

Festband zu Ehren von Prof. Dr. LUDWIG BECK

mit Beiträgen zur

Taxonomie und Faunistik von Arthropoden

**Biologie und Ökologie südamerikanischer
Bodenarthropoden**

Ökotoxikologie der Bodenfauna

OM

ZA

7629

15

2001

ndrias 15

s Museum für Naturkunde Karlsruhe 15. 12. 2001

Festband zu Ehren von Prof. Dr. LUDWIG BECK



andrias 15

Staatliches Museum für Naturkunde Karlsruhe 15. 12. 2001

P

Dieser Band ist
Herrn Prof. Dr. Ludwig Beck,
dem langjährigen Leiter der Zoologischen Abteilung
am Staatlichen Museum für Naturkunde Karlsruhe,
zu seinem Ruhestand gewidmet.

ZA 7629, 15.2001 OM



ISSN 0721-6513

Herausgeber: Staatliches Museum für Naturkunde Karlsruhe,
Redaktion und Schriftleitung des Bandes: Dr. H. HÖFER
Gestaltung des Bandes: bec.media GmbH, Karlsruhe
Druck: Gulde Druck GmbH, Tübingen
© Staatliches Museum für Naturkunde Karlsruhe
Postfach 111364, D-76063 Karlsruhe

Laudatio

WOLFRAM DUNGER: Bodenbiologische Forschung am Museum – Betrachtungen zum Wirken LUDWIG BECKS	5
Verzeichnis der Schriften von LUDWIG BECK	11
Verzeichnis der nach LUDWIG BECK benannten Arten und Gattungen ...	14

Einleitender Artikel

CHRISTOPHER MARTIUS, JÖRG RÖMBKE, MANFRED VERHAAGH, HUBERT HÖFER & LUDWIG BECK: Termiten, Regenwürmer und Ameisen – prägende Elemente der Bodenfauna tropischer Regenwälder	15
---	----

Taxonomie und Faunistik von Arthropoden

JÖRG SPELDA: Review of the millipede genus <i>Pterygophorosoma</i> VERHOEFF, 1897 (Diplopoda, Chordeumatida, Craspedosomatidae) ...	29
JÖRG SPELDA: Faunistic investigations on the soil fauna at the Muellertal (Luxembourg): Chilopoda, Diplopoda, Isopoda, Opiliones ...	49
ADETOLA BADEJO, STEFFEN WOAS & LUDWIG BECK: <i>Atropacarus</i> (<i>Hoplophorella</i>) <i>nigerienses</i> , a new species of phthiracarid mite (Acari, Oribatida) from Nigeria	55
ADETOLA BADEJO, STEFFEN WOAS & LUDWIG BECK: <i>Mesoplophora ifeana</i> , a new species of ptychoid mite (Acari, Oribatida) from Nigeria	65
ADALBERTO SANTOS & ANTONIO BRESCOVIT: A revision of the South American spider genus <i>Aglaoctenus</i> TULLGREN, 1905 (Araneae, Lycosidae, Sosippinae)	75
CRISTINA RHEIMS & ANTONIO BRESCOVIT: New species and records of <i>Scytodes</i> LATREILLE, 1804 of the "globula group" from Brazil (Araneae, Scytodidae)	91
HUBERT HÖFER & ANTONIO BRESCOVIT: Species and guild structure of a Neotropical spider assemblage (Araneae) from Reserva Ducke, Amazonas, Brazil	99
ULRICH IRMLER: Revision of the genus <i>Fauva</i> BLACKWELDER, 1952 (Coleoptera, Staphylinidae, Osoriinae) from South America	121

Biologie und Ökologie südamerikanischer Bodenarthropoden

- JOACHIM ADIS, MARINÉZ MARQUES & MATTHIAS WANTZEN: First observations on the survival strategies of terricolous arthropods in the northern Pantanal wetland of Brazil 127
- RAINER FOELIX & EILEEN HEBETS: Sensory biology of whip spiders (Arachnida, Amblypygi) 129
- ELIZABETH FRANKLIN, JOSÉ WELLINGTON DE MORAIS & EVANIRA M. R. DOS SANTOS: Density and biomass of Acari and Collembola in primary forest, secondary regrowth and polycultures in central Amazonia 141
- WERNER HANAGARTH & MARTIN BRÄNDLE: Soil beetles (Coleoptera) of a primary forest, secondary forest and two mixed polyculture systems in central Amazonia 155
- CHRISTOPHER MARTIUS: Nest architecture of *Nasutitermes* termites in a white water floodplain forest in central Amazonia, and a field key to species (Isoptera, Termitidae) 163

Ökotoxikologie der Bodenfauna

- ANDREA RUF: Stoffumsatzleistungen in Böden historisch alter und rezenter Laubwälder im niedersächsischen Flachland 173
- BERNHARD FÖRSTER: Streuabbau unter chemischem Stress: Potentielle Wirkung von Chemikalien am Beispiel des Fungizids Carbendazim . . . 185
- HARTMUT GREVEN, ULRICH RÜTHER & JOCHEN D'HAESE: Cadmium accumulation and metallothioneins in some members of the soil fauna 193
- JÖRG RÖMBKE: Auswirkungen zweier Umweltchemikalien auf die Enchytraeen eines Moderbuchenwalds 205

WOLFRAM DUNGER

Bodenbiologische Forschung am Museum – Betrachtungen zum Wirken LUDWIG BECKS

Naturmuseen haben traditionell die Aufgabe, Schätze der uns umgebenden Natur zu bewahren und der Öffentlichkeit einen Zugang zu ihnen zu eröffnen, der zuallererst auf Anschaulichkeit beruhen sollte. Hierfür ist das Auswahlprinzip des Naturalienkabinetts noch immer nicht überlebt: Der Besucher erwartet Großes, Schönes, Skurriles, Exotisches für ein ergötzliches Betrachten. Dort, wo die Grenzen der Erkennbarkeit (LUDWIG BECK betont oft: der Mensch ist ein Augentier) oder des Ekels und der Lächerlichkeit überschritten werden (die Regenwürmer hat schon GOETHE zum Ziel faustischen Spottes gemacht), geht der Schauwert gegen Null. Welche Chance soll also das "einförmige Wurmgewimmel" im Boden, sollen millimeterkleine Bewohner der Bodenstreu im Besucherinteresse haben? So ähnlich hat wohl die Frage gelautet, die sich Direktor Dr. ERWIN JÖRG stellen musste, als sich 1975 ein Bodenzologe um die Stelle des Leiters des Bereiches Zoologie im Staatlichen Museum für Naturkunde Karlsruhe bewarb. Schlimmer noch: Es war ein Professor der Universität Bochum, der seine Erfahrungen aus Südamerika bezog und unmissverständlich forderte, Bodenbiologie am Museum Karlsruhe zu etablieren. Was aber kann ein Universitätsmensch mit ausstellungserfernen Forschungsideen Nützliches an einem Museum leisten?

Freilich, zur Inventarisierung der Natur als klassischem Ziel der Sammlungstätigkeit des Museums gehören auch die Bodenorganismen. Aber in der großen Inventur des Abendlandes, deren Ende wir mit WILHELM SCHÄFER im Übergang zum 20. Jahrhundert sehen, waren die Bodentiere vergessen worden. Wie stark musste ein Museum sein, um sich diese Mammutaufgabe der Nacharbeit aufzubürden? Die zu erwartende Dimension ließ sich bereits erahnen. Ich will dies nicht am Beispiel von Bodenmilben verdeutlichen – hiervon hören wir noch aus berufenerem Mund. Für Collembolen aber konnte man die Entwicklung schon damals erahnen. Um 1900 waren erst 160, 1960 aber schon 850 Arten aus Europa bekannt. So überrascht es nicht, dass heute etwa 2.500 europäische Arten zu bewältigen sind. Arten nur einer der Tiergruppen, die sich erst unter dem Mikroskop dem Auge erschließen und die doch mit zehntausend bis hunderttausend Individuen unter jedem Quadratmeter gesunden Bodens leben. Aber damit nicht genug. Der Bewerber wollte ja auch die Bedeutung dieser Tiere in der Natur erkunden, in der heimischen wie auch in der tropischen zugleich, also weltweite Bodenökologie betreiben. Verwechsellte

dieser LUDWIG BECK die freien Forschungsmöglichkeiten einer Universität nicht größtenteils mit den Aufgaben, ja Zwängen eines Museums? Es war also schon mutig und weitblickend, dass Direktor ERWIN JÖRG damals LUDWIG BECK und mit ihm die Bodenzologie an das Naturkundemuseum Karlsruhe holte.

Was brachte der 40jährige Zoologieprofessor LUDWIG BECK bei seinem Amtsantritt am 7. Januar 1976 mit? Seine Grundkenntnisse hatte er sich nach dem Abitur am humanistischen Gymnasium in Neustadt an der Weinstraße durch das Studium der Biologie und Chemie in Tübingen und Mainz erworben. Seine weitere wissenschaftliche Entwicklung prägte dann ein nicht alltägliches Ereignis. Der Bodenzologe FRIEDRICH SCHALLER war 1957 mit umfangreichem Material von seiner Sammelreise in Peru nach Mainz heimgekehrt und suchte nun – nach seiner Berufung nach Braunschweig – Promoventen für die Bearbeitung der "Berlesefauna". Er fand sie in LUDWIG BECK für die Oribatiden und CHRISTIAN WINTER für die Collembolen.

In seiner Dissertation 1962 schildert BECK mit Dankbarkeit, wie ihm KARL STRENZKE und MARIE HAMMER den Einstieg in die Spezialkenntnis der Oribatiden eröffneten und REINHARD SCHUSTER, JANOS BALOGH und KONRAD MÄRKELE durch Teilbearbeitungen halfen. In der Dezemberausgabe 1961 der *Senckenbergiana Biologica* war dann erstmals in professionell-nüchterner Beschreibung zu lesen, dass zu den vier bekannten *Rhynchoribates*-Arten zwei neue aus Ostperu hinzukommen. In der Wahl der Artnamen verrät sich aber der frischgebackene Spezialist. Er taufte seine ersten eigenen Arten "*mirus*" und "*fabulosus*", in einem späteren der fünf Beiträge hierüber auch "*pulcher*" – wunderbar, fabelhaft, schön – welche Begeisterungsfähigkeit! Diese wandte LUDWIG BECK aber auch seiner Studienkollegin HANNELORE HERTLING zu, die er nach der Zeit seines DFG-Stipendiums am Senckenberg-Museum Frankfurt als wohlbestallter Assistent am Lehrstuhl für Allgemeine Zoologie bei Professor SCHWARTZKOPFF in Bochum 1964 heiratete. Seither teilen beide Freud und Leid des Lebens, im Beruf wie in der wachsenden Familie. Wir wissen, was dieser Kraftquell für das Leben bedeutet.

Die folgenden 12 Jahre an der Ruhr-Universität Bochum waren eine Periode der wachsenden Erfahrung in der universitären Tätigkeit mit Dozentur und schließlich Professur. Sie waren vor allem aber eine Zeit der z.T. mit FRIEDRICH SCHALLER unternommenen Forschungsreisen in das brasilianische Amazonas-

gebiet mit dem Standort Manaus sowie der wissenschaftlichen Aufbereitung des gesammelten Materials und der ökologischen Beobachtungen. LUDWIG BECK wurde so zum Spezialisten für Tropenökologie. Auf taxonomischem Gebiet dehnte er sein Interesse besonders auf spezielle Gruppen der Spinnentiere aus und untersuchte, oft mit Mitarbeitern, Geißelspinnen, Kapuzenspinnen und Zwerggeißelskorpione. Ökologisch aber, wie könnte das bei einem SCHALLER-Schüler anders sein, war er voll und ganz Bodenzöologe mit einem schon früh entdeckten Interesse an der Funktion des Systems. Hierfür steht besonders der Hauptteil seiner Habilitationsschrift über "Bodenzöologische Gliederung und Charakterisierung des amazonischen Regenwaldes", in der er bereits Gedanken seines späteren Freundes PETER VOLZ zur pedozöologischen Standortslehre weiterentwickelte und so ein wesentliches künftiges Arbeitsfeld vorbereitete.

Dies also brachte LUDWIG BECK 1976 in das Museum Karlsruhe ein, und es stand wohl schon die Frage, ob in seinem Kopf und Herz zwischen tropischem Regenwald und Hörsaal noch Raum für das Museum sein würde. Doch was er tat, überzeugte. Obwohl noch mit Verpflichtungen an der Universität Bochum und mit der Umhabilitierung an die Universität Karlsruhe belastet, stürzte er sich voll in die Museumsarbeit. Da war seit dem frühen Tod seines Vorgängers, des Orthoptologen HELMUT KNIPPER, vieles liegen geblieben. Der Wiederaufbau der zerstörten Ausstellungen bot auch die Chance für Neugestaltung, um die sich LUDWIG BECK besonders im Bereich Vivarium bemühte, von der Konzeption und der Gestaltung schöner Führer bis zur Beschaffung von Lebendmaterial an der französischen Mittelmeerküste. So konnte in den letzten Jahren eine äußerst ansprechende Modernisierung des Vivariums durch den Biologen HANNES KIRCHHAUSER erfolgen. Und natürlich hat er auch Lösungen für die Darstellung des Bodenlebens in der Ausstellung gesucht und gefunden. Für die Sammlungsarbeit brachte er HANS-WALTER MITTMANN aus Bochum mit, der nach seiner Promotion bei Prof. BECK die Kustosstelle einnahm.

Eine der beanspruchendsten Pflichten in einem wissenschaftlichen Museum ist die Herausgabe von Publikationen. Sie stiehlt dem Redakteur und Herausgeber unendliche Zeit der Arbeit im Verborgenen und kann doch nur gedeihen, wenn der Betroffene beste fachliche, technische und nicht zuletzt auch menschliche Fähigkeiten für den Umgang mit Autoren besitzt. Seit dem Dienstantritt von Direktor SIEGFRIED RIETSCHEL, und in guter Gemeinschaft mit ihm, leistet LUDWIG BECK diese Arbeit in Redaktion und Schriftleitung der neu gestalteten Publikationsreihen *carolina* und *andrias*, und ist sie wohl bis heute noch nicht losgeworden. Ich habe ihm gelegentlich dabei über die Schulter geschaut und – auch als gelernter Redakteur – manches profitiert.

Der große Schlag war aber die Forschungskonzeption des neuen Abteilungsleiters. Ich zitiere aus der *carolina* 58 (2000): "Weg von der klassischen, morphologisch-systematisch nach Tiergruppen ausgerichteten Museumszoologie hin zu einer sich am lebenden Organismus und seiner Umwelt orientierenden, also die Biologie und Ökologie der Tiere umfassenden und die systematischen Grenzen der Tiergruppen übergreifenden Konzeption"

Hierzu ist anzumerken: Wenn einer der Biologen unserer Generation für die Weiterentwicklung einer exakten, alle Erkenntnisebenen nutzenden Taxonomie auf seinem Fachgebiet gesorgt und dieses Arbeitsziel auf viele Mitarbeiter übertragen hat, so ist dies nicht zuletzt LUDWIG BECK.

Was mit der "übergreifenden Konzeption" gemeint ist, wird durch einen der fruchtbarsten Forschungsansätze der deutschen Ökologie deutlich, den LUDWIG BECK schon in Bochum vorgedacht hatte. Noch 1976 beginnt er eine bodenökologische Langzeitstudie an einem Moderbuchenwald bei Schluttenbach/Ettlingen, einem herrlichen Hallenwald, der auch mein Herz sofort gewann. Am Anfang mußte natürlich eine überzeugende Forschungskonzeption stehen, um die Unterstützung der Deutschen Forschungsgemeinschaft zu erlangen. Hierin war LUDWIG BECK bereits bestens geübt und teilte später diese Fähigkeit gern anderen Kollegen mit – auch ich bin hierfür noch immer dankbar. Seine Intention, die er hier wohl erstmals voll umsetzen konnte, nannte er mir einmal mit den Worten: "Ideen entwickeln, verarbeiten, weiterreichen" Hierin ist er tatsächlich wohl kaum zu übertreffen, ein bescheidener Mensch und weitblickender Wissenschaftler mit ausdauernder Energie im Dienst der Sache. Über 50 Arbeiten liegen heute aus dieser Langzeitstudie vor, darunter viele Diplomarbeiten und Dissertationen der BECKschen Schule.

Das Besondere am Projekt "Moderbuchenwald Schluttenbach" war nun nicht etwa nur die hohe Zahl der Tiergruppen, deren solide Bearbeitung LUDWIG BECK anzuregen und zu begleiten verstand. Ihn interessierte die Frage, wie dieser Buchenwald in allen seinen Teilen funktioniert. Kein Zeitaufwand war ihm zu hoch, um selbst die chemisch-physikalisch-klimatischen Bedingungen zu erkunden und zu dokumentieren, vor allem aber sah er die Streuzersetzung als Vorgang von zentraler Bedeutung. Hierzu untersuchten er und sein Team einerseits den Abbau der Streugenerationen über 5 Jahre, und zwar mit Hilfe von Netzbeuteln differenziert nach den Leistungsanteilen der großen Gruppen der Bodenfauna, andererseits wichtige biochemische Prozesse. Zusammenfassungen der Ergebnisse wurden 1983 in der Deutschen Zoologischen Gesellschaft und 1987 in der Gesellschaft für Ökologie vortragen, wobei die Tagung 1987 in Göttingen durch die gleichzeitige Darstellung des Göttinger Kalkbuchenwaldes und anderer Waldtypen zu einem zentra-



LUDWIG BECK im Buchenwald bei Ettlingen (1984).

len Ereignis der Waldbodenökologie in Deutschland wurde. Aus beiden Publikationen entnehmen Bodenökologen bis heute die klassischen Darstellungen LUDWIG BECKs zum Streuabbau im Buchenwald und zu den hierbei ablaufenden Veränderungen der wichtigen biochemischen Stoffgruppen innerhalb des Funktionsnetzes der Bodenorganismen. An dieses Schema dachte ich, als LUDWIG BECK einmal während eines Spazierganges seinen Zweifel äußerte, ob er eigentlich ein richtiger Biologe sei.

Durch diese unzweifelhaften Erfolge sah sich LUDWIG BECK aber nicht einfach auf dem eingeschlagenen Weg bestätigt. Wiederholt analysierte er die Entwicklung der ökologischen und speziellen Biologie sowohl aufgrund des Erkenntnisgewinns als auch aufgrund der wachsenden Anforderungen der Gesellschaft zur Bewältigung der ausufernden Umweltproblematik. Die Abschiebung dieser Wissenschaftsgebiete vom universitären in den Museums-Bereich sah er durchaus auch kritisch, mit Blick auf die Grenzen, die den wenigen Forschungsmuseen für deren Wahrnehmung gezogen sind. So entschloss er sich im fünfzigsten Lebensjahr in der Hoffnung, seine inzwischen erweiterten Ziele an der Universität besser verwirklichen zu können, zur Übernahme einer Professur im benachbarten Tübingen. Wenige zermürbende Monate genühten, um diese Illusion zu zerstören. Es war ein Glück für beide Teile, dass Direktor RIETSCHEL gerade noch die Möglichkeit fand, seinen bisherigen Stellvertreter an das Museum zurückzuholen und so den erfolgreich begonnenen Weg fortzusetzen. Das Museum hatte sich als Hort bodenbiologischer Tätigkeit durchgesetzt.

Wohl mancher hätte nach einer solchen Enttäuschung die letzten 15 Amtsjahre ruhiger angehen lassen – nicht so LUDWIG BECK. Wir können nicht weniger als vier vorwiegend angewandte Forschungsgebiete erkennen, die er seither weiter oder neu entwickelte. Hierbei darf nicht vergessen werden, dass er dies nur neben der Wahrnehmung seiner allgemeinen Pflichten im Haus angehen konnte.

Als erstes sei die Ökotoxikologie genannt. Grundidee eines vom damaligen Bundesministerium für Forschung und Technologie (BMFT) ausgeschriebenen Programmes war es, die Belastbarkeit von Ökosystemen zu bewerten. LUDWIG BECK sah sofort, dass sich hier ein Weg bot, die ökologischen Schlussfolgerungen aus den langjährigen Beobachtungen am Schlutenbacher Buchenwald im Experiment zu testen, dem BMFT ein ideales, weil voruntersuchtes Versuchsgelände anzubieten und dem Museum Drittmittel für die taxonomisch-faunistische Kernaufgabe zu sichern. Er gewann die ökotoxikologische Arbeitsgruppe des Battelle-Institutes e.V. in Frankfurt am Main, damals unter Leitung von KLAUS DUMPERT, zur Kooperation und leitete damit eine bis heute währende Verbindung zwischen dem Museum Karlsruhe und der heutigen ECT

Ökotoxikologie GmbH (Flörsheim) unter Leitung von BECKs Diplomanden und Dissertanten JÖRG RÖMBKE ein. Über 20 Personen waren letztlich an der Studie "Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien" tätig. Später (1994-1996) schloss sich eine Studie an, die sich mit der Wirkung von Dimilin und *Bacillus thuringiensis* auf Bodenfauna, Fraßaktivität und Streuabbau im Hardtwald (Stellario-Carpinetum) bei Bruchsal befasste – mit einem teilweise neuen Team. Aus beiden Untersuchungen leitete LUDWIG BECK verallgemeinernd ein Reaktionsmodell der Bodenfauna ab, wonach toxikologisch wenig resistente, normal aber konkurrenzstarke Arten nach der Kontamination zwar durch widerstandsfähigere Arten ersetzt werden können, ein mindestens vorübergehender Leistungsabfall im Streuabbau jedoch eintritt. Zu ergänzen wäre, dass diese Arbeiten zeitlich von Untersuchungen eingeholt wurden, die 1988 als "Immissionsökologischer Wirkungskataster" der Landesanstalt für Umweltschutz Baden-Württemberg an mehr als 10 Standorten begannen und sich vielfältig in den weiter zu nennenden Forschungsbereichen niederschlugen.

Als zweites aktuelles Forschungsgebiet ist erneut die funktionelle Bodenbiologie mit der Kernfrage des Streuabbaues zu nennen, jetzt aber im Vergleich zwischen einheimischen und tropischen Wäldern. LUDWIG BECK hat im vergangenen Jahr eine sehr prägnante Zusammenfassung der vielen Einzeluntersuchungen gegeben, die im deutschen Bereich nun auch neue Studien in einem Auenwald am Rhein und im tropischen Regenwald, einen Primärwald bei Manaus, einbeziehen. Wieder tauchen im Bearbeiterteam neue Namen auf, Tropenökologen wie MANFRED VERHAAGH, WERNER HANAGARTH und sein Amtsnachfolger HUBERT HÖFER. Der Verdacht, der vielbeschäftigte Professor BECK wird der Sache wohl mehr seinen Namen gegeben haben, ist völlig irrig. Ich habe ihn in Au am Rhein zur Probenahme begleitet, und erhielt auf meine vorsichtige Frage die resolute Antwort: "Ich lasse keinen meine Proben nehmen!" Ich weiß sehr wohl, wie recht er daran tut, aber auch, wie schwer das durchzuhalten ist. Und zum Amazonas ist es noch etwas weiter als zum Rhein. Nennen wir noch kurz das Ergebnis des Vergleichs, weil es wiederum in seiner Klarheit besticht. In gemäßigten Breiten ist in Wäldern mit jährlich totem Streuabbau die Leistung der Bodenmakrofauna groß, ihre Steuerungsfunktion aber gering, wodurch Verluste entstehen. Bei mehrjährigem Streuabbau leistet die hochentwickelte Mesofauna eine hochgradige und verlustarme Feinsteuerung des Prozesses. Im nährstoffarmen tropischen Regenwald dagegen verläuft der Abbau rasch und wenig kontrolliert unter hoher Beteiligung der Makrofauna. Die Feinsteuerung wird ersetzt durch ein hochentwickeltes organisches Filtersystem in allen Straten des Waldes. So klar steht dies noch in keinem Lehrbuch.

Eine dritte, in dieser Form ganze neue, im Keim aber doch schon länger "angelegte" Forschungsrichtung kann man mit den Termini "Biologische Bewertung von Böden" oder auch "Schutz des Bodens als Lebensraum" umreißen. Hier steht die Pionierleistung von PETER VOLZ an erster Stelle, die LUDWIG BECK schon 1971 in seiner bodenzologischen Charakterisierung des amazonischen Regenwaldes aufgegriffen hatte. Auslöser dieser erhöhten Aktivität war diesmal eine erfreuliche Reaktion des amtlichen Umwelt- und Naturschutzes, zunächst auf Länder- und schließlich auf Bundesebene, auf die wachsende Fachkenntnis vom Leben im Boden wie auch auf dessen zunehmende Bedrohung. Sie führte inzwischen zum gesetzlichen Schutz des Bodens als Lebensraum. Es spricht für die Aura wachsender Aufgeschlossenheit für die Lebensprozesse im Boden, die ganz wesentlich von LUDWIG BECK ausging, dass erste Aktivitäten hierfür in Baden-Württemberg entstanden. Folgerichtig wurde auch sein Wirkungskreis, hier in erster Linie die ECT Ökotoxikologie GmbH unter JÖRG RÖMBKE, mit der Ausarbeitung einer Fachgrundlage betraut. Beide Wege, die hierfür heute gangbar sind, sind auch von LUDWIG BECK und seinen Mitarbeitern erschlossen worden: Zum ersten die Nutzung der direkten Indikation durch Bodentiere, wie dies von den Zeigerwerten der Pflanzen weitaus besser ausgearbeitet vorliegt; zum zweiten die Verwendung genau bekannter Organismengarnituren von charakteristischen Bodennutzungstypen als Erwartungswert im Vergleich zum Istwert eines zu beurteilenden Bodens. Ebenfalls von der Erfahrung dieses Teams getragen, kommt noch die Notwendigkeit hinzu, die ersten Ergebnisse des bodenzologischen Biomonitoring hierfür zu nutzen. Das Resultat ist eine Zukunftsaufgabe, die nun aufbereitet und begründet vorliegt und auf alle Bodenzologen, in erster Linie aber auf die Träger der Nachfolge LUDWIG BECKS zukommt: Die "Bodenbiologische Standortklassifikation" soll den Zustand (oder die Qualität) eines Bodenstandorts dadurch beurteilen, dass sie zwischen einem Erwartungswert und der real vorgefundenen Bodenbiozönose vergleicht. Was die Väter der Bodenbiologie erstrebten – ich erinnere an WALTER KUBIENAS Geleitaufsatz zum Erscheinen der *Pedobiologia* 1961 –, wofür der hochbetagte Senior der Bodenzologie in Deutschland, PETER VOLZ, schon 1962 einen ersten Grundstein legte, hier steht es als von der Schule BECK erschlossenes Arbeitsziel mit dem Kürzel BBSK.

Auf der tropenökologischen Seite steht dem ein Projekt gegenüber, das nicht minder der aktuellen und künftigen Notwendigkeit für das Leben auf der Erde Rechnung trägt, SHIFT genannt. Hier haben sich viele Partner zusammengeschlossen, um in agroförmlichen Polykulturen des Amazonasgebietes, die den Druck zur Rodung immer weiterer Primärwaldflächen mindern sollen, ein Management mit pflanzlichen Bestan-

desabfällen zu erproben und seine Auswirkungen auf Bodenfauna und Streuabbau zu erforschen. Die Vielschichtigkeit dieses Vorhabens wird in den folgenden Beiträgen sicher deutlicher werden, als ich dies darstellen kann. Es darf aber festgehalten werden, dass eine der Wurzeln in LUDWIG BECKS Langzeitstudien in einheimischen Wäldern und seiner Übertragung bodenökologischer Erfahrung auf tropische Regenwälder zu suchen ist. Hier tritt eine weitere seiner Fähigkeiten zutage: Er ist ein höchst erfolgreicher Anstifter wie auch Träger kollektiver Arbeit.

Das vierte Themengebiet der aktuellen Arbeiten LUDWIG BECKS erwähne ich als letztes, nicht weil es weniger wichtig ist, sondern um es besonders hervorzuheben: das weite Feld zwischen Taxonomie, Systematik, Biologie und Ökologie. Dieses ureigenste Problem des Museumsbiologen durchzieht sein gesamtes Schaffen, gewinnt aber in den letzten Jahren eine neue Qualität. Für LUDWIG BECK ist Bioindikation nicht einfach eine Kennzeichnung von Standorts-Zuständen durch Arten oder Artenkollektive. Zunächst denkt er – wie alle Biosystematiker, die sich zu Recht so nennen – intensiv über die Art zwischen Morpho- und Biospecies nach, nicht nur, aber besonders intensiv am Beispiel der Oribatiden. Eine nächste Stufe betrifft die Zuordnung der biologischen und ökologischen Fakten zu einer Art, beginnend mit dem sorgfältigen Erfassen der Umweltparameter bei jeder Aufsammlung, weil nur so die Brauchbarkeit der ökologischen Aussage einer Art geprüft werden kann. Wenige haben sich dieser Sisyphusarbeit so konsequent verschrieben wie LUDWIG BECK, immer mit dem Ziel des Erstellens einer "Rückgrat-Datei", wie er sie nennt. Diese Sicherheit aus eigener Arbeit lässt dann eine Beurteilung der Daten zu, die aus einer umfangreichen Literaturliteraturauswertung, dem zweiten Standbein der bodenzologischen Charakterisierung, stammen. Nun ist aber LUDWIG BECK viel zu sehr Realist, als dass er glaubte, allein mit einer Wolke solcher, nur zeitraubend zu gewinnender Daten, für die Mehrzahl der Anforderungen praxisverwendbare Bioindikationen mit ökonomischem Aufwand erarbeiten zu können. Wie generell, so steht hier die Frage, ob der Biologe nur Antworten nach Erhebungen auf Artniveau geben kann. Hier zahlt sich sein langjähriges Zusammengehen mit STEFFEN WOAS, einem exzellenten Kenner der Großsystematik der Oribatiden, aus. Es gelingt, und das haben BECK, WOAS und HORAK in einem Vortrag zu meiner Verabschiedung aus dem Amt dargelegt, Standorte mit Hilfe der Artendominanz von Großgruppen der Oribatiden zu kennzeichnen, ein auch mit anderen Tiergruppen oft angestrebtes, aber selten erreichtes Ziel. In diesem Problemkreis, der das eigentliche Handwerkszeug eines ökologisch motivierten Taxonomen betrifft, sehe ich eine hohe Kompetenz von LUDWIG BECK und seinen engsten Mitarbeitern, und wir alle erhoffen uns von ihnen noch weitere Beiträge hierzu.

Der Altersrücktritt vom Amt kann, das ist eine angenehme Erfahrung, Kräfte freisetzen, die vorher durch Pflichten gebunden waren. Alte Erwartungen und neue Wünsche aus der vertrauten Umgebung bringen aber neue moralische Verpflichtungen, die Ehrenämter. Es ist undenkbar, dass sich LUDWIG BECK ab heute vom wissenschaftlichen Leben des Karlsruher Museums abkoppeln könnte. Schließlich ist dies der locus typicus, an dem er bodenbiologische Forschung am Museum in solider Fundierung und in einer andernorts nicht erreichten Breite der Anwendungsformen entstehen ließ. Vergleichbare Entwicklungen gibt es ohnehin nur an wenigen Museen, etwa in Paris oder in Görlitz.

Ich nutze die Gunst der Stunde, um LUDWIG BECK darüber hinaus dafür zu danken, dass er so vielen Kollegen – jüngeren und älteren – ein wichtiger Berater und Helfer war und ist. Das gilt natürlich für seine weitverzweigte Schule, das gilt aber zum Beispiel auch für mich. LUDWIG BECK hatte uns am Staatlichen Museum für Naturkunde Görlitz zum ersten Mal bereits 1965 besucht. So waren wir schon gute Freunde mit erfreulich komplementären fachlichen Zielen, als die freudig begrüßte deutsche Einheit von uns ein Umlernen im Verwaltungs-Procudere forderte. Hier war uns LUDWIG BECK ein selbstloser Helfer, ja das Museum Karlsruhe stand uns vom Direktor bis zum Verwaltungsleiter zur Seite. Hierfür bin und bleibe ich tief dankbar. Als Fortgeschrittener habe ich inzwischen natürlich begriffen, dass auch das bundesrepublikanische Ross in direkter Linie vom Amtsschimmel abstammt und nur feurig werden kann, wenn man ihm selbst Feuer einbläst. Dieses innere wissenschaftliche Feuer des äußerlich so ruhig-abgeklärten LUDWIG BECK also ist es, von dem wir hier im Grunde gesprochen haben, und es wird, das ist mein Wunsch, auch ohne Amtspflicht weiter glühen.

Autor

Prof. Dr. WOLFRAM DUNGER, Hofeweg 15, D-02829 Ebersbach bei Görlitz.

Verzeichnis der Schriften von LUDWIG BECK

1. BECK, L. (1961): Zwei neue Arten der Gattung *Rhynchoribates* GRANDJEAN (Oribatei, Acari). – Senck. Biol., **42** (5/6): 495-500.
2. BECK, L. (1962): Beiträge zur Kenntnis der neotropischen Oribatidenfauna I. *Eohypochthonius* und *Cosmochthonius* (Arachnida, Acari). – Senck. Biol., **43** (3): 227-236.
3. BECK, L. (1962): Beiträge zur Kenntnis der neotropischen Oribatidenfauna II. Nothridae, Camisiidae, Heterobelbidae (Arachnida, Acari). – Senck. Biol., **43** (5): 385-407.
4. BECK, L. (1962): Beiträge zur Kenntnis der neotropischen Oribatidenfauna III. *Dampfiella* (Arachnida, Acari). – Senck. Biol., **43** (6): 475-487.
5. BECK, L. (1963): Zur Ökologie und Taxonomie der neotropischen Bodentiere I. Zur Oribatidenfauna Perus. – Zool. Jb. Syst., **90**: 299-392.
6. BECK, L. (1964): Tropische Bodenfauna im Wechsel von Regen- und Trockenzeit. – Natur und Museum, **94** (2): 63-71.
7. BECK, L. (1964): Über Variabilität und Wertigkeit morphologischer Merkmale bei adulten Oribatiden (Arachnida, Acari) am Beispiel der Gattung *Rostrozetes* SELLNICK, 1925. – Abh. Senck. naturf. Ges., **508**: 1-64.
8. BECK, L. (1964): Beiträge zur Kenntnis der neotropischen Oribatidenfauna IV *Haplozetes* und *Peloribates* (Arachnida, Acari). – Senck. Biol., **45** (2): 161-183.
9. BECK, L. (1967): Die Bodenfauna des neotropischen Regenwaldes. – Atas do Simpósio sôbre a Biota Amazonica, **5** (Zoologia): 97-101.
10. BECK, L. (1967): Beiträge zur Kenntnis der neotropischen Oribatidenfauna V. *Archegozetes* (Arachnida, Acari). – Senck. Biol., **48** (5/6): 407-414.
11. BECK, L. (1968): Zum jahreszeitlichen Massenwechsel zweier Oribatidenarten (Acari) im neotropischen Überschwemmungswald. – Verh. Dtsch. Zool. Ges., 536-540.
12. BECK, L. & SCHUBART, H. (1968): Revision der Gattung *Cryptocellus* WESTWOOD, 1874 (Arachnida: Ricinulei). – Senck. Biol., **49** (1): 67-78.
13. BECK, L. (1968): Sôbre a Biologia de alguns Aracnideos na floresta tropical da Reserva Ducke (I.N.P.A. Manaus/Brasil). – Amazoniana, **1** (3): 247-250.
14. BECK, L. (1968): Aus den Regenwäldern am Amazonas I. – Natur und Museum, **98** (1): 24-32.
15. BECK, L. (1968): Aus den Regenwäldern am Amazonas II. – Natur und Museum, **98** (2): 71-80.
16. BECK, L. & PABST, H. (1969): Zur Tagesperiodik der Laufaktivität von *Admetus pumilio* C.L. KOCH (Amblypygi, Arachnida) aus dem neotropischen Regenwald. – Verh. Dtsch. Zool. Ges., **33**: 178-184.
17. BECK, L. (1971): Bodenzoologische Gliederung und Charakterisierung des amazonischen Regenwaldes. – Amazoniana, **3** (1): 69-132.
18. BECK, L. (1972): Der Einfluss der jahresperiodischen Überflutungen auf den Massenwechsel der Bodenarthropoden im zentral-amazonischen Regenwaldgebiet. – Pedobiologia, **12**: 133-148.
19. BECK, L. (1972): Zur Tagesperiodik der Laufaktivität von *Admetus pumilio* C.L. KOCH (Arachnida, Amblypygi) aus dem neotropischen Regenwald II. – Oecologia, **9**: 65-102.
20. BECK, L. (1974): Ökosystem amazonischer Regenwald: Droht ein Kreislaufkollaps? – Bild der Wissenschaft, **11** (10): 42-48.
21. BECK, L. & GÖRKE, K. (1974): Tagesperiodik, Revierverhalten und Beutefang der Geißelspinne *Admetus pumilio* C.L. KOCH im Freiland. – Z. Tierpsychol., **35** (2): 173-186.
22. BECK, L., FOELIX, R., GÖDEKE, E. & KAISER, R. (1974): Über die Haarsensillen der Geißelspinne *Admetus pumilio* (Arachn., Amblypygi). – Naturwissenschaften, **61**: 327-328.
23. BECK, L. (1976): Zum Massenwechsel der terrestrischen Bodenfauna in Überschwemmungswäldern des zentralen Amazonasgebietes. – Amazoniana, **6** (1): 1-20.
24. BECK, L., FOELIX, R., GÖDEKE, E. & KAISER, R. (1977): Morphologie, Larvalentwicklung und Haarsensillen des Tastbeinpaars der Geißelspinne *Heterophrynus longicornis*, BUTLER (Arach., Amblypygi). – Zoomorphologie, **88**: 259-276.
25. BECK, L. (1977): Das Vivarium – Führer durch die Ausstellungen der Landessammlungen für Naturkunde Karlsruhe, 48 S.
26. BECK, L. (1978): Zur Biologie eines Buchenwaldbodens 1. Einleitender Überblick und Forschungsprogramm. – Beitr. naturk. Forsch. SüdwDtl., **37**: 93-101.
27. BECK, L. (1978): Lurche und Kriechtiere oder Die Eroberung des Landes – Führer zu Ausstellungen (Museum am Friedrichsplatz Karlsruhe). SMNK, Karlsruhe, 48 S.
28. BECK, L. & BRESTOWSKY, E. (1980): Auswahl und Verwertung verschiedener Fallaubarten durch *Oniscus asellus* (Isopoda). – Pedobiologia, **20**: 428-441.
29. BECK, L. & FRIEBE, B. (1981): Verwertung von Kohlehydraten bei *Oniscus asellus* (Isopoda) und *Polydesmus angustus* (Diplopoda). – Pedobiologia, **21**: 19-29.
30. BECK, L. & MITTMANN, H. - W. (1982): Zur Biologie eines Buchenwaldbodens 2. Klima, Streuproduktion und Bodenstreu. – Carlinea, **40**: 65-90.

31. BECK, L. (1983): Zur Bodenbiologie des Laubwaldes. – Verh. Dtsch. Zool. Ges., 37-54.
32. BECK, L. (1983): Bodenzoologie amazonischer Überschwemmungswälder. – Amazoniana, **8**: 91-99.
33. BECK, L. (1984): Soil fauna on the beech wood floor. – German Research, **2/3**: 17-20.
34. BECK, L. (1984): Bodentiere im Laub des Buchenwaldes. – Forschung. Mitteilungen der DFG, **2**: 15-18.
35. BECK, L. & DUMPERT, K. (1985): Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien. – Spezielle Berichte der KFA Jülich, **196**: 12-30.
36. BECK, L. (1987): Untersuchungen zu Struktur und Funktion der Bodenfauna eines Buchenwaldes. – Abh. Ber. Naturkundemus. Görlitz, **60** (1): 19-28.
37. BECK, L. (1987): Ökosystemare Funktion charakteristischer Böden - Begründung der ausgewählten Forschungsansätze und Forschungsbedarf. – Spezielle Berichte der KFA Jülich, **396**: 53-56.
38. BECK, L. (1987): Hinweise zur ökotoxikologischen Bewertung von Chemikalien am Beispiel des BMFT-Vorhabens „Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien“ – Mitteilungen der Biologischen Bundesanstalt für Land - und Forstwirtschaft, **234**: 47-63.
39. BECK, L. (1988): Bestandes- und Bodenklima eines Buchenwaldes im nördlichen Schwarzwaldvorland. – Caroleinea, **46**: 141-144.
40. BECK, L., DUMPERT, K., FRANKE, U., MITTMANN, H.-W., RÖMBKE, J. & SCHÖNBORN, W. (1988): Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien. – Spezielle Berichte der KFA Jülich, **439**: 548-701.
41. BECK, L. (1989): Lebensraum Buchenwaldboden 1. Bodenfauna und Streuabbau - eine Übersicht. – Verh. Ges. Ökol., **17**: 47-54.
42. BECK, L. (1989): Zoologie. – Forschung an den Staatlichen Naturkundemuseen Baden-Württembergs. Bildung in neuer Sicht, **52**: 46-47
43. BECK, L. (1989): Bodenökologie als Langzeitforschung. – Forschung an den Staatlichen Naturkundemuseen Baden-Württembergs. Bildung in neuer Sicht, **52**: 60-64.
44. BECK, L. (1990): Bodenzoologie und Taxonomie in Karlsruhe. – Andrias, **7**: 5-8.
45. BECK, L. (1991): Zoologische Systematik - Forschung an einem Naturkundemuseum. – Caroleinea, **49**: 5-8.
46. BECK, L. & WOAS, S. (1991): Die Oribatiden-Arten (Acari) eines südwestdeutschen Buchenwaldes I. – Caroleinea, **49**: 37-82.
47. BECK, L. (1993): Zur Bedeutung der Bodentiere für den Stoffkreislauf in Wäldern. – Biologie in unserer Zeit, **23** (5): 286-294.
48. BECK, L. (1994): Bodenzoologie, Collembolen und einiges mehr - Anmerkungen zum wissenschaftlichen Werk WOLFRAM DUNGERS. – Abh. Ber. Naturkundemus. Görlitz, **68** (1): 5-13.
49. BECK, L., DIELMANN, H. & JACOBI, K. (1994): Übertragbarkeit und Präzisierung der Wirkungsmechanismen chemischer Belastung in verschiedenen Ökosystemen. Teilprojekt: Bodenfauna und Streuabbau. – Abschlussbericht Forschungsvorhaben BMFT, 1-60.
50. BECK, L., HÖFER, H. & VERHAAGH, M. (1994): Tropische Diversität, ihre Aufrechterhaltung und deren Mechanismen. – Andrias, **13**: 5-6.
51. BECK, L. & RIETSCHEL, S. (1994): EDUARD MAYER † 1928-1993. – Caroleinea, **52**: 151-152.
52. BECK, L. (1995): Milben als Reaktionsindikatoren. Methoden zu Wirkungserhebungen - ein Methodenhandbuch. – Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe, 42-43.
53. BECK, L., HÖFER, H., MARTIUS, C., RÖMBKE, J. & VERHAAGH, M. (1997): Aspekte der Bodenbiologie tropischer Regenwälder. – Geographische Rundschau, **49** (1): 24-31.
54. BECK, L., WOAS, S. & HORAK, F. (1997): Taxonomische Ebenen als Basis der Bioindikation - Fallbeispiele aus der Gruppe der Oribatiden (Acari). – Abh. Ber. Naturkundemus. Görlitz, **69**: 67-85.
55. BECK, L., HÖFER, H., MARTIUS, C., GARCIA, M. B., FRANKLIN, E. & RÖMBKE, J. (1998): Soil fauna and litter decomposition in primary and secondary forests and a polyculture system in Amazonia - study design and methodology. – In: LIEBEREI, R., VOSS, K., & BIANCHI, H. (eds.): Proceedings of the 3rd SHIFT-Workshop Manaus. BMBF, Bonn, 463-470.
56. BECK, L., GASPAPROTTO, L., FÖRSTER, B., FRANKLIN, E., GARCIA, M., HARADA, A., HÖFER, H., LUIZÃO, F., LUIZÃO, R., MARTIUS, C., DE MORAIS, J. W. & RÖMBKE, J. (1998): The role of soil fauna in litter decomposition in primary forests, secondary forests and a polyculture plantation in Amazonia: methodological considerations. – In: LIEBEREI, R., VOSS, K., & BIANCHI, H. (eds.): Proceedings of the 3rd SHIFT-Workshop Manaus. BMBF, Bonn, 471-481.
57. BECK, L., RÖMBKE, J., RUF, A., PAULUS, R., PRINZING, A. & WOAS, S. (1999): Auswirkungen des Einsatzes von Dimilin und *Bacillus thuringiensis* auf die Struktur und Funktion der Bodenfauna. – Freiburger Forstliche Forschung, **13**: 74-101.
58. BECK, L. (2000): Streuabbau und Bodenfauna in Wäldern gemäßigt und tropischer Breiten. – Caroleinea, **58**: 243-256.
59. BERG, J., WOAS, S. & BECK, L. (1990): Zur Taxonomie der *Phthiracarus*-Arten (Acari,Oribatei) eines südwestdeutschen Buchenwaldes. – Andrias, **7**: 61-90.
60. BRAND, C., HÖFER, H. & BECK, L. (1994): Zur Biologie eines Buchenwaldbodens 16. Die Spinnenassoziation einer Windbruchfläche. – Caroleinea, **52**: 61-74.

61. BRAUN, M. & BECK, L. (1986): Zur Biologie eines Buchenwaldbodens 9. Die Pseudoskorpione. – *Carolinea*, **44**: 139-148.
62. DÖRRSCHEIDT, G. J. & BECK, L. (1975): Advanced methods for evaluating characteristic parameters (τ , α , ρ) of circadian rhythms. – *J. Math. Biol.*, **2** (2): 107-121.
63. FOELIX, R. F., CHU-WANG, I.-W. & BECK, L. (1975): Fine structure of tarsal sensory organs in the whip spider *Admetus pumilio* (Amblypygi, Arachnida). – *Tissue and Cell*, **7** (2): 331-346.
64. FRANKE, U. & BECK, L. (1989): Lebensraum Buchenwald 2. Streueintrag und Streuabbau. – *Verh. Ges. Ökol.*, **17**: 47-54.
65. FRANKE, U., FRIEBE, B. & BECK, L. (1988): Methodisches zur Ermittlung der Siedlungsdichte von Bodentieren aus Quadratproben und Barberfallen. – *Pedobiologia*, **32**: 253-264.
66. HÖFER, H. & BECK, L. (1995): Die Spinnentierfauna des Regenwaldreservats „Reserva Ducke“ in Zentralamazonien I. – *Natur und Museum*, **125** (12): 389-401.
67. HÖFER, H. & BECK, L. (1996): Die Spinnentierfauna des Regenwaldreservats „Reserva Ducke“ in Zentralamazonien II. – *Natur und Museum*, **126** (3): 69-85.
68. HÖFER, H., HANAGARTH, W., GARCIA, M., MARTIUS, C., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2001): Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. – *Eur. J. Soil. Biol.*, (in press).
69. HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rainforest after experimental litter addition in small plots. – *Pedobiologia*, **40**: 570-576.
70. HÖFER, H., MARTIUS, C., RÖMBKE, J., GARCIA, M. B., & BECK, L. (1998): SHIFT Project ENV 52: Soil fauna and litter decomposition: the use of adapted soil biological methods in Amazonian rain forests. – In: DALITZ, H. et al. (eds.): Bielefelder ökologische Beiträge, Band **12**. Kurzbeiträge zur Tropenökologie. DFG Abschluss-symposium „Mechanismen der Aufrechterhaltung tropischer Diversität“ 1998 und 11. Jahrestagung der Deutschen Gesellschaft für Tropenökologie 1998, Bielefeld, 111.
71. KOGLIN, J. & BECK, L. (1983): Wirkung von Umweltänderungen auf die Collembolenfauna (Insecta, Apterygota) eines Buchenwaldbodens. *Verh. Dtsch. Zool. Ges.*, **76**: 218.
72. KRAUS, O. & BECK, L. (1967): Taxonomie und Biologie von *Trithyreus brasiliensis* n.sp. (Arach.: Pedipalpi: Schizopeltidia). – *Senck. Biol.*, **48** (5/6): 401-405.
73. KREIMES, K., BECK, L. & RÖMBKE, J. (1998): Ergebnisse bodenfaunistischer Erhebungen im Rahmen der ökologischen Umweltbeobachtungen Baden-Württemberg. – *EcoSys*, **7**: 105-116.
74. MAYER, E. & BECK, L. (1982): Schlangennachzuchten im Vivarium. – *Carolinea*, **41**: 137-139.
75. PAULUS, R., RÖMBKE, J., RUF, A. & BECK, L. (1999): A comparison of the litterbag-, minicontainer- and bait-lamina-methods in an ecotoxicological field experiment with diflubenzuron and btk. – *Pedobiologia*, **43** (2): 120-133.
76. PRINZING, A., KRETZLER, S. & BECK, L. (2000): Resistance to disturbance is a diverse phenomenon and does not increase with abundance: the case of oribatid mites. – *Ecoscience*, **7** (4): 452-460.
77. RÖMBKE, J., BECK, L., FÖRSTER, B., SCHEURIG, M. & HORAK, F. (1995): Bericht zur Literaturstudie: Bodenfauna und Umwelt. – Landesanstalt für Umweltschutz Baden-Württemberg, 1-188.
78. RÖMBKE, J., BECK, L., FÖRSTER, B., FRÜND, H.-C., HORAK, F., RUF, A., ROSCISZEWSKI, K. & SCHEURIG, M. (1997): Boden als Lebensraum für Bodenorganismen. Literaturstudie: Bodenbiologische Standortklassifikation. – *Texte und Berichte zum Bodenschutz*, (4): 430 S.
79. RÖMBKE, J., BECK, L., FÖRSTER, B., FRÜND, H.-C., HORAK, F., RUF, A., ROSCISZEWSKI, K. & SCHEURIG, M. (1997): Fortführung der Literaturstudie: Bodenfauna und Umwelt. – *Texte und Berichte zum Bodenschutz*, (4): 435 S.
80. RÖMBKE, J., FÖRSTER, B., RUF, A. & BECK, L. (1997): Ein Instrument zur Entwicklung von Bodenqualitätszielen: Das BBSK-Konzept. – *Mitt. Bodenk. Ges.*, **85**: 1599-1602.
81. RÖMBKE, J., BECK, L., FÖRSTER, B. & RUF, A. (1998): Aspekte der Untersuchung und Bewertung bodenbiologischer Zustandsparameter. – *Laufener Seminarbeiträge*, (5): 63-70.
82. RÖMBKE, J., HÖFER, H., MARTIUS, C., FÖRSTER, B., FRANKLIN, E., GARCIA, M. & BECK, L. (1999): Die Rolle der Bodenfauna beim Streuabbau in Primär- und Sekundärwäldern und einer Polykulturlandwirtschaft in Amazonien (SHIFT Projekt ENV 52): Methodische Überlegungen. – In: OEHLMANN, J. & MARKERT, B. (Hrsg.): Ökotoxikologie - Ökosystemare Ansätze und Methoden. ecomed Verlag, Landsberg.
83. RÖMBKE, J., DREHER, P., BECK, L., HAMMEL, W., HUND, K., KNOCH, H., KÖRDEL, W., KRATZ, W., MOSER, T., PIEPER, S., RUF, A., SPELDA, J. & WOAS, S. (2000): Bodenbiologische Bodengüte-Klassen. – *UBA-Text*, **6**: 276 S.
84. RÖMBKE, J., DREHER, P., BECK, L., HUND, K., KÖRDEL, W., KRATZ, W., PIEPER, S., SPELDA, J. & RUF, A. (2000): A new concept for determining soil quality. – *SETAC abstract 5dp/006*: 235.
85. RUF, A., RÖMBKE, J., PAULUS, R. & BECK, L. (1997): Die Wirkung von Dimilinen auf Individuen und Populationen von Bodentieren und auf die biologische Aktivität des Bodens eines Laubwalds. – *Mitt. DGAAE*, **11**: 211-215.

86. RUF, A., BECK, L., HAMMEL, W., HUND, K., KRATZ, W., RÖMBKE, J. & SPELDA, J. (1999): Grundlagen zur Erarbeitung eines Bewertungsrahmens für die Bodenfunktion „Lebensraum für Bodenorganismen“ Teil II. Erste Ergebnisse zur Anwendung von bodenkundlich/bodenbiologische definierten Standorttypen in Süddeutschland. – Mitt. Dtsch. Bodenk. Ges., **89**: 177-180.
87. RUF, A., BECK, L., RÖMBKE, J. & SPELDA, J. (2000): Standortsspezifische Erwartungswerte für die Gemeinschaftsstruktur ausgewählter Taxa der Bodenfauna als Bodenqualitätskriterium. – Ber. nat.-med. Verein Innsbruck, **87**: 365-379.
88. SCHALLNASS, H.-J., RÖMBKE, J. & BECK, L. (1992): Zur Biologie eines Buchenwaldbodens 15. Die Doppelfüßer (Diplopoda). – *Carolinea*, **50**: 145-170.
89. SCHEURIG, M., HOHNER, W., WEICK, D., BRECHTEL, F. & BECK, L. (1996): Laufkäferzönosen südwestdeutscher Wälder - Charakterisierung, Beurteilung und Bewertung von Standorten. – *Carolinea*, **54**: 91-138.
90. SCHUBART, H. & BECK, L. (1968): Zur Coleopterenfauna amazonischer Böden. – *Amazoniana*, **1** (4): 311-322.
91. WOAS, S., WUNDERLE, I. & BECK, L. (1987): Lebensraum Buchenwaldboden 12. Die Oribatiden. – *Verh. Ges. Ökol.*, **17**: 117-123.
92. WUNDERLE, I., BECK, L. & WOAS, S. (1990): Zur Taxonomie und Ökologie der Oribatulidae und Scleribatidae (Acari, Oribatei) in Südwestdeutschland. – *Andrias*, **7**: 15-60.

Verzeichnis der nach LUDWIG BECK benannten Arten und Gattungen

Fadenwürmer

Tylocephalus becki ZELL, 1985

Enchyträen

Enchytraeus becki SCHMELZ & COLLADO, 2001

Echte Spinnen

Amazoromus becki BRESCOVIT & HÖFER, 1994

Monoblemma becki BRIGNOLI, 1978

Scytodes becki RHEIMS & BRESCOVIT, 2001 (dieser Band)

Kapuzenspinnen

Cryptocellus becki PLATNICK & SHADAB, 1977

Milben

Acaroceras becki BALOGH & MAHUNKA, 1962

Beckiella GRANDJEAN, 1964

mit *B. carinata* (BECK, 1962), *B. cejanensis* (BECK, 1962),

B. sellnicki (HAMMER, 1961)

Eohypochthonius becki BALOGH & MAHUNKA, 1979

Lancetoppia becki HAMMER, 1968

Nothrus becki BALOGH & MAHUNKA, 1981

Phyllhermannia becki PEREZ-ÍÑIGO & BAGGIO, 1988

Käfer

Fauva becki IRMLER, 2001 (dieser Band)

CHRISTOPHER MARTIUS, JÖRG RÖMBKE, MANFRED VERHAAGH, HUBERT HÖFER & LUDWIG BECK

Termiten, Regenwürmer und Ameisen – prägende Elemente der Bodenfauna tropischer Regenwälder

Zusammenfassung

Neben Regenwürmern, denen weltweit eine besondere Rolle beim Abbau der organischen Substanz, der Nährstoffrückführung sowie der Bodenbildung und -strukturierung zukommt, prägen in tropischen Landökosystemen Termiten und Ameisen als soziale Insekten durch ihren Individuen- und Artenreichtum die Bodenfauna. Als sogenannte Ökosystem-Ingenieure formen sie durch ihre Fraß-, Grab- und Nestbauaktivität sichtbar ihren Lebensraum und bestimmen zusammen mit den anderen Makrofauna-Vertretern (Regenwürmer, Asseln und Tausendfüßer) die Dynamik der Nährstoffkreisläufe.

Summary

Soil fauna – together with microorganisms and plant roots – plays an essential role in the degradation of the dead plant material in terrestrial ecosystems. Therefore, the soil fauna is not only important in forming and regulating the nutrient cycles but also essential for the formation and maintenance of the soil structure. In the tropics, three animal groups – termites, earthworms and ants – dominate soil macrofauna in terms of abundance and biomass. Termites feed on wood, leaf-litter and humus. Their ability to degrade very hard and nutrient-poor substrates is based on an endosymbiosis with lignin- and cellulose-degrading, nitrogen-fixing microorganisms. Termites have a considerable influence on physical and chemical soil parameters through their burrowing and nesting activities; their nests are accumulations of organic matter and nutrients. Earthworms normally prefer substrates richer in nutrients than termites, and they do not occur in dry areas where termites dominate. Recent studies, focussing on Glossoscolecidae (including some "giant" species) show that their effects on physical soil properties, nutrient enrichment and dispersal of microorganisms are similar in tropical and temperate ecosystems. Especially in the formation of clay-humus-complexes they play a very important role for the maintenance of soil quality. In contrast to temperate forests, earthworms can be found in tropical rain forests up to the canopy in epiphyte soils. Most ants do not act as saprophages in the soil system but many species are important as predators on other soil organisms. Soil nesting ant species generally concentrate nutrients in their nests that often derive from other forest strata. On the other hand arboreal ant nests are important sources of nutrients for arboreal guilds of saprophagous animals and contribute to the soil nutrient pool when falling down some time. Ants of the tribe Attini have evolved a symbiosis with fungi, enabling them to exploit the rich resource of green plant leaves (leaf-cutting ants), or to act as saprophages through collecting arthropod remains and other litter items as a substrate for their fungus. Soil nesting ants and especially some leaf-cutting ants with their large colonies are also important soil-organisms because they move and mix large quantities of substrate. The few existing data show that in tropical ecosystems the soil fauna plays a much bigger role in the mineralization of litter than in temperate forests.

Authors

Dr. CHRISTOPHER MARTIUS, Zentrum für Entwicklungsforschung, Universität Bonn, Walter-Flex-Straße 3, D-53113 Bonn;
Dr. JÖRG RÖMBKE, ECT Oekotoxikologie GmbH, Böttgerstraße 2-14, D-65439 Flörsheim a. M.;
Dipl. Biol. MANFRED VERHAAGH, Dr. HUBERT HÖFER, Prof. Dr. LUDWIG BECK, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe.

Key words

soil fauna, tropical rain forests, termites, ants, earthworms

In terrestrischen Ökosystemen ist die Bodenfauna neben den Mikroorganismen und dem Wurzelsystem der Pflanzen die dritte biologische Komponente, die beim Abbau des pflanzlichen Bestandesabfalls mitwirkt, Nährstoffkreisläufe schließt, die Bodenstruktur entscheidend mitbestimmt und aufrecht erhält. Regenwürmer spielen in bodenbiologischen Prozessen weltweit eine bedeutende Rolle, doch kommen in tropischen Ökosystemen zwei andere dominierende und weitverbreitete Gruppen hinzu, die Termiten und die Ameisen. Diese drei Gruppen sind, von den Regenwäldern bis zu den Savannen, prägende Elemente der tropischen Bodenfauna.

Im Gegensatz zu den "Herbivoren"-Nahrungsketten, die mit dem Verzehr grünen, noch lebenden Pflanzenmaterials durch Pflanzenfresser ihren Anfang nehmen, beginnen die "Detritivoren"-Nahrungsketten mit dem Verzehr der abgestorbenen pflanzlichen Substanz ("Detritus") durch die saprophagen Bodentiere. Der biogene Abbau der Biomasse, die von den grünen Pflanzen während der Primärproduktion gebildet wurde, schließt den Kreislauf der Nährstoffe – ein für das Funktionieren eines Ökosystems grundlegender Prozess.

Der Abbau der organischen Substanz erfolgt, vereinfacht gesehen, in zwei Schritten, dem strukturellen Abbau und der nachfolgenden Mineralisierung. Beim ersten Schritt wird die abgestorbene organische Substanz mechanisch zerkleinert, und die Strukturpolysaccharide, vor allem Cellulosen, Hemicellulosen und Lignine, werden in einfache, monomere Moleküle zerlegt. Im zweiten Schritt werden diese Moleküle intrazellulär enzymatisch gespalten und – meist oxidativ – in die mineralischen Ausgangsstoffe, beispielsweise CO_2 , H_2O sowie Oxide anderer Elemente umgewan-

delt (vgl. BECK et al. 1997). Bodentiere sind auf verschiedenen Ebenen daran beteiligt: Primärzersetzer zerkleinern das frisch gefallene Pflanzenmaterial und schließen es zum Teil enzymatisch auf, während die sogenannten Sekundärzersetzer für den Aufschluss der dabei entstandenen Kotballen sorgen. Beide Gruppen interagieren auch mit der Mikroflora, so z. B. mit den Bodenpilzen, deren Biomasse sie beispielsweise durch "Abweiden" kontrollieren. Paradoxe Weise wird hierdurch deren Aktivität stimuliert, denn durch das Abweiden wird die Mikroorganismengemeinschaft verjüngt – und damit produktiver. Darüber hinaus beherbergen viele Zersetzerorganismen wie Termiten und Regenwürmer reichhaltige Mikroorganismengemeinschaften (KÖNIG & BREUNIG 1997), denen sie in ihrem Darm optimierte Lebensbedingungen bieten. Durch die "Endosymbiose" sind diese Bodentiere indirekt oder direkt an beiden Abbauschritten beteiligt.

Aufgrund der opportunistischen, anpassungsfähigen Ernährungsweise vieler Bodentiere sind ihre Nahrungsketten vielfältig miteinander verknüpft; zusammen mit den Mikroorganismen bilden sie eher ein verzweigtes "Nahrungsnetz" – das der Saprophyten oder Detritivoren. Je näher die Organismen am Primärgeschehen des Abbaus tätig sind, desto unmittelbarer wird ihre Wirkung sichtbar. Anders gesagt sind es unter den Bodentieren die Primärzersetzer, die entscheidend Ablauf und Geschwindigkeit des Abbaus beeinflussen. Deren Wirkung wird in Ausschlußexperimenten mit inzwischen weltweit erprobten Streubeuteln verschiedener Maschenweite nachgewiesen (BECK 2000, CORNU et al. 1997, HÖFER et al. im Druck, LEHMANN et al. 1995, YAMASHITA & TAKEDA 1998).

Natürlich gibt es im Boden neben den Zersetzerorganismen auch zahlreiche Prädatoren und Aasfresser, die auf vielfältige Weise mit den Saprophyten interagieren bzw. in das Bodenfauna-Nahrungsnetz eingeschlossen sind.

Die Vertreter der Bodenfauna werden nicht nur nach der Position in der Nahrungskette, sondern auch nach ihrer Größe klassifiziert, allerdings überlappen sich die beiden Klassifizierungen zum Teil. Die Primärzersetzer und Predatoren sind überwiegend der Makrofauna (Tiere mit über 2 mm Körperlänge) zuzurechnen, während Meso- (0,2-2,0 mm) und Mikrofauna (unter 0,2 mm) hauptsächlich als Sekundärzersetzer tätig sind (vgl. BECK 1993). Da diese Größeneinteilung willkürlich ist, werden in der Praxis allerdings häufig auch tiergruppenspezifische Einteilungen, bzw. Bearbeitungen vorgenommen, das heißt alle Springschwänze und Milben der Mesofauna und z.B. Käfer oder Ameisen unter 2 mm Länge der Makrofauna zugeordnet. In Ökosystemen mit raschem strukturellen Abbau wie den meisten tropischen Regenwäldern (vgl. HÖFER et al. im Druck) wird die Bodentierbiomasse von der Makrofauna dominiert. In den Böden tropischer Regen-

wälder zählen dazu vor allem drei Gruppen: Termiten, Ameisen und Regenwürmer. Sie sind zwar überwiegend in der Streuauflage und in den obersten Zentimetern des Bodens zu finden, doch können ihre Nester und Gänge mehrere Meter tief hinabreichen, weswegen diese Tiergruppen auch eine wichtige Rolle bei der Umwälzung der Bodenschichten ausüben.

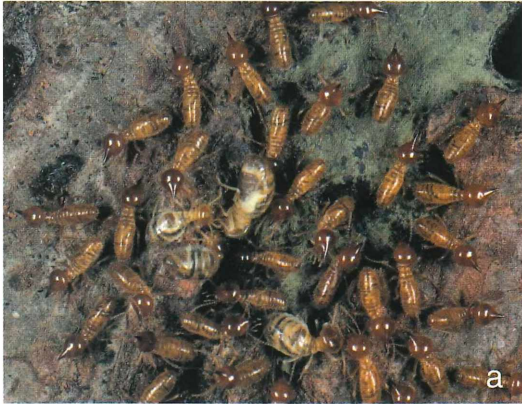
Obwohl zumindest Termiten und Ameisen überall in den Tropen jedem Beobachter auffallen, gibt es nur wenige verlässliche Daten über ihre Siedlungsdichte, ihre Biomasse und ihre Leistung. Die üblicherweise in der Bodenzöologie verwendeten Standardverfahren (z.B. Handauslese oder auf Hitze- und Feuchtigkeitsgradienten beruhende Austreibungsmethoden wie Berlese-Tullgren oder Kempson; vgl. ADIS 1987, ANDERSON & INGRAM 1993, SCHAUERMANN 1982) sind leider zur Erfassung dieser stark aggregiert und immer nur mit einem Teil ihrer Population außerhalb der Nester vorkommenden sozialen Insekten wenig geeignet. Überdies liegen meist nur Daten über die jeweilige Gesamtzahl der Bodentiere an den verschiedenen Standorten vor. Ohne eine differenzierte Betrachtung der einzelnen Arten oder einzelner funktioneller Gruppen (Gilden, so z.B. der Holz- und Humusfresser bei den Termiten oder der Laubschicht- und Bodenbewohner bei den Regenwürmern) ist eine genaue Bestimmung der tatsächlichen Leistung dieser Tiere unmöglich.

Termiten

Unter den genannten Tiergruppen spielen die Termiten in tropischen Regenwäldern eine so überragende Rolle, dass man ihnen auch den Beinamen "Regenwürmer der Tropen" gegeben hat. Sie scheinen tatsächlich in manchen Regionen die Regenwürmer zu ersetzen (s.u.), kommen aber auch mit ihnen zusammen vor, so in zentralamazonischen Regenwäldern (RÖMBKE et al. 1999, HÖFER et al. im Druck).

Alle Straten eines Regenwaldes, vom tiefen Mineralboden bis in die Baumkronen, sind von jeweils eigenen, spezialisierten Termitenarten besiedelt. Sie nutzen sämtliche Substrate als Nahrung und/oder Baumaterial, vom humusdurchsetzten Boden über den organischen Bestandesauffall in jeder Form, sei es als Laub- oder Holzstreu auf dem Waldboden, als Totholz in den Stämmen toter, noch stehender Bäume, bis hin zum (physiologisch ja bereits abgestorbenen) Holz im Kern noch lebender Bäume. Als "eu"-soziale Insekten bilden sie Staaten aus mehreren Tausend bis zu Millionen Tieren, die in verschiedene morphologisch-funktionelle Kasten differenziert sind. Ihnen obliegen die verschiedenen, zum Erhalt der Kolonie notwendigen Arbeiten (Nestbau, Nahrungsbeschaffung, Brutpflege, Verteidigung etc.).

Die meisten Termiten sind Holzfresser. Die klassische Einteilung in „Trockenholztermiten“ (Familie Kalotermitidae) und „Feuchtholztermiten“, darunter vor allem



Tafel 1. a) Arbeiter einer Kolonie von *Nasutitermes macrocephalus* beim Reparieren ihres Nestes. Soldaten, die aus ihrer Kopfdrüse ein klebriges Sekret mehrere cm weit schleudern können, sichern die Stelle vor allem gegen räuberische Ameisen ab (Foto: W. QUEISSER); b) *Nasutitermes macrocephalus* beim Fraß; c) Im hohlen Stamminnen eines Jahrhunderte alten Urwaldriesen aus dem Amazonasgebiet hat sich durch die Tätigkeit von Pilzen, Termiten und Pflanzenwurzeln ein regelrechter Boden gebildet (Foto: C. MARTIUS); d, e) Laubfressende Termiten (*Syntermes*) kommen in der Dämmerung zur Nahrungssuche aus ihren Bodennestern. Sie gehören zu den größten Termiten überhaupt (Foto: C. MARTIUS, H. HÖFER); f) Die Arbeiter der *Syntermes*-Termiten schneiden mit ihren kräftigen Mandibeln halbrunde Stücke aus dem Laub, die sie ins Nest transportieren und dort verzehren (Foto: C. MARTIUS).

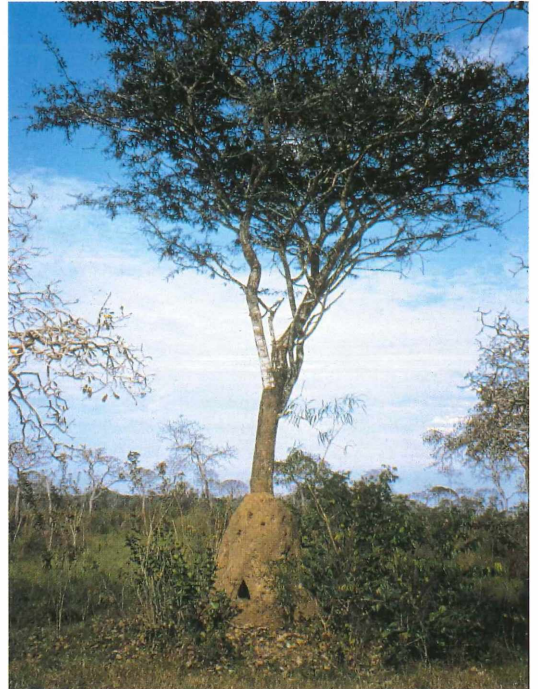


Tafel 2. a, b) Riesenregenwürmer aus einem amazonischen Tieflandregenwald (Reserva Ducke, Manaus; Fotos: H. HÖFER);
 c) Regenwurmexkreme in einem Tieflandregenwald nahe Manaus, Amazonien (Foto: J. RÖMBKE);
 d) Regenwurmexkreme in einer Elefantengras-Feuchtsavanne des Outamba-Kilimi Nationalparks in Sierra Leone (Foto: M. VERHAAGH).



Tafel 3. a) Eine Phalanx von Wanderameisen (*Eciton drepanophorum*) durchkämmt den Waldboden in Amazonien (Foto: M. VERHAAGH); b) Ameisengarten (Foto: M. VERHAAGH); c) Bodennistende Ameisen (*Ectatomma tuberculatum*) beim Sammeln von Membraciden-Honigtau (Foto: N. BLÜTHGEN); d) Das Nest einer Kolonie von Blattschneiderameisen (*Atta cephalotes*) besteht aus vielen Kammern und hat zahlreiche durch Erdkrater gekennzeichnete Ausgänge. Es kann eine Ausdehnung von mehreren Quadratmetern haben und mehrere Meter tief in den Boden reichen (Foto: L. BECK). e) Pilzzucht durch Ameisen der Gattung *Acromyrmex* in ihrem Nest (Foto M. VERHAAGH).





Tafel 4. a) Durch die Aktivität von Termiten entstandene Landschaftsform: "Campos de Murunduns" in der Nähe der brasilianischen Stadt Cuiabá (Bundesstaat Mato Grosso, Foto: L. BECK); b) Termitenbau in bolivianischen Überschwemmungssavannen (Süd-Beni; Foto: H. HÖFER)

die Vertreter der Rhinotermitiden und Nasutitermitiden, kann heute nicht mehr aufrecht erhalten werden. Die Kalotermitiden leben in unvermodertem (doch, wie sich herausgestellt hat, nicht unbedingt nur in trockenem) totem Holz noch am Baum befindlicher Äste und stehender Stämme. Es gibt wenige Arten, ihre Kolonien sind nur klein und von außen kaum wahrnehmbar. Während Kalotermitiden die Termitengemeinschaften trockener Regionen dominieren (MARTIUS et al. 1999, SCHLEMMERMEYER 2000), treten sie in Regenwäldern kaum in Erscheinung. Die Rhinotermitiden und vor allem die Nasutitermitiden (Taf. 1 a,b) stellen eine Vielzahl holzfressender Arten und einen Großteil der Termitenbiomasse in tropischen Wäldern. Diese Arten leben von vermodertem (deswegen meist "feuchtem") Totholz, welches durch eingedrungene Pilze und Mikroorganismen schon vorzersetzt ist.

Dabei besteht zwischen Termiten und Pilzen wahrscheinlich eine mutualistische Beziehung: Die Termiten bohren Gänge und vergrößern damit die Angriffsfläche für die Zersetzerpilze, welche allein nur langsam im Holz vordringen könnten. Sicherlich schleppen die Termiten auch Pilzsporen ein. Wie schon erwähnt, befehlen Termiten oft schon das Innere des Stammes noch lebender Bäume; sie dringen vom Boden her oder über Astlöcher in das Holz ein. Durch ihre Tätigkeit kann über die Jahrzehnte, die ein solcher Baum noch lebt, im Stamminneren ein regelrechtes „Boden“ entstehen, der von Pflanzenwurzeln durchzogen ist (Taf. 1 c). Dadurch werden die in der Holzbiomasse festgelegten Nährstoffe schon vorzeitig wieder mobilisiert. Man hat dies als ein Beispiel für die möglichst verlustfrei geführten Stoffkreisläufe auf den nährstoffarmen tropischen Standorten betrachtet (JANZEN 1976).

„Erntetermiten“, die abgestorbenes (nur sehr selten auch lebendes) Laub verwerten, spielen vor allem in tropischen Savannen eine herausragende Rolle; aber auch in den Regenwäldern gibt es solche Termitenarten, in Südamerika z.B. die Vertreter der Gattung *Syntermes*, die zu den größten Termiten der Welt zählen (Taf. 1 d,e). Sie leben unterirdisch in Kolonien, die eine Ausdehnung von vielen Quadratmetern haben können und mehrere Meter tief in den Boden reichen (DARLINGTON 1995, MARTIUS 1998, MARTIUS & WELLER 1998). Diese Termiten verlassen ihre Nester meist nur nachts, um auf der Bodenoberfläche kleine halbrunde Stücke aus dem Laub zu schneiden (Taf. 1 f). Ihre Effizienz beim Zerkleinern des Laubes ist so groß, dass dort, wo sie vorkommen, die Laubschicht oft nur noch aus vereinzelt auf dem nackten Boden herumliegenden Blättern besteht. Mancher nachts im Urwald kampierende Forscher hat seine eigenen Erfahrungen mit diesen Termiten gemacht, die weder vor Zeltbahnen noch ledernen Kamerariemen Halt machen!

Die laubfressenden *Syntermes*-Arten zerkaugen das in den Bau eingetragene Laub und verwerten es direkt. Ähnlich den Blattschneiderameisen gibt es aber auch

pilzzüchtende Termiten, die ebenfalls oft sehr großen Macrotermitiden, die als wichtige Holz- und Laubverwerter außer in Amerika und Australien auf allen Kontinenten zu Hause sind. Sie tragen zerkautes Laub oder Holz in besondere Kammern in ihrem Bau, wo auf diesem mit Termiten-Speichel durchmischten Pflanzenmaterial bestimmte Pilze der Gattung *Termitomyces* wachsen. Sie bilden kleine kugelförmige Körperchen, die als Nahrung für Königin und Larven verwendet werden; das vom Pilz chemisch veränderte Pflanzenmaterial dient dagegen den Arbeitern als Nahrung. Diese Termiten setzen zweimal soviel Streu pro Einheit Körpergewicht um wie andere Termiten, da sie ja auch den Pilz miternähren müssen (WOOD & SANDS 1978): Die Verlängerung der Nahrungskette bedeutet immer auch, daß ein höherer Einsatz an primärer pflanzlicher Nahrung erforderlich ist.

„Humusfresser“ als dritte große Termiten-Gruppe neben Holz- und Laubverwertern sowie Pilzzüchtern ernähren sich vom mehr oder weniger stark zersetztem organischen Material in der Streu und in den obersten Bodenschichten (BIGNELL 1994). Wie die Regenwürmer müssen sie große Mengen an Bodenmaterial durcharbeiten, um diesem niederwertigen Substrat ausreichend Energie entziehen zu können. Um effizient immer neue Bodenbereiche ausbeuten zu können, legen viele dieser Arten einfache, sich ständig wandelnde Gangsysteme im Boden an. Ein eigentliches Nestzentrum kann deshalb nicht mehr ausgemacht werden, was das Studium dieser Gruppe sehr erschwert. Hierzu gehören viele Termiten der Unterfamilie der soldatenlosen Termiten (Apicotermitinae). Aber auch die meisten Vertreter der Familie Termitidae sind Humusfresser; viele davon bauen Nester und scheinen sich bevorzugt an der Grenzfläche zwischen Totholz und Boden aufzuhalten (so genannte soil/wood interface feeders).

In der Verteilung der Nahrungstypen auf die Familien zeigt sich auch der Gang der Evolution: Während primitivere Kalotermitiden auf die Ressource Totholz nicht nur als Nahrung, sondern auch als Lebensraum vollständig angewiesen sind, können nestbauende Holzfresser, bei denen Nist- und Fraßplatz getrennt sind, die weit verstreuten Nahrungsressourcen viel besser ausbeuten. Damit erhöht sich die potentiell mögliche Koloniegröße und somit die Überlebenschance. Die höher entwickelten Termitiden konnten sich durch eine Umstellung der Zusammensetzung ihrer Darmflora sogar die Ressource Humus erschließen.

Termiten verwenden generell ihren Kot für den Bau der Nester, und diese Kotschichten können im Lauf der Jahre eine beträchtliche Dicke erlangen. Manche humivore Termitenarten haben sich ganz auf die Ausbeutung des Nestmaterials anderer Termiten spezialisiert. Diese Mitbewohner oder „Inquilinen“ sparen sich den Energieaufwand für den Bau eigener Nester und leben gut ernährt und gleichzeitig gut geschützt in den

Wänden der Bauten ihrer Gastgeber. In afrikanischen und südamerikanischen Regenwäldern sind jeweils bis zu 30% der Termitenbauten von diesen Inquilinen besiedelt. Meist leben 2-3, in Extremfällen bis zu 9 verschiedene Arten in einem Nest (APOLINÁRIO 1993, DEJEAN & RUELLE 1995).

Durch eine Symbiose mit im Hinterdarm lebenden Mikroorganismen sind Termiten in der Lage, Pflanzenmaterial, das aufgrund seines hohen Gehaltes an pflanzlichen Strukturpolysacchariden (Cellulosen, Hemicellulosen und Lignine) eigentlich nur schwer zersetzbar ist, sehr effizient aufzuschließen. Zunächst werden die von den Mundwerkzeugen grob zerkleinerten Nahrungspartikel in einem mit Chitinzähnen bewehrten Kaumagen (Vorderdarm) weiter zerkleinert. Im Mitteldarm wird der Nahrungsbrei dann mit Cellulose spaltenden, zumindest teilweise körpereigenen Enzymen versetzt, bevor die Cellulose im (zu einer großen, blasenförmigen Gärkammer erweitertem) Hinterdarm von symbiotischen Mikroorganismen aufgeschlossen wird (KÖNIG & BREUNIG 1997). Die Darmsymbionten-Gemeinschaften der Termiten bestehen aus mehreren Arten von Protozoen sowie verschiedenen aeroben und anaeroben Bakterien, die, wie die Mikroorganismen im Pansen der Wiederkäuer, in einem komplexen Nahrungsnetz miteinander verbunden sind (YOSHIMURA 1995).

Als ein Endprodukt der anaeroben Fermentation der schwer abbaubaren Pflanzenstoffe wird mikrobiell produziertes Methan (CH_4) freigesetzt, das gegenüber Kohlendioxid (CO_2) ein 32-mal höheres Potential als „Treibhausgas“ besitzt. Nach ersten Messungen Anfang der 80er Jahre wurde angenommen, dass Termiten ein Drittel der weltweit jährlich in die Atmosphäre freigesetzten Methanmenge produzieren würden. Grund dafür war die Vermutung, daß durch die großflächige Abholzung von Tropenwäldern so viel Holz zur Verfügung stünde, daß die holzfressenden Termitenpopulationen bei diesem Überangebot an Nahrung explosionsartig anwüchsen (ZIMMERMAN et al. 1982). Aber die Waldrodung verändert die mikroklimatischen Bedingungen so einschneidend, dass die meisten Termitenarten, welche auf die konstante Feuchte des Waldes angewiesen sind, auf den offenen Schlägen gar nicht vorkommen. Das Holz, das nicht verbrannt oder in eine Sägerei gebracht wurde, wird auf den gerodeten Flächen nur sehr langsam zersetzt. In den sonnenbeschienenen, völlig trockenen Stämmen findet man nur wenige Pilze und einige holzfressende Käferlarven. Methan wird hier also nur in geringen Mengen gebildet (MARTIUS et al. 1996). Derzeit wird deshalb der Anteil der Termiten an der weltweiten Gesamtproduktion dieses Gases nur noch auf 4% geschätzt (vgl. hierzu auch MOORE 1994). Auch an der weltweiten Jahresproduktion des Treibhausgases Kohlendioxid sind die Termiten mit nur maximal 2% beteiligt (SANDERSON 1996).

Da stickstoffarme Ressourcen wie Holz die hauptsächlichliche Nahrungsgrundlage der Termiten darstellen, sind verschiedene Mechanismen des Stickstoffhalts in der Kolonie zu beobachten, wozu bei "Niedereren Termiten" auch der Verzehr toter Nestgenossen gehört (WOOD & SANDS 1978). Eine weitere Verbesserung ihrer Stickstoffbilanz wird durch die Fähigkeit mancher ihrer Darmsymbionten (in diesem Fall Bakterien) Luftstickstoff zu fixieren erreicht. Obwohl deren N-Fixierungsraten nicht die der mit Leguminosen vergesellschafteten Knöllchenbakterien erreichen (SMITH & DOUGLAS 1987), beziehen beispielsweise Trockenholztermiten bis zu 50% ihres Stickstoffbedarfs über diesen Weg aus der Luft (TAYASU et al. 1994). Humusfressende Termitenarten fixieren allerdings nach neueren Daten dieser japanischen Forschergruppe wesentlich weniger Stickstoff.

Termiten sind in Regenwäldern mit etwa 100 Arten pro Hektar vertreten. Die meisten davon werden im Totholz am Waldboden gefunden. Im Boden der Regenwälder gibt es, je nach Bestand, 1.500 bis 4.500 Termiten pro Quadratmeter, mit einer Trockenbiomasse von 1,0-4,5 g/m² (das Frischgewicht liegt etwa 4-mal höher). Nimmt man jedoch die in tiefen Bodenschichten und hohlen Baumstämmen lebenden Termiten dazu, kann die Biomasse mindestens 3-mal höher liegen (vgl. BECK et al. 1997). Wie stark die Termiten im intakten Regenwald dominieren, zeigt der Vergleich der Makrofaunadichte am Boden einer Primärwaldfläche mit benachbarten Sekundärwald- und Polykulturflächen in Amazonien. Termiten stellten in Streu- und Bodenproben aus dem Primärwald 24% der gesamten Makrofauna und damit fast 50% der Zersetzer (Abundanz und Biomasse), im Sekundärwald waren sie noch ähnlich häufig, in den Pflanzungen aber unter 13% der Makrofauna bzw. 20% der Zersetzer (HÖFER et al. im Druck). Im Primärwald war allerdings auch das Gesamtvolumen an Totholz mit 35 m³ 2- bis 8-fach höher als in den anthropogenen Flächen (MARTIUS & BANDEIRA 1998).

In verschiedenen Ökosystemen konsumieren Termiten zwischen 10% und 50% der jährlich produzierten Streu (in einem Wüstenökosystem im Süden der USA sind es sogar 100%, FOWLER & WHITFORD 1996). Für amazonische Regenwälder haben in Ermangelung genauer quantitativer Daten durchgeführte Hochrechnungen ergeben, dass Termiten hier etwa 20-30% der Streu konsumieren, wobei aber nur 1-2% des in der Streu organisch gebundenen Kohlenstoffs zu CO_2 oxidiert werden (MARTIUS 1994, HANNE 2001). Vergleicht man jedoch das Verhältnis der mit 2% etwa gleich großen Mineralisierungsrate durch die Makrofauna in einem Kalkbuchenwald bei Göttingen mit der Konsumtion, dann zeigt sich, dass die gesamte Makrofauna hier 100% der jährlichen Streuproduktion konsumieren muss, um ihren Energiebedarf zu decken (SCHAEFER 1990). Dies bedeutet, dass im tropischen Regenwald der Beitrag der

Makrofauna als Primärzersetzer, die ja nicht nur aus Termiten bestehen, zum Abbau der Streu auf mindestens 5-10% zu schätzen ist und damit wesentlich höher liegt als in den gemäßigten Breiten. Neuere Ergebnisse zeigen, dass einige der Parameter, die zu den Abschätzungen in MARTIUS (1994) geführt haben, wahrscheinlich noch unterschätzt worden sind. Deswegen wurde der gesamte Beitrag der Termiten zum Kohlenstoffkreislauf von HANNE (2001) neu untersucht.

Termiten beeinflussen physikalische und chemische Bodeneigenschaften durch ihre Aktivitäten im Boden, u. a. über die Einarbeitung des Nestmaterials. Außerdem erstreckt sich ihr Einfluss auch steuernd auf die Populationen vieler anderer Zersetzerorganismen wie Pilze, Regenwürmer und Arthropoden (SALICK et al. 1983), denen sie das Rohmaterial zu ihrer Ernährung liefern. Das Baumaterial der Termitenhügel enthält meist 10-35 % organische Substanz, d. h. wesentlich mehr als der umgebende Boden; ausserdem sind in ihm Nährstoffe wie N, P, K, Mg und Ca teilweise beträchtlich angereichert. Dem steht die chemische und physikalische Stabilität und Resistenz der Humussubstanzen und der gebildeten Humus-Boden-Aggregate gegenüber (AMELUNG et al. im Druck), die aber gleichzeitig das Hohlraum- und Porenvolumen verbessern und damit so wichtige Bodeneigenschaften wie Belüftung, Drainage und Wasserhaltekapazität positiv beeinflussen.

Man kann deshalb fast generell von einer Bodenmelioration durch Termiten ausgehen, und bei der hohen Zahl existierender Arten, deren Nester die chemisch jeweils ganz verschiedenen Endprodukte ihrer Physiologie sind, ergibt sich eine hohe Diversität im Abbaugeschehen, deren Bedeutung für die Humusbildung in Regenwäldern noch gar nicht abgeschätzt werden kann (AMELUNG et al. im Druck). Allerdings ist diese Erkenntnis nicht unbedingt von praktischem Nutzen. Die Erfahrungen bei der experimentellen Verwendung von Termiten-Nestmaterial zur Bodenverbesserung sind nicht durchgängig positiv. Am Amazonas wird beispielsweise Nestmaterial von den Kayapó-Indianern zur organischen Düngung beim Pflanzen von Baumsetzlingen und von „Caboclo“-Bauern bei der Gemüseproduktion eingesetzt. Untersuchungen in Amazonien zeigen jedoch, dass Termiten-Nestmaterial trotz höherer Nährstoffgehalte das Wachstum von Anbaupflanzen nicht unbedingt verbessert; die Wirkung bleibt hinter der von Mineraldüngern zurück oder bedarf zumindest der Aufbesserung durch gleichzeitige Zugabe von Mineraldüngern (BATALHA et al. 1995, RIBEIRO 1997). In Afrika wird von manchen Völkern die Fruchtbarkeit degradierter Böden mit Hilfe von Mulch aus feinem Totholz (Äste und Zweige), der durch Termiten schnell umgewandelt wird, wieder hergestellt (BURNETT 1948). Andererseits sind die Nester mancher Arten, z.B. die der savannenbewohnenden *Cornitermes*-Arten, so hart und nährstoffarm, dass sie für die Landwirtschaft und Viehzucht in diesen Gebieten ein großes Problem darstellen können.

Regenwürmer

Bis Anfang der achtziger Jahre war man der Überzeugung, dass in tropischen Regenwäldern generell wenig Regenwürmer vorkommen und ihre Rolle im Destruentensystem demzufolge vernachlässigbar sei (ANDERSON & SWIFT 1983). Inzwischen musste, vor allem aufgrund methodischer Verbesserungen bei der Erfassung der Tiere, dieses Bild modifiziert werden. FRAGOSO & LAVELLE (1987) fanden beispielsweise in verschiedenen Ausprägungsformen eines süd-mexikanischen Regenwaldes bis zu 11 Arten (etwa ein Drittel davon Baumbewohner), deren Gesamtpopulation mit 120 Ind./m² und einer Biomasse von 43 g/m² Frischgewicht Werte erreichte, die in der Größenordnung gut besiedelter mitteleuropäischer Laubwaldböden liegen. Auch in anderen Primärwäldern, z.B. Brasiliens, dominiert die Biomasse der Regenwürmer gegenüber der anderer Makrofauna-Gruppen (CHAUVEL et al. 1987, HÖFER et al. im Druck). Bei einem Vergleich der Regenwurm-Zönosen an 12 Regenwald-Standorten stellten die Regenwürmer 51% der gesamten terrestrischen Tierbiomasse, gefolgt von den Termiten mit 13% (FRAGOSO & LAVELLE 1992). Aufgrund der extremen Größenunterschiede tropischer Regenwürmer (z.B. in einem amazonischen Primärwald mit Biomassen zwischen 10 mg und 35 g Frischgewicht bei Längen von ca. 2 bis ca. 110 cm) gibt es keine direkte Korrelation zwischen der Abundanz und Biomasse an einem Standort (RÖMBKE et al. 1999). Da zudem große Tiere äußerst ungleichmäßig verteilt vorkommen, sagen Durchschnittswerte wenig über die Bedeutung der Regenwürmer an einem Standort aus, außer über die Tatsache, dass diese Tiergruppe nicht vernachlässigbar ist.

In den Tropen dominieren andere Regenwurm-Familien als die in den gemäßigten Breiten dominanten Lumbriciden, z.B. die Glossoscolecidae in Süd- und Mittelamerika, die Eudrilidae in Afrika oder die Megascoclecidae in Südostasien. Zunehmend werden in vielen tropischen Gebieten jedoch einheimische Regenwürmer durch eingeschleppte (peregrine) Arten verdrängt. Die tropischen Regenwürmer unterscheiden sich morphologisch nur wenig von europäischen Arten (Ausnahme sind die tentakelförmigen „Kopflappen“ bei einigen Arten, z.B. bei *Thamnodrilus tenkatei* oder *Anteus distinctus*), doch können sie erheblich größer werden: Arten wie *Megascolecoides australis* aus Australien oder *Rhinodrilus faffner* aus Brasilien werden über 2 m lang (Taf. 2 a,b). Dementsprechend groß sind dann nicht nur die Ei-Kokons (über 5 cm lang bei Glossoscoleciden aus Kolumbien; ZICSI & CSUZDI 1997), sondern auch die Exkrementhaufen (bis ca 10 cm Durchmesser; Taf. 2 c).

Über die Lebensweise dieser extrem großen Würmer ist wenig bekannt, doch scheinen sie permanente, bis in eine Tiefe von mehreren Metern reichende Tunnel zu bewohnen. AYALA et al. (1972) berichten, dass eine

Art der Gattung *Thamnodrilus* bei Störungen oder Angriffen, z.B. durch Nattern, eine klebrige Flüssigkeit absondern kann, mit der eine Tunnelröhre teilweise oder vollständig ausgefüllt wird, so dass sich der Wurm in größere Tiefen zurückziehen kann. Im Gegensatz zu manchen dramatischen Berichten des 19. Jahrhunderts sind die meist erstaunlich "weichen" Riesenregenwürmer für andere Tiere völlig ungefährlich. Wenn sie an die Oberfläche kommen, werden sie von Indianern in Süd-Venezuela sogar als Nahrung genutzt.

Ökologisch lassen sich Regenwürmer weltweit in drei Gruppen einteilen (BOUCHÉ 1977): Streuschichtbewohner (Epigées), Mineralschichtbewohner (Endogées) und Tiefgräber (Anéciques). Allerdings weichen die jeweiligen Anteile dieser drei Gilden an der Regenwurmfauuna in den Tropen von denjenigen in unseren Breiten ab: In den tropischen Regenwäldern fehlen häufig die für die Holarktis typischen Vertikalgräber (Anéciques), zu denen beispielsweise der bekannteste holarktische Regenwurm, *Lumbricus terrestris*, gehört. Wenn sie vorkommen, wie z.B. in Süd-Venezuela (NEMETH & HERRERA 1982), dann sind sie kleinräumig sehr heterogen verteilt und dürften den Streuabbau weniger stark beherrschen als in Wiesen und Müllwäldern gemäßigter Breiten.

Auf der anderen Seite sind die Mineralschichtbewohner der Tropen ökologisch oft wesentlich stärker differenziert, je nach Nahrungsmenge und -qualität. Deshalb hat LAVELLE (1983) eine weitere Unterteilung in oligo-, meso- und polyhumics eingeführt. Die Ursache dürfte in dem sehr variablen Gehalt an organischer Substanz in tropischen Böden zu suchen sein, die zudem oft wegen ihres hohen Gehaltes an Alkyl-C und der daraus resultierenden Polymethylenstruktur nur schwer aufschließbar ist. Wenn aber einzelne Arten wie *Pontoscolex corethrus* aufgrund ihrer Ausstattung mit symbiontischen Mikroorganismen fähig sind, diese Nahrungsquellen zu nutzen, dann können sie hochdominant werden, wie dies beispielsweise in Böden auf Weideflächen gerodeter Waldstandorte im brasilianischen bzw. peruanischen Amazonasgebiet festzustellen ist (BARROS, pers. Mittl., RÖMBKE & VERHAAGH 1992). Freilandbeobachtungen in landwirtschaftlich genutzten Böden Australiens deuten daraufhin, dass diese Spezies ihren Kohlenstoffbedarf weder aus den komplexen organischen Verbindungen der Humusfraktion des Bodens noch aus der Streu deckt (SPAIN et al. 1990). Versuche mit radioaktiv markiertem Kohlenstoff weisen darauf hin, dass die Würmer Wurzelasscheidungen und die mit den Wurzeln assoziierten Mikroorganismen aufnehmen. BAROIS et al. (1987) halten *Pontoscolex corethrus* für fähig, ähnlich wie manche Termiten-Arten, mit Hilfe von Darmsymbionten Luftstickstoff zu fixieren, was den Tieren die Nutzung extrem nährstoffarmer Substrate erleichtern dürfte. Nur der Vollständigkeit halber sei erwähnt,

dass zu dieser Gruppe auch einige wenige räuberische Arten gehören (z.B. der Gattung *Agastrodriulus* in Savannenböden der Elfenbeinküste; LAVELLE 1983).

Die häufigste Regenwurm-Gruppe in tropischen Regenwäldern sind die oft kräftig gefärbten Streuschichtbewohner (Epigées), zu denen auch viele arboricole Arten des Stamm- und Kronenraumes, speziell in den „sols suspendus“ und „sols d'épiphytes“, zu zählen sind (z.B. die blau irisierende Art *Eutrigaster sporadonephra* aus mexikanischen Bromelien (FRAGOSO & ROJAS-FERNANDEZ 1996). Solche arboricolen Regenwürmer kommen in gemäßigten Breiten kaum vor (Ausnahme in Mitteleuropa: *Lumbricus eiseni* – einer aufgrund ihrer Lebensweise oft übersehenen Art; RÖMBKE 2000). Die Nahrungsansprüche dieser Regenwürmer sind weitgehend unbekannt; man nimmt an, dass neben polysaprophagen Arten und spezialisierten Pilzfressern auch solche Arten vorkommen, die Wurzeln als Nahrungsquelle nutzen.

Es gibt nur wenige Untersuchungen über die Leistungen tropischer Regenwürmer, aber die bisherigen Ergebnisse, vor allem aus Süd- und Mittelamerika, deuten eine den Verhältnissen in den gemäßigten Breiten durchaus vergleichbare Rollenvielfalt im bodenbiologischen Geschehen an, vor allem in den oberen Bodenschichten, der so genannten Drilosphäre (LAVELLE et al. 1992): Verbesserung der physikalischen Eigenschaften, speziell der Wasserleit- und -haltefähigkeit durch Grabaktivität, Durchmischung von Mineralboden und organischer Substanz mit Bildung von sehr stabilen Aggregaten, selektive Anreicherung von Nährstoffen wie Calcium im Kot, Stimulierung und Regulation der mikrobiellen Aktivität durch Verbreitung bzw. selektiven Fraß aber wiederum im Kot (LAL 1988, MULONGOY & BEDORET 1989). Besonders hervorzuheben ist ihre Rolle beim Streuabbau, vor allem bei der Fragmentierung des Laubs und bei der Einarbeitung des Humus in den Boden (FRAGOSO & LAVELLE 1995). Aufgrund dieser, das gesamte Teilökosystem Boden beeinflussenden Aktivitäten, werden Regenwürmer, speziell Tiefgräber, als "ecosystem engineers" bezeichnet; das heißt sie schaffen erst den Lebensraum für andere Bodenorganismen (LAVELLE et al. 1997). Diese hohe Wertigkeit führte in den letzten Jahren dazu, sie – z.B. in Peru oder Indien – aktiv zur Bodenverbesserung, speziell der Förderung der Bodenfruchtbarkeit einzusetzen (LAVELLE et al. 1998).

Aufgrund der Größe und Menge von Regenwurmerkrementen besteht an verschiedenen tropischen Standorten, wie z.B. den Savannen Sierra Leones (Taf. 2 d), die oberste Bodenschicht oft quadratkilometerweise aus organo-mineralischen „Krümeln“, die ihre Stabilität jahrelang behalten und damit den Wasserhaushalt positiv beeinflussen können. Auch kleinere Arten produzieren, bei täglichen Fraßraten vom 5-30fachen des eigenen Körpergewichts, sehr große Mengen an Kotkrümeln, so z. B. *Pontoscolex corethrus* in einem

Regenwald der Elfenbeinküste mit jährlich 15-30 t/ha (NOOREN et al. 1995). Dabei können Regenwürmer und Termiten dieselben Bodenschichten nutzen; eine Regenwurmart in Sri Lanka, *Notoscolex termiticola*, lebt sogar – und möglicherweise ausschließlich – in Termitenhügeln (ESCHERICH 1911).

Insgesamt lässt sich die ökologische Rolle der Regenwürmer in tropischen Regenwäldern derzeit wie folgt zusammenfassen: Wie Termiten beeinflussen sie natürliche und anthropogen veränderte Bodeneigenschaften stark, insbesondere die Bodenfruchtbarkeit. Die jeweilige Dominanz einer dieser beiden Tiergruppen an einem Standort hängt dabei sehr vom Klima ab, denn Regenwürmer scheinen jährliche Niederschläge von mindestens 800 mm zu benötigen, während Termiten auch in trockeneren Gebieten vorkommen (LAVELLE et al. 1997, LEE 1985).

Ameisen

Während die ökologische Bedeutung der Termiten und Regenwürmer im wesentlichen im Abbau von Holz und Streu und dem sich daraus ergebenden Einfluss auf den Stoff- und Energiehaushalt liegt, ist das ökologische Wirkungsspektrum der Ameisen im Ökosystem tropischer Regenwälder breiter gefächert, was angesichts von 500 und mehr Ameisenarten, die sich hier auf wenigen Hektar finden lassen (BRÜHL et al. 1998, VERHAAGH 1990, ROSCISZEWSKI 1995), nicht verwundern kann. Aber nicht nur die lokal auftretenden Artenzahlen sind in Tiefland-Regenwäldern beeindruckend, sondern auch der Anteil an den Individuenzahlen, die Ameisen unter der gesamten Boden-Makrofauna stellen. Sie erreichen bereits 27% in kleinen (0,035 m²) Berlese extrahierten Stecherproben (VERHAAGH et al. im Druck) in Brasilien (Manaus) und rund 49 % bis 70% in per Hand oder Exhaustor ausgelesenen bzw. Berlese extrahierten Quadratproben von 0,25 bis 1 m² Größe (BECK 1971, Brasilien, Manaus; LEVINGS & WINDSOR 1982, Panama, Barro Colorado Island BCI; WILLIAMS 1941, Panama, BCI). WILLIAMS (1941) gibt auch den Anteil der Ameisen an der gesamten Bodenmeso- und Bodenmakrofauna an, also inklusive der Springschwänze (Collembola) und Milben (Acari). Er betrug in seinen Untersuchungen 25%. Die von BECK (1967, 1971) aufgrund der Zahlen von WILLIAMS (1941) geäußerte und häufig in der Literatur zitierte (z. B. FITTKAU & KLINGE 1973; HÖLLDOBLER & WILSON 1990, ALONSO & AGOSTI 2000) Vermutung, dass Ameisen und Termiten sicher 75% der Biomasse der Bodenfauna stellen, ist allerdings bis heute nicht durch konkrete Zahlen untermauert worden. Konkrete Daten zur Biomasse der Bodenameisen sind dagegen rar. In den Untersuchungen von VERHAAGH et al. im Druck) in Zentralamazonien betrug der Anteil der Ameisen an der Biomasse der Bodenmakrofauna (also ohne Milben und Springschwänze) 7%. Da die verwendete Methode, kleine Stecherproben mit ansch-

ließender BERLESE-Extraktion, Ameisen in Anzahl und Größe klar unterrepräsentiert, dürfte die Biomasse in adäquaten Quadratproben bei 15-20% der Bodenmakrofauna liegen. Bei all diesen Werten ist allerdings zu bedenken, dass die bislang benutzten gängigen Methoden zur Erfassung der Bodenfauna für Ameisen (wie für Termiten) weitgehend inadäquat sind, da der Großteil der Population sich in mehr oder weniger tief im Boden befindlichen Nestern oder in harten Oberflächennestern befindet und durch diese Methoden gar nicht erfasst wird.

Ameisen stellen auch meist den Großteil der Individuenzahl und Biomasse bei Faunenerhebungen in den Kronen tropischer Regenwälder mittels Insektizid-Benebelung (canopy fogging). Er liegt nach den bisherigen Untersuchungen meist bei über 40% (3-94 %) der Gesamtindividuenzahlen (einschließlich Milben und Collembolen) und bei rund 1/3 (16-57 %) der Biomasse (s. Übersicht in TOBIN 1995, sowie ADIS et al. 1997, FLOREN & LINSENMAIR 1997, GUILBERT 1997). Aber auch bei dieser Methode stellt sich die Frage, welcher Prozentsatz der Ameisen- und Termitenkolonien, die sich häufig im Innern von Totholz oder in kompakten Nestkonstruktionen befinden, überhaupt erfasst wurde.

Viele Ameisenarten haben ein breites Nahrungsspektrum, das lebende und tote Tiere, aber auch pflanzliche Stoffe (meist Pflanzensäfte) umfasst. Auf der anderen Seite gibt es unter den Ameisen zahlreiche ausgesprochene Nahrungsspezialisten, und zwar in einem doppelten Sinn: (1) Arten, die fast ausschließlich eine bestimmte Nahrung zu sich nehmen und (2) Arten, zu deren Nahrungsspektrum eine sehr spezielle, von den meisten Ameisen nicht genutzte Ressource gehört. Generell umfasst das von Ameisen im Regenwäldern genutzte Nahrungsspektrum folgende Bandbreite: lebende Wirbellose (meist Arthropoden), in seltenen Fällen auch kleine Wirbeltiere, Aas (tote Arthropoden und andere Wirbellose, aber auch Wirbeltierkadaver), Samen oder deren fleischige Anhänge (= Elaiosomen), Fruchteile, Pollen, Nährkörperchen spezieller Pflanzen, auf denen sie wohnen (Myrmecophyten), zuckerhaltige Säfte aus (meist extrafloralen) Nektarien und anderen Pflanzenteilen (Blätter, Sprosse, Rinde), süßen Kot ("Honigtau") von Pflanzensaugern (Homoptera: Coccidae, Membracidae, Aphidae u. a.), Pilze sowie Blätter und Blüten, die die bei den Bauern berüchtigten Blattschneiderameisen allerdings nicht direkt verwerten können, sondern durch Pilze abbauen lassen. Zur Gruppe der Blattschneider (Attini) gehören außerdem Arten, die tatsächlich als Saprophagen agieren, indem sie organische Bestandteile der Streu zur Pilzzucht nutzen (ANDRADE & BARONI URBANI 1999, BROWN 2000, CHAPELA et al. 1994, HÖLLDOBLER & WILSON 1990, HUXLEY & CUTLER 1991, TOBIN 1994, VERHAAGH 1994).

Die bekanntesten unter den Beutegreifern sind die Treiber- oder Wanderameisen (Taf. 3 a). Arten mit derart „nomadischer“, ohne dauerhaftes Nest auskom-

mender Lebensweise haben sich in den Tropen Asiens, Afrikas und Südamerikas in unterschiedlichen Ameisengruppen entwickelt. Viele dieser Wanderameisenarten überfallen in langen Kolonnen hauptsächlich die Nester anderer Ameisen oder die von Wespen, sei es im Boden oder hoch in den Bäumen. Andere Arten, z.B. in Afrika solche aus der Gattung *Dorylus* oder in Südamerika *Eciton burchelli* und *Labidus praedator*, durchkämmen auf ihren Beutezügen den Waldboden in breiten Kolonnen und tragen alles, was sie überwältigen und zerstückeln können, zu ihren temporären Nistplätzen. Das Beutespektrum solcher „Schwarmjäger“ ist beträchtlich, und sie können offensichtlich lokal einen beträchtlichen Einfluss auf die Populationsgröße und Artenstruktur von bodenbewohnenden Tiergruppen wie Ameisen, Schaben, Spinnen und Heuschrecken ausüben (GOTWALD 1995, RETTENMEYER et al. 1983, ROSCISZEWSKI & MASCHWITZ 1994, SCHNEIRLA 1971, VIEIRA & HÖFER 1994, 1998).

Unter den räuberisch lebenden Ameisen gibt es in den Regenwäldern der Erde ausgesprochene Spezialisten, hauptsächlich in den Unterfamilien Ponerinae und Myrmicinae, die sich, soweit aus bisherigen Beobachtungen geschlossen werden kann, ausschließlich oder überwiegend von einer Beutetiergruppe ernähren (BROWN 2000, HÖLLDOBLER & WILSON 1990). So tragen *Discothyrea*- und *Proceratium*-Arten Arthropodeneier ein (BROWN 1957); *Thaumatomyrmex*-Arten fangen stark beborstete Tausendfüßer (Polyxeniden), die sie mit ihren mehrspitzigen Mandibeln vor dem Verzehr entborsten (BRANDÃO et al. 1991), und manche *Leptogenys*-Arten sind mit ihren säbelförmigen Mandibeln auf Asseln in Streu und Totholz spezialisiert, wie dies auch von morphologisch ähnlichen Arten aus anderen Ökosystemen bekannt ist (LEVIEUX 1983, WHEELER 1904). Einige große Ponerinen, so *Pachycondyla commutata* in Amazonien, überfallen in größeren Gruppen Termitennester der Gattung *Syntermes* und tragen die erbeuteten Bewohner im Gänsemarsch zu ihrem Nest (WHEELER 1936). Die weltweit in tropischen Regenwäldern in der Streu oder im Epiphytenhumus lebenden, nur wenige Millimeter großen Dacetinen haben sich dagegen auf kleine saprophage Streubewohner wie Collembolen und Dipluren als Beute spezialisiert. Einige Arten erdolchen ihre Beute mit langen, dornenbesetzten Schnappkiefern, andere schleichen sich langsam an ihre Beute heran, ergreifen sie mit ihren kurzen Mandibeln und lähmen sie mit einem Stich ihres Stachels.

Samenfresser (Ernteameisen) spielen in den Regenwäldern im Gegensatz zu offenen Graslandschaften nur eine geringe Rolle (FELDMANN et al. 2000, LEVEY & BYRNE 1993); allerdings transportieren auch manche Regenwald-Ameisen ähnlich wie es aus anderen tropischen Wäldern (VOIGT et al. im Druck), Savannen oder Halbwüsten bekannt ist, Samen zu ihren Nestern, die

für sie aufgrund von anhaftenden Substanzen, Resten des Fruchtfleisches oder speziellen fleischigen, nährstoffreichen Anhängseln (Elaiosomen) attraktiv sind. Solche Arten können je nach Verhalten zur Samenverbreitung beitragen oder den Anteil keimfähiger Samen drastisch verringern, wie dies in aufgegebenen Agrarflächen in Amazonien nachgewiesen wurde (NEPSTAD et al. 1996). Auch die berühmten „Ameisengärten“ der amazonischen Regenwälder, die erstmals von ULE (1902) beschrieben wurden (Taf. 3 b), entstehen auf diese Weise, da bestimmte Ameisen für sie attraktive Samen in ihre Kartonnester eintragen, wo sie später keimen und bestens mit Nährstoffen aus dem Ameisennest versorgt sind. Nach Absterben der Kolonie oder Aufgabe der Nester stellen diese und andere arboricole Nester eine wichtige Nährstoffressource für saprophage Organismen im Kronenraum und, nach dem Herunterfallen, auch am Boden dar.

Eine häufige Lebensweise unter Ameisen ist das Sammeln von „Honigtau“, den zuckerhaltigen Ausscheidungen pflanzensaugender Homopteren (BLÜTHGEN et al. 2000, HÖLLDOBLER & WILSON 1990); dies ist aber eher eine Art von Herbivorie und hat mit dem Destruentensystem i. d. R. wenig zu tun. Allerdings reichern bodennistende Ameisen wie z.B. *Ectatomma tuberculatum* (Taf. 3 c) auf diese Weise Nährstoffe im Boden an (s.u.). Eine weitere Ausnahme bilden kleine Schuppenameisen (Formicidae) der Gattung *Acropyga*, die sich von den Ausscheidungen von an Wurzeln lebenden Schildläusen ernähren. Deren Saugtätigkeit beeinflusst das Wurzelwachstum der betroffenen Pflanzen (BÜNZLI 1935).

Ameisennester sind wie Termitenbauten ein wichtiger Faktor in der Nährstoffdynamik des Bodens, nicht nur weil sie mit Nährstoffen angereichert sind, sondern auch weil der Boden im Nest und in seiner Umgebung von den Tieren ständig bewegt und durchlüftet wird. Viele Pflanzen ziehen mit den Wurzeln Nährstoffe aus der unmittelbaren Umgebung solcher Nester. In dieser Hinsicht kommt den Blattschneiderameisen in den Neotropen eine besondere Bedeutung zu, insbesondere den rund 40 Arten der Gattungen *Atta* und *Acromyrmex*. Ausgewachsene Nester von *Atta* nehmen Flächen von über 100, ja manchmal bis zu 600 m² ein (Taf. 3 d), deren nach Millionen zählende Bewohner Hunderte von Kammern bis zu drei, vier oder mehr Meter in die Tiefe graben. In den oberen Nestkammern züchten Blattschneider einen Pilz, zu dessen Versorgung große Mengen an frischen Blattstücken von vielen verschiedenen Pflanzen abgeschnitten und eingetragen werden (Taf. 3 e). Die Blattstücke werden zerkaud und als Pellets in den Pilzgarten eingebettet. Nur der Pilz besitzt die zum Celluloseabbau nötigen Enzyme, ja er versorgt die Ameisen sogar mit proteinabbauenden Enzymen, die sie selbst nicht besitzen (BOYD & MARTIN 1975). Die Ameisen ernähren ihre Brut ausschließlich mit diesem Pilz,

während die Arbeiterinnen den größeren Teil ihres Energiebedarfs über die Pflanzensäfte decken, die sie beim Schneiden und Zerkauen der Blätter aufnehmen (QUINLAN & CHERRETT 1979). Die nicht nutzbaren Reste der Pilzgärten werden von den Ameisen in Abfallkammern tief im Boden verstaut oder an die Bodenoberfläche transportiert.

Wenn auch die Blattschneiderameisen in Kulturen enorme Schäden anrichten können, so sind sie in den Regenwäldern ein außerordentlich wichtiges Glied der Nährstoffkreisläufe. Sie bringen lebende, d.h. noch relativ nährstoffreiche Blattsubstanz direkt in den Boden ein und veranlassen die Pflanzen, neue Blätter auszu-treiben; allein für die Gattung *Atta* wurde eine Konsumtion von 12-17% der Blattproduktion neotropischer Wälder errechnet (CHERRETT 1986). Demgegenüber konsumieren in gemäßigten Wäldern alle Herbivoren zusammen meist nur 5-10% der Primärproduktion. Durch die Abfallhaufen von *Atta*-Nestern fließen 16-98mal größere Nährstoffmengen als durch die Streuauflage darüber. Dass die Pflanzen davon profitieren, zeigt sich an der Feinwurzelndichte, die in den Nestern viermal höher ist als im umgebenden Boden (HAINES 1978). Wenn die Blattschneiderameisen im weiteren Sinne (*Tribus Attini*) auch in erster Linie als Quasi-Herbivore auffallen, greifen sie doch auch in das Abbaugeschehen der Bodenstreu direkt ein. So sammeln *Atta*- und *Acromyrmex*-Arten auch frisch gefallene Blütenblätter auf, und kleinwüchsige Arten anderer Gattungen wie *Apterostigma*, *Cyphomyrmex*, *Mycocepurus* u.a. tragen Arthropodenkot, Stücke der Chitinpanzer toter Insekten und andere Teile der Streuschicht ein, um darauf in ihren Nestern ähnlich wie *Atta* oder *Acromyrmex* Pilze zu züchten (CHAPELA et al. 1994, WEBER, 1972).

Als letzter wichtiger Aspekt der Bedeutung von Ameisen für die Ökologie des Bodenkompartmentes im tropischen Regenwald seien die vertikalen Wanderungen genannt, die zahlreiche Ameisen unternehmen und die von BECK (1971) geäußerte Ansicht "Ameisen bewegen sich außerhalb ihrer Nester praktisch nur auf der Bodenoberfläche" klar widerlegen. Solche Arten (z.B. *E. tuberculatum*, *Paraponera clavata*) tragen durch ihre Futtersuche in den oberirdischen Straten des Lebensraumes zu einer Konzentration von Nährstoffen im Boden bei.

Schlussbetrachtung

Bodentiere wie Regenwürmer und Termiten sind nicht nur über die Nahrungsaufnahme und -verarbeitung in der Zersetzerkette an den Prozessen der Bodenbildung beteiligt, sondern auch über ihre oft beträchtliche Bau- und Grabaktivität. Letztere zeichnet auch Bodentiere aus, die überwiegend keine Zersetzer sind, wie die Ameisen. Weil sie Hohlräume (Gänge, Kammern) im Boden anlegen, und bei Nahrungssuche und Nestbau die mineralischen und organischen Bodenbe-

standteile kräftig durchmischen, sind alle drei Tiergruppen an der Ausbildung der Bodenstruktur beteiligt. Regenwürmer tun sich weiterhin dadurch hervor, dass bei der Darmassage ihrer Nahrung Ton-Humus-Komplexe gebildet werden, ein für die Humusanreicherung im Boden entscheidender Prozess. Außerdem bestehen die Kotballen mancher Bodentiere aus nur schwer abbaubaren Verbindungen. Termiten und Ameisen lagern zudem häufig schwer zersetzbare Substanzen in ihren oft sehr großen Nestbauten ab, wodurch Nährstoffe konzentriert und teilweise sogar Vorräte ausgebildet werden, ein wichtiger Aspekt in den sonst durch eher schnellen Abbau gekennzeichneten tropischen Ökosystemen. Regenwürmer, Termiten und Ameisen können beträchtliche Bodenmengen umsetzen, und man kann sich vorstellen, dass dies auch in geologischen Zeiträumen zu langfristig spürbaren Veränderungen der Erdoberfläche geführt haben kann. So können eventuell die tiefgründigen Verwitterungsprofile tropischer Böden auf die besonders hohe Aktivität der Bodenfauna in diesen Breiten zurückgeführt werden. Allerdings werden lokal auffällige Bodeneigenschaften oft vorschnell dem Wirken der Bodenfauna zugeschrieben. Hier herrscht noch großer Forschungsbedarf.

Es fällt auf, dass zwei der drei hier behandelten Tiergruppen den sozialen Insekten zuzurechnen sind. Während in den gemäßigten Breiten nur Ameisen in manchen Ökosystemen hohe Dichten erreichen (BRINAN 1978, HIGASHI & YAMAUCHI 1979, SEIFERT 1986), Bienen und Wespen jedoch nicht, und Termiten gar nicht vorkommen, sind alle wichtigen Nährstoffflüsse der Tropenwälder (Zersetzer-, Herbivoren-, und Zoophagen-Kette) von der Dominanz sozialer Insekten geprägt. Die Vorteile einer sozialen Lebensweise wurden von WILSON (1992) deutlich hervorgehoben. Die für eine erfolgreiche Produktion von Nachkommen notwendigen Handlungsabläufe werden bei solitär lebenden Insekten oft von Störungen unterbrochen und dann nicht zu Ende geführt; das Tier bleibt ohne Nachkommen. Wenn aber in einer Kolonie sozialer Insekten Einzelindividuen ausfallen, so springen andere in die Bresche und können die begonnene Aufgabe zu Ende führen. Des weiteren kann eine Kolonie, in der Hunderte oder Tausende genetisch gleicher, ersetzbarer Soldaten leben, mit viel mehr "Einsatz" verteidigt werden, als von einem Einzeltier, das sein Leben und damit den Fortbestand seines Erbguts schützen muß. Ein so verteidigter guter Nistplatz wird mit größerer Wahrscheinlichkeit an direkte Nachkommen oder Artgenossen weitergegeben. Die Nester mancher Termitenarten überdauern Jahrhunderte, da der sehr stabile Bau von immer neuen Generationen wieder besiedelt wird.

Regenwürmer und Termiten kommen oft zusammen vor, sind in ihrer Verbreitung aber dennoch oft vikariierend (LAVELLE et al. 1992): Regenwürmer bevorzu-

gen feuchtes Milieu mit jährlichen Niederschlägen >800 mm, Termiten kommen auch in semi-ariden und ariden Gebieten vor und werden dort dann hochdominant. Regenwürmer bevorzugen auch die Böden mit höherem Nährstoffgehalt, während Termiten noch mit ärmsten Substraten zurecht kommen, wo sie wiederum auch hochdominant sein können. Sehr wahrscheinlich ist es auch hier wieder die soziale Lebensweise, welche die Termiten befähigt, selbst unter widrigen Außenbedingungen, zumindest innerhalb ihrer Bauten, einen Lebensbereich günstiger Bedingungen zu schaffen. So können sie in Trockengebieten Wasser aus bis zu mehreren Metern Tiefe holen und die Nährstoffe aus ärmstem Substrat so konzentrieren bzw. zusätzlich über ihre Darmsymbionten mit Nährstoffen wie Stickstoff anreichern, dass ein Überleben möglich ist. Entsprechend führt ihre Aktivität oft zur Ausbildung eines Nährstoffmosaiks: Nährelemente werden in oder unter Nestbauten punktuell konzentriert und können dort von den Pflanzen auch wieder ausgebeutet werden. Termitenbauten sind in Südamerika auch bei der Entstehung einer bestimmten Landschaftsform beteiligt, die in Brasilien "Campos de Murunduns" genannt wird (Taf. 4 a). Es handelt sich um flache, abflußlose Senken, deren Boden wasserundurchlässig ist, und die sich in der Regenzeit mit Wasser füllen. Hier können nur einjährige Pflanzen wachsen. Nur auf und um Termitenbauten, die, wahrscheinlich in Trockenzeiten entstanden, in diesen Savannen zu finden sind, stehen auch Büsche und Bäume (Taf. 4 b). Die Bauten erheben sich manchmal nur wenige Zentimeter über die Staunässe heraus, aber die hierdurch bereits ermöglichte Belüftung des Bodens (der an diesen Stellen im Wesentlichen aus Termitenmaterial besteht) scheint den mehrjährigen Pflanzen bereits das Wachstum zu ermöglichen. Allerdings ist die Entstehung dieser Landschaftsform noch nicht ganz genau geklärt, und in manchen Fällen scheint es sich bei den "Murunduns" auch um Erosionsformen zu handeln. Ähnliche von Termiten und/oder Regenwürmern bedingte Mikroreliefs und Landschaftsformen sind auch aus Kolumbien ("zurales"; GOOSEN 1971), Venezuela ("lombricales"; SARMIENTO 1984) und Bolivien ("sartenejales"; RÖMBKE & HANAGARTH 1994) bekannt. Die Makrofauna tropischer Regenwälder stellt neben Mikroorganismen und der Mesofauna nur einen Teil der für die Zersetzungsprozesse verantwortlichen Organismen dar. Dennoch ist es sicherlich der Makrofauna zuzuschreiben, wenn in Regenwäldern die Streumineralisation (also der vollständige Abbau der organischen Substanz bis hinab zu den wieder von Pflanzen aufnehmbaren anorganischen Ausgangsstoffen) viel schneller vorstatten geht als in Wäldern gemäßigter Breiten. Die Makrofauna – und hier sind außer den bisher behandelten auch noch Tausendfüßer (Diplopoda) und Asseln (Isopoda) als örtlich wichtige Gruppen zu nennen – ist zwar nicht zahlenmäßig, aber

von der Biomasse her dominierend (60-82% der gesamten Bodenfauna, HÖFER et al. im Druck), und tatsächlich hochaktiv, was die Umsetzung großer Streumengen betrifft. Unter experimentellem Ausschluß der Makrofauna in Streubeuteln mit Maschenweiten unter 250 µm gingen die Streuabbauraten auf 1/3 bis 1/5 der unbeeinflussten Abbauraten zurück (HÖFER et al. im Druck). Weiterhin sind die mit Mikroorganismen vergesellschafteten Bodentiere (Regenwürmer, Termiten, manche Ameisen) zum Aufschluß sonst nicht verwertbarer Nahrungsstoffe in der Lage. Wenn die Funktion der Makrofauna tatsächlich im wesentlichen darin bestehen sollte, der Mikroflora den Weg zu ebnen, wie es BRUSSAARD & JUMA (1996) ausdrücken, dann ist es gerade den mit endo- oder exogenen Symbionten eng vergesellschafteten Termiten und Blattschneiderameisen gelungen, diese Interaktion zu einem besonders effektiven Werkzeug im Kampf ums Überleben auf ärmsten Standorten zu machen.

Angesichts der Tatsache, dass Regenwälder auf allen Kontinenten sehr stark von der Zerstörung bedroht sind, soweit sie nicht überhaupt schon, wie in Westafrika und Teilen Südostasiens, fast völlig vernichtet wurden, ist die Entwicklung angepasster und nachhaltiger Nutzungsformen vielleicht die einzige Chance, das gegenwärtige Zerstörungstempo zu verlangsamen und damit die Einsicht in die Einmaligkeit und Unwiederbringlichkeit der tropischen Lebensräume und ihrer Lebensgemeinschaften zu ermöglichen. Die Untersuchung der Zersetzungsprozesse als Schlüsselabläufe der Nährstoffkreisläufe trägt dazu bei, diese Kreisläufe besser zu verstehen und Nutzungsmodelle zu entwickeln, die den Besonderheiten dieser fragilen Ökosysteme gerecht werden.

Literatur

- ADIS, J. (1987): Extraction of arthropods from neotropical soils with a modified Kempson apparatus. – *J. Trop. Ecology*, **3**: 131-138.
- ADIS, J., PAARMANN, W., FONSECA, C. R. V. DA, RAFAEL, J. A. (1997): Knockdown efficiency of natural pyrethrum and survival rate of living arthropods obtained by canopy fogging in Central Amazonia. – In: STORCK, N. E., ADIS, J. & DIDHAM, R. K. (eds.): *Canopy arthropods*: 67-81; London (Chapman & Hall).
- ALONSO, L. E. & AGOSTI, D. (2000): Biodiversity studies, monitoring, and ants: an overview. – In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (eds.): *Ants. Standard methods for measuring and monitoring biodiversity*: 1-8. Washington (Smithsonian Institution Press).
- AMELUNG, W., MARTIUS, C., BANDEIRA, A. G., GARCIA, M. V. B., ZECH, W. (im Druck): Lignin characteristics and density fractions of termite nests in an Amazonian rain forest - indicators of termite feeding guilds? – *Soil Biol. Biochem.*
- ANDERSON, J. M., & INGRAM, J. I. (1993): *Tropical Soil Biology and Fertility: A handbook of methods*. – 2nd ed.; Wallingford, U.K. (CAB International).

- ANDERSON, J. M. & SWIFT, M. J. (1983): Decomposition in tropical forests. – In: SUTTON, S. L., WHITMORE, T. C., CHADWICK, A. C. (eds.): Tropical rain forest: Ecology and management, Special Publication No.2 of the British Ecological Society: 287-309; Oxford (Blackwell Sci. Publ.).
- ANDRADE, M. L. DE & BARONI URBANI, C. (1999): Diversity and adaptation in the ant genus *Cephalotes*, past and present. – Stuttgart Beitr. Naturk., Ser. B, Nr. 271: 1-889.
- APOLINÁRIO, F. B. (1993): Composição faunística e hábitos de nidificação de térmitas (Insecta: Isoptera) em floresta de terra firme da Amazônia Central. – 72 pp.; Master thesis, INPA/FUA, Manaus.
- AYALA, S. C., JOHNSON, C., MORRIS, B., ROONEX, B., STUART, A. & WOODHULL, B. (1972): A colony of giant Andean earthworms. – *BioScience*, **22**: 299-301.
- BAROIS, I., VERDIER, B., KAISER, P., MARIOTTI, A., RANGEL, P. & LAVELLE, P. (1987): Influence of the tropical earthworm *Pontoscotlex corethrurus* (Glossoscolecidae) on the fixation and mineralization of nitrogen. – In: BONVICINI PAGLIAI, A. M. & OMODEO, P. (eds.): International Symposium on Earthworms, Bologna, Italia 1985: 151-158; Modena (Mucchi).
- BATALHA, L. S., SILVA FILHO, D. F. & MARTIUS, C. (1995): Using termite nests as a source for organic matter in agro-silvicultural production in Amazonia. – *Scientia Agricola* (Piracicaba), **52** (2): 318-325.
- BECK, L. (1967): Die Bodenfauna des neotropischen Regenwaldes. – Atas do Simpósio sobre a Biota Amazônica, **5** (Zoologia): 97-101.
- BECK, L. (1971): Bodenzoologische Gliederung und Charakterisierung des amazonischen Regenwaldes. – *Amazoniana*, **3**: 69-132.
- BECK, L. (1993): Zur Bedeutung der Bodentiere für den Stoffkreislauf in den Wäldern. – *Biologie in unserer Zeit*, **23** (5): 286-294.
- BECK, L. (2000): Streuabbau und Bodenfauna in Wäldern gemäßigter und tropischer Breiten. – *Carolinea*, **58**: 243-256.
- BECK, L., HOFER, H., MARTIUS, C., RÖMBKE, J. & VERHAAGH, M. (1997): Bodenbiologie tropischer Regenwälder. – *Geographische Rundschau*, **49** (1): 24-31.
- BIGNELL, D. E. (1994): Soil-feeding and gut morphology in higher termites. – In: HUNT, J. A. & NALEPA, C. A. (eds.): Nourishment and evolution in insect societies: 131-158; New Delhi (Oxford & IBH Publishing Co), Boulder (Westview Press).
- BLÜTHGEN, N., VERHAAGH, M., GOITIA, W., JAFFÉ, K., MORAWETZ, W. & BARTHOLOTT, W. (2000): How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. – *Oecologia*, **125**: 229-240.
- BOUCHÉ, M. B. (1977): Stratégies lombriciennes. – *Ecol. Bull.*, **25**: 122-132.
- BOYD, N. D. & MARTIN, M. M. (1975): Faecal proteinases of the fungus-growing ant *Atta texana*: their fungal origin and ecological significance. – *J. Insect Physiol.*, **21** (11): 1815-1820.
- BRANDÃO, C. R. F., DINIZ, J. L. M. & TOMOTAKE, E. M. (1991): *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). – *Ins. Soc.*, **38**: 335-344.
- BRIAN, M. V. (1978): Production ecology of ants and termites. – 409 pp.; Cambridge (Cambridge University Press).
- BROWN, W. L. (1957): Predation of arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. – *Psyche*, **64**: 115.
- BROWN, W. L. (2000): Diversity of ants. – In: AGOSTI, D., MAJER, J. D., ALONSO, L. E. & SCHULTZ, T. R. (eds.): *Ants. Standard methods for measuring and monitoring biodiversity*: 45-79. Washington: (Smithsonian Institution Press)
- BRÜHL, C. A., GUNSALAM, G. & LINSENMAIR, K. E. (1998): Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. – *J. Trop. Ecol.*, **14**: 285-297
- BRUSSAARD, L. & JUMA, N. G. (1996): Organisms and humus in soils. – In: PICCOLO, A. (ed.): *Humic Substances in Terrestrial Ecosystems*: 329-359; Amsterdam (Elsevier Science B.V.).
- BÜNZLI, G. H. (1935): Untersuchungen über coccidophile Ameisen aus den Kaffeefeldern von Surinam. – Mitteilungen der Schweizerischen Entomologischen Gesellschaft Zürich, **16** (6/7): 453-593.
- BURNETT, J. R. (1948): Crop production. – In: TOOTHILL, J.D. (ed.): *Agriculture in the Sudan*: 275-301; London (University Press).
- CHAPELA, I. H., REHNER, S. A., SCHULTZ, T. R. & MUELLER, U. G. (1994): Evolutionary history of the symbiosis between fungus-growing ants and their fungi. – *Science*, **266**: 1691-1694.
- CHAUVEL, A., GUILLAUMET, J. - L. & SCHUBART, H. O. R. (1987): Importance et distribution des racines et des êtres vivants dans un „latosol“ argileux sous forêt amazonienne. – *Rev. Ecol. Biol. Sol.*, **24**: 19-48.
- CHERRETT, J. M. (1986): History of the leaf-cutting ant problem. – In: LOFGREN, C. S. & VAN DER MEER, R. K. (eds): *Fire ants and leaf-cutting ants - biology and management*: 10-17; Boulder.
- CORNÜ, S., LUIZÃO, F., ROULLER, J. & LUCAS, Y. (1997): Comparative study of litter decomposition and mineral element release in two amazonian forest ecosystems: litter bag experiments. – *Pedobiologia*, **41**: 456-471.
- DARLINGTON, J. P. E. C. (1995): Underground foraging passages and storage pits built by the termite *Syntermes molestus* in Goiania, Brazil (Isoptera: Termitidae). – *Sociobiol.*, **23** (2), 211-212.
- DEJEAN, A., & RUELLE, J. E. (1995): Importance of *Cubitermes* termitaries as shelter for alien incipient termite societies. – *Ins. Soc.*, **42** (2): 129-136.
- ESCHERICH, K. (1911): Termitenleben auf Ceylon. – 263 S.; Jena.
- FELDMANN, M., VERHAAGH, M. & HEYMANN, E. (2000): *Sericomyrmex* ants as seed predators. – *Ecotropica*, **6**: 207-209.
- FITTKAU, E. J. & KLINGE, H. (1973): On biomass and trophic structure of the central Amazonian rain forest ecosystem. – *Biotropica*, **5**: 2-14.
- FLOREN, A. & LINSENMAIR, K. E. (1997): Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. – In: STORCK, N. E., ADIS, J. & DIDHAM, R. K. (eds.): *Canopy arthropods*: 344-381; London (Chapman & Hall).
- FOWLER, H. G. & WHITFORD, W. G. (1996): Soil invertebrates and the structure of desert annual plant communities. *Ciência e Cultura*, **48** (4): 254-255.
- FRAGOSO, C. & LAVELLE, P. (1987): The earthworm community of a mexican tropical rain forest (Chajul, Chiapas). – In: BONVICINI PAGLIAI, A. M. & OMODEO, P. (eds.): *On Earthworms. Selected Symposia and Monographs U.Z.I.*, **2**: 281-295; Modena.
- FRAGOSO, C. & LAVELLE, P. (1992): Earthworm communities of tropical rain forests. – *Soil Biol. Biochem.* **24**: 1397-1408.
- FRAGOSO, C. & LAVELLE, P. (1995): Are earthworms important in the decomposition of tropical litter – In: REDDY, M. V. (ed.): *Soil Organisms and Litter Decomposition in the Tropics*: 103-112; New Delhi (Oxford & IBH Publ. Co.).
- FRAGOSO, C. & ROJAS-FERNANDEZ, P. (1996): Earthworms inhabiting bromeliads in Mexican tropical rain forests: ecological and historical determinants. – *J. Trop. Ecol.*, **12**: 729-734.

- GOOSEN, D. (1971): Physiography and soils of the llanos orientales, Colombia. – 199 pp.; Ph.D. Thesis, Serie B, No. 64, University of Amsterdam; Enschede (ITC).
- GOTWALD, W. H. (1995): Army ants - The biology of social predation. – 302 pp.; Ithaca (Cornell University Press).
- GUILBERT, E. (1997): Arthropod biodiversity in the canopy of New Caledonian forests. – In: STORCK, N. E., ADIS, J., DIDHAM, R. K. (eds.): Canopy arthropods: 265-277; London (Chapman & Hall).
- HAINES, B. L. (1978): Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica*, **10** (4), 270-277
- HANNE, C. (2001): Die Rolle der Termiten im Kohlenstoffkreislauf eines amazonischen Festlandregenwaldes. – 156 S.; Dissertation, Universität Frankfurt/Main.
- HIGASHI, S. & YAMAUCHI, K. (1979): Influence of a supercolonial ant *Formica (Formica) yessensis* FOREL on the distribution of other ants in Ishikari Coast. – *Jap. J. Ecol.*, **29**: 257-264.
- HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rain forest after experimental litter addition in small plots. – *Pedobiologia*, **40** (6): 570-576.
- HÖFER, H., HANAGARTH, W., GARCIA, M., MARTIUS, C., FRANKLIN, E., RÖMBKE, J. & BECK, L. (im Druck): Structure and function of the soil fauna in Amazonian anthropogenic and natural ecosystems. – *Eur. J. Soil Biol.*
- HÖLDOBLER, B. & WILSON, E. O. (1990): The ants. – 732 pp.; Berlin (Springer).
- HUXLEY, C. R. & CUTLER, D. F. (1991): Ant-plant interactions. – 601 pp.; Oxford (Oxford University Press).
- JANZEN, D.H. (1976): Why tropical trees have rotten cores. – *Biotropica*, **8** (2): 110-112.
- KÖNIG, H. & BREUNIG, A. (1997): Ökosystem Termitendarm. – Spektrum der Wissenschaft, April 1997: 68-76.
- LAL, R. (1988): Effects of macrofauna on soil properties in tropical ecosystems. – *Agriculture, Ecosystems and Environment*, **24**: 101-116.
- LAVELLE, P. (1983): The soil fauna of tropical savannas. II. The Earthworms. – In: BOURLIERE, F. (Ed.): Tropical Savannas: 485-504; Amsterdam (Elsevier Scient. Publ. Co.).
- LAVELLE, P., BAROIS, I., BLANCHART, E., BROWN, G., BRUSSAARD, L., DECAENS, T., FRAGOSO, C., JIMENEZ, J. J., KA KAJONDO, K., MARTINEZ, M. DE L. A., MORENO, A., PASHANASI, B., SENAPATI, B. & VILLENAVE, C. (1998): Earthworms as a resource in tropical agroecosystems. – *Nature & Resources*, **34**: 26-41.
- LAVELLE, P., BIGNELL, D., LEPAGE, M., WOLTERS, V., ROGER, P., INESON, P., HEAL, O. W. & DHILLON, S. (1997): Soil function in a changing world: the role of invertebrate ecosystem engineers. – *Eur. J. Soil Biol.*, **33**: 159-193.
- LAVELLE, P., BLANCHART, E., MARTIN, A., SPAIN, A. V. & MARTIN, S. (1992): Impact of soil fauna on the properties of soils in the humid tropics. – In: Myths and Science of Soils of the Tropics, Soil Sci. Soc. America, Spec. Publ., **29**: 157-185.
- LEE, K. E. (1985): Earthworms: Their ecology and relationships with soils and land use. – 411 pp.; Sydney (Academic Press).
- LEHMANN, J., SCHROTH, G. & ZECH, W. (1995): Decomposition and nutrient release from leaves, twigs and roots of three alley-cropped tree legumes in central Togo. – *Agroforestry Systems*, **29**: 21-36.
- LEVEY, D. J. & BYRNE, M. M. (1993): Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. – *Ecology*, **74**: 1802-1812.
- LEVIEUX, J. (1983): The soil fauna of tropical savannas, IV: The ants. – In: BOURLIERE, F. (Ed.) Tropical savannas: 525-540; Amsterdam (Elsevier Scient. Publ. Co.).
- LEVINGS, S. C. & WINDSOR, D. M. (1982): Seasonal and annual variation in litter arthropod populations. – In: LEIGH, Jr., E. G., RAND, A. S., WINDSOR, D. M. (eds.): The ecology of a tropical forest: seasonal rhythms and long-term changes: 355-387; Washington (Smithsonian Institution Press).
- MARTIUS, C. (1994): Diversity and ecology of termites (Isoptera) in Amazonian forests. – *Pedobiologia*, **38**: 407-428.
- MARTIUS, C. (1998): Occurrence, body mass and biomass of *Syntermes* spp. (Isoptera: Termitidae) in Reserva Ducke, Central Amazonia. – *Acta Amazonica*, **28**(3): 319-324.
- MARTIUS, C. & BANDEIRA, A.G. (1998): Wood litter stocks in a Central Amazonian rain forest (Reserva Ducke). – *Ecotropica*, **4** (1-2): 115-118.
- MARTIUS, C., FEARNSIDE, P.M., BANDEIRA, A. G. & WASSMANN, R. (1996): Deforestation and methane release from termites in Amazonia. – *Chemosphere*, **33** (3): 517-536.
- MARTIUS, C., TABOSA, W. A. F., BANDEIRA, A. G. & AMELUNG, W. (1999): Richness of termite genera in a semi-arid region (Sertão) in NE Brazil (Isoptera). – *Sociobiologia*, **33**(3): 357-365.
- MARTIUS, C. & WELLER, M. (1998): Observations on the dynamics of entrance hole construction of two leaf-feeding, soil-inhabiting *Syntermes* species (Insecta: Isoptera) in an Amazonian rainforest, Brazil. – *Acta Amazonica*, **28** (3): 325-330.
- MOORE, T. R. (1994): Methanemissionen von Mooren in Kanada. – *Geographische Rundschau*, **46**: 322-327
- MULONGOY, K. & BEDORET, A. (1989): Properties of worm casts and surface soils under various plant covers in the humid tropics. – *Soil Biol. Biochem.*, **21**: 197-203.
- NEMETH, A. & HERRERA, R. (1982): Earthworm populations in a Venezuelan tropical rain forest. – *Pedobiologia*, **23** (6): 437-443.
- NEPSTAD, D. C., UHL, C., PEREIRA, C. A. & CARDOSO DA SILVA, J. M. (1996): A comparative study of tree establishment in abandoned pasture and mature forest of Eastern Amazonia. – *Oikos*, **76**: 25-39.
- NOOREN, C. A. M., VAN BREEMEN, N., STOOORVOGEL, J. J. & JONGMANS, A. G. (1995): The role of earthworms in the formation of sandy surface soils in a tropical forest in Ivory Coast. – *Geoderma*, **65**: 135-148.
- QUINLAN, R. J. & CHERRETT, J. M. (1979): The role of fungus in the diet of the leaf-cutting ant *Atta cephalotes*. – *Ecol. Entomol.*, **4** (2): 151-160.
- RETTENMEYER, C. W., CHADAB-CREPET, R., NAUMANN, M. G. & MORALES, L. (1983): Comparative foraging by Neotropical army ants. – In: JAISSON, P. (Ed.): Social insects in the tropics, **2**: 59-73; Paris (Université Paris-Nord).
- RIBEIRO, J. D'A. (1995): Ecologia de *Labioterme labralis* (Insecta: Isoptera) em florestas de terra firme na Amazônia Central. – Ph.D. Thesis, INPA, Manaus.
- RÖMBKE, J. (2000): Lumbricidae (Regenwürmer). – In: FLECHTNER, W., DOROW, W. & KOPELKE, J-P. (Eds.): Naturwaldreservat in Hessen. Niddahänge östlich Rudingshain. Zoologische Untersuchungen 1990-1992, No. 5/2.1. – *Mittl. Hess. Landesforstverw.*, **32**: 57-83.
- RÖMBKE, J. & HANAGARTH, W. (1994): The present faunistic knowledge on terrestrial Oligochaeta from Bolivia. – *Andrias* **13**: 7-16.
- RÖMBKE, J., MELLER, M. & GARCIA, M. (1999): Earthworm densities in Central Amazonian primary and secondary forests and a polyculture forestry plantation. – *Pedobiologia*, **43**: 518-522.
- RÖMBKE, J. & VERHAAGH, M. (1992): About earthworm communities in a rain forest and an adjacent pasture in Peru. – *Amazoniana*, **12**: 29-49.
- ROSCISZEWSKI, K. (1995): Die Ameisenfauna eines tropischen Tieflandregenwaldes in Südostasien: Eine faunistisch-öko-

- logische Bestandsaufnahme. – 184 S.; Dissertation, Universität Frankfurt/Main.
- ROSCISZEWSKI, K. & MASCHWITZ, U. (1994): Prey specialization of army ants of the genus *Aenictus* in Malaysia. – *Andrias*, **13**: 179-187
- SALICK, J., HERRERA, R. & JORDAN, C. F. (1983): Termitaria: Nutrient patchiness in nutrient-deficient rain forest. – *Biotropica*, **15** (1): 1-7
- SANDERSON, M. G. (1996): Biomass of termites and their emissions of methane, carbon dioxide and chloroform: A global database. – *Global Biogeochemical Cycles*, **10**: 1-19.
- SARMIENTO, G. (1984): The ecology of neotropical savannas. – 235 pp; Cambridge (Harvard University Press).
- SCHAEFER, M. (1990): The soil fauna of a beech forest on limestone: trophic structure and energy budget. – *Oecologia*, **82**: 128-136.
- SCHAUERMANN, J. (1982): Verbesserte Extraktion der terrestrischen Bodenfauna im Vielfachgerät modifiziert nach Kempson und MacFadyen. – *Mitt. SFB*, **135** (1): 47-50.
- SCHLEMMERMEYER, T. (2000): Levantamento da termitofauna da Estacao Biológica de Boracéia, Salesópolis, SP. – Ph.D. Thesis, Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras, Ribeirão Preto.
- SCHNEIRLA, T. C. (1971): Army ants: a study in social organization. – San Francisco (Freeman).
- SEIFERT, B. (1986): Vergleichende Untersuchungen zur Habitatwahl von Ameisen (Hymenoptera: Formicidae) im mittleren und südlichen Teil der DDR. – *Abh. Ber. Naturkundemus. Görlitz*, **59**: 1-124.
- SMITH, D. C. & DOUGLAS, A. E. (1987): The biology of symbiosis. – 302 pp.; London (E. Arnold Publ.).
- SPAIN, A. V., SAFFIGNA, P. G. & WOOD, A. V. (1990): Tissue carbon sources for *Pontosclex corethrusus* (Oligochaeta: Glossoscolecidae) in a sugarcane ecosystem. – *Soil Biol. Biochem.*, **22**: 703-706.
- TAYASU, I., SUGIMOTO, A., WADA, E., & ABE, T. (1994): Xylophagous termites depending on atmospheric nitrogen. – *Naturwissenschaften*, **81**: 229-231.
- TOBIN, J.E. (1994): Ants as primary consumers: diet and abundance in Formicidae. – In: HUNT, J. H. & NALEPA, C. A. (eds.): *Nourishment and evolution in insect societies*: 279-307; Boulder (Westview Press).
- TOBIN, J.E. (1995): Ecology and diversity of tropical forest canopy ants. – In: LOWMAN, M.D. & NADKARNI, N.M. (eds.): *Forest canopies*: 129-147; San Diego (Academic Press).
- ULE, E. (1902): Ameisengärten im Amazonasgebiet. – *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographien*, **30** (2) (Beiblatt Nr. 68): 45-52.
- VERHAAGH, M. (1990): The Formicidae of the rain forest in Panguana, Peru: the most diverse local ant fauna ever recorded. – In: VEERESH, G. K., MALLIK, B. & VIRAKTAMATH, C. A. (eds.): *Social insects and the environment*. Proc. 11th Int. Congr. IUSSI, New Delhi: 217-218.
- VERHAAGH, M. (1994): *Pachycondyla luteola* (Hymenoptera, Formicidae), an inhabitant of Cecropia trees in Peru. – *Andrias*, **13**: 215-224.
- VERHAAGH, M., GARCIA, M.V.B., MARTIUS, C. (im Druck): Ant fauna in central Amazonian polyculture systems and forests – systematic composition, number, and biomass. – In: *Proceedings of the German- Brazilian Workshop, Hamburg 2000*.
- VIEIRA, R. S. & HÖFER, H. (1994): Prey spectrum of two army ant species in Central Amazonia, with special attention on their effect on spider populations. – *Andrias*, **13** (1994): 189-198.
- VIEIRA, R. S. & HÖFER, H. (1998): Efeito do forrageamento de *Eciton burchelli* (Hymenoptera, Formicidae) sobre a araneofauna de liteira em uma floresta tropical de terra firme na Amazônia Central. – *Acta Amazonica*, **28** (3): 345-351.
- VOIGT, F. A., BURKHARDT, J. F., VERHAAGH, M. & BÖHNING-GAESE, K. (im Druck): Secondary seed dispersal by ants in Madagascar and South Africa. – *Ecotropica*.
- WEBER, N.A. (1972): Gardening ants. The Attines. – 146 pp.; Philadelphia (American Philosophical Society).
- WHEELER, W. M. (1904): A crustacean-eating ant (*Leptogenys elongata* BUCKLEY). – *Biol. Bull. Mar. Biol. Lab., Woods Hole*, **6** (6): 251-259.
- WHEELER, W. M. (1936): Ecological relations of ponerine and other ants to termites. – *Proc. Amer. Acad. Arts Sci.*, **71**: 159-243.
- WILLIAMS, E. C. (1941): An ecological study of the floor fauna of the Panama rain forest. – *Bull. Chicago Acad. Sci.*, **6** (4): 63-124.
- WILSON, E. O. (1992): Social Insects as dominant organisms. – In: BILLEN, J. (Ed.): *Biology and Evolution of Social Insects*: 1-7; Leuven (Leuven University Press).
- WOOD, T. G. & SANDS, W. A. (1978): The role of termites in ecosystems. – In: BRIAN, M.V. (Ed.): *Production ecology of ants and termites, International Biological Programme 13*: 245-292; Cambridge (Cambridge University Press).
- YAMASHITA, T. & TAKEDA, H. (1998): Decomposition and nutrient dynamics of leaf litter in litter bags of two mesh sizes set in two dipterocarp forest sites in peninsular Malaysia. – *Pedobiologia*, **42**: 11-21.
- YOSHIMURA, T. (1995): Contribution of the Protozoan fauna to nutritional physiology of the lower termite *Coptotermes formosanus* SHIRAKI (Isoptera: Rhinotermitidae). – *Wood Research*, **82**: 68-129.
- ZICSI, A. & CSUZDI, C. (1997): Über weitere Riesenregenwürmer aus Ekuador. Regenwürmer aus Südamerika. 29. *Ber. Nat.-med. Verein Innsbruck*, **84**: 81-103.
- ZIMMERMAN, P. R., GREENBERG, J. P., WANDIGA, S. O., & CRUTZEN, P. (1982): Termites: A potentially large source of atmospheric methane, carbon dioxide and molecular hydrogen. – *Science*, **218**: 563-565.

JÖRG SPELDA

Review of the millipede genus *Pterygophorosoma* VERHOEFF, 1897 (Diplopoda, Chordeumatida, Craspedosomatidae)

Abstract

Based on topotypic material from Schaubachhütte, South Tyrol, Italy, a redescription of *Pterygophorosoma alticolum* (VERHOEFF, 1894) is provided, and the present state of knowledge of the genus is discussed.

Kurzfassung

Übersicht über die Gattung *Pterygophorosoma* VERHOEFF, 1897 (Diplopoda, Chordeumatida, Craspedosomatidae)

Anhand von Topotypoiden von der Schaubachhütte in Südtirol (Italien) erfolgt eine Wiederbeschreibung von *Pterygophorosoma alticolum* (VERHOEFF, 1894). Der derzeitige Kenntnisstand über die Gattung *Pterygophorosoma* wird zusammengefasst und diskutiert.

Author

Dr. JÖRG SPELDA, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe.

Key words

Diplopoda, taxonomy, standardisation of descriptions, redescription, synonymy, distribution, ecology

1. Introduction

In his classification of the Diplopoda, HOFFMAN (1980) pointed out three problematic genera within the Craspedosomatidae that required further clarification through getting and studying topotypic material. These genera were *Aporogona* COOK, 1895, *Basigona* COOK, 1895, and *Pterygophorosoma* VERHOEFF, 1897. HOFFMAN (1980) noted also that it was *Pterygophorosoma*, proposed for *Atractosoma alticolum* VERHOEFF, 1894, a species described based on female material, that should cause no problems in obtaining topotypoids from Schaubachhütte near Sulden, Italian Alps.

HOFFMAN (1980) obviously overlooked that *A. alticolum* had long been assigned to the genus *Orotrechosoma*. This was perhaps because JEEKEL (1970) had selected different type species for both of these genera. But as these two species show only slight differences, there is no doubt that they are congeneric.

Ignoring his own, older, female-based description from Schaubachhütte, VERHOEFF (1911) described *Orotrechosoma alticolum dormeyeri*, this time based on male material and deriving exactly from the same locality, and he distinguished it from the "true" *O. alticolum*. He chose to attribute the latter name to material from Pic

Padella near Samaden (= Albula Pass, Switzerland), the place whence he described a male. Even at present it remains unclear if both taxa are indeed different.

The above shows both the degree of confusion and that at least topotypoids of *alticolum*, better coupled with type material of *dormeyeri*, would be crucial to finally clarify the identity of *Pterygophorosoma alticolum*.

During an excursion, supported by a grant received from the von-Kettner-Stiftung, the author made in September 1999 to clarify the status of some taxa of Central European soil organisms, several known and new localities where members of the genus *Pterygophorosoma* might be expected to occur were visited. At least in part the trip was successful, as it was possible to obtain topotypoids of *P. alticolum* from near Schaubachhütte near Sulden in the Ortler Mountain Range, South Tyrol. The occasion is taken here to both provide a review of the genus *Pterygophorosoma* and to complement the description of its type species. It is remarkable that *Iulogona tirolense* has also been described from the Sulden Valley. It was possible to collect this species only a few kilometres away from its type locality several times during that excursion.

2. Material and methods

2.1 Specimens studied

Three males, three females and nine juveniles have been collected only a few hundred metres west of Schaubachhütte, 4 km south of Sulden, South Tyrol, Italy, on a northern slope in a depression under stones.

For comparative purposes, another male has been provided by Dr. ARIANE PEDROLI-CHRISTEN, collected in the Swiss National Park at the summit plateau of Munt La Schera (2500-2540 m a.s.l.) (DETHIER & PEDROLI-CHRISTEN 1983).

2.2 Geographical reference to localities

In some cases it is quite easy to find localities given in faunistic or taxonomic papers, but in other cases it is really a detective game. Unfortunately, never ever the German myriapodologists of the classical period gave co-ordinates. This makes it quite difficult to produce maps. For this reason, whenever possible, the co-ordinates of the cited localities have been determined. They are given in decimal degrees. Western longitude and southern latitude are marked with a negative sign. This way of representation is to be preferred over the classical form with degrees, minutes and seconds as it is

easier to store in electronic databases and allows an easier access via GIS systems. In the present paper the so-called German "Generalkarten" have been used to determine the co-ordinates.

Based on the co-ordinates, a map has been produced. Type localities of taxa have been marked with arrows, pointing from the name to the locality. This convention should be used as a standard in future.

3. Standardisation of descriptions in the Craspedosomatini and other millipedes

Unfortunately even now descriptions in millipedes are not standardised. This often makes it difficult to compare taxa with each other. Another special case in present-day millipede systematics is neglect of peripheral characters in favour of gonopods, the male secondary copulatory organs. The reason is, that the authors of the classical period, especially ATTEMS, BROLEMANN and VERHOEFF, based their classifications exclusively on gonopod structure. Descriptions often consisted only of gonopod drawings and their verbal description. Consequently it is mostly impossible to identify a species without having a male, although from time to time promising attempts have been made to alter this (e.g. RIBAUT 1913, SCHUBART 1934). The fact that the descriptions appear to be dispersed over a great amount of small papers, often published in rare/obscure periodicals, makes it extremely difficult not only to gather all relevant literature but also to consider everything. Summarising the present knowledge and supplementing the descriptions if necessary, i.e. building up a homogeneous foundation for comprehensive comparisons, becomes increasingly topical.

In succession some character complexes will be treated that must be taken into account in future descriptions. At present this attempt is to be considered as preliminary, to be completed at a later time.

head

In some millipedes either the males or both sexes show bosses, depressions or darker sclerotized structures like horns. At present, no head modifications other than a flattened frons of the male (figs. 5b-c) in nearly all Craspedosomatidae are known.

mouthparts

Structure of the mouthparts has been used from time to time in diplopod taxonomy. It is well-known that the structure of the gnathochilarium is distinct in the different orders of millipedes. In the Chordeumatida it is important if the mentum is divided or not. There are some bizarre cases of gnathochilarium modifications in diplopods, e.g. in *Leucogeorgia* VERHOEFF, 1930 (Julida: Julidae), *Ingurtidorgius* STRASSER, 1974 (Polydesmida: Trichopolydesmidae) and a few others. So-

me of such modifications are sex-linked, e.g. in males in species of the genus *Ophiulus* BERLESE, 1884 and of the order Stemmiulida. Chordeumatida in general show special structures above the inner palps (COOK & COLLINS 1895). These structures are usually more or less tri- or quadridentate (figs. 4i-j). They are called styliform processes. They do not appear to exist in other orders of millipedes, except in some Polydesmida. In *Mastigona mutabile* (LATZEL, 1884) (fig. 4j) and *M. bosniense* (ATTEMS, 1899) (ATTEMS 1926, p. 37, fig. 40), the innermost cone of the internal palps is modified into a serrate hyaline lobe. This character, perhaps occurring in all Mastigophorophyllidae, has not been observed in several other members of this order.

Although the structure of the mandible is known to carry important taxonomic characters too (ENGHOFF 1979, KÖHLER & ALBERTI 1990), it is largely neglected in species descriptions, perhaps because of the difficulties in preparation (destruction of the head) and drawing (SHEAR 1972).

antennae

The antennae often allow discrimination of taxa at higher, genus or family, taxonomic levels. It was apparently RIBAUT (1913) who was the first to recognise the antennae as an important taxonomic character. According to RIBAUT (1913), the length and width of each of the seven antennomeres, and their length-width index must be considered. Unfortunately, this procedure had not been standardised until ENGHOFF (1992) proposed dorsal measurements (fig. 1a).

At about the middle of the 7th antennomer, and pointing laterad when the antennae are extended, there is a solitary, rather slender, mammillate-conic, transparent protuberance, narrowed at the tip and produced into a long, very slender, and exceedingly fine-pointed hair. As discovered still by COOK & COLLINS (1895), this structure is characteristic of the order Chordeumatida, not occurring in other millipede orders.

segments

Shape of the tergites, especially their lateral expansions and the position of the macrochaetae are among the most important taxonomic characters in the order Chordeumatida. Unfortunately, only very few authors provided meaningful drawings. Even rarer, the number of the depicted body segment has been mentioned. Again it was RIBAUT (1913) who standardised drawings of body segments in Chordeumatida at the 15th segment. This was a good choice. As most Chordeumatida have 30 segments, the 15th segment is in the middle, where the animal is the broadest. For the same reason, the 10th segment is to be depicted in the order Polydesmida, as the adults of most species possess 20 segments. In most other millipede orders the number of segments is not fixed.

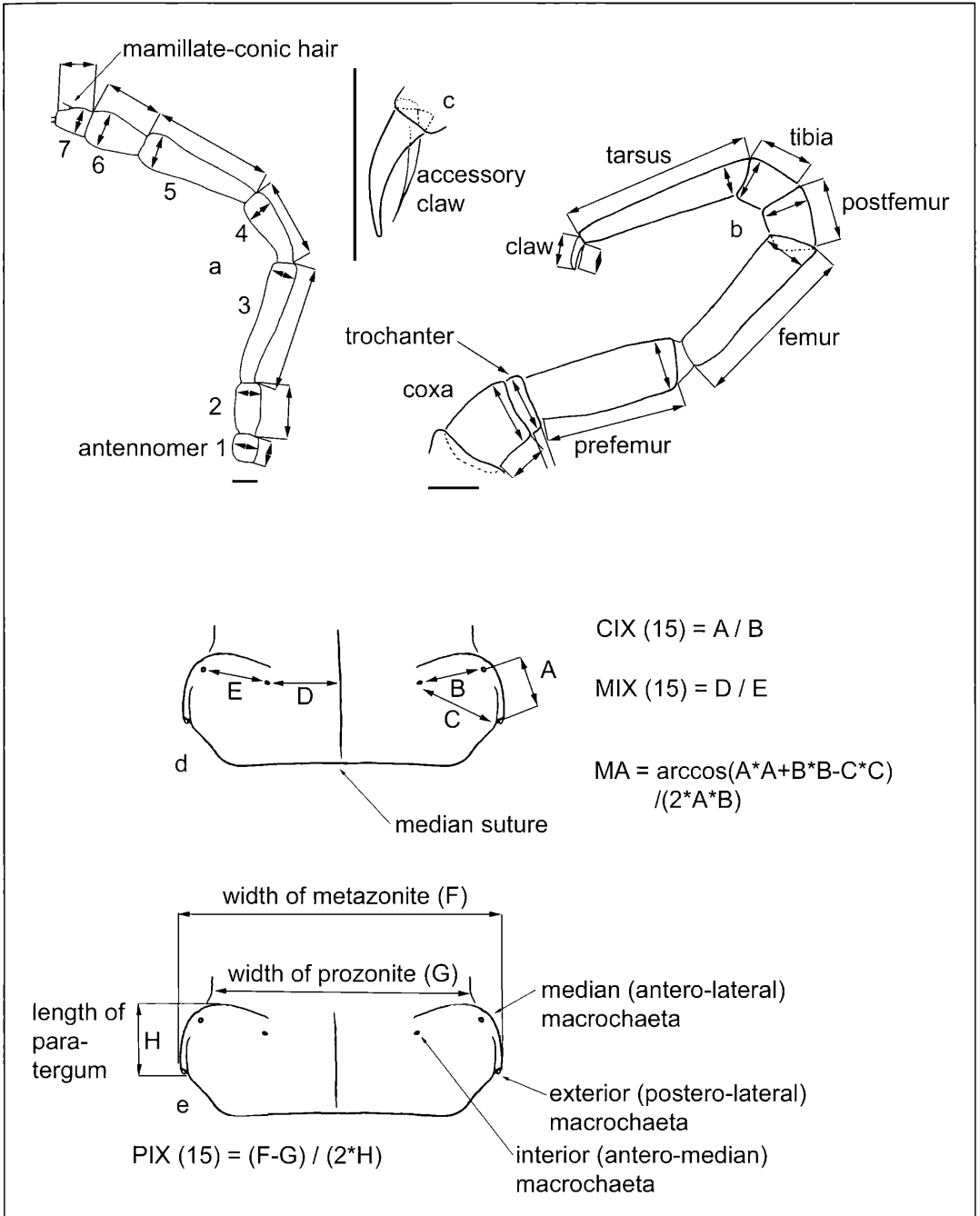


Figure 1. *Pterygophorosoma alticolum* (VERHOEFF, 1894): a) antenna of ♂, semidiagrammatic, double-headed arrows indicate length and width of antennomeres; b) anterior leg of 10th segment (♀), anterior view, double-headed arrows indicate length and width of podomeres; c) same, claw, magnified; d) dorsal view of 15th segment (♂), semidiagrammatic, macrochaetae replaced by their insertion points, showing macrochaetal indices; e) same, showing other measures. Figs. a-c: specimen from Schaubachhütte figs. d-e: specimen from Munt la Schera. Scale lines 0.1 mm.

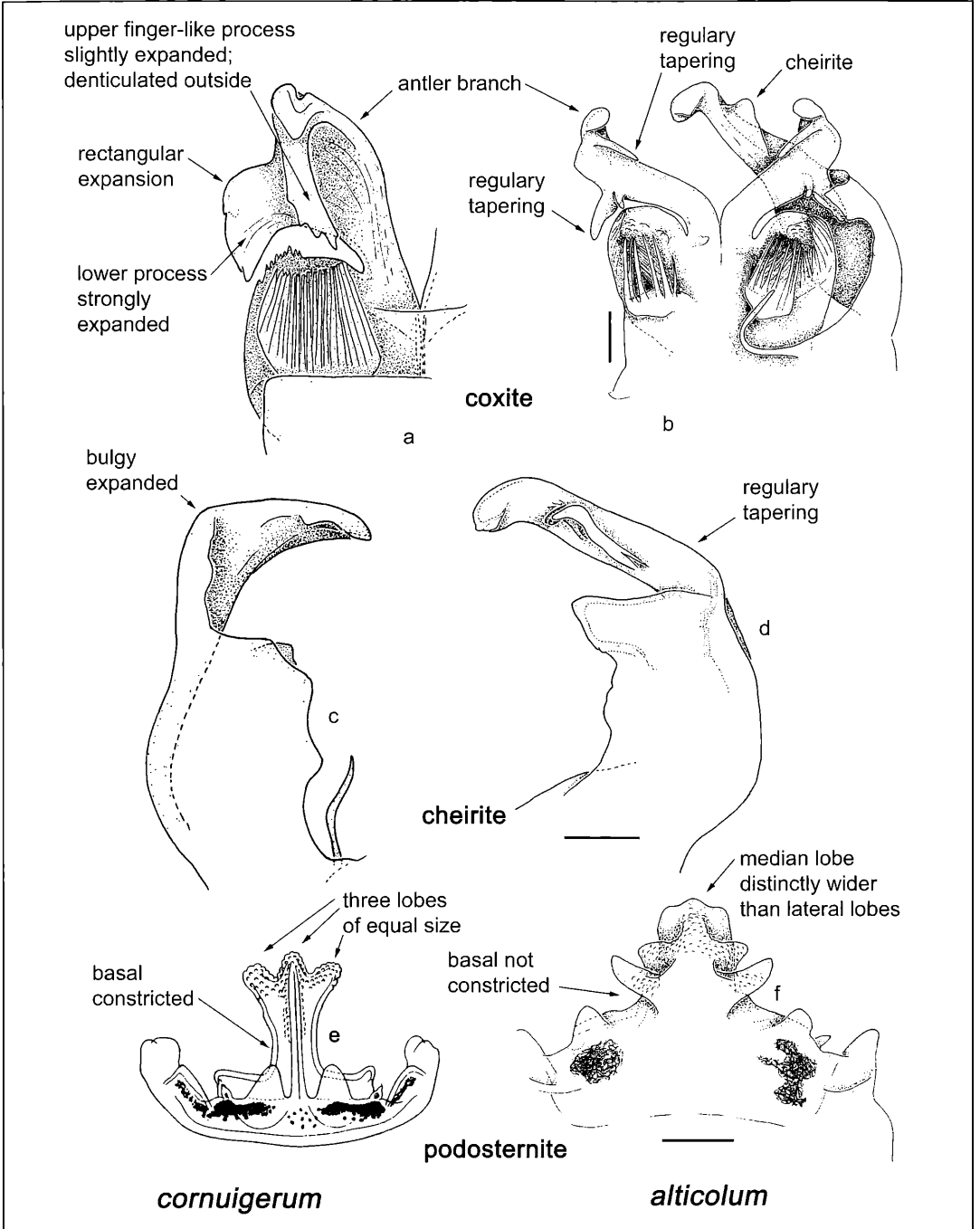


Figure 2. Figs. a, c, e: *Pterygophorosoma cornuigerum* (VERHOEFF, 1894); figs. b, d, f: *Pterygophorosoma alticum* (VERHOEFF, 1894): a-b) anterior gonopods, coxite, posterior view; c-d) cheirite, external view; e-f) podosternite, anterior view. Figs. a, c: after VERHOEFF (1900), modified; fig. e: after VERHOEFF (1925), modified; figs. b, f: specimen from Munt la Schera; fig. d: specimen from Schaubachhütte. Scale lines 0.1 mm.

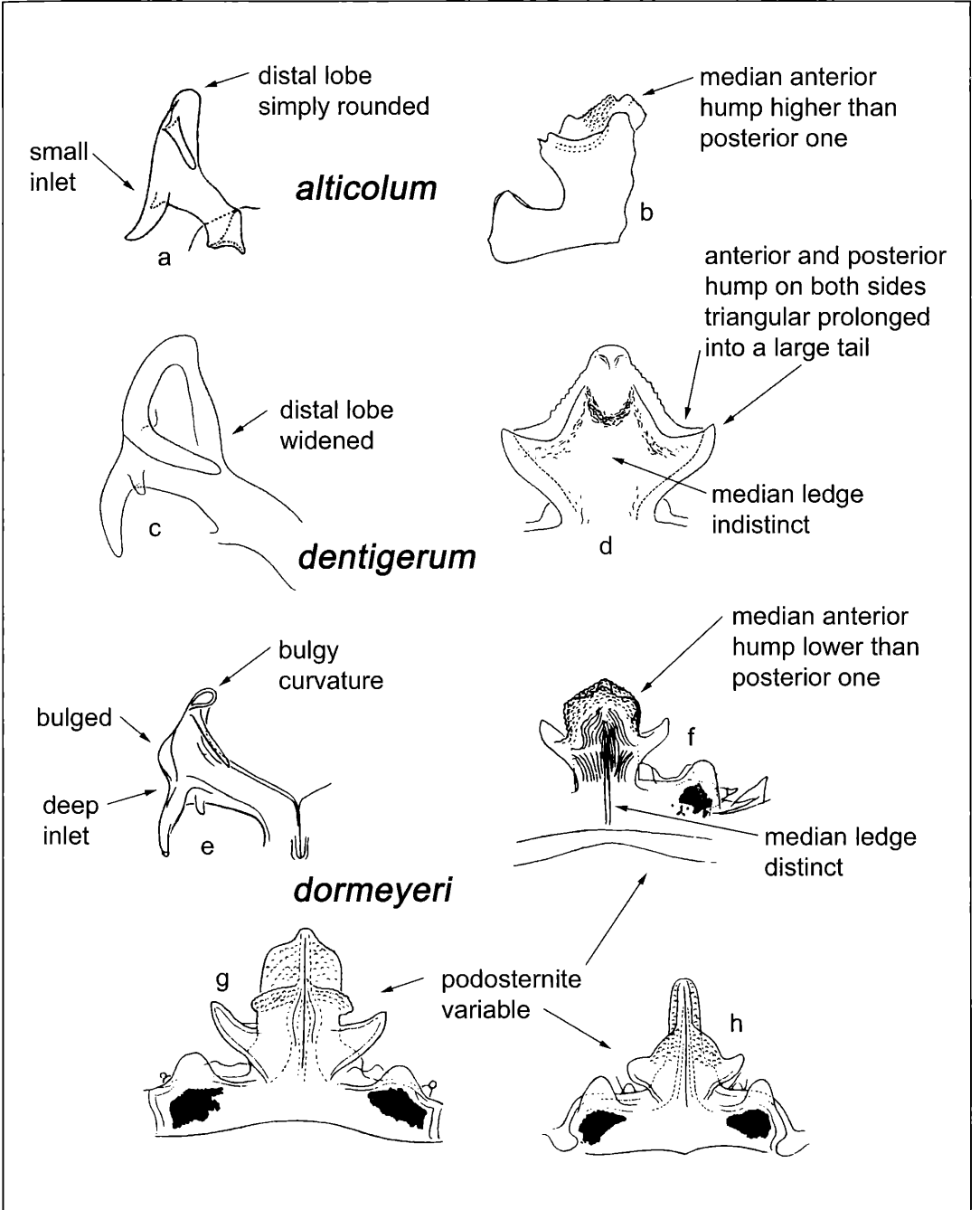


Figure 3. Figs. a-b: *Pterygophorosoma alticolum alticolum* (VERHOEFF, 1894); figs. c-d: *Pterygophorosoma alticolum dentigerum* (VERHOEFF, 1901); figs. e-h: *Pterygophorosoma alticolum dormeyeri* (VERHOEFF, 1911); figs. g-h: var. *excavatum*: a) c) e) anterior gonopods, coxite, antler branch, posterior view; b) d) f) top of podosternite, anterior view; g-h) podosternite, anterior view. Fig a-b: after VERHOEFF (1896), modified; figs. c-d: after VERHOEFF (1901), modified; figs. e-f: after VERHOEFF (1911), modified; figs. g-h: after VERHOEFF (1925), modified.

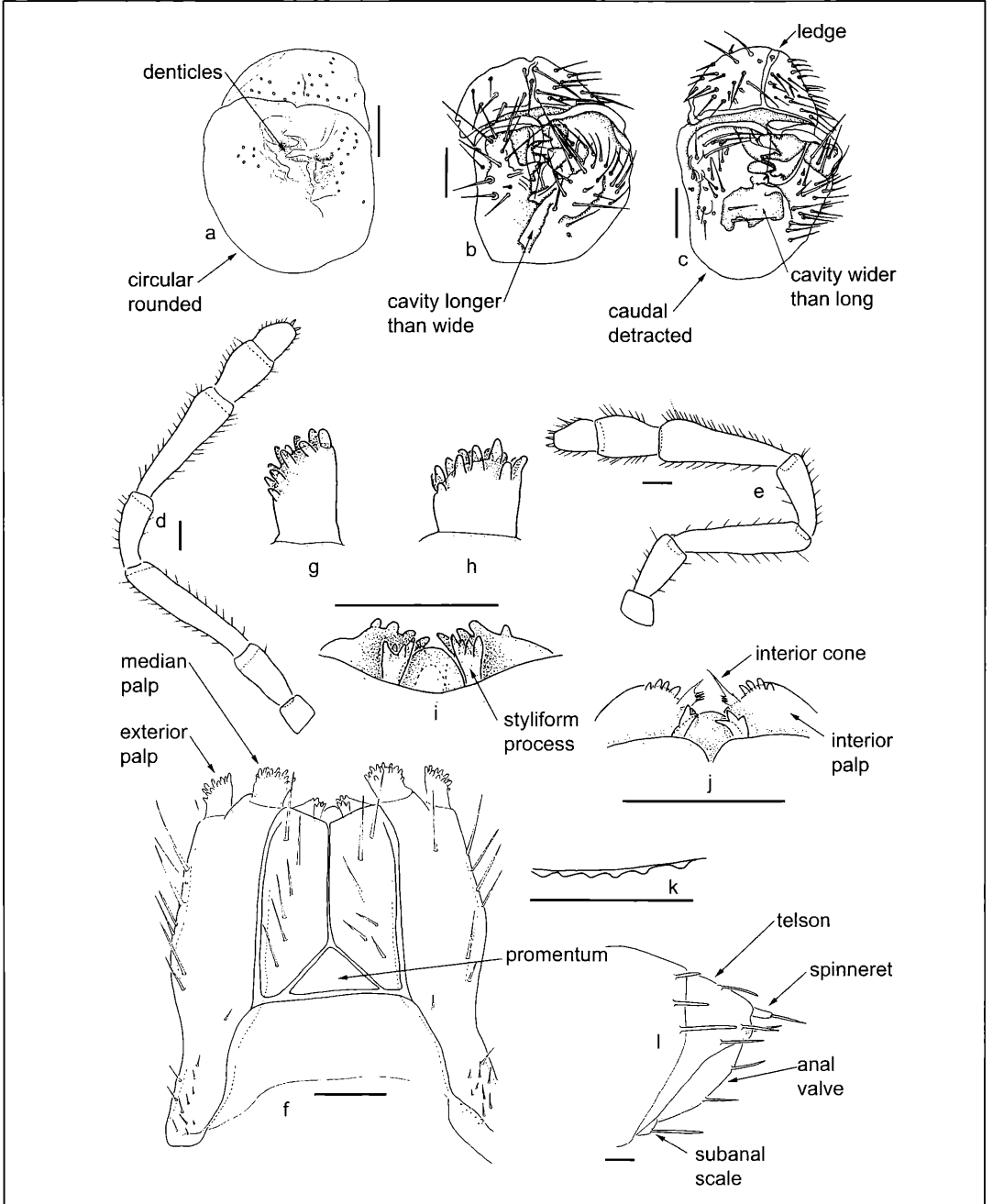


Figure 4. Figs. a-b, d-i, k-l: *Pterygophorosoma alticolum* (VERHOEFF, 1894); fig. c: *Pterygophorosoma cornuigerum* (VERHOEFF, 1894); fig. j: *Mastigona mutabile* (LATZEL, 1884): a-c) vulva, ventral view, scale indicates inner side; d) antenna of ♀, lateral view; e) antenna of ♂, lateral view; f) gnathochilarium of ♂, ventral view; g) same, exterior palp; h) same, median palp; i): same, inner palps and styliform processes; j): inner palps and styliform processes of *Mastigona mutabile*, for comparison; k) limbus of 15th segment, lateral part of a ♂; l) posterior end of a ♂, external view. Figs. a, d-l, k-l specimen from Schaubachhütte; figs. b-c: after KURNIK (1988), modified; fig. j: specimen from Bavaria: Obermaiselstein. Scale lines 0.1 mm, figs. g-i use the same scale line.

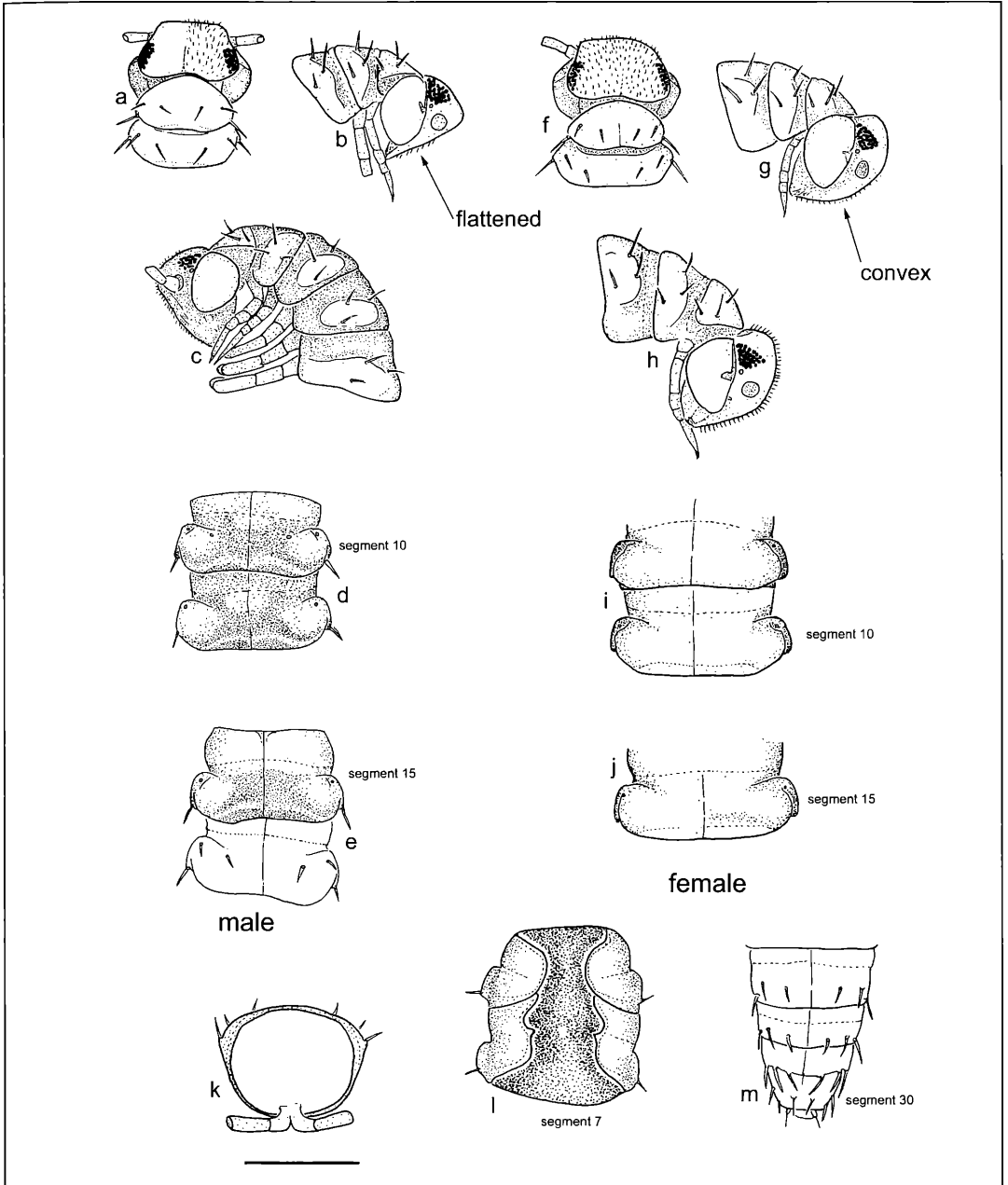


Figure 5. *Pterygophorosoma alticum* (VERHOEFF, 1894): a) head and first two segments of ♂, dorsal view, showing pilosity on right side; b) head and first three segments of ♂, external view, showing sculpture; c) head and first five segments of ♂, external view, showing sculpture; d) 10th and 11th segment of ♂, dorsal view, showing colour pattern; e) 15th and 16th segment of ♂, dorsal view, showing colour pattern on 15th segment; f) head and first two segments of ♀, dorsal view; g) head and first three segments of ♀, external view, showing sculpture; h) same of another ♀; i) 9th and 10th segment of ♀, dorsal view, macrochaetae omitted, showing sculpture; j) same for 15th segment of ♀; k) 17th segment of ♂, posterior view; l) 6th and 7th segment of ♂, ventral view, inner parts removed; m) last four segments of ♀, dorsal view. Figs. a-b, d-m: specimen from Schaubachhütte; fig. c: specimen from Munt la Schera. Scale lines 1 mm.

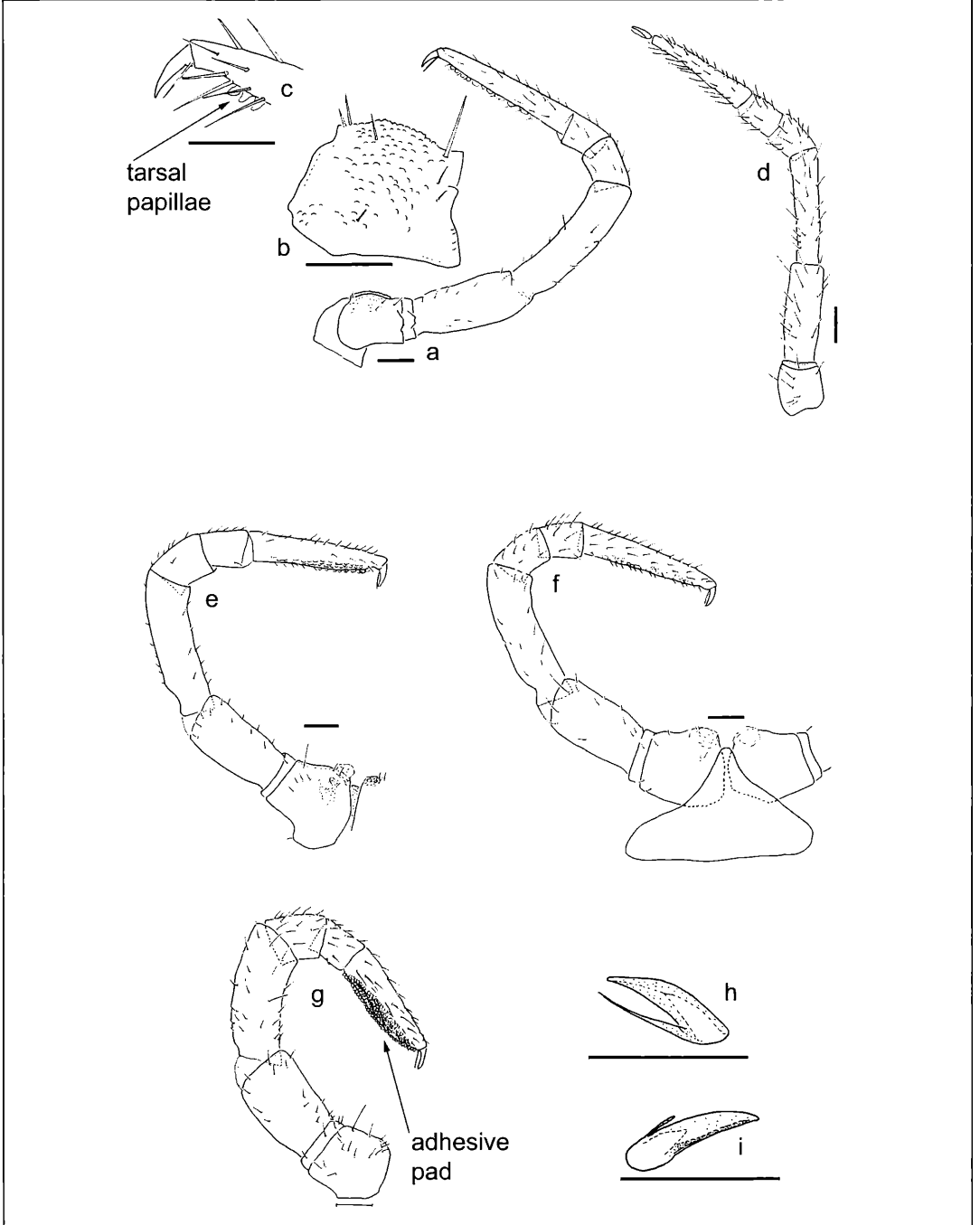


Figure 6. *Pterygophorosoma alticolum* (VERHOEFF, 1894): a) anterior leg of 10th segment of ♂, posterior view; b) same, coxa, magnified; c) same, claw, magnified; d) anterior leg of 10th segment of ♀, anterior view; e) anterior leg of 8th segment of ♂ (= leg10), posterior view; f) posterior leg of 8th segment of ♂ (= leg11), anterior view; g) posterior leg of 6th segment of ♂ (=leg7), anterior view; h) claw of 10th segment of ♀; i) claw of a posterior segment of ♂. All specimen from Schaubachhütte. Scale lines 0.1 mm.

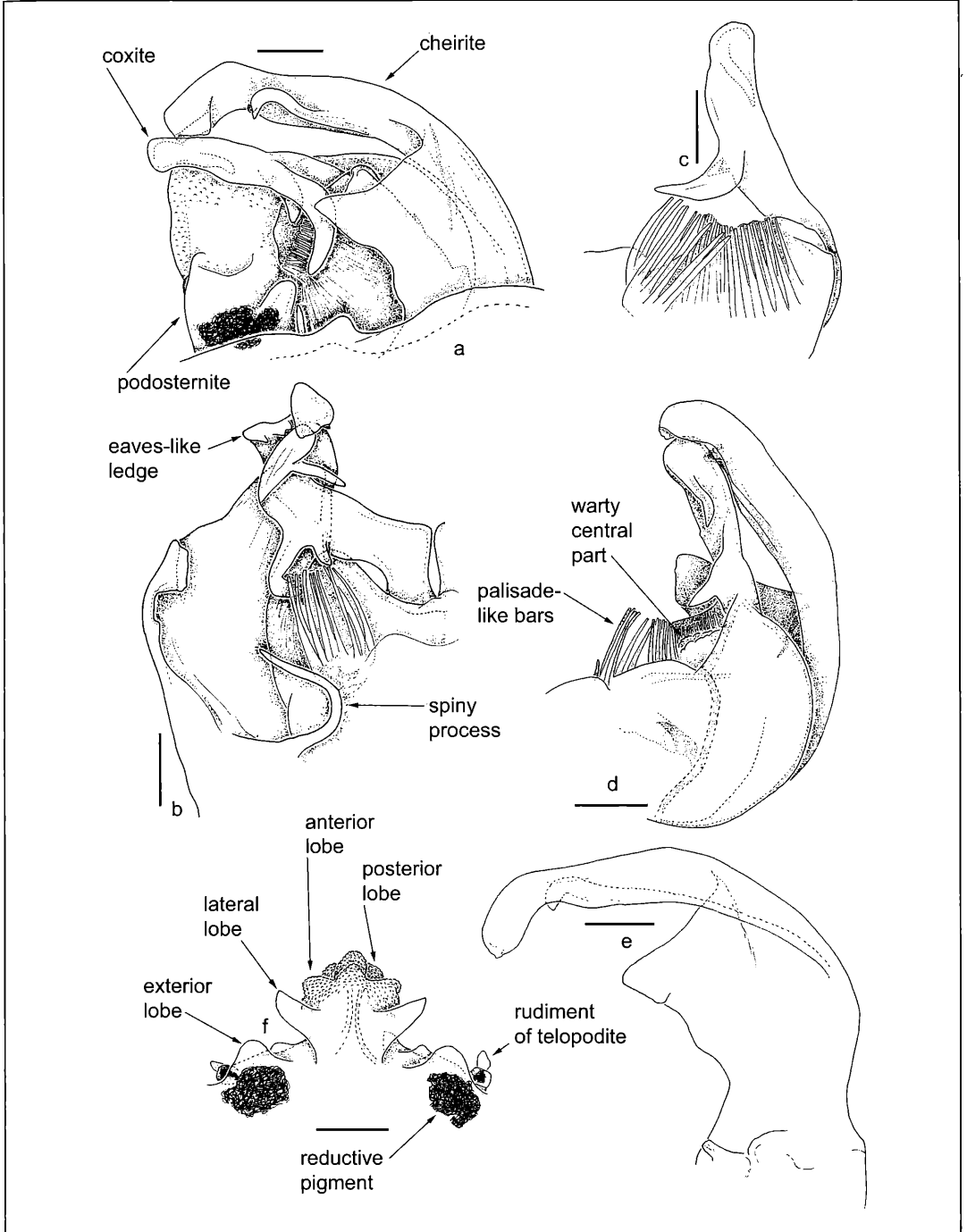


Figure 7. *Pterygophorosoma alticolum* (VERHOEFF, 1894), ♂: a) both gonopods, external view; b) anterior gonopods, posterior view; c) coxite, external view; d) anterior gonopods, internal view; e) cheirite, internal view; f) podosternite, anterior view. Figs. a-d, f: specimen from Schaubachhütte; fig. e: specimen from Munt la Schera. Scale lines 0.1 mm.

In these cases, a midbody segment is mostly used. But it is equally legitimate to use a segment of a given position. This segment should be clearly behind the 7th segment, which contains the gonopods and is often elevated. On the other hand, its position should not be too rear to allow work on incomplete specimens. Because of this, the 10th segment would be a good choice.

It is herewith recommended to give a drawing of both 10th and 15th segment in dorsal view. Supplementary drawings of a segment in lateral and caudal view would be advisable as well. The head, the first (= column) and the second segment should be drawn in dorsal view. The 7th segment, if it is modified in males, is to be drawn in dorsal view as well. This is easier if it is still connected with the 6th or 8th segment. Taxonomically more important is the 7th segment in ventral view, as often there are conspicuous structures like processes or inlets.

The first attempt towards a mathematical expression of the position of the macrochaetae has been made by SCHUBART (1934). He expressed the position by two numbers in the form of a fraction. In a recent work (SPELDA 1999), two different names have been introduced for these so-called "formulae of SCHUBART":

The macrochaetae index (CIX) is defined as follows (fig. 1d):

$$\text{CIX} = \frac{(\text{distance between exterior and median macrochaeta})}{(\text{distance between interior and median macrochaeta})}$$

The median index (MIX) is defined as follows:

$$\text{MIX} = \frac{(\text{distance of interior macrochaeta and median (longitudinal) suture})}{(\text{distance between interior and median macrochaeta})}$$

or

$$\text{MIX} = \frac{(\text{distance of both interior macrochaetae})}{2 \cdot (\text{distance between interior and median macrochaeta})}$$

Besides these distance relations, the angles formed between the three macrochaetae are also of importance. It can be expressed trigonometrically by the macrochaetal angle (MA)

$$\text{MA} = \frac{\arccos((\text{distance of exterior and median macrochaeta})^2 + (\text{distance of interior and median macrochaeta})^2 - (\text{distance of interior and exterior macrochaeta})^2)}{2 \cdot (\text{distance of exterior and median macrochaeta}) \cdot (\text{distance of interior and median macrochaeta})}$$

The measurements must be taken in dorsal view. This view has to be projected into a plain. This supplementary definition is necessary to treat convex animals. It is as well conceivable to measure the indices in lateral (external) view.

Another important character lies in the shape of the paraterga. It can be expressed by another formula called the paratergal index (PIX, fig. 1e).

$$\text{PIX} = \frac{(\text{distance of exterior edge of paratergum and median suture}) - (\text{distance of edge of prozonite and median suture})}{(\text{length of paratergum, measured parallel to median suture at the edge between it and the prozonite})}$$

or

$$\text{PIX} = \frac{(\text{distance of the edges of both paraterga}^1) - (\text{distance of edges of prozonite}^2)}{2 \cdot (\text{length of paratergum}^3)}$$

¹ = width of metazonite

² = width of prozonite

³ measured parallel to median suture at the edge between it and the prozonite

A paratergal index of one indicates a square paratergal wing. A poorly developed paratergum has an index close to zero.

For all these measures the segment at which they were taken should be given in brackets (e. g. PIX (15) = 0.5). Although there is not much variation if an index is taken from a neighbouring segments, there is a clear difference if an absolute measure (e.g. width) is taken either from the 10th or 15th segment.

The following measurements must be given as standard for the 10th and 15th segment: width of prozonite and metazonite, length of paratergum (if present), angle MA, indices CIX, MIX and PIX.

Still another taxonomically important character of the segments is the so-called limbus, a supplementary rear margin of the metazonite which seems to have been introduced to diplopod taxonomy by PORATH (1872). As the limbus must be scrutinised at higher magnification in transmission light, it is often necessary to break off a piece of a segment. This can easily cause a damage to the whole segment. For this reason none of the segments that are to be drawn ought to be selected for the investigation of the limbus. It is either recommended to use the 5th, 8th or 9th segment or to embed the whole 10th or 15th segment. Limbal structure has been used in several orders of millipedes (SCHMIDT 1962). According to previous knowledge, no limbus has been revealed in the group Nematophora (Chordeumatida, Callipodida, and Stemmiulida) (SCHMIDT 1962), but during the present study a limbus has been found in *Pterygophorosoma*, yet only on the sides of the segment. It seems very likely that it has just been overlooked in other Nematophora.

legs

Length and width of single podomeres have only seldom been used in diplopod taxonomy. A good attempt has been made by ENGHOFF (1982, 1992) who gives standards for these measures: the length has to be taken on the external side and the width right-angled to it at the widest part (fig. 1b). In contrast to ENGHOFF (1982) who took the average value of six median podomeres, it seems to be more reasonable to take a single leg and to describe the variation separately. Si-

milarly to the segments, it is herewith recommended to take the anterior leg of the 10th and / or the 15th segment. Similarly to the antennae both absolute measures and their length-width indices should be given. It might be reasonable to give the length as well as fraction of the femur, usually the longest podomere. Attention is to be paid to the fact that the legs of males are enlarged in many millipedes, especially the anterior legs of numerous Chordeumatida, including the Craspedosomatidae. For this reason males and females must be treated separately.

Especially in the order Chordeumatida, several legpairs can be modified. In the males one or both legpairs of the 8th segment show coxal glands and sometimes additional processes on podomeres, e.g. in the family Haaseidae. Other chordeumatidans show coxal horns or sternal outgrowths on anterior legpairs. In several Craspedosomatidae the coxa of the posterior leg of the 6th segment is enlarged.

In females it is the 2nd or 3rd legpair which is sometimes modified, e.g. in the family Mastigophorophyllidae where the 2nd legpair is reduced to a lobe.

In one of his last papers, ATTEMS (1959) instructed his successors to pay special attention to the shape of the claw (fig. 1c) in chordeumatidan taxonomy. Unfortunately, this promising attempt has only very seldom been adopted. In particular, within the family Craspedosomatidae ATTEMS (1959) was able to recognise several types of claw. He even found differences between anterior and posterior legpairs. Remarkably, *Pterygophorosoma alticum* was among the species ATTEMS (1959) investigated. In a later attempt, ENGHOFF (1992) recommended to give the length of the accessory claw as a fraction of claw length. This should be defined as a standard too.

gonopods

Gonopods still carry the most important taxonomic characters in millipede taxonomy. For that reason it is important to have standardised figures. The standardisation depends on the structure of the gonopods. In some cases these are difficult to fix, because their parts are movable against each other. In most julids, the gonopods must be dissected longitudinally at best, except for the Ommatoiulini which can be depicted in posterior view without dissection. A dissection between anterior (pro- and mesomerite) and posterior part (opisthomerite) is mostly impossible, because both are connected by flagellae. These flagellae either break off and remain with the opisthomerite or they cause an unwanted torsion. As the opisthomerites are only loosely connected with each other, it is very difficult to fix them exactly in cranial or caudal view. Mostly they break into two parts and will be found later in a virtual position. Because of such inconsistent preparations several taxa have been described twice.

In the order Chordeumatida we face perhaps the greatest variety of gonopod structures. Depending on family, sometimes even on genus, different orientations have to be chosen. Most times it is only possible to present an external view using an intact specimen. A dissection of the entire gonopod complex requires an experienced specialist and calm handling. Often the anterior and posterior gonopods will be separated during dissection, because they represent different legpairs and remain free from each other.

In the chordeumatidans, the posterior gonopods should be drawn in anterior (cranial) view as a standard. A posterior (caudal) view of the posterior gonopods might sometimes be advisable too. The two halves of the posterior gonopods are connected by a sternal process in most Chordeumatida. In the Craspedosomatini they are fused to a homogeneous structure called podosternite. The posterior gonopods are compressed caudo-cranially. For that reason it is nearly impossible to fix them in lateral view or to dissect them further.

In contrast to the posterior gonopods, the anterior gonopods have to be shown in posterior view. As a standard, anterior, external (antaxial) and internal (paraxial) views are to be depicted too. The anterior view is taxonomically less important, but it is advisable to show it too. To get an anterior or posterior view, the whole anterior gonopods have to be fixed, preferably in a hollow slide.

In the families Craspedosomatidae and Attemsidae, the anterior gonopods are bipartite, consisting of the external cheirites and the internal coxites (fig. 7a). Sometimes they have to be separated to study them isolated. As both cheirites and coxites are mostly compressed laterally, they have to be shown in lateral view. While figures of the cheirites are given regularly in most descriptions, the coxites are often omitted, especially in the Craspedosomatini. This is comprehensible, as their delicate structures scarcely lend themselves to be drawn. Unfortunately, the coxites carry structures of great taxonomic importance at the species level, otherwise show little variation (SPELDA 1999). The importance of the coxites is obvious if one takes in consideration that they carry out a direct function in sperm transfer.

To sum up, in respect of the gonopods the following procedure is proposed for chordeumatidans:

1. If possible, the gonopods are to be depicted using an intact specimen in external view.
2. The gonopods must be isolated from the 7th segment. If this happens without separating them, they have to be figured in external view.
3. The posterior gonopods ought to be separated from the anterior gonopods. They have to be figured in anterior view, eventually in posterior view too.
4. The anterior gonopods are to be shown in posterior view, and, if omitted up to now (2.), in external view. Eventually the anterior view must be figured too.

5. If possible, the anterior gonopods are to be separated in the middle. They have to be figured in internal and external views.

6. Cheirites and coxites (if present) must be separated. The missing views (cheirite in internal view, coxite in external view) are to be added.

vulvae

The female genitalia, or the vulvae, have long been used as taxonomic characters (BRÖLEMANN & LICHTENSTEIN 1919). Isolated vulvae are difficult to fix, sometimes only in the taxonomically less useful lateral view. To place and keep the vulvae in the important ventral view it is advisable to dissect them together with the 2nd and 3rd legpairs in chordeumatidans and together with the 2nd legpair in julidans. The legs help to turn the vulvae into the right position during their fixation on a slide with a cover glass. Depending on the amount of extrusion the preparation might be directed more to the anterior (operculum) or posterior (bursa) part. It is important to render no pressure to the vulvae, otherwise they might get deformed. For that reason hollow slides are preferable. An absolute fixed orientation, as in gonopods, is not possible, because the vulvae are spherical, soft, therefore easily destructible structures.

In most diplopods the vulvae are strongly covered with setae. For that reason it might be advisable to draw only their insertion points (fig. 4a), otherwise they hide the underlying external structures of the bursa. It is important to show the receptacula too. These are situated inside the vulva. Although their shape varies in detail, the general structure is of taxonomic value. Of course setae can only be omitted if their structure is of no taxonomic significance. Otherwise two figures must be given, one with and the other without setae.

number of specimen to be investigated

It is remarkable that the authors of the classical period did not pay attention to the variability of measurements. The only laudable exception was OTTO SCHUBART. Especially in his late papers on Brazilian millipedes added he huge tables with measurements of individual specimens.

To get statistically significant parameters for the variation of the investigated measures, a minimum of six specimens must be investigated for each sex and age class. A higher number is advisable, but the amount of work for a description clearly increases. For practical reasons six specimens seems to be a reasonable compromise.

In practice it is common that for a description or redescription less than six specimens are at hand. In this case the single measures of all specimen should be published in a table. This enables future students, who get additional material, to complement measures and

to correct or specify the parameters. For characters of uncertain taxonomic value it might be reasonable to measure a single specimen, just to have a comparison with higher taxa.

It is to be underlined that males and females have to be described separately. In some genera the differences in size between the two sexes are greater than between members of different species within the same sex (e. g. in *Rhymogona* COOK, 1896).

4. Synonymy list of the genus *Pterygophorosoma*

Explanation of abbreviations:

C = citation, D = description, N = note

Pterygophorosoma VERHOEFF, 1897

- 1897 *Craspedosoma* (*Pterygophorosoma*) VERHOEFF: Arch. Naturgesch., **63** (1): 138 (D, no type species proposed)
 1900 *Orotrechosoma* VERHOEFF: Arch. Naturgesch., **66** (1): 370 (D, no type species proposed)
 1910 *Orotrechosoma* – VERHOEFF: SB Ges. naturf. Freunde Berlin, **1910**: 35 (N)
 1911 *Orotrechosoma* – VERHOEFF: Zool. Anz., **38**: 28, 30-31 (D, including juveniles).
 1925 *Orotrechosoma* – VERHOEFF: Zool. Jb. Syst., **50**: 65 (N)
 1926 *Orotrechosoma* – ATTEMS: Handb. Zool., **4** (1): 173-174 (D)
 1932 *Orotrechosoma* – VERHOEFF: In BRONN, Klassen und Ordnungen des Tierreichs, **5** (2): 1491-1495 (D)
 1934 *Orotrechosoma* – VERHOEFF: In BROHMER et al., Tierwelt Mitteleuropas, **2, 3**: 44, 49 (D)
 1970 *Orotrechosoma* – JEEKEL: Monograf. Nederl. Ent. Ver., **5**: 74 (N, subsequent designation of type species: *Orotrechosoma cornuigerum* VERHOEFF, 1900)
 1970 *Pterygophorosoma* – JEEKEL: Monograf. Nederl. Ent. Ver., **5**: 77 (N, subsequent designation of type species: *Atractosoma alticolum* VERHOEFF, 1894)
 1980 *Orotrechosoma* – HOFFMAN: Classification of the Diplopoda: 133 (N)
 1980 *Pterygophorosoma* – HOFFMAN: Classification of the Diplopoda: 125 (N)

According to JEEKEL (1970), the genera *Pterygophorosoma* und *Orotrechosoma* have a neuter gender. For that reason the species names have to end with “-um”

Pterygophorosoma alticolum (VERHOEFF, 1894)

- 1894 *Atractosoma alticolum* VERHOEFF: Verh. zool.-bot. Ges. Wien, **44**: 21 (D /)
 1895 *Atractosoma alticolum* – VERHOEFF: Zool. Anz., **18**: 218-220 (D, ?, without figures)
 1896 *Craspedosoma alticolum* – VERHOEFF: Arch. Naturgesch., **62** (3): 208-209, pl. 14, figs. 59-62 (D, ?)
 1900 *Orotrechosoma alticolum* – VERHOEFF: Arch. Naturgesch., **66** (1): 384 (N)
 1901 *Orotrechosoma alticolum* – ROTHENBÜHLER: Revue suisse Zool., **9**: 366 (N)
 1901 *Orotrechosoma alticolum dentigerum* VERHOEFF: Jh. Ver. vaterl. Naturk. Württemberg, **57**: 105-106, pl. 3, fig. 24-25 (D ?).

- 1911 *Orotrechosoma alticum dormeyeri* VERHOEFF: Zool. Anz., **38**: 31, figs. 7-8 (D ?, /).
- 1925 *Orotrechosoma alticum (genuinum)* – VERHOEFF: Zool. Jb. Syst., **50**: 66 (D, ?)
- 1925 *Orotrechosoma alticum dentigerum* – VERHOEFF: Zool. Jb. Syst., **50**: 66, (D, ?)
- 1925 *Orotrechosoma alticum dormeyeri* – VERHOEFF: Zool. Jb. Syst., **50**: 66-67 (D, ?)
- 1925 *Orotrechosoma alticum dormeyeri* var. *excavatum* VERHOEFF: Zool. Jb. Syst., **50**: 66, pl. 2, figs. 9-10 (D, ?)
- 1929 *Orotrechosoma alticum dormeyeri* – BIGLER: Ergeb. Wiss. Unters. Schweiz. Nationalpark, **5**: 13-14 (N)
- 1934 *Orotrechosoma alticum* – SCHUBART: In DAHL, Tierwelt Deutschlands, **28**: 126-128, figs. 216-219 (D ? /; synonymy of the taxa *alticum*, *dormeyeri* und *excavatum*, but without arguments)
- 1949 *Orotrechosoma alticum* – ATTEMS: SB Ak. Wien, math.-naturw. Kl., **158** I: 136 (N)
- 1974 *Atractosoma alticum* – MORITZ & FISCHER: Mitt. Zool. Mus. Berlin, **50**: 326 (N)
- 1974 *Orotrechosoma alticum dentigerum* – MORITZ & FISCHER: Mitt. Zool. Mus. Berlin, **50**: 334 (N)
- 1983 *Orotrechosoma alticum dormeyeri* – DETHIER & PEDROLI-CHRISTEN: Bull. Soc. vaud. Sc. nat., **76** (364): 376-377 (N)
- 1984 *Orotrechosoma alticola* – STRASSER & MINELLI: Lavori Soc. Ven. Sc. Nat., **9** (2): 206 (C)
- 1988 *Orotrechosoma alticola* – KURNIK: Zool. Jb. Syst., **115**: 265-266, fig. 67 (D /: vulva)
- 1989 *Orotrechosoma alticum* – THALER: Ber. nat.-med. Verein Innsbruck, **76**: 100 (N)
- 1993 *Pterygophorosoma alticum* – PEDROLI-CHRISTEN: Documenta Faunistica Helvetiae, **14**: 99 (N, map for Switzerland, synonymy of the taxon *dormeyeri*, but without arguments)
- 1995 *Pterygophorosoma alticola* – FODDAI et al.: In MINELLI et al., Checklist delle specie della fauna italiana, **32**: 16 (C)

Pterygophorosoma cornuigerum (VERHOEFF, 1900)

- 1900 *Orotrechosoma cornuigerum* VERHOEFF: Arch. Naturgesch., **66** (1): 383-384, pl. 16, figs. 28-30 (D ?, /)
- 1925 *Orotrechosoma cornuigerum* – VERHOEFF: Zool. Jb. Syst., **50**: 65-66, pl. 2, fig. 5 (D ?, /, juveniles)
- 1949 *Orotrechosoma cornuigera* – ATTEMS: SB Ak. Wien, math.-naturw. Kl., **158** I: 136 (N)
- 1974 *Orotrechosoma cornuigerum* – MORITZ & FISCHER: Mitt. Zool. Mus. Berlin, **50**: 333 (N)
- 1984 *Orotrechosoma cornuigerum* – STRASSER & MINELLI: Lavori Soc. Ven. Sc. Nat., **9** (2): 206 (C)
- 1988 *Orotrechosoma cornuigera* – KURNIK: Zool. Jb. Syst., **115**: 266, fig. 68-69 (D /: vulva)
- 1995 *Pterygophorosoma cornuigerum* – FODDAI et al.: In MINELLI et al., Checklist delle specie della fauna italiana, **32**: 16 (C)

5. Diagnoses of higher taxa

Family Craspedosomatidae

A family belonging to the order Chordeumatida, characterised by:

- anterior gonopods consisting of two parts: internal coxites and external cheirites (figs. 2b, 7a-b, 7d). Coxae of 7th legpair without large processes (fig. 6g, difference from Attemsidae).

Tribe Craspedosomatini

A tribe of the family Craspedosomatidae, characterised by:

- Sternite and telopodites of the posterior gonopods fused to a podosternite. Sternal process broadened and covered with warty outgrowths (fig. 2f, 7f).
- Coxites of anterior gonopods with an outer semi-circle of palisade-like bars, called “Grannenapparat” by VERHOEFF (1926-1932).

In his classification, HOFFMAN (1980) divided the Craspedosomatidae into five subfamilies, Craspedosomatinae, lulogoninae, Rhymogoninae, Atractosomatinae, and Rothenbuehleriinae. As this classification seems to generally overrate the rank of most of these taxa, it appears advisable to largely treat them as tribes only. The only exception is the subfamily Rothenbuehleriinae, which is indeed distinctly set off from the other Craspedosomatidae. The subfamily Atractosomatinae sensu HOFFMAN (1980), now treated as a tribe, Atractosomatini, is more or less a heterogeneous “can of worms” to encompass the genera that are still impossible to group properly. They certainly belong to different tribes, and some might prove to belong to the tribe Rhymogonini. Until a major revision clears up the relations, HOFFMAN’s (1980) classification is to be retained, with the exception of downgrading most of the taxa to tribal level.

Genus *Pterygophorosoma*

A genus of the tribe Craspedosomatini, characterised by:

- Antler-like outgrowths instead of pseudoflagelloids (antler branch: fig. 2a-b).

accessory characters:

- Podosternite with a laterally and distally expanded median process (fig. 7f). This character is shared with some *Pyrgocyphosoma* species.
- Margin of 7th segment in males with a small tooth (fig. 5l). This character is shared with the genus *Pyrgocyphosoma*.
- Operculum of vulva arched, with a median ledge (fig. 4a-c); bursa with large, tooth-like projections in its inner part and a distal cavity.
- In contrast to other Craspedosomatini, juveniles of *Pterygophorosoma* show the following characters (VERHOEFF 1911: 28):

Table 1: Distinction between *P. alticolum* and *P. cornuigerum*

	<i>alticolum</i>	<i>cornuigerum</i>
collum (1 st tergite)	not lightened	collum and sometimes 2nd tergite lightened
anterior gonopods: coxite: antler branch: upper finger-like process	regularly tapering; not denticulated	distally mucronate or slightly expanded; at the end denticulated outside
anterior gonopods: coxite: antler branch: lower process	regularly tapering and pointed	strongly expanded, on top with a nearly rectangular expansion
anterior gonopods: cheirite: finger-like process outside	bulgy expanded	regularly tapering
posterior gonopods: top of the podosternite	basal not constricted; median lobe distinctly wider than lateral lobes	basally constricted; distally expanded with three lobes of equal size
vulva: central part	caudal detracted	caudally expanded into a circular emargination
vulva: bursa	inwards declining	not inwards declining

Table 2: Distinction of the nominal subspecies of *P. alticolum* (according to VERHOEFF 1925)

	<i>alticolum</i>	<i>dentigerum</i>	<i>dormeyeri</i>
anterior gonopods: antler branch	at the end simply rounded; outwards only with a small inlet	as in <i>alticola</i> , but distal branch much wider	at the end with a bulgy curvature; outwards with a deep inlet and bulged behind it
posterior gonopods: podosternite	median anterior hump <u>higher</u> than a hidden posterior one, latter only slightly higher than its strongly projecting lateral lobes	anterior and posterior hump of the top on both sides extended into a triangular, large tail; median ledge indistinct	median anterior hump <u>lower</u> than posterior one, latter distinctly higher than small lateral lobes; median ledge distinct
paratega: colour	like the rest of the body	distinctly reddish brown, contrasting	

- without three dark longitudinal bands as in *Craspedosoma* LEACH, 1814 (one in the middle, the others below paraterga);
- 3+3 macrochaetae on segments only slightly larger than in adults; especially median macrochaetae rather short, not reaching the posterior margin on most segments;
- basal nodes of macrochaetae weakly developed.

6. Taxa previously described in *Pterygophorosoma*

Two species, *P. alticolum* and *P. cornuigerum*, are generally accepted in *Pterygophorosoma*. They can easily be distinguished by the characters given in tab. 1. The differences in all parts of the gonopods are striking (figs. 2a-f). The vulvae also allow separation of both species (figs. 4a-c), as shown by KURNIK (1988). Two additional subspecies have been described in *P. alticolum*. The character used to discriminate them from each other, according to the latest treatment by VERHOEFF (1925), are given in table 2 and figures 3a-h.

7. Redescription of *Pterygophorosoma alticolum* (VERHOEFF, 1894)

Measures of individual specimens are given in table 3.

Length 13-16 mm; width, measured on 15th and 10th segment, 1.3-1.7 mm. Colour of body in alcohol marbled dark chocolate to dark reddish brown (colour pattern shown in figs. 5d-e), somewhat varying individually, antennae a little darker, legs a little bit lighter than the rest of the body.

Body with 30 segments; paraterga small, distinctly rounded (figs. 5d-e, 5i-k) but not totally so as in *Craspedosoma*; paratergal index PIX 0.4-0.6 on segments 10 and 15. Ocelli in an almost equilateral triangular field, composed of about 25 ocelli in 5-6 rows, consisting of 7-6-5-4-2(-1) ocelli; deviations of about one ocellus per row common. Antennae long and slender (figs. 4d-e), antennomere 3 longest; relative lengths of antennomeres in relation to antennomere 3: 0.18-0.23, 0.41-0.51, 1.0, 0.27-0.31, 0.45-0.51, 0.21-0.24, 0.14-0.18; length/width indices of antennomeres: 0.77-1.12, 1.65-2.17, 4.25-4.94, 2.45-2.95, 2.45-4.00, 1.28-2.38, 1.14-1.58.

Gnathochilarium (fig. 4f) with a promentum, styliform processes quadri-dentate (fig. 4i), innermost cone of internal palps not modified.

Collum semi-circular, not covering the head (figs. 5a, 5f). Segments with 3+3 dorsal, spiniform macrochaetae (figs. 5d-e, 5i-j); macrochaetae of midbody segments (10 and 15 measured) forming an angle of 89-116°; macrochaetae index CIX 0.62-1.10; median index MIX 1.12-1.55. Limbus (fig. 4k) present only on sides of segments, missing in central part, consisting of isolated, more or less rounded lobes.

Claws of anterior legs (figs. 6c, 6h) about 3 times longer than wide, with a ventral, setiform accessory claw about the length of the claw; posterior legs with a second, dorsal accessory claw (fig. 6i), reaching about half of the length of the claw.

male

Frons flattened (figs. 5b-c); ventral side of 7th segment with a triangular projection (fig. 5l); legs with tarsal papillae ("Sohlenbläschen" of VERHOEFF 1926-1932) on tarsi of all legs (fig. 6c) except for the first two and the last five pairs, broadened into pads on legpairs 2-7 (fig. 6g). Legs 3-7 distinctly incrassate, thus having relatively small length/width indices, especially on prefemur, femur and tarsus; length/width indices for leg 7 from coxa to tarsus: 1.13-0.18-1.52-2.28-1.38-1.35-3.35. Second legpair of 6th segment (= legpair 7) with an unmodified coxa (fig. 6g). Both pairs of 8th segment with coxal sacs, but no other modifications (figs. 6e-f). Relative lengths of anterior leg of 10th segment (fig. 6a) in relation to femur (coxa to tarsus): 0.41-0.08-0.62-1.00-0.36-0.26-0.97; length/width indices: 1.19-0.25-1.78-3.39-1.40-1.24-5.43; coxa of anterior leg of 10th segment (fig. 6a) covered with warts on ventral side.

Anterior gonopods (figs. 2b, 7a-b) fused with each other, no separate sternite visible, divided in two parts, i.e. exterior cheirites and interior coxites. Coxite (figs. 7b-d) with a usual exterior semi-circle of palisade-like bars (fig. 7d), surrounding an area covered with semi-circular warts, but without any projection. Instead of pseudoflagelloids of other Craspedosomatini, an antler-like branch present. This antler-branch with 3 more

Legend table 3: Abbreviations: BL = length of body, HW = width of head; EW = width of external margins of eyes, CW = width of collum, CL = length of collum, AW = width of antennomer, AL = length of antennomer, AI = antennomer index (length/width), PW = width of prozonite, MW = width of metazonite, PL = length of paratergum, MID = distance of both interior macrochaetae, MMD = distance of both median macrochaetae, MED = distance of both exterior macrochaetae, MIMD = distance between interior and median macrochaeta, MMED = distance between median and exterior macrochaeta, MIED = distance between interior and exterior macrochaeta, MA = macrochaetal angle, CIX = macrochaetal index, MIX = median index, PIX = paratergal index. Numbers in brackets indicate segment or antennomer number. All measures are given in mm, angles in degree. Specimen reference: 15-1 = JSP000215-001, 15-2 = JSP000215-002, 15-3 = JSP000215-003, 15-4 = JSP000215-004, 18-1 = JSP000218-001, 18-2 = JSP000218-002, all from Schaubachhütte; 96-5 = JSP280896-005 from Munt la Schera.

Table 3: Some measurements of studied material.

specimen	96-5	15-2	15-3	18-1	15-1	15-4	18-2
sex	♂	♂	♂	♂	♀	♀	♀
BL	14	14	14		13	16	15
HW	1.21	1.14	1.10		1.17	1.26	
EW	0.83	0.88	0.90		0.90	0.98	
CW	0.83	0.88	0.88		0.88	1.00	
CL	0.38	0.45	0.50		0.40	0.50	
AW (1)	0.11	0.13	0.10	0.11	0.10	0.11	
AW (2)	0.12	0.12	0.12	0.11	0.11	0.12	
AW (3)	0.11	0.11	0.11	0.11	0.10	0.11	
AW (4)	0.12	0.11	0.11	0.11	0.10	0.12	
AW (5)	0.12	0.15	0.16	0.15	0.14	0.19	
AW (6)	0.10	0.15	0.16	0.15	0.14	0.19	
AW (7)	0.12	0.11	0.12	0.12	0.11	0.12	
AL (1)	0.10	0.10	0.10	0.11	0.11	0.11	
AL (2)	0.21	0.19	0.21	0.24	0.23	0.26	
AL (3)	0.52	0.45	0.48	0.52	0.49	0.52	
AL (4)	0.31	0.31	0.30	0.33	0.27	0.29	
AL (5)	0.48	0.49	0.49	0.51	0.45	0.48	
AL (6)	0.23	0.24	0.24	0.24	0.21	0.24	
AL (7)	0.17	0.18	0.14	0.14	0.14	0.14	
AI (1)	0.89	0.77	1.00	1.06	1.12	0.95	
AI (2)	1.80	1.65	1.71	2.11	2.17	2.14	
AI (3)	4.89	4.28	4.50	4.94	4.88	4.68	
AI (4)	2.60	2.89	2.83	2.95	2.71	2.45	
AI (5)	4.00	3.32	3.07	3.35	3.35	2.45	
AI (6)	2.38	1.64	1.46	1.54	1.46	1.28	
AI (7)	1.40	1.58	1.14	1.15	1.21	1.14	
PW (10)	1.14	1.07	1.10		1.12	1.26	1.26
MW (10)	1.45	1.38	1.38		1.43	1.62	1.55
PL (10)	0.31	0.30	0.33		0.31	0.32	0.33
MID (10)	0.70	0.74	0.69		0.69	0.81	0.79
MMD (10)	1.24	1.17	1.17		1.21	1.40	1.36
MED (10)	1.40	1.33	1.33		1.36	1.55	1.52
MIMD (10)	0.26	0.24	0.24		0.31	0.33	0.29
MMED (10)	0.25	0.24	0.26		0.19	0.25	0.26
MIED (10)	0.41	0.33	0.40		0.43	0.43	0.40
MA (10)	109	89	108		116	93	95
CIX (10)	0.95	1.00	1.10		0.62	0.75	0.92
MIX (10)	1.34	1.55	1.45		1.12	1.21	1.38
PIX (10)	0.5	0.52	0.43		0.50	0.56	0.43
PW (15)	1.05	1.07	1.07		1.26	1.31	1.29
MW (15)	1.33	1.33	1.38		1.45	1.64	1.55
PL (15)	0.30	0.31	0.31		0.27	0.36	0.32
MID (15)	0.63	0.69	0.69		0.74	0.86	0.81
MMD (15)	1.15	1.17	1.17		1.26	1.45	1.36
MED (15)	1.30	1.31	1.36		1.40	1.60	1.50
MIMD (15)	0.24	0.26	0.26		0.29	0.31	0.29
MMED (15)	0.24	0.24	0.26		0.24	0.26	0.29
MIED (15)	0.37	0.38	0.40		0.38	0.40	0.42
MA (15)	102	99	101		93	90	94
CIX (15)	1.00	0.91	1.00		0.83	0.85	1.00
MIX (15)	1.33	1.32	1.32		1.29	1.38	1.42
PIX (15)	0.48	0.42	0.50		0.35	0.47	0.41

or less finger-like, proximally directed processes; base of antler-like branch attached to the rest of the coxite more strongly sclerotized. Cheirite (figs. 2d, 7e) shovel-shaped with a gradually tapering finger-shaped internal branch and a shorter, triangular outer branch; finger-shaped branch carrying an eaves-like ledge with a distal hook on its inner side; cheirite at base with a long, inner, frontolaterad, spiniform process.

Posterior gonopods fused with sternum into a podosternite (figs. 2f, 7f); distal part of podosternite with a tower-like top, consisting of lower anterior and higher posterior lobes, with warts on cranial side and a triangular lateral lobe proximal of anterior lobes; base of podosternite with a semi-circular exterior lobe on each side and a very small telopodite, latter consisting of two joints; podosternite proximally with a large area of reduced pigment.

female

Frons convex (figs. 5g-h); neither leg nor body modifications as in male. Relative lengths of anterior leg of 10th segment (fig. 6d) in relation to femur (coxa to tarsus): 0.36-0.05-1.00-0.36-0.29-1.00; length/width indices: 0.95-0.18-2.76-4.00-1.25-1.14-5.09.

Vulvae (figs. 4a-b) without a visible receptaculum; operculum arched, with a median ledge (fig. 4a-b); bursa with large, tooth-like projections in its inner part and a distal cavity, latter about 3 times longer than wide.

characters probably constant in most Chordeumatida, often varying in other orders of millipedes
Cheeks (= genae) laterally expanded and very prominent, not obviously divided into separate cardines and stipes, but with a groove on cephalic (dorsal) face instead of a separating line of other millipedes (figs. 5b-c, 5g-h). Head and genae densely setose, vertigial (= epicranial) suture well visible. Body segments open ventrally, without pilosity; macrochaetae of penultimate segment (fig. 5m) at posterior end; telson with anterior macrochaetae situated more cranially, at end with a pair of spinnerets, protruding from under the dorsal part of the telson (fig. 4l). Transverse suture between pro- and metazonite well developed; axial suture well developed. Ozopores absent. Labrum with 3 median teeth at anterior margin. Antennae with usual mammillate-conic, finely pointed hair on antennomere 7 (fig. 1a). Anal valve with 3 setae at margin (fig. 4l); subanal scale with 1+1 setae.

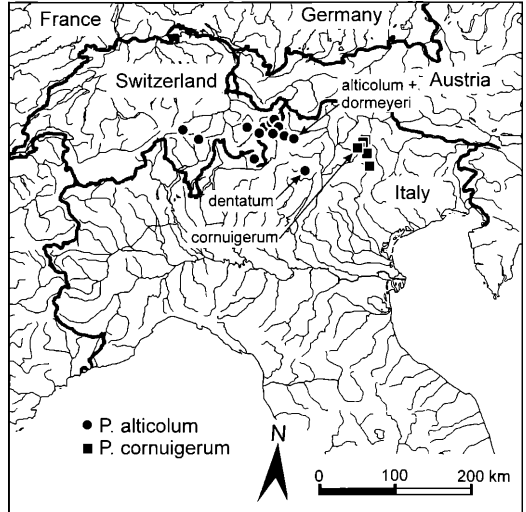


Figure 8: Distribution of the genus *Pterygophorosoma*.

8. Synopsis of the distribution of *Pterygophorosoma*

The localities where specimens of *Pterygophorosoma* have been collected are shown in fig. 8. During the excursion in September 1999, besides the locality "Schaubachhütte" the localities "Stilfserjoch" (Stilfserjochhütte and the northern slope of Mt. Scorluzzo) and "Langkofel" (T. Demetz-Hütte-Langkofelscharte) have been checked, unfortunately without positive result.

Pterygophorosoma alticolum (VERHOEFF, 1894)

The taxon *alticolum*:

Type locality: VERHOEFF (1894): 21

– "5 reife / und 4 / Pulli unter Steinen in der Umgebung der Schaubachhütte bei Suldern. 2650m.": co-ordinates (related to Schaubachhütte): 10.596° E, 46.491° N

VERHOEFF (1895): 219

– "?? verdanke ich meinem Freunde dem Faunisten Herrn Amtsrichter Carl Roettgen (Bonn), welcher dieselben auf dem Pic Padella bei Samaden (Schweiz) auffand.": co-ordinates (related to Albulapass): 9.842° E, 46.583° N. As a note (? from Verhoeff or Brolemann) on the material from the NMNHP shows, "Pic Padella" is identical with "Albulapass", the regular name of this locality in present German maps.

ROTHENBÜHLER (1901): 366

– "Mittelmoräne des Sordagletschers, Adulagruppe, 2800 m.": co-ordinates (related to route between Capanna Adula and Rheinwaldhorn): 9.031° E, 46.500° N

– "Lischannagebiet, Südseite wildes Hochgebirge, 2900m.": co-ordinates (related to *P. Lischana*): 9.873° E, 46.538° N

– "Val Triazza, über der lokalen Baumgrenze, 2300m., an einer Endmoräne.": according to the localities given for *Bergamosoma canestrinii*, Val Triazza is situated near Schuls, co-ordinates (related to Schuls): 10.301° E, 46.799° N

SCHUBART (1934): 128

– The author provides a raw geographical and ecological description of the presently known records.

ATTEMS (1949): 136

– “Z.: Sulden, Ostschweiz (Relikt).”: This is only a listing of the formerly published records.

– “Lv.: Euganeen.”: This record is mysterious. Apparently it does not belong to the “Collì Euganei” south of Verona, because these little mountains never reach alpine heights (601 m being highest altitude). Possibly it refers to a record of GANGLBAUER (KURNIK 1988). This is very likely, because the material of Ganglbauer is deposited in the Natural History Museum in Vienna (NHMW).

MORITZ & FISCHER (1974): 326

– “ZMB 1780 (1 /, Syntypus) – Tirol, VERHOEFF leg.”: In their list of the types kept in the Zoological Museum in Berlin (ZMHB), MORITZ & FISCHER (1974) as well listed the marks on the labels. From them it follows that labels made by Verhoeff, especially in his early years, were not very precise. The same has been observed concerning the Verhoeffian material housed at the Museum of Natural History in Karlsruhe (SMNK).

KURNIK (1988): 265

– “Schweiz: Piz Padella, 5 / NMW 1897, VERHOEFF leg.”: This series, kept at the Museum of Natural History in Vienna (NHMW), obviously belongs to the original series of VERHOEFF (1895).

– “Italien: Val di Leno, 1 / NMW 1903, Ganglbauer leg.”: A record of unknown location.

– “Brenta, Tosahütte, 2500 m, 4 / Thaler leg. 17.8.1985”: This record is identical with the record given for the taxon *dentigerum* by VERHOEFF (1901) (see below).

PEDROLI-CHRISTEN (1993):

– In her map the author shows a record that should be located above the tunnel of Gotthard. The record is not mentioned in the text, but the material has been deposited in the National Museum of Natural History in Paris (NMNHP). According to the data provided by J.-P. Mauriès, the record refers to a refuge called “Capanna di Caolimo”, situated in the Val Canaria at 2570 m a.s.l.; co-ordinates: 8.696° E, 46.572° N records from the National Museum of Natural History in Paris (NMNHP):

– “Suisse, Tessin, val Cavarria, Cabanna Caolimo, collecteur: A. Pedrolì, 12-08-87, 1 mâle, 1 fem.”: see above

– “Italie: Lombardia: Passo Caronelle, 20-09-1888, collecteur: Brolemann, HWB n° 283, 1 ?, 1 / “: A record of uncertain location, possibly referable to the village Carona in the Val Brembana or to one of the passes at the M. Corno Stella (9.807° E, 46.053° N). The fact that BRÖLEMANN collected nearby M. Corno Stella at the Passo di San Marco (9.622° E, 46.045° N, the type locality of *Pyrgocyphosoma dentatum*) would plead for this.

– “Italie: Lombardia: Passo Canciano (Val Malenco), 16-09-1888, collecteur: Brolemann, HWB n° 283, 1 mâle (disséqué par HWB), 3 mâles, 3 mâles j., 9 fem., 8 j. “: co-ordinates (related to P. Canciano): 10.000° E, 46.286° N

– “Suisse, Grisons, Pic Padella (Albua Pass), collecteur: Verhoeff, HWB n° 791, 1 fem.”: see above

The taxon *dentigerum*:

Type locality: VERHOEFF (1901): 106

– “Freund Roettgen verdanke ich 1 ?, 2/ von der Tosahütte.”: co-ordinates (related to Tosahütte): 10.901° E, 46.158° N

MORITZ & FISCHER (1974): 334

– “ZMB 12912 (1 ? : Gonopoden, 2 Beinpaare, Syntypus: Mikroskop. Präparat Nr. 594 Coll. Verhoeff) – Tosahütte, Tirol,

ROETTGEN leg.”: As this is the only male of VERHOEFF (1901) from the Tosahütte, it must be selected as lectotype.

The taxon *dormeyeri*:

Type locality: VERHOEFF (1911): 31

– “..., gesammelt in der Nachbarschaft der 2700 m hoch gelegenen Schaubachhütte am Ortler.”: co-ordinates (related to Schaubachhütte): 10.454° E, 46.529° N

VERHOEFF (1925): 67

– “Meinem Freunde Gerichtsrat Roettgen verdanke ich 6 ? u. 1 / der var. *excavatum* (und zwar *subvar. a* und *b*) welche er bei etwa 2700m im August 1909 am Stilferjoch sammelte, ? 13½ - 14½ mm lg.”: co-ordinates (related to Stilferjochhaus): 10.596° E, 46.491° N

BIGLER (1929): 14

– „Wo bei den Fundorten kein besonderes Datum angegeben ist, fällt dasselbe in die Zeit zwischen 10.-24.VII. 1918.”: If there is no date given, the material has been collected between 10.-24. July 1918.

– “Mittleres Val Mütschans, 2300 m, am steilen Grashang (8 ?, 3 /, 2 j. ? und / à 28 Sgm., 4 Juv. [1 ?, 3 /] a 26 und 1 Juv. à 19 Sgm.”: uncertain, but situated in the Swiss National Park

– “Murtaröl, 2300-2587 m (3 ?, 5 /, ein Pärchen in Copula)”: co-ordinates (related to P. Murtaröl): 10.290° E, 46.572° N

– “Hinteres Val Tantermozza und Nordgrat des Piz d’Esen, 2300-2800m (17 ?, 18 /, 15 Juv. [3 ?, 12 /] à 28, 1 à 26, 6 à 23, 2 à 19 Sgm.). In der Ritze eines Granitsteines wurden 9 Entwicklungsstadien von 19, 15, 11 u. 9 Sgm. gefunden und 3 Pärchen in Copula.”: co-ordinates (related to P. d’Esen): 10.063° E, 46.627° N

– “Val de Diavel, 2200m, 8.X.1919 (1 ?, 1 /).”: co-ordinates (related to P. dal Diavel): 10.141° E, 46.625° N

– “Kammübergang Murtèr, 2600m, Juli und Okt. (18 ?, 20 /, 10 Juv. à 28, 5 à 26 und 4 à 23 Sgm.).” co-ordinates (related to P. Murtèr): 10.246° E, 46.690° N

– “Mt. la Schera, 2400-2588 m (3 ?, 2 /, 3 Juv. à 28 Sgm.).”: co-ordinates (related to Munt la Schera): 10.211° E, 46.648° N

– “Val Ftur, 2700m (2 ?, 1 /) und 2100m (je 2 Juv. à 26 und 26 Sgm.).” : uncertain, but situated in the Swiss National Park

– “Val Tavrù und Mot de Gaier, 2260-2600 m (2 ?, 6 /, 2 Juv. à 26 Sgm.).” co-ordinates (related to P. Tavrù): 10.298° E, 46.688° N

– “Am Munt della Bês-cha (nördlich Ofenpaßhöhe), 2500m (3 ?, 3 /, 1 Juv. à 28 Sgm.).”: co-ordinates (related to north of Ofenpaß): 10.298° E, 46.650° N. BIGLER (1929) explicitly emphasised the location to be north of the Ofenpaß. This he certainly did to avoid confusion with the Munt da la Bês-cha (determined co-ordinates 9.918° E, 46.511° N) north of Pontresina.

– “Val Sesvenna, 2600-2700m (3 ?, 5 /):” co-ordinates (related to P. Sesvenna): 10.404° E, 46.708° N

– “Bei Punkt 2784,21 südöstlich von St. Maria, 2700-2780m (2 ?, 5 /, 5 Juv. à 28, 1 à 26 Sgm.).”: co-ordinates (related to P. Mischuns): 10.488° E, 46.582° N

– “Fuorcla Saßalb (nördlich Lü), 2500m (2 ?, 1 /).” co-ordinates (related to P. Terza): 10.399° E, 46.645° N

DETHIER & PEDROLI-CHRISTEN (1983): 373

– “De 1977 à 1980, nous avons étudié un *Caricetum firmae* (KERNER) BR.-BL. ou «*Firmetum*» situé sur le plateau sommital du Munt La Schera (2540m).”: see above

THALER (1989): 100

– “Südtirol: Ortler A., Mt. Scorluzzo 3000-3090m (4 ? 4/; 17 Juli 1987).”: co-ordinates (related to Mt. Scorluzzo): 10.441° E, 46.524° N

***Pterygophorosoma cornuigerum* (VERHOEFF, 1900)**

Type locality: VERHOEFF (1900): 284

– “1 ? 1 / und 2 Junge wurden in 2600m Höhe von meinem Freunde C. Roettgen im sog. „Gartl“, einer Partie im Rosengarten, erbeutet.”: co-ordinates (related to Gartlhütte): 11.622° E, 46.460° N

VERHOEFF (1901): 105

– “Langkofelhütte, ...”: co-ordinates (related to Langkofelhütte, 2253 m): 11.721° E, 46.520° N

– “Contrinhütte, ...”: co-ordinates (related to Contrinhütte, 2016 m): 11.818° E, 46.431° N

– “Regensburger Hütte (1 Paar in Copula, Juli) (ROETTGEN)”: co-ordinates (related to Regensburger Hütte, 2037 m): 11.760° E, 46.591° N

VERHOEFF (1925): 65-66

– “habe ich später noch in mehreren Stücken ebenfalls durch meinen Freund Gerichtsrat ROETTGEN (Coblenz) erhalten und zwar 1 ? von 11½ mm, von der Vajoletthütte...”: co-ordinates (related to Vajoletthütte): 11.632° E, 46.460° N

– “...sowie 1 ?, 2 / und eine Larve von der Mulazhütte in der Nordpalagruppe der Dolomiten, ? 11½, / 12 mm lg.”: co-ordinates (related to Rif. Mulaz, 2560 m): 11.836° E, 46.312° N

– “Aus dem oberen Val grande der Nordpala erhielt ich ebenfalls ein Pärchen, ...”: exact locality uncertain, but probably near Mulazhütte

ATTEMS (1949): 136

– “Lv.: Dolomiten: Rosengarten, Langkofelhütte, Vajoletthütte, Palagruppe.”: only a list of previously known records.

MORITZ & FISCHER (1974): 333

– “ZMB 2380 (1 /, 1 juv. /, Syntypen) – Tirol, alpin, ROETTGEN leg.”: see under *P. alticolum*

– “ZMB 12911a (1 ? : 1. bis 7, Beinpaar, Syntypus: Mikroskop. Präparat Nr. 595 Coll. VERHOEFF) – “im Gartl”, Tirol.”: As this is the only male of VERHOEFF (1900), it must be selected as lectotype.

KURNIK (1988): 266

– “Italien: Dolomiten, Langkofelhütte, 1 / NMW 19101, VERHOEFF leg.”: The single female studied by KURNIK (1988), from the Natural History Museum in Vienna, obviously belongs to the original series of VERHOEFF (1901).

9. Ecology of the genus *Pterygophorosoma*

Nearly all specimens I have managed to find myself were taken at once in a depression on a slope of northern exposure, just before the ascent, under stones. Only three juveniles have been collected outside this depression, but on the same northern slope under stones as well. In several places chordeumatidans have been observed as preferring to occur under large stones/boulders at the base of depressions. These locations are very cool and only a few plants, largely mosses, grow there. Chordeumatidans would best be found there before sunrise or during sunset. As soon as sunbeams reach the place, the chordeumatidans disappear into deeper layers. As it is mostly inevitable to collect during daytime, because the ascent takes its time, these depressions, which the sun did not reach, are the most promising localities then.

During my sampling on 15.09.1999, no other millipedes were recorded around Schaubachhütte. In contrast, VERHOEFF (1894) emphasised that *Mastigona mutabile* occasionally occurred there too, and he was also able to collect a juvenile female of *Atractosoma meridionale* nearby.

BIGLER (1929) confirmed VERHOEFF's (1911) opinion that *Pterygophorosoma* is a genus of the alpine region: “I have found this animal only under stones above the timberline. From my data I can confirm VERHOEFF's point of view to call them alpine animals. The best places to collect them were situated near spots of snow, where the melted snow has caused heavy moisture at the substrate. Several times I found them there in copulation.”

(Original: „Das Tierchen habe ich immer nur oberhalb der Waldgrenze unter Steinen gefunden. Ich kann VERHOEFFS Bezeichnung der Orotrechosomen als Alpentiere für meine Vertreter durchaus bestätigen. In nächster Nähe von Schneeflecken, auf vom Schmelzwasser total durchfeuchteter Unterlage war die Ausbeute immer am reichsten. Zu verschiedenen Malen habe ich gerade an solchen Stellen kopulierende Pärchen getroffen“).

PEDROLI-CHRISTEN (1993) recorded *Pterygophorosoma* between 2000 and 2900 m a.s.l. Most of the records belong to localities above 2500m. The animals have been found there from June to October, occurring mainly in July. In their paper on the fauna of the Munt La Schera, DETHIER & PEDROLI-CHRISTEN (1983) reported *P. alticolum* from *Firmetum typicum* and *Elynetum* plant communities.

Unfortunately, we have no ecological information about *P. cornuigerum*. The reason is, that Verhoeff did not collect material by himself. The records suggest this species occurs in habitats similar to those of *P. alticolum*. In contrast, the majority of the records are situated distinctly lower, between 2000 and 2100 m a.s.l.

10. Discussion

Although it was not possible to recollect material of *P. cornuigerum*, there is no doubt that this is a different species. VERHOEFF (1925) explicitly stressed low variability in the gonopods between males from different localities in this species. The differences given for the vulvae of both species partly result from a misinterpretation by KURNIK (1988). The author did not recognise the long, distal central structure as being a cavity as well (fig. 4a-b). In *P. alticolum* this cavity is about 3 times longer than wide and directed inward. In *P. cornuigerum* it is distinctly wider than long and truncate distally. The new interpretation emphasises the close relationship of both species. They are distinguished from other members of the family Craspedosomatidae by the ledge of the operculum, the denticles in the central part of the bursa, and the distal cavity.

In contrast to *P. cornuigerum*, *P. alticolum* shows considerable variation. Yet the early description of *alticolum* (VERHOEFF 1896) rather reflects the lower quality of the author's drawings than real differences. BIGLER (1929) already pointed out that the description of the male of *P. alticolum* might be incorrect, while that of the taxon *dormeyeri* shows the correct relations. According to BIGLER (1929), VERHOEFF (1896) mistook the anterior and posterior lobe of the podosternite in his description. My own preparations of the antler-like branch in a strict caudal view also show exactly the relations given for *dormeyeri*: at the end with a bulgy curvature and outwards with a deep inlet and a bulge behind it.

VERHOEFF (1925) already noticed considerable variation in shape of the podosternite in the taxon *dormeyeri*. In fact his var. *excavatum* is easily explicable by a ventrocaudal, not strictly ventral view, while his subvarieties (fig. 3g-h) reflect a real difference. My own preparations in strict cranial view hardly reveal any variation. They correspond to fig. 3f given by VERHOEFF (1911).

The study material clearly shows that both *alticolum* and *dormeyeri* represent the same taxon distributed both in the Ortler Massif and Engadine, Swiss National Park.

The taxon *dentigerum* still requires topotypoids to be taken to solve its status. The distant type locality and the triangular posterior lobes of the podosternite seem to favour its independent taxonomic position. The widened distal lobe with its upper finger-like process set low at its base might either reflect a real difference or a ventrocaudal aspect.

Acknowledgments

Dr. ARIANE PEDROLI-CHRISTEN (Neuchâtel) kindly provided material for comparative studies and JEAN-PAUL MAURIÉS (Paris) gave information about the collection of the MNHP. Prof. Dr. SERGEI GOLOVATCH (Moscow) carefully checked the whole manuscript in respect of taxonomy and linguistics. As well he provided several helpful discussions on millipede taxonomy during the last eleven years. He. The excursion of the author was partly supported by the VON-KETTNER-Stiftung, Karlsruhe.

11. Literature

- ATTEMS, C. (1926): Progoneata – In: KÜKENTHAL, W., KRUMBACH, T. (eds.): Handbuch der Zoologie. Bd. 4,1: 7-238; Berlin.
- ATTEMS, C. (1949): Die Myriopodenfauna der Ostalpen – Sitzungsberichte der österreichischen Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Klassen, I, 158: 79-153.
- ATTEMS, C. (1959): Die Myriopoden der Höhlen der Balkanhalbinsel. Nach dem Material der "Biospeologica balcanica" – Annalen des Naturhistorischen Museums in Wien, 63: 281-406.
- BIGLER, W. (1929): Die Diplopodenfauna des schweizerischen Nationalparks – Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark, 5: I-VII, 1-87
- BRÖLEMANN, H. W. & LICHTENSTEIN, J. L. (1919): Les vulves des Diplopodes – Archives de Zoologie expérimentale et générale, 58 (4): 173-218.
- COOK, O. F. & COLLINS, G. N. (1895): The Craspedosomatidae, of North America – Annals of the New York Academy of Sciences, 9: 1-100.
- DETHIER, M. & PEDROLI-CHRISTEN, A. (1983): Diplopodes et Chilopodes d'une pelouse alpine au Parc national suisse – Bull. Soc. vaud. Sc. nat., 76 (364): 373-379.
- ENGHOFF, H. (1979): Taxonomic significance of the mandibles in the millipede order Julida – In: CAMATINI, M. (ed.): Myriapod biology: 27-38; London.
- ENGHOFF, H. (1982): The millipede genus *Cylindroiulus* on Madeira – an insular species swarm (Diplopoda, Julida: Julidae) – Entomologica Scandinavica, Supplement, 18: 1-142.
- ENGHOFF, H. (1992): *Dolichoziulus* – a mostly Macaronesian multitude of millipedes. With the description of a related new genus from Tenerife, Canary Islands (Diplopoda, Julida, Julidae) – Entomologica Scandinavica, Supplement, 40: 1-158.
- FODDAI, D., MINELLI, A., SCHELLER, U. & ZAPPAROLI, M. (1995): Chilopoda, Diplopoda, Paupopoda, Symphyla – In: MINELLI, A., RUFFO, S., LA POSTA, S.: Checklist delle specie della fauna italiana, 32: 1-35; Bologna.
- HOFFMAN, R. L. (1980): Classification of the Diplopoda. 1-237; Genève.
- KÖHLER, H. R. & ALBERTI, G. (1990): Morphology of the mandibles in the millipedes (Diplopoda, Arthropoda) – Zoologica Scripta, 19: 195-202.
- KURNIK, I. (1988): Zur Taxonomie ostalpiner Chordeumatida: Vulvenmorphologie und Identifikation der Weibchen – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, 115: 229-302.
- MORITZ, M. & FISCHER, S. C. (1974): Die Typen der Myriopoden-Sammlung des Zoologischen Museums Berlin. I. Diplopoda. Teil 2 – Mitteilungen aus dem Zoologischen Museum in Berlin, 50 (2): 323-375.
- PEDROLI-CHRISTEN, A. (1993): Faunistik der Tausendfüßler der Schweiz (Diplopoda) – Documenta Faunistica Helvetiae, 14: 1-167
- PORATH, C. O. (1872): Myriopoda Africae australis in Museo Regio Holmiensis asservata. II. Diplopoda – Öfversigt Kongl. Vetenskaps-Akademie Förhandlingar, 29 (5): 3-46.
- RIBAULT, H. (1913): Biospeologica XXVIII. AscospERMOPHORA (Myriopodes) – Archives de Zoologie expérimentale et générale, 5e sér., 10: 399-478.
- ROTHENBÜHLER, H. (1901): Fauna der Rhätischen Alpen. 1. Beitrag. Myriopoden Graubündens besonders des Engadins und des Münsterthales – Revue suisse de Zoologie, 9: 357-377
- SCHMIDT, D. (1962): Über die taxionomische Wertigkeit von Strukturen des Metazonit-Hinterrandes bei Diplopoden – Senckenbergiana biologica, 43 (1): 65-80.
- SCHUBART, O. (1934): Tausendfüßler oder Myriapoda. I: Diplopoda – In: Die Tierwelt Deutschlands, 28: 1-318; Jena.
- SHEAR, W. A. (1972): Studies in the milliped order Chordeumida (Diplopoda). A revision of the family Cleidogonidae and a reclassification of the order Chordeumida in the New World. - Bull. Mus. Comp. Zool. Harvard, 144: 151-352.
- SPELDA, J. (1999a): Verbreitungsmuster und Taxonomie der Chilopoda und Diplopoda Südwestdeutschlands. Diskriminanzanalytische Verfahren zur Trennung von Arten und Unterarten am Beispiel der Gattung *Rhymogona* Cook, 1896

- (Diplopoda: Chordeumatida: Craspedosomatidae) – Ph. D. Thesis, University of Ulm. Part 1: 217 pp. Part 2: 324 pp.
- STRASSER, K. & MINELLI, A. (1984): Elenco dei Diplopodi d'Italia – Lavori, Soc. Ven. Sc. nat., **9** (2): 193-212.
- THALER, K. (1989): Streufunde nivaler Arthropoden in den mittleren Ostalpen – Ber. nat.-med. Verein Innsbruck, **76**: 99-106.
- VERHOEFF, K. W. (1894): Beiträge zur Diplopoden-Fauna Tirols – Verhandlungen der zoologisch-botanischen Gesellschaft in Wien, **44**: 9-43.
- VERHOEFF, K. W. (1895): Aphorismen zur Biologie, Morphologie, Gattungs- und Art-Systematik der Diplopoden – Zoologischer Anzeiger, **18**: 203-244.
- VERHOEFF, K. W. (1896): Über Diplopoden Tirols, der Ostalpen und anderer Gegenden Europas, nebst vergleichend-morphologischen und biologischen Beobachtungen – Archiv für Naturgeschichte, **62** (3): 187-242.
- VERHOEFF, K. W. (1897): Über Diplopoden aus Bosnien, Herzegowina und Dalmatien. 1. Theil: Polydesmidae; II. u. III. Theil: Chordeumidae und Lysiopetalidae – Archiv für Naturgeschichte, **63** (1): 139-204.
- VERHOEFF, K. W. (1900): Zur vergleichenden Morphologie, Phylogenie, Gruppen- und Art-Systematik der Ascospermyiophora. (Beiträge zur Kenntniss paläarktischer Myriopoden 13) – Archiv für Naturgeschichte, **66** (1): 347-402.
- VERHOEFF, K. W. (1901): Über Diplopoden aus Süddeutschland und Tirol. Beiträge zur Kenntnis paläarktischer Myriopoden 18 – Jahresheft des Vereins für vaterländische Naturkunde in Württemberg, **57**: 81-111.
- VERHOEFF, K. W. (1910): Über Diplopoden. 17. Deutsche Craspedosomiden – Sitzungsberichte der Gesellschaft naturforschender Freunde in Berlin, **1910**: 19-62.
- VERHOEFF, K. W. (1911): Über Diplopoden. 44. Aufsatz: Zur Kenntnis der Craspedosomiden-Gattungen *Helvetiosoma* und *Orotrechosoma* – Zoologischer Anzeiger, **38**: 17-31.
- VERHOEFF, K. W. (1925): Neue Diplopoden-Beiträge. 95. Diplopoden-Aufsatz – Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, **50**: 61-122.
- VERHOEFF, K. W. (1926-1932): Diplopoda, Teil I und II – In: BRONN, H. G. (ed.): Klassen und Ordnungen des Tierreichs, Bd. 5, Abt. 2. 2084 S.; Leipzig.
- VERHOEFF, K. W. (1934): Oberklasse Progoneata (Diplopoda, Symphyla, Pauropoda); Oberklasse Opisthogoneata (Chilopoda) – In: BROHMER, P., EHRMANN, P., ULMER, G.: Die Tierwelt Mitteleuropas. **2** (3): 120 S.; Leipzig.

JÖRG SPELDA

Faunistic investigations on the soil fauna at the Muellertal (Luxembourg): Chilopoda, Diplopoda, Isopoda, Opiliones

Abstract

The results of a faunistic survey, made in 1998 - 1999 at the Muellertal / Grand Duchy of Luxembourg by Prof. Dr. LUDWIG BECK and his collaborators are presented. The investigated sites showed a rich millipede fauna in relation to the sandy soil there.

Kurzfassung

Faunistische Untersuchungen der Bodenfauna im Müllertal (Luxemburg): Chilopoda, Diplopoda, Isopoda, Opiliones
Im vorliegenden Artikel wird über Ergebnisse einer faunistischen Untersuchung der Bodenfauna berichtet, die in den Jahren 1998 - 1999 von Prof. Dr. LUDWIG BECK und seiner Arbeitsgruppe im Müllertal in Luxemburg durchgeführt wurden. Die Untersuchung ergab eine angesichts des Sandbodens des Gebietes reiche Fauna der genannten Gruppen.

Author

Dr. JÖRG SPELDA, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe.

Key words

Faunistics, Chilopoda, Diplopoda, Isopoda, Opiliones, Muellertal / Luxembourg

1. Introduction

During the last few years the National Museum of Natural History in Luxembourg under the direction of MARC MEYER has carried out an intensive survey of the fauna of the natural reserve "Muellertal" southwest of Echternach. For this reason the soil zoological working group of the National Museum of Natural History in Karlsruhe under the leadership of Prof. Dr. LUDWIG BECK was invited to study several groups of the soil fauna. Three excursions have been made to obtain soil samples. The author of the present paper took part in two of these investigations and used the opportunity to collect additional samples by hand. The faunistic results on centipedes, millipedes, woodlice and harvestmen are presented in this paper.

2. Materials and Methods

The Muellertal is a mountainous area that consists of sandstone rocks of the Lower Jurassic (Lias). Three different sites in the Muellertal were visited during each excursion (tab. 1). At a fourth site (LXMP) only the author of the present paper made

a collection and no abiotic parameters were measured. There is a gradient in moisture from LXP (dry) over LXM to LXS (wet). The two excursions, in which the author participated, took place on 21.10.1998 and 20.10.1999. At two sites (LXM, LXP) soil samples and handsorting were both carried out. At each site the author made manual collections lasting approximately one hour. At the site LXM the author sampled as well a spruce forest (*Picea abies*-monoculture), which was disregarded by the regular sampling.

The numbers of individuals are given in the scheme males/females or males/females/juveniles or males/females/juvenile males/juvenile females. If no dash is given (*Cryptops parisi*) the sex has not been determined (tab. 2).

3. Results

A total of 11 species of centipedes, 12 species of millipedes, 8 species of woodlice and 2 species of harvestmen were caught at the three investigated sites (tab. 4).

The centipede community is typical for mountainous sites. This is shown by the dominance of *Lithobius macilentus* and in comparison the rarity of *L. mutabilis*. The ratio of these two species characterises a chilopod community as either mountainous (*L. macilentus* dominant) or continental (*L. mutabilis* dominant, SPELDA 1999a, 1999b). FRÜND (1991) derives the difference in dominance from differences in precipitation. Another species playing an important role in the centipede community was *Cryptops parisi*. The presence of this species instead of *C. hortensis* shows that there are cooler conditions, although, as well as *L. dentatus*, this species avoids very cold areas (SPELDA 1999a). The geophilids show a characteristic species-spectrum of cooler woodland sites too.

The millipede community consists of members of all four large millipede orders. It is dominated by julids. The species spectrum suggests a richer soil, as demonstrated by the presence of *Polydesmus angustus* instead of *P. denticulatus* and the dominance of *Tachypodoiulus niger* instead of *Julus scandinavicus*. As well julids are less important on very poor sites (SPELDA 1999c).

The occurrence of several Western European species (*Cylindroiulus punctatus*, *Melogona gallica*) shows that the sites are influenced by Atlantic conditions.

The occurrence of *Leptoilulus simplex* is remarkable.

Table 1. Description of the four investigated sites.

abbreviation	LXM	LXMP	LXP	LXS
location	Muellertal, Mardelle, 3 km SW Berdorf, 7 km WNW Echternach	Muellertal, Mardelle, 3 km SW Berdorf, 7 km WNW Echternach	Muellertal, Predigtstuhl, 1 km SW Berdorf, 6 km WNW Echternach	Muellertal, „Schluchtwald“, 3 km SW Berdorf 7 km WNW Echternach
co-ordinates	06°19' E 49°48' N	06°19' E 49°48' N	06°19' E 49°48' N	06°19' E 49°48' N
exposition	< 5°		NNW / 5-30°	W / 20-40°
floristic associations	Galio-Fagetum	Piceetum	Luzulo-Fagetum	Galio-Fagetum
soil type	sandy, somewhat loamy		sandy	sandy, somewhat loamy
humus type	mull-moder to moder		moder	mull-moder to moder
pH litter (CaCl ₂)	4,2 (3,6-4,0)		3,6 (2,9-4,7)	5,3 (5,1-5,7)
pH upper soil (CaCl ₂)	3,6 (3,3-4,0)		2,9 (2,8-3,2)	4,7 (3,8-5,5)

This mountainous Pleistocene relict reaches its north-western border in Belgium (Ardennes) and Luxembourg. It has already been recorded for Luxembourg by REMY & HOFFMANN (1959) and KIME (1994).

Orthochordeumella pallida is sometimes said to be an Atlantic species too. More recent faunistic investigations have shown that this species occurs as well, in a very localised way, in Central Europe (FRÜND & RUSZOWSKI 1989, SPELDA 1999a). The explanation for this strange distribution might be the competition with *Mycogona germanica*, which is very common in Central Europe but mostly missing from areas where *Orthochordeumella* species occur. It might be possible that *O. pallida* was widely distributed in Central Europe once in the past but has been replaced in most areas. Only on very few sites have relict populations survived until present time. In this respect the absence of *M. germanica* in the samples is remarkable, although the species has been recorded from Luxembourg, even near Echternach (REMY & HOFFMANN 1959).

The woodlice show a species spectrum characteristic of regular woodlands. The dominance of *Oniscus asellus* at the Predigtstuhl suggests somewhat disturbed conditions. With *Porcellio monticola* an Atlantic element is present in the woodlouse community.

The fauna of harvestmen was surprisingly poor. Only the species *Lophopilio palpinalis* and *Oligolophus tridens* have been found, each as a single specimen each in 1998 at the site LXM. Although these two species are among the most common litter-dwelling opiloidids, *Nemastoma lugubre* and *Paranemastoma quadripunctatum* might have been expected too. At the other sites and in the captures of 1999 no harvestmen were found.

The site LXM was distinctly richer in both chilopod and diplopod species (tab. 4). The sites LXP and LXS showed similar species numbers and composition. This is not too surprising, as both are neighbouring slopes. In contrast LXM contains more different level parts (tab. 1).

Both excursions have been made during the second

half of October at nearly the same date. As well the climatic conditions were more or less comparable. This gives the opportunity to check if a single sample is representative for the composition of the community. Differences in the captures might result from either community changes or stochastic effects. Differences in low numbers might be mostly the result of the latter. If the sampling is insufficient there will be a species change between two collections.

If all the data of one year is pooled (except for LXMP, which has only been collected in one year) the species numbers of both years deviate only slightly from each other (tab. 4). In the diplopods even the total number of specimens seems to be nearly the same. Both *Glomeris* species and *Tachypodoiulus niger* occurred in both years on all sites. *Allaiulus nitidus* was only missing at LXMP. In 1998 the julids *T. niger* and *A. nitidus*, in 1999 the chordeumatids *Craspedosoma rawlinsii* and *Chordeuma sylvestre* have been collected in distinctly higher numbers (tab. 3). This change in abundance might be interpreted as the result of cooler conditions in 1999.

The centipede numbers of the different years cannot be compared which each other in the same way, because many specimen in the samples of the year 1998 had unfortunately been broken, making the lithobiids undeterminable. Nevertheless it is obvious that *C. parisi* was more common in 1998.

Beside these changes in abundance there is a high correspondence between the collections of both years. If a species occurred in one year at numbers higher than seven (a critical number in statistics, see SPELDA 1996) it has normally been found in the other year too. The only exception might be *Oniscus asellus* at the site LXM. But as *O. asellus* tends to aggregate, this should not be rated too high. In both years *O. asellus* was a dominant woodlouse at the site LXP.

Table 2. Number of centipedes, millipedes, woodlice and harvestmen found at the Muellertal at the different sites in two different years.

Site Date	LXM 1998	LXMP 1998	LXM 1999	LXP 1998	LXP 1999	LXS 1998	LXS 1999
Chilopoda							
Lithobiidae							
<i>Lithobius aeruginosus</i>	.	0/0/0/1	1/0	0/1	0/1	.	.
<i>Lithobius crassipes</i>	.	1/1	0/2
<i>Lithobius dentatus</i>	.	0/1	0/5	0/1	2/5	.	2/0
<i>Lithobius macilentus</i>	0/1	.	2/3/2/0	.	1/0/1/0	.	.
<i>Lithobius mutabilis</i>	.	.	1/0
<i>Lithobius piceus</i>	0/1
<i>Lithobius tricuspis</i>	2/0	.	1/1	0/3	2/0	.	1/0
Cryptopidae							
<i>Cryptops parisi</i>	5	.	2	3	6	3	.
Geophilidae							
<i>Geophilus alpinus</i>	0/0/0/1	.	.	.	1/2	.	.
<i>Strigamia acuminata</i>	0/1	.	0/1
<i>Strigamia crassipes</i>	.	1/0
Diplopoda							
Glomeridae							
<i>Glomeris intermedia</i>	4/12	1/1	2/7	2/1	0/1	0/2	1/4
<i>Glomeris marginata</i>	1/6/0/1	0/1	2/4 2/2/1	3/5	2/3/2/0	1/8	.
Julidae							
<i>Julus scandinavicus</i>	0/2	.	1/1
<i>Leptoziulus simplex</i>	0/1	.	0/1	1/0	1/2	0/4	2/1
<i>Allajulus nitidus</i>	4/8/0/4	4/4	10/6/0/1	0/3/1/0	1/6/0/3	3/1	.
<i>Cylindroiulus punctatus</i>	.	0/1	1/0	.	1/2/1/0	.	0/2/1/0
<i>Tachypodoiulus niger</i>	1/4/3/0	4/8/2/0	3/4/1/2	3/13/9/1	2/5/1/0	1/3 0/2	.
Craspedosomatidae							
<i>Craspedosoma rawlinsii alemannicum</i>	1/1	2/1	7/2	.	1/4/1	1/0	.
Chordeumatidae							
<i>Chordeuma sylvestre</i>	1/1	.	4/8/2	1/3	0/2/1	0/1	.
<i>Melogona gallica</i>	1/0/0/1
<i>Orthochordeumella pallida</i>	0/1
Polydesmidae							
<i>Polydesmus angustus</i>	0/1	0/1	2/0	.	1/1	0/1	1/1
Isopoda							
Ligiidae							
<i>Ligidium hypnorum</i>	0/2	0/1	.
Trichoniscidae							
<i>Trichoniscus pusillus</i>	0/1	.	.	.	0/2	.	.
Oniscidae							
<i>Oniscus asellus</i>	.	1/2	4/7	3/3/1/0	3/3 1/1	1/0	.
<i>Philoscia</i> sp.	.	.	0/1
Porcellionidae							
<i>Porcellio monticola</i>	.	1/0
<i>Porcellium conspersum</i>	0/1

Table 3. Sum of centipedes, millipedes and woodlice found at the Muellertal in the different years (sites LXM, LXP, LXS pooled) and the different sites (both years pooled). Only species with at least seven collected specimens are treated.

date / site	1998	1999	LXM	LXMP	LXP	LXS
Chilopoda						
<i>Lithobius dentatus</i>	2	14	5	1	8	2
<i>Lithobius macilentus</i>	1	9	8	0	2	0
<i>Lithobius tricuspis</i>	5	5	4	0	5	1
<i>Cryptops parisi</i>	11	7	7	0	9	3
Diplopoda						
<i>Glomeris intermedia</i>	21	15	25	2	4	7
<i>Glomeris marginata</i>	20	23	14	1	13	16
<i>Leptoiulus simplex</i>	6	7	2	0	4	7
<i>Allajulus nitidus</i>	43	12	24	0	21	14
<i>Cylindroiulus punctatus</i>	0	8	1	1	4	3
<i>Tachypodoiulus niger</i>	38	20	18	14	34	6
<i>Craspedosoma rawlinsii alemannicum</i>	3	15	11	3	6	1
<i>Chordeuma sylvestre</i>	7	17	16	0	7	1
<i>Polydesmus angustus</i>	3	6	3	1	2	3
Isopoda						
<i>Oniscus asellus</i>	9	18	11	3	13	3

4. Discussion

REMY & HOFFMAN (1959) recorded 28 species of centipedes from Luxembourg, some of them remarkable thermophile or Atlantic faunistic elements not known in Germany (*Himantarium gabrielis*, *Dignathodon microcephalum*, *Gnathomerium inopinatum*). It was remarkable that nevertheless two species (*Lithobius aeruginosus*, *L. mutabilis*) have been recorded additionally. *L. aeruginosus* occurs in Germany and the southern part of the Netherlands (BERG 1995). For that reason its occurrence is not surprising. *L. mutabilis* is a continental species that does not occur in western Europe (compare BRÖLEMANN 1930, EASON 1964, BERG 1995). It probably reaches its western border at Luxembourg. *Geophilus alpinus*, formerly known as *G. insculptus* (SPELDA 1999a) has been confused with *G. proximus* (REMY & HOFFMANN 1959) belong in fact to *G. alpinus*.

The Grand-Duchy of Luxembourg is famous for the occurrence of several thermophilous millipedes (*Ommatoiulus rutilans*, *Stosatea italica*) too, but these are confined to limestone areas (REMY & HOFFMANN 1959,

KIME 1994, KIME 1996). REMY & HOFFMAN (1959) listed 36 species of millipedes for Luxembourg. One of them (*Craspedosoma alemannicum*) is now regarded as a subspecies of *C. rawlinsii* (SPELDA 1991). As KIME (1996) discovered *Orthochordeumella pallida* in Luxembourg, the list still stands at 36.

As the Muellertal is a mountainous woodland with sandy soil, a poorer fauna than in limestone areas is to be expected. For such an area the millipede fauna is quite rich. The reason might be that the Lias-sandstone contains a higher amount of calcium, thus having a higher pH and therefore supporting a richer soil fauna. Although the number of collected animals was low, compared with the investigations of KIME (1994, 1996) it can be assumed that the species composition has been recorded quite completely.

For the woodlice and harvestmen the lack of comparable data does not allow a more detailed analysis of the species community. Generally it is in correspondence with other investigations in western Central Europe.

Table 4. Number of species in centipedes, millipedes, woodlice and harvestmen found at the Muellertal in the different years (sites LXM, LXP, LXS pooled) and the different sites (both years pooled).

date / site	1998	1999	LXM	LXMP	LXP	LXS	total
Chilopoda	8	8	8	4	6	5	11
Diplopoda	11	10	12	6	9	9	12
Isopoda	5	4	4	3	4	3	8
Opiliones	1	0	1	1	0	0	2

Acknowledgements

Both Dr. JÖRG RÖMBKE (Flörsheim) and Dr. RICHARD DESMOND KIME (Brussels) kindly checked the manuscript and suggested several important improvements.

5. Literature

- BERG, M. P. (1995): Preliminary atlas of the centipedes of the Netherlands. – Communication EIS-Nederland, **78**: 1-60.
- BRÖLEMANN, H. W. (1930): Elements d'une faune des Myriapodes de France. Chilopodes. – 405 pp.; Toulouse.
- EASON, E. H. (1964): Centipedes of the British Isles. – 294 pp.; London, New York.
- FRÜND, H.-C. (1991): Zur Biologie eines Buchenwaldbodens. 14. Die Hundertfüßer (*Chilopoda*). – *Carolinea*, **49**: 83-94.
- FRÜND, H.-C. & RUSZOWSKI, B. (1989): Untersuchung zur Biologie städtischer Böden. 4. Regenwürmer, Asseln und Diplopoden. – *Verhandlungen der Gesellschaft für Ökologie*, **18**: 193-200.
- KIME, R. D. (1994): Millipedes (Diplopoda) found in and around hedges in Luxembourg. – *Bull. Soc. Nat. luxemb.*, **95**: 349-357.
- KIME, R. D. (1996): Millipedes recorded in the Grand Duchy of Luxembourg. – *Mémoires du Muséum nationale d'histoire naturelle*, **169**: 257-263.
- REMY, P. & HOFFMANN, J. (1959): Faune des Myriapodes du Grand-Duché de Luxembourg. – *Archives Institut Grand-Duchal Luxembourg, Section des Sciences naturelles, physiques et mathématiques, N.S.*, **25**: 199-236.
- SPELDA, J. (1991): Zur Faunistik und Systematik der Tausendfüßler (Myriapoda) Südwestdeutschlands. – *Jh. Ges. Naturkde. Württemberg*, **146**: 211-232.
- SPELDA, J. (1996): Die Hundert- und Tausendfüßerfauna von Wacholderheiden im Landkreis Calw und ihre Reaktion auf unterschiedliche Pflegemaßnahmen (Chilopoda, Diplopoda). – *Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ.*, **88**: 289-320.
- SPELDA, J. (1999a): Verbreitungsmuster und Taxonomie der Chilopoda und Diplopoda Südwestdeutschlands. Diskriminanzanalytische Verfahren zur Trennung von Arten und Unterarten am Beispiel der Gattung *Rhymogona* COOK, 1896 (Diplopoda: Chordeumatida: Craspedosomatidae). – Part 1: 217 pp. Part 2: 324 pp.; Ulm (Ph. D. Thesis, University of Ulm).
- SPELDA, J. (1999b): Ökologische Differenzierung südwestdeutscher Steinläufer (Chilopoda: Lithobiida). – *Verhandlungen der Gesellschaft für Ökologie*, **29**: 389-395.
- SPELDA, J. (1999c): Die Hundert- und Tausendfüßerfauna zweier Naturwaldreservate in Hessen (Myriapoda: Chilopoda, Diplopoda). – *Carolinea*, **57**: 101-110.

MOSADOLUWA ADETOLA BADEJO, STEFFEN WOAS & LUDWIG BECK

Atropacarus (Hoplophorella) nigeriensis, a new species of phtiracarid mite (Acari, Oribatida) from Nigeria

Abstract

This paper is the first of a series in which more information will be added to the existing on biogeographical distribution of oribatid mites. Here we describe a new species of a phtiracarid mite collected from forest floor litter in southwestern Nigeria. Differences between this species, *Atropacarus (Hoplophorella) nigeriensis*, and other *Hoplophorella* species are the foveoli on the aspis and notogaster, the shape of notogastric setae, as well as shapes and chaetotaxy of the genital and anal plates. More differences in taxonomically important features such as the morphological features of the infracapitulum and epimeron as well as leg chaetotaxy between this species and others could not be determined, not only because of lack of information on the latter in literature, but also because many type specimens are not available for dissection which must be done in order to reveal fine morphological details. *Atropacarus (Hoplophorella) nigeriensis* belongs to the "cucullata" group of *Hoplophorella* which possess one enlarged adanal seta. It differs from other members of this group in respect of adanal and tarsal chaetotaxy. *Hoplophorella* is considered as a subgenus of *Atropacarus* in this paper, because there is no evidence in literature that *Hoplophorella* as a group is a separate phylogenetic entity.

Authors

Prof. Dr. MOSADOLUWA ADETOLA BADEJO, Department of Zoology, Obafemi Awolowo University, Ile-Ife, Nigeria;
Dr. STEFFEN WOAS & Prof. Dr. LUDWIG BECK, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe, Germany.

Key words

taxonomy, Acari, Oribatida, Africa, Nigeria

1. Introduction

It is widely known among acarologists that the oribatid mite fauna of much of the tropics and southern hemispheres has been poorly investigated when compared with the huge amount of information on palaeartic and nearctic fauna. If identification keys which were designed based on observed morphological features of oribatid mites from northern Europe are not suitable for identifying oribatid mites of temperate environments in North America (NORTON 1990), one could imagine the magnitude of difficulties encountered while using them to identify tropical fauna.

The Nigerian experience has been that available identification keys only allow family-level identification of

adult oribatid mites with minimum error. Identifications beyond this level are usually problematic because the authors of the keys did not have the Nigerian species in mind when designing their keys. This is one major reason why little information exists on the oribatid mite fauna of Nigeria.

It is in the light of the above that the authors of this paper came together to start extensive taxonomic investigations on oribatid mite specimens collected in Nigeria. The aim of this exercise is to add to the existing information on biogeographical distribution of oribatid mites and create basic data for an identification-key of palaeotropical taxa. In this paper, we present the results of our investigations on a species of lower oribatid mites which was collected from the litter cover of a secondary regrowth tropical rainforest soil in Nigeria.

2. Systematics

Atropacarus (Hoplophorella) nigeriensis BADEJO, new species

Figures 1-5

Phtiracaroida PERTY, 1841
Steganacaridae NIEDEBALA, 1986
Atropacarus EWING, 1917
Hoplophorella BERLESE, 1923

Holotype: female collected from forest floor litter in Ile-Ife, Nigeria in June 2000, M.A. BADEJO col., (specimen dissected for the description) deposited in the Museum of Natural History (MNH) at Obafemi Awolowo University, Ile-Ife, Nigeria.

Paratypes: 7 females with the same collecting dates, deposited in MNH, 5 females with the same collecting dates, deposited at Staatliches Museum für Naturkunde Karlsruhe (SMNK), Germany.

Description

Measurements: Aspis length 200 - 250 μm , Aspis height 95 - 120 μm , Notogaster length 387 - 490 μm , Notogaster height 300 - 335 μm .

Integument yellowish, surface covered with concavities which are more evident on the notogaster than on the aspis.

Aspis: A conspicuous lateral carina (lc) (fig. 1) and two posterior furrows extending towards the two bothridia and meeting to form an arch at the middle are present

Table 1. Morphological traits of other *Hoplophorella* species that are different from *Atropacarus (Hoplophorella) nigeriensis*.

Characters	<i>H. andrei</i> (BALOGH, 1958) = <i>Steganacarus andrei</i>	<i>H. collaris</i> (BALOGH, 1958) = <i>Steganacarus collaris</i>	<i>H. prominens</i> (BALOGH, 1958)	<i>H. africana</i> WALLWORK, 1967
Size	AL 221-279 μ m NL 435-549 μ m Nh 254-353 μ m	AL 180 μ m NL 344 μ m Nh 196 μ m	AL 176-283 μ m NL 378-606 μ m NH 202-364 μ m	AL 168-224 μ m AH 84-112 μ m NL 392-470 μ m NH 207.2-280 μ m
Aspis		foveolated medially, punctate or smooth laterally, rugose basally; no ex; short and thick prodorsal setae long with small head; lamella setae slightly dialted, spoon-shaped and finely spiculate; ro spiniform	surface strongly foveolate dorsally, less strongly medially, smooth marginally, rugae present basally; low crista; ro largest prodorsal setae	
Notogaster			*characteristic shape - elongated anterior part covering basal part of prodorsum; foveoles on this protusion very fine and similar than foveolates on the rest of the notogaster	Presence of lyrifissure ip - not true of Hoplophorella;
Notogastric setae	c_1 more anteriorly placed; * h_3 also more anteriorly placed than in other <i>Hoplophorella</i>	All well dialated; spoon-shaped with many spicules on the dialated end		
Genital Plates				4 pairs of aggenito-genital setae
Ano-adanal setae	3 pairs of adanal setae; anterior anal setae rounded distally; ad_2 spoon-shaped	3 pairs of adanal seate; ad_2 spoon-shaped with many spicules on the dilated end	3 pairs of adanal setae; ad_3 simple and the shortest of all	3 pairs of adanal setae;
Leg chaetotaxy				Tarsal setal formula is I (16) - II(12) - III(10) - IV(10).
* Diagnostic features				

on the aspis (fig. 2). There are five pairs of setae on the aspis. These are the rostral setae (ro); the sensillus (ss); two interbothridial setae (in_1 & in_2) and the exobothridial seta (ex) (Figs 2, 3). Setae ro and in_2 are spatulate and conspicuous. In lateral view, seta ro is directed upwards but the frontal view reveals that it also extends beyond the rostrum (fig. 3). Setae in_1 and ex are spiniform and can only be seen after careful examination. The bothridium (pseudostigma) has an alveolar surface. It is circular in shape and bounded on one side by a chitinized shelf which extends backwards along the aspis (fig. 4). The ss is relatively long (110 μ m), sigmoid and expands gradually along its length like a narrow leaf with a thick midrib.

Notogaster: covered by a relatively thin layer of cerotegument and appearing arched in lateral view but quadrangular in dorsal view (fig. 2). The concavities which ramify all over the integumental surface are

seen better in dorsal view. Those on the lateral margin look like grotesque red blood cells in dorsal view. There is no notogastral hood but a collar inside which the aspis retracts when necessary is very conspicuous in lateral view (fig. 1). The two anterior corners of the rectangular notogaster is strengthened by thickened integument which projects upwards and extends down the length of the notogaster gradually becoming less thickened towards the posterior corners (fig. 2). There are 15 pairs of notogastral setae which are very conspicuous, bent backwards and spatulate in shape (fig. 5). The number and arrangement of the setae is typical of the subgenus *Hoplophorella*. Seta c_1 originates farther from the collar line than c_2 and c_3 (fig. 2). There are two pairs of lyrifissures, the anterior (ia) and posterior (im) lyrifissures which are represented by small refractive circles inbetween cp and d_2 (ia), and inbetween c_2 and ps_4 (im). This is a general rule for all

<i>H. angolensis</i> MAHUNKA, 1984.	<i>H. benoiti</i> MAHUNKA, 1984.	<i>H. ensifera</i> MAHUNKA, 1984.	<i>H. horida</i> MAHUNKA, 1984	<i>H. cochlearia</i> PEREZ-INIGO & BAGGIO, 1993.
AL 227 µm NL 414 µm Nh 273 µm	AL 170-179 µm NL 353-386 µm Nh 223-244 µm	AL 430 µm NL 859 µm NH 546 µm	AL 328-427 µm NL 754-910 µm NL 418-517 µm	AL 194-200 µm NL 390-410 µm NH 207.2-280 µm
No crista (?)	weakly developed carina; anterodorsal part foveolate; *short ro; ro and in equal in length	prodorsal surface with deep depressions in front of la & ro; *la & in both strong and well spiculate; ss long, small head, strongly dilated	Quadrangular in lateral view; wide rostral margin with 3 crista; prodorsal setae thin, simple, setiform	
	foveoles widely separated		*anterior part very large, protruding forward in dorsal view covering the basal part of the aspis; *surface with large protuberances at areas of insertion of setae	
*Long, bent, blunt at the tip, finely roughened, all nearly equal in length	strong, erectile, slightly dilated, distal end with spickles	all strong, thick, partly erect, spiculate with a sharp edge on the inner side; all with setae far from the collar line	all fine, thin, simple and setiform	Distal end enlarged to give a spoon-shaped appearance
3 pairs of adanal setae; ad ₁ slightly lanceolate; ad ₂ rounded with dilated head	3 pairs of adanal setae; ad ₂ sword-shaped	3 pairs of adanal setae; ad ₂ very long, dagger-shaped, finely roughened	genito-aggenital and ano-adanal plates with some ribs and rugae 3 pairs of ano-adanal setae	3 pairs of adanal setae; shape of ad ₂ different from notogaster setae

Hoplophorella. Lyrifissure ip is absent in all specimens examined.

Ventral Region

Mouthparts: The infracapitulum is the stenarthrous type which is common in all Phthiracaroida (Fig 6). The rutellum is well developed and the anterior (or₁) and posterior (or₂) adoral setae are ciliated. The posterior-antiaxial setae (or₃) is setiform. The anterior (a) and median (m) smooth setae on the genae (G) are also setiform. Posteriorly, there is a pair of small setiform setae (h) which lies inbetween the inner edges of a triangular shaped membrane which not only covers the posterior part of the infracapitulum but also connects the whole labiogenal articulation of the infracapitulum to the musculature in the leg-bearing hysterosoma. The chelicera is the chelate-dentate type that bears the dorsal (cha) and lateral (chb) setae on the fixed digit

(fig. 7). There are a few spines on the antiaxial surface and the surface ornamentation on the blunt posterior end which is usually within the infracapitulum is denser than the ornamentation on the free anterior end. The pedipalp is 3-segmented with setal formula 2-2-8. There is a solenidion (ω) and an euphatidial seta (sul) at the base of the solenidion on the tarsus. (fig. 8).

Epimeral region: The epimera is clearly divided into two regions. Epimere I and II are more or less fused and larger than epimere III and IV which overlap partially to facilitate retraction of the aspis into the notogaster (fig. 9). The chaetotaxy of the epimera is 1-0-1-1 which is typical of all Phthiracaroida.

Legs: Leg I is the strongest of all legs (fig. 10). Each leg has five segments. Tiny pores similar to the ornamentation on the epimera are seen on either the trochanter or the femur or both. The tarsus of each leg is monodactyl. Each claw is strongly developed

and bidentate midventrally. The anterior tooth is always more developed than the posterior. Leg chaetotaxy is as follows: I (1-4-3-5-18-1), II (1-3-3-12-1), III (2-2-2-2-9-1), IV (2-1-1-2-8-1). The absence of seta I' on genu IV distinguishes this genus from *Steganacarus* and the ratio of the length of v'' to v' on femur I is exactly 2.25, which confirms that the specimens observed belong to the genus *Atropacarus*. Solenidiotaxy on the genu, tibia and tarsus I (2-1-3), II (1-1-2), III (1-1-0), IV (0-1-0) is typical for all Phthiracaridae.

Ano-genital plates: The anogenital region is clearly visible in lateral view (fig. 1). The anal and adanal plates are fused on the one hand while the genital and aggenital plates are fused on the other. These plates articulate directly with the notogaster and both occupy the whole of the ventral region leaving no room for a separate ventral plate. This is a remarkable trait of all Phthiracaridae. The adano-anal plate is somewhat triangular in shape. The proximal margin projects anteriorly to form an interlocking device with the posterior corner of the aggenito-genital plate and all along the anterior margin, there are overlapping chitinized lobes on the right and left adano-anal plates (fig. 11a) which probably control the opening and closing of both plates and most likely the aggenito-genital plates too. The paraxial margin which bears 5 pairs of setae is convex, protruding slightly beyond the anterior aggenito-genital plate in ventral view (fig. 1). The relative positions of the setae are not clearly seen from the lateral view but when the plates are removed and viewed from above, 3 pairs of setae of similar shape and length are seen arranged on a line closer to the paraxial margin than the other 2 pairs. The marginal pairs of setae are filiform and designated as an_1 , an_2 and an_3 while the other two pairs which are believed to be in the adanal area are designated as ad_1 and ad_2 . Setae ad_1 is spiniform, while ad_2 is spatulate like the notogastral setae. On the other hand, the aggenito-genital plate is quadrangular in shape, with rounded corners and slanting vertical edges which make it look like a parallelogram (fig. 11b). The fused plates bear 10 pairs of setae, one of which is clearly in the aggenital region on the anterior top corner of each plate. This setae which is inserted within a furrow on the antiaxial side is the aggenital setae (ag). The remaining pairs of setae are on the paraxial side of the aggenito-genital plate. Setae g_1 to g_5 are minute setae which are arranged closely together along a line within a furrow at the anterior lower corner of each plate. Behind these minute setae are the more conspicuous and widely spaced g_6 to g_9 which are also arranged in a line along the entire length of the plate. The ovipositor has many lobes and is richly setose just as in many oribatid mites.

3. Discussion

Opinion on the taxonomic status of *Hoplophorella* appears divided among oribatologists. While NIEDBALA (1986) considers *Hoplophorella* as a subgenus of *Atropacarus* based on phylogenetic considerations, PEREZ-ÍÑIGO & BAGGIO (1993) suggested that *Hoplophorella* should be distinguished from *Atropacarus* as a separate genus. About fifty species of *Hoplophorella* have been described (cited in PEREZ-ÍÑIGO & BAGGIO 1993), but many of them have either been considered as synonyms or as a subgenus of *Atropacarus* by NIEDBALA (1992) and not *Steganacarus* as originally suggested by BERLESE (1923). This is in order as *Atropacarus* was a subgenus of *Steganacarus* (JACOT 1930) until recently (KAMIL & BAKER 1980, NIEDBALA 1992). In order to avoid further misconceptions, *Hoplophorella* should remain a subgenus of *Atropacarus*. A comprehensive definition of *Hoplophorella* does not exist in literature up to date, unlike *Atropacarus* and *Steganacarus* which are phylogenetic entities.

The differences between *Atropacarus* (*Hoplophorella*) *nigeriensis* described in this study and many related *Hoplophorella* species are presented in Table 1. The observed specimens fall within the same size range as all the species in Table 1 except *H. ensifera* MAHUNKA, 1984 which is bigger. The differences are observed in respect of the foveoli on the aspis and notogaster, shape of notogastral setae as well as shapes and chaetotaxy of the genital and anal plates. Other differences may exist in respect of certain other morphological traits such as the morphological features of the infracapitulum and epimeron as well as leg chaetotaxy. These traits were hardly described in many species so, the differences can only be determined by examination of the type specimens, many of which may not be available for dissection to reveal the fine details of the structures that we have reported in this study.

Morphological traits of *A. (H.) nigeriensis* that have not been reported for other related *Hoplophorella* species are the membrane linking the labiogenital articulation of the infracapitulum to the musculature in the leg-bearing hysterosoma, the 3 pairs of anal setae on the paraxial margin of the adano-anal plate, 2 pairs of adanal setae, spatula shaped prodorsal and ad_2 seta (except *H. andrei*) and interlocking device of the anal and genital plates. *H. africana* WALLWORK, 1967 was collected from organic debris in Tchad and it shares similar morphological traits with *A. (H.) nigeriensis*. However, the illustration of *H. africana* in WALLWORK (1967) suggests that it is somewhat dorsoventrally compressed and many morphological traits were not described. Leg chaetotaxy for example, is not fully known. Only the tarsal formula was provided in Wallwork's description and it is different from the tarsal formula of *A. (H.) nigeriensis*. Both species however belong to the " *cucullata*" group which has been identified by PEREZ-ÍÑIGO & BAGGIO (1993) as *Hoplophorella*

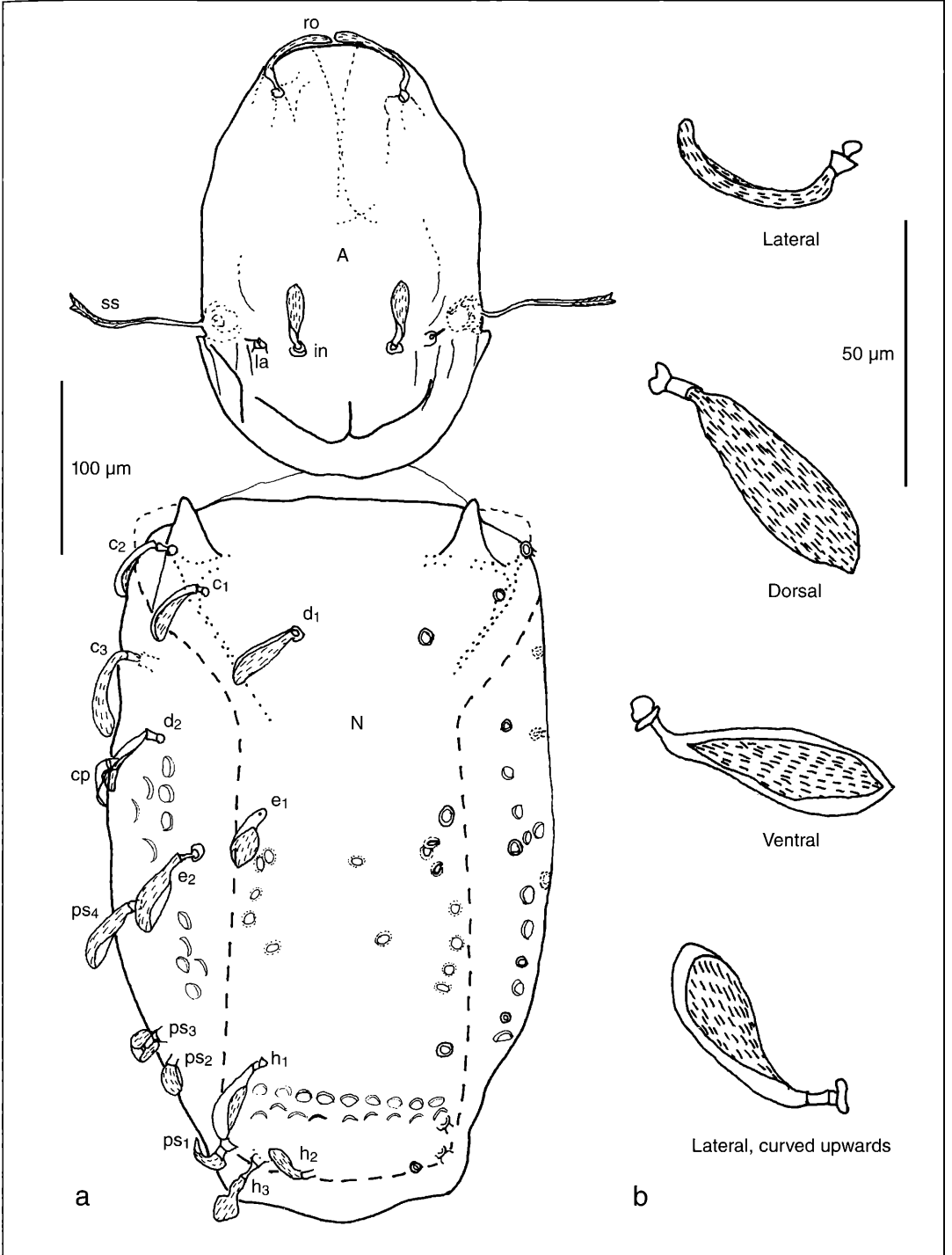


Figure 1. a) *Atropacarus (Hoplophorella) nigeriensis* BADEJO, new species: dorsal view; b) prodorsal setae.

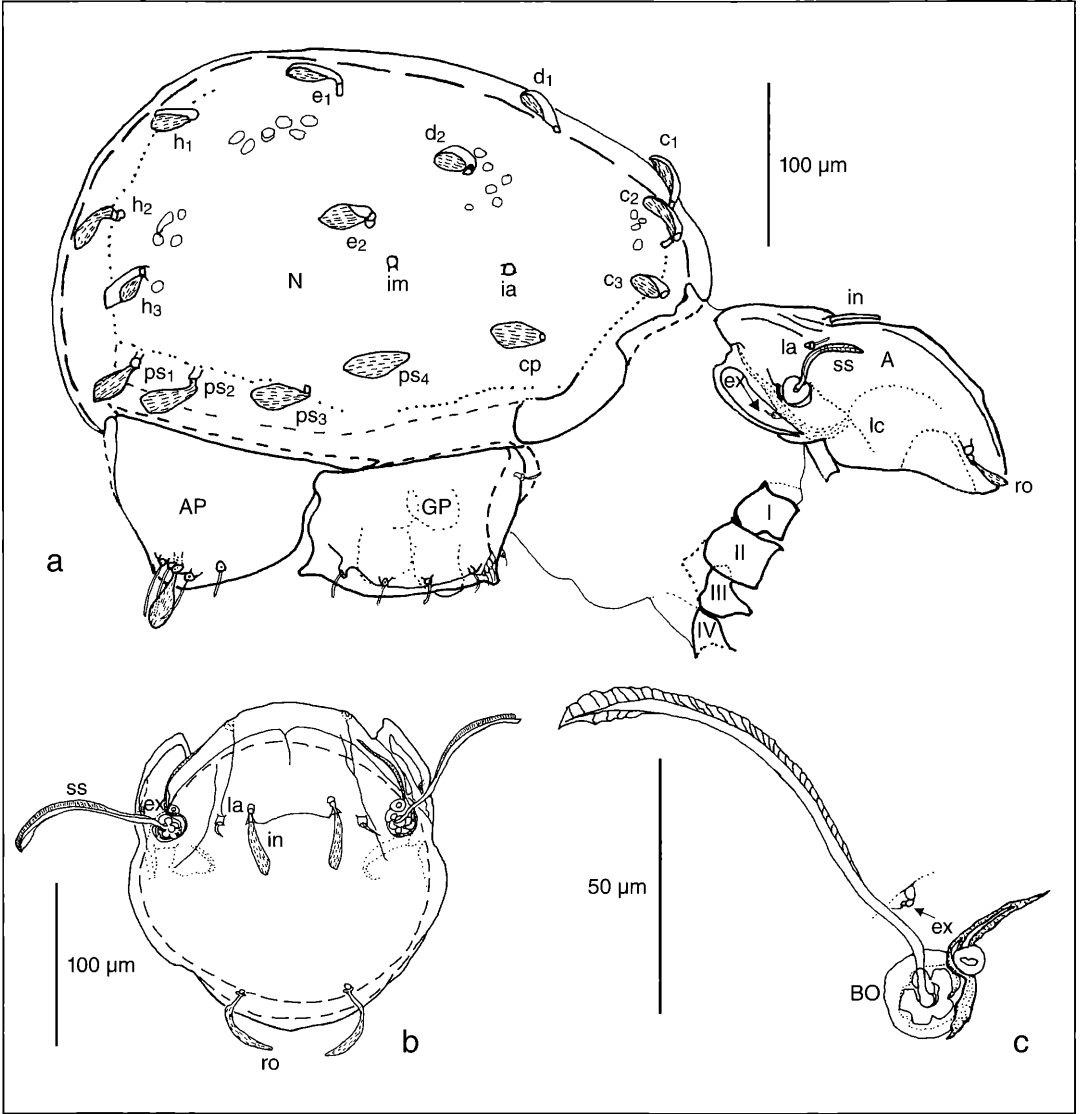


Figure 2. a) *Atropacarus (Hoplophorella) nigeriensis* BADEJO, new species: lateral view. ro, in, ss, la, ex - prodorsal setae; lc - lateral carina; A - Aspis; I, II, III, IV - epimeral plates at the bases of legs I-IV; N - Notogaster; c₁, c₂, c₃, c_p, d₁, d₂, e₁, e₂, h₁, h₂, h₃, ps₁, ps₂, ps₃, ps₄ - notogastral setae; ia, im - lyrifissures; AP - adano-anal plate; GP - aggenito-genital plate; b) frontal view of aspis. ro, in, ss, la, ex - prodorsal setae; c) sensillus. BO - bothridium.m; ex - exobothridial seta.

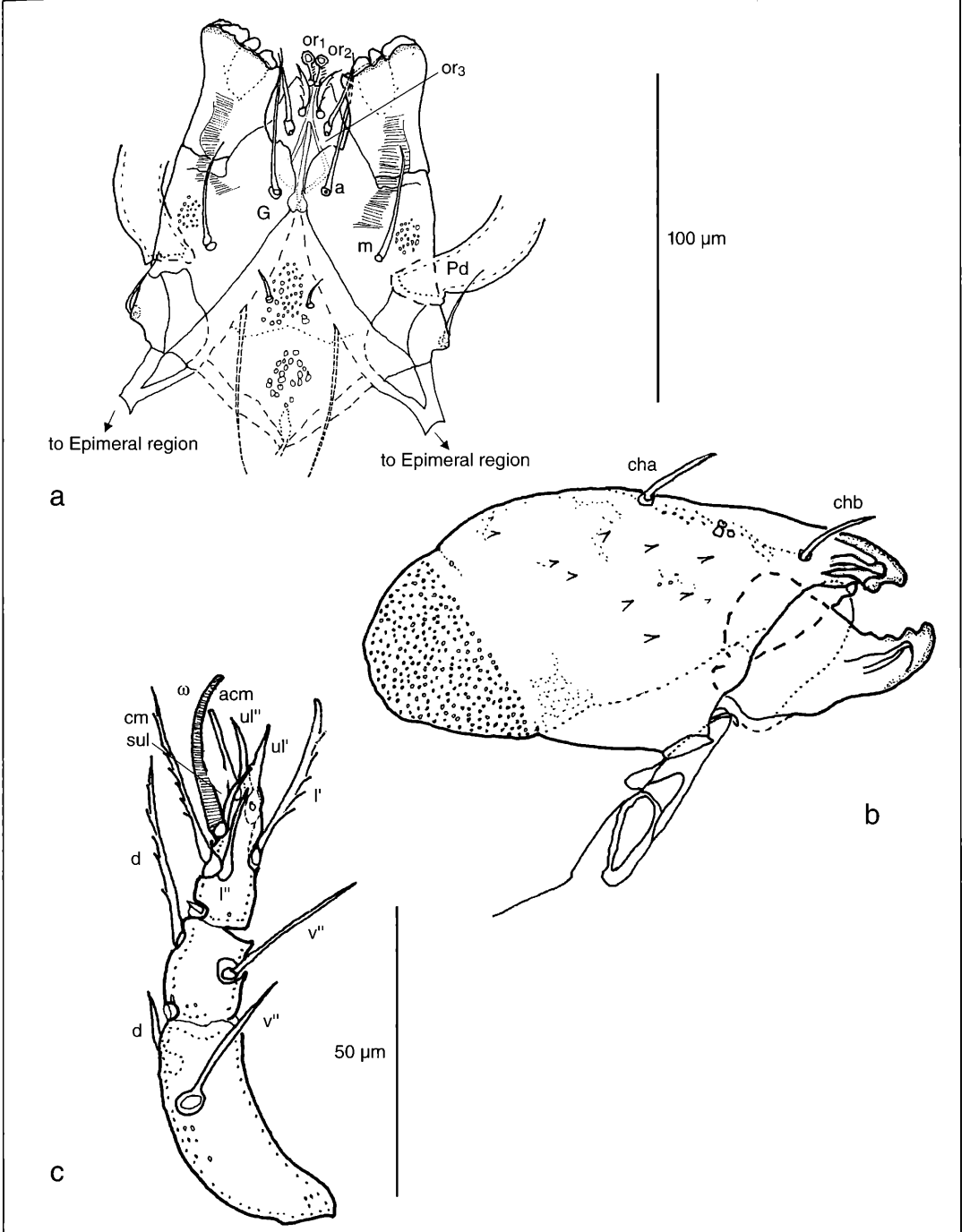


Figure 3. a) *Atropacarus (Hoplophorella) nigeriensis* BADEJO, new species: infracapitulum. *or*₁ - anterior adoral setae, *or*₂ - posterior adoral setae; *or*₃ - posterior antiaxial setae, *a* - median setae, *m* - smooth setae; *G* - genua; *Pd* - distal segment of pedipalp; b) chelicera: *cha* - dorsal setae, *chb* - lateral setae; c) pedipalp..

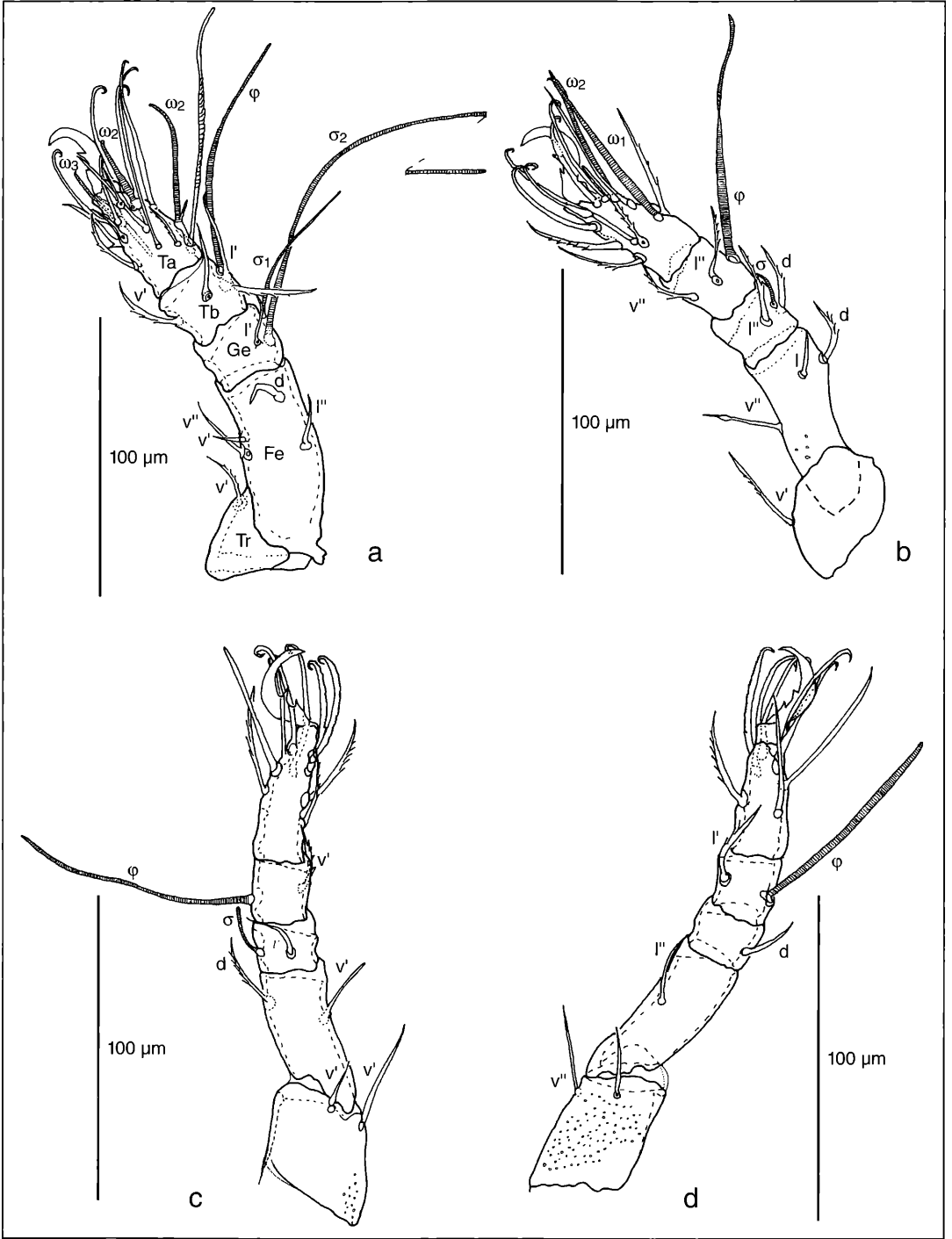


Figure 4. *Atropacarus (Hoplophorella) nigeriensis* BADEJO, new species: a) leg I, b) leg II, c) leg III, d) leg IV; Tr - trochanter; Fe - femur; Ge - genu; Tb - tibia; Ta - tarsus.

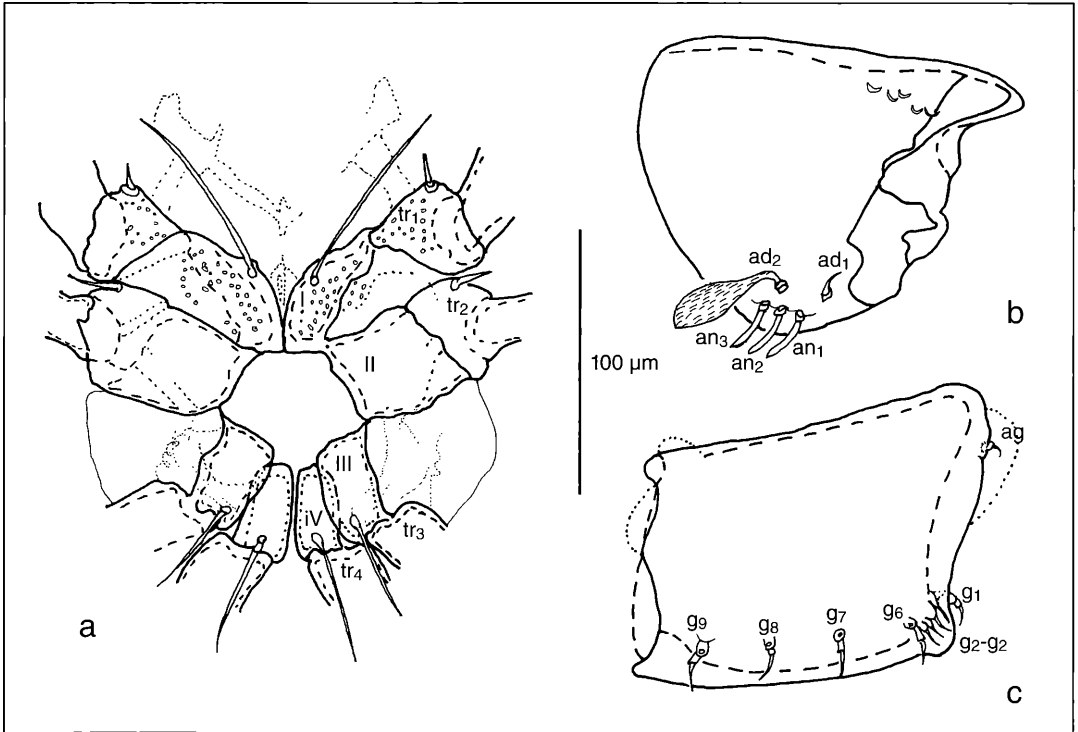


Figure 5. a) *Atropacarus (Hoplophorella) nigeriensis* BADEJO, new species: epimeral region. I, II, III, IV - epimeral plates; tr_1 , tr_2 , tr_3 , tr_4 - trochanters of legs I-IV; b) adano-anal plate. an_1 , an_2 , an_3 - anal setae; ad_1 , ad_2 - adanal setae; c) aggenito-genital plate. ag - aggenito-genital setae; g_1 - g_9 - genital setae.

with one enlarged adanal seta. The morphological differences between *H. africana* and other *Hoplophorella* in this group (e.g. *H. obsoletior* BALOGH, 1962, *H. cuculata* BALOGH, 1962, both collected from Madagascar, and *H. thoreani* JACOT, 1933 from Florida) have already been highlighted by WALLWORK (1967).

Acknowledgement

We are grateful to the Alexander-von-Humboldt-Stiftung (AvH) for awarding the George-Foster-Research Fellowship to M.A. BADEJO which made it possible for us to work together at the State Museum of Natural History in Karlsruhe/Germany where this study was carried out.

4. Literature

- BALOGH, J. (1958): Oribatides nouvelles de l'Afrique tropicale. - *Rev. Zool. Bot. Afr.*, **58**: 1-34.
- BALOGH, J. (1962): LXXV - Acari Oribates - *Ann. Mus. Roy. Afr. Centr.*, In-8°, **Zool.**, **110**: 90-131.
- BERLESE, A. (1923): Centuria sesta di Acari nuovi. - *Redia*, **15**: 237-262.
- JACOT, A.P. (1930): Oribatid mites of the subfamily Phthiracarinae of the northeastern United States. - *Proc. Boston Soc. Nat. Hist.* **39**: 209-261.
- JACOT, A.P. (1933): Phthiracarid mites of Florida. *Journ. Elisha Mich. Sci. Soc.*, **48**: 232-267
- KAMIL, B.W. & BAKER, A.S. (1980): The genus *Atropacarus* EWING (Acari: Cryptostigmata). - *Bull. Br. Mus. Nat. Hist. (Zool.)* **39**: 189-204.
- MAHUNKA, S. (1984): Description and redescription of Ethiopian oribatids (Acari: Oribatida). - *I Folia Entomologica Hungarica, Rovartani Közlemenyek*, **2**: 127-142.
- NORTON, R.A. (1990): Acarina: Oribatida. - In: DINDAL, D.L. (Ed.): *Soil Biology Guide*: 779-803; New York (John Wiley & Sons).
- NIEDBALA, W. (1986): System des Phthiracaroida (Oribatida, Euptyctima). - *Acarologia*, **27**: 61-86.
- NIEDBALA, W. (1992): Phthiracaroida (Acari, Oribatida) Systematic Studies. - Polish Scientific Publishers, Warszawa, 612 pp.
- PEREZ-ÍÑIGO, C. & BAGGIO, D. (1993): Oribates edaphiques du Bresil (VII). Oribates de l'etat de São Paulo (Quatrieme partie). - *Acarologia*, **34**: 249 - 264.
- WALLWORK, J. (1967): Some Oribatei (Acari: Cryptostigmata) from Tchad (3. Series). - *Rev. Zool. Bot. Afr.*, **1-2**: 35-45.

MOSADOLUWA ADETOLA BADEJO, STEFFEN WOAS & LUDWIG BECK

Mesoplophora ifeana, a new species of ptychoid mite (Acari, Oribatida) from Nigeria

Abstract

In this paper, we describe a new species of *Mesoplophora* collected from forest floor litter in southwestern Nigeria. *Mesoplophora* is a cosmopolitan genus of ptychoid mites that has been recorded from the Palaearctic region as well as Morocco and Tchad in the Ethiopian region. *M. ifeana* is the first *Mesoplophora* species to be fully identified and described from Nigeria. Differences between this species, *M. ifeana*, and other *Mesoplophora* species recorded from Africa are observed in respect of the number of spines on the sensillus, presence of two pairs of exobothridial setae and leg chaetotaxy. The lack of information on fine taxonomic details of adults and deutonymphs of *M. africana* from Tchad as well as the discrepancies in the description of certain morphological features such as organisation and chaetotaxy of the ventral plates as well as the nomenclature of setae on the aspis were noted. Attention was drawn to the unique combination of traits of both lower and higher Oribatida in *Mesoplophora*, a trait which may be responsible for its ubiquitous distribution.

Authors

Prof. Dr. MOSADOLUWA ADETOLA BADEJO, Department of Zoology, Obafemi Awolowo University, Ile-Ife, Nigeria;
Dr. STEFFEN WOAS & Prof. Dr. LUDWIG BECK, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe, Germany.

Key words

taxonomy, Acari, Oribatida, Africa, Nigeria

1. Introduction

The Mesoplophoroidea was regarded as one of the four superfamilies of ptychoid mites when the Ptyctima was regarded as a separate taxonomic group from Arthronota (BALOGH 1972). Later, the Mesoplophoroidea was classified as Arthroptyctima, a cohort of the Supercohort Arthronota (BALOGH & MAHUNKA 1983). This separated the mesoplophoroids from their ptychoid mates Phthiracaroida and Euphthiracaroida which were classified as Mixonomata, another supercohort of lower Oribatida. The organisation of the anogenital plates in the juveniles of Mesoplophoroidea is the same as in Mixonomata, but in the adults the anal and genital plates are separated as in higher brachypiline mites. The genus *Mesoplophora* is cosmopolitan. Most other ptychoid mite genera are not. The Protoplophoroidea which are also arthroptyctimid Arthronota are predominantly palaeartic soil dwellers. Members of the genus *Mesoplophora* are more abundant and more widely distributed in the tropical rainforest zone in Nigeria than

other ptychoid mites (BADEJO & LASEBIKAN 1988; BADEJO et al. 1999). It therefore appears that *Mesoplophora* possesses unique taxonomic and ecological traits among the ptychoids which confers on it an ubiquitous status. For these reasons, detailed study of taxonomic features which may have conferred unique ecological traits on mesoplophorid mites collected from the tropical rainforest zone in Nigeria were embarked upon with the aim to add to the existing information on the biogeographical distribution of the genus, as well as reveal its true taxonomic position among the lower Oribatida.

2. Systematics

Mesoplophora ifeana BADEJO, new species

Figures 1-6.

Mesoplophoroidea EWING, 1917
Mesoplophoridae GRANDJEAN, 1933
Mesoplophora VAN DER HAMMEN, 1959

Holotype: female collected from forest floor litter in Ile-Ife, Nigeria in June 2000, M.A. BADEJO col., (specimen dissected for the description) deposited in the Museum of Natural History (MNH) at Obafemi Awolowo University, Ile-Ife, Nigeria
Paratypes: 78 females and 10 deutonymphs with the same collecting dates, deposited in MNH, 10 females and 5 deutonymphs with the same collecting dates, deposited in Staatliches Museum für Naturkunde Karlsruhe (SMNK), Germany.

Description

Measurements: aspis length 160–191 µm, aspis height 92–120 µm, notogaster length 275–322 µm, notogaster height 138–161 µm.

Integument yellowish, smooth with fine irregular microsculpture on the cerotegument.

Aspis: The lateral view reveals a conspicuous margin which extends frontally beyond the base of the rostral seta (ro) to meet the lateral carina which extends to the lower margin of the aspis (fig. 1 a). Present on the aspis are 5 pairs of setiform setae, each of which bears 18 spines. The sensillus (ss) is the most conspicuous of all the setae. It is directed sharply backwards in such a way that the long axis forms an acute angle with the short basal part which is inserted into the bothridium (fig. 1 b). Being relatively long when compared with other setae, the spines of the sensillus are also long and conspicuous making it relatively easier to count the number (fig. 1 c). A pair of inter-

bothridial setae (in) is present between the two bothridia (BO), each of which is inserted very close and slightly anterior to the bothridium (fig. 1 c). Two pairs of exobothridial setae are inserted laterally on the aspis. The first pair (ex_1) which is spiniform is very close but slightly anterior to the centre of the bothridium, while the more conspicuous and spinose second pair (ex_2) is along the same axis as ex_1 but in a more anterior position. The distance between ex_1 and ex_2 is exactly half of the distance between ex_2 and ro (Figs 1 a, 2). Each ro is directed forward, curving gently towards each other and extending well beyond the aspis in frontal view (fig. 2). The distal 1/5th of the aspis is covered by the proximal end of the notogaster.

Notogaster: The notogaster is perfectly round in shape and appears convex in lateral view. Irregular microsculpture on the cerotegument ramify all over as a tiny dark pattern on the yellowish body (figs 1 a, 2). The posterior margin of the aspis is seen through the integument inside the anterior part of the notogaster, suggesting that the aspis does not move out of the notogaster when at rest, unlike in some ptychoids, where the base of the aspis could be away from the notogastral collar. A small notch is present anteriorly on either side of the notogaster. This notch which represents the depression in a penknife joint most likely accommodates the upward movement of the posterior end of the aspis and the simultaneous lateral movement of the anterior corners of the notogaster when the aspis is closing up. Lines of thickened exoskeleton are seen on the base of this notch suggesting an extra strengthening of the area to facilitate the closing of the aspis (fig. 2). There are eight pairs of setiform and spinose setae on the notogaster. Each seta has 18 spines.

Ventral region

Mouthparts: The infracapitulum is of the anarthric type lacking a labiogenal articulation. The rutellum is narrow. The anterior adoral setae (or_1) is the smallest and least conspicuous of the three pairs of adanal setae. The posterior adoral setae (or_2) is big and modified to form a structure that looks like a stretched foot pointing upwards. The posterior antiaxial setae (or_3) is filiform and it often extends beyond the or_2 and rutellum (fig. 5 a). The anterior (a) and median (m) smooth setae on the genua (G) are also filiform, the ratio of a:m in length being 5:4. The chelicerae are of the basic chelate-dentate type but are narrow and somewhat elongated (fig. 5 b). There are no setae on the chelicera but spines pointing towards the anterior end are present on the antiaxial surface. The spines occur in groups increasing gradually in number from one at the proximal end to six at the distal end (fig. 6 b). The spines that occur in groups of three or more are arranged in such a way that their base forms an arc.

There are no ornamentations on the chelicerae. The pedipalps are 4-segmented with setal formula 1-0-1-10 (fig. 5 c). At the tip of the tarsi is a set of tripartite setae which is typical for Hypochthonidae.

Epimeral region: As in all ptychoid mites, the epimere is divided into 2 regions. Epimere I and II are clearly separated from epimere III and IV. There is considerable overlap between epimere I and II such as only the inner lateral margin and the base of epimere II are not covered by epimere I (fig. 3 a). The trochanters of legs I and II are relatively small and partially sunk inside their respective epimeres in such a way that the epimere appears like the first leg segment (see figs 4 a,b). The relatively smaller epimeres III and IV are completely fused (fig. 3 b). The trochanters of legs III and IV are inserted closely together within the fused epimera in a way that suggests that the movement of the two pairs of legs are controlled in unison by the fused epimera. Chaetotaxy of the entire epimeral region is 2-1-2-1.

Legs: Leg I is stronger than leg II which is in turn stronger than legs III and IV (figs 4 a-d). Each leg has 5 segments and the tarsi are monodactyl. The claw on leg I has a weakly developed midventral tooth. The claw on leg II is bidentate, while those on legs III and IV appear multidentate with poorly developed teeth which look more or less like tiny spines. Leg chaetotaxy is as follows: I - 0-2-2-4-19-1, II - 0-3-3-3-14-1, III - 2-3-3-2-2-11-1, IV - 2-4-2-2-8-1. This is rather different although similar in pattern to the leg chaetotaxy of *M. pulchra* (I - 0-3-3-4-19-1, II - 0-4-3-3-14-1, III - 2-2-3-3-10-1, IV - 2-3-0-2-8-1) (GRANDJEAN 1965).

Ventral plates: The anal (AP) and genital (GP) plates are clearly separated and lie at the central part of the venter (fig. 3 c) bounded all over by a pleural plate (P) that is almost as big as the notogaster in ventral view. The irregular microsculpture seen on the notogaster is also present in the ventral region. There are ten pairs of setae on the pleural plate (p_1 - p_7 ; ad_1 - ad_3) three of which lie in the adanal region (ad_1 , ad_2 , ad_3) surrounding the anal plates. One tiny pair (p_7) is present at the proximal end of the pleural plate lying almost midway between the aggenital area and the margin of the pleural plate. Each genital plate looks like the sector of a sphere. The pair therefore appears semispherical with the proximal end of each plate folding backwards like a twisted lip to accommodate the rostrum of the aspis when it is closed (fig. 3 c). There are seven pairs of setae on the genital plates. The anal plates are semi-circularly shaped and bear only two pairs of setae (an_1 and an_2). All the ventral setae are small, setiform and spinose, excepting one pair (p_6) which is as long as some notogastral setae. The anal and genital openings are very narrow slits along the length of their respective plates and they are not contiguous because of the clear separation of the anal and genital plates. The ovipositor sometimes protrudes out of the genital opening and can be seen from ventral view (fig. 3 c) to

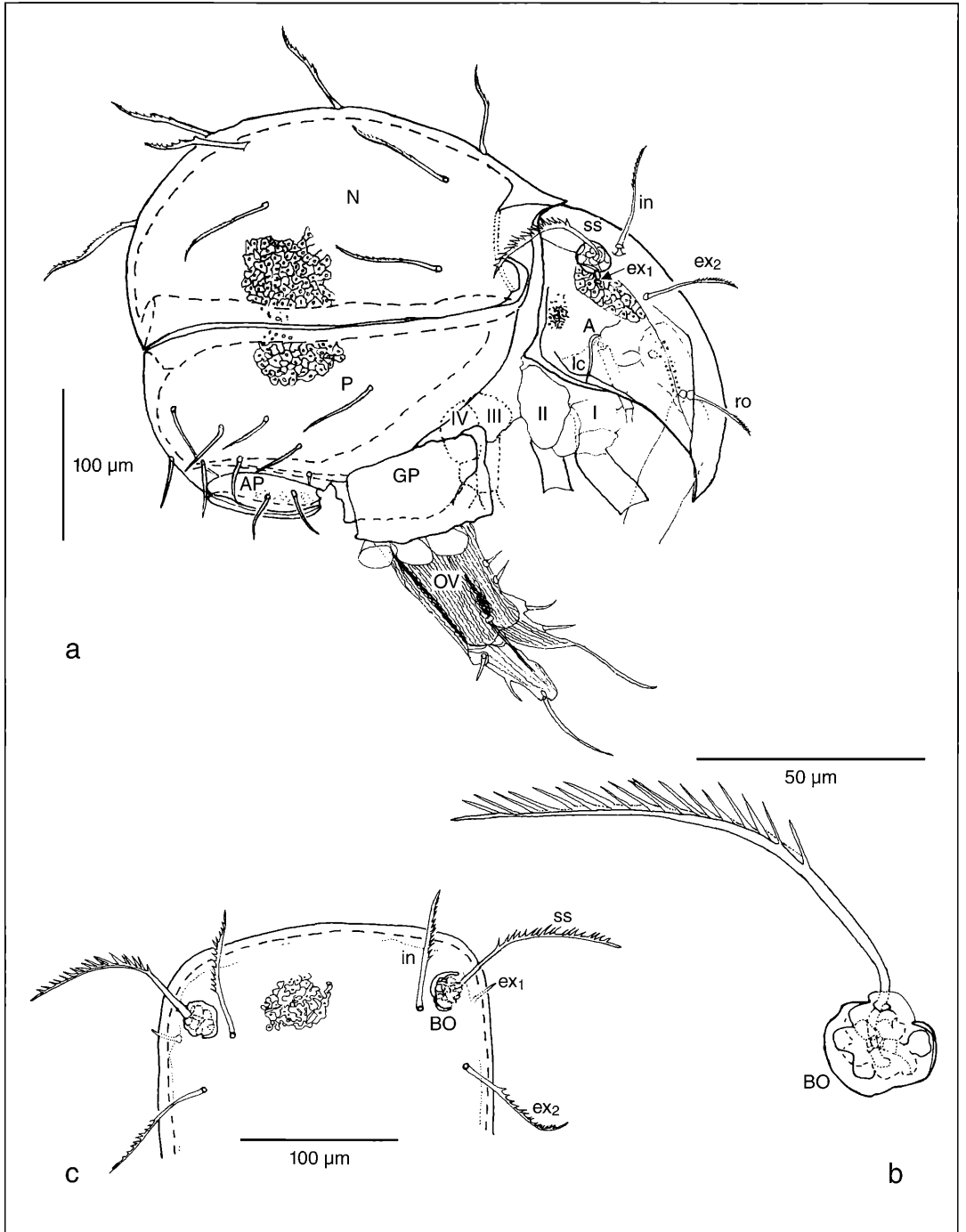


Figure 1. a) *Mesoplophora ifeana* BADEJO, new species: lateral view: ro, in, ss, ex₁, ex₂ - prodorsal setae; lc - lateral carina; A - Asp-is; I, II, III, IV - epimeral plates at the bases of legs I-IV; N - Notogaster; P - Pleural plate; AP - Adano-anal plate; GP - Aggenito-genital plate; b) sensillus showing the 18 spines, BO - Bothridium; c) frontal view of aspis, posterior half: ro, in, ss, ex₁, ex₂ - prodorsal se-

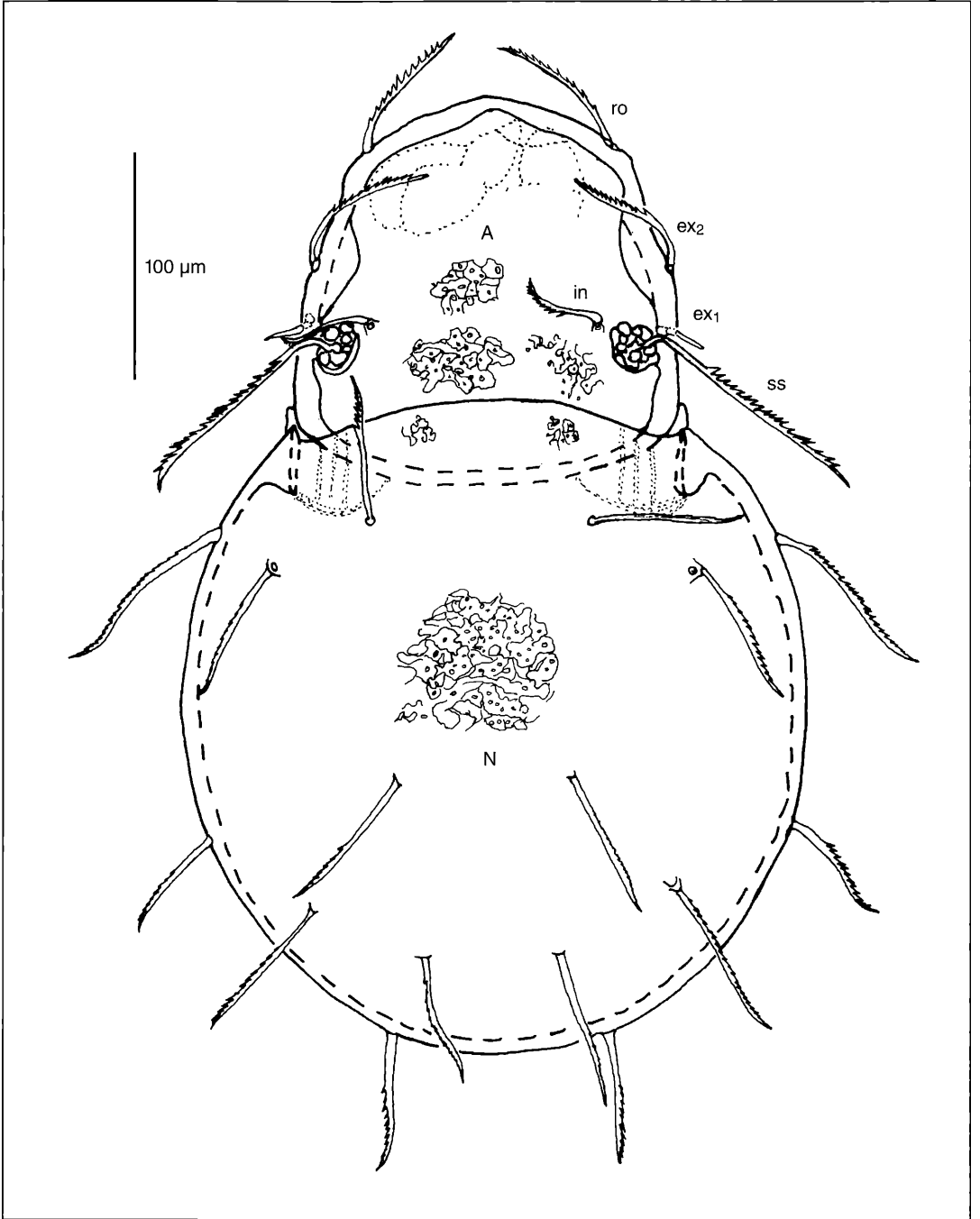


Figure 2. *Mesoplophora ifeana* BADEJO, new species: dorsal view.

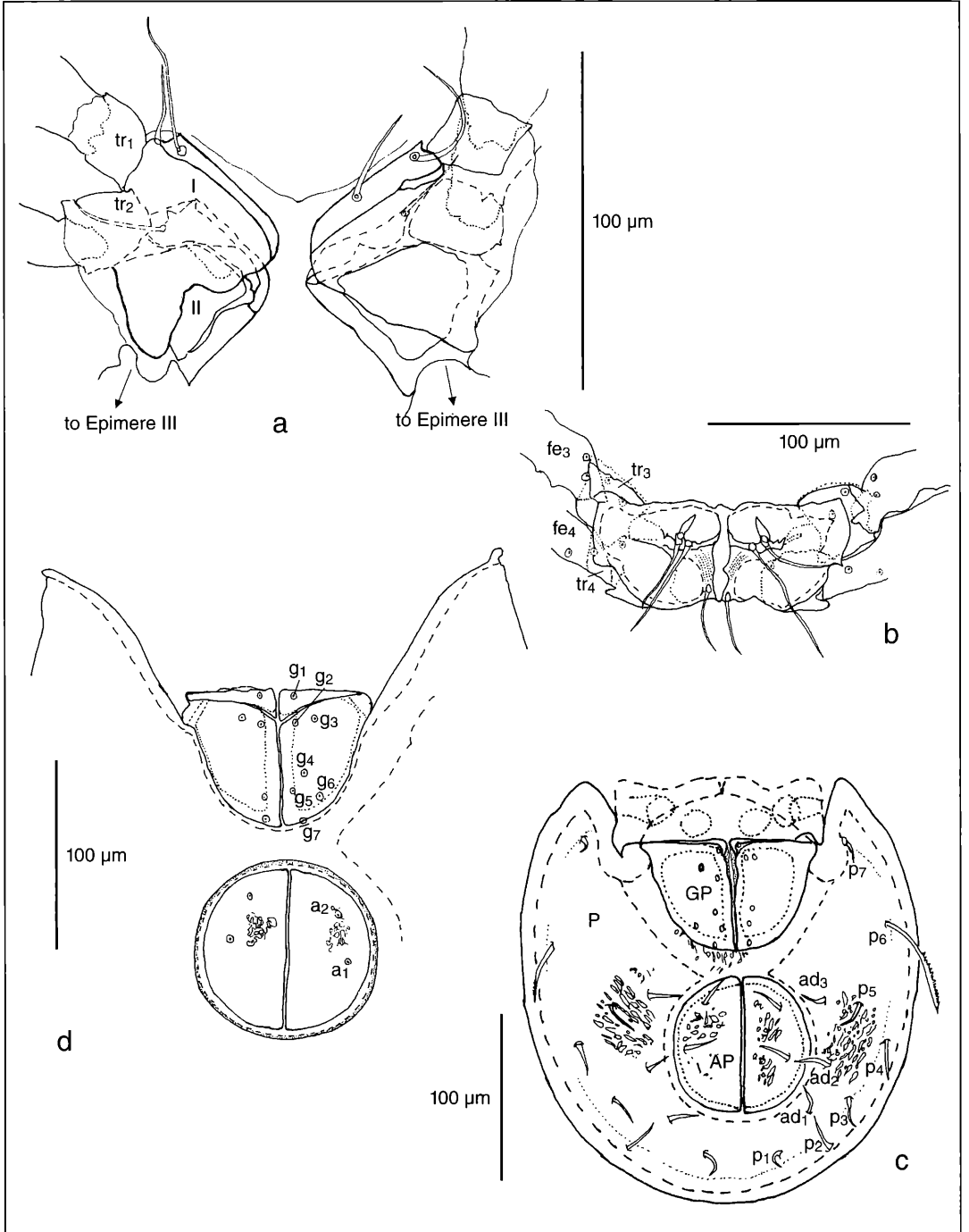


Figure 3. *Mesoplophora ifeana* BADEJO, new species: a) epimeral plates I, II; tr₁, tr₂ - trochanters of legs I, II. b) epimeral plates III, IV; tr₃, tr₄ - trochanters of legs III, IV; fe₃, fe₄ - femora of legs III, IV; c) ventral region: AP - adano-anal plate, GP - aggenito-genital plate; d) adano-anal and aggenito-genital plates showing the positions of anal and genital setae.

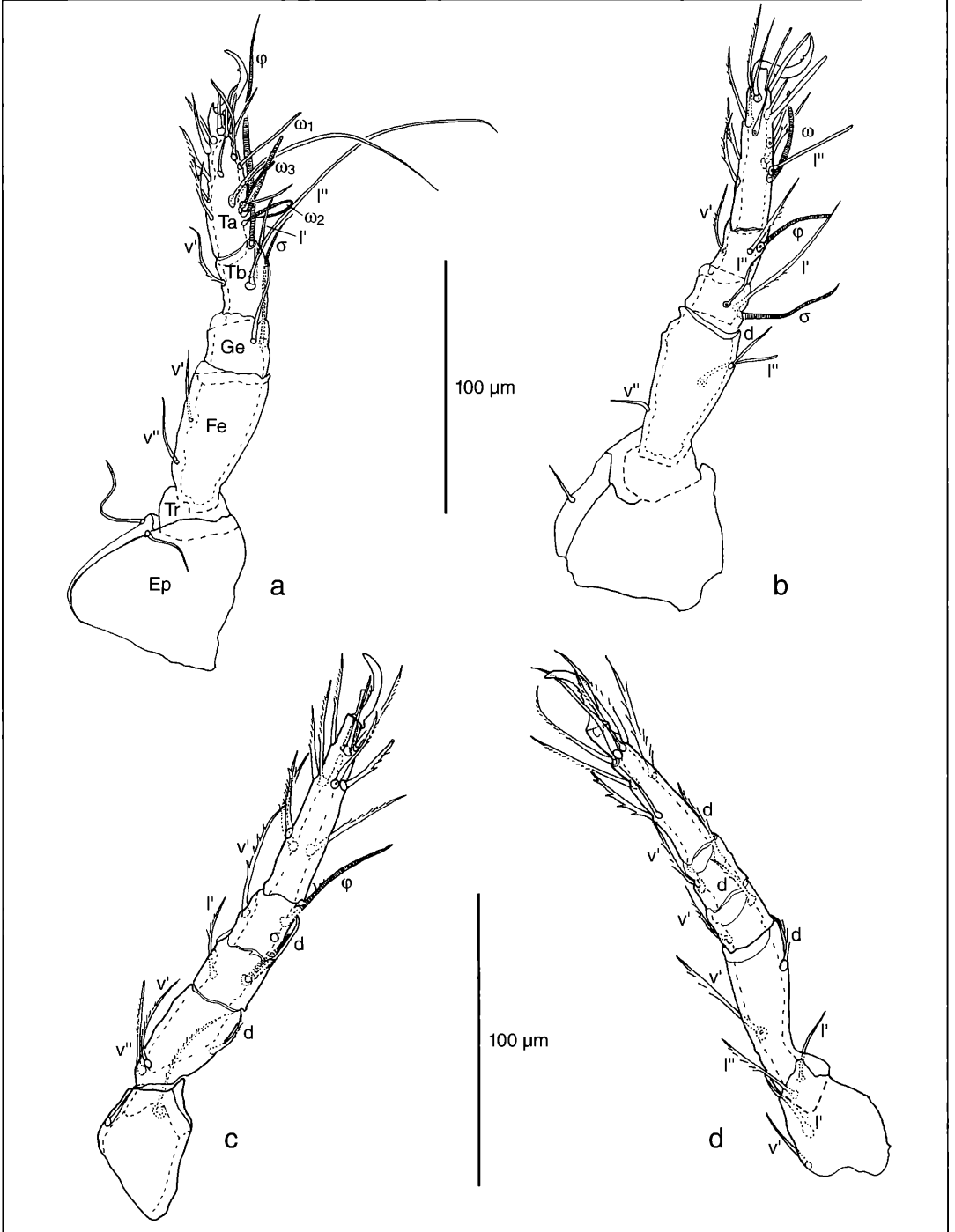


Figure 4. *Mesoplophora ifeana* БАДЕЈО, new species: a) leg I, b) leg II, c) leg III, d) leg IV; Tr – Trochanter, Fe – Femur, Ge – Genu, Tb – Tibia, Ta – Tarsus.

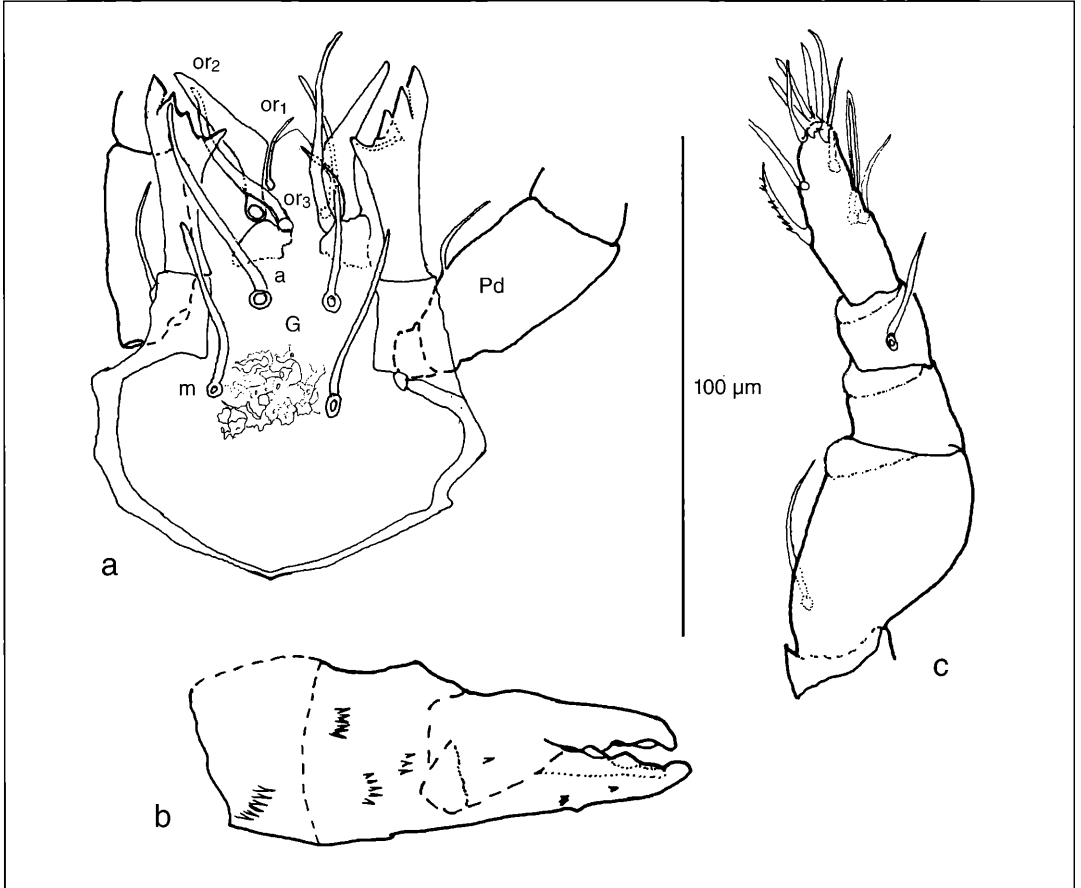


Figure 5. a) *Mesoplophora ifeana* BADEJO, new species: infracapitulum: or₁ - anterior adoral setae, or₂ - posterior adoral setae, or₃ - posterior antiaxial setae, a - median setae, m - smooth setae, G - Genua, Pd - distal segment of pedipalp; b) chelicera; c) pedipalp.

possess many lobes and setae which is the basic form of the ovipositor of oribatid mites.

Deutonymph: The integument of the deutonymph is sclerotized as in the adult but it is lighter in colour. There are eight pairs of notogatal setae as in the adults although some of them are not fully developed. The setae on the venter are also poorly developed and fewer than in the adults (fig. 6). No setae were observed on the genital plates. The anal plates are distinct from the adanal plates and each pair bears two pairs of setae. The most notable difference between the deutonymph and the adult is the organisation of the ano-genital region. The genital plates are elongated and contiguous with the equally elongated anal and adanal plates thus producing an ano-genital aperture as in adult Euphthiacoidea.

3. Discussion

Mesoplophora as a genus is a good example of a taxonomic group that must be defined by a combination of characters. This genus possesses the traits of both lower and higher Oribatida. For example, features shared with the lower Hypochthoniidae include the following: two pairs of exobothridial setae, anathric infracapitulum, small or poorly developed rutella, triplet setae on the tip of the pedipalp and sclerotized nymph. Features shared with the Phthiracarids are the pythoid exoskeleton and spines on the chelicera. The separation of anal and ventral plates in adults is a brachypylina (higher Oribatida) trait which is not possessed by any other group of lower Oribatida.

Five species of *Mesoplophora* have been described from the Palaearctic region (BALOGH & MAHUNKA 1983). One of these five species, (*M. pulchra*) was first

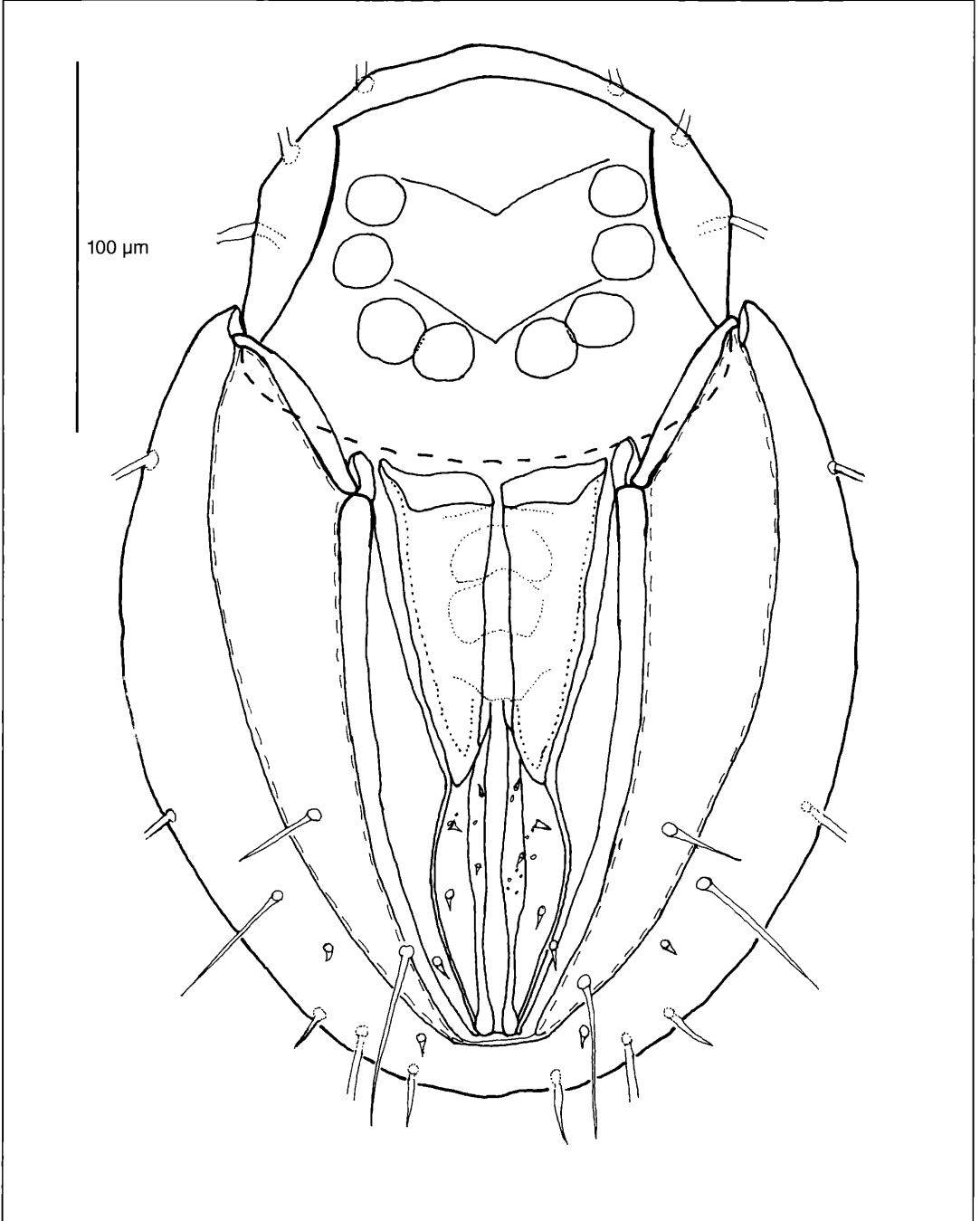


Figure 6. *Mesoplophora ifeana* BADEJO, new species: ventral view of the Deutonymph.

recorded from Morocco in the Ethiopian region (GRANDJEAN 1933). The only species of *Mesoplophora* that has been described from the tropical rainforest zone is *M. africana* which was first described by BALOGH (1958) and later redescribed by MAHUNKA (1985). However, there are a few differences in the morphological features of *M. africana* and *M. ifeana* such as the number of spines on the sensillus (13-15 in *M. africana*, 18 in *M. ifeana*) and presence of two pairs of exobothridial setae in *M. ifeana*. There are also discrepancies in the description of certain morphological features such as chaetotaxy of the ventral plates and the nomenclature of setae on the aspis. Comparison of *M. africana* and *M. ifeana* can never be detailed enough without reference to the type specimens of BALOGH & MAHUNKA. The descriptions of *M. africana* by these workers reveal nothing about many features of taxonomic interest in the adults and deutonymphs of *Mesoplophora* which we have highlighted in this study. It thus appears as if the option of establishing a separate identity for the specimens collected from Ile-Ife in Nigeria seems the most appropriate for now.

Acknowledgement

We are grateful to the Alexander-von-Humboldt-Stiftung (AvH) for awarding the George-Foster-Research Fellowship to M.A. BADEJO which made it possible for us to work together at the State Museum of Natural History in Karlsruhe/Germany where this study was carried out.

4. Literature

- BADEJO, M.A. & LASEBIKAN, B.A. (1988): Comparative studies of the acarine populations of a secondary regrowth forest and a cassava plantation in Ile-Ife, Nigeria. – *Pedobiologia*, **32**: 111-116.
- BADEJO, M.A., MAKINDE, A.S. & VAN STRAALEN, N.M. (1999): The oribatid mite fauna of top soil under different vegetation cover in Ile-Ife, Nigeria. – *Trop. Ecol.*, **40** (2): 275-280.
- BALOGH, J. (1958) Oribates nouvelles de l'Afrique tropicale. – *Rev. Zool. Bot. Afr.*, **58**: 1-34.
- BALOGH, J. (1972): *The Oribatid Genera of the World*. – 188 pp., 71 pl.; Budapest (Akademiai Kiado).
- BALOGH, J. & MAHUNKA, S. (1983): *Primitive Oribatids of the Palaearctic Region*. – 372 pp.; Amsterdam (Elsevier).
- GRANDJEAN, F. (1933): Oribates de l'Afrique du Nord (I. Serie). – *Bulletin de la Societe d'Histoire Naturelle de l'Afrique du Nord*, **24**: 308-323.
- GRANDJEAN, F. (1965): Nouvelles observations sur les oribates (4. Serie). – *Acarologia*, **7**(1): 91-112.
- MAHUNKA, S. (1985): Description and redescription of Ethiopian oribatids (Acari, Oribatida)., – II. *Annales Historico-Naturales Musei Nationalis Hungarici*, **77**: 233-249.

ADALBERTO J. SANTOS & ANTONIO D. BRESCOVIT

A revision of the South American spider genus *Aglaoctenus* TULLGREN, 1905 (Araneae, Lycosidae, Sosippinae)

Abstract

The wolf spider genus *Aglaoctenus* is revised, and of the 12 original species only two are considered valid: *A. castaneus* (MELLO-LEITÃO) and *A. lagotis* (HOLMBERG). Eight specific names are considered junior synonyms of *A. lagotis*: *Porrimoso granadensis* (KEYSERLING), *P. freiburguensis* (KEYSERLING), *P. diversa* (O.P.-CAMBRIDGE), *P. obscura* (KEYSERLING), *P. glieschi* (MELLO-LEITÃO), *P. callipoda* (MELLO-LEITÃO), *Aglaoctenus bifasciatus* TULLGREN and *A. harknessi* (CHAMBERLIN). *Aglaoctenus guianensis* CAPORACCO, described based on an immature specimen from French Guyana is considered species inquirenda and *Porrimoso securifera* TULLGREN, based on a female specimen from Argentina is transferred to *Orinocosa* CHAMBERLIN. The *Aglaoctenus* species are distributed exclusively in South America, except Chile.

Resumo

O gênero *Aglaoctenus* é revisado e de suas 12 espécies originais, apenas duas são consideradas válidas, *A. castaneus* (MELLO-LEITÃO) e *A. lagotis* (HOLMBERG). Oito nomes específicos são aqui sinonimizados com *A. lagotis*: *Porrimoso granadensis* (KEYSERLING), *P. freiburguensis* (KEYSERLING), *P. diversa* (O.P.-CAMBRIDGE), *P. obscura* (KEYSERLING), *P. glieschi* (MELLO-LEITÃO), *P. callipoda* (MELLO-LEITÃO), *Aglaoctenus bifasciatus* TULLGREN e *A. harknessi* (CHAMBERLIN). *Aglaoctenus guianensis* CAPORACCO, descrito com base em um imaturo da Guiana é considerada espécie inquirenda e *Porrimoso securifera* TULLGREN, descrita com base em uma fêmea da Argentina é transferida para *Orinocosa* CHAMBERLIN. As espécies de *Aglaoctenus* estão distribuídas exclusivamente na América do Sul, com exceção do Chile.

Authors

M. Sc. ADALBERTO J. SANTOS & Dr. ANTONIO D. BRESCOVIT, Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil 1500, CEP 05503-900, São Paulo, SP, Brazil; e-mail: oxyopes@yahoo.com

Key words

Araneae, Lycosidae, Sosippinae, *Aglaoctenus*, *Porrimoso*, South America, taxonomy

1. Introduction

This study revises a group with a long and confusing taxonomic history, that began with the proposition of the genus *Porrima* by SIMON (1898). This genus was based on *Podophthalma diversa* CAMBRIDGE, 1877, and diagnosed by the procurved anterior eye row and the presence of 4 teeth on the posterior margin of the cheliceral fang furrow. During the next 50 years, the

genus increased in number of species with the description of *P. harknessi* CHAMBERLIN, 1916, *P. glieschi* MELLO-LEITÃO, 1926, *P. callipoda* MELLO-LEITÃO, 1934, and *P. castanea* MELLO-LEITÃO, 1942, and with the transference of *Ocyale lagotis* HOLMBERG, 1876. Moreover, MELLO-LEITÃO (1947) informally transferred all South American species assigned to the pisaurid genus *Tetragonophthalma* KARSCH, 1878 to *Porrima*, with no justifications or even a list of these species. Currently, four South American species have been assigned to *Tetragonophthalma*: *T. spinipes* TACZANOWSKI, 1873, *T. granadensis* KEYSERLING, 1876, *T. freiburguensis* KEYSERLING, 1877, and *T. obscura* KEYSERLING, 1891. Since MELLO-LEITÃO presents no evidence that the type specimens of these species were examined, we suppose the transference was based on their original descriptions. Obviously, MELLO-LEITÃO's concept of *Porrima* was too ample, since one of those species, *T. spinipes*, was posteriorly transferred to *Staberius* SIMON, 1898, a pisaurid genus, by CARICO (1981).

Although *Porrima* was originally placed in Lycosidae by SIMON, it's taxonomic position was confusing. Many species posteriorly transferred to this genus came from Pisauridae, and *Porrima* itself was considered a pisaurid by LEHTINEN (1967). Part of this confusion can be attributed to the genus's pisaurid eye pattern, together with a lycosid genitalia. Another confusing character of this group and probably the reason why MELLO-LEITÃO (1941a) considered *Porrima* as an "intermediate" genus between the Lycosidae and Age-lenidae, is the funnel-web constructed by the spiders. The generic classification of this group of species changed considerably during the 50's, when ROEWER published important papers on lycosid classification. In 1954b, he proposed a new genus, *Porrimula*, for *P. callipoda*, based on the fact that the distance between the posterior median eyes is equal to the eye diameter, while in other species of the group this distance is smaller than the eye diameter. In ROEWER's classification, *Porrimula* and *Porrima* are united by the presence of four teeth in the cheliceral fang furrow's posterior margin. In 1959 he transferred the species with 3 teeth to a new genus, *Porrimoso*, including *P. harknessi*, *P. castanea*, *P. glieschi* and *P. lagotis*. The genus *Porrima* was maintained, including only *P. diversa* and *P. granadensis*.

ROEWER's partition of the genus *Porrima* was discussed by CAPOCASALE (1982), in the most recent revision of this group. CAPOCASALE shows that the character "four teeth in cheliceral fang furrow" was an early perpetuated error, since the syntypes of *P. diversa*, the specimens used by SIMON to describe *Porrima*, and 97.6% of the material examined by him possess only three teeth. Based on these observations, the two genera described by ROEWER are considered subjective junior synonyms of *Porrima*. Nevertheless, this name, the earliest one available for the group, could not be used because it was preoccupied by a Lepidoptera species 21 years before SIMON's description (NEAVE 1940). To solve this homonymy, CAPOCASALE preferred to use the name *Porrmosa* ROEWER, 1959, since he considered the earlier *Porrimula* ROEWER, 1954 a nomen dubium. That was because, at the time, the holotype of *P. callipoda*, was erroneously considered lost.

CAPOCASALE (1982; 1991) considered only three valid species in the genus: *P. lagotis*, *P. castanea* and *P. harknessi*. All other species described in the group were considered as species inquirendae since their immature or lost type specimens do not permit their proper recognition. The same happened to *Isohogna securifer* (TULLGREN, 1905), transferred erroneously to *Porrmosa* and considered species inquirenda by CAPOCASALE (1982).

Two new species were included in this genus when CARICO (1993) transferred *Aglaoctenus* TULLGREN, 1905 from Pisauridae to Lycosidae and considered it a junior synonym of *Porrmosa*. This transfer was based on the examination of the holotype of *A. bifasciatus* TULLGREN, 1905, the type species of the genus, and also included *A. guianensis* CAPORACCIO, 1954. As stated by PLATNICK (1997), the name *Aglaoctenus* has priority over *Porrmosa*, and consequently, in contrast to the statement of CARICO (1993), must be considered the senior synonym.

In this paper, we present a new revision of this genus, which so far included 11 nominal species. After examining more than 300 specimens from several South American locations and the majority of the type species, we came to the conclusion that all these specimens are best placed in two species, which are described herein.

2. Material and Methods

In this study, we examined specimens deposited in the following collections: AMNH, American Museum of Natural History, New York (N. I. PLATNICK); BMNH, Natural History Museum, London (J. BECCALONI); FSCA, Florida State Collection of Arthropods, Gainesville (G. B. EDWARDS); IBSP, Instituto Butantan, São Paulo (A.D. BRESOVIT); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (C. SCIOSCIA); MUSM, Museo de Historia Natural, Universidad Mayor de San Marcos, Lima (D. SILVA-

DÁVILA, G. LAMAS); MHNM, Museo de Historia Natural de Montevideo, Montevideo (R. M. CAPOCASALE); MLP, Museo de La Plata, Facultad de Ciencias Naturales, La Plata (C. SUTTON DE LICITRA); MCN, Museu de Ciências Naturais, Fundação Zoológica do Rio Grande do Sul, Porto Alegre (E.H. BUCKUP); MCP, Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A.A. LISE); MHCI, Museu de História Natural "Capão do Imbuia", Curitiba (J.C. MOURA-LEITE); MNRJ, Museu Nacional, Rio de Janeiro (A.B. KURY); MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, (E. CANCELLO); MCZ, Museum of Comparative Zoology, Harvard University, CAMBRIDGE (L. LEIBENSPERGER); MNHN, Muséum National de Histoire Naturelle, Paris (C. ROLLARD); USNM, National Museum of Natural History, Smithsonian Institution, Washington (J.A. CODDINGTON); NHRM, Naturhistoriska Riksmuseet, Stockholm (T. KRONESTEDT); SMNK, Staatliches Museum für Naturkunde Karlsruhe (H. HÖFER); UEFS, Universidade Estadual de Feira de Santana, Feira de Santana (E. XAVIER); UNESP, Universidade Estadual Paulista, Campus de Botucatu, Botucatu (I. M. P. RINALDI).

Male palpi were expanded by immersion in 10% KOH solution followed by immersion in water. To describe the internal structure of the female genitalia, epigynes were removed and placed in a 10% KOH solution for ~ 10 min. and examined in clove oil (LEVI, 1965). All measurements, except eye sizes and interdistances, were taken with a dial caliper, and are in mm. Descriptions and abbreviations follow BRESOVIT & HÖFER (1994). The terminology of genitalic structures follows BRADY (1962) and SIERWALD (2000).

3. Systematics

Aglaoctenus TULLGREN, 1905

- 1898 *Porrima* SIMON: Hist. Nat. Araignées, 2: 327 (type species by original designation *Podophthalma diversa* O. P.-CAMBRIDGE, 1877); name preoccupied (NEAVE 1940)
- 1905 *Aglaoctenus* TULLGREN: Ark. Zool., 2: 52 (type species by monotypy *A. bifasciatus* TULLGREN, 1905)
- 1954 *Porrimula* ROEWER: Katalog der Araneae, 2: 313 (type species by monotypy *Porrima callipoda* MELLO-LEITÃO 1934)
- 1959 *Porrmosa* ROEWER: Exploration du Parc National de L'Upemba, 30: 1001-1002
- 1967 *Porrima* - LEHTINEN: Ann. Zool. Fenn., 4: 260 (transferred to Pisauridae)
- 1982 *Porrimula* - CAPOCASALE: J. Arachnol., 10: 146 (nomen dubium, considered junior synonym of *Porrmosa*)
- 1982 *Porrmosa* - CAPOCASALE: J. Arachnol., 10: 148 (new name for *Porrima*)
- 1989 *Porrmosa* - PLATNICK: Adv. Spider Taxonomy 1981-1987: 386-387
- 1990 *Porrmosa* - CAPOCASALE: J. Arachnol., 18: 139
- 1991 *Porrmosa* - CAPOCASALE: J. Arachnol., 19: 93
- 1993 *Aglaoctenus* - CARICO: J. Arachnol., 21: 231 (transferred from Pisauridae to Lycosidae)
- 1993 *Porrmosa* - PLATNICK: Adv. Spider Taxonomy 1988-1991: 506
- 1997 *Aglaoctenus* - PLATNICK: Adv. Spider Taxonomy 1992-1995: 539

Diagnosis

Aglaoctenus is very close to *Sosippus* SIMON, 1888 by the presence of a curved lateral apophysis in the conductor (fig. 4: LAC, apophysis b of *Sosippus* in SIERWALD 2000) of the male palpus and the spermathecae divided in two branches in the female genitalia. Males of *Aglaoctenus* can be differentiated from *Sosippus* males by the anterior eye row, which is much more curved in *Aglaoctenus* and by the lateral eyes positioned on tubercles (see BRADY 1962: figs 10-11); the absence of a projection on the ventral section of the tegulum (apophysis c in SIERWALD 2000: fig. 9) and the smaller and less sclerotized median apophysis in male palps (figs 3b,f; 4a). Females of *Aglaoctenus* differ from *Sosippus* by the inverted T-shaped median septum of the epigynum (median field of *Sosippus* in SIERWALD 2000) covered by plumose hairs (figs 3c,d).

Description

Total length 10.1 – 20.1 (males) and 10.3 – 24.0 (females). Carapace oval, narrowest anteriorly, widest between coxae II and III, cephalic region as high as thoracic, sulcated posteriorly. Coloration variably dark, with a clear v-shaped band between the posterior part of the carapace and the PLE, covered with scattered dark hairs and with marginal white to yellowish bands (Plate 1, figs a and b) and white hairs. Thoracic groove longitudinal, with conspicuous dorsal grooves. From above, anterior eyes in procurved row and posterior ones recurved. All eyes dark, surrounded by black rings. Lateral eyes on tubercles, anterior laterals ventrally directed. AME separated by 0.7 their diameter and by 1.5 their diameter from the ALE; PME almost one diameter apart and 1.3 their diameter from the PLE. Clypeus height between 1.5 and 2 times the AME diameter. Chilum present, subtriangular, with a central notch and covered by short hairs. Chelicerae robust, usually darker than the carapace, covered by short white and long black hairs (also present, but more scattered, in the clypeus and ocular area), and with three promarginal and three retromarginal teeth (fig. 1a). Cheliceral boss present, glabrous, clearer than the chelicerae and carapace. Fangs dark, half the length of the chelicerae. Endites rectangular, not notched, distally rounded and with anteromedian scopula. Labium longer than wide, truncated anteriorly, with lateral notches on the proximal half. Sternum as long as wide, posteriorly triangular, with its tip reaching between the coxae IV. Sternum, labium, coxae and trochanters with long black hairs. Female palpus with cylindrical tarsus, a pectinate claw with at least three teeth (fig. 1c), scopulae on the distal half, and with the following spination: femur d1-1-1 r0-0-1 p0-0-1, patella p1, tibia d1, p1, tarsus d1, r0-1 p1-1. Leg formula 4123.

Leg spination pattern (only surfaces with spines): femur I d1-1-1 r1-1-1 p0-1-1, II d1-1-1 p1-1-1 r1-1-1-1,

III d1-1-1 p1-1-0 r1-1-1-1; IV d1-1-1, p1 1-1-1 r0-0-1; patella II p1, III d0-1 p1 r1, IV d0-1 r1; tibia I d1-1-0 p1-1-0 r1-1-0 v2-2-2, II p1-1-0 r1-1-0 v2-2-2, III p1-1-0 r1-1-0 v 2-2-2, IV d0-1-0 p1-1-0 r1-1-0 v2-2-2; metatarsus I p0-1-1 r0-1-1 v2-2-2, II, III and IV p1-1-1 r1-1-1 v2-2-2. Scopulae of tarsi with long lateral and short ventral hairs. Trichobothria with long trichoma, bothrium with semicircular ring presenting thin grooves (fig. 1b), in one dorsal row on metatarsi and tarsi. Tarsi with three claws, superior claws pectinate, unpaired claw with three teeth (fig. 1d). Abdomen oval, longer than wide, pilose, dark, dorsally with 2 marginal and 7 transversal white bands, which are sometimes interrupted (Plate 1, figs a and b). Anterior dorsal red spot present, pronounced in some specimens. Venter of abdomen creamy, with two marginal rows of dark spots. Colulus present, pilose. Six spinnerets, PLS longer than anterior laterals. Anterior lateral spinnerets conical, contiguous at base, two-segmented, distal segment short, truncate, with two large (in females, fig. 2d, AGS) and one large and tartiporous (in males, fig. 2a, TA) major ampullate gland spigots on mesal margin and 70-80 small piriform gland spigots (PGS). Posterior median spinnerets contiguous, one-segmented; males with 30-40 aciniform gland spigots (ACS) and two minor ampullate gland spigots (not visible in fig. 2b); females with two large cylindrical gland spigots (CGS) with conical base and enlarged shafts and 30-40 aciniform gland spigots (fig. 2e, ACS). Posterior lateral spinnerets long, tubular, two-segmented; distal segment short, with about 30 aciniform gland spigots (figs 2c,f). Anal tubercle triangular and prominent.

Male palpus with retrolaterally curved tibia. Cymbium oval, elongated and distally narrowed, densely pilose. Subtegulum rounded, positioned in the mesal-proximal portion of the tegulum (fig. 4a). Conductor (C) flattened, concave, with a hyaline projection and a curved and strongly sclerotized lateral apophysis (LAC, tegular apophysis a and b of *Sosippus* in SIERWALD 2000). Median apophysis (MA) reduced, forming a triangular lamina close to the apex of LAC. Embolus (E) long, with wide base (EB, palea region in SIERWALD 2000), running counter-clockwise in the left palpus. Epigynum (figs 3c,d) pilose, with a strongly sclerotized inverted T-shaped median septum (median field of *Sosippus* in SIERWALD 2000) covered with plumose white hairs. Internal genitalia (figs 6e; 7e) with spermathecae divided in a lobulate copulatory bursa (B, vulval chamber in SIERWALD 2000), and a curved seminal receptacle (SR, head of spermathecae in SIERWALD 2000). Fertilization ducts short and narrow.

Composition

Two species occurring in all South America, except Chile (fig. 8).

Natural History

Aglaoctenus species are semelparous spiders with an annual life cycle. The reproductive season varies regionally. In *A. lagotis* it begins in May in southeastern Brazil (SORDI 1996) and in October in the Argentinean chaco (BUCHER 1974). In *A. castaneus*, mating pairs have been seen on the webs in July in the State of Espírito Santo (southeastern Brazil) and Rio Mapiá, Amazonas (western Brazilian Amazon, ADB, pers. obs.), but only tiny juveniles were present in the same period in central Amazonia (AJS, pers. observ.).

At the beginning of the reproductive season the adult males abandon their webs and move on the ground or through the understorey vegetation searching for female webs (BUCHER 1974). The males, sometimes more than one, live in the female's web during an

unknown period of time, during which copulation occurs (AJS & ADB, pers. observ. for both species). The males generally abandon the female's web, or die, before the egg sac is deposited. Females of *A. lagotis*, carrying the spherical egg sacs attached to the spinnerets (a typical behavior of lycosids), were observed by SORDI (1996) from August onwards in southeastern Brazil and from February onwards by BUCHER (1974) in Argentina. After having emerged from the egg sacs, the spiderlings are carried on the female's dorsum for approximately 5 days (SORDI 1996). After this short period of maternal care, the juveniles disperse, building their webs close to the natal web.

The webs of *Aglaoctenus* are composed of a funnel-shaped silk tube that connects a retreat to a horizontal non-adhesive sheet with width and length between 4.5 and 90 cm. This sheet is attached to the vegeta-

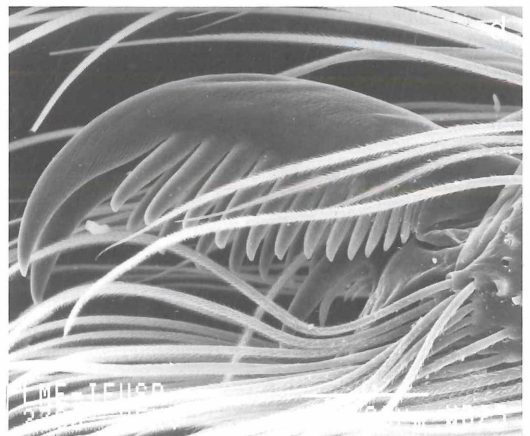
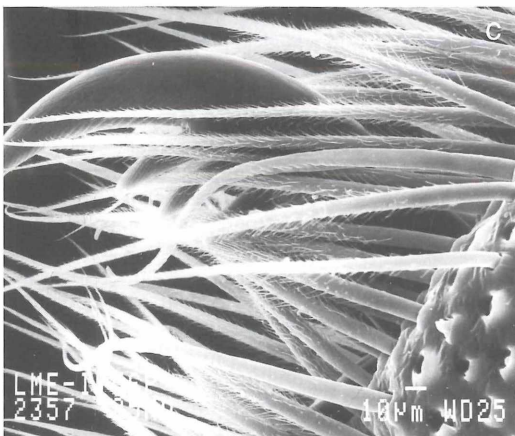
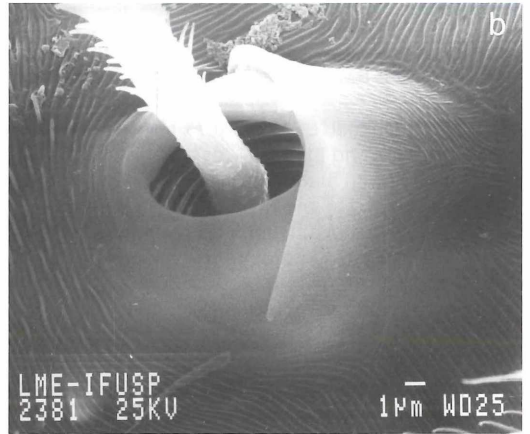
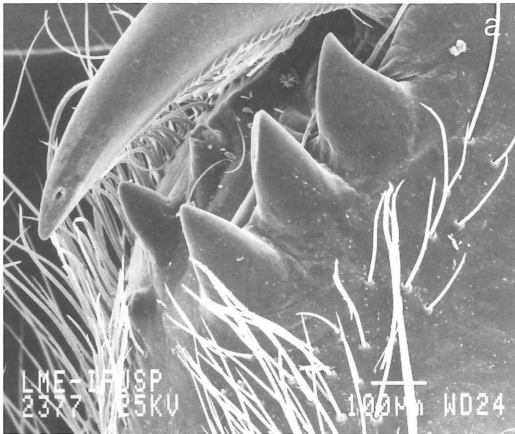


Figure 1. *Aglaoctenus* spp.: a) male cheliceral teeth; b) trichobothria, leg I of female; c) pedipal claw of female; d) tarsal claws of female leg I.

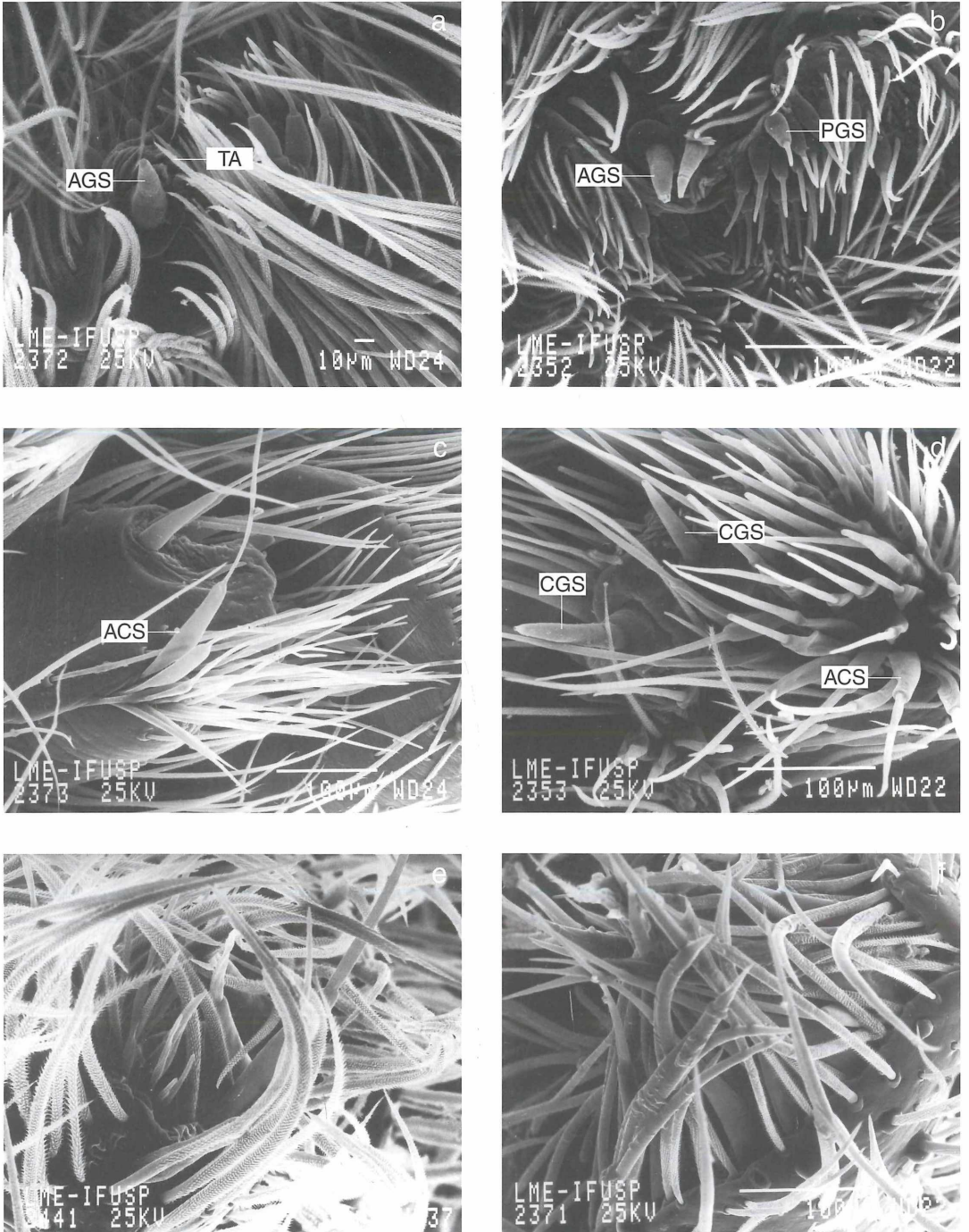


Figure 2. *Aglaoctenus* spp., male: a) anterior lateral spinnerets; b) posterior median spinnerets; c) posterior lateral spinnerets; female: d) anterior lateral spinnerets; e) posterior median spinnerets; f) posterior lateral spinnerets. (ACS, aciniform gland spigot; AGS, ampulate gland spigot; CGS, cylindrical gland spigots; PGS, piriform gland spigot; TA, tartipore).

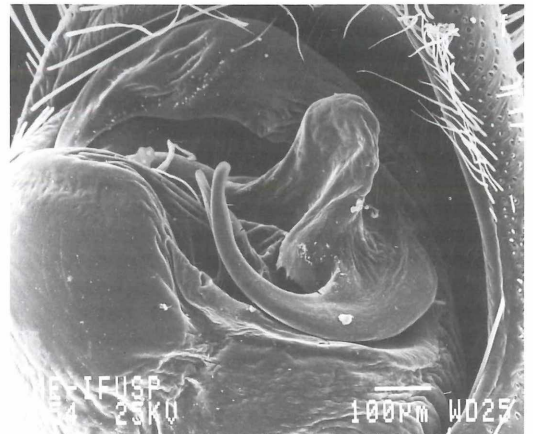
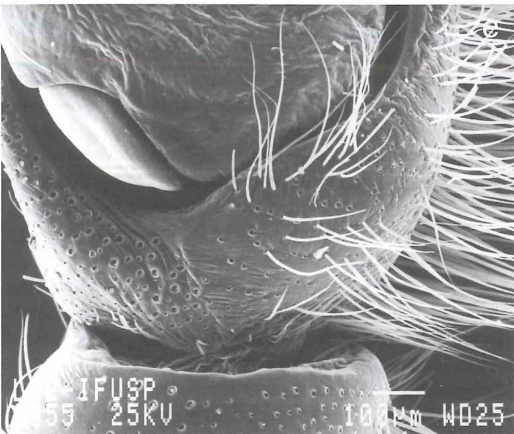
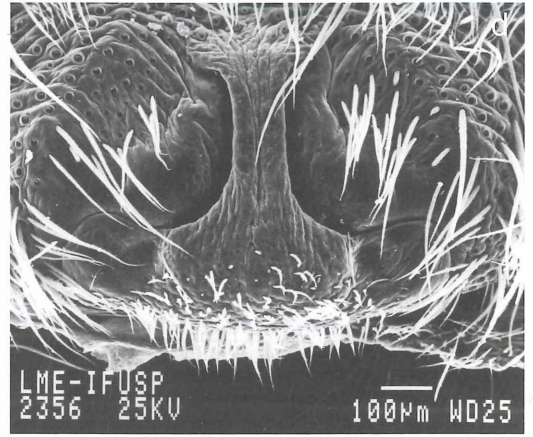
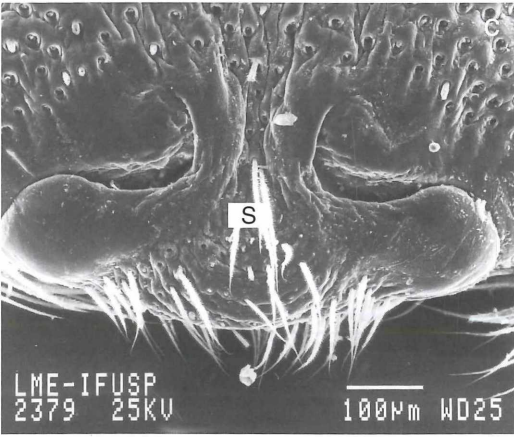
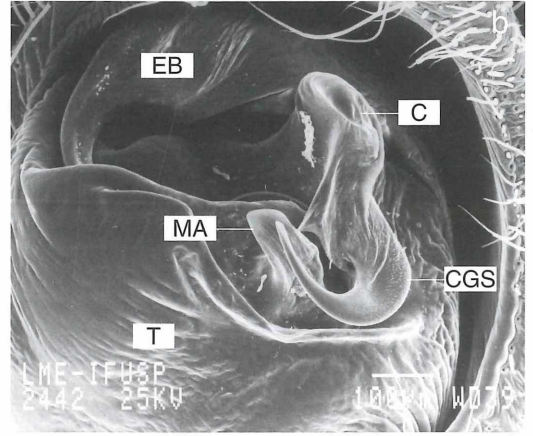
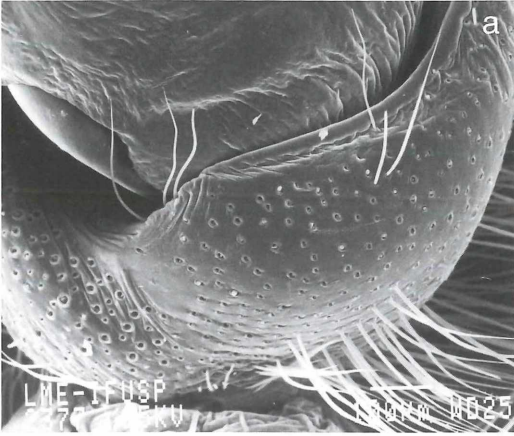


Figure 3. *Aglaoctenus castaneus* (MELLO-LEITÃO), male palp: a) base of cymbium, ventral; b) apex of bulb, ventral; female: c) epigynum, ventral; *A. lagotis* (HOLMBERG), female: d) epigynum, ventral; male palp: e) base of cymbium, ventral; f) apex of bulb, ventral, (C, conductor; EB, embolus base; LAC, lateral apophysis of conductor; MA, median apophysis, S, septum; T, tegulum).

Plate 1. *Aglaoctenus castaneus* (MELLO-LEITÃO): a) male, dorsal view; b) female, dorsal view; c) web in a bromeliad; d) *A. lagotis* (HOLMBERG): web in trunks.



tion with a series of vertical barrier threads. The spiders wait for prey at the funnel entrance, looking towards the sheet, during the day and at night (AJS, pers. obs.). In this position, the spiders can attack insects that fall on the sheet and flee to the retreat if they feel disturbed. Captured prey is consumed at the funnel entrance, inside the silk tube or in the retreat. This web type can capture a great variety of prey, mostly insects. SORDI (1996) recorded insect prey of 10 orders for *A. lagotis*, being Hymenoptera, Heteroptera and Diptera the most common items. The size of the captured prey varied up to 2.8 cm in length. A female *A. castaneus* was observed eating a tiny litter frog in southeastern Brazil (G. MACHADO, pers. comm.). For records of structures used to build the webs, see natural history notes under each species description.

Species recognition

The species of *Aglaoctenus* can be distinguished mainly by genitalic characters. Using these characters (see details below) we recognize two species. Differences in coloration or size can be observed between specimens collected from different localities but high variation within a population is also commonly observed in both species. The extreme variation in non-genitalic characters posed a problem to find the early names available for each species and their junior synonyms, since most species were described based on juvenile specimens. It was solved mapping the species distribution and type localities of the nominal species (fig. 8). This procedure was facilitated by the virtual absence of sympatry between the two species observed.

The *Aglaoctenus* species differ in the relative size of the male legs. After measuring the length of patella plus tibia of leg I and the carapace width of all specimens examined and calculating the ratio between those two measurements (leg-carapace ratio in species diagnosis; fig. 5), the difference between *A. castaneus* and *A. lagotis* was significant in males (fig. 5a). Although the same relationship was observed in females, the ratios overlapped and the difference was not significant (fig. 6b).

Another important diagnostic character is the shape of the male median apophysis. Although the differences in this structure may be considered too tenuous to distinguish the species, it is considered important for three reasons. First, the character is not so variable as others (including female genitalia, see below). Second, the shape of the male median apophysis is commonly used for the identification of lycosid species (see examples in DONDALE & REDNER 1990), and in this genus, this character may appear too tenuous only because the median apophysis is small. Third, the courtship behavior and cross-breeding studies in other groups of wolf spiders have shown that small variations in the male genitalia can indicate reproductively

isolated species (e.g. KRONESTEDT 1990, TÖPFER-HOFMANN et al. 2000).

The female epigynum presents some variation in its structure (even within the same population; figs 5c,d; 7c,d), but is still useful for species recognition. CAPOCASALE (1982, 1991) used characters of the internal genitalia to separate the species. The main distinctive characters used by him were the number and shape of copulatory bursa (CAPOCASALE 1982: figs 1, 3; 1991: fig. 7). However, after examining a great number of specimens we concluded that the later character is very variable. Copulatory bursae occur in at least two shapes in both species, rounded (fig. 5e) or triangular (fig. 7e). We suppose that the shape depends upon the variable volume of sperm in the bursa after copulation, as it was demonstrated for *Nephila clavipes* LINNAEUS by HIGGINS (1989). The triangular form probably represents the empty the round form the filled condition.

Unrecognizable species

Aglaoctenus guianensis CAPORIACCO, 1954: 58 (immature holotype from Charvein, French Guyana, BENOIST col., 1914, in MNHN, examined). It was impossible to determine the identity of this species due to the scarcity of material from northern South America. No other specimens from French Guyana could be obtained for comparison.

Misplaced species

Lycosa securifera TULLGREN, 1905: 66, pl. 8 fig. 32 (immature holotype from Moreno, Jujuy, Argentina, NHRM, examined), placed in *Isohogna* by ROEWER (1954b) and transferred to *Porrimosa* by CAPOCASALE (1982). This species is herein transferred to *Orinocosa*, based on characters cited in CHAMBERLIN (1916), such as tarsi ventrally setose, without scopulae; tibia I with three pairs of ventral spines, the distal one reduced; tibiae III and IV with a dorsal stout median apical and a median basal spine; and similar epigynum shape (see CHAMBERLIN 1916: plate 24, fig. 8).

New combination.

Aglaoctenus castaneus (MELLO-LEITÃO, 1942)

Plate 1a-c; figures 3a-c; 4a; 5a-e; 6a-b; 8

- 1942 *Porrima castanea* MELLO-LEITÃO: Rev. Bras. Biol., **2**: 432-433, fig. 6 (female holotype from La Merced, San Martin, Peru, P. J. SOUKUPI col., deposited in MNRJ 13514, examined)
- 1959 *Porrimosa castanea* – ROEWER: Exploration du Parc National de L'Upemba, **30**: 1002, 1005
- 1961 *Porrimosa castanea* – ROEWER: BULL. INST. SCI. NAT. BELGIQUE, **37**: 16
- 1982 *Porrimosa castanea* – CAPOCASALE: J. Arachnol., **10**: 148-149, figs 1-2, 12, 14
- 1990 *Porrimosa castanea* – CAPOCASALE: J. Arachnol., **18**: 139
- 1991 *Porrimosa castanea* – CAPOCASALE: J. Arachnol., **19**: 94, 96, figs 4-5, 8 (description of the male)
- 1993 *Porrimosa castanea* – PLATNICK: Adv. Spider Taxonomy 1992-1995: 506

Diagnosis

The males of this species can be distinguished from *A. lagotis* by the wider median apophysis (figs 3b; 5a,b) and more conspicuous base of cymbium of the male palp (figs 3a; 5a) and by the leg-carapace ratio lying between 2.2 and 2.9. The female epigynes differ by the T-shaped septum, which is shorter longitudinally and wider transversally, with a more pronounced convex projection in the center (figs 3c; 5c,d).

Description

Male (Linhares, Espírito Santo, Brazil). Carapace orange, cephalic region red, with a clear orange median y-shaped band. Chelicerae dark brown, endites orange, labium dark brown. Sternum and legs orange, legs clearer on the ventral side, metatarsus and tarsus red. Abdomen dark gray, including the folium, with a red anterior dorsal spot. Venter of abdomen with lateral longitudinal rows of spots. Spinnerets red. Total length 18.0, carapace 7.7 long, 5.7 wide. Clypeus 0.7 high, almost twice the AME diameter. Eye sizes and interdistances: AME 0.33, ALE 0.52, PME 0.44, PLE 0.47, AME-AME 0.19, AME-ALE 0.5, PME-PME 0.47, PME-PLE 0.58. MOQ length 0.88, front width 0.86, back width 1.41. Chelicerae 2.63 long with 4 promarginal and 3 retromarginal teeth. Abdomen 9.0 long, 3.6 wide.

Length of leg segments: I - femur 2.27/ patella 0.77/ tibia 2.22/ metatarsus 2.25/ tarsus 0.94/ total 8.45/ II - 2.13/ 0.69/ 2.08/ 2.11/ 0.8/ 7.83/ III 1.94/ 0.58/ 1.72/ 1.91/ 0.72/ 6.88/ IV - 2.52/ 0.61/ 2.27/ 2.33/ 1.14/ 8.88. Leg spination following the typical pattern. Palpus with the typical structure of the genus, with a triangular median apophysis, widest at base (figs 3b; 5a).

Female (same locality as male). Carapace brown, cephalic area dark brown, laterally red, lateral and median band orange, area around thoracic groove black. Chelicerae dark brown, endites red, labium brown. Sternum and legs red, metatarsi and tarsi darker than the other segments. Abdomen grayish, with a dark folium delimited by creamy lateral bands. Spinnerets dark brown. Total length 23.0, carapace 9.0 long, 6.5 wide. Clypeus 0.94, equal to 1.3 AME diameter. Eye sizes and interdistances: AME 0.72, ALE 0.94, PME 0.94, PLE 0.94, AME-AME 0.5, AME-ALE 1.0, PME-PME 0.94, PME-PLE 1.1. MOQ length 2.2, front width 1.8, back width 2.9. Chelicerae 2.8 long with 4 promarginal and 3 retromarginal teeth. Abdomen 12.5 long, 6.3 wide.

Length of leg segments: I - femur 3.94/ patella 1.55/ tibia 3.77/ metatarsus 3.5/ tarsus 1.05/ total 13.81/ II - 3.94/ 1.44/ 3.5/ 2.94/ 1.38/ 13.21/ III - 3.55/ 1.22/ 2.83/ 3.05/ 1.22/ 11.88/ IV - 4.66/ 1.16/ 4.05/ 5.0/ 1.83/ 16.72. Leg spination following the typical pattern. Epigynum typical for the genus (figs 3c; 5c-e).

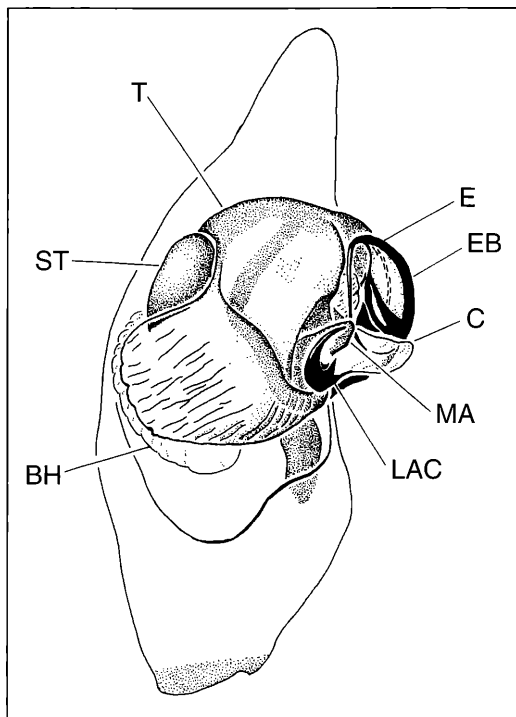


Figure 4. *Aglaoctenus castaneus* (MELLO-LEITÃO): a) expanded male palp (BH, basal haematodocha; C, conductor; E, embolus; EB, embolus base; LAC, lateral apophysis of conductor; MA, median apophysis, ST, subtegulum; T, tegulum). Scale line: 0.5 mm.

Variation

Coloration varies from red to dark, almost black. Amazonian specimens are usually darker and males show a more conspicuous red spot on the abdomen than the specimens from other localities. Some specimens present a longitudinal black y-shaped band on the venter of the abdomen, from the epigastric furrow to the anterior margin of the spinnerets (see CAPOCASALE 1982: fig. 12). Immatures from Amazonian forests have red carapaces and black abdomens (see HÖFER & BECK 1996: fig. 21). Variation in total length: females 14.2 - 24.0 (N=55), males 11.9 - 20.1 (N=43).

Natural History

This species is recorded mainly from humid forests. Webs were observed on two species of palms (*Attalea* sp. and *Astrocaryum aculeatissimum*) in Reserva Florestal de Linhares and Estação Biológica de Poço das Antas, southeastern Brazil (AJS, pers. obs. and F.N. RAMOS, pers. comm.). On the Ilha do Cardoso, also in southeastern Brazil, webs were observed on bromeliads (*Vriesea* sp.) in a restinga vegetation area (Plate 1 c) (G. MACHADO, pers. comm.). Juveniles were observed

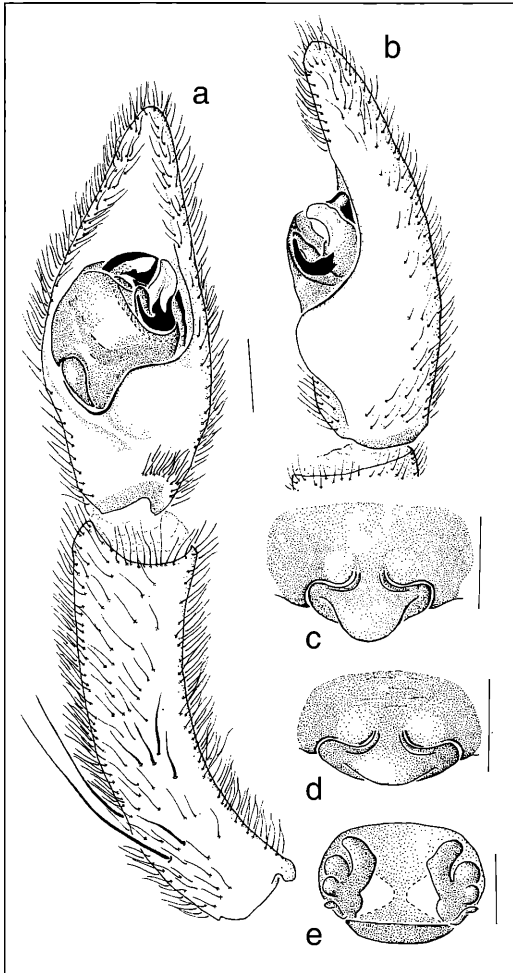


Figure 5. *Aglaoctenus castaneus* (MELLO-LEITÃO), male: a) palp, ventral view; b) retrolateral view; female epigyna: c) ventral view, specimen from Linhares, Espírito Santo, Brazil; d) ventral view, specimen from Manu, Madre de Diós, Peru; e) dorsal view, specimen from Linhares, Espírito Santo, Brazil. Scale lines: 0.5 mm.

with webs in the litter in the Smithsonian Reserve at km 41 in central Amazonia (G. F. DUTRA, pers. comm.).

Distribution

Ecuador and northern Peru, northern, northeastern and southeastern Brazil (fig. 8).

Material examined

Ecuador. no locality, 1♀ 1juv (MCZ).
Peru. Loreto: 2♂ 3♀, 13.VIII.1998, D.S.DÁVILA col. (MUSM); Jenaro Herrera, 04° 55' S, 73° 45' W, 1♂, XII.1990, B. HAKQUIZIEV col. (MUSM); Cuzco: Machu Pichu (bamboo/cloud

forest, 2400 m), 1♀, 16.X.1987, J.A.CODDINGTON col. (USNM); Cashiriari, 1♂, 25.XI.1997, S.CORDOVA col. (MUSM); Madre de Dios: Zona Reservada de Manu, puesto de vigilancia Pakitza, 11°58'S 71°18'W, 1♀, 28.IX.1987, D.SILVA & J.A.CODDINGTON col. (USNM); zone 2, inundated forest, 1♀, 30.IX.1987 (USNM); Rio Troche, 1♂1♀, 4.X.1987 (USNM); 2♀, 10.X.1987 (USNM); 1♂1♀, 6.X.1987 (USNM); 1♂, 1-9.X.1991, D.SILVA col. (USNM).

Brazil. Roraima: Ilha de Maracá, 1♀ 1juv., 31.I-14.II.1992, A.A.LISE col. (MCP 1813); Acre: Parque Nacional da Serra do Divisor, Várzea Gibraltar-Pedro, 1♂ 1♀ 1juv., 19.XI.1996, R.S.VIEIRA col. (IBSP 9343); 1♀ 1juv., 20.XI.1996, R.S.VIEIRA col. (IBSP 9359); Tipologia 7, Sítio 4, 1♀ 1juv., 16.III.1997, L.RESENDE & R.VIEIRA col. (IBSP 12225); Tipologia 8, Sítio 1, 1♂ 6♀ 1juv., 19.III.1997, L.RESENDE & R.VIEIRA col. (IBSP 12144); Tipologia 8, Sítio 4, 1♂ 1♀, 14.III.1997, L.RESENDE & R.VIEIRA col. (12323); Rio Branco, Reserva Extrativista Humaitá, 1♂ 3♀, 12.V.1996, Eq. IBSP/SMNK. (IBSP 8766); 1♀, 18.VIII.1995, R.S.VIEIRA col. (IBSP 7940); Xapuri, Pimenteira, 1♂ 3juv., 5-7.IV.1996, Eq. IBSP/SMNK col. (IBSP 8623); Amazonas: Borba, Rio Mapiá, 2♂ 2♀ 1juv., 22.IV.1996, Eq. IBSP/SMNK col. (IBSP 8815); Manaus (Reserva Dimona), 1♀, 15.V.1991, H.G.FOWLER, E.M.VENTICINQUE & R.S.VIEIRA col. (MCZ); (Reserva do Km 41, 80 Km from Manaus), 1♀, 24.V.1991, H.G.FOWLER, E.M.VENTICINQUE & R.S.VIEIRA col. (MCZ); (Reserva Florestal Adolfo Ducke), 1♀, 18.VII.1987, A.A.LISE col. (MCN 25682); 1♀, 4.VIII.1987, A.A.LISE col. (MCN 25683); 1♀, 5.VIII.1987, A.A.LISE col. (MCN 25681); 1♂, 18-28.II.1992, A.D.BRESCOVIT col. (MCN 22020); 1♀, 19-24.II.1992, A.A.LISE col. (MCP 1696); (Rio Tarumã-Mirim, várzea), 2♀ with egg sac, 19.III.1988, H.HÖFER col. (SMNK 386); (Distrito Agropecuário da Sufran), 1♀, 31.VI.1986, F.A. de NEO col. (IBSP 14280); Mato Grosso: Teles Pires, Alto Tapajós, 1♀, 29.VIII.1950, H. SICK col. (MNRJ 2690); Apicás, 1♂, 30.I.- 27.II.1997, M.E.V.CALLEFFO & G.SKUK col. (IBSP 8565); São José do Rio Claro, 1♂, 12-27.VI.1997, M.CALLEFFO col. (IBSP 11001); Bahia: Porto Seguro, 1♀, VIII.1989, R.M.da ROCHA col. (IBSP 4647); Ilhéus, São João da Água Preta, 1♂ 1♀, IX.-X.1927 (MNRJ 1284); Una, Reserva Biológica do Una, 1♀, 4-8.X.1987, J.BECKER col. (MNRJ) Espírito Santo: São Mateus, Reserva Florestal da Companhia Vale do Rio Doce, 1♂ 2♀, 19-25.VI.1997 (IBSP 12798); 1♂ 1♀, (IBSP 12723); 1♀ (IBSP 12666); 1♂ (IBSP 12732); 1♀ (IBSP 12836); 1♀, 5-12.I.1998, (IBSP 16910), all collected by A.D.BRESCOVIT et al. col.; 1♂ 1♀, 29.VII.1994, J.R. LIMA col. (IBSP 26136); 1♂ 1♀, VII.1994 (IBSP 26184); Rio de Janeiro: Silva Jardim, Reserva Biológica de Poço das Antas, 2♀, VI.1998, F.N.RAMOS col. (IBSP 26129); Itatiaia, Parque Nacional do Itatiaia, E, M. ZIKÁN col. (MNRJ 14112); São Paulo: Cananéia, 1♀ (MZSP 3148); Ilha do Cardoso, 1♀, 14-18.IX.1999 (IBSP 26130); 1♂, V.2000 (IBSP 26133); 0♂, VI.2000, all collected by G. MACHADO (IBSP 26135); Paraná: Paranaguá, Ilha do Mel, Caminho da Figueira, 2♂ 1juv, 25.V.1989, C.A.FAUCZ col. (MZSP 13892); 26.V.1989, C.A.FAUCZ col., 1♀ 1juv, MZSP 13891).

Aglaoctenus lagotis (HOLMBERG)

Plate 1d; figures 3d-f; 6a-b; 7a-e; 8

1876 *Ocyale lagotis* HOLMBERG: An. Agr. Argentina, 4: 26 (two females and male syntypes, from Argentina, lost).

1876 *Diapontia freiburgensis* KEYSERLING: Verh. zool.-bot. Ges Wien, 26: 671, pl. 8. fig. 45 (male holotype from Nova Friburgo, Rio de Janeiro, Brazil, should be in BMNH, not found, probably lost). New synonymy

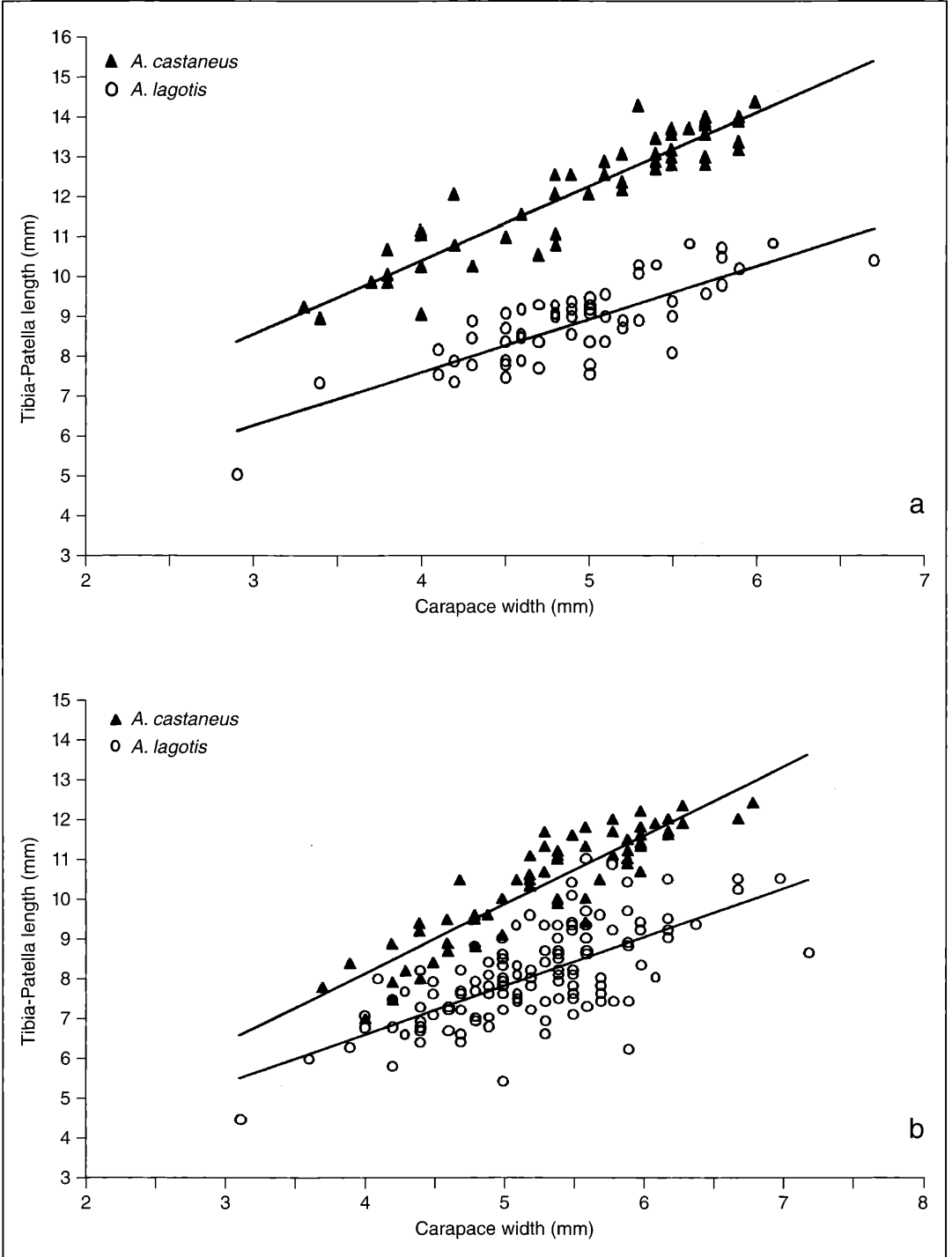


Figure 6. Variation of carapace width and relation to tibia-patella I length in *Aglaoctenus* species: a) males; b) females.

- 1876 *Diapontia granadensis* KEYSERLING: Verh. zool.-bot. Ges Wien, **26**: 673, pl. 8, fig. 47 (female holotype from "Neu Granada" (actually Bogotá), Colombia, should be in BMNH, not found, probably lost). New synonymy
- 1877 *Podophtalma diversa* PICKARD-CAMBRIDGE: Proc. zool. Soc. London, 1877: 572, pl. 57 figs 9a-b (5 immature syntypes from Minas Gerais, Brazil, in the Hope Department Entomology Collection, Oxford University, not examined). New synonymy
- 1891 *Tetragonophtalma diversa* – KEYSERLING: Die Spinnen Amerikas, **3**: 255
- 1891 *Tetragonophtalma freiburgensis* – KEYSERLING: Die Spinnen Amerikas, **3**: 255
- 1891 *Tetragonophtalma granadensis* – KEYSERLING: Die Spinnen Amerikas, **3**: 255
- 1891 *Tetragonophtalma obscura* KEYSERLING: Die Spinnen Amerikas, **3**: 256, pl. 10 fig. 192 (female holotype from Taquara, Rio Grande do Sul, Brazil, in BMNH 1890.7.1.2822, examined). New synonymy
- 1898 *Porrina diversa* – SIMON: Hist. Nat. Ar., **2**: 327, figs 332-333
- 1905 *Aglaoctenus bifasciatus* TULLGREN: Ark. Zool., **2**: 53, pl. 7, fig. 25 (female and 15 juveniles syntypes from Tatarenda, Chaco, Bolivia, in NHRM, examined). New synonymy
- 1916 *Porrina harknessi* CHAMBERLIN: Bull. Mus. Comp. Zool. Harvard, **60**: 280, pl. 23 figs 2-6 (male holotype and male and immature paratypes from Huadquiña, Peru, in MCZ, examined). New synonymy
- 1926 *Porrina glieschi* MELLO-LEITÃO: Bol. Mus. Nac. Rio de Janeiro, **2**: 2 (immature holotype from Rio Grande do Sul, Brazil, R. B. Lange col., in MNRJ 966, examined). New synonymy
- 1934 *Porrina callipoda* MELLO-LEITÃO: Mem. Inst. But., **8**: 405, figs 5, 6 (immature holotype from Ribeirão Claro, Mato Grosso do Sul, Brazil, in IBSP 1003, examined). New synonymy
- 1941 *Porrina diversa* – MELLO-LEITÃO: Rev. Mus. La Plata, **2**: 201
- 1941 *Porrina granadensis* – MELLO-LEITÃO: Ann. Acad. Bras. Cienc., **13**: 278
- 1941 *Porrina lagotis* – MELLO-LEITÃO: Rev. Mus. La Plata, **2**: 138-139, pl. 6, figs 28, 35
- 1941 *Porrina lagotis* – MELLO-LEITÃO: Rev. Mus. La Plata, **2**: 201
- 1942 *Porrina diversa* – MELLO-LEITÃO: Rev. Mus. La Plata, **2**: 383
- 1942 *Porrina lagotis* – MELLO-LEITÃO: Rev. Bras. Biol., **2**: 383
- 1943 *Porrina freiburgensis* – MELLO-LEITÃO: Arq. Mus. Nat. Rio de Janeiro, **37**: 164
- 1943 *Porrina diversa* – MELLO-LEITÃO: Arq. Mus. Nac. Rio de Janeiro, **37**: 164
- 1944 *Porrina lagotis* – MELLO-LEITÃO: Rev. Mus. La Plata, **3**: 316, 321
- 1945 *Porrina diversa* – MELLO-LEITÃO: Rev. Mus. La Plata, **4**: 221
- 1945 *Porrina lagotis* – MELLO-LEITÃO: Rev. Mus. La Plata, **4**: 221
- 1947 *Porrina diversa* – MELLO-LEITÃO: Arq. Mus. Paranaense, **6**: 266
- 1947 *Porrina freiburgensis* MELLO-LEITÃO: Arq. Mus. Paranaense, **6**: 265
- 1947 *Porrina lagotis* – MELLO-LEITÃO: Arq. Mus. Paranaense, **6**: 266
- 1947 *Porrina obscura* – MELLO-LEITÃO: Arq. Mus. Paranaense, **6**: 265.
- 1948 *Porrina diversa* – MELLO-LEITÃO: An. Acad. Bras. Sci., **20**: 153
- 1949 *Porrina diversa* – MELLO-LEITÃO: Bol. Mus. Nac. Rio de Janeiro, **92**: 4
- 1954 *Aglaoctenus bifasciatus* – ROEWER: Expl. Parc Nat. De L'Upemba, **30**: 126
- 1954 *Porrina diversa* – ROEWER: Katalog der Araneae von 1758 bis 1940, **2**: 313
- 1954 *Porrina glieschi* – ROEWER: Katalog der Araneae von 1758 bis 1940, **2**: 313
- 1954 *Porrina harknessi* – ROEWER: Katalog der Araneae von 1758 bis 1940, **2**: 313
- 1954 *Porrina lagotis* – ROEWER: Katalog der Araneae von 1758 bis 1940, **2**: 313
- 1954 *Porrinula callipoda* – ROEWER: Expl. Parc Nat. De L'Upemba, **30**: 313
- 1958 *Porrina callipoda* – BONNET: Bibl. Aran., **2**: 3765
- 1958 *Porrina glieschi* – BONNET: Bibl. Aran., **2**: 3765.
- 1958 *Porrina harknessi* – BONNET: Bibl. Aran., **2**: 3765
- 1959 *Porrina granadensis* – ROEWER: Expl. Parc Nat. De L'Upemba, **55**: 1005
- 1959 *Porrinosa glieschi* – ROEWER: Expl. Parc Nat. De L'Upemba, **55**: 1005
- 1959 *Porrinosa harknessi* – ROEWER: Expl. Parc Nat. De L'Upemba, **55**: 1001, 1005
- 1959 *Porrinula callipoda* – ROEWER: Expl. Parc Nat. De L'Upemba, **55**: 1005
- 1961 *Porrinosa glieschi* – ROEWER: Bull. Inst. Sci. Nat. Belg., **37**: 16
- 1961 *Porrinosa harknessi* – ROEWER: Bull. Inst. Sci. Nat. Belg., **37**: 16
- 1961 *Porrinula callipoda* – ROEWER: Bull. Inst. Sci. Nat. Belg., **37**: 16
- 1962 *Porrina diversa* – BRADY: Psyche, **69**: 11, fig. 11
- 1962 *Porrina harknessi* – BRADY: Psyche, **69**: 129, fig. 12, 33.
- 1972 *Tetragonophtalma callipoda* – BÜCHERL & LUCAS: Mem. Inst. But., **36**: 267
- 1982 *Porrinosa callipoda* – CAPOCASALE: J. Arachnol., **10**: 148-149 (species inquirenda)
- 1982 *Porrinosa diversa* – CAPOCASALE: J. Arachnol., **10**: 149-150 (species inquirenda)
- 1982 *Porrinosa glieschi* – CAPOCASALE: J. Arachnol., **10**: 150 (species inquirendae)
- 1982 *Porrinosa granadensis* 0– CAPOCASALE: J. Arachnol., **10**: 147
- 1982 *Porrinosa harknessi* – CAPOCASALE: J. Arachnol., **10**: 151, figs 9-10
- 1982 *Porrinosa lagotis* – CAPOCASALE: J. Arachnol., **10**: 151-154, figs 3-5, 6-8, 11, 13 (non *P. lagotis* (MELLO-LEITÃO, 1941c) and lectotype MLP 14945 erroneously designated)
- 1990 *Porrinosa callipoda* – CAPOCASALE: J. Arachnol., **18**: 139
- 1990 *Porrinosa diversa* – CAPOCASALE: J. Arachnol., **18**: 139
- 1990 *Porrinosa glieschi* – CAPOCASALE: J. Arachnol., **18**: 139
- 1990 *Porrinosa harknessi* – CAPOCASALE: J. Arachnol., **18**: 139
- 1990 *Porrinosa lagotis* – CAPOCASALE: Aracnologia, **11/12**: 12
- 1990 *Porrinosa lagotis* – CAPOCASALE: J. Arachnol., **18**: 139
- 1991 *Porrinosa harknessi* – CAPOCASALE: J. Arachnol., **19**: 96, figs 6-7, 9 (description of the female)
- 1991 *Porrinosa lagotis* – CAPOCASALE: J. Arachnol., **19**: 96, figs 1, 10
- 1993 *Aglaoctenus bifasciatus* – CARIC: Bull. Amer. Mus. Nat. Hist., **170**: 231.
- 1993 *Porrinosa freiburgensis* – PLATNICK: Adv. Spider Taxonomy 1988-1991: 506
- 1993 *Porrinosa harknessi* – PLATNICK, 1993: Adv. Spider Taxonomy 1988-1991: 506
- 1993 *Porrinosa lagotis* – PLATNICK: Adv. Spider Taxonomy 1988-1991: 506
- 1993 *Porrinosa obscura* – PLATNICK: Adv. Spider Taxonomy 1988-1991: 506

1997 *Aglaoctenus harknessi* – PLATNICK: Adv. Spider Taxonomy 1992-1995: 539

1997 *Porrima freiburgensis* – PLATNICK: Adv. Spider Taxonomy 1992-1995: 539

1997 *Porrimosa glieschi* – PLATNICK: Adv. Spider Taxonomy 1992-1995: 539

Diagnosis

Aglaoctenus lagotis males differ from *A. castaneus* by the narrower median apophysis (figs 3e; 7a,b), by the inconspicuous base of the cymbium, and by a leg-carapace ratio of 1.45 to 2.15. Female epigynes with the T-shaped septum longer longitudinally and narrower transversely (figs 3d; 7c,d).

Description

Male (Indianópolis, Minas Gerais, Brazil): Carapace orange, thoracic groove red, ocular area black. Chelicerae brown, endites and labium orange. Sternum and legs orange, legs clearer in the ventral side, metatarsi and tarsi red. Abdomen gray, with dark brown folium. Spinnerets orange. Total length 14.9, carapace 7.6 long, 5.4 wide. Clypeus 0.38 high, equals to 1.46 the AME diameter. Eye sizes and interdistances: AME 0.26, ALE 0.26, PME 0.36, PLE 0.28, AME-AME 0.16, AME-ALE 0.36, PME-PME 0.28, PME-PLE 0.45. MOQ length 0.76, front width 0.69, back width 1.02. Chelicerae 2.35 long, with 4 promarginal and 3 retromarginal teeth. Abdomen 7.6 long, 3.2 wide.

Leg segments length: I - femur 7.22/ patella 2.66/ tibia 6.0/ metatarsus 5.44/ tarsus 3.11/ total 24.44/ II 5.88/ 2.0/ 4.88/ 5.33/ 2.66/ 20.77/ III 6.22/ 2.11/ 4.88/ 5.44/ 2.44/ 21.11/ IV 8.22/ 2.22/ 6.88/ 9.0/ 3.44/ 29.77. Palpus as typical for the genus (figs 3e-7; 7a,b).

Female (same locality as male). Carapace orange, with clearer borders, cephalic region and thoracic groove red, median y-shaped band as clear as the borders of the carapace, ocular area black. Chelicerae dark brown, endites and labium red. Sternum and legs orange, metatarsi and tarsi red. Abdomen dark gray, with dark brown folium delimited by light lateral bands. Spinnerets dark gray. Total length 22.6, carapace 8.0 long, 6.2 wide. Clypeus 1.11 high, 1.8 times the AME diameter. Eye sizes and interdistances: AME 0.61, ALE 0.66, PME 0.94, PLE 0.77, AME-AME 0.44, AME-ALE 0.94, PME-PME 0.83, PME-PLE 0.77. MOQ length 1.77, front width 1.72, back width 2.72. Chelicerae 3.6 long, with 4 promarginal and 3 retromarginal teeth. Abdomen 11.1 long, 6.3 wide.

Length of leg segments: I - femur 7.11/ patella 2.88/ tibia 6.55/ metatarsus 5.77/ tarsus 3.11/ total 25.44/ II - 6.88/ 2.88/ 6.0/ 5.44/ 3.0/ 24.22/ III - 6.0/ 2.44/ 5.0/ 5.44/ 2.44/ 21.33/ IV 8.33/ 2.66/ 7.11/ 9.0/ 3.33/ 23.33. Epigynum with the typical shape of the genus (figs 3c; 7c-e).

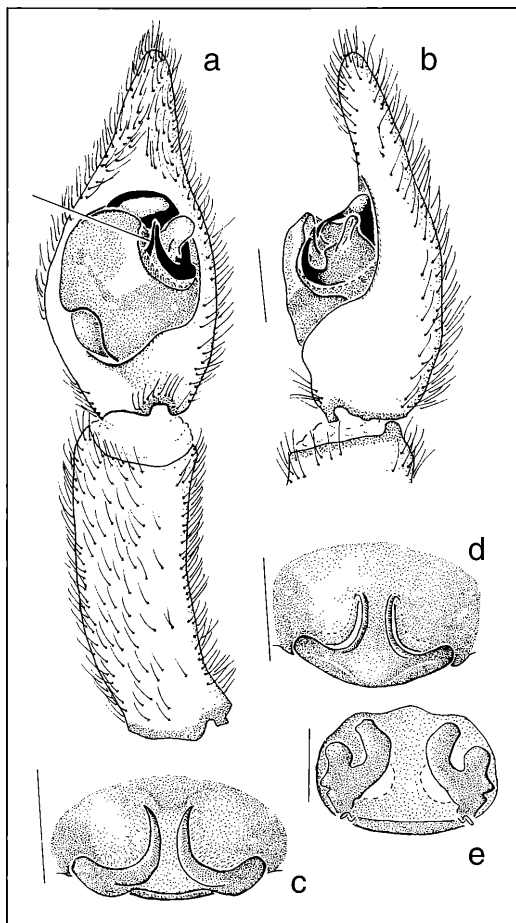


Figure 7 *Aglaoctenus lagotis* (HOLMBERG), male: a) palp, ventral view; b) retrolateral view; female epigyna: c) ventral view, specimen from Parnaíba, Piauí, Brazil; d) ventral view, specimen from Atibaia, São Paulo, Brazil; e) dorsal view, specimen from Indianópolis, Minas Gerais, Brazil. (MA, median apophysis). Scale lines: 0.5 mm.

Variation

Coloration varies from orange to dark brown, rarely black. Males rarely present tufts of long hairs on metatarsi. Juveniles are uniformly dark-gray. Variation in total length: females 10.3-23.0 (N=140), males 10.1-19.0 (N=57).

Note

Although the holotypes of *Tetragonophthalma freiburgensis* and *T. granadensis* were not located, we are sure of their generic placement based on KEYSERLING's original illustrations. Judging by the localities, *Aglaoctenus lagotis* and *A. granadensis* are the earlier names available for these species, both with lost

types. The former name was preferred because more material is available from Argentina than from Colombia. The synonymies of *Porrimosa diversa*, *P. glieschi*, and *P. callipoda*, all described on immature specimens, and *P. freiburguensis*, whose type is probably lost, are established based on the type localities, which are all within the distribution range of *A. lagotis* (fig. 8). The syntypes of *P. diversa* were not examined for two reasons: we are sure that these specimens are correctly placed in *Aglaoctenus* because they were examined by CAPOCASALE (1982) and since all specimens are immature, examining them would not reveal new informations for the correct placement.

Natural History

A. lagotis was recorded from primary and disturbed humid forests, Brazilian Caatinga, savannas (Argentinean Chaco, Brazilian Cerrado and Pantanal) and montane fields (Brazilian "campos rupestres"). Regarding the preferred sites for web building, SORDI (1996) observed several microhabitats, including holes in trunks, stocks of leaves and branches on and above the ground, and hollows in litter and bromeliads. It was also recorded from bromeliads (*Bromelia balansae*) in central and southeastern Brazil (L. B. Albuquerque and G. Q. ROMERO pers. comm.), from soil termite mounds and cliffs in cerrado areas of central and southeastern Brazil (AJS, pers. observ.) and within rock outcrops and dry trunks (Plate 1d) in Caatingas of northeastern Brazil (ADB, pers. observ.). One specimen was observed (AJS) in a garbage can in an urban park in Campinas, São Paulo, Brazil. A complete description of the life-cycle and several natural history observations for this species can be found in SORDI (1996) and a description of the courtship and copulation behavior in CAPOCASALE (1982: 153-154).

Distribution

Colombia, Venezuela, southern Peru, Bolivia, Paraguay, central, southeastern and southern Brazil, Uruguay, Argentina (fig. 8).

Material examined

Colombia. Boyacá: La Uvita, 1♂1♀ (MNRJ 13520).
Venezuela. Bolívar: Parupa, Gran Sabana, 1500m., 1♂, 27.VI.-10.VII.1987, S. & J. PECK col. (AMNH).
Peru. Cuzco: Wiñayhuaina, 13° 07' S, 72° 34' W, 2700-3100m, 1♂ 2juv., 9.II.1990, D.SILVA DÁVILA (MUSM); Loreto: no locality, 1♀, VIII.1973, J.C.OLIN (MCZ).
Bolivia. La Paz, Valle del Zongo, Laguna Viscachani, 1♀, 5.VIII.1993, H.HÖFER col. (SMNK); Rio Huarinilla, near Coroico, 1♀, VIII.1993, A.D.BRESCOVIT (SMNK); Sara: San Ignacio, 2♀, 9.III.1961, L.HAMMERSCHMID col. (IBSP 3364); Estación Biológica del Beni, 1♀, 24-jul-1993, A.D. BRESCOVIT & H.HÖFER col. (MCN 24118); 1♀1juv., 27.VII.1993, H.HÖFER col. (SMNK 1233); 2♂ 1♀1juv., A.D. BRESCOVIT col. (SMNK 1213).
Brazil. Piauí: Parnaíba, 1♀, 6-20.XI.1994, R.BERTANI & PINZ col. (IBSP 5722); Paraíba: Serra do Teixeira, 1♀ with egg sac, 21.II.1978, P.F.L.DUARTE col. (IBSP 8579); Mato Grosso:

Agachi, 1♂, 10.XI.1952, C.F.MORAES col. (IBSP 784); 1♂, 19.IX.1952, C.F.MORAES col. (IBSP 3495); Chapada dos Guimarães, 2♀, 15-26.VII.1992, A.A.LISE & A.BRAUL Jr. col. (MCP 2154); 1♀ (A.A.LISE & A.BRAUL Jr. col. (MCP 2155); Poconé, 1♀, 3.VIII.1992, A.A.LISE & A.BRAUL Jr. col. (MCP 2424); near Poconé, Pantanal area, 3♂ 2juv., 4-12.VIII.1992, A.A.LISE & A.BRAUL Jr. col. (MCP 2322); Cáceres, 1♀, 27.VII.1962, V.VEIT col. (IBSP 4094); Burity, 1♀1juv., 3.VI.1972, W.G.WHITCOMB col. (FSCA); Mato Grosso do Sul: Campo Grande, 1♀, I.1950, P.BRUNO col. (IBSP 1115); 1♀, IX.1982, R.RODRIGUES col. (IBSP 3498); Campo Grande, Reserva da UCDB, 7.I.1997, A.M.CAÇÃO col. (IBSP 26137); 2♀, 1.VIII.1997, A.M.CAÇÃO col. (IBSP 26131; 26132); Bela Vista, Fazenda Luis Felipe, 1♂, 28.VIII.1998 (IBSP 26125); 1♀, 10.XI.1998, all collected by A.M.CAÇÃO (IBSP 26128); Camapuã, 3♀ 3juv., I.1968, F.SIBERBAUER col. (IBSP 8156); Brasília: Brasília, Fazenda Cisalpina, 5♀, VII.2000, Eq. IBSP col. (IBSP 26195); Tocantins: Porto Nacional, Fazenda Sandoval, 1♀, 9.VIII.2000 (IBSP 26182) 1♂, 10.VIII.2000 (IBSP 26183) Usina Hidrelétrica Luiz Eduardo Magalhães, 1♀, 7-11.VIII.2000, I. KNYSAK & R.MARTINS col. (IBSP 26198); Goiás: Distrito Federal, Brasília, 1♀ 1juv., 1971, W. R. LOURENÇO col. (IBSP 4240); 1♀, 30.X.1990, C. D. HOLVORCEN col. (IBSP 15899); Caldas Novas, Usina Hidrelétrica de Corumbá, 17°42' 50" S, 48°32'12" W, 8♂, 12-23.VIII.1996, M.T.I. RODRIGUES col. (MZSP 15658); Cabeceiras, 1♀, 1964 (MZSP 4201); Urutáguia, 1♂ 1juv., 10.VII.1952, A.NOGUEIRA col. (IBSP 3477); 1♀, X.1952, A.NOGUEIRA col. (IBSP 822); Mineiros, Parque Nacional de Emas, 1♂, 28.VII.1997, P.VALDUJO & C.NOGUEIRA col. (IBSP 11714); 1♀, C.ADES col. (IBSP 14379); near Niquelândia, Usina Hidrelétrica de Serra da Mesa, 14°01' S, 48°18' W, 1♂, 24-30.XI.1995, G.SKUK col. (IBSP 6278); Minaçu, Usina Hidrelétrica de Serra da Mesa, 1♀, 18-30.X.1996, A.B.BONALDO & L.MOURA col. (MCN 27975); Bahia: Barreiras, área militar, 2♀2juv., 3.VIII.2000, E. F.RAMOS col. (IBSP 26196; 26197); Central, around the city, 3♀ 3juv., 10.VII.2000, A.D.BRESCOVIT & E.F.RAMOS col. (IBSP 26147; 26148; 26152); Itapicuru, 1♀, O.LEONARDO col. (MNRJ 42305); Ibiraba, dunas do rio São Francisco, 1♂, 5.III.1997, E.XAVIER col. (IBSP 15247); Jussiapê (13°34'S 41°36'W), 1♀1juv., 21.XII.1998, L.S. ROCHA col. (IBSP 20782); Lençóis, 1♀, X.1999, (UEFS); Minas Gerais: Morro da Garça, 1♀, 1964 (MZSP 4215); Prata, 1♀, X.1979, T.ALMEDA col. (IBSP 4977); Serra do Caraça, 1♂, VII.1991, R.BERTANI col. (IBSP 7420); Barão de Cocais, 3♀, 15.XII.1969, J.P.COUTO col. (IBSP 2439); Itabirito, 1♂1♀, 15.IX.1999, C.SCHETINI & E.ALVAREZ col. (IBSP 26126); Belo Horizonte, Estação Ecológica da Universidade Federal de Minas Gerais, 1♂ 2♀, 11.VIII.1997, A.J.SANTOS & M.O.GONZAGA col. (IBSP 26127); Confins, Ribeirão Confins, 1♀, 1964 (MZSP 4164); Sete Lagoas, CNPMS-Embrapa, 1♀, 5.IX.1996, R. de OLIVEIRA col. (IBSP 7751); 1♂, R. de OLIVEIRA col. (IBSP 7744); Indianópolis, Usina Hidrelétrica de Miranda, 1♂ 1♀, 23.VIII.1995, A.L.T. SOUZA col. (IBSP 26122); Poços de Caldas, 1♂, P.F.L. DUARTE col. (MCN 24984); Rio de Janeiro: Barra do Pirai, 1♂ 2♀, IV.1950, J. UBELE col. (IBSP 1149); São Paulo: Divisa Rio de Janeiro/São Paulo, 1♀, 20.X.1989, ALTAMIRO & BEATRIZ col. (MNRJ); Atibaia, Parque Municipal da Serra da Itapetininga, 1♂ 3♀, 6.IX.1997, A.J.SANTOS et al. col. (IBSP 26123); Jundiá, Serra do Japi, 1♀, I.1999, A.J.SANTOS col. (IBSP 26124); São José do Rio Preto, Instituto Penal Agrícola, 1♂ 1♀, 29.VIII.1997, G.Q.ROMERO col. (IBSP 26134); Presidente Epitácio, Usina Hidrelétrica Sérgio Motta, 1♂ 1♀, 16.I-13.II.1999, Eq. IBSP col. (IBSP 23269; 23133); Penápolis, 1♀, I.1955, E.FIGUEIREDO col. (IBSP 1667); Usina Hidrelétrica de Três

Irmãos, 3♀, IX.X.1990, R.BERTANI, M.COSTA & C.R.BERTINI col. (IBSP 4861); Sorocaba, Fazenda Serrinha, 3♂ 21♀, X.1981, J.NAVAS col. (IBSP 1964; 2963); Itapira, 1♀, IX.1975, S.NOUGUÉS col. (IBSP 1075); Campo Alegre, 7♀, 2.VI.1969, W.RODRIGUES col. (IBSP 2254); Porto Feliz, 1♂, 29.V.1981, O. de ALMEIDA FILHO col. (IBSP 14271); Andradina, 1♂ 3♀, 12.VIII.1973, M.P.BUENO col. (IBSP 2686); Presidente Prudente, 1♀, XII.1959, G.RODRIGUES col. (IBSP 1473); Mogi-Guaçu, 1♀, 26.VIII.1977, M.B. de LIMA col. (IBSP 8373); Serra da Cantareira, 1♀, XII.1982, M.L.O.MARTINS col. (IBSP 3590) Itú, 1♀, 3.VII.1995, A.G.CADOSO col. (IBSP 685); Serra Negra, 1♀, VII.1983, M. Maluf col. (IBSP 3786); Alto da Serra, 1♀, XI.1941, J.DAMIGO col. (MZSP 6309); Amparo, Monte Alegre, Fazenda Santa Maria, 1♀, 27.XI.1942, F.LANE col. (MZSP 10345); Francisco Morato, 2♀, 19.XI.1952, D. dos SANTOS col. (IBSP 833); Rinópolis, 1♀, VII.1960, M.NAKASHIM col. (IBSP 5081); Piracicaba, 1♂, 18.X.1996 (IBSP 7754); Jundiá, 1♀, 30.X-2.XI.1998, C.A.RHEIMS col. (IBSP 20180); Barueri, 1♂, 6.VIII.1954, K.LENKO col. (MZSP 5528); 1♀ 1juv., 19.VIII.1954, K.LENKO col. (MZSP 5835); Boa Esperança do Sul, Fazenda Itaquerê, 1♂, VI.1965, K.LENKO col. (MZSP 4585); São Paulo, 1♀, 21.V.1937, M.M.LEAL col. (IBSP 1002); 1♂, 31.VIII.1947, H.URBAN col. (SMNK 426); no date or collector (SMNK 325); 1♀, 22.X.1973, B.F.F.VAGELAR col. (IBSP 8372); (Perus), 1♀ (MZSP 9241); Franca, 1♀ 1juv., 1902, O.DREHER col. (MZSP 6482); Embú-Guaçu, 1♂, 14.X.1997, J.B. de SÁ (IBSP 13916); São Roque, Fazenda São Joaquim, 1♂, 22.VIII.1961, Eq. IBSP col. (IBSP 48); Martinópolis, 1♀, VIII.1982, H.C.A.PIRES col. (IBSP 3549); Taiúva, 1♂ 5♀, 20.XI.1954, B.J.LOURENÇO col. (IBSP 955); 5♀ (IBSP 957); 4♀ (IBSP 959); Tietê, 1♂, 3.IV.1995 (IBSP 6157); 1♀, 1.VIII.1995, A.GUIMARÃES col. (IBSP 6454); Vista Alegre do Alto, 1♂, 31.VIII.1951, P.SIQUEIRA col. (IBSP 569); Bragança Paulista, 3♀, VIII.1989, V.P.LUIZ col. (IBSP 4293); Quatá, 2♀, III.1957, J.CERCKASIM col. (IBSP 1407); Bauru, 1♀, A.M.MARQUES col. (IBSP 1222); Botucatu, (Jardim Botânico) 1♂, 1995, L. de OLIVEIRA col. (UNESP); 1♂, 27.XI.1995, A.B.LIMA col. (UNESP); Botucatu (Fazenda Edgardia) 1♀, 25.XI.1994, I.M.P.RINALDI col. (UNESP); 1♀, 6.VI.1989, I.M.P.RINALDI col. (UNESP); Botucatu (Fazenda Lageado) 1♀, 11.XII.1988, I.M.P.RINALDI & L.C.FORTI col. (UNESP); Vale do Ribeira, 1♀ (MHCI 1571); Paraná: Rio Iguazu, Usina Hidrelétrica Foz do Areia, 1♀, 23.IV.1980, Eq. IBSP (IBSP 14604); Guaaraqueçaba, 1♂, R.LANGE col. (MHCI 1525); Candió/Mangueirinha, Usina Hidrelétrica de Segredo, 1♀ 1juv., 1996, R.BERTANI col. (IBSP 7955); Usina Hidrelétrica de Segredo, Reservatório do Rio Jordão, 1♀, 29.IV.1996, A.CHAGAS JR. & M. DI BERNARDO col. (IBSP 8032); 1♀, 30.IV.1996, J.C.MOURA LEITE (IBSP 8038); Curitiba, 2♀, B.ROHR col. (MNRJ 41412); Pinhão, 1♀, 25.X.1991, R.PINTO-DA-ROCHA col. (MCN 22214); Rio Grande do Sul: no locality, 1♀ 2juv., P.B.RAMBO col. (MNRJ 41669); Pelotas, 1♂, 4-6.X.1996, L.MOURA col. (MCN 27760); Caxias do Sul, Fazenda Souza, 2♀ 1juv., 18-21.XI.1993, A.A.LISE col. (MCP 4168); São Simão, 2♀, X.1934, M.IRON col. (IBSP 1000); Novo Hamburgo, 1♀, 17.I.1988, C.J.BECKER col. (MCP 231); Mariana Pimentel, 1♂, 23.IV.1993, M.SILVEIRA col. (MCP 3124); Tenente Portela, 1♂, 29.XI.1978, H.BISCHOF col. (MCN 8379); Passo Fundo, Floresta Nacional de Passo Fundo, 1♂ 4♀ 1juv., 12.X.1985, A.A.LISE col. (MCN 13632); Garruchos, 1♀, 8.XII.1975, A.A.LISE col. (MCN 3179); Guaíba, 2♀, 17.III.1995, A.A.LISE et al. col. (MCP 8041); 1♂ 1♀, 9.I.1996, A.A.LISE et al. col. (MCP 9555); Guaíba, Guaíba Country Club, 3♀, 01.I.1993, A.B.BONALDO col. (MCN 22682); Flores da Cunha, 1♂, 1.V.1993, A.A.LISE col. (MCP 3191); Vião, 1♂, 17.XI.1991, C.FREITAS col. (MCP 1429); Quaraí, 1♂, 9.IV.1977, J.W.THOMÉ col. (MCN 5266);

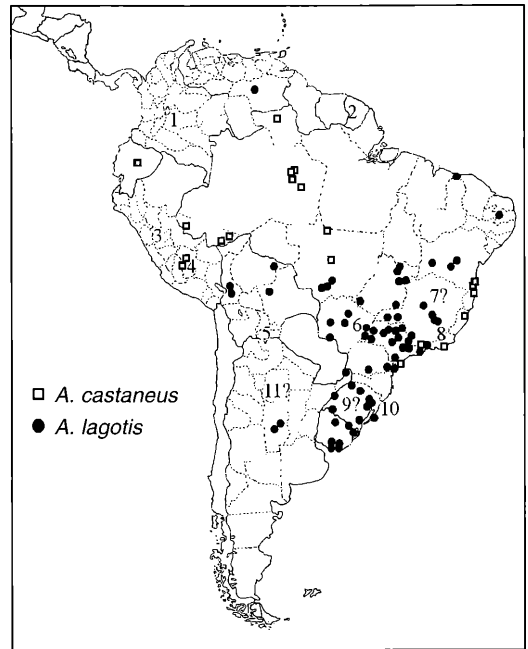


Figure 8. Distribution of *Aglaoctenus* species. The numbers indicate the type localities of the following synonymised species: 1, *granadensis*; 2, *guianensis*; 3, *castaneus*; 4, *harknessi*; 5, *bifasciatus*; 6, *callipoda*; 7, *diversa*; 8, *freiburgensis*; 9, *glieschi*; 10, *obscura*; 11, *lagotis*. ? = species whose type locality are not expressed clearly, with only data about province, state or country.

1♀ 1juv., 24-28.V.1991, A.A.LISE col. (MCP 445); Canela, 1♀, 7.X.1967, A.A.LISE col. (MCN 442); Carazinho, 1♀, 10.XI.1979, A.A.LISE col. (MCN 8691); Porto Alegre, 1♀ 1juv., 19.VI.1963, O.HARTLIEB & PACINI col. (MCN 1189).
Uruguay. Lavalleja: Marmarajá, 1♀, 12.V.1962, E.S.CARBONALL & M.A.MONNÉ col. (MNHN 805); Minas, 1♂, 3.III.1981, R.M.CAPOCASALE & L.BRUNO col. (MNHN 940); Arequita, Cerro Arequita, 1♀, 5.XII.1997, A.D.BRESCOVIT col. (IBSP 14458); Maldonado: Cerro Pan de Azúcar, 1♀, 3.IX.1978, F.PÉREZ & J.BASSO col. (MNHN 856); Sierra de la Ballena, 1♀, 29.VIII.1976, F.LOPEZ & R. DE SAA col. (MNHN 706); Taquarém: Tambores, Pozo Hondo, 1♀, 4.IX.1971, F.ACHAVAL col. (MNHN 708); Cerro Largo: Río Taquarí, Ruta 8, 1♀, 26.XI.1983, R.M.CAPOCASALE & F.PÉREZ col. (MNHN 928); Quebracho, 1♀, 16.V.1983, C.MORENO col. (MNHN 963); Canelones: Piedras de Afilar, 3♀, 3.V.1989, F.COSTA et al. col. (MNHN 860); Marindia, 1♀, 16.III.1978, F.COSTA & M.URRUTY col. (MNHN 810); Treinta y Tres: Quebrada de los Cuervos, 1♀, 10-11.X.1988, F. PÉREZ-MILES col. (MNHN 576).
Argentina. Rio Negro: 1♀ (MNRJ 13518); Córdoba: Talumba, 1♀, M.BIRABÉN col. (MNRJ 58036); Arguillo, 2♀ 2juv., X.1943, J. De CARLO col. (MACN 1354); Tanti, 1♀, I.1950, J.M.VIANA col. (MACN 2855); Misiones: Tobuna, 2♀ 2juv., II.1952, W.PARTRIDGE col. (MACN 4054); Yacupoi, Puerto Bemberg, 1♀, 11.II.1980, J.CRANWELL col. (MACN 3023); Santa Maria, 1♂, X.1953, J. De CARLO, R.D.SCHIAPELLI, J.M.VIANA & M.E.GALIANO col. (MACN 3844); Rio Iguazú, 60 km from Puerto Iguazú, 1♀, III.1951, W.PARTRIDGE col. (MACN 3458).

Acknowledgements

We are grateful to Dr. HUBERT HÖFER for inviting us to publish in this special volume, and especially to Prof. Dr. LUDWIG BECK, for supporting the second author during projects in Brazilian Amazonia, Bolivia and scientific visits at the State Museum of Natural History in Karlsruhe. We thank all the curators of the consulted collections for the loan of the material examined, including G.B. EDWARDS, who lent specimens of *Sosippus* for comparison. We also thank A.L.T.SOUZA, A.M.CAÇÃO, C.SCHETINI, E.ALVAREZ, F.N.RAMOS, G.F.DUTRA, G.MACHADO, G.Q.ROMERO, J.VASCONCELLOS NETO, L.B.ALBUQUERQUE, M.O.GONZAGA, and R.L.G.RAIMUNDO for collecting specimens for this study and for natural history observations and A.M.F.PACHECO for suggestions on the drawings. We thank Prof. PEDRO KIYOHARA and Miss SIMONE PERCHE DE TOLEDO (USP) for making the scanning electron micrographs. The following people gently provided colored pictures of spiders and webs: M.S.ARAUJO (plate 1), B.D.BUYS (plate 1b), and G.MACHADO (plate 1c). The authors also acknowledge C.A.RHEIMS, M.O.GONZAGA, P.SIERWALD and R.CAPOCASALE, who read the first drafts of this manuscript and made important suggestions. The first author received logistical support from J. VASCONCELLOS NETO, from Departamento de Zoologia, Universidade Estadual de Campinas. This study was financed by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP No. 99/05695-8 to A.J.SANTOS and CNPq and FAPESP No. 1999/05446-8 to A.D.BRESCOVIT. This work is part of BIOTA/FAPESP - The Biodiversity Virtual Institute Program (www.biotasp.org.br).

4. Literature

- BONNET, P. (1958): *Bibliographia Araneorum*, 2 (4) 3027-4230; Toulouse (Douladore).
- BRADY, A. R. (1962): The spider genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). – *Psyche*, 69: 129-164.
- BRESCOVIT, A. D. & HÖFER, H. (1994): *Heidrunea*, a new genus of the spider subfamily Rhoicininae (Araneae, Trechaleidae) from Central Amazonia, Brazil. – *Andrias*, 13: 71-80.
- BÜCHERL, W. & LUCAS, S. (1972): Sobre a posição sistemática de *Porrima callipoda* MELLO-LEITÃO, 1934 (Araneae: Lycosidae). – *Mem. Inst. Butantan*, 36: 267.
- BUCHER, E. (1974): Observaciones ecológicas sobre artrópodos del bosque chaqueño de Tucumán. – *Rev. Fac. Ci. Ex. Fis. Nat. Córdoba (NS) Biología*, 1: 35-122.
- CAPOCASALE, R.M. (1982): Las especies del genero *Porrimosa* ROEWER, 1959 (Araneae, Hippasinae). – *J. Arachnol.*, 10: 145-156.
- CAPOCASALE, R.M. (1990a): Las especies de la subfamilia Hippasinae de America del Sur (Araneae, Lycosidae). – *J. Arachnol.*, 18: 131-141.
- CAPOCASALE, R.M. (1990b): An annotated checklist of uruguyan spiders. – *Aracnologia*, 11/12: 1-23.
- CAPOCASALE, R.M. (1991): Nuevos aportes al genero *Porrimosa* ROEWER (Araneae, Lycosidae). – *J. Arachnol.*, 19: 93-96.
- CAPORIACCO, L. DI. (1954): Araignées de la Guyane Francaise du Muséum d'Histoire Naturelle de Paris. – *Comm. Pontif.*, 16: 45-193.
- CARICO, J. E. (1981): The Neotropical spider genera *Architis* and *Staberius* (Pisauridae). – *Bull. Amer. Mus. Nat. Hist.*, 170: 140-153.
- CARICO, J.E. (1993): Revision of the genus *Trechalea* THORELL (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the western hemisphere. – *J. Arachnol.*, 21: 226-257.
- CHAMBERLIN, R.V. (1916): Results of the Yale Peruvian Expedition of 1911: the Arachnida. – *Bull. Mus. Comp. Zool. Harvard*, 60: 177-299.
- DONDALE, C. D. & REDNER J. H. (1990): The Insects and Arachnids of Canada, Part 17 The wolf spiders, Nurseryweb spiders, and the Lynx spiders of Canada and Alaska, Araneae: Lycosidae, Pisauridae, and Oxyopidae. – *Research Branch, Agriculture Canada Publ.*, 1859: 1-383.
- HIGGINS, L. E. (1989): The effect of insemination on the morphology of the internal genitalia of the spider *Nephila clavipes* (Araneae: Araneidae). – *Ann. Ent. Soc. America*, 82: 748-753.
- HOLMBERG, E.L. (1876): Arácnidos argentinos. – *An. Agr. Argentina*, 4: 1-30.
- HÖFER, H. & BECK, L. (1996): Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien II. – *Natur und Museum*, 126: 69-85.
- KEYSERLING, E. (1876): Über amerikanische Spinnenarten der Unterordnung Citigrade. – *Verh. zool-bot. Ges. Wien*, 26: 609-708.
- KEYSERLING, E. (1891): Die Spinnen Amerikas (Brasilianische Spinnen). – *Vol. 3: 1-278*; Nürnberg.
- KRONSTEDT, T. (1990): Separation of two species standing as *Alopecosa aculeata* (CLERCK) by morphological, behavioural, and ecological characters, with remarks on related species in the *pulverulenta* group (Araneae, Lycosidae). – *Zool. Scripta*, 19: 203-225.
- LEHTINEN, P. (1967): Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorphae. – *Ann. Zool. Fenn.*, 4: 199-468.
- LEVI, H.W. (1965): Techniques for the study of spider genitalia. – *Psyche*, 72: 152-158.
- MELLO-LEITÃO, C.F. (1926): Algumas aranhas novas do Brasil meridional. – *Bol. Mus. Nac. Rio de Janeiro*, 2: 1-18.
- MELLO-LEITÃO, C.F. (1934): Três aranhas novas nas coleções do Instituto Butantan. – *Mem. Inst. Butantan*, 8: 3-9.
- MELLO-LEITÃO, C. F. (1941a): Notas sobre a sistemática das aranhas, com descrição de algumas novas espécies. *Ann. Acad. Bras. Ciencias*, 13: 103-127
- MELLO-LEITÃO, C. F. (1941b): Catálogo das aranhas da Colômbia. – *Ann. Acad. Bras. Ciencias*, 13: 233-300.
- MELLO-LEITÃO, C.F. (1941c): Las arañas de Córdoba, La Rioja, Catamarca, Tucumán, Salta y Jujuy. – *Rev. Mus. La Plata (N.S. zool.)*, 2: 99-198.
- MELLO-LEITÃO, C.F. (1941d): Arañas de la provincia de Santa Fe colectadas por el Prof. Birabén. – *Rev. Mus. La Plata (N.S. zool.)*, 2: 199-225.
- MELLO-LEITÃO, C.F. (1942a): Arañas del Chaco y Santiago del Estero. – *Rev. Mus. La Plata (N.S. zool.)*, 2: 381-426.
- MELLO-LEITÃO, C.F. (1942b): Cinco aranhas novas do Peru. – *Rev. Bras. Biol.*, 2: 429-434.
- MELLO-LEITÃO, C.F. (1943a): Catálogo das aranhas do Rio Grande do Sul. – *Arq. Mus. Nac. Rio de Janeiro*, 37: 147-245.
- MELLO-LEITÃO, C.F. (1943b): Arañas nuevas de Mendoza, La Rioja y Córdoba colectadas por el Prof. M. BIRABÉN. – *Rev. Mus. La Plata (N.S. zool.)*, 3: 101-121.
- MELLO-LEITÃO, C.F. (1944): Arañas de la Provincia de Buenos Aires. – *Rev. Mus. La Plata (N.S. zool.)*, 3: 311-393.
- MELLO-LEITÃO, C.F. (1945): Arañas de Misiones, Corrientes y Entre Ríos. – *Rev. Mus. La Plata (N.S. zool.)*, 4: 213-302.
- MELLO-LEITÃO, C.F. (1947): Aranhas do Paraná e Santa Catarina, das coleções do Museu Paranaense. – *Arquivos do Museu Paranaense*, 6: 231-304.

- MELLO-LEITÃO, C.F. (1948): Contribuição ao conhecimento da fauna araneológica das Guianas. – An. Acad. Bras. Sci., **20**: 151-196.
- MELLO-LEITÃO, C.F. (1949): Aranhas da foz do Koluene. – Bol. Mus. Nac. Rio de Janeiro (N.S. zool.), **92**: 1-19.
- NEAVE, S. A. (1940): Nomenclator Zoologicus. – Vol. III; London.
- PICKARD-CAMBRIDGE, O. (1877): On some new species of Araneida, with characters of two new genera and some remarks on the families Podophtalmides and Dinopides. Proc. zool. Soc. London., 1877: 557-578.
- PLATNICK, N.I. (1989): Advances in Spider Taxonomy 1981-1987. – Manchester (Manchester University Press).
- PLATNICK, N.I. (1993): Advances in Spider Taxonomy 1988-1991 - with synonymies and transfers 1940-1980. – New York (New York Entomological Society).
- PLATNICK, N.I. (1997): Advances in Spider Taxonomy 1992-1995 - with redescriptions 1940-1980. – New York (New York Entomological Society).
- ROEWER, C.F. (1954a): Katalog der Araneae von 1758 bis 1940 – Vol. 2: 1-923; Bruxelles.
- ROEWER, C.F. (1954b): Exploration du Parc National de l'Upemba, Araneae, Lycosaeformia I. – Institut des Parcs Nationaux du Congo Belge, Bruxelles, **30**: 1-420.
- ROEWER, C.F. (1959): Exploration du Parc National de l'Upemba, Araneae, Lycosaeformia II. – Institut des Parcs Nationaux du Congo Belge, Bruxelles, **55**: 519-1040.
- ROEWER, C.F. (1961): Über Namen der Gattungen und Arten der Lycosidae (Araneae). – Bull. Inst. Sci. Nat. Belgique, **37**: 1-19.
- SIERWALD, P. (2000): Description of the male of *Sosippus placidus*, with notes on the subfamily Sosippinae (Araneae, Lycosidae). – J. Arachnol., **28**: 133-140.
- SIMON, E. (1898): Histoire Naturelle des Araignées 2: 193-380. Roret, Paris.
- SORDI, S.J. (1996): Ecologia de Populações da aranha *Porri-mosa lagotis* (Lycosidae) nas Reservas Mata de Santa Genebra, Campinas (SP) e Serra do Japi, Jundiá (SP). – Master Thesis, Universidade Estadual de Campinas, Brazil.
- TÖPFER-HOFMANN, G., CORDES D. & VON-HELVERSEN, O. (2000): Cryptic species and behavioural isolation in the *Pardosa lugubris* group (Araneae, Lycosidae), with description of two new species. – Bull. Brit. Arachnol. Soc., **11**: 257-274.
- TULLGREN, A. (1905): Araneida from the Swedish Expedition through the Gran Chaco and the Cordilleras. – Ark. Zool., **2**: 1-81.

CRISTINA A. RHEIMS & ANTONIO D. BRESCOVIT

New species and records of *Scytodes* LATREILLE, 1804 of the “*globula* group” from Brazil (Araneae, Scytodidae)

Abstract

Four new species of scytodid spiders from Brazil are described: *Scytodes becki* sp.n. from Niquelândia and *Scytodes eleonorae* sp.n. from São Domingos, both in the state of Goiás; *Scytodes skuki* sp.n. from Aripuanã, Mato Grosso and *Scytodes strussmannae* sp.n. from Xapuri, Acre. Together with the synanthropic species *S. globula* NICOLET and the Brazilian species *S. itapevi* BRESCOVIT & RHEIMS these four new species form a distinct group within the Neotropical *Scytodes*, herein named “*globula* group”. New records for *S. globula* and *S. itapevi* are also reported.

Resumo

Novas espécies e novos registros de *Scytodes* LATREILLE do “grupo *globula*” do Brasil (Araneae, Scytodidae)

Neste trabalho são descritas quatro novas espécies de *Scytodes* do Brasil: *Scytodes becki* sp.n. de Niquelândia e *Scytodes eleonorae* sp. n. de São Domingos, ambos em Goiás; *Scytodes strussmannae* sp.n. de Xapuri, Acre e *Scytodes skuki* sp. n. de Aripuanã, Mato Grosso. Junto com a espécie sinantrópica *S. globula* NICOLET e a espécie brasileira *S. itapevi* BRESCOVIT & RHEIMS, as quatro espécies novas formam um grupo distinto dentro dos *Scytodes* Neotropicais, chamado “grupo *globula*”. São incluídos novos registros para *Scytodes globula* e *Scytodes itapevi*.

Authors

CRISTINA A. RHEIMS & DR. ANTONIO D. BRESCOVIT, Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil, 1500, Butantã, CEP 05503-900, São Paulo SP, Brazil; e-mail: chris.rheims@aol.com.br; adbrsc@terra.com.br

Key words

Araneae, *Scytodes*, Neotropical, taxonomy

1. Introduction

The scytodids are a small spider family comprising only five genera: *Dictis* L.KOCH, *Scyloxes* DUNIN, *Stedocys* ONO, *Scytodes* LATREILLE and *Soeuria* SAARISTO. Of these, only *Scytodes* occurs in the Neotropical region. During the last three years, this genus has been the subject of several taxonomic studies, resulting in the description of 11 new Neotropical species (BRESCOVIT & HÖFER 1999; BRESCOVIT & RHEIMS 2000; RHEIMS & BRESCOVIT 2000). Together with the four new species described in this paper we count to date a total of 35 valid species (ROEWER 1942; BONNET 1958; PLATNICK 1989, 1993, 1997).

The species are separated mainly by morphological characteristics of the male palp and female epigynum. These characteristics enable a preliminary recognition of at least one distinct group within the Neotropical species, herein named “*globula* group”. This group includes the synanthropic species *Scytodes globula* NICOLET, *S. itapevi* BRESCOVIT & RHEIMS and the four new species described here. The diagnostic characters for the group include a male palp with a large curved sclerotized process (SP in figs 1b, 2c, 3d; BRESCOVIT & RHEIMS 2000: figs 27, 31, 37), initially mistaken for the embolus in BRESCOVIT & RHEIMS (2000). The female epigynes are highly variable but generally present large rounded foveae and two pairs of seminal receptacles, one being globular (figs 2 f-h; 3 b,c; BRESCOVIT & RHEIMS 2000: figs 33,34, 38,39).

2. Material and methods

The material examined belongs to the following institutions: IBSP, Instituto Butantan, São Paulo (A.D. BRESCOVIT); MCTP, Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A.A. LISE); MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo (E. CANCELLO); SMNK, Staatliches Museum für Naturkunde Karlsruhe (H. HÖFER). Descriptions and terminology follow BRESCOVIT & RHEIMS (2000). All measurements are in millimetres. The epigynes were submerged in lactic acid in order to study the internal structures. Micrographs were obtained with a JEOL (JSM 840A) scanning electron microscope at the University of São Paulo (USP).

3. Systematics

Scytodes becki, new species

Figure 1

Holotype: male from Niquelândia, Goiás (14°01' S; 48°18' W), Brazil, Sept. 24 - Oct. 6, 1995, SILVESTRE, DIETZ & BRANDÃO col., deposited in MZSP 14306.

Etymology

The specific name is a patronym in honor of the soil biologist and arachnologist Dr. LUDWIG BECK, who helped supporting the second author's arachnological work in Amazonia and Germany.

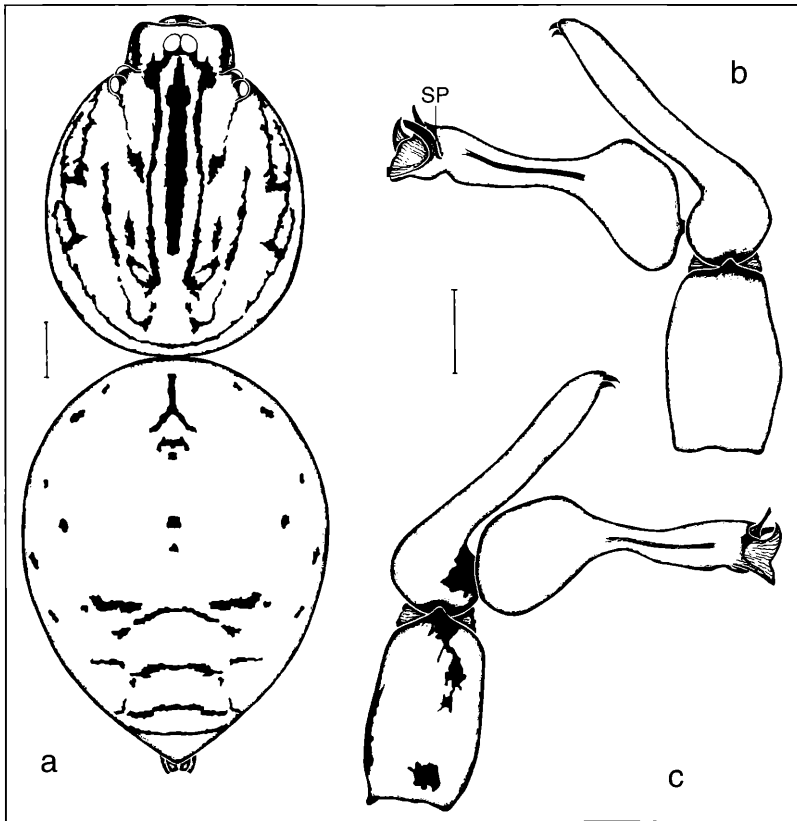


Figure 1. *Scytodes becki*, n. sp. a) male body, dorsal view; b) left palp, retrolateral view (SP = Sclerotized process); c) proximal view. Scale lines: 0.25 mm.

Diagnosis

The male of *Scytodes becki* differs from all the species of the *globula* group by the shorter sclerotized process and small and pointed apical, dorsal membrane on the distal area of the palpal bulb and by a pair of strong, short and curved distal spines on the cymbium (figs 1 b,c).

Description

Male (MZSP 14306). The species described in this paper was probably collected soon after moulting and presents very light yellow coloration. Carapace with a pattern of thin brown stripes as in figure 1 a. Pedipalps with few scattered thin brown spots. Legs with a pair of ventral longitudinal brown stripes on femur. Abdomen with light brown pattern of few anterior scattered spots and posterior transversal stripes as in figure 1 a.

Total length 6.1. Carapace slightly flattened, 2.9 long, 2.2 wide. Eye diameters: PME 0.16, ALE 0.14, PLE 0.16. Lateral eyes on tubercle. Chelicerae with subapical hyaline keel and inconspicuous stridulatory ridges. Labium 0.26 long, 0.28 wide. Sternum 1.32 long, 1.04 wide. Abdomen 3.2 long, 2.5 wide.

Leg measurements: I - femur 6.8/ patella 0.7/ tibia 6.9/ metatarsus 9.0/ tarsus 1.3/ total 24.7/ II - 5.0/ 0.7/ 4.9/

5.6/ 0.7/ 16.9/ III - 3.0/ 0.6/ 2.5/ 3.5/ 0.7/ 10.3/ IV - 5.0/ 0.7/ 4.4/ 5.3/ 0.9/16.3.

Palp: Palpal femur with short and narrow stridulatory pick with rounded and slightly projecting socket. Bulb 0.8 long, slightly constricted medially (fig. 1 c). Distal area with large prolateral hyaline membrane, slightly curved upwards (figs 1 b,c).

Female: Unknown.

Distribution: Known only from the type locality.

Material examined

Only the holotype.

Scytodes eleonorae, new species

Figures 2, 4

Types: Male holotype and female paratype from Angélica Cave, Parque Estadual de Terra Ronca, São Domingos, Goiás, Brazil, Sept. 6, 2000, C.A. RHEIMS col., deposited in IBSP 26037; male and female paratypes from same locality as holotype, Sept. 6, 2000, F.P. FRANCO col., deposited in IBSP 26041 and male and female paratypes with same data as holotype, deposited in MZSP.

Etymology

The specific name honors Dr. ELEONORA TRAJANO, a speleologist from the University of São Paulo, who organized the field course on cave communities in Goiás, during which most specimens were collected.

Diagnosis

The male of *Scytodes eleonorae* resembles that of *S. itapevi* by the presence of two hyaline membranes at the distal area of the palpal bulb, but differs by the long dorsal membrane and the absence of a prolateral curved prong (figs 2 c,d). The female resembles that of *S. strussmannae* by the large and globular seminal receptacles with lateral sclerotized plates, but differs by the simple smaller seminal receptacles with sinuous stalks (figs 2 f-h).

Description

Male (IBSP 26037). Carapace yellow with dark brown pattern as shown in figure 2 a. Pedipalps yellow with anterior transversal bands close to the articulations. Labium and endites yellow with thick brown margins. Sternum yellow with brown spots in front of each coxa, narrowing towards centre. Legs yellow with brown transversal bands, except on tarsi. Abdomen greyish with very faint brown pattern.

Total length 6.9. Carapace slightly flattened, 3.0 long, 2.3 wide. Eye diameters: PME 0.18, ALE 0.2, PLE 0.18. Lateral eyes on prominent tubercle. Chelicerae anteriorly projected, with subapical hyaline keel and inconspicuous stridulatory ridges. Labium 0.26 long, 0.3 wide. Sternum 1.5 long, 1.2 wide. Abdomen 3.8 long, 2.3 wide.

Leg measurements: I - femur 17.4/ patella 0.9/ tibia 17.4/ metatarsus 23.6/ tarsus 1.5/ total 60.8/ II - 11.9/ 0.8/ 11.7/ 15.1/ 1.0/ 40.5/ III - 7.5/ 0.8/ 6.9/ 8.2/ 1.2/ 24.6/ IV - 11.3/ 0.8/ 10.5/ 11.9/ 1.2/ 35.7.

Palp: Cymbium with a pair of long and slender distal spines (figs 2 c,d). Palpal femur with short and thickened stridulatory pick with rounded and slightly projected socket (fig. 4 d). Bulb 0.74 long, at middle slightly constricted with very long, strongly curved process (figs 2 c,d, 4 a,c). Distal area narrow and sinuous, carrying duct opening (fig. 4 b).

Female (IBSP 26037). Colour pattern as in male but slightly darker.

Total length 6.0. Carapace domed, 2.5 long, 2.2 wide. Eye diameters: PME 0.16, ALE 0.16, PLE 0.14. Lateral eyes as in male. Chelicerae as in male. Labium 0.3 long, 0.32 wide. Sternum 1.4 long, 1.1 wide. Abdomen 3.5 long, 2.5 wide.

Leg measurements: I - femur 6.9/ patella 0.7/ tibia 7.2/ metatarsus 8.9/ tarsus 1.2/ total 24.9/ II - 5.6/ 0.6/ 5.0/ 6.6/ 1.1/ 18.9/ III - 3.9/ 0.6/ 3.4/ 4.2/ 0.9/ 13.0/ IV - 5.5/ 0.7/ 5.4/ 6.0/ 1.2/ 18.8.

Epigynum: Palpal femur with stridulatory pick as in male. Foveae rounded with triangular positioning

ridges very close together (fig. 2 e). Internal genitalia with globular pair of seminal receptacles medianly united (figs 2 f-h).

Variation: Four males: total length 4.9 - 6.3; carapace 2.3 - 2.9; femur I 16.0 - 17.38; bulb 0.66 - 0.82; eighteen females: total length 5.1 - 8.0; carapace 2.5 - 3.2; Femur I 5.6 - 8.2. Some specimens present darker and more elaborate colour patterns, as shown in figure 2 b. The sclerotized plates on the larger globular seminal receptacles and the shape of the smaller seminal receptacles vary considerably as shown in figures 2 g,h.

Natural history

This species was found inhabiting subterranean habitats in Bahia and Goiás, Brazil. They were observed feeding and carrying egg-sacs in cave interiors at distances of up to 800 meters from the cave entrance. Although very abundant deep inside the cave, few specimens were collected close to the entrance. In most cases, they were collected from between pholcid (*Mesabolivar* sp.) webs.

The specimens from Bahia were collected in "caatinga" areas, a habitat characterized by a very hot and dry climate and sparse vegetation (AB'SABER 1977 JOLY et al. 1999). They were found inhabiting small subterranean cavities, less than 100 meters deep, called "tocas" (LUMLEY et al. 1987). The specimens from São Domingos, Goiás were collected in "cerrado" (RIZZINI 1997), in an area with several deep caves.

All specimens present the same basic genital morphology but the São Domingos specimens are larger with very long legs and much lighter colour patterns than those collected from small caves or epigeic habitats. Although the latter present characteristics shared by many exclusively subterranean species (troglobites sensu BARR & HOLSINGER 1985), such as elongated legs and pigment reduction, no collections were made outside these caves to indicate any possibility of isolation in the subterranean environment initiating species differentiation.

Distribution

The species is known from caves in central and north-eastern Brazil (states of Ceará and Paraíba).

Material examined

Brazil. Ceará, 8 Km SW Porteiras (39°10' W; 07°30' S), 1♀, Jan. 28, 1995, M. VERHAAGH col. (SMNK); Paraíba, Areia, Mata de Pau Ferro (06°57' S; 35°44' W), 1♂, Sept., 1999, A. D. BRESCOVIT et al. col. (IBSP 26210), Bahia, Itaguassú (Toca Santo Eusébio), 1♀, July 20, 2000, A.D. BRESCOVIT et al. col. (IBSP 26145); (Toca de Pilões), 4♀ 1 juv., July 19, 2000, A.D. BRESCOVIT et al. col. (IBSP 26146); Jussara (Toca da Esperança), 2♀, July 21, 2000, A.D. BRESCOVIT col. (IBSP 26156); Goiás, São Domingos, (Caverna Angélica), 1♂ 6♀ 6 juvs, Sept. 6, 2000, C.A. RHEIMS col. (IBSP 26036); 1♀, Sept. 9, 2000, C.A. RHEIMS & F.P. FRANCO col. (IBSP 26043); (Caverna Passa Três), 1♂ 1♀, Sept. 5, 2000, C.A. RHEIMS col. (IBSP

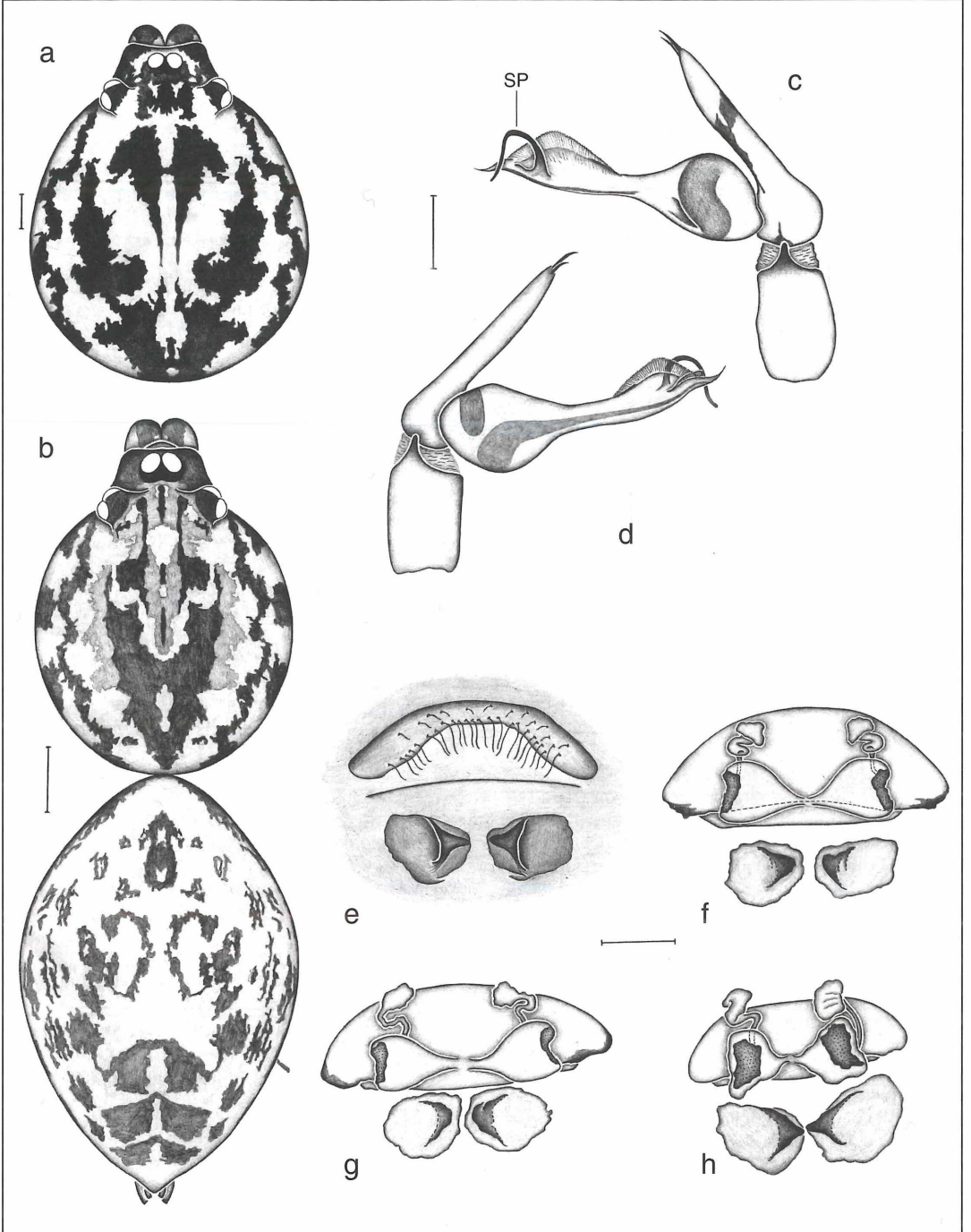


Figure 2. *Scytodes eleonora*, n. sp. a) male carapace, dorsal view; b) body, dorsal view; c) left palp, retrolateral view (SP = sclerotized process); d) prolateral view; e) female epigynum, ventral view; f) dorsal view; g) variation, dorsal view; h) variation, dorsal view. Scale lines: 0.25 mm.

26038); 1♀ 1juv., Sept. 3, 2000, C.A. RHEIMS col. (IBSP 26039); (Caverna São Bernardo), 1♀, Sept. 8, 2000, F.P. FRANCO col. (IBSP 26040); 2♀ 1 juv., Sept. 8, 2000, C.A. RHEIMS col. (IBSP 26042).

***Scytodes strussmannae*, new species**

Figures 3 a-c

Types: Female holotype from Pimenteira, Xapuri, Acre, Brazil, Apr. 5-7, 1996, Eq. IBSP/SMNK col., deposited in IBSP 8636. Two female paratypes from Piraputanga, Dois Irmãos do Buriti (20°27' S; 55°30' W), Mato Grosso do Sul, Brazil, Jun. 31 Jul. 6, 1999, A.D. BRESCOVIT et al. col., deposited in IBSP 26212 and IBSP 26213. Female paratype from Denise, Mato Grosso, Brazil, Sept. 12, 1992, C. STRUSSMANN col., deposited in MCTP 3015.

Etymology

The specific name is a patronym in honor of the collector of one of the paratypes.

Diagnosis

The female of *Scytodes strussmannae* resembles that of *S. eleonorae* by the sclerotized plate of the larger seminal receptacles; but differs by the subrectangular shape of the smaller seminal receptacles with a dorsal projection (fig. 3 c) and the semicircular shape of the positioning ridges (fig. 3 b).

Description

Female (MCTP 3015). Carapace yellow with dark brown pattern as shown in figure 3 a. Pedipalps yellow with transversal brown bands. Labium brown. Endites anteriorly brown, posteriorly yellow with brown margins. Sternum yellow with light brown margins and large brown spots in front of each coxa, extending towards centre. Legs yellow with brown transversal bands along entire leg. Abdomen grey with brown pattern of two posterior paired large transversal spots followed by two large spots and covered by many scattered small spots as shown in figure 3 a.

Total length 8.0. Carapace domed, 3.7 long, 2.6 wide. Eye diameters: PME 0.2, ALE 0.18, PLE 0.18. Lateral eyes on tubercle. Chelicerae with subapical hyaline keel and 5 to 6 very conspicuous stridulatory ridges. Labium 0.3 long, 0.4 wide. Sternum 1.7 long, 1.24 wide. Abdomen 4.3 long, 3.2 wide.

Leg measurements: I - femur 6.5/ patella 0.7/ tibia 6.9/ metatarsus 8.0/ tarsus 1.4/ total 23.5/ II - 5.3/ 0.7/ 5.1/ 5.4/ 1.0/ 17.5/ III - 4.0/ 0.7/ 3.4/ 3.8/ 1.2/ 13.1/ IV - 5.0/ 0.7/ 5.2/ 5.3/ 1.2/ 17.4.

Epigynum: Palpal femur with short and strong stridulatory pick with rounded and slightly projecting socket. Foveae separated from each other by their width (fig. 3 b). Internal genitalia with large oval seminal receptacles widely separated. Smaller seminal receptacles with non-sinuuous stalks (fig. 3 c).

Variation: Two females: total length 6.8, 8.0; carapace 2.9, 3.7; femur I 4.9, 6.5.

Male unknown.

Distribution

Known from the States of Acre and Mato Grosso, Brazil.

Material examined

Only the types.

***Scytodes skuki*, new species**

Figures 3 d,e

Types: Male holotype from Chapada Dardanelos, Aripuanã, Mato Grosso (10°10' S; 59°27' W), Brazil, Nov. 2-13, 1996, G. SKUK col., deposited in MZSP 15409.

Etymology

The specific name is a patronym in honor of the collector of the type specimen.

Diagnosis

The male of *Scytodes skuki* resembles that of *S. globula* by the presence of a single hyaline membrane, but differs by the membrane's larger size, by a concave ventral prolateral projection (figs 3 d-e) and by the absence of a dorsal projection on the distal area of the palpal bulb.

Description

Male (MZSP 15409). Carapace and abdomen colour pattern cannot be well defined due to the poor condition of the specimen that was probably moulting when caught. Carapace orange with brown pattern. Pedipalps orange with brown transversal bands. Labium and endites orange with anterior brown transversal stripe. Sternum creamy coloured with light brown margins. Legs orange with brown thick transversal bands, except on tarsi.

Total length 7.4. Carapace slightly flattened, 3.6 long, 2.7 wide. Eye diameters: PME 0.2, ALE 0.2, PLE 0.2. Lateral eyes on tubercle. Chelicerae with subapical hyaline keel and inconspicuous stridulatory ridges. Labium 0.46 long, 0.48 wide. Sternum 1.9 long, 1.7 wide. Abdomen 3.8 long, 2.1 wide.

Leg measurements: I - absent, II - femur 9.2/ patella 1.0/ tibia 9.0/ metatarsus 11.2/ tarsus 1.3/ total 31.7/ III - 6.2/ 0.9/ 5.6/ 6.5/ 1.2/ 20.4/ IV - 8.5/ 1.0/ 8.3/ 9.4/ 1.3/ 28.5.

Palp: Cymbium with a single apical spine (figs 3 d,e). Palpal femur with short and narrow stridulatory pick with rounded and slightly projecting socket. Bulb 0.96 long, narrow and at the middle slightly constricted (fig. 3 e). Distal area with strongly curved sclerotized process (fig. 3 d). Cymbium with single apical spine (figs 3 d,e).

Female unknown.

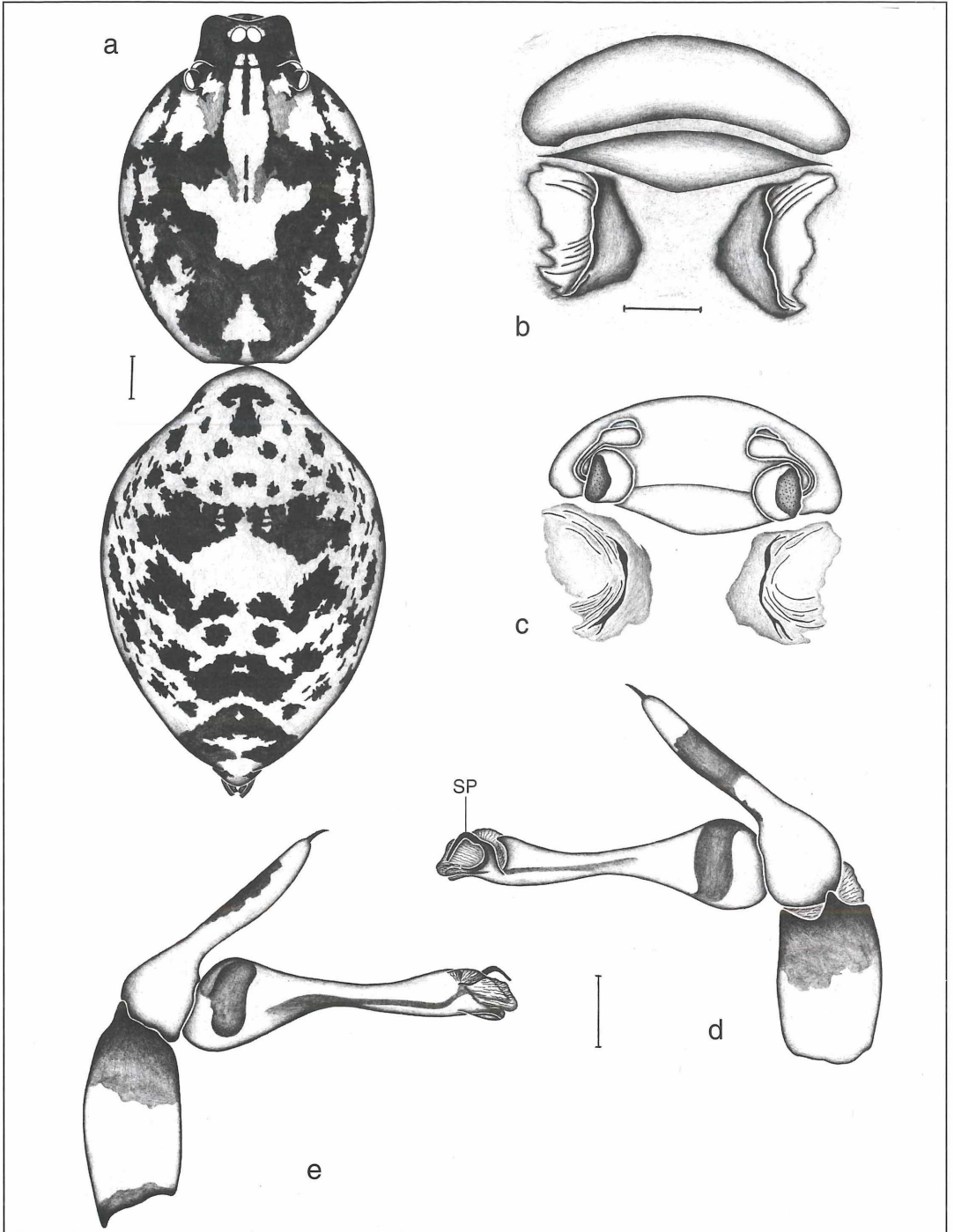


Figure 3 a-c. *Scytodes strussmannae*, n. sp. a) female body, dorsal view; b) epigynum, ventral view; c) dorsal view; d,e. *Scytodes skuki*, n. sp. d) left male palp, retrolateral view (SP = sclerotized process); e) prolateral view. Scale lines: 0.25 mm.

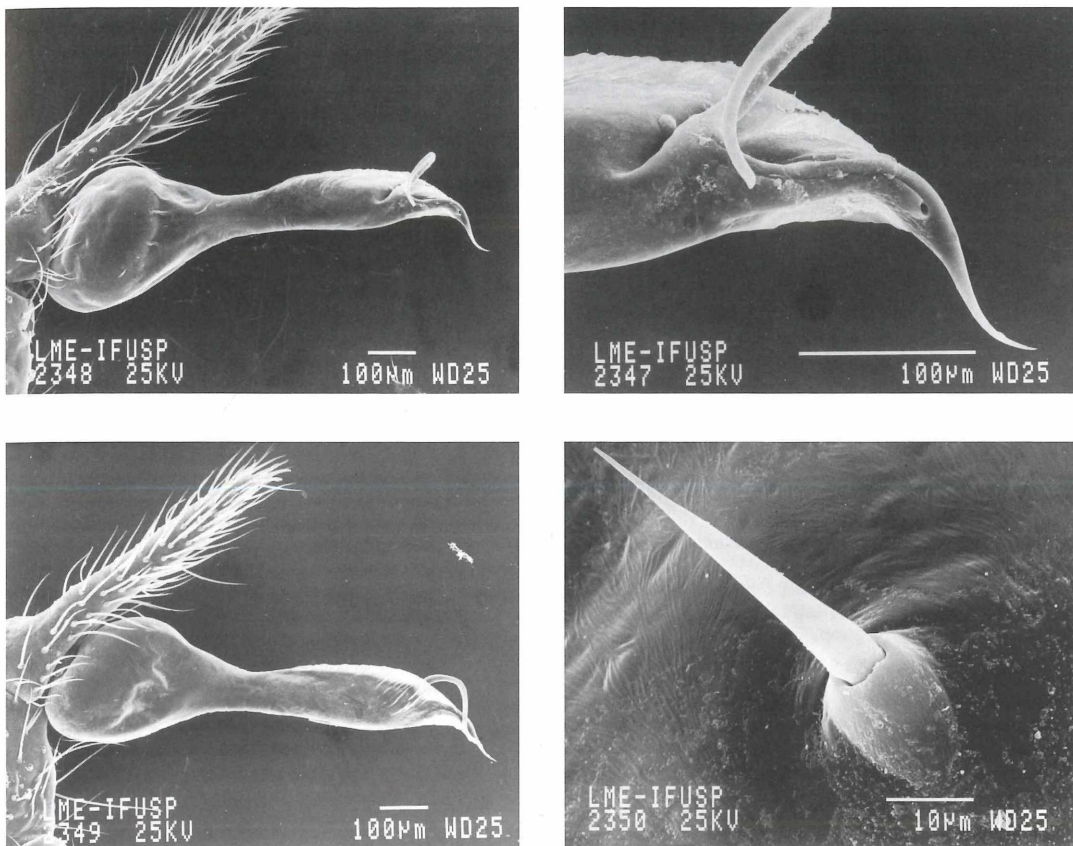


Figure 4. *Scytodes eleonorae*, n. sp. a) male right palp, retrolateral view; b) distal area (D = Duct opening); c) left palp, prolateral view; d) stridulatory pick.

Distribution

Known only from the type locality.

Material examined

Only the type.

New records

Scytodes globula NICOLET, 1849

Material examined

Brazil. Minas Gerais: Uberlândia, Fazenda Experimental do Gloria, Sept. 27, 2000, A.J. SANTOS col., 2♂ 4♀ (IB 0 26186); São Paulo: Itirapina, Jul. 27 - Nov. 22, 1999, M.E. do E.S. OLIVEIRA col., 31♂ 8♀ 4 juvs (IBSP); Mato Grosso do Sul: Brasilândia (Usina Hidrelétrica Engenheiro Sergio Motta), Jul. - Aug., 2000, Eq. IBSP col., 1♂ 6♀ (IBSP); Bataguáçu, Aug. 3, 2000, D. CANDIANI & C. SOUZA col., 2♀ (IBSP); Paraná: Morretes, Pico do Marumbi, Dec., 1945, GOFFERGÉ col., 1♂ (MZSP 3185); Santa Catarina: Ilhota, Parque Botânico Morro do Baú (26°48' S; 48°57' W), Apr. 1-2, 1999, R. PINTO-DA-ROCHA, R.

BÉRNILS & R. LINGNAU col., 1♀ 7 juvs (MZSP 18548); São Bento do Sul, Ano Bom (26°22' S; 49°13' W), R. PINTO-DA-ROCHA, R. BÉRNILS & R. LINGNAU col. (MZSP 18606).

Uruguay. Minas, Dpto. Lavalleja, Cerro Arequita (34°17' S; 55°15' W), Dec. 3, 1997, R. PINTO-DA-ROCHA col., 1♀ 4 juvs (MZSP 16035).

Scytodes itapevi BRESICOVIT & RHEIMS, 2000

Material examined

Brazil. Bahia: Porto Seguro (Parque Nacional do Monte Pascoal), Apr. 23, 1998, A.D. BRESICOVIT et al. col., 2♂ 1♀ (IBSP 18991); Minas Gerais: Belo Horizonte, Estação Ecológica da UFMG (19°52' S; 43°58' W), 1999-2000, E.S.S. ALVARES, C.S. AZEVEDO & E.O. MACHADO col., 1♂ 1♀ 1 juv. (IBSP 26187); 2♀ (IBSP 26188); Uberlândia, Fazenda Experimental do Gloria, Sept. 27, 2000, A.J. SANTOS col., 1♂ 1♀ 4 juvs (IB 26185). Rio de Janeiro: Pinheiral, Fazenda Santa Helena, Nov. 5-11, 1999, A. D. BRESICOVIT et al. col., 1♂ (IBSP 26193), 1♀ (IBSP 26194), 1♂ (IBSP 26192), 1♀ (IBSP 26191)

Acknowledgements

We wish to thank the curators of the collections for loaning material for this study; Prof. PEDRO KUYOHARA and Miss SIMONE PERCHE DE TOLEDO (IF/USP) from "Laboratório de Microscopia Eletrônica do Departamento de Física Geral do Instituto de Física da Universidade de São Paulo" (USP) for making the scanning electron micrographs; Dr. ELEONORA TRAJANO, for enabling the collection of material in São Domingos, Goiás; Dr. HUBERT HÖFER for the invitation to contribute to this special volume and Dr. E. TRAJANO and Dr. B.A. HUBER for helpful comments on the manuscript. This study was supported by PROAP 2000, CNPq and "Fundação de Amparo à Pesquisa de São Paulo" (FAPESP No. 99/05446-8; 00/00247-6).

4. Literature

- AB'SABER, A.N. (1977): Os domínios morfoclimáticos na América do Sul. Primeira aproximação. – Geomorfologia, **52**:1-21.
- BARR, T.C. & HOLSINGER, J.A. (1985): Speciation in cave faunas. – Ann. Rev. Ecol. Syst., **16**:313-337
- BONNET, P. (1958): Bibliographia araneorum. – v. 2, pte 4, p. 3027-4230, Toulouse (Douladoure).
- BRESCOVIT, A.D. & HÖFER, H. (1999): Four new species of litter inhabiting *Scytodes* spiders (Araneae, Scytodidae) from Amazonia. – Stud. Neotrop. Fauna & Environm., **34**:105-113.
- BRESCOVIT, A.D. & RHEIMS, C.A. (2000): On the synanthropic species of the genus *Scytodes* LATREILLE (Scytodidae, Araneae) of Brazil, with synonymies and records of these species in other Neotropical countries. – Bull. Br. arachnol. Soc., **11**: 320-330.
- JOLY, C.A., AIDAR, M.P.M., KLINK, C.A., McGRATH, D.G., MOREIRA, A.G., MOUTINHO, P., NEPSTAD, D.C., OLIVEIRA, A.A., POTT, A., RODAL, M.J.N. & SAMPAIO, E.V.S.B. (1999): Evolution of the Brazilian phytogeography classification systems: Implications for biodiversity conservation. **51**: 331-348.
- LUMLEY, H., DE LUMLEY, M.-A., BELTRÃO, M.C.M.C., YOKOYAMA, Y., LABEYRIE, J., DANON, J., DELIBRIAS, G., FALGUERES, C. & BISCHOFF, J.L. (1987): Présence d'outils taillés associés a une faune quaternaire datée du Pleistocène moyen dans la Toca da Esperança, région de Central, état de Bahia, Brésil. – L'Anthropologie (Paris), **91**(4):917-942.
- PLATNICK, N.I. (1989): Advances in Spider Taxonomy 1981-1987 – Manchester (Manchester University Press).
- PLATNICK, N. I. (1993): Advances in Spider Taxonomy 1988-1991 with synonymies and transfers 1940-1980. – New York (New York Entomological Society).
- PLATNICK, N.I. (1997): Advances in Spider Taxonomy 1992-1995 with redescrptions 1940-1980. – New York (New York Entomological Society).
- RHEIMS, C.A. & BRESCOVIT, A.D. (2000): Six New Species of Neotropical *Scytodes* LATREILLE (Araneae, Scytodidae). – Zoosystema, **22** (4): 721-731.
- RIZZINI, C.T. (1997): Tratado de Fitogeografia do Brasil. Aspectos ecológicos, sociológicos e florísticos. – 2. edição; Rio de Janeiro (Âmbito Cultural Edições LTDA.).
- ROEWER, C. F. (1954): Katalog der Araneae von 1758 bis 1940. – Vol. 2: 1-923; Bruxelles.

HUBERT HÖFER & ANTONIO D. BRESCOVIT

Species and guild structure of a Neotropical spider assemblage (Araneae) from Reserva Ducke, Amazonas, Brazil

Abstract

We present a species list of spiders collected over a period of more than 5 years in a rainforest reserve in central Amazonia –Reserva Ducke. The list is mainly based on intense sampling by several methods during two years and frequent visual sampling during 5 years, but also includes records from other arachnologists and from the literature, in total containing 506 (morpho-)species in 284 genera and 56 families. The species records from this Neotropical rainforest form the basis for a biodiversity database for Amazonian spiders with specimens from several Brazilian collections and the collection of the State Museum of Natural History Karlsruhe, where it is housed. This database will in the future facilitate species identification of Neotropical spider collections, allow comparison of morphospecies and serve as an important background for biodiversity evaluation in natural and anthropogenic habitats and the recognition of species distribution and loss. For further evaluation of the structure of Neotropical spider assemblages and their ecological function we present an analysis of the guild structure of the fauna of Reserva Ducke, although we also emphasize the lack of knowledge on natural history and behavior for many of the species.

Authors

Dr. HUBERT HÖFER, Staatliches Museum für Naturkunde, P.O. 11 1364, D-76063 Karlsruhe; e-mail: hubert.hoefer@smnk.de;
Dr. ANTONIO D. BRESCOVIT, Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil 1500, CEP 05503-900, São Paulo, SP, Brazil; e-mail: adbresc@terra.com.br

Key words

Araneae, Neotropical, assemblage guilds, inventory

1. Introduction

The forest reserve „Reserva Florestal ADOLPHO DUCKE“ belongs to the Instituto Nacional de Pesquisas da Amazônia (INPA) and is certainly one of the best studied areas of Amazonian rainforest. It is situated in central Amazonia, 26 km northeast of the city of Manaus (59°58'W, 2°54'S) and comprises 100 km² (10 x 10 km). A summarized description of geology, soil characteristics, floristic composition is presented in GENTRY'S comparison of „Four Neotropical Rainforests“ (GENTRY 1990). A "Flora da Reserva Ducke" has recently been presented in book form (RIBEIRO et al. 1999). PENNY & ARIAS (1982) made a first survey of the knowledge on insects of the reserve and HÖFER & BECK (1995, 1996) gave a synopsis of the arachnids collected there. Zoo-

logical species inventories have been presented by APOLINÁRIO (1993) for termites, BECK (1971) for oribatid mites, HARADA & ADIS (1997) for ants, HERO (1990) for frogs, LOURENÇO (1988) for scorpions, MAHNERT & ADIS (1985) for pseudoscorpions and WILLIS (1977) for birds. A book on the arthropod fauna of the reserve, edited by INPA scientists is in preparation.

We present here a species list of spiders collected in the reserve. The list is based on more than 2 years of intense sampling by diverse methods in ecological studies (GASNIER et al. 1995, GASNIER & HÖFER 2001, HÖFER 1997, HÖFER et al. 1994a, b, HÖFER et al. 1996, VIEIRA & HÖFER 1994, VIEIRA & HÖFER 1998), but also includes species records from frequent visual sampling over more than five years and specimens collected by other people over a period of about 20 years, which were deposited in Brazilian collections, and few additional species records from the literature.

The species records from this Neotropical rainforest represent the basis of a biodiversity database for Amazonian spiders with specimens from several Brazilian collections and the collection of the State Museum of Natural History Karlsruhe. This database will on the long run be completed by at best all records of identified species from Amazonia and also include morphospecies characterized by a character matrix to allow comparison and recognition of species identity or complementarity. The collections of several institutions will become accessible and their specimens available for comparison, thus enhancing taxonomic work but also allowing better recognition of species in ecological investigations - today internationally recognized demands (GBIF-Global Biodiversity Information Facility: www.gbif.org). The database will allow biogeographic evaluation and serve as an important background for biodiversity inventories of natural and anthropogenic habitats and the recognition of species distribution and loss.

The knowledge of natural history and ecology of spiders is essential for an understanding of the role of spiders in natural and agroecosystems (SUNDERLAND & GREENSTONE 1999), but these informations are especially scarce from tropical assemblages. Assemblage guilds (JAKSIČ & MEDEL 1990) have been proposed to be used as ecological units instead of species or other taxonomically defined units, especially in studies on the effects of spiders on pests in agroecosystems.

UETZ et al. (1999) summarized and discussed the concept and proposed and tested a guild classification for North American spider assemblages. We made a similar analysis for the spider assemblage of a Neotropical primary terra firme rainforest (Reserva Ducke) and propose here a guild classification which can be compared with classifications from other climatic and geographic zones and which has to be tested with assemblages of other Neotropical natural or anthropogenic ecosystems.

2. Material and Methods

Our own collections have been made by pitfall traps, litter quadrat sampling, ground-photoelectors and trunk (arboreal) funnel traps (HÖFER 1990), insecticide fogging in the canopy of two trees (HÖFER et al. 1994a), intensive nocturnal transect sampling (GASNIER 1996, GASNIER & HÖFER 2001) by the aid of cap lamps, one day sampling with a protocol proposed by CODDINGTON et al. (1991) and conventional hand sampling during hundreds of excursions. Five ground-electors and 3 trunk funnel traps were run for 12 respectively 17 months in 1991 and 1992 within an area of about 5 hectares. The ground-electors enclosed 1 m² each, were put up in a line of 50 m and remained always 4 weeks in the same position before being moved 10 meters forward in the forest. The trunk funnel traps were mounted on three medium sized tree trunks, 50 - 70 m distant from each other, in a height of 1.5 m above ground. Arthropods caught in all these traps, filled with picric acid, were collected weekly. In two experimental sites of 400 m² each, within this area, we repeatedly collected 20 litter quadrat samples, which were handsorted, and run 30 pitfall traps during three periods of 4 weeks each.

In addition we checked the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus and the Museo de Ciências Naturais (MCN) in Porto Alegre and all available literature (e.g. the numerous publications of H.W. LEVI and M.E. GALIANO) for additional species records.

Many specialists identified species from our collections and included specimens in their taxonomic work. Corinnidae were identified and revised by ALEXANDRE BONALDO (Belem), Salticidae were identified by HEIKO METZNER, Theridiidae by ERICA BUCKUP and APARECIDA MARQUES (Porto Alegre), Thomisidae by ARNO LISE (PORTO ALEGRE); PABLO GOLOBOFF (Buenos Aires) identified most of the mygalomorph spiders. Morphospecies in genera, where an identification could not be done to date, were only included with a confirmed deposition/availability of specimens.

Because the material collected with traps could only be identified or separated in morphospecies during revisionary work in the course of the last 8 years, a reasonably correct calculation of diversity indices of samples with abundances of every morphospecies is not possible. Species numbers given and dominance values are estimates based on lists with experienced assignment of juvenile specimens to species. The number of observed species including juveniles is already an estimate, because the species belonging of many juveniles cannot be finally determined. Estimation of species numbers based on adult specimens were made using the first order jackknife and the CHAO 2 function of the computer program BioDiversity Professional (Beta version 1 by LAMBSHEAD, PATERSON and GAGE). These two models have shown the best performance

in the tests of TOTI et al. (2000). Due to the long lasting identification process and the failure of an encoded specimen database we could only use the total catches over the whole period of always one trap as unit and not the weekly samples. From such a weak database no accurate estimates can be derived and the resulting species estimates have to be regarded with caution.

Criteria used to analyse the guild structure of the Neotropical spider assemblage partly followed UETZ et al. (1999), but were supplemented with criteria considered important for the Amazonian spider assemblage (see table 5). Cluster analysis was done with the same method and program that UETZ et al. (1999) used, the unweighted pair group average method (Statistica, StatSoft 1997).

Most specimens from our samples will lastly be deposited in the collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, however a large part of the material is at the moment still on loan to taxonomists or to the two authors. Abbreviations used for the collections where specimens are deposited: AMNH, American Museum of Natural History, New York, USA (N.I. PLATNICK); CAS, California Academy of Sciences, San Francisco, USA (C. GRISWOLD); IBSP, Instituto Butantan, São Paulo, Brazil (A.D. BRESOVIT); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (C. MAGALHÃES); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (C. SCIOSCIA); MCN, Museo de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (E.H. BUCKUP); MCTP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (A.A. LISE); MCZ, Museum of Comparative Zoology, Harvard, USA (L. LEIBENSPERGER); MEG, private collection of M.E. GALIANO, Buenos Aires, Argentina; MNRJ, Museu Nacional, Universidade Federal de Rio de Janeiro, Brazil (A. KURY); MZSP, Museu de Zoologia, Universidade de São Paulo, Brazil (E. CANCELLO); SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany (H. HÖFER).

3. Results

3.1 Species inventory

The species list contains at the moment 506 recognized morphospecies in 284 genera and 56 families (tab. 1). The list is highly resolved, which means that 279 species are identified, 67 (13 %) are confirmed new species. Reserva Ducke is the type locality of 39 species. For 3 species the paratypes or the first described male or female are from Reserva Ducke. When we started our study more than 20 % of the spider fauna were undescribed.

In the families Araneidae (*Eustala*), Linyphiidae, Mysmenidae, Oonopidae, Sparassidae, Theridiidae and Theridiosomatidae, additional species might well be recognized by revisional work based on our material. The list thus gives the minimum number of species recorded for the locality.

Salticidae is the most species rich family with 112 identified species (22 %) followed by Araneidae with 91 species (18 %), Theridiidae with 59 (12 %), Corinnidae with 43 (9 %) and Ctenidae with 16 species

(3 %). Mygalomorph spiders are represented by 22 species from 10 families. The ratio of species to genera (S/G) for the whole list is 1.8, for the ground eclector samples 1.9 and for the trunk funnel samples 1.8.

Continuously run traps like ground-eclectors and trunk funnels were most effective in capturing high species numbers, but single fogging procedures also contributed considerably to the species inventory (tab. 2, HÖFER et al. 1994a), demonstrating the expected (and still unrevealed) high species richness of the tropical forest canopy. Pitfall traps and quadrat samples collected considerably less species. Our manual sampling

principally served to collect species living in lower vegetation and large hunting spiders of the ground, which on the other hand were rarely caught as adult specimens in the traps.

None of the mean randomized (50 runs) observed species accumulation curves from the three different methods (ground eclectors, trunk funnel traps, CODDINGTON's protocol) reached an asymptote. Richness estimates (first order jackknife and CHAO 2) from three different sample sets, using only adult specimens, show very different values (tab. 2), all clearly below the species number of our list resulting from all methods together.

Table 1. List of species recorded from Reserva Ducke RD (ud – undescribed, tl – type locality RD, pt – paratype collected at RD, occurrence – method or stratum where specimens were recorded, when no information is given it was collected manually: be – beating of vegetation, f – fogging, ge – ground eclector, ld – looking down, lu – looking up, pf – pitfall trap, te – trunk eclector, veg – in vegetation; da – dial activity: di – diurnal, no – nocturnal).

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
Actinopodidae							
<i>Actinopus</i>	sp.	.	.	.	MCN, SMNK	pf	no
Anapidae							
<i>Anapis</i>	<i>caluga</i>	PLATNICK & SHADAB	.	.	SMNK	lu	di
<i>Anapis</i>	sp.	.	.	.	MCN	te	
<i>Pseudanapis</i>	sp.	.	.	.	MCN	m	
Anyphaenidae							
<i>Anyphaenoides</i>	<i>coddingtoni</i>	BRESCOVIT	.	+	IBSP, USNM	te	
<i>Hibana</i>	<i>melloleitaoi</i>	(CAPORIACCO)	.	.	INPA, MCN	lu ge be f	di
<i>Isigonia</i>	<i>limbata</i>	SIMON	.	.	INPA, SMNK	te	
<i>Patrera</i>	sp.	.	.	.	MCN	te f	
<i>Pippuhana</i>	sp.	.	.	.	IBSP on loan	te	
<i>Teudis</i>	sp.	.	+	.	MCN	te	
<i>Wulfila</i>	<i>modesta</i>	CHICKERING	.	.	SMNK, MCN	te f	
<i>Wulfilopsis</i>	n.sp.	.	.	+	INPA	te	
gen. ?	sp.	.	.	.	IBSP on loan	te	
Araneidae							
<i>Acacesia</i>	cf. <i>cornigera</i>	PETRUNKEVITCH	.	.	MCN	f	
<i>Actinosoma</i>	<i>pentacanthum</i>	(WALCKENAER)	.	.	INPA, MCN	.	di
<i>Alpaida</i>	<i>acuta</i>	(KEYSERLING)	.	.	MCZ		
<i>Alpaida</i>	<i>bicornuta</i>	(TACZANOWSKI)	.	.	NHRM	f	
<i>Alpaida</i>	<i>carminea</i>	(TACZANOWSKI)	.	.	MEG, MZSP		
<i>Alpaida</i>	<i>delicata</i>	(KEYSERLING)	.	.	SMNK		
<i>Alpaida</i>	n.sp. <i>prope antonio</i>	.	.	+	SMNK on loan	ge	
<i>Alpaida</i>	n.sp. <i>prope simila</i>	.	.	+	SMNK on loan	ge	
<i>Alpaida</i>	n.sp.?	.	.	.	SMNK on loan	ge	
<i>Alpaida</i>	<i>negro</i>	LEVI	.	.	SMNK		
<i>Alpaida</i>	<i>tabula</i>	(SIMON)	.	.	SMNK	te	no
<i>Alpaida</i>	<i>trispinosa</i>	(KEYSERLING)	.	.	MEG	.	
<i>Alpaida</i>	<i>truncata</i>	(KEYSERLING)	.	.	INPA, SMNK	be	di
<i>Alpaida</i>	<i>urucuca</i>	LEVI	.	.	MCN		
<i>Amazonepeira</i>	<i>herrera</i>	LEVI	.	.	MCN		
<i>Amazonepeira</i>	<i>masaka</i>	LEVI	.	.	MCN		
<i>Araneus</i>	<i>guttatus</i>	(KEYSERLING)	.	.	MEG		
<i>Araneus</i>	<i>venatrix</i>	(C.L.KOCH)	.	.	MCN		
<i>Argiope</i>	<i>argentata</i>	(FABRICIUS)	.	.	MCN		
<i>Bertrana</i>	<i>elinguis</i>	(KEYSERLING)	.	.	SMNK, MEG	ge	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Chaetacis</i>	<i>cornuta</i>	(TACZANOWSKI)	.	.	MCN		
<i>Chaetacis</i>	<i>cucharas</i>	LEVI	.	.	MCN		
<i>Chaetacis</i>	<i>necopinata</i>	(CHICKERING)	.	.	INPA		
<i>Chaetacis</i>	<i>abrahami</i>	MELLO-LEITÃO	.	.	MCN		
<i>Chaetacis</i>	<i>aureola</i>	(C.L.KOCH)	.	.	INPA, MCN, MEG		
<i>Cyclosa</i>	<i>bifurcata</i>	(WALCKENAER)	.	.	INPA, MCZ, SMNK	veg	
<i>Cyclosa</i>	<i>caroli</i>	LEVI	.	.	INPA, MCN		
<i>Cyclosa</i>	<i>diversa</i>	(O. P. CAMBRIDGE)	.	.	INPA, MCTP, MCN		
<i>Cyclosa</i>	<i>fillineata</i>	HINGSTON	.	.	INPA, MCN, SMNK		
<i>Cyclosa</i>	<i>rubronigra</i>	CAPORACCIO	.	.	MCTP, MCZ		
<i>Cyclosa</i>	<i>tapetifaciens</i>	HINGSTON	.	.	INPA, MACN, MCN, SMNK		
<i>Cyclosa</i>	<i>vieirae</i>	LEVI	.	.	MACN		
<i>Dubiepeira</i>	<i>dubitata</i>	(SOARES & CAMARGO)	.	.	MCN		
<i>Edriscus</i>	sp.	.	.	.	MCN		
<i>Epeiroides</i>	<i>bahiensis</i>	(KEYSERLING)	.	.	MCN		
<i>Eriophora</i>	<i>fuliginea</i>	(C.L.KOCH)	.	.	MCN		
<i>Eustala</i>	spp.	.	.	.	MCN, SMNK	lu be te f	no
<i>Gasteracantha</i>	<i>cancriformis</i>	(LINNAEUS)	.	.	.	only photo	
<i>Hingstepeira</i>	<i>dimona</i>	LEVI	.	.	MCN, MCZ		
<i>Hingstepeira</i>	<i>folisecens</i>	LEVI	.	.	INPA, MCN, SMNK	veg	no
<i>Hypognatha</i>	<i>scutata</i>	(PERTY)	.	.	INPA		
<i>Kapogea</i>	<i>alayi</i>	(ARCHER)	.	.	MCN		
<i>Kapogea</i>	<i>sexnotata</i>	(SIMON)	.	.	MCZ		
<i>Larinia</i>	sp.	.	.	.	MCN on loan		
<i>Mangora</i>	sp.	.	.	.	IBSP, SMNK, MCN	veg te f	
<i>Manogea</i>	<i>porracea</i>	(C.L.KOCH)	.	.	INPA, MCN, MCZ		
<i>Mecynogea</i>	sp.	.	.	.	MCN		
<i>Metazygia</i>	<i>castaneoscutata</i>	(SIMON)	.	.	MCN		
<i>Metazygia</i>	<i>ducke</i>	LEVI	.	+	MCN		
<i>Metazygia</i>	<i>enabla</i>	LEVI	.	.	MCN		
<i>Metazygia</i>	<i>laticeps</i>	(O. P. CAMBRIDGE)	.	.	SMNK	veg	
<i>Metazygia</i>	<i>manu</i>	LEVI	.	.	MCN		
<i>Metazygia</i>	<i>mariahelenae</i>	LEVI	.	+	MACN		
<i>Metazygia</i>	<i>yucumo</i>	LEVI	.	.	MCN		
<i>Micrathena</i>	<i>acuta</i>	(WALCKENAER)	.	.	SMNK on loan		
<i>Micrathena</i>	<i>clypeata</i>	(WALCKENAER)	.	.	INPA, SMNK	lu f	di
<i>Micrathena</i>	<i>coca</i>	LEVI	.	.	MCN, MEG		
<i>Micrathena</i>	<i>evansi</i>	CHICKERING	.	.	INPA, MEG		
<i>Micrathena</i>	<i>excavata</i>	(C.L.KOCH)	.	.	INPA, MCN		
<i>Micrathena</i>	<i>exlinae</i>	LEVI	.	.	MCN		
<i>Micrathena</i>	<i>furcula</i>	(O. P. CAMBRIDGE)	.	.	MCN		
<i>Micrathena</i>	<i>horrida</i>	(TACZANOWSKI)	.	.	MCN		di
<i>Micrathena</i>	<i>kirbyi</i>	(PERTY)	.	male	INPA, MCN, SMNK	veg	di
<i>Micrathena</i>	<i>lata</i>	CHICKERING	.	.	MZSP		
<i>Micrathena</i>	<i>plana</i>	(C.L.KOCH)	.	.	SMNK on loan		
<i>Micrathena</i>	<i>pungens</i>	(WALCKENAER)	.	.	AMNH, SMNK		
<i>Micrathena</i>	<i>schreibersi</i>	(PERTY)	.	.	INPA, MCZ, SMNK	veg	di
<i>Micrathena</i>	<i>triangularis</i>	(C.L.KOCH)	.	.	INPA, MCN		
<i>Micrathena</i>	<i>triangularispinosa</i>	(DE GEER)	.	.	INPA, MCN, MEG		
<i>Micrathena</i>	<i>ucayali</i>	LEVI	.	.	MCN		
<i>Micrepeira</i>	<i>fowleri</i>	LEVI	.	.	INPA, MCZ		
<i>Micrepeira</i>	<i>hoeferi</i>	LEVI	.	.	INPA, MCN, SMNK, MCZ	veg	
<i>Micrepeira</i>	<i>tubulofaciens</i>	(HINGSTON)	.	.	MCN		
<i>Ocrepeira</i>	<i>maraca</i>	LEVI	.	.	MEG		
<i>Ocrepeira</i>	<i>albopunctata</i>	(TACZANOWSKI)	.	.	MCN, MEG		
<i>Ocrepeira</i>	<i>covillei</i>	LEVI	.	.	MCN		

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Parawixia</i>	<i>hypocrita</i>	(O. P. CAMBRIDGE)	.	.	MCN	veg	
<i>Parawixia</i>	<i>kochi</i>	(TACZANOWSKI)	.	.	INPA, MCN	veg te	no
<i>Parawixia</i>	<i>tarapoa</i>	LEVI	.	.	MCN	wasps prey	
<i>Pronous</i>	<i>tuberculifer</i>	KEYSERLING	.	.	MCZ		
<i>Spilasma</i>	<i>duodecinguttata</i>	(KEYSERLING)	.	.	INPA, MCN, SMNK		
<i>Testudinaria</i>	sp.	.	.	.	SMNK	lu	no
<i>Verrucosa</i>	sp.	.	.	.	SMNK	lu te	no
<i>Wagneriana</i>	<i>acrosomoides</i>	(MELLO-LEITÃO)	.	.	INPA		
<i>Wagneriana</i>	<i>bamba</i>	LEVI	.	.	MCN		
<i>Wagneriana</i>	<i>jelskii</i>	(TACZANOWSKI)	.	.	INPA, CAS		
<i>Wagneriana</i>	<i>lechuza</i>	LEVI	.	.	MCN		
<i>Wagneriana</i>	<i>maseta</i>	LEVI	.	.	INPA		
<i>Wagneriana</i>	<i>neblina</i>	LEVI	.	.	MCN		
<i>Wagneriana</i>	<i>transitoria</i>	(C.L. KOCH)	.	.	MCN		
<i>Xylethrus</i>	<i>scrupeus</i>	SIMON	.	.	SMNK	veg	
Barychelidae							
<i>Strophaeus</i>	sp.	.	.	.	AMNH on loan	ge	
Caponiidae							
<i>Caponinae</i>	sp.	.	.	.	AMNH on loan	ge	
<i>Nops</i>	sp.	.	.	.	INPA, MCN	ge	
Clubionidae							
<i>Clubiona</i>	aff. kiwoa	.	.	.	MCN on loan		
<i>Elaver</i>	sp.	.	.	.	IBSP	te	
Corinnidae							
<i>Abapeba</i>	<i>hoeferi</i>	BONALDO	.	+	MCN, SMNK	te	
<i>Abapeba</i>	<i>lacertosa</i>	SIMON	.	.	INPA, MCN, SMNK	te	
<i>Abapeba</i>	<i>taruma</i>	BONALDO	.	.	INPA, SMNK	te	
<i>Apochinomma</i>	sp.	.	.	.	BONALDO on loan		
<i>Castianeira</i>	sp.2	.	.	.	MCN, SMNK	ge	
<i>Castianeira</i>	sp.4	.	.	.	MCN, SMNK	te	
<i>Castianeira</i>	sp.6	.	.	.	MCN, SMNK	te	
<i>Corinna</i>	<i>ducke</i>	BONALDO	.	+	INPA, MCN, SMNK	ge te	
<i>Corinna</i>	<i>recurva</i>	BONALDO	.	+	INPA, MCN, SMNK	ge pf te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 2	.	.	+	INPA (BONALDO on loan)	ge	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 3	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 4	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 5	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 6	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 7	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 9	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 11	.	.	+	INPA (BONALDO on loan)	te	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 12	.	.	+	INPA (BONALDO on loan)	m	
<i>Corinna</i>	grupo <i>ducke</i> n.sp. 13	.	.	+	INPA (BONALDO on loan)	m	
<i>Creugas</i>	n.sp.	.	.	+	INPA (BONALDO on loan)	te	
<i>Ecitocobius</i>	<i>comissator</i>	BONALDO & BRESCOVIT	.	+	INPA	with ants	
<i>Falconina</i>	n.sp.	.	.	+	INPA (BONALDO on loan)	.	
<i>Mazax</i>	cf. <i>pax</i>	.	.	.	SMNK	sandy area veg	
<i>Myrmecotypus</i>	sp.	.	.	.	SMNK	f	
<i>Myrmecium</i>	<i>bifasciatum</i>	(TACZANOWSKI)	.	.	INPA, SMNK	veg te	
<i>Myrmecium</i>	cf. <i>gounelley</i>	SIMON	.	.	SMNK on loan	veg	
<i>Myrmecium</i>	cf. <i>velutinum</i>	SIMON	.	.	SMNK on loan	veg	
<i>Parachemmis</i>	<i>manauara</i>	BONALDO	.	.	MCN, INPA, IBSP, SMNK	te	
<i>Parachemmis</i>	n.sp. 1	.	.	+	INPA (BONALDO on loan)	te	
<i>Parachemmis</i>	n.sp. 2	.	.	+	INPA (BONALDO on loan)	te	
<i>Simonestus</i>	n.sp. 3	.	.	+	INPA (BONALDO on loan)	te	
<i>Simonestus</i>	n.sp. 5	.	.	+	INPA (BONALDO on loan)	termite nest	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Simonestus</i>	n.sp. 7	.	+	.	INPA (BONALDO on loan)	te	
<i>Sphecotypus</i>	cf. <i>niger</i>	.	.	.	INPA (BONALDO on loan)	f	di
<i>Stethorrhagus</i>	<i>lupulus</i>	SIMON	.	.	MCN, SMNK	te f	
<i>Tapixaua</i>	<i>callida</i>	BONALDO	.	+	INPA, SMNK	te	
Trachelinae gen.	n.sp.2	.	.	.	INPA (BONALDO on loan)	te	
Trachelinae gen.	n.sp.4	.	.	.	INPA (BONALDO on loan)	te	
Trachelinae gen.	n.sp.5	.	.	.	INPA (BONALDO on loan)	te	
Trachelinae gen.	n.sp.6	.	.	.	INPA (BONALDO on loan)	te	
<i>Tupirinna</i>	<i>rosae</i>	BONALDO	.	+	INPA, IBSP, SMNK	te	
<i>Tupirinna</i>	n.sp. 1	.	+	.	INPA (BONALDO on loan)	m	
<i>Xeropigo</i>	n.sp. 5	.	+	.	INPA (BONALDO on loan)	te	
Ctenidae							
<i>Acanthoctenus</i>	<i>spiniger</i>	KEYSERLING	.	.	IBSP on loan	m	no
<i>Asthenoctenus</i>	<i>longistylus</i>	BRESCOVIT & SIMÓ	.	.	INPA, SMNK	te	no
<i>Centroctenus</i>	<i>acara</i>	BRESCOVIT	.	+	INPA, IBSP, SMNK	ld	no
<i>Centroctenus</i>	<i>auberti</i>	(CAFORIACCO)	.	.	MCN, INPA, SMNK	te	no
<i>Centroctenus</i>	<i>miriuma</i>	BRESCOVIT	.	.	SMNK	te	no
<i>Centroctenus</i>	<i>ocelliventer</i>	(STRAND)	.	.	INPA, IBSP, MCN, SMNK	te	no
<i>Ctenus</i>	<i>amphora</i>	MELLO-LEITÃO	.	.	INPA, IBSP, SMNK	ge ld te	no
<i>Ctenus</i>	<i>crulsi</i>	MELLO-LEITÃO	.	.	INPA, IBSP, SMNK	ge ld	no
<i>Ctenus</i>	<i>inaja</i>	HÖFER, BRESCOVIT & GASNIER	+	.	NPA, MCN	te	no
<i>Ctenus</i>	<i>manauara</i>	HÖFER, BRESCOVIT & GASNIER	.	+	INPA, SMNK	m	no
<i>Ctenus</i>	<i>minor</i>	F.O. P. CAMBRIDGE	.	.	INPA, MCN	m	no
<i>Ctenus</i>	<i>villasboasi</i>	MELLO-LEITÃO	.	.	INPA, SMNK	ld	no
<i>Cupiennius</i>	<i>celerrimus</i>	SIMON	.	.	IBSP, MCN, SMNK, UA	veg	no
<i>Enoploctenus</i>	n.sp.	.	+	.	INPA, IBSP, MCN, SMNK	te	no
<i>Gephyroctenus</i>	n.sp.	.	+	.	MCN	ge bete	
<i>Phoneutria</i>	<i>fera</i>	PERTY	.	.	SMNK, MCN	veg te	no
<i>Phoneutria</i>	<i>reidyi</i>	(F.O. P. CAMBRIDGE)	.	.	SMNK, MCN	veg te	no
Ctenizidae							
<i>Ummidia</i>	sp.	.	.	.	AMNH on loan	m	no
Cyrtoucheniidae							
<i>Bolostromus</i>	sp.	.	.	.	INPA, IBSP, SMNK on loan	ge qu	
<i>Fufius</i>	sp.	.	.	.	MCN, AMNH on loan	ge in wasp nest	
<i>Rhytidicolus</i>	sp.	.	.	.	AMNH on loan	pf	
Deinopidae							
<i>Deinopis</i>	sp.	.	.	.	MCN	lu be te	no
<i>Dictyna</i>	sp.	.	.	.	MCN	f	
<i>Thallumetus</i>	sp.	.	.	.	INPA, IBSP	ge	
Dipluridae							
<i>Diplura</i>	sp.	.	.	.	MCN	qu pf ld te	no
<i>Masteria</i>	n.sp.1	.	+	.	SMNK, MCN, AMNH on loan	qu ge pf te	
<i>Masteria</i>	n.sp.2	.	+	.	SMNK, MCN, AMNH, on loan	qu ge pf te	
Gnaphosidae							
<i>Amazoromus</i>	<i>becki</i>	BRESCOVIT & HÖFER	.	+	INPA, SMNK	te	
<i>Amazoromus</i>	<i>kedus</i>	BRESCOVIT & HÖFER	.	+	INPA, SMNK, MCN	te	
<i>Apopyllus</i>	sp.	.	.	.	IBSP on loan		
<i>Apodrassodes</i>	sp.	.	.	.	SMNK on loan	te	
<i>Cesonia</i>	sp.	.	.	.	MCN		
<i>Zimiromus</i>	n.sp. aff. <i>nadleri</i>	.	+	.	IBSP on loan	te	
<i>Zimiromus</i>	<i>kleini</i>	BUCKUP & BRESCOVIT	.	.	INPA, IBSP, MCN, SMNK	veg	
<i>Zimiromus</i>	<i>syenus</i>	BUCKUP & BRESCOVIT	.	.	INPA, IBSP, MCN, SMNK	veg	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
Hahniidae							
<i>gen. ?</i>	sp.	.	.	.	INPA, MCN, SMNK on loan		
<i>Tama</i>	aff. <i>crucifera</i>	.	.	.	IBSP, SMNK on loan	te f	
I Idiopidae							
<i>Idiops</i>	sp.	.	.	.	MCN, SMNK	ge te	no
Linyphiidae							
<i>Erigone</i>	sp.	.	.	.	MCN		
<i>Sphecozone</i>	sp.	.	.	.	MCN	ge	
<i>Orthobula</i>	n.sp.	.	+	.	MCN on loan	ge	
Lycosidae							
<i>Aglaoctenus</i>	<i>castaneus</i>	(MELLO-LEITÃO)	.	.	MCN	ge	di
<i>Lycosa</i>	group <i>thorelli</i> sp.	.	.	.	SMNK	pf	
Microstigmatidae							
n.gen.	n.sp.	.	+	.	INPA, SMNK on loan	qu ge pf	
Mimetidae							
<i>Arocha</i>	sp.	.	.	.	IBSP		
n.gen.	n.sp.	.	+	.	MCN on loan	ge	
<i>Ero</i>	sp.	.	.	.	MCN	ge lu be te	
<i>Gelanor</i>	sp.	.	.	.	MCN	m	
<i>Mimetus</i>	group <i>melanostoma</i> sp.	.	.	.	MCN		
<i>Cheiracanthium</i>	<i>inclusum</i>	(HENTZ)	.	.	INPA, MCN	veg	
<i>Terminius</i>	<i>insularis</i>	(LUCAS)	.	.	SMNK	pf	
Mysmenidae							
<i>Microdipoena</i>	sp.	.	.	.	SMNK	ge	
<i>Mysmenopsis</i>	sp.	.	.	.	SMNK	ge	
Nemesiidae							
<i>Neodiplothele</i>	n.sp.	.	.	+	AMNH on loan	ge	
cf. <i>Nesticus</i>	sp.	.	.	+	MCN on loan		
gen. ?	sp.	.	.	+	MCN on loan	m	no
Ochyroceratidae							
<i>Ochyrocera</i>	n.sp. p	.	.	+	SMNK	pf	
<i>Ochyrocera</i>	<i>hamadryas</i>	BRIGNOLI	.	+	SMNK	pf	
<i>Ochyrocera</i>	n.sp. b	.	.	+	SMNK, MCN	ge pf te	
<i>Speocera</i>	<i>amazonica</i>	BRIGNOLI	.	+	SMNK	qu ge	
<i>Speocera</i>	<i>irritans</i>	BRIGNOLI	.	.	SMNK	qu ge	
<i>Speocera</i>	<i>molesta</i>	BRIGNOLI	.	+	SMNK	qu ge	
<i>Speocera</i>	n.sp. iw	.	.	+	SMNK	ge pf	
<i>Speocera</i>	n.sp. j	.	.	+	SMNK	pf	
<i>Speocera</i>	n.sp. m	.	.	+	SMNK	ge	
<i>Speocera</i>	n.sp. pn	.	.	+	SMNK	qu	
Oecobiidae							
<i>Oecobius</i>	cf. <i>concinus</i>	SIMON	.	.	IBSP on loan	f juv.	
Oonopidae							
cf. <i>Ischnothyreus</i>	sp.	.	.	.	SMNK	ge be	
<i>Gamasomorpha</i>	cf. <i>patquiana</i>	BIRABEN	.	.	SMNK on loan	ge	
Gamasomorphinae	sp.	.	.	.	SMNK on loan	ge te	
Gamasomorphinae	sp.	.	.	.	SMNK on loan	ge te	
Gamasomorphinae	sp.	.	.	.	SMNK on loan	ge te	
<i>Neoxyphinus</i>	<i>termitophilus</i>	(BRISTOWE)	.	.	MCN	pf q	
Oonopinae	sp.	.	.	.	SMNK on loan	ge te	
Oonopinae	sp.	.	.	.	SMNK on loan	ge te	
Oonopinae	sp.	.	.	.	SMNK on loan	ge te	
Oonopinae	sp.	.	.	.	SMNK on loan	ge te	
<i>Xyccarph</i>	<i>myops</i>	BRIGNOLI	.	+	INPA, MCN, SMNK	qu ge	
<i>Xyccarph</i>	<i>wellingtoni</i>	HÖFER & BRESCOVIT	.	+	INPA, MCN, SMNK	qu	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
Oxyopidae							
<i>Hamataliwa</i>	sp.	.	.	.	MCN	ge	
<i>Oxyopes</i>	sp.	.	.	.	MCN	te	
<i>Peucetia</i>	sp.	.	.	.	MCN, SMNK	m	di
<i>Schaenicoscelis</i>	sp.	.	.	.	MCN	m	
<i>Tapinillus</i>	sp.	.	.	.	IBSP on loan	m	
Palpimanidae							
<i>Fernandezina</i>	sp.	.	.	.	IBSP	m	
<i>Otiotops</i>	<i>hoeferi</i>	BONALDO & BRESCOVIT	.	+	INPA, SMNK	pf	
<i>Otiotops</i>	<i>oblongus</i>	SIMON	.	.	INPA, MCN, SMNK	ge te f	no
Paratropididae							
<i>Paratropis</i>	sp.	.	.	.	MCN, SMNK	qu ge pf	no
Philodromidae							
<i>Paracleocnemis</i>	sp.	.	.	.	MCTP on loan	f	
Pholcidae							
<i>Carapoa</i>	<i>fowleri</i>	HUBER	.	.	INPA, SMNK, MCZ, MCTP	ge lu te	
<i>Carapoa</i>	<i>ocaina</i>	HUBER	.	.	INPA, SMNK	ge	
gen. ?	sp.	.	.	.	SMNK on loan	ge pf	
<i>Mesabolivar</i>	<i>aurantiacus</i>	(MELLO-LEITÃO)	.	.	INPA, MCN, MCTP, SMNK	ge lu te	di
<i>Mesabolivar</i>	<i>difficilis</i>	(MELLO-LEITÃO)	.	.	SMNK	.	di
<i>Modisimus</i>	sp.	.	.	.	SMNK	ge	
<i>Metagonia</i>	<i>taruma</i>	HUBER	.	.	INPA, MCN	ge	
<i>Litoporus</i>	<i>dimona</i>	HUBER	.	.	SMNK	te	
Pisauridae							
<i>Ancylometes</i>	<i>rufus</i>	(WALCKENAER)	.	.	INPA, SMNK	mte	no
<i>Ancylometes</i>	<i>terrenus</i>	HÖFER & BRESCOVIT	.	+	INPA, SMNK	m	no
<i>Architis</i>	<i>nitidopilosa</i>	SIMON	.	.	SMNK	lu be te	di
<i>Architis</i>	<i>tenuis</i>	SIMON	.	.	SMNK	tef	di
<i>Staberius</i>	<i>spinipes</i>	(TACZANOWSKI)	.	.	SMNK	ld	
<i>Thaumasia</i>	<i>annulipes</i>	F.O. P. CAMBRIDGE	.	.	SMNK, MCN	m	no
<i>Thaumasia</i>	sp.	.	.	.	SMNK, MCN	mte	no
Prodidomidae							
<i>Lygromma</i>	<i>gasnieri</i>	BRESCOVIT & HÖFER	.	pt	INPA, IBSP, SMNK	ge pf	
<i>Lygromma</i>	<i>huberti</i>	PLATNICK	.	.	INPA, IBSP, MCN, SMNK	ge pf	
Salticidae							
<i>Acragas</i>	<i>castaneiceps</i>	SIMON	.	.	MCN		
<i>Acragas</i>	cf. <i>procalvus</i>	SIMON	.	.	SMNK		
<i>Acragas</i>	<i>quadriguttatus</i>	(F.O. P. CAMBRIDGE)	.	.	INPA		
<i>Amphidraus</i>	<i>duckei</i>	GALIANO	.	+	INPA, SMNK	tef	
<i>Amphidraus</i>	n.sp. 2	.	.	+	INPA, SMNK	ge te	
<i>Amphidraus</i>	n.sp. 3	.	.	+	INPA, SMNK	ge te	
<i>Amyceae</i>	sp.	.	.	.	SMNK	ge veg	
<i>Amycus</i>	<i>flavicomis</i>	SIMON	.	.	INPA, SMNK		
<i>Amycus</i>	<i>spectabilis</i>	C.L.KOCH	.	.	MCN		
<i>Arachnomura</i>	n.sp. 1 prope <i>hieroglypha</i>	.	.	+	SMNK		
<i>Arachnomura</i>	n.sp. 2 prope <i>hieroglypha</i>	.	.	+	INPA, SMNK		
<i>Asaracus</i>	<i>semifimbriatus</i>	(SIMON)	.	.	MCN		
<i>Balmaceda</i>	n.sp. prope <i>anulipes</i>	.	.	+	INPA, SMNK	te	
<i>Bellota</i>	<i>violacea</i>	GALIANO	.	+	MNRJ, MACN		
<i>Breda</i>	cf. <i>variolosa</i>	SIMON	.	.	INPA; MCN		
<i>Breda</i>	n.sp. prope <i>spinimana</i>	.	.	+	INPA, SMNK	te	
cf. <i>Tariona</i>	sp. I	.	.	.	SMNK	f	
cf. <i>Tariona</i>	sp. II	.	.	.	INPA, SMNK	te	
cf. <i>Zygoballus</i>	sp.	.	.	.	SMNK	f	
<i>Chinoscopus</i>	n.sp. prope <i>flavus</i>	.	.	+	SMNK		

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Chinoscopus</i>	<i>gracilis</i>	(TACZANOWSKI)	.	.	MACN		
<i>Chinoscopus</i>	<i>maculipes</i>	CRANE	.	.	MACN, MNRJ	f	
<i>Chira</i>	sp.	.	.	.	INPA, SMNK	te	
<i>Chirothecia</i>	sp.	.	.	.	MCN		
<i>Chloridusa</i>	sp.	.	.	.	MCN		
<i>Corcovetella</i>	n.sp. prope <i>aemulatrix</i>	.	+	.	INPA	ge	
<i>Coryphasia</i>	sp.	.	.	.	SMNK on loan	te	
<i>Corythalia</i>	cf. <i>electa</i>	(PECKHAM)	.	.	SMNK		
<i>Corythalia</i>	sp. I	.	.	.	SMNK, INPA	ge te	
<i>Corythalia</i>	sp. II	.	.	.	INPA		
<i>Corythalia</i>	sp. III	.	.	.	SMNK		
<i>Corythalia</i>	sp. IV	.	.	.	SMNK		
<i>Corythalia</i>	n.sp. prope <i>valida</i>	.	+	.	SMNK on loan		
Cytaeinae gen.	sp.	.	.	.	SMNK	te	
<i>Descanso</i>	<i>ventrosus</i>	GALIANO	.	+	MZSP, MACN		
<i>Encolpius</i>	<i>guaraniticus</i>	GALIANO	.	.	SMNK		
<i>Erica</i>	cf. <i>eugenia</i>	PECKHAM & PECKHAM	.	.	SMNK		
<i>Euophrys</i>	sp.	.	.	.	MCN		
<i>Eustromastix</i>	<i>falcatus</i>	GALIANO	.	.	MCN		
<i>Fissidentati</i> gen. prope <i>Balmaceda</i>	sp.	SIMON	.	.	SMNK, INPA	te	
<i>Fissidentati</i> gen. prope <i>Salticus</i>	sp.	.	.	.	SMNK	te	
<i>Fluda</i>	<i>opica</i>	(PECKHAM & PECKHAM)	.	.	MACN, MCN, SMNK		
<i>Fluda</i>	cf. <i>angulosa/nigritarsis</i>	.	.	.	SMNK		
<i>Freya</i>	cf. <i>rufohirta</i>	(SIMON)	.	.	INPA, SMNK		
<i>Freya</i>	cf. <i>perelegans</i>	SIMON	.	.	SMNK		
<i>Freya</i>	n.sp. prope <i>exulta</i>	SIMON	+	.	INPA, SMNK	ge te f	
<i>Freya</i>	<i>dureti</i>	GALIANO	.	pt	MACN, MNRJ		
<i>Frigga</i>	<i>kessleri</i>	(TACZANOWSKI)	.	.	SMNK??		
<i>Gypogyna</i>	<i>forceps</i>	SIMON	.	.	SMNK		
<i>Hypaeus</i>	<i>miles</i>	SIMON	.	.	INPA, SMNK	te	
<i>Hypaeus</i>	<i>triplagiatus</i>	SIMON	.	.	SMNK on loan		
<i>Itata</i>	<i>tipuloides</i>	SIMON	.	.	INPA	f	
<i>Lyssomanes</i>	<i>amazonicus</i>	PECKHAM, PECKHAM & WHEELER	.	.	INPA, SMNK		
<i>Lyssomanes</i>	<i>longipes</i>	(TACZANOWSKI)	.	.	INPA, SMNK	be	
<i>Lyssomanes</i>	n.sp. prope <i>nigrofimbriatus</i>	.	+	.	INPA		
<i>Lyssomanes</i>	n.sp. prope <i>taczanowskii</i>	.	.	.	INPA		
<i>Lyssomanes</i>	n.sp. prope <i>velox</i>	.	+	.	INPA		
<i>Lyssomanes</i>	<i>quadrinotatus</i>	SIMON	.	.	INPA		
<i>Lyssomanes</i>	aff. <i>tapuiramae</i>	GALIANO	.	.	MCN on loan		
<i>Lyssomanes</i>	aff. <i>unicolor</i>	(TACZANOWSKI)	.	.	MCN on loan		
<i>Lyssomanes</i>	<i>ceplaci</i>	GALIANO	.	.	SMNK		
<i>Mago</i>	<i>acutidens</i>	SIMON	.	.	INPA, SMNK		
<i>Mago</i>	<i>longidens</i>	SIMON	.	.	MCN		
<i>Mago</i>	n.sp. prope <i>fonsecai</i>	SOARES & CAMARGO	+	.	INPA		
<i>Mago</i>	<i>steindachneri</i>	(TACZANOWSKI)	.	.	SMNK		
<i>Mago</i>	sp.	.	.	.	SMNK, INPA	ge te	
Magoninae	sp. 1	.	.	.	SMNK	te	
Magoninae	sp. 2	.	.	.	SMNK	te	
<i>Martella</i>	<i>pasteuri</i>	GALIANO	.	+	MNRJ, MACN		
<i>Metaphidippus</i>	sp.	.	.	.	MCN		
<i>Myrmarachne</i>	<i>sumana</i>	GALIANO	.	+	INPA, MACN	te f	
<i>Myrmarachne</i>	n.sp. prope <i>sumana</i>	.	+	.	SMNK		
<i>Myrmarachne</i>	cf. <i>brasiliensis</i>	MELLO-LEITÃO	.	.	INPA	te	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Nagaina</i>	cf. <i>tricincta</i>	SIMON	.	.	SMNK		
<i>Noegus</i>	<i>comatulus</i>	SIMON	.	.	INPA	ge	
<i>Noegus</i>	sp. I	.	.	.	INPA, SMNK	te	
<i>Noegus</i>	sp. II	.	.	.	INPA, SMNK	f	
<i>Noegus</i>	sp. III	.	.	.	SMNK	f	
<i>Noegus</i>	<i>fuscimanus</i>	(TACZANOWSKI)	.	.	INPA	ge	
<i>Nycerella</i>	<i>aprica</i>	(PECKHAM & PECKHAM)	.	.	MNRJ, MACN	ge	
<i>Nycerella</i>	<i>melanopygia</i>	GALIANO	.	+	MACN, MNRJ	ge	
<i>Pachomius</i>	<i>sextus</i>	GALIANO	.	+	MZSP, MACN		
<i>Pachomius</i>	<i>dybowskii</i>	(TACZANOWSKI)	.	.	MACN		
<i>Pensacola</i>	n.sp. prope <i>tuberculotibiata</i>		.	+	SMNK	te	
<i>Phiale</i>	cf. <i>crocea</i>	C.L.KOCH	.	.	SMNK	te	
Plexippeae	sp.	.	.	.	SMNK		
<i>Plexippus</i>	<i>paykulli</i>	(SAVIGNY & AUDOUIN)	.	.	INPA, SMNK		
Pluridentati	n.sp. 1	.	.	+	SMNK, INPA	ge	
n.gen. A							
Pluridentati	n.sp. 2	.	.	+	INPA	ge	
n.gen. A							
Pluridentati	n.sp.	.	.	+	SMNK, INPA	te	
n.gen. B							
Pluridentati	n.sp.	.	.	+	SMNK	ge	
n.gen. C							
<i>Psecas</i>	sp.	only photo	
<i>Rudra</i>	n.sp.	.	.	+	MCTP on loan		
Saiteae gen.	sp. A	.	.	.	SMNK, INPA	ge	
Saiteae gen.	sp. B	.	.	.	SMNK, INPA	ge	
Saiteae gen.	sp. C	.	.	.	SMNK	ge	
Saiteae gen.	sp. D	.	.	.	SMNK	ge	
Saiteae gen.	sp. E	.	.	.	SMNK, INPA	ge te	
<i>Sarinda</i>	cf. <i>cayennensis</i>	(TACZANOWSKI)	.	.	SMNK on loan		
<i>Sarinda</i>	cf. <i>longula</i>	(TACZANOWSKI)	.	.	SMNK	f	
<i>Scopocira</i>	sp.	.	.	.	MCN		
<i>Sidusa</i>	<i>angulitarsis</i>	SIMON	.	.	INPA	te	
<i>Stenodeza</i>	<i>acuminata</i>	SIMON	.	.	SMNK		
Synageleae gen.	sp.	.	.	.	SMNK		
prope <i>Semorina</i>							
<i>Synemosyna</i>	n.sp.	.	.	+	MCN, SMNK	te	
Thiodininae gen.	sp.	.	.	.	SMNK		
<i>Tullgrenella</i>	sp. 1	.	.	.	SMNK	te	
<i>Tullgrenella</i>	sp. 2	.	.	.	SMNK	te	
<i>Vinnius</i>	n.sp. prope <i>calcarifer</i>	.	.	+	SMNK on loan		
<i>Wedoquella</i>	n.sp. prope <i>denticulata</i>	.	.	+	SMNK	ge	
<i>Zygoballus</i>	sp.	.	.	.	SMNK		
Scytodidae							
<i>Scytodes</i>	<i>piroca</i>	RHEIMS & BRESCOVIT	.	.	INPA, IBSP, SMNK	ge	
<i>Scytodes</i>	<i>baibina</i>	RHEIMS & BRESCOVIT	pt	.	INPA, MCN, SMNK	ge veg	
<i>Scytodes</i>	<i>martiusi</i>	BRESCOVIT & HÖFER	.	+	INPA, IBSP, SMNK	ge	
<i>Scytodes</i>	<i>paarmanni</i>	BRESCOVIT & HÖFER	.	+	INPA, IBSP, MCN, SMNK	ge	
Segestriidae							
cf. <i>Ariadna</i>	n.sp.	.	.	+	INPA, SMNK on loan	te	
Selenopidae							
<i>Selenops</i>	<i>ducke</i>	CORRONCA	.	+	MCN	ge te	
<i>Selenops</i>	<i>kikay</i>	CORRONCA	.	.	MCN	te	
<i>Selenops</i>	<i>lavillai</i>	CORRONCA	.	.	SMNK	te	
Senoculidae							
<i>Senoculus</i>	sp.	.	.	.	MCN	ge te	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
Sparassidae							
<i>Olios</i>	sp.1	.	.	.	IBSP on loan	te	
<i>Olios</i>	sp.2	.	.	.	IBSP on loan	te	
<i>Olios</i>	sp.3	.	.	.	IBSP on loan	te	
<i>gen.?</i>	sp.1	.	.	.	IBSP on loan	ge te	
<i>gen.?</i>	sp.2	.	.	.	IBSP on loan	ge te	
<i>gen.?</i>	sp.3	.	.	.	IBSP on loan	f	
Sparianthinae	sp.1	.	.	.	IBSP on loan	ge	
Sparianthinae	sp.2	.	.	.	IBSP on loan	ge	
Symphytognathidae							
<i>Anapistula</i>	<i>secrata</i>	GERTSCH	.	.	MCN	ge qu	
<i>Symphytognatha</i>	sp.	.	.	.	MCN		
Synotaxidae							
<i>Synotaxus</i>	sp. 1	.	.	.	MCN		
Tetrablemmidae							
<i>Monoblemma</i>	<i>becki</i>	BRIGNOLI	.	+	SMNK		
Tetragnathidae							
<i>Azilia</i>	sp. 1	.	.	.	MCN		
<i>Chrysometa</i>	<i>flava</i>	(O. P.CAMBRIDGE)	.	.	GALIANO		
<i>Chrysometa</i>	<i>flavicans</i>	(CAPORIACCO)	.	.	GALIANO		
<i>Chrysometa</i>	<i>guttata</i>	(KEYSERLING)	.	.	GALIANO		
<i>Chrysometa</i>	<i>minuta</i>	(KEYSERLING)	.	.	GALIANO		
<i>Chrysometa</i>	n.sp.	.	.	+	SMNK on loan		
<i>Dolichognatha</i>	<i>ducke</i>	LISE	.	+	MCTP	veg	
<i>Glenognatha</i>	sp.	.	.	.	MCN on loan		
<i>Leucauge</i>	<i>argyra</i>	(WALCKENAER)	.	.	INPA	veg	
<i>Leucauge</i>	sp.	.	.	.	SMNK	lu be	no
<i>Mecynometa</i>	sp.	.	.	.	MCN	veg	
<i>Metabus</i>	sp.	.	.	.	MCN		
<i>Nephila</i>	<i>clavipes</i>	(LINNAEUS)	.	.	.	only photo	di
<i>Tetragnatha</i>	sp.	.	.	.	MCN	be	di
Theraphosidae							
<i>Acanthoscurria</i>	sp.	.	.	.	INPA	ge	no
<i>Avicularia</i>	sp.	.	.	.	INPA	te	no
<i>Cyriocosmus</i>	<i>elegans</i>	(SIMON)	.	.	SMNK	qu	
<i>Cyriocosmus</i>	<i>sellatus</i>	(SIMON)	.	.	MCN	ge te	
<i>Drytopelma</i>	<i>rondoni</i>	(LUCAS & BÜCHERL)	.	.	INPA	ge	no
<i>Epebopus</i>	cf. <i>murinus</i>	(WALCKENAER)	.	.	SMNK	m	no
<i>Epebopus</i>	<i>uatuman</i>	LUCAS, SILVA & BERTANI	.	.	INAP, SMNK	m	no
<i>Holothele</i>	sp.	.	.	.	SMNK		
<i>Tapinauchenius</i>	sp.	.	.	.	INPA	te	
<i>Theraphosa</i>	<i>blondi</i>	(LATREILLE)	.	.	INPA, SMNK	m	no
Theridiidae							
<i>Achaeearanea</i>	<i>schneirlai</i>	LEVI	.	.	SMNK	ge be	di
<i>Achaeearanea</i>	<i>trapezoidales</i>	(TACZANOWSKI)	.	.	SMNK	te	
<i>Achaeearanea</i>	<i>dalana</i>	BUCKUP & MARQUES	.	.	MCN		
<i>Achaeearanea</i>	<i>hieroglyphica</i>	(MELLO-LEITÃO)	.	.	MCN		
<i>Achaeearanea</i>	<i>hirta</i>	(TACZANOWSKI)	.	.	MCN on loan	f	
<i>Achaeearanea</i>	<i>nigrovittata</i>	(KEYSERLING)	.	.	MCN		
<i>Anelosimus</i>	<i>eximus</i>	(KEYSERLING)	.	.	MCN	be te	di
<i>Anelosimus</i>	<i>studiosus</i>	(HENTZ)	.	.	MCN on loan	f	
<i>Argyrodes</i>	<i>altus</i>	KEYSERLING	.	.	MCN		
<i>Argyrodes</i>	<i>amplifrons</i>	O. P.CAMBRIDGE	.	.	MCN on loan		
<i>Argyrodes</i>	<i>analiae</i>	GONZALES & CASTRO	.	.	MCN on loan		
<i>Argyrodes</i>	<i>attenuatus</i>	(O. P.CAMBRIDGE)	.	.	MCN	lu f	no
<i>Argyrodes</i>	<i>dracus</i>	(CHAMBERLIN & IVIE)	.	.	SMNK	te	

Family / Genus	Species	Author	ud	ti	collection	occurrence	da
<i>Argyrodes</i>	<i>duckensis</i>	GONZALES & CASTRO	+	.	MLP		
<i>Argyrodes</i>	<i>godmani</i>	EXLINE & LEVI	.	.	MCN on loan		
<i>Argyrodes</i>	<i>metallissimus</i>	(SOARES & CAMARGO)	.	.	MCN on loan		
<i>Argyrodes</i>	sp.	.	.	.	SMNK		
<i>Cerocida</i>	<i>ducke</i>	MARQUES & BUCKUP	.	+	INPA, MCN, SMNK	be	
<i>Chrosiothes</i>	<i>venturosus</i>	MARQUES & BUCKUP	.	+	INPA, MCN	f	
<i>Chryso</i>	<i>calima</i>	BUCKUP & MARQUES	.	.	MCN on loan		
<i>Dipoena</i>	<i>alta</i>	KEYSERLING	.	.	SMNK	ge f	
<i>Dipoena</i>	<i>atlantica</i>	CHICKERING	.	.	MCN	ge f	
<i>Dipoena</i>	<i>bryantae</i>	CHICKERING	.	.	MCN	ge f	
<i>Dipoena</i>	<i>conica</i>	(CHICKERING)	.	.	MCN	ge	
<i>Dipoena</i>	<i>cordiformis</i>	KEYSERLING	.	.	INPA, MCN, SMNK	ge	
<i>Dipoena</i>	<i>donaldi</i>	CHICKERING	.	.	MCN	ge f	
<i>Dipoena</i>	<i>duodecimguttata</i>	CHICKERING	.	.	MCN	ge	
<i>Dipoena</i>	<i>hortoni</i>	CHICKERING	.	.	MCN	ge	
<i>Dipoena</i>	<i>kuyuwini</i>	LEVI	.	.	MCN	ge	
<i>Dipoena</i>	<i>militaris</i>	CHICKERING	.	.	MCN	ge be	di
<i>Dipoena</i>	n.sp.	.	.	+	MCN	ge f	
<i>Dipoena</i>	<i>puertoricensis</i>	LEVI	.	.	MCN on loan	ge	
<i>Dipoena</i>	<i>tiro</i>	LEVI	.	.	INPA, SMNK	ge te	
<i>Echinotheridion</i>	<i>lirum</i>	MARQUES & BUCKUP	.	+	INPA, MCN		
<i>Episinus</i>	<i>erythropthalmus</i>	(SIMON)	.	.	MCN	f	
<i>Episinus</i>	<i>malachinus</i>	(SIMON)	.	.	MCN on loan		
<i>Episinus</i>	<i>salobrensis</i>	(SIMON)	.	.	MCN, SMNK	lu	no
<i>Euryops</i>	<i>taczanowskii</i>	(SIMON)	.	.	MCN on loan		
<i>Helvibis</i>	sp.	.	.	.	MCN, SMNK	lu	no
<i>Latrodectus</i>	sp.	.	.	.	SMNK	open sandy area	di
<i>Nesticodes</i>	<i>rufipes</i>	(LUCAS)	.	.	SMNK		
<i>Phoroncidia</i>	cf. <i>moyobamba</i>	LEVI	.	.	SMNK	be	di
<i>Spintharus</i>	<i>flavidus</i>	HENTZ	.	.	SMNK	f	
<i>Spintharus</i>	<i>hentzi</i>	LEVI	.	.	MCN	be f	di
<i>Tekellina</i>	<i>bella</i>	MARQUES & BUCKUP	.	+	INPA, MCN	te	
<i>Tekellina</i>	<i>crica</i>	MARQUES & BUCKUP	.	+	INPA, MCN	te	
<i>Theridion</i>	<i>crispulum</i>	SIMON	.	.	MCN on loan		
<i>Theridion</i>	<i>hispidum</i>	O. P.CAMBRIDGE	.	.	MCN on loan	f	
<i>Theridion</i>	sp.1	.	.	.	MCN on loan	te	
<i>Theridion</i>	sp.2	.	.	.	MCN on loan	m	
<i>Theridion</i>	sp.3	.	.	.	MCN on loan	m	
<i>Theridion</i>	sp.4	.	.	.	MCN on loan	m	
<i>Theridion</i>	sp.5	.	.	.	MCN on loan	m	
<i>Theridula</i>	<i>puebla</i>	LEVI	.	.	MCN		
<i>Thwaitesia</i>	<i>affinis</i>	O. P.CAMBRIDGE	.	.	SMNK	f te	
<i>Thwaitesia</i>	<i>bracteata</i>	(EXLINE)	.	.	MCN, SMNK	f	
<i>Thwaitesia</i>	<i>simoni</i>	(KEYSERLING)	.	.	MCN, SMNK	ge ld lu be te	no
<i>Tidarren</i>	sp.	.	.	.	MCN on loan		
Theridiosomatidae							
<i>Chthonos</i>	sp.	.	.	.	SMNK on loan	be	di
<i>Epeirotypus</i>	sp.	.	.	.	SMNK on loan		
<i>Naatlo</i>	sp.	.	.	.	SMNK on loan	ge ld lu	
<i>Theridiosoma</i>	sp.	.	.	.	MCN	qu	
Thomisidae							
<i>Aphantochilus</i>	<i>rogersi</i>	O. P.CAMBRIDGE	.	.	INPA, MCTP	m	di
<i>Deltoclista</i>	sp.	.	.	.	MCN		
<i>Dietinae</i>	sp.	.	.	.	MCN		
<i>Epicadinus</i>	sp.	.	.	.	MCN	be f	di
<i>Majellula</i>	sp.	.	.	.	MCN	lu be teno	

Family / Genus	Species	Author	ud	tl	collection	occurrence	da
<i>Misumenops</i>	sp.	.	.	.	MCN	te	
<i>Onocolus</i>	sp.	.	.	.	MCN		
<i>Stephanopoides</i>	<i>simoni</i>	KEYSERLING	.	.	INPA, MCN	te	
<i>Strophius</i>	sp.	.	.	.	MCTP on loan		
<i>Synaema</i>	sp.	.	.	.	SMNK		
<i>Titidius</i>	<i>galbanatus</i>	(KEYSERLING)	.	.	MCN		
<i>Titidius</i>	<i>rubescens</i>	CAPORIACCO	.	.	INPA, SMNK		
<i>Tmarus</i>	sp.	.	.	.	MCN	lu be f	
<i>Tobias</i>	sp.	.	.	.	MCTP on loan		
Titanoeidae							
cf. <i>Goeldia</i>	sp.	.	.	.	IBSP on loan	ge	
Trechaleidae							
<i>Dossenus</i>	<i>marginatus</i>	SIMON	.	.	SMNK	te f	
<i>Paradossenus</i>	<i>longipes</i>	(TACZANOWSKI)	.	.	MCTP		
<i>Rhoicinus</i>	<i>urucu</i>	BRESCOVIT & OLIVEIRA	.	.	MCN, UA		
<i>Trechalea</i>	<i>amazonica</i>	F.O. P. CAMBRIDGE	.	.	INPA, MCN	te	no
<i>Trechalea</i>	<i>macconnelli</i>	POCOCK	.	.	INPA, SMNK	ge te	no
Uloboridae							
<i>Miagrammopes</i>	sp. 1	.	.	.	SMNK	lu be	no
<i>Miagrammopes</i>	sp. 2	.	.	.	SMNK	ge lu	no
<i>Miagrammopes</i>	sp.	.	.	.	INPA, SMNK	lu	di
<i>(Mumaia)</i>							
<i>Philoponella</i>	sp.1	.	.	.	MCN	m	
<i>Philoponella</i>	<i>vittata</i>	(SIMON)	.	.	SMNK	m	
<i>Uloborus</i>	sp.	.	.	.	MCN, SMNK		
<i>Zosis</i>	aff. <i>peruvianus</i>	.	.	.	SMNK	lu	no
<i>Zosis</i>	<i>geniculatus</i>	(OLIVER)	.	.	INPA, SMNK	ld	di
Zodariidae							
<i>Tenedos</i>	n.sp. 1	.	+	.	MCN, IBSP	qu ge pf ld	no
<i>Tenedos</i>	n.sp. 2	.	+	.	MCN, IBSP	qu ge pf ld	no
Zoridae							
<i>Odo</i>	sp.	.	+	.	IBSP on loan	te	

Table 2. Number of individuals and species collected by different methods (sampling intensity = ratio of individuals to species; all = all specimens including juveniles).

method	ground- electors	trunk funnel traps	pitfall traps	litter quadrat sampling	canopy fogging	Coddington's protocol	visual search in lower strata
nr. of traps/ samples	5 traps	3 traps	30 traps	20 samples	20 funnels	11 samples	> 100 excursions
time run/nr. of sampling events	12 months 1x	17 months 1x	4 weeks 1x	5x	2 trees 3x	1 day + 1 night	5 years intensive 20 years records
sampling intensity all / only adults	10.9 / 6.7	22.4 / 10.0	5.8 / 5.5	3.1 /-	2.9 / 1.6	3.2 / 3.4	66
all individuals	1649	3941	302	124	235	266	.
only adults	626	1503	177	.	81	88	appr. 2000
nr. of species observed (all)	136	178	52	40	80	82	.
nr. of species observed (adults)	93	152	32	32	50	26	appr. 300
nr. of species estimated (adults):							
Jackknife 1	135.4	214	.	.	.	40.5	.
Chao 2	175.6	342	.	.	.	42	.

3.2 Assemblage structure and guilds

Salticidae heavily dominated the samples from the ground electors (56 % of individuals and 23 % of species). All other families had less than 10 % of the individuals (tab. 3). Salticids were also abundant and species rich on the tree trunks with 21 % of individuals and 20 % of species (tab. 4).

Even in the continuously over one year run traps few species have been collected in high abundances and many species with few or even one specimen. A probably undescribed salticid species dominated the total capture of the three trunk funnels with >16 % (Saiteae gen. E sp.), an undescribed species of *Gephyroctenus* (Ctenidae) accounted for 7 % and adults of the the corinnid *Tupirinna rosae* BONALDO for 4 % of all individuals captured by this method. In ground electors the most abundant species was also an undescribed pluridentate salticid with 8 % (only adults), followed by a fissidentate salticid with 5 % (only adults) of all individuals. Four species of the genus *Ctenus* at least visually dominated the ground surface (GASNIER 1996, HÖFER et al. 1994b).

Most of the species captured and recorded on the ground were at least occasionally also captured in the trunk funnels. Not at last by fleeing from the frequent hunting raids of army ants (*Eciton burchelli*, *Labidus praedator*) (GASNIER et al. 1995, VIEIRA & HÖFER 1994) many spiders move actively to the trunk region of the trees. Although there are certainly real trunk inhabiting species in many families (e.g. *Alpaida septemmammata* and *Alpaida tabula* in Araneidae, *Gephyroctenus* sp. in Ctenidae, Corinnidae spp., Salticidae spp.), in our matrix only Selenopidae are marked as exclusively to be found on trunks.

Table 3. Structure of the ground spider assemblage sampled by ground electors.

Family	Ind.	% of all	Species	% of species
Salticidae	905	56.2	27	23.3
Corinnidae	86	5.3	6	5.2
Pholcidae	76	4.7	5	4.3
Oonopidae	55	3.4	10	8.6
Ctenidae	53	3.3	3	2.6
Araneidae	53	3.3	5	4.3
Mygalomorphae	48	3.0	12	10.3
Zodariidae	38	2.4	1	0.9
Theridiidae	34	2.1	9	7.8
Gnaphosidae	29	1.8	2	1.7
Linyphiidae	29	1.8	1	0.9
Ochyroceratidae	25	1.6	3	2.6
Sparassidae	25	1.6	2	1.7
Pisauridae	13	0.8	1	0.9
Theridiosomatidae	13	0.8	2	1.7
Thomisidae	13	0.8	2	1.7
Scytodidae	12	0.7	2	1.7
Oxyopidae	11	0.7	1	0.9
Palpimanidae	6	0.4	1	0.9
Symphytognathidae	6	0.4	1	0.9
Caponiidae	5	0.3	2	1.7
Mysmenidae	5	0.3	2	1.7
Anapidae	2	0.1	1	0.9
Anyphaenidae	2	0.1	2	1.7
Lycosidae	2	0.1	2	1.7
Senoculidae	2	0.1	1	0.9
Uloboridae	2	0.1	2	1.7
Selenopidae	1	0.1	1	0.9



Plate 1. a) *Thaumasia* sp. (Pisauridae), a representative of the "ground ambusher" guild.

b) *Nops* sp. (Caponiidae), a representative of the "litter stalker" guild.

c) *Otiotrops hoeferi* (Palpimanidae), another representative of the "litter stalker" guild.

d) *Cupiennius celerrimus* (Ctenidae), a "nocturnal aerial ambusher".

e) *Olios* sp. (Sparassidae), another representative of the "nocturnal aerial ambusher" guild.

f) *Scytodes* sp. (Scytodidae), a spitting spider in its retreat. These spiders hunt stalking around and were included in the guild of "nocturnal aerial runners".



a



c



b



d



e



f

Plate 2. a) *Noegus* sp. (Salticidae), a representative of the "nocturnal aerial runner" guild.

b) *Deinopis* sp. (Deinopidae), although phylogenetically considered orb-weavers, these spiders hunt by using a very special casting net held by the forelegs; they belong to the "nocturnal ground weaver" guild.

c) *Dubiepeira dubitata* (SOARES & CAMARGO) (Araneidae), an "aerial orb weaver".

d) *Cyclosa* sp., another "aerial orb weaver".

e) *Architis* sp. (Pisauridae), a representative of the "sedentary sheet weavers".

f) *Mesabolivar aurantiacus* (MELLO-LEITÃO) (Pholcidae), a "sedentary sheet weaver".

3.2.1 Ecological characterization of the families

For many families we followed the characterization of UETZ et al. (1999), because it reflects common arachnological knowledge and we had no differing observations from the tropical species (tab. 5). In some cases, however, characterization of a family is totally different, due to the representation of the family by a single species or genus with a different natural history, e.g. *Aglaoctenus* for Lycosidae and *Architis* for Pisauridae, both web-building representatives of families with no web-building species in temperate regions. For the same reason two families were splitted in their ecological characterization (Dipluridae and Pisauridae; tab. 5).

Table 4. Structure of the trunk spider assemblage sampled by trunk funnel traps.

Family	Ind.	% of all	species	% of species
Salticidae	836	21.2	38	25.3
Idiopidae	539	13.7	1	0.7
Corinnidae	505	12.8	18	12.0
Ctenidae	427	10.8	8	5.3
Pisauridae	365	9.3	5	3.3
Oonopidae	255	6.5	5	3.3
Pholcidae	251	6.4	4	2.7
Gnaphosidae	84	2.1	5	3.3
Sparassidae	84	2.1	5	3.3
Dipluridae	61	1.5	2	1.3
Mimetidae	55	1.4	1	0.7
Segestriidae	53	1.3	1	0.7
Scytodidae	48	1.2	2	1.3
Selenopidae	48	1.2	1	0.7
Theridiidae	45	1.1	8	5.3
Ochyroceratidae	43	1.1	2	1.3
Caponiidae	42	1.1	2	1.3
Anyphaenidae	36	0.9	8	5.3
Liocranidae	31	0.8	1	0.7
Araneidae	23	0.6	7	4.7
Palpimanidae	13	0.3	1	0.7
Deinopidae	11	0.3	1	0.7
Hersiliidae	10	0.2	1	0.7
Theraphosidae	9	0.2	2	1.3
Thomisidae	8	0.2	5	3.3
Trechaleidae	7	0.2	2	1.3
Linyphiidae	6	0.1	1	0.7
Miturgidae	3	0.1	1	0.7
Oxyopidae	3	0.1	1	0.7
Mygalomorphae	3	0.1	3	2.0
Senoculidae	2	0.05	1	0.7
Uloboridae	2	0.05	2	1.3
Zoridae	2	0.05	1	0.7
Hahniidae	1	0.03	1	0.7
Theridiosomatidae	1	0.03	1	0.7
Zodariidae	1	0.03	1	0.7
Lycosidae	1	0.03	1	0.7
Anapidae	1	0.03	1	0.7

Our tropical assemblage includes spiders in 34 families not occurring in North America and thus not included in UETZ et al.'s analysis. This was one of the main reasons to repeat their analysis with our database. Characterization of these families was based primarily on own observations and the representation of the species in our ground, trunk and canopy samples, completed by the rather scarce informations in the literature on tropical spiders (SILVA & CODDINGTON 1996). For many species we had enough observations on presence in different strata, activity or hunting manner to classify their families: Anyphaenidae (pers. obs. ADB), Ctenidae (part. *Ctenus*: GASNIER 1996, GASNIER & HÖFER 2001, HÖFER et al. 1994b; and *Phoneutria*: TORRES-SANCHEZ 2000), Dipluridae, Paratropididae and Pholcidae (pers. obs. HH), Pisauridae (AZEVEDO 2000, HÖFER & BRESICOVIT 2000) and Trechaleidae (pers. obs.). However, for many other families we still know very few on their natural history, but deduced informations from their representation in the different traps (Caponiidae, Corinnidae, Ochyroceratidae, Oonopidae, Palpimanidae, Scytodidae, Zodariidae). Other representatives were so rare in traps and never observed alive, that classification has to be regarded as provisional (most mygalomorphs, Gnaphosidae, Miturgidae, Prodidomidae, Symphytognathidae, Tetralemmidae, Titanocidae). In the very diverse and well known families Araneidae, Salticidae and Theridiidae and the surprisingly diverse and abundant family Corinnidae an ecological classification is a rather problematic generalization, which certainly does not reflect the diverse natural history strategies of the species included. The family Ctenidae includes real ground spiders like *Ctenus* and *Centroctenus*, the last one living in burrows, but also species living on trunks, twigs and branches like *Enoploctenus*, *Gephyroctenus* and on foliage like *Cupiennius* and juvenile *Phoneutria*. It was therefore difficult to decide whether this family should be splitted or treated as a whole (which we did), due to their uniform hunting manner. Based on our observations at night we consider most of the species of the tropical assemblage nocturnal, but we are aware of the lack of data on diel activity of spiders.

3.2.2 Guild classification analysis

Summarizing the dendrogram in figure 1 we propose 12 guilds for the tropical spider assemblage. The cluster analysis shows a clear separation in hunting and web-building spiders. Within the hunters ground living spiders are separated from spiders hunting in the vegetation above ground. Within the ground hunters a first guild is herein called "ground ambushers" and includes sedentary spiders, e.g. the burrowing mygalomorphs (Actinopodidae, Barychelidae, Ctenizidae, Idiopidae, Nemesiidae) and spiders with frequent site changes like pisaurids of the genera *Ancylometes* and *Thaumasia* (Plate 1 a), all being nocturnal hunters.

Table 5. Matrix for the cluster analysis of spider guilds. web use: 0-none, 1-hunt on web, 2-hunt off web; plant use: 0-none, 1-on foliage, 2-between plants ; site tenacity: 0-sedentary, 1-frequent site change, 2-mobile; other columns: 0 - absence and 1 - presence of ecological characteristic.

Family	included genera	web type				hunting manner				stratum				plant use		site tenacity		diurnal		nocturnal	
		Web	Web use	sheet	space	orb	ambush	stalk	pursue	burrow	ground	trunk	vegetation	plant use	site tenacity	diurnal	nocturnal				
Actinopidae	<i>Actinopus</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	
Anapidae	<i>Anapis, Pseudanapis</i>	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	1	1	0	0	
Anyphaenidae	various	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	1	
Araneidae	many	1	1	0	0	1	0	0	0	0	1	1	2	1	1	1	1	1	1	1	
Barychelidae	<i>Strophaeus</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	
Caponiidae	<i>Nops</i>	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	2	0	0	1	
Clubionidae	<i>Clubiona, Elaver</i>	0	0	0	0	0	0	0	1	0	0	1	1	2	0	1	2	0	0	1	
Corinnidae	various	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	
Ctenidae	various	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	
Ctenizidae	<i>Urimidia</i>	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
Cyrtacueniidae	various	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	
Deinopidae	<i>Deinopis</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	
Dictynidae	<i>Dictyna, Thallumetus</i>	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	
Dipluridae 1	<i>Masteria</i>	0	0	0	0	0	0	1	0	0	1	1	0	0	2	0	0	1	0	1	
Dipluridae 2	<i>Diplura, Linothele</i>	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	
Gnaphosidae	various	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	2	0	0	1	
Hahniidae	gen.?	1	2	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	
Hersiliidae	<i>Tama</i>	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	1	
Idiopidae	<i>Idiops</i>	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1	
Linyphiidae	various	1	2	0	1	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	
Liocranidae	<i>Orthobula</i>	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	0	
Lycosidae	<i>Aglaoctenus</i>	1	1	1	0	0	0	0	0	0	0	0	1	2	0	1	0	1	0	0	
Microstigmatidae	n.gen.	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	1	0	1	
Mimetidae	various	0	0	0	0	0	0	1	0	0	0	1	1	2	1	1	2	1	1	0	
Miturgidae	<i>Teminius</i>	1	1	0	0	0	0	0	1	0	1	0	0	2	1	0	2	1	0	0	
Mysmenidae	<i>Microdipoena, Mysmenopsis</i>	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	
Nemesiidae	<i>Neodiplothele</i>	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	
Ochyroceratidae	various	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	
Oonopidae	various	0	0	0	0	0	0	1	0	0	1	0	0	2	0	0	2	0	1	0	
Oxyopidae	various	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	
Palpimanidae	<i>Fernandezina, Otiotrops</i>	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	2	1	0	0	
Paratropididae	<i>Paratropis</i>	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	
Philodromidae	<i>Paracleonemis</i>	0	0	0	0	0	0	1	0	0	0	0	0	1	1	2	1	0	0	0	
Pholcidae	various	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	
Pisauridae 1	<i>Ancylometes, Thaumasia</i>	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0	1	0	1	0	

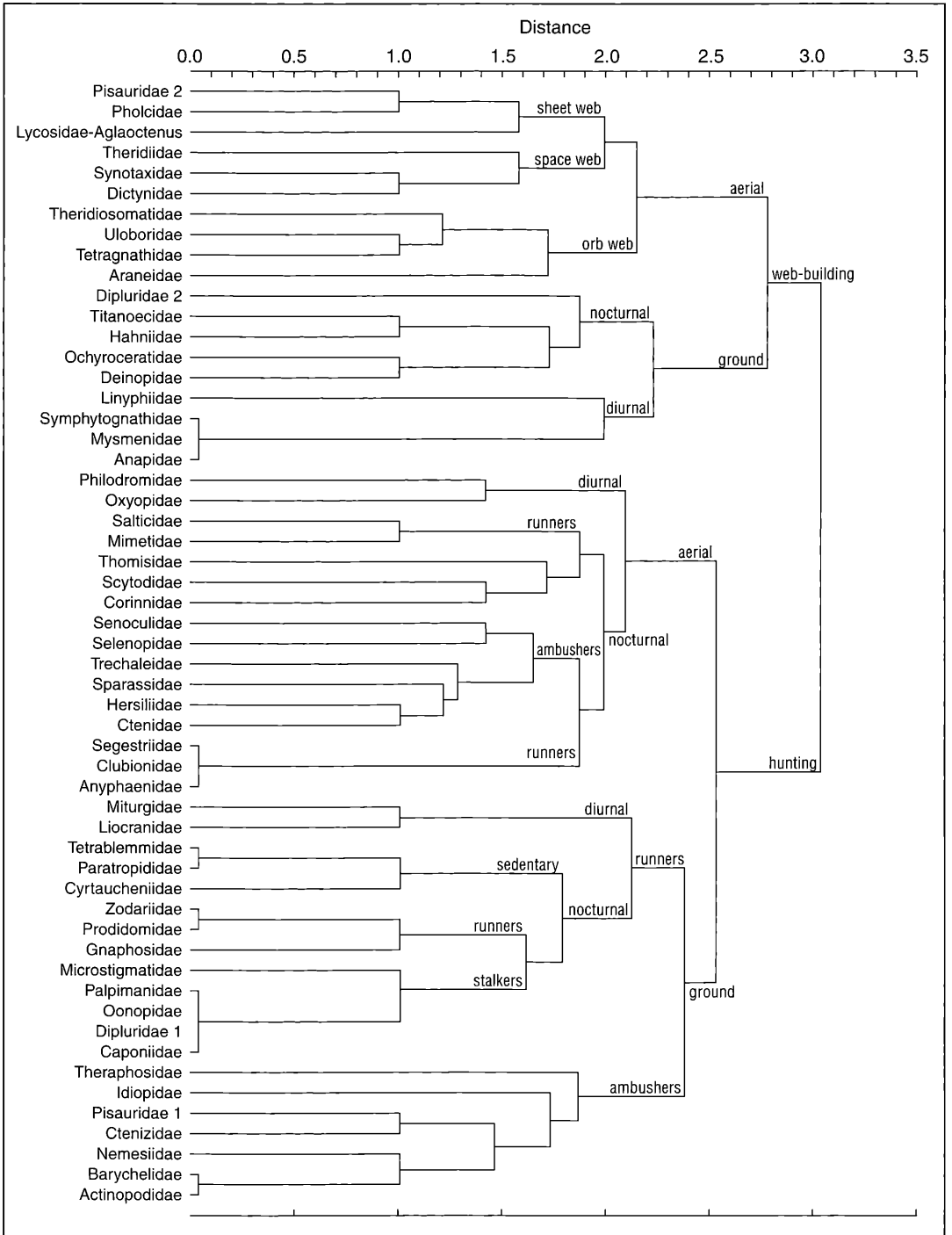


Figure 1. Guild classification dendrogram for 53 spider families resulting from a cluster analysis of the matrix in table 5 by the unweighted pair-group average method.

4. Discussion

As pointed out by CODDINGTON et al. (1991), COLWELL & CODDINGTON (1994) and TOTI et al. (2000) we need quick and accurate sampling protocols and species richness estimators to evaluate species numbers in natural and disturbed areas to be able to evaluate and hopefully decrease species losses. Many estimators have been developed and proposed in the last years, and been tested with a few theoretic and real data sets (COLWELL & CODDINGTON 1994, TOTI et al. 2000). However, even in well known North-American faunas, for which identification of at least adults is possible, a final evaluation of the performance of the estimators is difficult, because the observed species accumulation curves do not reach asymptotes, which means that the actual species number of a site is rarely known. This is especially true for tropical faunas, where many species are not at all or not adequately described and even adults cannot be easily identified. Consequently comparisons and calculations are done on morphospecies level, which is a very labour intensive task when the number of samples increases. Without character matrices or drawings the comparison of samples from different researchers in different collections is impossible and this hinders evaluation of beta and gamma diversity. Therefore we started joint effort in building a database of Amazonian spiders based on our species list from Reserva Ducke which will be amplified to central Amazonian spiders.

The low richness estimates, even from the methods with high sampling intensity show the method dependence of the results. Our sampling with CODDINGTON's protocol which should overcome this problem on the other hand was not sufficient. Method dependent species numbers are not only caused by unsatisfiable efficiency of the method itself, but also by the restricted occurrence of many species in different strata or microhabitats. Our personal estimate for the spider assemblage of the studied area (10 hectares) is 550 - 600 species.

Species-to-genera-ratios from our trap samples are relatively high when compared with North American spider fauna (CODDINGTON et al. 1996, EDWARDS 1993), where they were below 1.6 for single collection sets and only reached values above 2.0 for larger areas. The total number of species, so far recorded from the tropical site Reserva Ducke is higher than in temperate spider assemblages in North America (hardwood forest: 89 species – CODDINGTON et al. 1996) and Europe (beech forest: 95 species, DUMPERT & PLATEN 1985, spruce forest: 76 species – HÖFER 1989), which is not surprising. It is within the range of the few comparably sampled Neotropical sites: Cónдор montane forest: 228 species (SILVA 1992), Pakitza: 324 (one forest type), 498 species (several forest types)(SILVA & CODDINGTON 1996), Cuzco Amazonico (probably two

forest types) approximately 440 species (SILVA 1996), Samiria inundation forest 1140 morphospecies (SILVA 1996), all in Peru. Our own collections of spiders with CODDINGTON's sampling protocol in Bolivian lowland forest islands in savanna (3 days and nights) resulted in 189 morphospecies (HÖFER & BRESCOVIT 1994). Trap sampling in an Amazonian inundation forest resulted in 210 species (HÖFER 1997).

Distribution of species among families is rather similar compared to other Neotropical assemblages (HÖFER 1997, SILVA 1996).

As was already pointed out by several authors (CODDINGTON et al. 1996, EDWARDS 1993) each method is sampling a different array of species and not one can be used as a single universal sampling method for species estimation. Sampling protocols, like the one proposed by CODDINGTON et al. (1991) are recommendable, especially when completed by methods accessing the species rich litter fauna. They are better suited for species estimation because they produce a high number of single samples, but the necessary effort in the field for a suitable number of samples is high, and if not repeated, gives only a snapshot of the species richness. Continuously run traps may overcome this weakness and sample also more seasonally restricted species, but have other restrictions. Trunk funnel traps showed the highest species capture in the studied tropical assemblage and have a relatively high portion of adults, which facilitates identification. In combination with litter samples and ground eclector samples they would give a good base for the real species richness of an area which can be visited repeatedly over a longer period. However the cross-comparison of all morpho-species between all single samples of these traps is especially difficult and labour intensive for tropical faunas.

The dominance of the active salticid hunters and the hunting spiders in general (80 % of all individuals in ground eclectors and 92 % in trunk funnel traps) is certainly biased by the activity dependence of these two trap types, but is also a characteristic of tropical spider assemblages (JOCQUÉ 1984), mainly resulting from the rarity of the species rich and abundant linyphiids in temperate forests.

Guild classification not surprisingly resembles much the one found by UETZ et al. (1999) with the most distinctive ecological characteristic of web use, however followed by a second classification step into ground living spiders and spiders active in higher strata (called aerial spiders), which was not so obvious in UETZ et al's analysis of the North American assemblage. The classification in ground and aerial spiders however appeared strongly in the treatment of another North American spider assemblage (CODDINGTON et al. 1996) and is certainly pushed by the separation of ground and aerial sampling methods. Further subdivisions of the hunting spider cluster as well as the web-

building spider cluster appeared through differences in foraging manner and diel activity. Many spiders in Amazonian terra firme forests were observed to be nocturnal, a supposed effect of the high diurnal predation pressure (CODDINGTON et al. 1996). This hypothesis is also strengthened by our observations on other visual predation preventing strategies like ant mimicry, mimetic form and colour of the body and the frequency of retreats and burrows (HÖFER & BECK 1996), together with the already recognized immense diversity of diurnal predators like lizards and understory birds in these tropical habitats (see GENTRY 1990).

Due to the higher diversity of the tropical assemblage, becoming obvious in the higher number of families put in the analysis, more than the 6 - 8 clusters of UETZ et al. (1999) seem reasonable at this time. Additional guilds are defined by the main stratum and the diel activity, both characters supposed to be of importance for the use of the prey resources. There is no doubt that the allocation of some families has still to be confirmed or changed, due to the lack of knowledge of their natural history or due to the diversity of lifestyles represented by the different species. The latter is the case in ctenids which are inside the foliage cluster due to the fact that at least the *Phoneutria* species live most of their time in the vegetation. However the most abundant representatives, the *Ctenus* species are characteristic ground living spiders. The family could equally well be included in the ground ambusher guild or be splitted. The usefulness and applicability of our guild classification for studies of tropical spider assemblages has now to be tested.

Acknowledgements

We are especially grateful to Prof. Dr. LUDWIG BECK, to whom we dedicate this publication for sustaining our scientific work during all the years of this study. He, himself has studied the ecology of Arachnids in the Reserva Ducke in 1965/66. We thank all taxonomists who identified spiders for us or gave taxonomic advice, namely A. BONALDO, E. BUCKUP, M. E. GALIANO, P. GOLOBOFF, P. LEHTINEN, H. W. LEVI, A. A. LISE, H. METZNER, R. OTT and N. PLATNICK. The Instituto Nacional de Pesquisas da Amazônia (INPA) kindly gave the permission to enter and work in the reserve and loaned the material to us. The German Science Foundation (DFG), the Brazilian Research Council (CNPq) and the von-KETTNER-foundation, Karlsruhe financed the studies. We thank our colleagues Dr. A. BONALDO, Dr. T. GASNIER, Dr. W. HANAGARTH and Dr. H. JAPYASSU for valuable comments on the manuscript.

5. Literature

- APOLINÁRIO, F. B. (1993): Composição faunística e hábitos de nidificação de térmitas (Insecta: Isoptera) em floresta de terra firme da Amazônia Central. – 72 pp.; Master thesis, INPA/FUA, Manaus.
- AZEVEDO, C. S. de (2000): Ecologia de *Ancylometes gigas* (PICKARD-CAMBRIDGE, 1897) (Araneae: Pisauridae), uma aranha errante que vive próximo a corpos de água em uma floresta tropical úmida. – 44 pp.; Master thesis, INPA/FUA, Manaus.
- BECK, L. (1971): Bodenzoologische Gliederung und Charakterisierung des amazonischen Regenwaldes. – *Amazoniana*, **3**: 69-132.
- CODDINGTON, J., GRISWOLD, C. E., SILVA DÁVILA, D., PENARANDA, E. & LARCHER, S. F. (1991): Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. – In: DUDLEY, E. C. (ed.): Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology: 44-60; Portland, OR (Dioscorides Press).
- CODDINGTON, J. A., YOUNG, L. H. & COYLE, F. A. (1996): Estimating spider species richness in a Southern Appalachian cove hardwood forest. – *J. Arachnol.*, **24**: 11-128.
- COLWELL, R. K. & CODDINGTON, J. A. (1994): Estimating terrestrial biodiversity through extrapolation. – *Phil. Trans. Royal Soc. (Ser. B)*, **345**: 101-118.
- DUMPERT, K. & PLATEN, R. (1985): Zur Biologie eines Buchenwaldbodens 4. Die Spinnenfauna. – *Carolinea*, **42**: 75-106.
- EDWARDS, R. L. (1993): Can the species richness of spiders be determined. – *Psyche*, **100**: 185-208.
- GASNIER, T. R. (1996): Ecologia comparada de quatro espécies de aranhas do gênero *Ctenus* (Walckenaer) (Araneae, Ctenidae) em uma floresta na Amazônia Central: bases para um modelo integrado de coexistência. 76 pp., Ph.D. thesis, INPA/FUA, Manaus.
- GASNIER, T. R., HÖFER, H. (2001): Patterns of abundance of four species of wandering spiders (Ctenidae: *Ctenus*) in a forest in central Amazonia. – *J. Arachnol.*, **29**: 95-103.
- GASNIER, T. R., HÖFER, H. & BRESCOVIT, A. D. (1995): Factors affecting the "activity-density" of spiders on tree trunks in an Amazonian rainforest. – *Ecotropica*, **1** (2): 69-77.
- GENTRY, A. H. (1990): Four Neotropical rainforests. – New Haven, London (Yale University Press).
- HARADA, A. Y. & ADIS, J. (1997): The ant fauna of tree canopies in Central Amazonia: a first assessment. – In: STORK, N. E., ADIS, J., and DIDHAM, R. K. (eds): Canopy arthropods: 382-400; London (Chapman & Hall).
- HERO, J. - M. (1990): An illustrated key to tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brasil. – *Amazoniana*, **11**(2): 201-262.
- HÖFER, H. (1989): Beiträge zur Wirbellosenfauna der Ulmer Region: I. Spinnen (Arachnida: Araneae). – *Mitt. Ver. Naturwiss. Math. Ulm/Donau*, **35**: 157-176.
- HÖFER, H. (1990): The spider community (Araneae) of a Central Amazonian blackwater inundation forest (Igapó). – *Acta Zool. Fennica*, **190**: 173-179.
- HÖFER, H. (1997): The spider communities. – In: JUNK, W. J. (ed.): The central Amazonian river floodplains. Ecology of a pulsing system. *Ecological Studies*, **126**: 373-383; Berlin (Springer-Verlag).
- HÖFER, H. & BECK, L. (1995): Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien I. – *Natur und Museum*, **125** (12): 389-401.

- HÖFER, H. & BECK, L. (1996): Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien II. – Natur und Museum, **126** (3): 69-85.
- HÖFER, H. & BRESCOVIT, A. D. (1994): Ergebnisse der Bolivien-Expedition des Staatlichen Museums für Naturkunde Karlsruhe: Spinnen (Araneae). – Andrias, **13**: 99-112.
- HÖFER, H. & BRESCOVIT, A. D. (2000): A revision of the Neotropical spider genus *Ancylometes* BERTKAU (Araneae: Pisauridae). Insect Systematics & Evolution, **31**: 323-360.
- HÖFER, H., BRESCOVIT, A. D., ADIS, J. & PAARMANN, W. (1994a): The spider fauna of Neotropical tree canopies in Central Amazonia. First Results. – Stud. Neotrop. Fauna Environm., **29** (1):23-32.
- HÖFER, H., BRESCOVIT, A. D. & GASNIER, T. R. (1994b): The wandering spiders of the genus *Ctenus* (Ctenidae, Araneae) of Reserva Ducke, a rainforest reserve in central Amazonia. – Andrias, **13**: 81-98.
- HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rain forest after experimental litter addition in small plots. – Pedobiologia, **40**: 570-576.
- JAKSČ, E. M. & MEDEL, R. G. (1990): Objective recognition of guilds: Testing for statistically significant species clusters. – Oecologia, **82**: 87-92.
- JOCOUE, R. (1984): Considerations concernant l'abondance relative des araignées errantes et des araignées à toile vivant au niveau du sol. – Revue Arachnol., **5** (4):193-204.
- LOURENÇO, W. R. (1998): Synopsis of the Scorpion fauna of the Manaus region, Amazonas State, Brazil, with description of two new species. – Amazoniana, **10**(3): 327-338.
- MAHNERT, V. & ADIS, J. (1985): On the occurrence and habitat of pseudoscorpions (Arachnida) from Amazonian forest of Brazil. – Stud. Neotrop. Fauna Environm., **20**: 211-215.
- PENNY, N. D. & ARIAS, J. R. (1982): Insects of an Amazon forest. – 269 pp.; New York (Columbia University Press).
- RIBEIRO, J. E. L. da S., HOPKINS, M. J. G., VICENTINI, A., SOTHERS, C. A., COSTA, M. A. da S., BRITO, J. M. de, SOUZA, M. A. D. de, MARTINS, L. H. P., LOHMANN, L. G., ASSUNÇÃO, P. A. C. L., PEREIRA, E. da C., SILVA, C. F. da, MESQUITA, M. R. & PROCÓPIA, L. C. (1999): Flora da Reserva Ducke: Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. – 816 pp.; Manaus (INPA, DFDI).
- SILVA, D. (1992): Observations on the diversity and distribution of the spiders of Peruvian montane forests. – Mem. Mus. Hist. Nat. U.N.M.S.M. (Lima), **21**: 31-37.
- SILVA, D. (1996): Species composition and community structure of peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria river. – Rev. Suisse Zool., Vol. hors serie: 597-610.
- SILVA, D. & CODDINGTON, J. A. (1996): Spiders of Pakitza (Madre de Dios, Perú): Species richness and notes on community structure. – In: WILSON, D. E. & SANDOVAL, A. (eds.): Manu. The Biodiversity of Southeastern Peru: 253-311; Washington (Smithsonian Institution).
- SUNDERLAND, K. D. & GREENSTONE, M. H. (1999): Summary and future directions for research on spiders in agroecosystems. – J. Arachnol., **27**: 397-400.
- TORRES-SANCHEZ, M. P. (2000): Padrões espaciais de abundância, ciclo reprodutivo e variação de tamanho de adultos de *Phoneutria fera* PERTY e *Phoneutria reidyi* F. O. PICKARD-CAMBRIDGE (Araneae, Ctenidae) na Reserva Florestal ADOLPHO DUCKE, Amazonas, Brasil. – 89 pp.; Master thesis, INPA, UA, Manaus.
- TOTI, D. S., COYLE, F. A. & MILLER, J. A. (2000): A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. – J. Arachnol., **28**: 329-345.
- UETZ, G. W., HALAJ, J. & CADY, A. B. (1999): Guild structure of spiders in major crops. – J. Arachnol., **27**: 270-280.
- VIEIRA, R. S. & HÖFER, H. (1994): Prey spectrum of two army ant species in central Amazonia, with special attention on their effect on spider populations. – Andrias, **13**: 189-198.
- VIEIRA, R. S. & HÖFER, H. (1998): Efeito do forrageamento de *Eciton burchelli* (Hymenoptera, Formicidae) sobre a araneofauna de liteira em uma floresta tropical de terra firme na Amazônia Central. – Acta Amazonica, **28** (3): 345-351.
- WILLIS, E. O. 1977 Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke Amazonas Brasil. – Rev. Bras. Biol., **37**: 585-601.

ULRICH IRMLER

Revision of the genus *Fauva* BLACKWELDER, 1952 (Coleoptera, Staphylinidae, Osoriinae) from South America

Heartily dedicated to Prof. Ludwig Beck on the occasion of his retirement in remembrance of our time at the Amazon

Abstract

Specimens belonging to the Neotropical genus *Fauva* (Staphylinidae: Osoriinae) were studied from the following collections: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSN); Field Museum of Natural History, Chicago, USA (FMNH); and from a collection from Peru, made available by M. VERHAAGH (Karlsruhe, Germany). The genus and four species are redescribed and the new species *Fauva becki* is described. The genus is divided into two species groups and a key to species is provided.

Key words

Neotropical, Staphylinidae, Osoriinae, *Fauva*, taxonomy, new species

Author

Dr. habil. ULRICH IRMLER, Christian-Albrechts Universität zu Kiel, Ökologie-Zentrum, Schauenburgerstr. 112, D-24118 Kiel; e-mail: irmiler@fsoe.uni-kiel.de

1. Introduction

In the collection of MANFRED VERHAAGH a species of the genus *Fauva* was found that draw my attention to that genus as part of my studies on the Neotropical Osoriinae. Only 4 species were known from South America, each with only one specimen. During the study, a second specimen of *F. laeviuscula* was detected. The presently known number of 6 specimens of the genus documents the rareness of the species. The long and thick antennae and the setae structure of the head resemble many other coleopteran species hosting in ant nests. Nothing is known about the biology of the species. The three species described by FAUVEL (1902) were found in tabacs; BERNHAUER (1906) also gave no information about the biology. The new Peruvian species presumably lives in or on the forest floor. It is, therefore, not unlikely that the species host in ant nests and rarely leave the nests.

2. Material and Methods

The specimens studied were from the following collections: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSN); Field Museum of Natural History, Chicago, USA (FMNH); and from a collection from Peru, made available

by M. VERHAAGH (Karlsruhe, Germany). The latter (new species) will be deposited in Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima (MUSM).

3. Systematics

Fauva BLACKWELDER, 1952

1902 *Diplopsis* FAUVEL: Rev. d'Ent., **21**: 33 (type species by subsequent designation *Diplopsis alternans* (LUCAS 1920: 243))

1942 *Diplopsis* – BLACKWELDER: Proc. US Nat. Mus., **92**: 88 (type species by subsequent designation *Diplopsis multicostata* FAUVEL)

1952 *Fauva* BLACKWELDER: Smiths. Inst. U.S. Nat. Mus., **200**: 165 (fixed through objective synonymy with *Diplopsis*)

Description

The genus *Fauva* is conspicuous by many apomorphic characters. It is characterized by the relatively long first two abdominal segments. The antennae are very thick and long, antennal segments of equal length and width. The eyes are very small containing only few ocellae. Similar to many species of the genus *Thoracophorus*, there are three carinae on the head, several carinae or striae on the elytra and pronotum with wide lateral furrows. In contrast to *Thoracophorus* the pronotum has no central depression, but a transverse depression often exists in front of the posterior edge. The structure of the aedeagus is very simple as in *Thoracophorus*.

The presently known species reflect two species groups. The *Alternans* group contains species described by FAUVEL (1902) from tabac plantations of Bahia (Brazil) and by BERNHAUER (1906) from Paraguay. The head in species of this group shows a characteristic structure with a distinct dorsal process that is divided or not. In the first case the forehead is separated from the neck, forehead with distinct central, posteriorly prominent carina carrying several yellow bristles at the posterior angles pointed posteriorly, neck with a distinct central prominence and with several yellow bristles pointed apically. The second group consists of the new species *F. becki* from Peru and presents striae on the head instead of the carina. The head is not divided between forehead and neck. The neck is only separated from the forehead by a transverse stria.

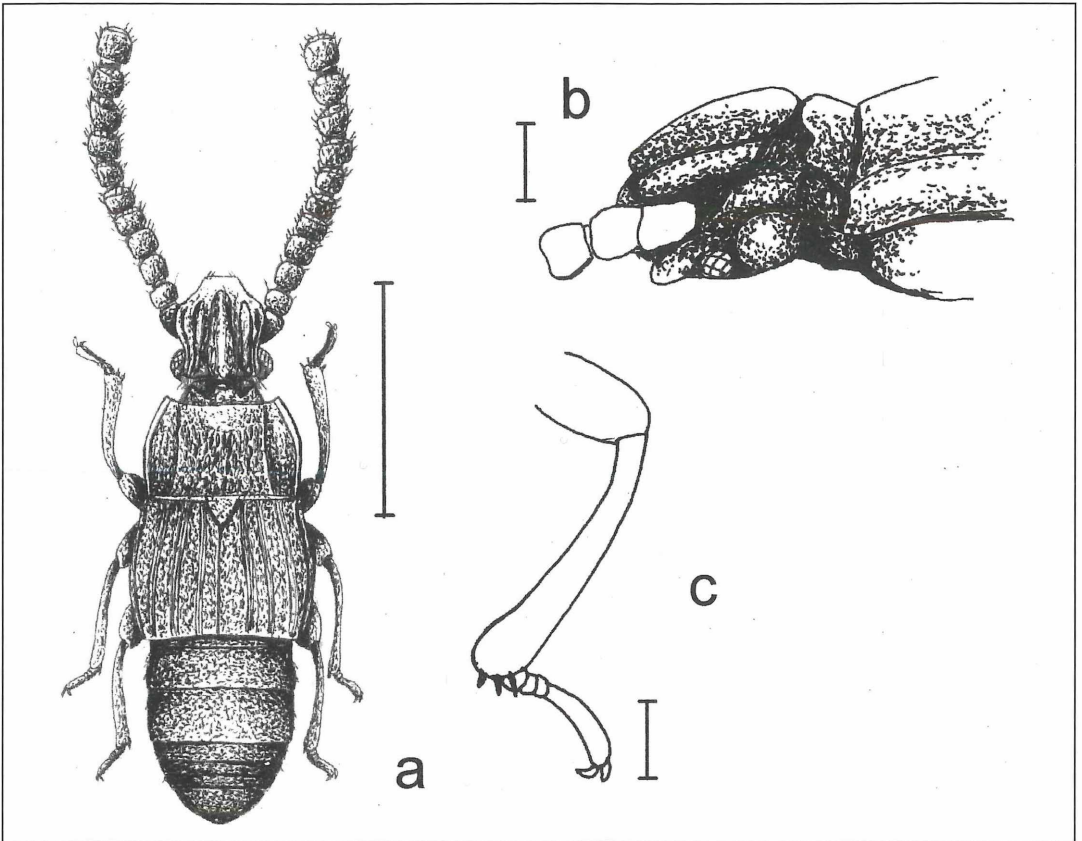


Figure 1. a) *Fauva alternans*; b) head laterally, c) front leg (scale line a: 1 mm; b, c: 0.1 mm).

***Fauva alternans* (FAUVEL, 1902)**

Figures 1, 2-2a-c

1902 *Diplopsis alternans* FAUVEL: Rev. d'Ent., 21: 34

Description

Length 2.2 mm, colour black, elytra red, abdomen and legs reddish, abdominal tergites posteriorly yellow. Head 0.5 mm long, 0.35 mm wide; antennae longer than head and pronotum, thick, wider than eyes, segments globular, basal segments as thick as apical segments, each segment with few yellow bristles, last segments with more bristles than basal segments, head with wide lateral furrow behind antennae, neck separated from forehead by a deep furrow, eyes small, on a distinct lateral prominence, forehead with a longitudinal central carina widened posteriorly, a small longitudinal depression on the wide part of the central carina, between central carina and lateral margin another smaller carina carrying several yellow bristles pointed posteriorly, central and lateral carina diminished in front of the clypeus, temples very short, neck wide, dorsally with a strong prominence behind the central promi-

nence of the forehead. Pronotum 0.45 mm long, 0.5 mm wide; widest at posterior edge, sides more or less parallel, narrowed to the front edge in the apical third, between lateral margin and disc a wide smooth furrow, disc with a transverse depression in front of the posterior edge, coriaceous punctate, punctures longitudinally coriaceous, apical third of disc without punctuation, smooth. Elytra 0.55 mm long, 0.7 mm wide; polished, without punctuation, on the disc with three groups of striae, each group containing three fine striae ending shortly in front of the posterior edge, distinctly wide at posterior edge than at apical edge. Abdomen with fine longitudinal striae, segments 2 to 5 laterally with few yellow bristles, segments 5 and 6 also dorsally with few bristles, all segments with very short scaly hairs.

The species is conspicuous within the *alternans*-group by the smooth apical third of the pronotum and the three groups of three striae each on the elytra.

Material examined

Brazil: Salvador de Bahia, in tabac plantation, without further data (holotype: IRSN).

***Fauva multicostata* (FAUVEL, 1902)**

Figures 2-1a-c

1902 *Diplopsis multicostata* FAUVEL: Rev. d'Ent., 21: 34

Description

Length 2.2 mm, colour black, elytra red, abdomen and legs reddish, abdominal tergites posteriorly yellow. Head 0.45 mm long, 0.3 mm wide; antennae longer than head and pronotum, thick, wider than eyes, segments globular, basal segments as thick as apical segments, each segment with few yellow bristles, last segments with more bristles than basal segments, head without punctuation, with wide lateral furrow behind antennae, neck separated from forehead by a deep furrow, eyes small, on a distinct lateral prominence, the longitudinal central carina not thicker at posterior end than at apical end, central and lateral carina diminished in front of the clypeus, temples very short, neck wide, dorsal prominence of neck with a longitudinal central depression. Pronotum 0.4 mm long, 0.5 mm wide; widest at posterior edge, sides more or less parallel in the posterior half, in the apical half narrowed to the front edge, between lateral margin and disc a wide smooth furrow, disc with a transverse depression in front of the posterior edge, coriaceous punctuate, a short smooth space behind the apical edge smooth. Elytra 0.6 mm long, 0.65 mm wide; polished, without punctuation, elytra with 7 fine carinae. Abdomen with fine longitudinal striae, segments 2 to 5 laterally with few yellow bristles, segments 5 and 6 also dorsally with few bristles, all segments with very short scaly hairs.

Within the *Alternans*-group the species is characterized by the coriaceous punctuation of the pronotum that nearly reach the apical edge and the distinct carinae of elytra.

Material examined

Brazil: Salvador de Bahia, in tabac plantations, without further data (holotype: IRSN).

***Fauva laeviuscula* (FAUVEL, 1902)**

Figures 2-3a-c

1902 *Diplopsis laeviuscula* FAUVEL: Rev. D'Ent., 21: 35

Description

Length 2.3 mm; colour black, elytra red, abdomen and legs reddish, abdominal tergites posteriorly yellow. Head 0.5 mm long, 0.4 mm wide; antennae longer than head and pronotum, thick, wider than eyes, segments globular, basal segments as thick as apical segments, each segment with few yellow bristles, last segments with more bristles than basal segments, head with wide lateral furrow behind antennae, neck separated from forehead by a deep furrow, eyes small, on a distinct lateral prominence, the longitudinal central carina thicker at posterior end than at apical end and without longitudinal depression on it, central and lateral carina dimin-

ished in front of the clypeus, temples very short, neck wide. Pronotum 0.4 mm long, 0.55 mm wide; widest at posterior edge, sides more or less parallel in the posterior half, in the apical half narrowed to the front edge, between lateral margin and disc a wide smooth furrow, a deep depression within the furrow in front of the posterior edge, disc with fine longitudinal punctuation, apically finer punctuate, a wide space behind the apical edge without punctuation, smooth. Elytra 0.65 mm long, 0.75 mm wide; polished, without punctuation, elytra with three fine striae, each stria divided by a fine line, the striae diminished in the posterior third. Abdomen with fine longitudinal striae, segments 2 to 5 laterally with few yellow bristles, segments 5 and 6 also dorsally with few bristles, all segments with very short scaly hairs. The species can be differentiated from the related species of the *alternans*-group by the fine punctuation of the pronotal disc and the fine striae of the elytra.

Material examined

Brazil: Salvador de Bahia, in tabac plantations, without further data (holotype: IRSN); Serra de Navio (Amapá), 1.6.1990, leg. DEGALLIER (FMNH).

***Fauva laevipennis* (BERNHAEUER, 1906)**

Figure 3

1906 *Diplopsis laevipennis* BERNHAUER: Verh. Zool.-Bot. Ges. Wien, 56: 323

Description

Length 2.6 mm; colour black, antennae piceous, elytra and abdomen dark red. Head 0.6 mm long, 0.3 mm wide; 2. segment of antennae globular, the following segments oblong, segments 6 to 8 slightly longer than the proceedings, head without punctuation and very weak longitudinal micro-reticulation, nearly polished, widest between base of antennae, strongly narrowed to the front edge, sides between base of antennae and front edge slightly emarginate, from the neck to the disc an obtuse process, that is margined ventrally by a very deep furrow pointed to the venter of the neck, a smaller furrow laterally parallel to the process, eyes very small, it seems to consist only of one ocella, a supraocular line between base of antennae and the deep furrow. Pronotum 0.5 mm long, 0.75 mm wide; with fine and sparse punctuation on then apical 2/3 of the disc, this part posteriorly margined by a transverse line, between this line and the posterior edge with a deep and coarse punctuation, in the front part with weak micro sculpture, shining, posterior part dull, front part of the disc with a distinct midline, pronotum broadly margined, margin very flat, without punctuation and very weak micro sculpture, nearly polished. Elytra 0.7 mm long, 0.9 mm wide, with very fine micro punctuation and weak longitudinal micro sculpture, shining, apical margin distinct and straight, on the disc with three lines, distinct at the base and obsolete in front of

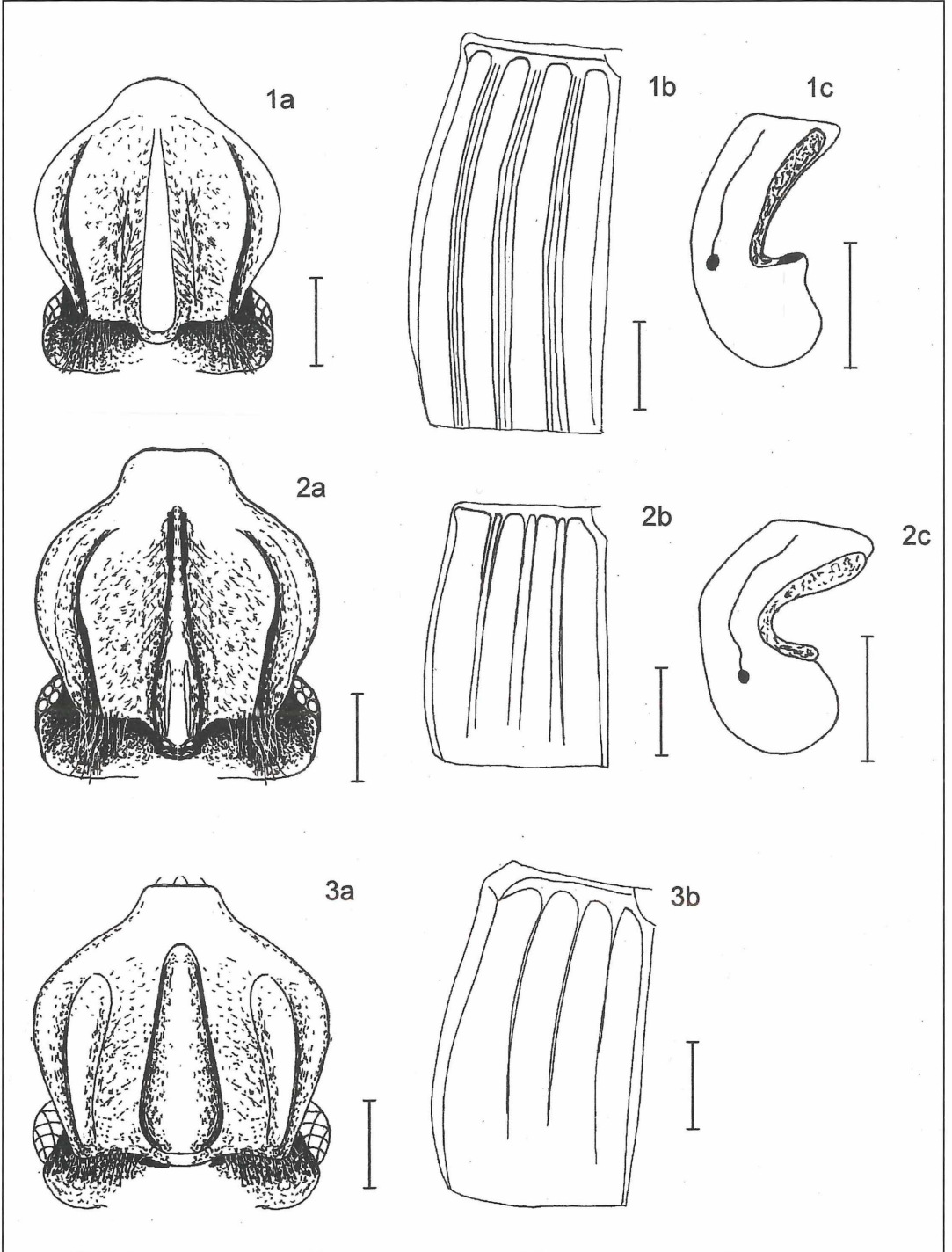


Figure 2.1) *Fauna multicostata*, 2) *F. alternans*, 3) *F. laeviuscula* (a: front head, b: elytra, c: aedeagus; scale line 0.1 mm).

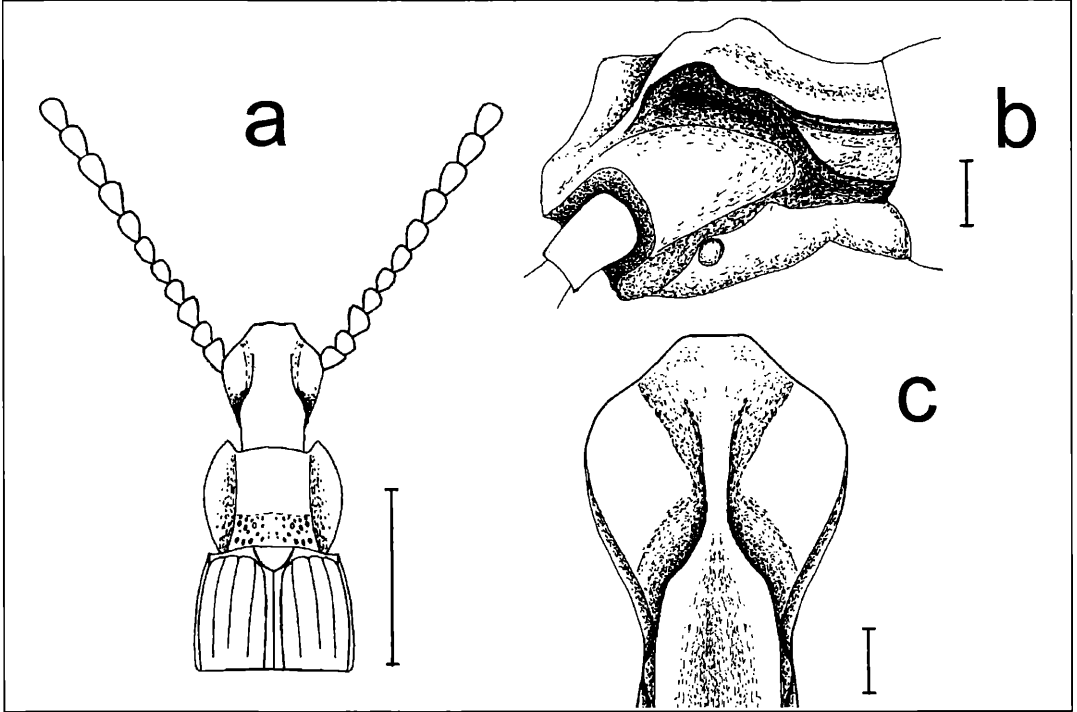


Figure 3. *Fauva laevipennis* a) front body, b) head in lateral view, c) head in dorsal view (scale line for a: 1mm, b and c: 0.1 mm).

the posterior edge. Abdomen with dense and fine punctuation, dull, punctures weak on the 6. segment, 6. tergite laterally and in the middle with a row of three pairs of tubercles, each carrying a scale-like hair, segments 4 to 6 laterally also with scale-like hairs.

Material examined

Paraguay: 23.4.1886, leg. DRAKE (holotype: FMNH)

Fauva becki new species

Figures 4a-d

Holotype: Male from Peru: Departamento Huánuco, Rio Yuyapichis, Biol. Station "Panguana" (9°37'S, 74°56'W, ca. 260 m), caught by a pitfall trap in a pasture (BF3), 10.-24.10.1984, leg. M. VERHAAGH (MUSM)

Description

Length 1.7 mm; colour piceous, front angles of pronotum, posterior edge of elytra and posterior edge of abdominal tergites red, legs yellow. Head 0.3 mm long, 0.28 mm wide; antennae thick, two times thicker than eyes, longer than head and pronotum, each segment twice as wide as long, head without punctuation, posteriorly with fine coriaceous ground sculpture, clypeus, quadrate, emarginate laterally between front edge and base of antennae, with longitudinal, central distinct carina, lateral carinae less distinct, temples

very short, eyes in a small lateral depression, very small not more than 10 ocellae, behind the eyes without furrow, neck separated from forehead by a fine transverse line. Pronotum 0.3 mm long, 0.4 mm wide; smallest at the apical edge, in front of the posterior angles shortly parallel, lateral margin distinct, thick, at parallel part an indistinct depression, finely punctate, with weak longitudinal microsculpture, shining. Elytra 0.3 mm long, 0.5 mm wide; widest at the posterior edge, at the base with similar punctuation as pronotum, posterior half without punctuation, smooth, two very fine longitudinal lines instead of the usual carinae that do not reach the posterior edge, without lateral margin, a short carina behind the shoulders indicate the rest of the margin, scutellum very small; abdomen with short scaly yellow hairs.

The species is conspicuous by the small size and the extremely thick antennae. In contrast to the other species of *Fauva*, the head is without exclusive structures, only some indistinct ridges present, the lateral furrows of the pronotum scarcely present and the carinae on the elytra very indistinct.

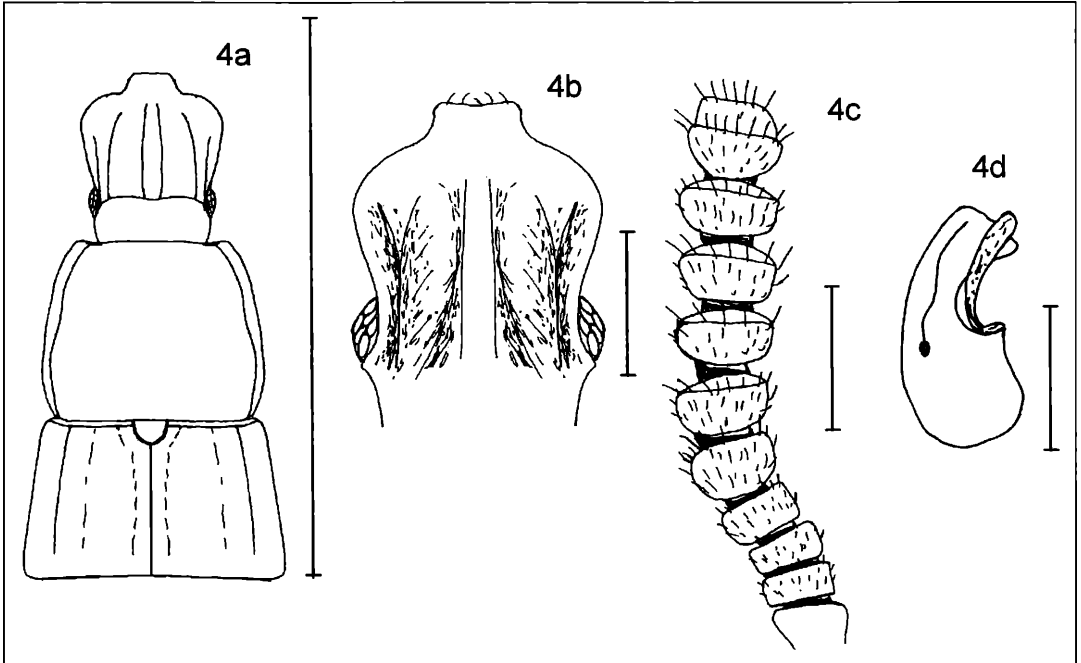


Figure 4. *Fauva becki* a) front body, b) head, c) antenna, d) aedeagus (scale line 0.1 mm).

Key to the species

1. Head with a more or less large process between neck and forehead, that is separated from the venter of the head by a deep depression 2
 - Head without such a conspicuous structure dorsally, smooth, only with few fine longitudinal lines *F. becki* n. sp.
2. Process of head separated in an apical and posterior part, with distinct central carina and neck with distinct prominence pointed to the apex *F. laevipennis* (BERNHAUER)
 - Process of head not separated, separation only conspicuous by a transverse stria 3
3. Pronotum at least partly with coriaceous punctuation, elytra with distinct striae or carinae 4
 - Pronotum with fine punctuation, the apical half nearly smooth, elytral striae fine and ending in the posterior half *F. laeviuscula* FAUVEL
4. Apical third of pronotum smooth without punctuation, elytra with three groups of three striae each *F. alternans* (FAUVEL)
 - pronotum with coriaceous punctuation, only a small space behind the apical edge without punctuation, elytra with 7 carinae *F. multicosata* (FAUVEL)

Acknowledgements

I am thankful to the following institutes and curators who graciously provided material used in this study: Institute Royal des Sciences Naturelles de Belgique, Brussels, Dr. D. DRUGMAND (IRSN); the Field Museum of Natural History, Chicago, Dr. A. NEWTON (FMNH). I also thank MANFRED VERHAAGH, who made his material collected at the Biological Station Panguana, Peru, available for my studies. Thanks are also due to Dr. L. ZERCHE, Deutsches Entomologisches Institut, Eberswalde, for his helpful comments.

4. Literature

- BERNHAUER, M. (1906): Neue Staphyliniden aus Südamerika 3. Stück. – Verh. Zool. Bot. Ges. Wien, **56**: 322-339.
- BLACKWELDER, R.E. (1942): Notes on the classification of the staphylinid beetles of the groups Lispini and Osoriniinae. – Proc. U.S. Nat. Mus. **92**: 75-90.
- BLACKWELDER, R.E. (1952): The generic names of the beetle family Staphylinidae. – Smithsonian Inst. U.S. Nat. Mus., **200**: 1-483.
- FAUVEL, C. (1902): Staphylinides exotiques nouveaux. – Rev. d'Ent., **21**: 8-37.

JOACHIM ADIS, MARINÊZ ISAAC MARQUES & KARL MATTHIAS WANTZEN

First observations on the survival strategies of terricolous arthropods in the northern Pantanal wetland of Brazil

Abstract

Terricolous arthropods (fire ants, leaf cutting ants, millipedes) make vertical migrations to temporarily pass the aquatic phase in northern Pantanal wetlands at non-flooded sites like grass stems and tree trunks.

Resumo

Primeiras observações sobre as estratégias de sobrevivência em artrópodos terrícolas das áreas alagáveis no Pantanal do Norte do Brasil

Os artrópodos terrícolas (formigas de fogo, saúvas, diplópodos) fazem migrações verticais para passar a fase aquática nas áreas alagáveis do Pantanal do Norte temporariamente em lugares não inundados como gramíneas e troncos de árvores.

Authors

Prof. Dr. J. ADIS & Dr. K. M. WANTZEN, Max-Planck-Institute for Limnology, Tropical Ecology Working Group, P.O. 165, D-24302 Plön, Germany;

Dr. M. I. MARQUES, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Correia da Costa S/N, 78060-900 Cuiabá-MT, Brazil.

Key words

migration, inundation, floodplains, Formicidae, Diplopoda

1. Introduction

One of the largest wetlands of the world, the Pantanal of Mato Grosso, is situated in the center of South America, 15 - 20° south of the equator. It is formed by the upper section of the Paraguay River and its tributaries in a large depression. Flood levels vary from few centimeters to several meters. Flood periods range from 2 - 5 months (JUNK et al. in press). To inhabit the floodplain forests and open grasslands of this environment, terricolous arthropods have to adapt to the unfavorable external conditions to enhance their ability of survival. First observations, still preliminary, of these "survival strategies" can be given for some ant and millipede species.

2. Material and Methods

The study area was located in the northern Pantanal of Mato Grosso at Fazenda Retiro Novo, Pantanal of Poconé, in the district of Pirizal (16°15'12"S, 56°22'12"W). This region is sub-

jected to a rainy season from October to April and to annual flooding of 0.6-1.5 m height, generally between December and March (aquatic phase). Field observations were realized in February/March 2000 in two floodplain forests (locally called Landi and Cambarazal) and their adjacent open grasslands, when most of the study area was flooded.

3. Results and Discussion

In the flooded open grassland area, the soil inhabiting fire ant *Solenopsis saevissima* (Myrmicinae) aggregated on grass stems of *Setaria geniculata* (Gramineae) above the water-level (Plate 1a). Animals moved between grass stems in forming living carpets or "rafts" (see also HÖLLDOBLER & WILSON 1990) on the water surface (Plate 1b). Those reaching the floodplain forest temporarily climbed tree trunks. This survival strategy has previously been observed in white-water river-floodplains of central Amazonia where *S. saevissima* sometimes forms "rotating balls" which are carried downriver (ADIS, 2000). A second ant species, *Dorymyrmex* aff. *pyramicus* (Dolichoderinae), was found to aggregate more towards the top of the grass stems (Plate 2 a). However, dislocation on the water surface has not been observed.

In the floodplain forests, two terricolous millipede species were found to pass the aquatic phase on tree trunks. Advanced immatures of *Plusioporus salvadorii* (Spirostreptidae) were located up to 1 m above the water-level on the bark of *Vochysia divergens* (Vochysiaceae) (Plate 1c). This tree species dominates the Cambarazal floodplain forest where all developmental stages of the spirostreptidan millipede inhabit the forest floor during the terrestrial phase. A second species, *Pantanalodesmus marinezae* (Chelodesmidae), was located near the base of leaf axils of *Scheelea phalerata* (Arecaceae). During the terrestrial phase the polydesmidan millipede lives and reproduces beneath decomposing leaves of this palm tree on and in the soil. Vertical migration in response to the flood pulse was previously found in millipedes inhabiting inundation forests of river-floodplains in central Amazonia (ADIS 1997).

The leaf cutting ant *Acromyrmex lundi carli* (Myrmicinae) was twice observed to move its subterranean nest located at the bottom of tree trunks to non-flooded tree axes (Plate 2 b) prior to inundation. After

the new nest above ground had been established and was supplied with fresh leaf material for the fungus culture (Plate 2 c) the old nest was still being cleaned by workers for a possible re-use during the next terrestrial phase, if not completely destroyed by the flood. Temporary nests of *A. lundi carli* were not located in the upper canopy as reported from whitewater river-floodplains of Central Amazonia where this species uses hollow boughs and dead tree trunks as a refuge (ADIS 1982).

In conclusion, the survival strategy hitherto observed in terricolous ants and millipedes inhabiting northern Pantanal wetlands represents a temporal vertical migration to non-flooded sites. This is the most common response of terricolous arthropods to the flood pulse in river-floodplains of Central Amazonia (ADIS 1997).

Acknowledgements

Prof. Dr. RICHARD HOFFMAN, Martinsville/USA is thanked for identification of the millipedes and Dr. JACQUES DELABIE, Itabuna/Brazil as well as Dr. CARLOS BRANDÃO, São Paulo/Brazil kindly determined the ants. Dr. CATIA NUNES DA CUNHA, Cuiabá, Brazil, kindly identified the plants.

5. Literature

- ADIS, J. (1982): Eco-Entomological observations from the Amazon: III. How do leafcutting ants of inundation forests survive flooding? – *Acta Amazonica*, **12** (4): 839-840.
- ADIS, J. (1997): Terrestrial invertebrates: Survival strategies, group spectrum, dominance and activity patterns. – In: JUNK, W. J. (ed.): *The central Amazon floodplain. Ecology of a pulsing system.* – *Ecological Studies*, **126**: 299-317; Berlin (Springer).
- ADIS, J. (2000): Terrestrial arthropods in soils from inundation forests and deforested floodplains of white water rivers in central Amazonia. – In: JUNK, W. J., OHLY, J. J., PIEDEDE, M. T. F. & SOARES, M. G. M. (eds.): *The central Amazon floodplain: Actual use and options for a sustainable management*: 463-476; Leiden (Backhuys Publishers).
- HÖLLEDBLER, B. & WILSON, E.O. (1990): *The ants.* – 732 pp., Berlin (Springer).
- JUNK, W.J., DA SILVA, C.J., WANTZEN, K.M., DA CUNHA, C.N. & NOGUEIRA, F. (in press): *The Pantanal of Mato Grosso: Status of ecological research, actual use, and management for sustainable development.* – In: MALTBY, E. (ed.): *The wetlands handbook*; Oxford (Blackwell Science).



Plate 1. a) Aggregation of the fire ant *Solenopsis saevissima* (Myrmicinae) on grass stems of *Setaria geniculata* (Gramineae) shortly above the water surface during flooding. b) Living carpets of the fire ant *Solenopsis saevissima* (Myrmicinae) on the water surface during flooding. c) Advanced immatures of the millipede *Plusioporos salvadorii* (Spirostreptidae) passing the flood period on a tree trunk of *Vochysia divergens* (Vochysiaceae).



Plate 2. a) Aggregation of the ant species *Dorymyrmex* nr. *pyramicus* (Dolichoderinae) at the top of grass stems of *Setaria geniculata* (Gramineae) during flooding.

b) Abandoned subterranean nest of the leaf cutting ant *Acromyrmex lundii carli* (Myrmicinae) at tree base and new established arboreal nest prior to flooding (about 1.80 m above ground) in a tree axis of *Licania parvifolia* (Chrysobalanaceae).

c) Transport of fresh leaf material by the leaf cutting ant *Acromyrmex lundii carli* (Myrmicinae) to the arboreal nest established prior to flooding in a tree axis of *Licania parvifolia* (Chrysobalanaceae).



RAINER FOELIX & EILEEN HEBETS

Sensory biology of whip spiders (Arachnida, Amblypygi)

Abstract

Whip spiders belong to a small arachnid order (Amblypygi) that is not well known. Their most conspicuous feature are the elongated, extremely thin front legs ("whips", or antenniform legs). These are no longer used for walking but are modified extremities carrying various sense organs – very much like the antennae of insects. Whereas hundreds of olfactory hairs are concentrated near the tip of each antenniform leg, large bristles (contact chemoreceptors) are evenly distributed over the entire antenniform leg. The sensory hairs of each antenniform leg contribute about 30,000 small sensory axons which proceed toward the central nervous system (CNS). The sensory fibers originating from the mechanoreceptive bristles make chemical synapses with a few giant interneurons in the periphery. The giant axons (10-20 μm in diameter) of these large interneurons transmit nerve impulses with a high velocity (6 m/s) to the CNS. The purpose of this fast pathway still needs to be determined. Originally it was thought that the fast giant axons would trigger quick escape reactions, but this was not confirmed in physiological experiments. However, other possible behaviors that may be aided by the giant interneurons are prey capture, fighting, and orientation.

What makes whip spiders unique is that both synapses and giant neurons are located far out in the peripheral nervous system. In all other arthropods – except for some arachnids – synapses and giant fiber systems are always found inside the CNS, never in the periphery.

Kurzfassung

Geißelspinnen gehören zu einer kleinen, wenig bekannten Ordnung der Spinnentiere, den Amblypygi. Ihr auffallendstes Merkmal sind die stark verlängerten, extrem dünnen Vorderbeine ("Geißeln"). Diese werden nicht mehr zum Laufen benutzt, sondern dienen – ähnlich wie die Antennen der Insekten – als Träger verschiedener Sinnesorgane. Während die Geißelspitze Hunderte von Geruchshaaren aufweist, ist die übrige Geißel ziemlich gleichmäßig mit Borstenhaaren (Kontaktchemorezeptoren) bestückt. In jeder Geißel ziehen ca. 30.000 kleine sensorische Nervenfasern zum Zentralnervensystem (ZNS). Dabei werden die mechanorezeptiven Nervenfasern über chemische Synapsen auf einige periphere Riesen-Interneurone aufgeschaltet; deren Riesenaxone (10-20 μm \varnothing) leiten Nervenimpulse mit großer Geschwindigkeit (6 m/s) zum ZNS. Wofür dieses Schnellleitsystem im Verhalten der Tiere eingesetzt wird, ist noch nicht geklärt – die ursprüngliche Vorstellung im Sinne einer raschen Fluchtreaktion ließ sich physiologisch nicht bestätigen. Andere Einsatzmöglichkeiten (Beutefang, Kommentkämpfe, Orientierung) werden diskutiert.

Sowohl Synapsen als auch Riesenneurone liegen bei anderen Arthropoden stets innerhalb des ZNS; nur bei einigen Spinnentieren sind Synapsen im peripheren Nervensystem gefunden worden – ein peripheres Riesenfasersystem dürfte auf Geißelspinnen beschränkt sein.

Authors

Dr. RAINER F. FOELIX, Naturama, Postfach, CH-5001 Aarau, Switzerland; rainer.foelix@ag.ch;
Dr. EILEEN A. HEBETS, Department of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721 USA.

Key words

Arachnida, Amblypygi, sensory biology, behavior

1. Introduction

Whip spiders – even most zoologists have not heard of these animals, and even fewer have ever seen one in nature. They are "exotic" indeed: although whip spiders are true arachnids (Order Amblypygi) and closely related to web spiders (Araneae), they differ in several aspects. Unlike "true" spiders they do not possess silk glands or poison glands. Most unusual is the fact that whip spiders walk only on six legs, not on eight as most other arachnids do. This is because their first pair of legs are very thin (< 0.5 mm) and long (up to 30 cm!) and are held out above the ground. These elongated antenniform legs greatly resemble insect antennae and correspondingly are equipped with thousands of sensory organs that perceive a variety of mechanical and chemical stimuli from their environment (BECK 1968, BECK et al. 1977, HÖFER & BECK 1995). The six walking legs also possess sensory hairs (mechanoreceptors for touch and vibrations), but the antenniform first legs provide the main sensory input. Whip spiders deprived of those important first extremities can no longer locate or catch any prey, nor can they orient themselves in their environment (BECK & GÖRKE 1974; GÖRKE 1973).

What is the typical habitat of whip spiders? Almost all species live in warm tropical regions, usually in rain forests (Plate 1b) or caves (WEYGOLDT 2000). Due to their strictly nocturnal habits, most people have never seen a whip spider. They hide in crevices, behind bark, in holes in the ground and even under rocks during the day and venture out only at sunset (BECK & PABST 1969, HEBETS, in prep.). In tropical forests whip spiders spend much of the night sitting on the vertical surfaces of large tree trunks, waiting for prey. Their long antenniform legs probe the (dark!) environment by slowly moving and circling around in front of them. If a prey item, usually a small arthropod, is detected, the whip spider approaches directly yet slowly. The

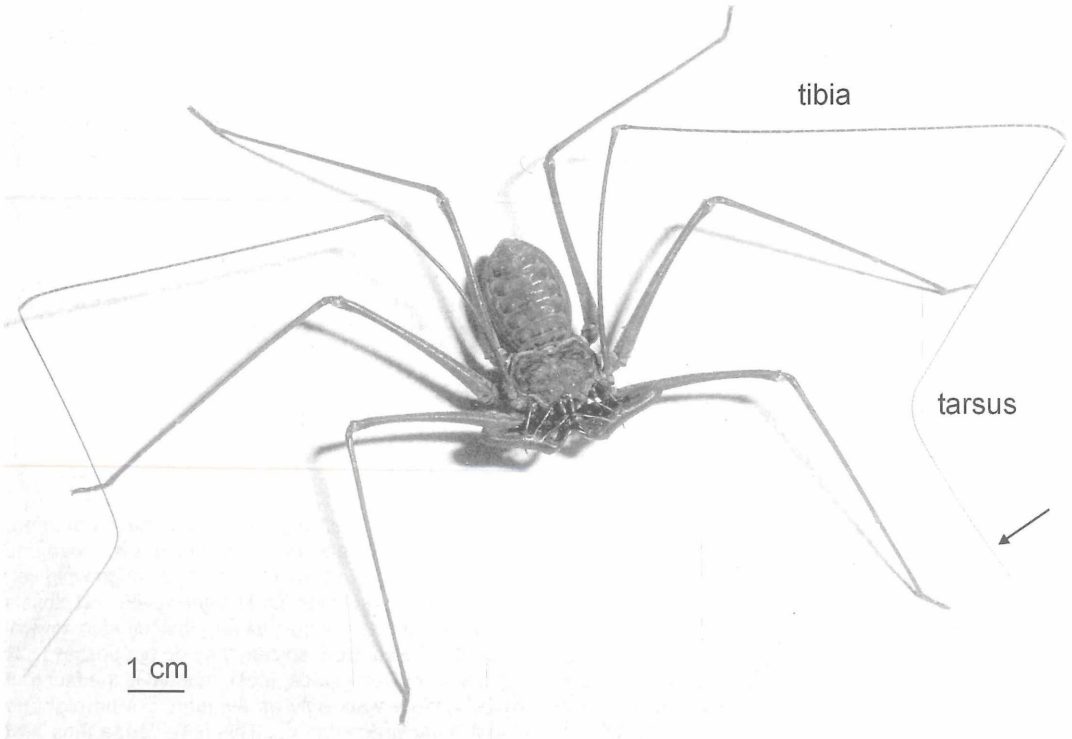


Figure 1. Whip spiders typically cling to the vertical surface of tree trunks with their heads down. Their first legs are no longer used for walking but are specialized sensory organs, comparable to the antennae in insects. Note the extremely elongated tibia and tarsus, each about 10 cm long; these bear thousands of sensory hairs, particularly on the tarsal tip (arrow).

heavily spined pedipalps are opened wide and once within close range, the animal quickly lunges forward and stabs the prey. If whip spiders are disturbed in any way, either by touch or by a slight puff of wind, they rapidly withdraw into the closest retreat. They are not aggressive at all towards humans but seem to avoid all contact.

2. Sensory equipment of the antenniform legs

It is clear simply from watching their behavior that whip spiders must possess excellent sensory organs and that most of them lie on their antenniform legs (fig. 1). Their distal segments are the longest with the tarsus alone measuring about 10 cm and the tibia between 5 and 6 cm. Both leg segments are subdivided into many subsegments (also called "annuli" or "articles") of 1-2 mm in length. The number of these annuli varies between species; for instance, *Heterophrynus longicornis* has about 100 tarsal and more than 40 tibial annuli, in the cavernicolous *Stygophrynus longispina* there are less, i.e. 45 in the tarsus and 25 in the tibia (WEYGOLDT 1994).

The antenniform legs are highly motile: not only do they bend at the segmental joints but they can also flex within the tarsus, thus giving the impression of a thin rubber hose. How this tarsal movement is achieved is not quite clear, since muscles are lacking in the distal part of the legs. There are, however, two slender cuticular tendons which traverse the entire tarsus up to the reduced claws at the tarsal tip. These tendons are in contact with the hypodermis at various points and probably act like internal reins. At any rate, in *Heterophrynus* one can easily observe a strong bending ($> 90^\circ$) of the tarsus between annuli 30 and 40 while they probe their environment (fig. 1; IGELMUND & WENDLER 1991a).

Looking at the antenniform legs with the naked eye, one can only detect relatively large bristles (about 500 μm long and 10-15 μm thick) which are arranged in five longitudinal rows along the entire tarsus. Under the microscope, however, hundreds of small hair sensilla become visible, especially on the 20 distal tarsal annuli (figs 2, 3). Since the wall of these sensory hairs is perforated, they most likely act as chemosensory receptors (olfactory, taste, humidity).

Actually, a large variety of sensory organs is present on the antenniform legs (BECK et al. 1974, 1977;

FOELIX et al. 1975; IGELMUND 1987): 1. Bristles, 2. Trichobothria, 3. Slit sensilla, 4. Pore hairs, 5. Club hairs, 6. Rod hairs, 7. Pit organ, 8. Plate organ, 9. Proprioceptors, 10. Tarsal claws.

2.1 Bristles

Bristles are the longest and most numerous hair sensilla on the tarsus and tibia. In *Heterophrynus* species their length ranges from 200 – 1000 µm and their number varies between 1200 and 1700 on the tarsus of adult animals (BECK et al. 1977; IGELMUND 1987). The hair shaft is relatively thick and has grooves and small spines on its surface. The hair lumen encloses 9-12 dendrites that run up to a terminal pore; two further dendrites end at the hair base and exhibit tubular bodies that are typical of mechanoreceptive neurons. Actually, the bristles are the only sensilla with a distinct socket and a movable hair shaft. Touching the bristles elicits action potentials, as was shown by electrophysiological recordings (IGELMUND & WENDLER 1991a). Thus, the bristles can be interpreted as typical contact chemoreceptors, responding to both mechanical and chemical stimuli.

A variation of the regular bristles are the "leaf-like hairs", which have a flattened shaft. This may cause more resistance to air currents and since they sit rather firmly in their sockets, they may transmit mechanical load to slit sensilla in the cuticle (IGELMUND 1987)

2.2 Trichobothria

There are only a few trichobothria on the antenniform legs (tibia), but many on the walking legs (tibia, metatarsus). Trichobothria, or filiform hairs, have a long, slender shaft suspended in a deep, cup-shaped socket; the slightest air currents make them quiver and therefore they are considered as long range tactile organs (BARTH 2000, BARTH & HÖLLER 1999). The trichobothria on the walking legs seem to be very important for prey detection – even at distances of 50-60 cm (BECK & GÖRKE 1974). Strong stimulation of these long trichobothria (2 mm!) can also trigger escape responses; this is in contrast to the short trichobothria (200-300 µm) located on the tibia of the antenniform legs, which do not elicit escape reactions (IGELMUND & WENDLER 1991a).

2.3 Slit sensilla

Slit sensilla are very inconspicuous slits in the leg cuticle, usually 10 µm long and 3 µm wide. Each slit is covered by a thin cuticular membrane to which two dendrites of sensory cells are attached; as in other arachnids these sensilla measure strain in the cuticle. There are 1-3 slit sensilla on each tarsal annulus, always lying parallel to the longitudinal axis of the leg. One exceptionally large slit sensillum (80 µm) lies on annulus 22 (in *Heterophrynus elaphus*); it

responds to bending between annuli 21/22 and thus acts as a proprioceptor (IGELMUND & WENDLER 1991a). If several single slits lie close together they are called "lyriform organs". Although very common in web spiders (Araneae), they are rare in whip spiders (HANSEN 1893, BARTH & STAGL 1976). One lyriform organ composed of 7 slits lies at the border of the tibia and tarsus in the antenniform legs (IGELMUND 1987); it is somewhat reminiscent of the metatarsal lyriform organ in spiders, which is a well-known vibration receptor (BARTH 1985).

2.4 Pore hairs

Pore hairs are small (120 µm long, 3-4 µm in diameter) sensilla with rather thin, perforated walls. They are restricted to the distal 20 annuli and are most densely clustered at the tarsal tip (fig. 3). Fine structural studies showed two types of hairs, one with many pores and many dendrites (40), the other one with fewer pores and fewer dendrites (20-30) (FOELIX et al. 1975). Both types closely resemble olfactory hairs on insect antennae and there is good physiological evidence that they react to different odors (HEBETS & CHAPMAN 2000). Between 400 and 500 of these pore hairs were counted on the distal tarsus of one antenniform leg (*Heterophrynus longicornis*; BECK et al. 1977).

2.5 Club hairs

Club hairs are the smallest sensilla, measuring only 30 µm in length and 3-4 µm in diameter. The bulbous tip (6-8 µm diameter) exhibits a central pore, at which 4-6 dendrites are exposed to the environment (fig. 3). Like the pore hairs they are non-socketed and they occur only on the distal 20 annuli; their total number is close to 400. The function of those club sensilla is not known but most likely they represent some kind of chemoreceptors.

2.6 Rod hairs

Rod hairs always occur in one cluster on each annulus of the distal tarsus (fig. 2). Again, two types can be distinguished, one with very thin walls (0.1 µm) and a terminal pore in a 20 µm long hair shaft, the other one with numerous pores in a thicker wall (0.4 µm) of a longer shaft (40 µm). The total number of rod sensilla was 65 in *Heterophrynus longicornis* (BECK et al. 1977) but only 35 in *H. elaphus* (IGELMUND 1987). No specific function could be assigned to the rod hairs so far.

2.7 Pit organ

On the tarsal tip (annulus 1) lies a small pit with 5-6 raised pore openings inside. At each pore 2-5 dendrites are exposed to the outside. This structure resembles closely the so-called "tarsal organ" in spiders and similarly may function as a hygroreceptor (EHN & TICHY 1994).

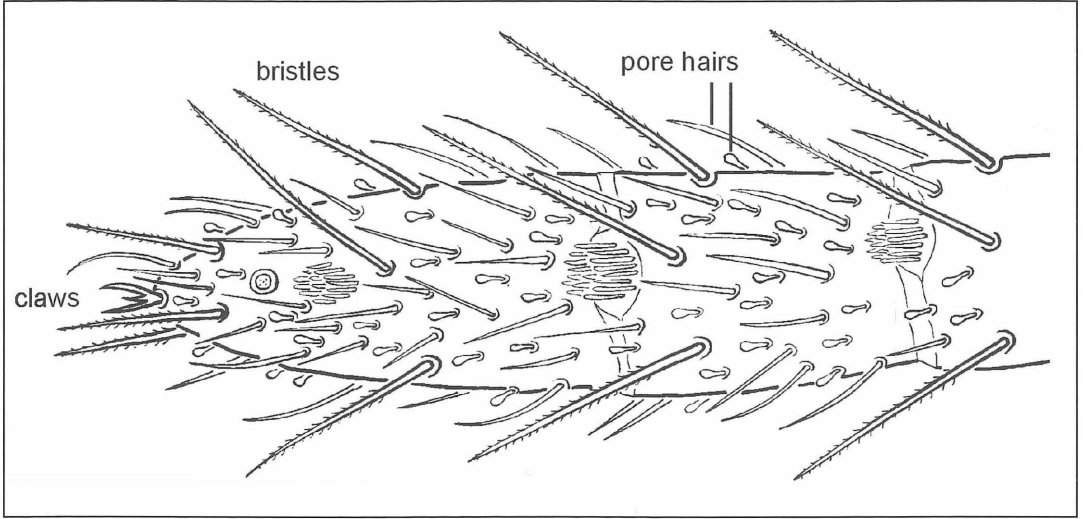


Figure 2. In *Heterophrynus longicornis* the tarsus of the antenniform legs is subdivided into one hundred small segments (annuli); they are studded with large bristles (contact chemoreceptors) and near the tip with hundreds of pore hairs (olfactory receptors). The distalmost part of the tarsus ends in three tiny claws; after GÖDEKE & KAISER 1975.

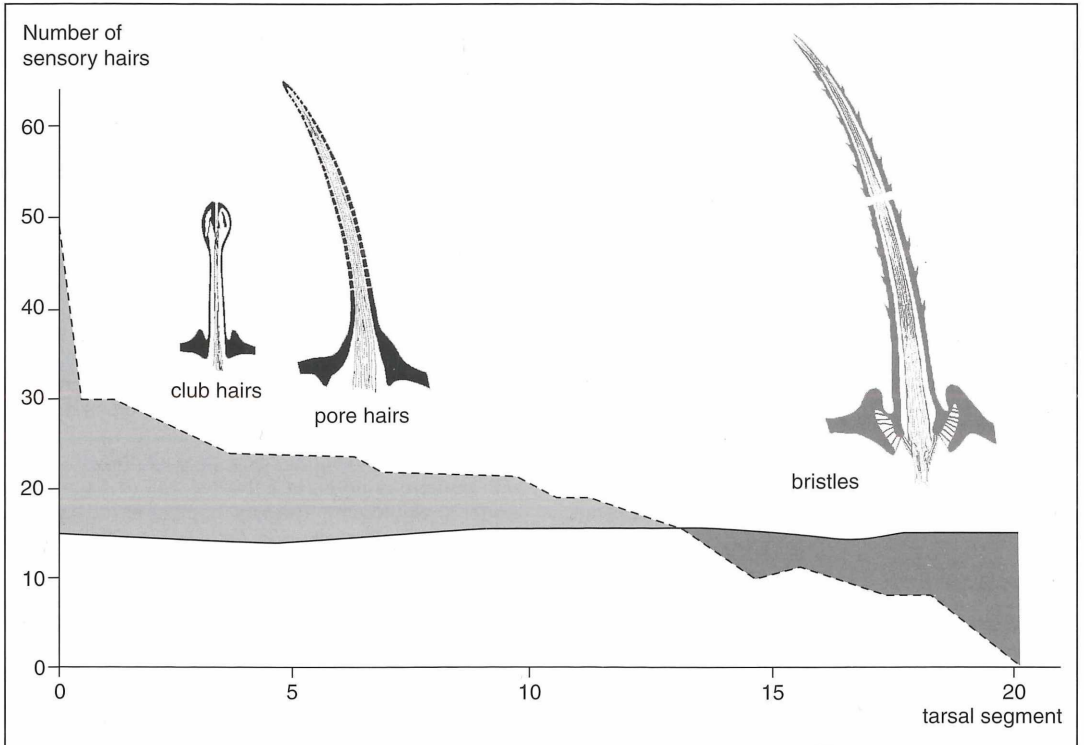


Figure 3. The number of pore hairs is highest near the tip of the tarsus and decreases proximally; no olfactory hairs are present between tarsal segments 20 and 100. In contrast, the concentration of the mechanosensitive bristles remains the same throughout the entire tarsus; after data from GÖDEKE & KAISER 1975.

2.8 Plate organ

On annulus 12 or 13 lies a oval shaped depression, about 70 μm long and 25 μm wide. From its distal surface arises a cuticular cone with a terminal pore; it is innervated by 12 dendrites. Nothing is known about the function of this organ.

2.9 Proprioceptors

Two large sensory cells lie in annulus 22 and their dendrites extend distally into the hypodermis (IGELMUND 1987). Both the morphology and the physiology point to a function as joint receptor (FOELIX & CHOMS 1979; IGELMUND & WENDLER 1991a). Groups of bipolar neurons were observed near the tibio-tarsal joint, lying freely in the hemolymph; they were also interpreted as proprioceptors (FOELIX, unpublished).

2.10 Tarsal claws

Three reduced claws sit at the very tip of the tarsus of the antenniform legs (fig. 2). Each claw has a subterminal opening and is innervated by several dendrites; the middle claw actually has three bundles of 3-5 dendrites each (FOELIX et al. 1975). The fine structure indicates some sort of contact chemoreception.

3. Internal organization of the tarsus in antenniform legs

An unusual feature of arachnid sensilla is the relatively high number of neurons associated with each sensory hair (FOELIX 1985). Whereas a typical insect contact chemoreceptor has 4-6 neurons per sensillum, arachnid taste hairs have more than 20. The pore hairs in whip spiders exhibit even more neurons, namely up to 40 per sensillum. Such a high number of sensory cells necessarily leads to thousands of afferent fibers within the sensory nerves. Before we deal with the actual numbers of sensory axons, we want to have brief look at the internal organization of an antenniform leg.

A cross section of the tarsus shows the following features under the microscope: Beneath the cuticle lies a single epidermal layer (hypodermis) that harbors most of the sensory neurons. The small axons of the sensory cells form small nerve bundles which soon join one of the two tarsal nerves (fig. 4). These two conspicuous nerves lie in the central hemolymph space of the tarsus. Additionally, there are two long tendons, one lying dorsally in the hemolymph space, the other being enclosed by the large leg artery ventrally. As in true spiders (Araneae) these tendons traverse the entire tarsus, but their muscular part lies within the tibia. In spiders these two muscles serve to raise or lower the tarsal claws, but since the claws are very reduced in the antenniform legs of whip spiders, this

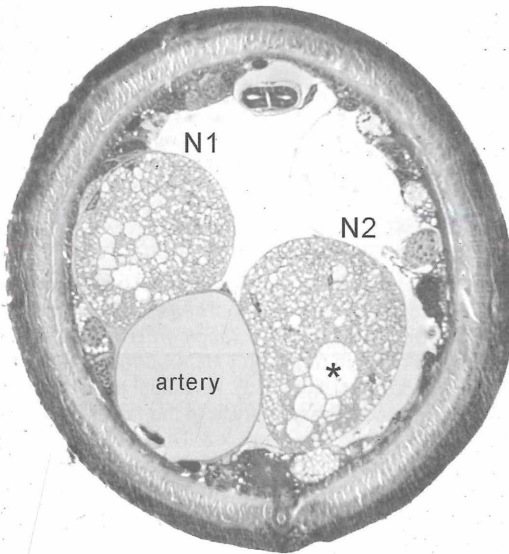


Figure 4. A cross section through the tarsus of an antenniform leg shows two conspicuous sensory nerves (N1, N2). The nerves contain mostly very small afferent fibers but also a few giant axons (*), 500x.

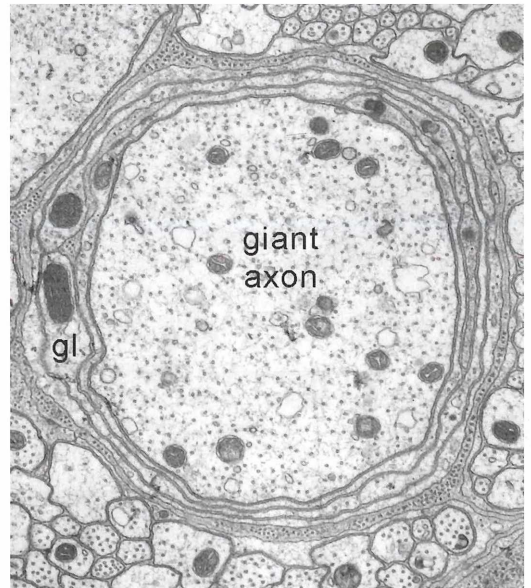


Figure 5. A single giant axon as seen in the electron microscope. Note the extensive glial wrapping (gl) and the surrounding small sensory axons, 5,000x.

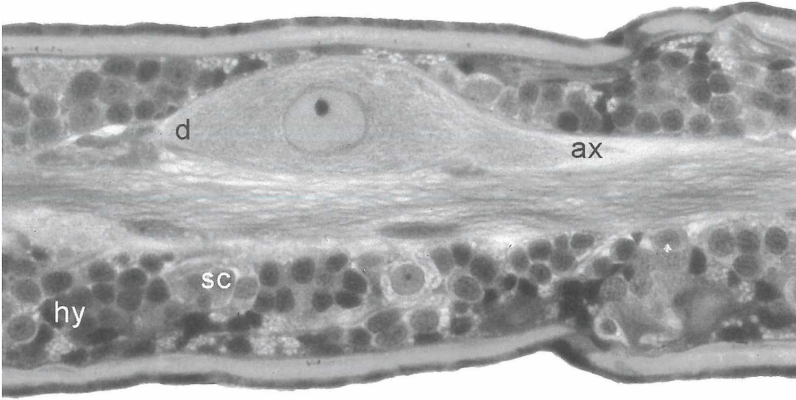


Figure 6. Several large interneurons lie within the antenniform legs and receive sensory input from hundreds of bristles. Compare the size of the giant neuron to that of sensory cells (sc) and hypodermal cells (hy). ax, axon and d, dendrite of giant neuron, 300x.

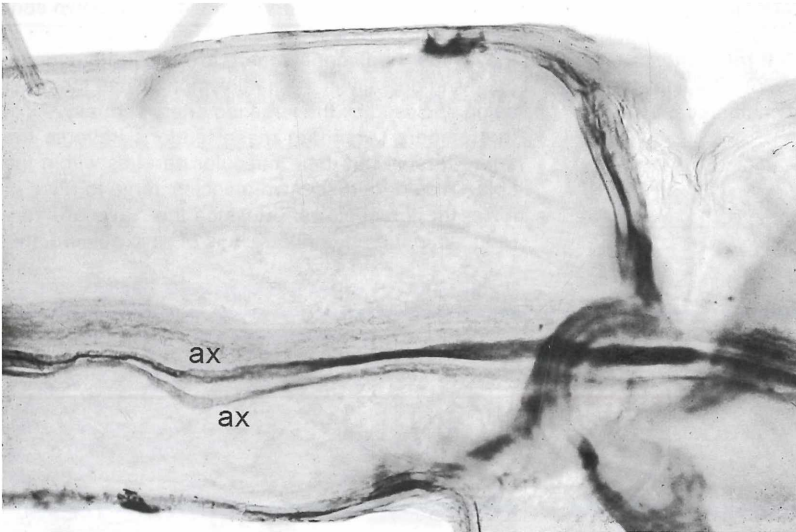


Figure 7. The giant neurons give rise to large axons of 10-20 μm diameter that proceed toward the central nervous system. In this photograph two giant axons (ax) entering the tarso-tibial joint stand out because they have been marked with cobalt sulfide, 350x.

function is no longer present. Instead, these tendons may be responsible for flexing the long tarsus (see above).

Since there are no muscles within the tarsus, the two tarsal nerves must be purely sensory; this is an important precondition when counting the number of axons in the tarsal nerves and relating them to the number of tarsal sensory organs (see below).

How do these thousands of sensory organs send their information to the central nervous system? Most of the sensory axons are of very small calibre (0.1 – 0.2 μm in diameter) which allows for several thousands of nerve fibers to fit into the narrow lumen of the antenniform legs. After compiling a quantitative list of all the sensilla present on a tarsus of an antenniform leg and knowing from electron microscopy how many sensory

cells were associated with each sensillum type, the total number of sensory fibers was calculated as 24,400 for *Heterophrynus longicornis* (BECK et al. 1977) and close to 30,000 for *Heterophrynus elaphus* (IGELMUND & WENDLER 1991a). An actual axon count of cross-sectioned sensory nerves at the tibio-tarsal joint yielded 23,050 axons (FOELIX & TROYER 1980). This close correspondence between the theoretical and the actual axon count allowed the following conclusions: 1) that all the nerve fibers within the two tarsal nerves are afferents, and 2) that all the primary sensory axons proceed to the central nervous system (CNS). At least theoretically there was the possibility that the high number of afferent fibers in the periphery could be reduced, for instance by converging the input from many sensory fibers onto a few interneurons. How-

ever, such interneurons are generally restricted to the CNS in arthropods. It turned out that whip spiders are quite exceptional in this respect, i.e. they do have large interneurons in their peripheral nerves.

4. The giant fiber system

Although more than 99 % of all sensory axons are very small, a few large fibers are present in each sensory nerve, measuring between 5 and 20 μm in diameter (figs 5, 7). The obvious question was: Where are the corresponding cell bodies of these giant fibers located – do they lie within the CNS in the prosoma (as one would expect), or do they perhaps lie in the periphery, somewhere within the antenniform legs? After much serial sectioning it became clear that these giant neurons lie indeed in the periphery, i.e. mostly far out in the tarsus – sometimes as far as 26 cm away from the CNS (IGELMUND & WENDLER 1991b).

It is also remarkable that these giant neurons (fig. 6) are located in specific annuli of the tarsus, i.e. in subsegments 1, 5, 6, 13, 21, 25 and 101 in *Heterophrynus longicornis* (FOELIX & TROYER 1980); this knowledge enabled one to relocate specific giant somata for more detailed studies. Compared to hypodermal or sensory cells the giant neurons have very large somata (up to 160 μm long and 50 μm wide). Most conspicuous is the large pale nucleus (25 μm in diameter) with a distinct nucleolus. Aside from a large variety of the usual cell organelles, the cytoplasm contains also some unusual “twisted filaments”, which may represent a new class of intermediate-sized filaments (FOELIX & HAUSER 1979).

The giant neurons are bipolar or multipolar nerve cells, distally with a relatively short, branching dendrite and proximally with a long giant axon. The next obvious question was: what is the function of these giant neurons? The first hints came from the observation of synapses within the antenniform leg nerves (FOELIX 1975). The presence of synapses in peripheral nerves was rather surprising, since synaptic contacts in arthropod nervous systems are generally restricted to ganglia, i.e. to the CNS. A closer look revealed that these synapses were almost exclusively restricted to the dendritic branches of the giant neuron and only few were seen on the soma or on the giant axon (figs 8, 9).

The fine structure of these peripheral synapses closely resembles synapses of other arthropods (FABIAN-FINE et al. 1999, 2000; FAHRENBACH 1979; FOELIX 1985; TOLBERT & HILDEBRAND 1981). Basically, there are many synaptic vesicles clustered around a presynaptic density (“bar”). In whip spider synapses, however, several presynaptic bars lie parallel to each other, resulting in rather large synaptic contacts. The synaptic vesicles are usually large (62 nm diameter) and round, but flat-

tened synaptic vesicles were also observed. Whether the shape of the synaptic vesicles is correlated with excitatory or inhibitory synapses, as is often claimed, needs to be determined. In peripheral synapses of spiders at least four different vesicle populations have been demonstrated; larger synaptic vesicles apparently contain L-glutamate as a neurotransmitter, whereas smaller synaptic vesicles seem to be filled with γ -aminobutyric acid (GABA) (FABIAN-FINE et al. 2000). Unfortunately, similar immunocytochemical labeling studies have not been done on whip spider synapses.

What kind of connections do these peripheral synapses represent? Most likely the presynaptic input onto the giant neuron stems from sensory hairs. Whether this input is provided by mechanoreceptive or chemoreceptive sensilla (or both?) cannot be decided from electron micrographs. It was argued however, that mechanoreceptors would be the most likely candidates, since synaptic contacts on giant fibers were also observed on proximal tarsal levels, where bristles are the only sensory hairs present (BECK et al. 1977). This hypothesis was fully confirmed, when IGELMUND & WENDLER (1991a, b) stimulated single tarsal bristles mechanically and thereby elicited action potentials in the giant fibers. Furthermore, they demonstrated convincingly that most of the synaptic input (90%) actually occurred along the giant axons. Although the density of synapses is very high on the short dendrite of the giant neuron, the absolute number of synapses is higher on the long giant axon. This means that the first “wiring diagram” of the whip spider’s giant interneuron (FOELIX & TROYER 1980) needs to be modified by adding many more synaptic contact points, mainly to the giant axon and to a lesser extent to the soma (fig. 10). One interesting feature remains unchanged, however: the sensory axons apparently do not terminate on the giant neurons after making synaptic contacts, but continue as individual nerve fibers into the CNS. This means that despite a convergence of numerous afferent nerve fibers onto a few giant neurons there is no reduction in the actual number of axons within the sensory nerves of the antenniform legs.

The electrophysiological recordings yielded further interesting results: 1) each giant neuron covers a certain receptive field, and 2) the receptive fields of neighboring giant neurons overlap (IGELMUND & WENDLER 1991b). For instance, in *Heterophrynus elaphus* giant neuron 1 receives mechanoreceptive input from all 750 bristles on annuli 1-40, while giant neuron 2 covers the 1500 bristles on annuli 10-74. There is thus an overlap between annuli 10 to 40. Consequently, bristles standing between segments 10 and 40 trigger action potentials in both giant axons.

For giant neuron 1 maximal mechanosensitivity was observed distally (at the tarsal tip) and less on the proximal side, for giant neuron 2 the mechanosensitivity

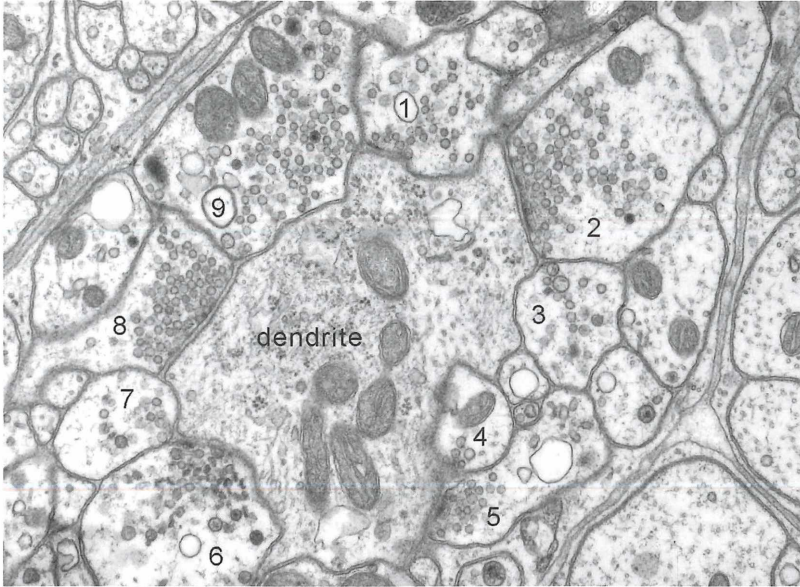


Figure 8. The dendrite of the giant neuron shown here is densely covered with synapses (1-9) originating from the mechanoreceptive bristles. Note that most synapses contain spherical vesicles, whereas some contain flattened ones (Nr. 6), 30,000x.

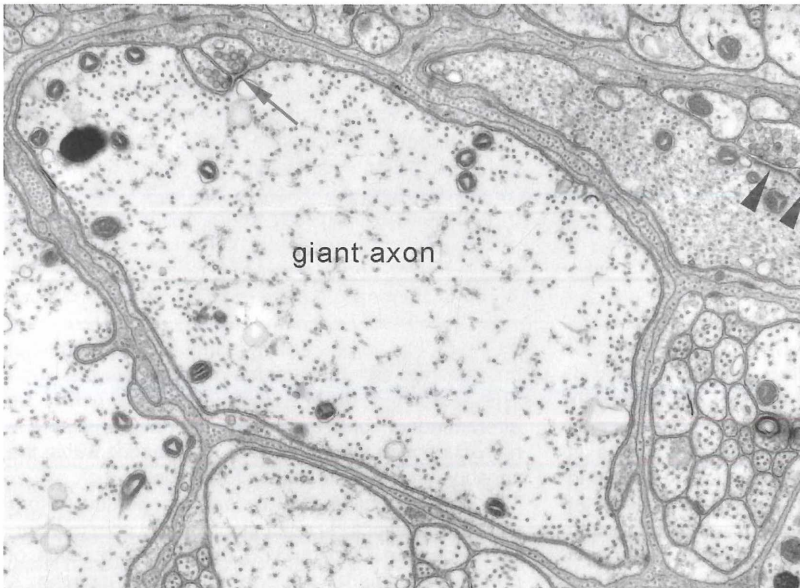


Figure 9. Giant axon in a sensory nerve of the tibia. Small synaptic terminals are seen at the upper left (arrow) and also on a smaller fiber at the upper right (arrow heads), 22,000x.

ity was opposite, i.e. more pronounced proximally. Other giant interneurons that were investigated were also mechanoreceptive (e.g. responding to bending of the tarsus), but some may react to chemicals. Physiologically, the diameter of nerve fibers is directly correlated with the velocity of conduction, i.e. small axons are rather "slow", whereas impulse transmission in large axons is "fast". Since most of the sensory fibers in the antenniform legs of whip spiders are very

small (0.1 - 0.2 μm in diameter), one would expect fast impulse conduction only in the giant fibers. Using electrophysiological methods, conduction velocities of 5-6 m/s were measured in the tarsal giant fibers of *Heterophrynus elaphus* (figs 11, 12; IGMUND & WENDLER 1991a). These values are quite comparable to those found in giant fiber systems of other invertebrates (e.g. insects, crustaceans or earthworms) or even to those in myelinated nerve fibers of verte-



Plate 1. a) The tropical rain forest is the main habitat of whip spiders. The best way to get there is by boat, as seen here on a side branch of the Rio Negro near Manaus; b) Large trees are a prerequisite for the occurrence of whip spiders. At night whip spiders sit on the lower trunks, about 1-2 m above ground, and during the day they hide in small crevices between the roots.

brates. FOELIX & TROYER (1980) measured the reaction time of the antenniform legs of whip spiders after mechanical and chemical stimulation of the tarsal tip. In high speed film analyses they observed leg withdrawal responses 120 ms after mechanical (touch) and 160 ms after chemical stimulation (chloroform vapor). They calculated that the corresponding nerve conduction speed had to be around 1 m/s, a value that presumably could only be accounted for by transmission of the impulses in the giant fibers. The conclusions rendered were that the giant fibers would act as a fast pathway from the periphery to the distant CNS (fig. 12), and that mechanical stimuli in particular would be transmitted rapidly to elicit a motor reaction (withdrawal of the antenniform leg).

Although this model seemed quite attractive, it was not corroborated by electrophysiological studies; no motor reactions were observed in response to giant fiber activity (IGELMUND & WENDLER 1991b). Thus, avoidance reflexes are apparently independent of the giant fibers, being perhaps transmitted by smaller nerve fibers. If so, then the question remains, what are the giant fibers actually good for? In insects it is certain that giant fibers are directly involved in escape responses, but in insects the entire system is fundamentally different (motor fibers within the CNS of insects, sensory fibers in peripheral nerves of whip spiders). A rapid escape response can indeed be triggered in whip spiders, but only by stimulating the walking legs and not the antenniform legs (IGELMUND & WENDLER 1991b).

What other functions could the giant fiber system serve in whip spiders? It is tempting to think of prey capture (see below). Yet although the attacks of these animals are often very precipitous, it is baffling that there is usually a distinct delay between the last contact with the prey and the execution of the actual

grasping response. Still, there may be times, such as seizing a moth straight from the air, when the giant fibers do come into play. Another possibility would be during mating and fighting (WEYGOLDT 1977, 1997/98). Courtship involves much mutual touching with the antenniform legs and so does fighting between males. In both cases there is a rapid exchange of signals during which a fast conducting system via giant fibers would be of advantage. Nevertheless, at this stage we have to concede that the specific purpose of the giant fibers of whip spiders has still to be elucidated. What makes whip spiders special is that their giant fiber system lies outside the CNS, i.e. in the peripheral nervous system. This is in contrast to giant fibers in all other invertebrates. In cockroaches, for instance, cercal sensory hairs activate giant interneurons in the last abdominal ganglion, which in turn transmits the excitation to leg motoneurons in the thoracic ganglia (WESTIN et al. 1977, RITZMANN & CAMHI 1978). Thus all these giant fibers are efferent and perform motor functions, whereas the whip spider's giant fibers are afferent and transmit sensory input. Furthermore, the system is highly sensitive: even stimulation of a single bristle produces impulses in the giant fiber (IGELMUND & WENDLER 1991b). In comparison, a considerable summation from multiple receptors is necessary for the excitation of giant fibers in cockroaches, crickets or crayfish (CALLEC et al. 1971, PALK & OLBERG 1977, ZUCKER 1972).

5. Sensory processing

The importance of sensory input in whip spiders is apparent in several of their behaviors. Prey capture, courtship, orientation and territoriality depend on highly processed sensory information. A first nervous

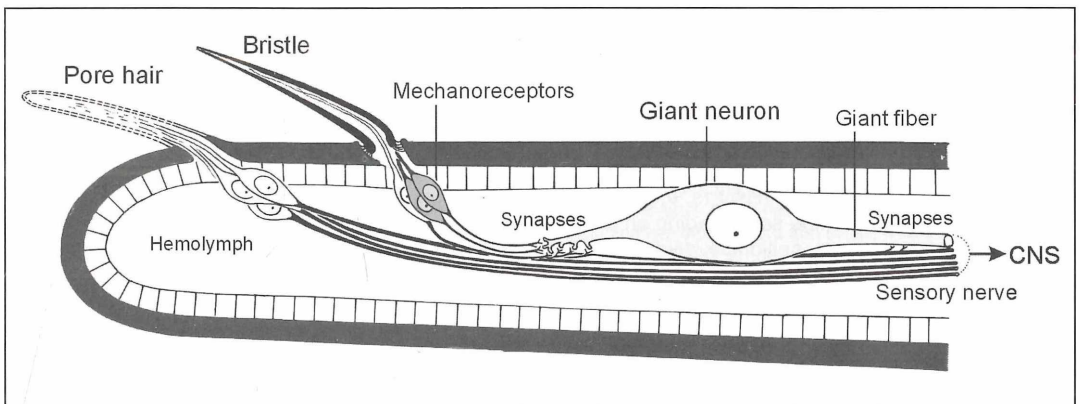


Figure 10. "Wiring diagram" of a peripheral giant interneuron in the antenniform legs of whip spiders. The mechanoreceptive sensory cells lying near the bristle base make synapses with the dendrite and the axon of the giant neuron. The giant fibers have a high conduction velocity and probably provide a fast pathway to the central nervous system (CNS). Modified after FOELIX & TROYER 1980.

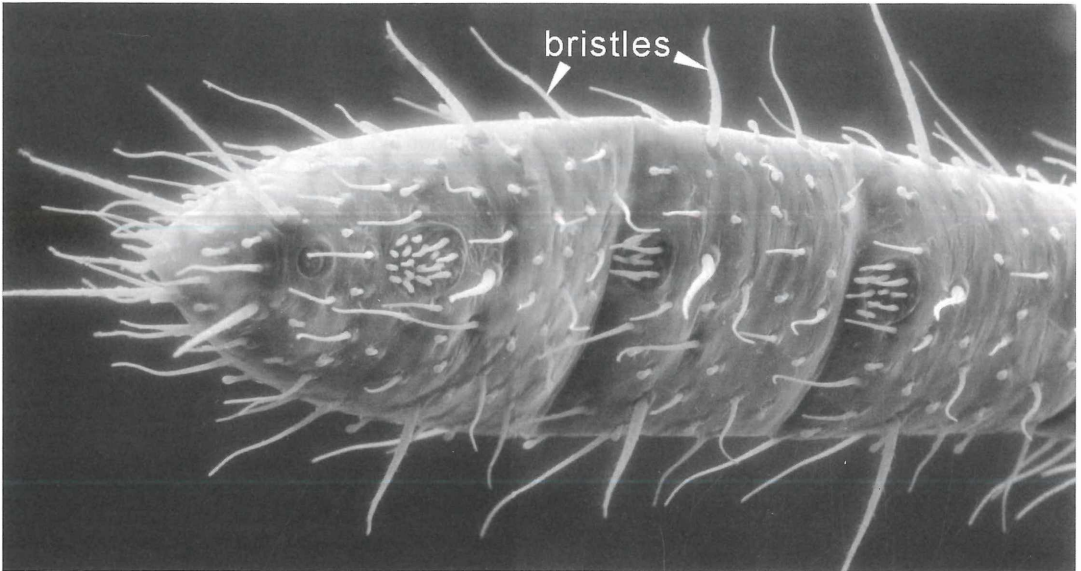


Figure 11. The large bristles on the antenniform legs are the only socketed hairs and they are the only external mechanoreceptors present. Movement of these bristles elicits action potentials in the giant fibers of the tarsal nerves. This SEM picture shows the three distalmost tarsal segments. 150X. Photo: GÖDEKE & KAISER.

integration may happen already in the periphery, as is indicated by the wide spread occurrence of peripheral synapses. Further processing takes place in extensively developed areas of the CNS, the “*corpora pedunculata*”; so far only preliminary studies have been done on these structures (GÖDEKE & KAISER 1975).

Courtship and mating have been described extensively for many species of whip spiders (WEYGOLDT 2000) and therefore will not be covered here.

5.1 Prey capture

Whip spiders can be seen exiting their diurnal retreats (crevices, holes at the bases of a trees, etc.) just as the sun begins to go down. They remain at the entrance of their retreat until darkness falls, at which point they venture out either onto the horizontal ground above their hole or onto the vertical surface of their tree (BECK & GÖRKE 1974; HEBETS, unpubl.). In the field, whip spiders can be seen feeding on crickets, katydids, cockroaches, opilionids, spiders, millipedes, and moths. In the laboratory they have been known to feed on conspecifics, but to our knowledge this does not happen under natural conditions. In the field they mainly sit and wait for prey, slowly exploring their immediate environment with their long antenniform legs. When they sense a potential prey, these legs become extremely active. If the tips of the legs come in contact with the prey, they are immediately withdrawn and the whip spider slowly approaches the

prey. Once within reach, the animal suddenly opens its spined pedipalps, lunges forward and stabs the victim, pulling it in with both pedipalps. The rather small chelicerae are pushed into the prey which is then slowly mascerated. Since whip spiders possess no venom glands, a prey item may often remain alive during much of the initial feeding period and sometimes will even escape while the whip spider attempts to reorient it.

Whip spiders are such quick predators that they can even capture moths out of the air. The vibrating wings of moths can be registered over a distance of 60 cm! The trichobothria on the walking legs most likely act as the vibration receptors. If the trichobothria are removed on all legs, a fluttering insect is only perceived if it is less than 20 cm away. At such close range the prey can be captured successfully, provided that at least one antenniform leg is still intact. If both antenniform legs are lacking, prey capture is severely handicapped or impossible, even though the wing beat is sensed by the trichobothria on the walking legs (WEYGOLDT 1972, BECK & GÖRKE 1974).

5.2 Movement patterns and orientation

When whip spiders leave their crevices at dusk, they tend to move very slowly and cautiously and will retreat back in at the slightest perturbation. They typically remain near their retreat entrance until the sun has set completely. Initially, whip spiders remain stationary, exploring their environment with their antenni-



Figure 12. Recording simultaneously from two different sites (E1, E2, 30 mm apart) along the tarsus yielded a shift of 5 ms between matching nerve impulses (arrow). This corresponds to a conduction speed of 6 m/s. Courtesy of Dr. P. IGELMUND.

form legs until they decide to move. Once in motion, whip spiders move with purpose; they move rather quickly and in spurts of up to 30 cm at a time. Although they are known to wander great distances (>30 m), many species are quite loyal to their retreats (BECK & GÖRKE 1974).

When removed from their retreat but placed back onto the opposite side of the same tree, individuals easily find their way back to their retreat. When displaced from the tree altogether, they not only navigate back to their original tree, but even to their original crevice. This is certainly true for close ranges (up to 7 m), where the animals find back during the same night. If displaced for more than 10 m, it may take several days until the home tree has been located again. As one might expect, the antenniform legs play an important role in this navigation. Whip spiders in which both antenniform legs had been amputated, were no longer capable to find their way back (BECK & GÖRKE 1974).

Females are more likely than males to remain in the same crevice over a long period of time (HEBETS, unpubl.). The retreats are generally occupied by just one individual at a time, the only exceptions being cases where both a mature male and a mature female inhabit the same retreat for up to 2 weeks, suggesting some type of mate guarding behavior. Both males and females are capable of roaming tens of meters and preliminary results indicate that individuals have home ranges that encompass several different trees (HEBETS, unpubl.). Over three consecutive nights of

observation, eleven different individuals were seen exiting and re-entering the same retreat. Individual movement patterns mapped onto the trees indicate that individuals are not using the same paths to exit or re-enter their retreats. Thus, simple trail following behavior cannot explain the movement patterns of whip spiders, suggesting that they have more complex navigational capabilities.

In summary, anyone who is lucky enough to study live whip spiders, either in tropical rain forests at night or under controlled conditions in the laboratory, cannot help being impressed by these exceptional creatures.

Acknowledgements

We are most indebted to Dr. LUDWIG BECK, Karlsruhe, to whom this article is dedicated. LUDWIG BECK introduced one of us (RFF) to the fascinating sensory biology of whip spiders back in 1973. For RFF the ensuing collaboration with LUDWIG BECK and his research group has brought many personal highlights, including two trips to Peru and Brasil, where they spent many "hard days in the jungle" together (Plate 1a,b). RFF also recalls quite a few less scientific escapades with LUDWIG BECK, like crossing the Andes in highly unsafe planes and rickety vehicles, and climbing alpine mountain passes on race bikes. Although LUDWIG BECK has retired, we are convinced that he will remain very active and adventuresome, and for that all his friends are grateful.

We also want to thank the following colleagues for generously sharing their knowledge and for contributing to this article: Dr. PETER IGELMUND, Köln; Dr. DAVID TROYER, Münster, Dr. PETER WEYGOLDT, Freiburg/Br., and ANDREAS ROHNER, Aarau.

6. Literature

- BARTH, F. G. (1985): Slit sensilla and the measurement of cuticular strains. – In: BARTH, F.G. (Ed.): Neurobiology of Arachnids: 162-188; Berlin (Springer).
- BARTH, F. G. (2000): How to catch the wind: Spider hairs specialized for sensing the movement of air. – *Naturwissenschaften*, **87**: 51-58.
- BARTH, F. G. & HÖLLER, A. (1999): Dynamics of arthropod filament hairs. V. The response of spider trichobothria to natural stimuli. – *Phil. Trans. R. Soc. Lond. B*, **354**: 183-192.
- BARTH, F. G. & STAGL, J. (1976): The slit sense organs of arachnids. A comparative study of their topography on walking legs (Chelicerata, Arachnida). – *Zoomorphologie*, **86**: 1-23.
- BECK, L. (1968): Aus den Regenwäldern am Amazonas II. Natur und Museum, **98**: 71-80.
- BECK, L. & PABST, H. (1969): Zur Tagesperiodik der Laufaktivität von *Admetus pumilio* C. KOCH (Amblypygi, Arachnida) aus dem neotropischen Regenwald. – *Zool. Anz. (Suppl.)*, **33**: 178-184.
- BECK, L. & GÖRKE, K. (1974): Tagesperiodik, Revierverhalten und Beutefang der Geißelspinne *Admetus pumilio* C. L. KOCH im Freiland. – *Z. Tierpsychol.*, **35**: 173-186
- BECK, L., FOELIX, R., GÖDEKE, E. & KAISER, R. (1974): Über die Haarsensillen der Geißelspinne *Admetus pumilio* (Arach., Amblypygi). – *Naturwissenschaften*, **61**: 327-328.
- BECK, L., FOELIX, R., GÖDEKE, E. & KAISER, R. (1977): Morphologie, Larvalentwicklung und Haarsensillen des Tastbeinpaars der Geißelspinne *Heterophrynus longicornis* BUTLER (Arach., Amblypygi). – *Zoomorphologie*, **88**: 259-276.
- CALLEC, J. J., GUILLET, J. C., PICHON, Y. & BOISTEL, J. (1971): Further studies on synaptic transmission in insects. II. Relations between sensory information and its synaptic integration at the level of a single giant axon in the cockroach. – *J. Exp. Biol.*, **55**: 123-149.
- EHN, R. & TICHY, H. (1994): Hygro- and thermoreceptive tarsal organ in the spider *Cupiennius salei*. – *J. comp. Physiol. A*, **174**: 345.
- FABIAN-FINE, R., VOLKNANDT, W. & SEYFARTH, E.A. (1999): Peripheral synapses at identifiable mechanosensory neurons in the spider *Cupiennius salei*: synapsin-like immunoreactivity. – *Cell Tissue Res.*, **295**: 13-19.
- FABIAN-FINE, R., MEINERTZHAGEN, I. A. & SEYFARTH, E.A. (2000): Organization of efferent peripheral synapses at mechanosensory neurons in spiders. – *J. Comp. Neurol.*, **420**: 195-210.
- FAHRENBACH, W. H. (1979): The brain of the horseshoe crab (*Limulus polyphemus*) III. Cellular and synaptic organization of the corpora pedunculata. *Tissue & Cell* **11**: 163-200.
- FOELIX, R. F. (1975): Occurrence of synapses in peripheral sensory nerves of arachnids. – *Nature*, **254**: 146-148.
- FOELIX, R. F. (1985): Sensory nerves and peripheral synapses. – In: BARTH, F. G. (Ed.): Neurobiology of Arachnids: 189-200; Berlin (Springer).
- FOELIX, R. F. & CHOMS, A. (1979): Fine structure of a spider joint receptor and associated synapses. – *Europ. J. Cell Biology*, **19**: 149-159.
- FOELIX, R. F. & HAUSER, M. (1979): Helically twisted filaments in giant neurons of a whip spider. – *Europ. J. Cell Biol.*, **19**: 303-306.
- FOELIX, R. F. & TROYER, D. (1980): Giant neurons and associated synapses in the peripheral nervous system of whip spiders. – *J. Neurocytol.*, **9**: 517-535.
- FOELIX, R. F., CHU-WANG, I. W. & BECK, L. (1975): Fine structure of tarsal sensory organs in the whip spider *Admetus pumilio* (Amblypygi, Arachnida). – *Tissue & Cell*, **7**: 331-346.
- GÖDEKE, E. & KAISER, R. (1975): Verteilung und Entwicklung der Haarsensillen des Tastbeinpaars der Geißelspinne *Admetus pumilio* C. L. KOCH. – 94 S.; Diplomarbeit Ruhr Univ. Bochum.
- GÖRKE, K. (1973): Freilandbeobachtungen und verhaltensbiologische Untersuchungen zur Biologie der Geißelspinne *Admetus pumilio* C. L. KOCH. – 50 S.; Diplomarbeit Ruhr Univ. Bochum.
- HANSEN, H. J. (1893): Organs and characters in different orders of arachnids. – *Ent. Medd.*, **4**: 137-251.
- HEBETS, E.A. & CHAPMAN, R. F. (2000): Electrophysiological studies of olfaction in the whip spider *Phrynus parvulus* (Arachnida, Amblypygi). – *J. Insect Physiol.*, **46**: 1441-1448.
- HÖFER, H. & BECK, L. (1995): Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien I. – *Natur und Museum*, **125**: 389-401.
- IGELMUND, P. (1987): Morphology, sense organs, and regeneration of the forelegs (whips) of the whip spider *Heterophrynus elaphus* (Arachnida, Amblypygi). – *J. Morph.*, **193**: 75-89.
- IGELMUND, P. & WENDLER, G. (1991a): The giant fiber system in the fore legs (whips) of the whip spider *Heterophrynus elaphus* Pocock (Arachnida: Amblypygi). – *J. comp. Physiol. A*, **168**: 63-73.
- IGELMUND, P. & WENDLER, G. (1991b): Morphology and physiology of peripheral giant interneurons in the fore legs (whips) of the whip spider *Heterophrynus elaphus* Pocock (Arachnida: Amblypygi). – *J. comp. Physiol. A*, **168**: 75-83.
- PALKA, J. & OLBERG, R. (1977): The cercus-to-giant interneuron system of crickets. III. Receptive field organization. – *J. comp. Physiol.*, **119**: 301-317
- RITZMANN, R.E. & CAMHI, J. M. (1978): Excitation of leg motor neurons by giant interneurons in the cockroach, *Periplaneta americana*. – *J. comp. Physiol.*, **125**: 305-316.
- TOLBERT, L. P. & HILDEBRAND, J. G. (1981): Organization and synaptic ultrastructure of glomeruli in the antennal lobes of the moth *Manduca sexta*: a study using thin section and freeze fracture. – *Proc. R. Soc. Lond. B*, **213**: 279-301.
- WESTIN, J., LANGBERG, J. & CAMHI, J. (1977): Responses of giant interneurons of the cockroach *Periplaneta americana* to wind puffs of different directions and velocities. – *J. comp. Physiol.*, **121**: 307-324.
- WEYGOLDT, P. (1972): Geißelskorpione und Geißelspinnen (Uropygi und Amblypygi). – *Z. Kölner Zoo*, **15**: 95-107
- WEYGOLDT, P. (1977): Kampf, Paarungsverhalten, Spermatophoren-Morphologie und weibliche Genitalien bei neotropischen Geißelspinnen (Amblypygi, Arachnida). *Zoomorphologie*, **86**: 271-286.
- WEYGOLDT, P. (1994): Amblypygi. – In: JUBERTHIE, C. & DECU, V. (Eds.): *Encyclopedia Biopaleoalpica I*: 241-247
- WEYGOLDT, P. (1997/98): Mating and spermatophore morphology in whip spiders (*Phrynichodamon scullyi* (PURCELL, 1901), *Damon gracilis* nov. spec., *Damon variegatus* (PERTY, 1834) and *Euphrynichus bacillifer* (GERSTAECKER, 1873) (Arachnida: Amblypygi: Phrynichidae). – *Zool. Anz.*, **236**: 259-276
- WEYGOLDT, P. (2000): Whip Spiders. (Chelicerata: Amblypygi). *Their Biology, Morphology and Systematics*. – Stenstrup, Denmark (Apollo books).
- ZUCKER, R. S. (1972): Crayfish escape behavior and central synapses. I. Neural circuit exciting lateral giant fiber. – *J. Neurophysiol.*, **35**: 599-620.

ELIZABETH N. FRANKLIN, JOSÉ WELLINGTON MORAIS & EVANIRA M. R. DOS SANTOS

Density and biomass of Acari and Collembola in primary forest, secondary regrowth and polycultures in central Amazonia

Abstract

The mesofauna communities were assessed every three months (June 1997 to March 1999), in the litter and soil of a polyculture system (POA and POC) and from a primary (FLO) and a secondary (SEC) forest. The highest densities were obtained in POA, due to the dominance of Oribatida. The densities of Acari Oribatida and Collembola were notably lower in the mineral soil. For non-Oribatid Acari, the same tendency was not clearly detected. In contrary to the other groups, the highest densities of Collembola were found in FLO. In general, densities in the litter layer were higher. Therefore, strong differences were detected between 1997, an exceptionally dry year caused by the "El Niño" Southern Oscillation, and 1998. The mesofauna population was lowest in 1997. Only in 1997, was the density in FLO, POA and POC higher in the soil fraction. The pattern in SEC was not the same because of the higher amount of litter. We hypothesized that the differences between 1997 and 1998 were a result of: 1) a reaction of the mesofauna that migrated to the mineral soil during the extremely dry period of 1997 and 2) a consequence of the litter layer reduction that occurred in 1997, causing lower mesofauna densities. Superimposed on the micro-climatic factors, we observed the influence of the condition of the litter layer on the mesofauna densities. Depending on the physical factors, there are years of high and others with low populations. Extremely wet years could also exert an influence on the soil mesofauna and studies of long-term periods are recommended. Although there was a tendency for the Acari Non-Oribatida biomass estimated in this study to be lower than in temperate forest, the values are however higher than values recorded for many tropical forests. On the contrary, Oribatida and Collembola biomass were characterized by lower values compared to temperate forests.

Resumo

Foram efetuadas coletas trimestrais da mesofauna (junho/1997 a março/1999), na liteira e no solo de parcelas em policultivo (POA e POC) e em florestas primária (FLO) e secundária (SEC). A maior densidade foi registrada na POC, resultante da maior dominância de Oribatida. As densidades de Oribatida e Collembola foram notavelmente menores no solo mineral do que na serapilheira. A mesma tendência não foi detectada para os outros Acari. Ao contrário dos outros grupos, as maiores densidades de Collembola foram registradas na FLO. Em geral, as maiores densidades foram registradas na serapilheira. Entretanto, diferenças marcantes foram detectadas entre 1997, um ano excepcionalmente seco devido ao fenômeno "El Niño" e com menores registros de densidade, e 1998. Somente em 1997 as densidades na FLO, na POA e na POC foram maiores na camada do solo mineral. O padrão na SEC não foi o mesmo, provavelmente devido à maior quantidade de liteira. Nós hipotetizamos que as diferenças entre 1997 e 1998 foram resultados de: 1) uma reação

da mesofauna que migrou para o solo mineral no período extremamente seco em 1997 e 2) uma consequência da redução da liteira que ocorreu em 1997, causando menor densidade da mesofauna. Sobreposto aos fatores micro-climáticos, observamos a influência da condição da camada de serapilheira sobre a densidade da mesofauna. Dependendo dos fatores físicos, existe anos de alta e outros com baixa populações, levando à hipótese de que anos extremamente úmidos também podem exercer influência na população da mesofauna e são recomendados estudos de longa duração. A biomassa de Acari (exceto Oribatida), calculada nesse estudo, foi menor do que em floresta temperada, porém, os valores foram maiores que aqueles estimados para outras florestas tropicais. Ao contrário, os valores para Oribatida e Collembola foram menores em comparação com as florestas temperadas.

Authors

DR. ELIZABETH N. FRANKLIN, DR. JOSÉ WELLINGTON MORAIS & M.Sc. EVANIRA M. R. DOS SANTOS, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69011.970 Manaus, AM, Brazil.

Key words

Mesofauna, Acari, Collembola, primary forest, secondary growth, polyculture plantation, vertical migration

1. Introduction

The sustained efficiency of a dystrophic Amazonian forest ecosystem appears to be dependent on the distribution of roots and living organisms in the soil, since it is through them that most of the recycling of nutrients is carried out (CHAUVEL et al. 1987). As management practices have a significant impact on the density and activity of the soil biota, information about these effects on invertebrate populations is needed (ROPER & GUPTA 1995). A contribution to this context is given by several ongoing projects at the Brazilian Agroforestry Research Facility (Embrapa Amazônia Ocidental) within the German-Brazilian Scientific Cooperation Program "Studies of Human Impact on Floodplains and Forest in the Tropics" (SHIFT).

The investigations took place on an abandoned rubber tree plantation (*Hevea brasiliensis*, "Seringueira") which has been used as a polyculture forestry research area since 1992. Originally, the area was cleared of primary rain forest in 1979/1980, and then the rubber tree plantation was abandoned in 1984.

After 1984, the plantation naturally transformed itself into secondary growth through neglect. Using this area as an experiment, the fallow rubber plantation was cultivated (in 1992) with mixed plantings of annual and perennial plants (polyculture systems). In 1997, another project on soil fauna and litter decomposition was established (SHIFT ENV 52 "Soil Fauna and Litter Decomposition in Primary and Secondary Forest and a Mixed Culture System in Amazonia"), closely related to the existing SHIFT projects in Manaus. Parameters, such as the quantity and quality of the litter produced in the systems, the decomposition rates, and the abundance, biomass and respiration of microorganisms and soil animals, were simultaneously and comparatively studied in the primary and secondary forest and in one polyculture system (HÖFER et al. 2001). Although there is a considerable amount of literature concerning the spatial and seasonal distribution of the invertebrates in the soil, most of these studies are restricted to a short-term period and limited to macrofauna. Therefore, our study was developed over a period of two years and describes for the first time the density and biomass of the most abundant groups of the soil mesofauna (Acari Non-Oribatida, Acari Oribatida and Collembola) in Amazonia. Comparing the three forestry systems involved, our principal research questions were 1) What are the density and biomass of these groups? 2) Does the difference of the physical factors between the dry and wet periods exert influences on the density and biomass of the mesofauna? 3) Does the climatic changes during exceptionally dry years exert some influence on the densities of the mesofauna in relation to the litter or mineral soil? 4) Are the mesofauna groups studied here sensitive to the anthropogenic action?

2. Study sites, materials and methods

The study area belongs to the agroforestry research station of "Embrapa Amazônia Ocidental", located close to the city of Manaus, Amazonas, Brazil (3°8'S, 59°52'W). The previously mentioned plantation was divided into 90 experimental plots of 32 x 48 m each (BECK et al. 1998, LIEBERE & GASPAROTTO 1998, VOHLAND & SCHROTH 1999). In the polyculture system IV (a plantation with four tree species), two plots (POA and POC) were sampled in comparison with one 40 x 40 m plot in a secondary (SEC) forest and another of the same size in a primary (FLO) forest. All plots were situated within a distance of less than 300 m of each other. The plot named POC was located close to the edge of the primary forest and the one situated at POA was close to a secondary forest. The entire area has soils of the yellow clayey latosol (Oxisol) type. Soil fauna densities were assessed every three months, from June 1997 to March 1999 (eight sample events). At every sample event, 10 random samples were taken from each of the polyculture plantations POA and POC and 20 from the primary (FLO) and secondary (SEC) forested areas. As we did not sample replicates of the growth areas, our analyses show

only the differences between the single plots. The samples were taken following a 1 m grid of lines marked at each plot. Soil samples were taken in the field with a split corer (steel cylinder, diameter 6.4 cm, corresponding to 0.0032 m²), to a depth of 5 cm. Each sample was divided into two sub-samples: the litter layer and the mineral soil. The Kempson process was used to extract the mesofauna from the samples. To obtain biomass values, additional live material was collected with Berlese-Tullgren extracts of the soil and litter layers in the experimental area. The animals were selected and weighed with an electronic microbalance. The animals were then dried at 60°C for 72 hours to obtain their dry weight. A representative number of individuals belonging to each group was then used to get an average individual weight. The biomass of the specified taxa was obtained by multiplying the number of individuals per m² with the average individual weight.

The data set of daily values of maximum, minimum, and average soil temperature, air humidity, evapotranspiration and rainfall was obtained from the climatic station of the Embrapa Amazônia Ocidental for January 1996 through April 1998 and computed by MARTIUS et al. (2000). This station is a standard climatic station. Monthly averages were computed on the basis of these daily values. The saturation deficit was calculated from the air temperature and relative humidity according to the "Magnus formula" (D'ANS-LAX 1967). The microclimate was measured with data loggers in 6 different sites. Due to technical reasons (battery life duration), the data was obtained in three subsets: August 1997 to March 1998, May 1998 to November 1998, and November 1998 to April 1999. Using the small data loggers (Stowaway XTI Internal/External Temperature Logger), we recorded the temperature in the litter layer above the soil and in the soil to a depth of 5 cm. The relative air humidity was recorded at approximately 10 cm above the soil (on the litter surface) (MARTIUS et al. 2000).

3. Results

3.1 Climatic factors

Rainfall occurrence is shown in figure 1. The rainfall, the average minimum and maximum air temperature, and the relative air humidity measured at the Embrapa weather station, all show that 1997 was a strong El Niño (ENSO) year. This is also reflected in the microclimate of the study sites, where the maximum and average air and soil temperatures were highest in September and October of 1997. Minimum air temperatures were elevated in the subsequent period, from October 1997 to May 1998. The relative humidity of the air was extremely low in September 1997, and evapotranspiration and the calculated saturation deficit were very high. Litter temperatures in FLO, SEC, POC were similar, but in POA, they averaged about 2°C higher. The highest maximums were recorded in POA, showing that the microclimatic conditions are much more variable and unpredictable there than in the other plots. Soil temperatures were lowest in FLO, higher in SEC, and still higher in POA. In FLO, the soil temperature almost equaled the temperature of the litter layer, whereas soil temperatures in POA were considerably lower than the litter temper-

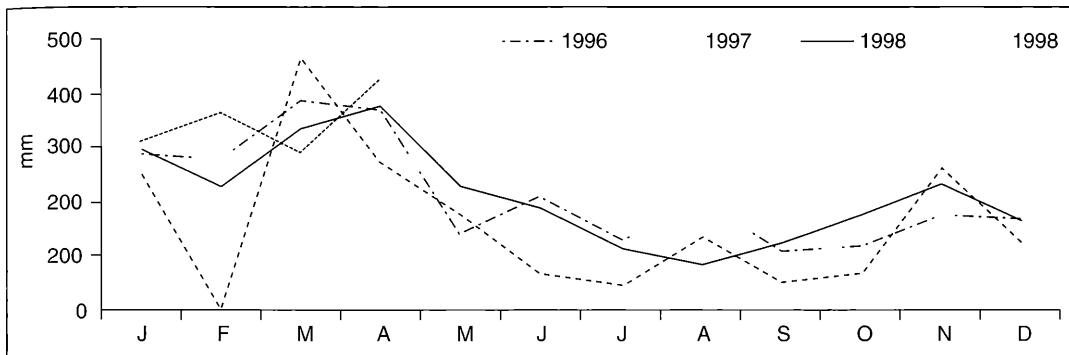


Figure 1. Rainfall results of the station at the Embrapa Amazônia Ocidental (monthly sums) during the study period.

atures. Air humidity of all sites was lowest in September/October 1997. In the other months, it almost always stayed near 100% in FLO, SEC and POC, but was much lower in POA (MARTIUS et al. 2000).

3.2 Density, biomass and group compositions

The values obtained for the wet and dry individual weight of Acari Oribatida, Acari Non-Oribatida and Collembola are summarized in table 1 and compared with the results of other authors for temperate regions. These values are the first to be obtained for the Central Amazon region.

Contrary to what was expected in terms of total values of the mesofauna in the litter layer and mineral soil during the 21-month sampling period, the highest densities and biomass of the mesofauna was not observed in FLO, but in the anthropogenic systems. The total densities of mesofauna decreased in the following order: POA > SEC > POC > FLO (tab. 2).

In FLO, SEC and POC, the total densities of Acari Non-Oribatida were lower than those registered for POA (5,725 ind/m²). The difference in values between the highest density in POA and the lowest in FLO (5,0 ind/m²) was only 12.6% (tab. 2).

The increase of the density of Acari Oribatida in POC (12,722 ind/m²) was only 1.2% higher than that registered for SEC (12,562 ind/m²), meaning that they were

almost similar. The densities in POC and SEC were 18.5% higher than the value obtained in FLO (10,398 ind./m²). Remarkably, the difference in values obtained between the highest density in POA (23,371 ind/m²) and the lowest in FLO, was as high as 44.5% (tab. 2). Following an inverse pattern from those registered for Acari Oribatida and Non-Oribatida, Collembola was clearly higher in the primary forest (FLO), with a value of 3,296 ind/m² and was 37, 28 and 24% higher than the values registered in POC, POA and SEC respectively (tab. 2).

Comparing the values of the litter layer added to the mineral soil, the relative dominance of Acari Oribatida over the Acari Non-Oribatida and Collembola was very high, the minimum value reaching 64% in FLO to the maximum of 82% in POA. The lowest values registered for Collembola in POA and FLO varied between 5 and 14% respectively (tab. 2).

3.3 Seasonal fluctuations and vertical distribution of the mesofauna in the soil profile

Analyzing separately the two layers of the samples in the four plots, the dominance of Acari Oribatida (D %, tab. 2) in relation to the other two groups was highest in POA (77.6 and 68% in the litter and mineral soil, respectively). In FLO, SEC and POC, the density of Acari Oribatida was 54% of the mesofauna in both layers.

Table 1. Individual weight (the standard deviation is represented in parenthesis) of Acari Non-Oribatida, Acari Oribatida and Collembola.

		Acari Non-Oribatida	Acari Oribatida	Collembola
Wet Weight (mg)	This study	0.04092 (0.06291)	0.08422 (0.1018)	0.06316 (0.04981)
	Other studies		0.11675** 0.053*	
Dry Weight (mg)	This study	0.02111 (0.03790)	0.03373 (0.04155)	0.02059 (0.04245)
	Other studies	0.087*	0.0295**	0.027*

* PETERSEN (1892); **LUXTON (1975)

Table 2. Mean density (ind./m²) and biomass (dry weight mg/m²) with standard error of Acari Non-Oribatida, Acari Oribatida and Collembola in the litter layer and mineral soil at FLO, SEC (n = 20), POA and POC (n = 10) in eight trimestral sampling periods. D (%) = dominance of each group in relation to the total catch and IP (%) = increased percentage of the highest density value compared to the lowest between the two soil profiles.

		Litter				Mineral Soil				Litter and Mineral Soil				Total Litter + Mineral Soil			
		Density	Biomass	D (%)	Density	Biomass	D (%)	IP (%)	Density	Biomass	D (%)	Density	Biomass	D (%)	Density	Biomass	D (%)
FLO	Acari Non-Oribatida	2484.6 (349.1)	52.4 (7.4)	24	2516.0 (433.3)	53.1 (9.1)	29	1.2	5000.6	105.5	22	5000.6	105.5	22	5000.6	105.5	22
	Acari Oribatida	5727.7 (698.2)	193.2 (23.5)	57	4670.9 (955.1)	157.5 (32.2)	54	18.4	10398.6	305.7	64	10398.6	305.7	64	10398.6	305.7	64
	Collembola	1905.4 (561.0)	39.2 (11.5)	19	1390.3 (213.1)	28.6 (4.4)	17	27	3295.7	64.0	14	3295.7	64.0	14	3295.7	64.0	14
	Total								18694.9	475.2		18694.9	475.2		18694.9	475.2	
SEC	Acari Non-Oribatida	2987.9 (492.1)	63.0 (10.3)	21	2014.0 (354.0)	42.4 (7.4)	35	32.6	5001.9	105.6	18	5001.9	105.6	18	5001.9	105.6	18
	Acari Oribatida	9405.1 (1980.8)	317.2 (66.8)	66	3157.1 (523.8)	106.5 (17.7)	55	66.4	12562.2	423.7	73	12562.2	423.7	73	12562.2	423.7	73
	Collembola	1914.9 (544.2)	39.4 (11.2)	13	592.8 (145.5)	12.2 (3.0)	10	69	2507.7	51.6	9	2507.7	51.6	9	2507.7	51.6	9
	Total								20071.8	580.9		20071.8	580.9		20071.8	580.9	
POA	Acari Non-Oribatida	2997.7 (732.1)	62.3 (15.4)	14.5	2737.2 (843.1)	57.8 (17.8)	25	8.7	5724.9	120.1	13	5724.9	120.1	13	5724.9	120.1	13
	Acari Oribatida	16030.3 (5235.3)	540.7 (176.6)	77.6	7340.6 (1893.1)	247.6 (63.8)	68	54.2	23370.9	788.3	82	23370.9	788.3	82	23370.9	788.3	82
	Collembola	1621.3 (598.9)	33.4 (12.3)	7.8	754.3 (114.8)	15.5 (2.4)	7	53.5	2375.6	48.9	5	2375.6	48.9	5	2375.6	48.9	5
	Total								31471.4	957.3		31471.4	957.3		31471.4	957.3	
POC	Acari Non-Oribatida	2480.6 (658.9)	52.4 (13.9)	22	2535.0 (260.9)	53.5 (5.5)	31	2.1	5015.6	105.9	18.5	5015.6	105.9	18.5	5015.6	105.9	18.5
	Acari Oribatida	7935.4 (1862.5)	267.7 (62.8)	68	4786.1 (603.5)	161.4 (20.3)	58	39.7	12721.5	429.1	74	12721.5	429.1	74	12721.5	429.1	74
	Collembola	1184.6 (318.4)	24.4 (6.5)	10	895.6 (265.1)	18.5 (5.5)	11	24.3	2080.2	42.9	7.5	2080.2	42.9	7.5	2080.2	42.9	7.5
	Total								19817.3	577.9		19817.3	577.9		19817.3	577.9	

Table 3. Mean density (ind./m²) and biomass (mg/m²) of the Acari Non-Oribatida, oribatid mites and Collembola in the four systems, during the dry (July, September/1997, June and September/1998) and wet (December/1997, March/1998, December/1998 and March/1999) months. The standard errors are given in parenthesis.

		Litter				Soil				Total Litter + Mineral Soil				
		Density	Biomass	Wet	Dry	Density	Biomass	Wet	Dry	Density	Biomass	Wet	Dry	
Acari Non-Oribatida	FLO	1881.80 (436.67)	39.72 (9.22)	41.71 (9.64)	3374.81 (879.56)*	3238.50 (519.93)	71.24 (18.57)	68.36 (10.98)	3374.81 (879.56)*	3238.50 (519.93)	71.24 (18.57)	68.36 (10.98)	71.24 (18.57)	68.36 (10.98)
		2566.10 (363.77)*	54.17 (7.68)	33.82 (8.60)	3390.36 (702.76)	4261.28 (831.59)*	71.57 (14.84)	89.96 (17.55)	3390.36 (702.76)	4261.28 (831.59)*	71.57 (14.84)	89.96 (17.55)	71.57 (14.84)	89.96 (17.55)
		3530.33 (453.72)*	74.52 (9.58)	65.33 (14.44)	793.16 (178.36)	2208.40 (557.74)*	16.74 (3.77)	46.62 (11.77)	793.16 (178.36)	2208.40 (557.74)*	16.74 (3.77)	46.62 (11.77)	16.74 (3.77)	46.62 (11.77)
		1213.06 (277.20)	4012.44 (702.04)*	25.61 (5.85)	84.70 (14.82)	1321.93 (316.62)	27.91 (6.68)	32.50 (6.00)	4012.44 (702.04)*	1321.93 (316.62)	27.91 (6.68)	32.50 (6.00)	27.91 (6.68)	32.50 (6.00)
SEC		1586.31 (404.86)	2037.33 (496.69)*	33.49 (8.55)	43.01 (10.49)	1726.28 (354.27)	36.44 (7.48)	71.24 (10.20)	2037.33 (496.69)*	1726.28 (354.27)	36.44 (7.48)	71.24 (10.20)	36.44 (7.48)	71.24 (10.20)
		2037.33 (330.47)	3950.23 (601.32)*	43.01 (6.98)	83.39 (12.69)	2566.10 (690.70)*	1788.49 (397.87)	37.76 (8.40)	3950.23 (601.32)*	2566.10 (690.70)*	1788.49 (397.87)	37.76 (8.40)	1788.49 (397.87)	37.76 (8.40)
		4634.53 (923.23)*	3856.92 (636.41)	97.83 (19.49)	81.42 (13.43)	917.57 (182.59)	19.37 (3.85)	69.29 (9.89)	3856.92 (636.41)	917.57 (182.59)	19.37 (3.85)	69.29 (9.89)	19.37 (3.85)	69.29 (9.89)
		1259.72 (358.55)	4541.21 (924.20)*	26.59 (7.57)	95.87 (19.51)	590.98 (114.84)	12.48 (2.42)	40.38 (6.96)	4541.21 (924.20)*	590.98 (114.84)	12.48 (2.42)	40.38 (6.96)	12.48 (2.42)	40.38 (6.96)

POA	1181.96 (296.54)	3545.88 (622.26)*	24.95 (6.26)	74.85 (13.14)	2146.19 (410.10)	7153.97 (1006.30)*	45.31 (8.66)	151.02 (21.24)
	1275.27 (271.26)	6065.32 (1515.40)*	26.92 (5.73)	128.04 (31.99)	5536.55 (826.73)*	590.98 (189.63)	116.88 (17.45)	12.48 (4.00)
	3390.36 (618.15)*	2830.48 (471.10)	71.57 (13.05)	59.75 (9.94)	1150.86 (153.96)	2923.79 (437.58)*	24.29 (3.25)	61.72 (9.24)
	217.73 (73.68)	5474.34 (701.06)*	4.60 (1.56)	115.56 (14.80)	870.92 (288.97)	1923.79 (437.68)*	18.39 (5.70)	32.17 (7.37)
	1959.56 (389.39)*	870.92 (238.24)	41.37 (8.22)	13.89 (5.03)	2674.96 (399.22)	2892.69 (472.92)*	56.47 (8.20)	61.06 (9.98)
POC	870.92 (156.56)	3676.98 (1057.48)*	18.39 (3.30)	75.51 (22.32)	2830.48 (271.26)	3297.05 (640.98)*	59.75 (5.73)	69.60 (13.53)
	995.33 (256.65)	1430.79 (323.25)*	21.01 (5.40)	30.20 (6.82)	1026.44 (296.99)	2270.61 (360.73)*	21.67 (6.27)	47.93 (7.62)
	4386.69 (1866.24)	5754.28 (1062.04)*	92.58 (39.38)	121.47 (22.42)	3203.73 (1193.49)*	2083.98 (251.95)	67.63 (25.19)	43.99 (5.32)
	2814.93 (569.29)	5946.39 (966.52)*	94.95 (19.20)	200.57 (32.60)	5023.33 (948.90)	10648.61 (2054.65)*	169.44 (32.01)	359.18 (69.30)
	5147.74 (933.26)	6345.26 (1549.71)*	173.63 (31.48)	214.03 (52.27)	4930.02 (505.22)	5381.03 (606.38)*	166.29 (17.04)	181.50 (20.45)
SEC	8895.80 (1554.31)*	6207.53 (1109.41)	300.06 (52.43)	206.68 (37.42)	2612.75 (464.87)	3732.50 (460.80)*	88.13 (15.68)	125.90 (15.54)
	3943.70 (642.18)	7120.62 (1201.98)*	112.78 (21.66)	242.88 (40.54)	2146.19 (493.30)	2892.69 (322.38)*	72.39 (16.64)	97.57 (10.87)
	2519.44 (571.27)	5038.88 (843.30)*	84.98 (19.27)	169.96 (28.44)	1632.97 (258.15)	5925.35 (634.44)*	55.08 (8.71)	199.86 (21.40)
	4992.22 (900.78)	18102.64 (5093.05)*	168.39 (30.38)	610.60 (171.79)	2534.99 (392.33)*	2130.64 (233.72)	85.51 (13.23)	71.87 (7.88)
	14370.14 (2368.69)*	13079.32 (2184.49)	484.70 (79.90)	441.17 (73.66)	2177.29 (359.64)	4805.60 (719.79)*	73.44 (12.13)	162.09 (24.28)
POA	5521.00 (129.56)	11617.42 (1882.33)*	830.84 (62.57)	391.86 (63.49)	7465.01 (423.79)	12223.95 (1882.91)*	251.79 (109.21)	412.31 (63.51)
	2052.88 (197.27)	8304.82 (1633.12)*	69.24 (6.65)	280.12 (55.09)	3359.25 (1424.96)*	2690.51 (355.56)	113.31 (48.06)	90.75 (11.99)
	3328.15 (1053.81)	30793.16 (2787.47)*	112.26 (35.54)	1038.65 (94.02)	5194.40 (478.57)*	3794.71 (922.59)	175.21 (16.14)	128.00 (31.12)
	17138.41 (2137.81)	44852.26 (19368.63)*	578.08 (72.11)	1512.87 (653.30)	3639.19 (643.37)	18413.69 (6816.91)*	122.75 (21.70)	621.09 (229.93)
	8087.09 (1369.22)	13685.85 (1340.66)*	272.78 (46.18)	461.62 (45.22)	4696.73 (692.77)*	3297.05 (543.91)	158.42 (23.37)	111.21 (18.35)
POC	4914.46 (1288.66)*	3390.36 (956.15)	165.76 (43.47)	114.36 (32.25)	4136.86 (720.61)	7993.78 (942.90)*	139.54 (24.31)	269.63 (31.80)
	2301.71 (324.91)	15054.43 (3668.66)*	77.64 (10.96)	507.79 (123.74)	4385.69 (419.17)*	4292.38 (883.91)	147.93 (14.14)	144.78 (29.81)
	16205.29 (5765.89)*	5069.98 (725.07)	546.60 (194.48)	171.01 (24.46)	3545.88 (1185.87)	6842.92 (1573.43)*	119.60 (40.00)	230.81 (53.07)
	6656.30 (1608.30)	9891.14 (1326.47)*	224.52 (54.25)	333.63 (44.74)	4012.44 (873.30)*	3079.32 (480.14)	230.81 (53.07)	103.87 (16.19)
	777.60 (202.46)	841.64 (326.01)*	16.01 (4.17)	17.33 (6.71)	1741.84 (308.08)*	933.13 (279.29)	35.86 (6.34)	19.21 (5.75)
Collembola	1244.17 (304.43)*	870.92 (240.61)	26.52 (6.27)	4.95 (4.95)	1741.84 (314.63)*	1010.98 (219.80)	35.86 (6.48)	20.81 (4.53)
	4650.08 (876.13)*	2317.26 (571.97)	95.75 (18.04)	47.71 (11.78)	1135.30 (361.95)	1990.67 (553.84)*	23.38 (7.45)	40.99 (11.40)
	575.43 (135.50)	3048.21 (476.27)*	11.85 (3.16)	62.76 (9.79)	419.81 (91.03)	2149.16 (306.01)*	8.65 (1.87)	44.19 (6.30)
	451.01 (160.32)	590.98 (216.32)*	9.29 (3.30)	12.17 (4.45)	342.16 (95.47)*	202.18 (88.19)	7.04 (1.91)	4.16 (1.86)
	1041.99 (289.63)	4136.86 (863.14)*	21.45 (5.34)	85.18 (17.77)	388.80 (136.87)	1305.38 (231.89)*	8.01 (2.86)	26.90 (4.97)
POA	2814.93 (664.62)*	1804.04 (252.90)	57.96 (13.68)	37.16 (5.21)	684.29 (309.07)	1088.65 (301.48)*	14.09 (6.36)	22.42 (6.21)
	513.32 (130.17)	3965.79 (888.94)*	10.57 (2.68)	81.66 (18.30)	186.63 (47.33)	544.32 (146.02)*	3.84 (0.97)	11.21 (3.01)
	279.94 (89.49)	435.46 (284.32)*	5.76 (1.84)	8.97 (5.85)	1026.44 (540.79)	1275.27 (646.20)*	21.13 (11.13)	26.26 (13.31)
	497.67 (127.83)	2021.77 (391.60)*	10.25 (2.63)	41.63 (8.05)	777.60 (304.50)*	1717.73 (80.65)	16.01 (6.27)	4.48 (1.66)
	4416.80 (853.60)*	1026.44 (260.34)	90.94 (17.58)	21.13 (5.36)	746.56 (143.67)	808.71 (205.28)*	15.37 (2.96)	16.65 (4.23)
POC	311.04 (118.22)	3981.34 (670.17)*	6.40 (2.43)	81.98 (13.80)	435.46 (143.67)	746.50 (276.66)*	8.97 (2.96)	15.37 (5.70)
	342.15 (110.94)	1150.86 (348.61)*	7.04 (2.28)	23.70 (7.18)	1026.44 (298.79)	1461.90 (227.27)*	21.13 (6.15)	30.10 (4.68)
	456.56 (123.77)	1524.11 (400.82)*	9.61 (2.55)	31.38 (8.25)	93.31 (46.94)	1161.95 (163.28)*	1.82 (0.97)	24.34 (3.36)
	342.15 (197.95)	1306.38 (294.72)*	7.04 (4.08)	26.90 (6.06)	0.00 (0.00)	1399.69 (218.10)*	0.00 (0.00)	28.82 (4.49)
	1275.27 (230.56)	3079.32 (759.39)*	26.26 (4.75)	63.40 (15.64)	62.21 (29.33)	1959.56 (639.18)*	1.28 (0.60)	40.35 (13.16)

* Highest mean density value comparing dry and wet periods at each surface layer.

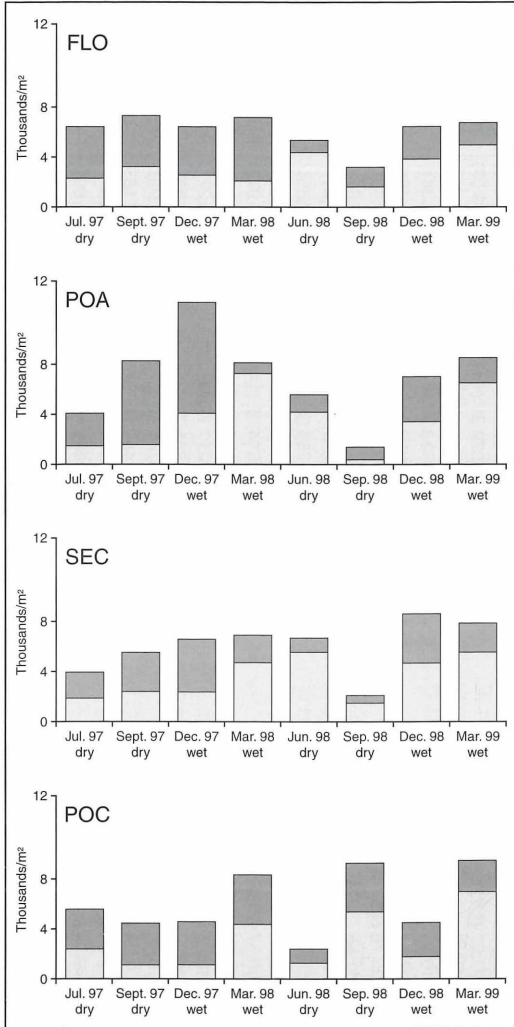


Figure 2. Mean density (Ind./m²) of Acari Non-Oribatida in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n = 20), Secondary Forest (SEC; n = 20) and the Polyculture system (POA and POC; n = 10 each).

The density of all of the mesofauna groups was higher in the litter layer than in the soil layer (tab. 2), the only exception was for Acari Non-Oribatida in FLO and POC, where the densities for the mineral soil were higher. Notably, the total density of Acari Non-Oribatida in the four plots were almost similar. The difference between the values, for the mineral soil and the litter layer, did not exceed 1.2% in FLO and 2.1% in POC. The different values obtained in the soil and litter layers continued even when the densities in the litter layer

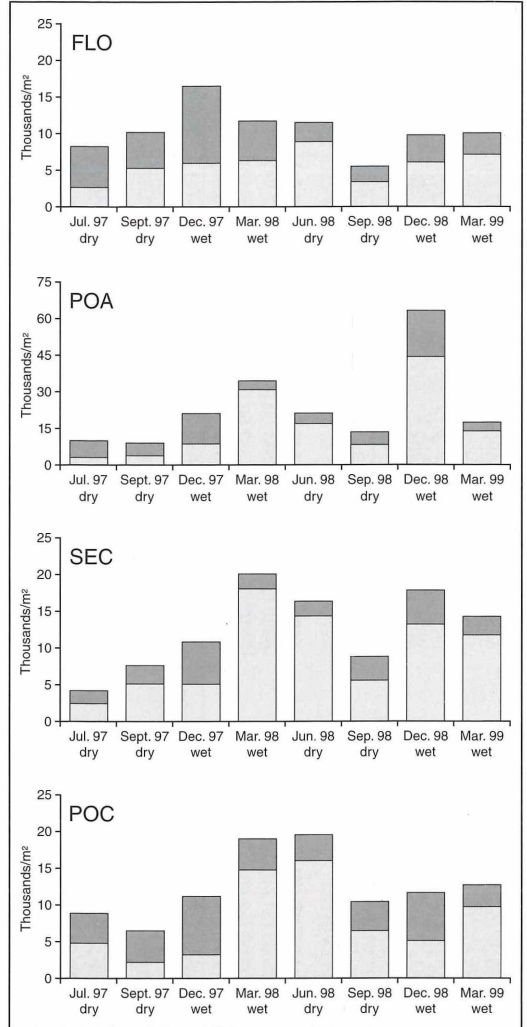


Figure 3. Mean density (Ind./m²) of Acari Oribatida in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n = 20), Secondary Forest (SEC; n = 20) and the Polyculture system (POA and POC; n = 10 each). Notice differences in scale of Ind./m² for POA.

increased, reaching 32.6 and 8.7% in SEC and POA, respectively (tab. 2, fig. 2). In sharp contrast, the pattern observed for the decomposers groups shows their clear preference for the litter layer. These differences were more apparent in SEC and POA. For Acari Oribatida and Collembola, the largest difference between the soil and litter layers (SPD %) was obtained in SEC (66.4 and 69%, respectively) and POA (54.2 and 53.5%, respectively) while the lowest was in FLO (18 and 27%, respectively) (tab. 2, figs 3 and 4).

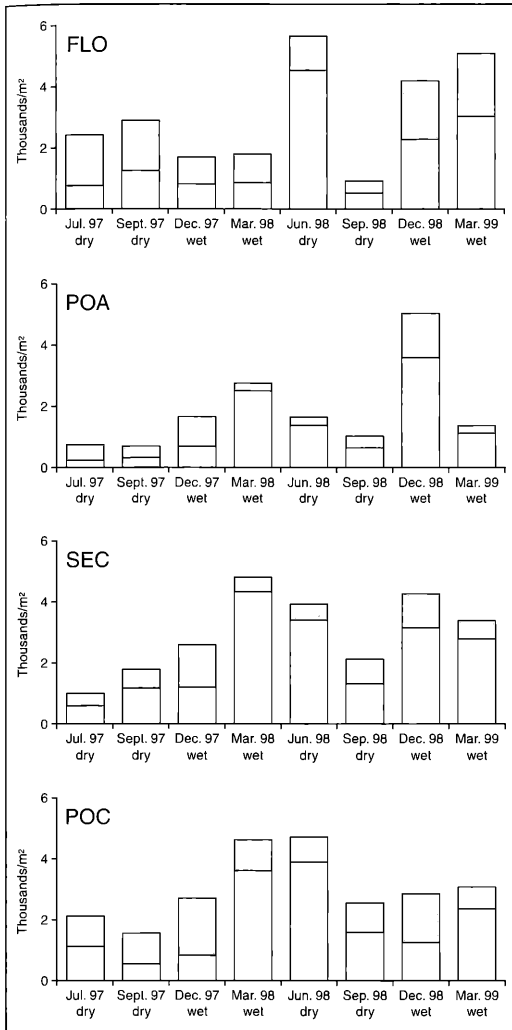


Figure 4. Mean density (Ind./m²) of Collembola in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n = 20), Secondary Forest (SEC; n = 20) and in the Polyculture system (POA and POC; n = 10 each).

For both the litter layer and mineral soil, and for all the mesofauna groups, the highest density and biomass values were generally during the wet season (tab. 3; figs 2, 3 and 4). Lower values coincided with the lower rainfall occurring in the area during the driest period of June - October (fig. 1). This was also reflected in the microclimate of the study sites (soil temperature, relative humidity of the air, litter and soil temperatures).

3.4 Differences between 1997 and 1998

A clear pattern in all mesofauna groups was the higher densities in the mineral soil during the extremely dry year of 1997, principally in FLO, POA and POC (tab. 3, figs 2, 3 and 4). One exception was registered in SEC, but only for Acari Oribatida and Collembola. In this area, the pattern for Acari Non-Oribatida was the same observed for the other groups during 1997. Therefore, during 1998 and 1999, the ratio soil/litter in 1997 was inverted due to high densities of the mesofauna in the litter layer for all of the plots. In the litter layer, the densities of the Acari Oribatida were higher principally in the SEC, POA and POC (tab. 3, fig. 3) and the highest densities of Collembola were detected at FLO and SEC (tab. 3, fig. 4).

Comparing 1997 and 1998, the total mesofauna density increased 29.7% in 1998. The total amount of animals in the litter and mineral soil also differed strongly. In 1998, the density in the litter layer increased 60%, while in the mineral soil a 28% of reduction was detected (tab. 4, fig. 5).

For each group, it can be clearly seen that densities in the litter layer of 1998 were higher than in the soil fraction and that densities in the soil fraction of 1997 were higher than that in the litter layer. In 1998, the density of Acari Non-Oribatida in the litter layer increased 29.4%. Therefore, in 1997, the density in the mineral soil was almost twice as that registered in 1998. The same tendency was also observed in the two decomposers groups. In 1998, the number of oribatid mites in the litter layer increased 66%. In 1997, the density obtained in the mineral soil was almost 17% greater than that of 1998. In 1998, the number of Collembola in the litter layer increased by 62% and, in 1997, the densities in the mineral soil increased by 18.6% (tab. 4, fig. 5).

We detected the highest amount of litter (mean dry weight) in the year of 1998, principally in POC and SEC, whose values were 64 and 39%, respectively, higher than 1997 (tab. 6). In the mineral soil the differences in mean dry weight between 1997 and 1998 did not exceed 24%.

The highest litter and soil temperatures were recorded in POA and there was a general tendency for temperatures to be higher in 1997 than in 1998 in each plot (fig. 6).

3.5 Biomass estimates

The values obtained for the biomass estimates of Acari Oribatida, Acari Non-Oribatida and Collembola in main biomes are summarized in table 5. Comparing the four plots of this study, the total biomass (dry weight) of the soil mesofauna varied between the minimum of 475 mg/m² and the maximum of 957 mg/m² in FLO and POA, respectively. The values obtained for SEC (582 mg/m²) and POC (578 mg/m²) were very similar. Comparing the areas of this study with the

other Amazonian forests, the lowest values of the mesofauna were registered at the flooded forests of várzea and igapó (191 and 287 mg/m², respectively). For Acari Oribatida and Acari Non-Oribatida, the values obtained for the SEC (424 and 106 ind/m²,

respectively) were almost similar to that registered in other secondary forest areas (429 and 96 ind/m²) whose values were the median of the results for five plots of 38 x 42 m at the same experimental area of our study. Comparing the values obtained for central

Table 4. Differences in the years 1997 and 1998 (June/July, September and December) of the mesofauna mean densities (ind./m²) in FLO, SEC, POA and POC. IP (%) represents the increased percentage of the highest value compared to the lowest between the two years at each soil profile.

	Litter layer			Mineral soil			Total Litter + Mineral Soil		
	1997	1998	IP (%)	1997	1998	IP (%)	1997	1998	IP (%)
Acari Non-Oribatida	21,789	30,841	29.4	40,906	20,513	49.9	62,695	51,354	18.0
Acari Oribatida	50,752	149,347	66.0	72,095	59,984	16.8	122,847	209,331	41.0
Collembola	8,110	21,353	62.0	11,011	8,958	18.6	19,121	30,311	36.9
Total	80,651	201,541	60.0	124,012	89,455	28.0	204,663	290,996	29.7

Table 5. Biomass (mg dry weight/m²) estimates of Acari and Collembola in main biomes (in parenthesis the percentage of each group in relation to the total mesofauna). Values of the columns 1 to 7 were extracted from LUXTON (1975) and represented median values of five or more independent mean biomass estimates. Values of columns 8 and 9 are from PETERSEN (1982b). Values for Oribatida in columns 10 were extracted from WOAS et al. (1982) and for Collembola from DIELMANN (1982). Values of the columns 11 to 14 were extracted from our data, 15 and 16 from FRANKLIN et al. (1996) and of the column 17 from SANTOS (2000; median values of five parcels of 38 x 42 m at the same experimental area of Embrapa).

	Oribatida	Non-Oribatida	Acari (in toto)	Collembola	TOTAL
01 - "tundra"	60 (25)	30 (12)	90	150 (63)	240
02 - temperate "grassland"	110 (37)	100* (33)	120*	90 (30)	300
03 - tropical "grassland"	20* (22)	60* (67)	80*	10* (11)	90
04 - temperate coniferous forest	450 (70)	110* (17)	500	80 (13)	640
05 - temperate deciduous forest (mor soil)	700*		900*	130*	830
06 - temperate deciduous forest (mull soil)	180		300*	110	290
07 - tropical forest			100*	20*	100
08 - temperate forest (mor soil)	400/1000				
09 - temperate forest (mull soil)	100/400				
10 - temperate forest (moder beech wood soil)	300/700			340	
11 - tropical primary forest (FLO)	306 (64)	105 (22)	411	64 (14)	475
12 - tropical secondary forest (SEC)	424 (73)	106 (18)	530	52 (9)	582
13 - tropical polyculture system (POA)	788 (82)	120 (13)	908	49 (5)	957
14 - tropical polyculture system (POC)	429 (74)	106 (18)	535	43 (8)	578
15 - tropical flooded forest ("várzea")	156	35	191		191
16 - tropical flooded forest ("igapó")	266	21	287		287
17 - tropical secondary forest	429	96	525	97	622

* tentatives values generally based on less than five biomass estimates

Table 6. Mean dry weight (mg) and standard deviation (parenthesis) of the litter and mineral soil in the study sites in the years 1997 and 1998 (June/July, September and December). IP (%) represents the increased percentage of the highest value compared to the lowest between the two years at each soil profile.

	Litter			Mineral Soil		
	1997	1998	IP (%)	1997	1998	IP (%)
FLO	10.60 (3.47)	15.03 (4.52)	29	109.31 (14.56)	83.51 (8.05)	24
SEC	13.02 (4.37)	21.28 (6.27)	39	109.30 (10.23)	98.30 (7.57)	10
POA	12.89 (2.67)	15.43 (5.70)	16	103.09 (8.06)	96.11 (11.92)	7
POC	6.83 (2.60)	18.95 (6.24)	64	103.03 (8.39)	98.28 (3.39)	5
TOTAL	11.16 (4.24)	17.83 (6.16)	37	107.16 (11.46)	93.02 (10.99)	13

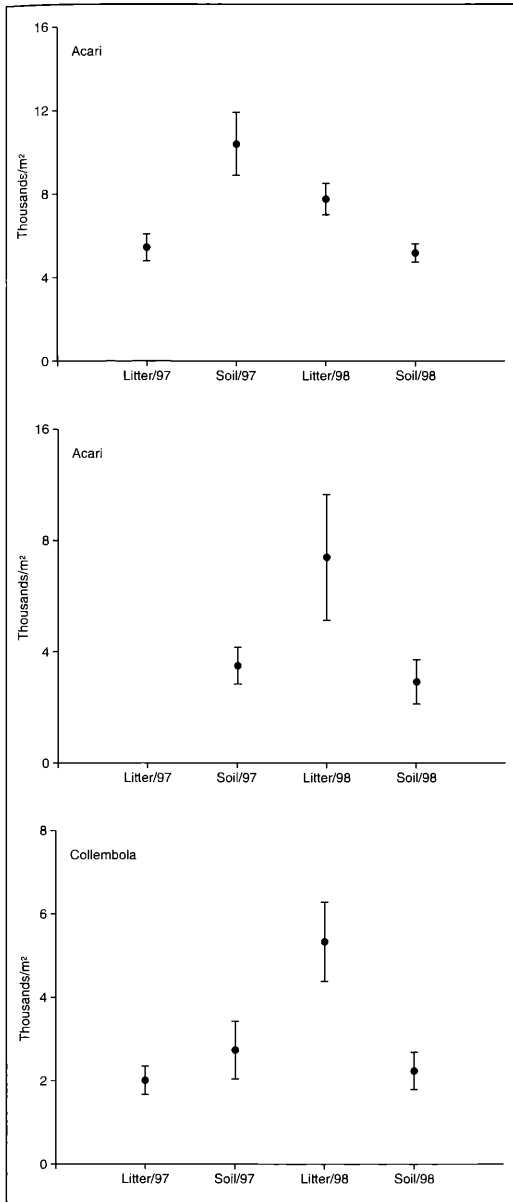


Figure 5. Comparison of the mean density with errors bars of Acari Non-Oribatida, Acari Oribatida and Collembola in FLO, SEC, POA and POC at each soil profile (litter and mineral soil) during the period of June/July, September and December of 1997 and 1998. Notice difference of scale.

Amazon region and even for the temperate coniferous forest, the highest difference of the Acari Oribatida' dominance in relation to the other mesofauna groups was obtained at POA (82%).

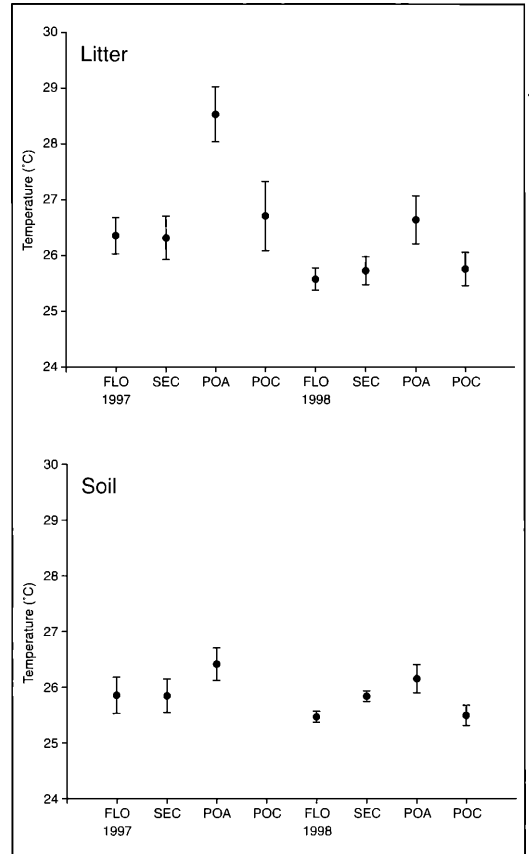


Figure 6. Microclimate measurements with data loggers in the study sites. Litter and mineral soil monthly average temperatures with errors bars in 1997 (August, September and December) and 1998 (July, September and December). Data extracted from Martius et al. (2000). Measurement for POC (soil) in 1997 was not available.

4. Discussion

Contrary to our expectation, mesofauna densities were higher in the polyculture POA than in the relatively undisturbed FLO. This is situated at the northwestern extremity of the experimental area and does not receive much shading from the neighboring plantations, nor from the adjacent secondary growth. The microclimate at the soil surface of this plot therefore was much harsher than in the secondary and primary forests (MARTIUS et al. 2000). All these factors resulted in extreme abiotic conditions and contributed to a different annual cycle to that recorded in POC, which is situated near a primary forest and received strong shading from the directly neighboring primary forest. The difference in soil mesofaunal density between POA and POC might

be also explained by the more extreme microclimatic conditions in POA (HÖFER et al. 2001).

The greatest relative dominance of the Acari Oribatida in relation to the other groups of the mesofauna in POA, point to this group as being principally responsible for the greatest mesofauna density of this plot. A few dominant Acari Oribatida species, mainly *Archegozetes longisetosus* (AOKI, 1965) occurs sporadically, but in great aggregations in Central Amazon region (OLIVEIRA & FRANKLIN 1989). Unfortunately, the Acari Oribatida of our mesofauna study were not identified at species level. Another experiment in the same plots investigated, litterbags of three mesh sizes (1 cm, 250 µm and 20 µm) were filled with a "standard litter" (*Vismia guianensis*) at the end of the rainy season of April/1988 and were implanted in the plots. The mesofauna in these litter bags were sampled after 26, 58, 111, 174, 278 and 350 days from the beginning of the experiment (BECK et al. 1998). According to the results obtained by HAYEK (2000), the total mean density of *A. longisetosus* was extremely high in POA (44.85 individuals), followed by SEC, FLO and POC, with 14.25, 1.3 and 0.4 individuals, respectively. Also, in POA, more evidence of aggregation for this specie was reported, as 45% (20.25 individuals) of the total obtained were concentrated in the second period.

Our results for the dominance of the three groups of the mesofauna (POA>SEC>POC>FLO) showed exactly the opposite pattern of dominance obtained for the macrofauna by HÖFER et al. (2001), over all eight sampling periods. They reported the macrofauna in the following gradient of dominance: FLO (4,866 ind/m²), POC (4,266 ind/m²), SEC (3,769 ind/m²) and POA (3,745 ind/m²). Predatory forms made up between 46 and 53% of the total arthropod macrofauna. Also, they reported that the macrofauna density in POA was 23% lower than the values registered in FLO, where the predators were more numerous (53%) and dominated by the Pseudoscorpionida, Diplura, Formicidae and Araneae. Based on these results, we would hypothesise that the relative abundance of the mesofauna density could be explained by the results for macrofauna. The highest densities of macro-predators in plots of lowest mesofauna densities (POC and FLO) suggest that the macropredators could have acted as controllers of the mesofauna abundance. However, our results showed that the highest density of Collembola was obtained in the primary forest (FLO), whose value (3,296 ind/m²) was 37, 28 and 24% higher than the values recorded in POC, POA and SEC, respectively. This result does not conform with the hypothesis of a high level of predation by the macropredators in plots where they were more abundant, probably because Collembola being very mobile is less susceptible to predation than other mesofauna group. It is quite interesting to observe that Collembola

responds differently from the other groups of mesofauna under similar conditions. This is a reflection of the differences in the relative contribution of each of the components of biotic (predation) and abiotic (microclimate) factors operating in each plot to fluctuations in densities of each taxonomic group of the mesofauna. In this study, predation and extreme microclimate have been identified as two major factors that could have affected mesofauna densities. Also, we can not eliminate the hypothesis that the increased dominance of the oribatid mites caused by of one or more species, like *A. longisetosus*, that became dominant in the anthropogenic plots, could explain our results.

According to LAVELLE et al. (1992), the possibility of maintaining or improving soil fertility by manipulating the activities of soil fauna needs to be explored. An enhanced knowledge of the biology and dynamics of soil colonization by populations that are adaptable to relatively harsh ecological conditions is required. In the case of agroecosystems and soil submitted to rehabilitation techniques, the perspectives for the management of soil biodiversity is to maintain key functional groups. This study revealed differences among the mesofauna groups. The density of the two decomposers groups, the Acari Oribatida and Collembola were notably lower in the mineral soil, than in the litter layer. For the Acari Non-Oribatida, the same tendency was not clearly discernible, probably because of their predatory habit. This made more evident the different responses of different taxonomic groups to the same set of environmental conditions.

This study has shown that the population densities of mesofauna fluctuated greatly between 1997 and 1998. The litter arthropod population was lowest in 1997 probably because of the extreme and exceptional dryness caused by the El Niño Southern Oscillation and also due the reduction of the litter layer in the soil surface.

In a tropical deciduous forest in Panama, a dry season with little rain or a long wet season reduced the numbers of litter arthropods. Arthropod abundance was not as random with respect to years and individual groups of litter animals that showed a persistent pattern of seasonal increase and decrease (LEVINGS & WINDSOR, 1985). In this study, we detected the same pattern, which means that there are years of high and others with low populations, depending on the effects of the physical factors.

When looking at the distribution of the soil mesofauna over the whole period of our study, it can be seen that densities in the litter layer are generally higher than in the soil fraction. Only in 1997, was the mesofauna density in three of the four plots higher in the mineral soil. This tendency was more accentuated in the polyculture system. The pattern in SEC was not the same for the decomposer groups, the Oribatid mites and

Collembola, probably due to the higher amount of surface litter at this plot. We also observed that the amount of litter in 1997 was relatively lower than in 1998 and that the litter and soil temperatures were higher in 1997, principally in the litter layer.

We hypothesize that the differences between 1997 and 1998 are results of: 1) a possible reaction of the mesofauna that migrated to the mineral soil during the extremely dry period of 1997 and 2) a consequence of the reduction of the litter layer that occurred in 1997, causing lower mesofauna densities. We may also conclude that the mesofauna density showed a relationship with the rainfall occurrence, temperature of the litter and the mineral soil as a possible result of dryness stress during the dry periods. Superimposed on these climatic factors, we evidenced the influence of the amount of litter on the soil surface and the possible effect of predation.

The large influence of the microclimate, at least in extreme climatic years as 1997, or via the extremes in normal years, has a restrictive influence on the soil fauna, and thus, on the decomposition process (MARTIUS et al. 2000). The microclimate is influenced by the cropping system, e.g. shading by the plant canopy, soil cover by litter, etc. In general, the results obtained for the primary forest, not subjected to environmental impact, were the most stable during the study period.

In the central Amazon region, the vertical distribution and abundance of arthropods (meso- and macrofauna) in the soil of a secondary dryland forest in 0-14 cm depth were studied in September/1985 (dry season) (ADIS et al. 1987). According to the authors, the results did not correspond with data from the forest in the seasonal tropics (LEVINGS & WINDSOR 1982, 1984; MERINO & SERAFINO 1978). In more markedly seasonal tropics, the abundance of the animals during the dry season was higher in the mineral subsoil as a response to the decreasing humidity in organic layers (ADIS et al. 1987). Another short-term period study was developed in April/1986 (rainy season) (ADIS et al. 1987). They consequently concluded that neither during the rainy season nor during the dry season was the abundance of arthropods in mineral subsoil higher in response to the changing in organic layers, as reported from forests in the seasonal tropics. The macroarthropod community was investigated in a Neotropical mesothermic rainforest (Ecuador) in September/1987 and February/1998. The results of this short-term period of study showed that the vertical distribution did not change dramatically during the low rainfall period, and no clear evidence of vertical migration was detected. Therefore, a clear tendency concerning population dynamics was observed in the litter and soil layers, with the lowest mesofauna density occurring during the driest periods (SILVA DEL POZO & BLANDIN 1991).

While analyzing the results of other long-term period studies with mesofauna, we detected some indications similar to our results. Seasonal densities and vertical distribution of soil mesofauna were studied in a coffee plantation in the Central Plateau of Costa Rica (1,130 mm) from March 1977 to February 1978 (12 sampling periods). The distribution of Collembola, Protura, Symphyla and Acari was positively correlated with the rainy season. The Acari (not separated into Oribatida and Non-Oribatid groups) prevailed in the upper 5 cm of soil depth independent of the season of the year. The highest abundance of Collembola was detected in the upper 5 cm of soil depth during the rainy season, while during the dry season the highest density was detected in the deeper layers of the soil profile (FRAILE & SERAFINO 1978).

On the contrary, in the central Amazon region, two long-term period studies in the soil of a primary (MORAIS 1985) and secondary forest (RODRIGUES 1985) there was a lower density of arthropods during the rainy season. These studies were made during December/1982–May/1983 with the soil sampled once a month in the 3.5 and 3.5-7cm depth (Kempson extraction). As both authors in their results did not include Acari and Collembola, this is probably the main reason for the differences registered here.

In tropical vertisols (Martinique, French West Indies), changes in arthropod communities indicate a decline in soil quality following agricultural use. During the dry period, this type of soil also is unfavorable to the development of soil animal populations and in particular to Collembola due to physiological dryness (high concentrations of smectites). The litter protected the soil against erosion, offered microhabitats and food to litter-dwelling groups and prevented vertisols from shrinking during dry periods (LORANGER et al. 1999). In Central Amazon, soil and litter-inhabiting fauna depends on litter quantity (HÖFER et al. 1996) and quality and on microclimatic conditions in the specific habitat (HÖFER et al. 2001). Complementary, our results have also revealed that the mesofauna density oscillates between years of extreme and "normal" climatic registers, resulting in migration of the mesofauna to the mineral soil during the extreme driest period. In addition, a more accentuated influence of these factors in the antropogenic system has been observed. Based on these results, we may also hypothesize that the extremely wet years could exert an influence on the soil fauna population. This underscores the need to carry out long-term studies. According to LEVINGS & WINDSOR (1984), the population distributions in tropical areas are the result of interactions among many factors. Physical factors, often assumed to be unimportant in the tropics, can not be disregarded or excluded as contributors to the observed variance in animal and plant distribution.

It is quite possible that not only the amount of litter but also the diversity of leaves available on the soil surface could exert some effect on the soil invertebrate communities. Therefore, the effect of different qualities of litter was tested in the development of the invertebrate community. The experiment took place in 5 plots (30 x 40 m) of secondary forest in Central Amazonia. Four substrata were tested: 1) *Hevea brasiliensis* ("seringueira"), 2) *Carapa guianensis* ("andioba"), 3) a "mixture" of *Hevea*, *Carapa* and *Vismia* spp. ("lacre", the predominant leaf species on the soil of the secondary forest plots) and 4) the original and more diversified litter layer. The results showed that the density of the selected groups (decomposers, herbivores, predators, social groups and others) in the litter layer did not differ significantly between the four substrata. Analysis of the multidimensional scaling, using the PATN program showed that there was no difference in the fauna composition in the litter and mineral soil between the four treatments (SANTOS 2001). The reduction of the diversity of the leaves did not affect adversely the soil community, principally the Acari and Collembola, that possess a large alimentary spectrum. The author states the possibility that the soil invertebrates could respond in a more favorable way to the reduction of the diversity and amount of resources in the soil than is actually supposed. According to LEBRUN & VAN STRAALLEN (1995), the oribatid mites occupy a great variety of habitats, possess a great diversity in morphology and feeding habits, have different ways of reproduction, and above all exhibit complex and diverse life cycles.

Our results for the Acari Oribatida and Collembola individual weights are close to those obtained in other studies and are the first biomass results based on concrete measures for the central Amazon region. The values given in earlier literary works were only estimates. However, since the average individual weights have only been measured on only one occasion, which ignored changes in relative population with the time (PETERSEN 1982a), our results of biomass need to be interpreted with caution. The most recommended procedure would be the estimation for each sampling period of the year in a long-term study.

In our study areas, the Acari Non-Oribatida biomass varied between 105 – 120 ind/m² and did not differ much from the temperate forest value estimation (110 ind/m²; LUXTON 1975). Although there is a tendency for the Acari Non-Oribatida biomass estimated in this study to be lower than in temperate forest, the values are however higher than values recorded for many tropical forests where total Acari are about 100 mg/m² as reported by LUXTON (1975). Collembola biomass obtained at FLO (64 mg/m²), SEC (52 mg/m²), POA (49 mg/m²) and POC (43 mg/m²) were lower than the values estimated for temperate forests that vary between 80 and 340 mg/m² (LUXTON 1975, DIELMANN 1982).

Acknowledgements

We were pleased with the invitation to publish in the special issue of Andrias honoring Dr. LUDWIG BECK, former head of the Department Zoology at the State Museum of Natural History of Karlsruhe, Germany. His great scientific and management capacity during the development of the project SHIFT ENV 52 has made this work possible. The comments of Dr. BECK, Dr. S. WOAS, Dr. A. BADEJO, Dr. H. HÖFER and an anonymous referee greatly improved the manuscript. We are grateful to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil) and BMBF (Bundesministerium für Bildung und Forschung, Germany). The technical staff (F. A. O. CAMPOS, J. C. SANTOS and A. P. SANTOS) of INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil) gave indispensable help with the "Mesofauna", "Enchytraeidae" and "Soil Respiration" teams. We also thank W. MONTOIA and G. N. PEREIRA that made the separation of the mesofauna and S. CHILSON for revision of the English language.

5. Literature

- ADIS, J., MORAIS, J. W. & RIBEIRO, E. F. (1987): Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the dry season. – *Trop. Ecol.*, **28**: 174-181.
- ADIS, J., MORAIS, J. W. & MESQUITA, H. (1987): Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the rainy season. – *Studies Neotrop. Fauna Environ.*, **28**: 174-181.
- BECK, L., GASPAROTTO, L., FÖRSTER, B., FRANKLIN, E., GARCIA, M. V., HARADA, A., HÖFER, H., LUIZÃO, F., LUIZÃO, R., MARTIUS, C., MORAIS, J. W., OLIVEIRA, E. & RÖMBKE, R. (1998): The role of soil fauna in litter decomposition in a primary forest, secondary forest and a polyculture plantation in an Amazonia (SHIFT Project ENV 052): Methodological considerations. – *Proc. Third SHIFT Workshop, Manaus, Brazil, 1998*: 471-481; Bonn (BMBF).
- CHAUVEL, A., GUILLAUMET, J. L. & SCHUBART, H. O. R. (1987): Importance et distribution des racines et des êtres vivants dans un "latosol" argileux sous forêt amazonienne. – *Rev. Ecol. Biol. Sol.*, **24** (1): 19-48.
- D'ANS-LAX (1967): Taschenbuch für Chemiker und Physiker. Band I Makroskopische physikalisch-chemische Eigenschaften. Berlin (Springer).
- DIELMANN, H. J. (1982): Lebensraum Buchenwaldboden. 10. Die Collembolen. – *Verh. Ges. Ökol.*, **17**: 103-107
- FRAILE, J. M. & SERAFINO, A. (1978): Variaciones mensuales en la densidad de microartrópodos edáficos en un cafetal de Costa Rica. – *Ver. Biol. Trop.*, **26** (2): 291-301.
- FRANKLIN, E. N., ADIS, J. & WOAS, S. (1997): The Acari Oribatida. – In: JUNK, W. (ed.) *The Central Amazon Floodplain. Ecology of a pulsing system*. Ecological Studies, Vol. **126**: 321-349; Berlin (Springer).
- HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rain forest after experimental litter addition in small plots. – *Pedobiologia*, **40**: 570 – 576.
- HÖFER, H., HANAGARTH, W., GARCIA, M., MARTIUS, C., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2001): Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. *Eur. J. Soil Biol.*, (in press).
- HAYEK, T. (2000): Ácaros do solo (Acari: Oribatida): Diversidade, abundância e biomassa na decomposição de serapilheira

- em parcelas de floresta primária, capoeira e policultivo da Amazônia Central. – 93 pp.; MSc. Thesis, INPA/UA, Manaus, Brazil.
- LAVELLE, P., BLANCHART, E., MARTIN, A., SPAIN, A. V. & MARTIN, S. (1992): Impact of soil fauna on the properties of soils in the humid tropics. – In: *Myths and Science of Soils of the Tropics*, **29**: 157-185; Madison, Wisconsin (SSSA Special Publication).
- LEBRUN, P. & VAN STRAALLEN, N. M. (1995): Oribatid mite: prospects for their use in ecotoxicology. – *Experimental & Applied Acarology*, **19**: 361-379.
- LEVINGS, S. C. & WINDSOR, D. D. (1982): Seasonal and annual variation in litter arthropod population. – In: E. G. LEIGH, A. S. RAND & D. M. WINDSOR (eds.) *The ecology of a tropical forest: Seasonal rhythms and longer-term changes: 355-387*; Washington, D. C. (Smithsonian Institution Press).
- LEVINGS, S. C. & WINDSOR, D. D. (1984): Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. – *Biotropica*, **16**: 125-131.
- LEVINGS, S. C. & WINDSOR, D. D. (1985): Litter arthropod population in a tropical deciduous forest: Relation between years and arthropod groups. – *J. Animal Ecol.*, **54**: 61-69.
- LIEBEREI, R. & GASPAROTTO, L. (1998): Agroecological profile of plants used as production factors and as management components in tropical polyculture systems. Proc. Third SHIFT-Workshop, Manaus, 1998: 307-312; Bonn (BMBF).
- LORANGER, G., PONGE, J-F., BLANCHART, E. & LAVELLE, P. (1998). Influence of agricultural practices on arthropod communities in vertisol (Martinique). – *Eur. J. Soil Biol.*, **34** (4): 157 – 165.
- LUXTON, M. (1975): Studies on the Acari Oribatida of a Danish beech wood soil. II. Biomass, calorimetry and respiration. – *Pedobiologia*, **15**: 161-200.
- MARTIUS, C., GARCIA M. & HANAGARTH, W. (2000). Report: Microclimate 1997-1999 in primary forest, secondary forest and agroforestry systems in central Amazonia. – In: HÖFER et al. (eds.): *Soil fauna and litter decomposition in primary and secondary forests and a mixed culture system in Amazonia*. – Final report of SHIFT project ENV 52, 36-49; Bonn (BMBF).
- MERINO, J. F. & SERAFINO, A. (1978): Variações mensuais en la densidade de microartrópodos edáficos en un cafetal de Costa Rica. – *Rev. Biol. Trop.*, **26**: 291-301.
- MORAIS, J. W. (1985): Abundância e distribuição vertical de Arthropoda do solo numa floresta primária não inundada. – 92 pp.; MSc Thesis, INPA/UA, Manaus, Brazil.
- OLIVEIRA, E. P. & FRANKLIN, E. N. (1989): Efeito do fogo sobre a mesofauna do solo: Recolonização em áreas queimadas. – *Pesq. agropec. bras.*, Brasília: 257-369.
- PETERSEN, H. (1982a): Structure and size of soil animal population. – *Oikos*, **39** (3): 306-329.
- PETERSEN, H. (1982b): The total soil fauna biomass and its composition. – *Oikos*, **39** (3): 330-339.
- ROPER, M. & GUPTA, V.V.S.T. (1995): Management practices and soil biota. – *Aust. J. Soil Res.*, **33**: 321-329.
- RODRIGUES, J. M. G. (1985): Abundância e distribuição vertical de Arthropoda do solo em capoeira de terra firme. – 92 pp.; MSc Thesis, INPA/UA, Manaus, Brazil.
- SANTOS, E.M.R. (2001): Densidade, diversidade e biomassa da fauna do solo em serrapilheira manipulada numa floresta secundária na Amazônia Central. – 85 pp.; MSc. Thesis, INPA/FUA, Manaus, Brazil.
- SILVA DEL POZO, X. & BLANDIN, P. (1991): Les Macroarthropodes édaphiques d'une forêt mésothermique primaire de l'Équateur occidental: Abondances saisonnières et distribution spatiale. – *Rev. Ecol. Bio. Sol*, **28** (4): 421 – 433.
- VOHLAND, K. & SCHROTH, G. (1999): Distribution patterns of the litter macrofauna in agroforestry and monoculture plantations in central Amazonia as affected by plant species and management. – *Appl. Soil Ecol.* **13**: 57-68.
- WOAS, S., WUNDERLE, I. & BECK, L. (1982): Lebensraum Buchenwaldboden. 12. Die Oribatiden. – *Verh. Ges. Ökol.*, **17**: 117-123.

WERNER HANAGARTH & MARTIN BRÄNDLE

Soil beetles (Coleoptera) of a primary forest, secondary forest and two mixed polyculture systems in central Amazonia

Abstract

The beetle fauna of soil and litter in Amazon forest eco-systems was studied by means of Berlese-Tullgren extractions, at 8 sampling dates during 2 years in four experimental plots (one in primary forest, one in secondary forest and two polyculture plots) of the Embrapa Amazônia Ocidental research centre near Manaus (Brazil). Beetle individuals were found in 99 % of the extracted litter and soil cores. In total, we recorded 47 beetle families, of which 12 contributed to more than 90% of the total individual numbers and beetle biomass, respectively. Most individuals recorded were very small averaging less than 2 mm body length. The total number of predator families was low (6 families, 13 %), when compared to that of the decomposers (29 families, 62 %). Only one family was considered herbivorous (Chrysomelidae, 2 %). 28 % of the decomposer families, but 67 % of the predator families ranged among the 12 most abundant beetle families. Among the 12 dominant beetle families the carnivorous Scydmaenidae, Staphylinidae, Carabidae and Pselaphidae represented 51 % of the abundance and 41 % of the biomass. In comparison to other macroarthropods (Chilopoda, Formicidae, Isoptera, Diplopoda) the contribution of Coleoptera to the total of individual numbers or faunal biomass was rather small. We conclude that although diversity of the soil dwelling beetles seems to be high, their total contribution to nutrient cycling may be of minor importance.

Authors

Dr. WERNER HANAGARTH, Dr. MARTIN BRÄNDLE, State Museum of Natural History Karlsruhe, Department of Zoology, Erbprinzenstr. 13, D-76133 Karlsruhe; e-mail: werner.hanagarth@smnk.de

key words

Beetles, guilds, diversity, Amazonia, polyculture systems

1. Introduction

Beetles are one of the most diverse taxa among the insects (JACOBS & RENNER 1988, ERWIN 1982). Following DUNGER (1964) they are the most important Pterygota in soil biology. SCHUBART & BECK (1968), however, stated that beetles may be very important and dominant in temperate zones, but in the tropics termites and ants appear to be much more abundant and functionally more important. Beetles provide a wide range of functions in ecosystems, occupying almost all types of trophic niches. There are carnivorous, phytophagous (including pollen- and sap-feeders), detritophagous, saprophagous (including scavengers and

coprophagous species), xylophagous and fungivorous groups.

In the Amazon region, a series of studies on the functional diversity of the soil fauna has been carried out, considering abundance and partially the biomass at the level of orders (e.g. ADIS 1982, ADIS et al. 1987 a, b, HARADA & BANDEIRA 1994, BANDEIRA & HARADA 1998, LAVELLE & PASHANASI 1989, TAPIA-CORAL et al. 1999). Ants, termites and earthworms are the most studied soil fauna groups at the level of genus or species (BANDEIRA & HARADA 1991, MARTIUS 1994). However, only a few papers show data on the abundance and even less publications offer data on the biomass of litter and soil dwelling beetles at the family level (DIDHAM 1998, DIDHAM et al. 1998a, 1998b). This may be surprising because beetles are also abundant insects of the litter and soil in Amazonia (BECK 1963, HANAGARTH 1981, DIDHAM 1998, DIDHAM et al. 1998 a, b) and in Panama (WILLIAMS 1941). The reason for this low attention given to ground dwelling beetles may be (i) their small body size, (ii) the low status of knowledge of trophic behaviour even in well studied temperate zones and (iii) the poor taxonomic status of many families in the tropics.

The present study was part of the project ENV 52 "Soil fauna and litter decomposition" of the German-Brazilian SHIFT program "Studies on Human Impact on Forests and Floodplains" in the Brazilian Amazonia. Here we analyse the beetle fauna extracted from soil cores with a Berlese-Tullgren apparatus. First we describe the soil beetle fauna and evaluate the importance of different families due to abundance and biomass. Second, we compare the functional position of soil beetles with other groups of soil macroarthropods.

2. Material and methods

The study site is located at the experimental area of the agroforestry research station Embrapa Amazônia Ocidental close to the city of Manaus, Amazonas, Brazil (3°8'S, 59°52'W, BECK et al. 1998, HÖFER et al. 2000; VOHLAND & SCHROTH 1999). The study area is flat without accentuated altitudinal differences (altitude 44 - 50 m a.s.l.). The investigations took place on an abandoned plantation of rubber trees (*Hevea brasiliensis* occluded with *Hevea pauciflora*, Seringueira) which has been used for agroforestry research since 1992. Originally, the area was cleared from primary forest in 1979/1980, and

the rubber plantation was abandoned in 1984. The SHIFT experimental area is surrounded by primary and secondary forests. In the SHIFT project ENV 52 a primary forest (FLO), a 12 year old secondary forest plot (SEC), dominated by *Vismia guianensis*, and two 7 year old mixed polyculture systems (POA and POC) were studied. The tree plantations were planted with Seringueira (*Hevea brasiliensis-pauciflora*), Paricá (*Schizobolium amazonicum*), Mogno (*Swietenia macrophylla*) and Andiroba trees (*Carapa guianensis*). After tree planting, second growth was tolerated. Therefore, these plantations corresponded floristically and structurally to improved secondary forests, in which *Vismia* species dominate (PREISINGER et al. 1994, 2000; SKATULLA et al. 2000). The soil properties correspond to a clayey Xanthic Ferralsol according to the FAO/UNESCO classification (FAO/UNESCO 1990) in all four study plots.

The macrofauna at each site has been extracted in a BERLESE-TULLGREN apparatus (DUNGER & FIEDLER 1989, SOUTHWOOD 1966). This extraction method was frequently applied in soil fauna studies in Europe (e.g. BRASSE 1975, HOUSE & PARMELEE 1985, SCHAEFER 1974), as well as in the Amazon rain forest (BECK 1972, 1976; HÖFER et al. 1996, HÖFER et al. 2000, RÖMBKE et al. 1999, SCHUBART & BECK 1968). A major drawback of this method is that large beetle species or those of low abundance may be not representatively extracted because of the small size of the individual samples. Due to this methodological restrictions the beetle fauna is considered as part of a "Berlese soil fauna". However, compared to handsorting methods, the Berlese-Tullgren method offers great advantages, because it permits the extraction of very small and medium sized beetles as well as a large proportion of larvae.

In total 480 samples comprising a total sampling area of 16.6 m², were taken from July 1997 to March 1999 during 8 sampling events at the four plots. Samples were taken at random with a soil core sampler (21 cm diameter), subsequently separated in litter and soil (0-5 cm) and extracted during 17 days in a BERLESE-TULLGREN apparatus. During each sampling event 20 samples were taken each in FLO and SEC and 10 cores in POA and POC, respectively.

The extracted beetle specimens were identified to the family level. Their dry weight was estimated by direct individual measurement of total body length or other body size variables and applying body length-body weight regression curves with the formula $y = ax^b$ (y = dry weight in mg, a and b = coefficients, x = body length or other body variable in mm). All regressions were highly significant ($r^2 > 0.9$, $P < 0.001$). For the definition of body length-body weight regression curves, fresh material has been independently measured and weighed. The same specimens were dried at 65°C during 72 hours and weighed (dry weight), using a microbalance (min. >0.0001 g, SARTORIUS). For some species of rarely sampled families with similar body weight-body length relationships, the same length categories have been used for the estimation of their biomass.

The determination of trophic groups was hindered by the low level of knowledge of the feeding behaviour of most species and families. Assuming that most species of the recorded families have similar food preferences than their relatives from temperate zones, the trophic level of the families was determined with reference mainly to literature from the European, southeast Asian, North American and Central American Coleoptera fauna (ARNETT 1993, BORROR et al. 1981, DELVARE & ABERLENC 1989, FREUDE et al. 1965-1983, HAMMOND 1990, JACOBS & RENNER 1988, ZAHRADNIK 1985). Families such as Carabidae and Staphylinidae have to be considered as trophically heterogeneous since some of them are not strictly predaceous

(HAMMOND 1990, VANICEK et al. 1994), although conventionally they were considered to be predators (BELL 1990, DUNGER & FIEDLER 1989, NEWTON 1990).

The decomposer families include groups which may act as primary decomposers, feeding on litter similarly to many Myriapoda and Isopoda. However, most species may be fungivorous and micro- or macrosaprophagous thus occupying an inferior trophic level as secondary decomposers.

3. Results and discussion

Diversity of beetle families

In sum, 47 beetle families were identified in the study area. The largest number of families was found in the primary forest (FLO: 36 families), whereas the number of families was smaller at the other plots (28 families in SEC, 24 in POA and 26 in POC).

The total number of families with predatory beetles was low (6 families, 13 %), when compared to that of

Table 1. Mean frequency of ground dwelling beetles in 480 Berlese samples of a) all study plots and b) in the different plots. SD = standard deviation based on eight sampling events during two years.

a)			
All study plots	Frequency (%)	SD	Median (%)
Litter fraction			
Adults	87.0	12.0	90
Larvae	68.3	15.1	70
Adults + larvae	90.9	9.3	90
Soil fraction			
Adults	83.7	13.1	88
Larvae	61.7	19.2	63
Adults + larvae	90.8	9.2	93
Litter & soil fractions			
Adults	97.2	4.6	100
Larvae	87.2	11.4	90
Adults + larvae	99.2	2.2	100
b)			
Study plots	Frequency (%)	SD	Median (%)
FLO			
Adults	85.0	12.1	85
Larvae	66.9	8.8	65
Adults + larvae	92.5	7.6	93
SEC			
Adults	86.3	10.3	90
Larvae	75.0	15.4	75
Adults + larvae	91.3	7.9	90
POA			
Adults	92.5	7.1	90
Larvae	75.0	15.4	75
Adults + larvae	93.8	7.4	95
POC			
Adults	83.8	16.9	85
Larvae	67.5	10.4	65
Adults + larvae	86.3	13.0	85

Table 2. Proportion of individuals and biomass of the most abundant beetle families. Data based on 480 Berlese samples. N = 3.629 individuals (adult specimens), 47 families (*remaining families: predators: 2; decomposers: 21; herbivores: 1; other groups: 11).

Trophic group	Family	Individuals		Dry weight (mg)	
		%	Cumulative %	%	Cumulative %
Decomposers	Scolytidae	19.1	19.1	19.2	19.2
Decomposers	Ptiliidae	17.5	36.6	4.5	23.8
Predators	Scydmaenidae	16.7	53.3	6.9	30.7
Predators	Staphylinidae	15.6	68.9	16.7	47.4
Predators	Carabidae	13.1	82.0	13.5	60.9
Predators	Pselaphidae	5.9	87.9	3.4	64.2
Decomposers	Leiodidae	3.4	91.4	3.0	67.2
Decomposers	Platypodidae	0.9	92.3	1.1	68.3
Decomposers	Curculionidae	0.9	93.1	9.3	77.6
Decomposers	Colydiidae	0.8	93.9	0.5	78.1
Decomposers	Tenebrionidae	0.8	94.7	1.4	79.6
Decomposers	Scarabaeidae	0.7	95.4	14.4	94.0
Remaining (*)	35 families	4.6	100.0	6.0	100.0

decomposers (29 families, 62 %). Only one family was considered herbivorous (Chrysomelidae, 2 %).

A preliminary estimation of species richness applying the morphospecies concept (data not shown) indicates that Staphylinidae, Pselaphidae, Scydmaenidae and Carabidae might be the species richest families, whereas species richness of the decomposer families seemed to be low. However, in comparison to a study from western Amazonia (HANAGARTH 1981), the species richness of Carabidae seemed to be low in all plots studied here. DIDHAM et al. (1998b) also recorded low species richness of Carabidae in the leaf litter of forest fragments north of Manaus.

Frequency of beetles

Beetle individuals (adults and larvae) were found in 99 % of the Berlese samples, attaining a frequency value of 91 % both in the litter and soil fraction, respectively (tab. 1a). They occurred in very similar frequencies in all four study plots (tab. 1b). The frequency of adult beetles ranged between 83 and 87 % in soil and litter fractions. The frequency of the larvae was lower (62 – 68 %). These differences might be caused by sampling artefacts: larvae are expected to be more sensible to the sample handling.

Abundance and biomass

In the whole sample, adult beetles dominated in abundance and biomass compared to the larvae, attaining 64 % and 61 %, respectively.

Out of the 47 families, 12 families (26 %) represented 95 % of all individuals registered and 94 % of the biomass of adult beetles (tab. 2). Among them, the xylophagous Scolytidae and the very small detritivorous Ptiliidae (0.5 - 0.8 mm) were the most abundant families. However, Scarabaeidae (mainly Aphodiini) occupied the second rank in the decomposers biomass

and the third when all families were considered. Only 28 % of the decomposer families, but 67 % of the predator families ranged among the 12 most abundant beetle families. Among the 12 dominant beetle families the carnivorous Scydmaenidae, Staphylinidae, Carabidae and Pselaphidae represented 51 % of the abundance and 41 % of the biomass. The remaining 35 families only represented 5 % of the abundance and 6 % of the biomass.

In the four plots total mean abundance of the beetles, including larvae, were 321 individuals per m² with a mean biomass of 121 mg. In the primary forest (FLO) and in POC the total abundance was low, and high in SEC and POA (tab. 3a), whereas total beetle biomass was high in FLO and low in the other study plots (tab. 3b). However, no statistically clear differences, either in abundance nor in biomass, were found between the primary forest and the tree plantations (tab. 3a and 3b). Predators and decomposers shared about the same proportion of individuals (53 % and 46 %) and biomass (48 % and 50 %), respectively. There were no strong differences of abundance of predators between the primary forests and the tree plantations, whereas predator biomass was slightly higher in the primary forest than in the secondary forest and in the tree plantations. No strong differences in abundance were found for the decomposers, whereas larger differences existed in their biomass. However, their mean biomass was 1.5 – 3 times higher in the primary forest when compared to the other plots (tab. 5).

Body length

Figure 1 shows the body length distribution of a total of 3.575 adult individuals of predators and decomposers. The log₁₀-transformed body length distribution of both groups was right-skewed and differed significantly from the normal distribution (tab. 4). Most of the beetles

Table 3. a) Mean abundance (individuals/ m²) and b) mean biomass (dry weight mg/ m²) of functional groups, based on 480 Berlese samples.

a)				
Functional group	FLO	SEC	POA	POC
	Mean	Mean	Mean	Mean
Predators	157.2	179.3	189.9	148.7
Decomposers	121.2	147.5	207.7	117.1
Herbivores	0.0	1.7	4.2	0.9
Others	4.6	2.5	2.3	0.0
Sum	282.9	331.0	404.1	266.6
b)				
Functional group	FLO	SEC	POA	POC
	Mean	Mean	Mean	Mean
Predators	72.7	60.7	41.4	58.2
Decomposers	99.4	39.3	67.6	35.0
Herbivores	0.0	0.4	1.3	0.2
Others	3.7	0.3	0.2	1.6
Sum	175.8	100.7	110.5	95.0

recorded had relatively small to very small body sizes. The mean length of 5.283 specimens from 47 families, including all adults and larvae recorded in the samples, was 2.04 mm. They achieved maximum and minimum lengths of 42.0 and 0.4 mm, respectively (Appendix, tab. 1). Following the classification of VAN DER DRIFT (1951), and the Tropical Soil Biology and Fertility Programme (TSBF) (LAVELLE & PASHANASI 1989, ANDERSON & INGRAM 1993) most of them would be characterised as mesofauna (< 2 mm body length) rather than macrofauna (> 2 mm body length). The adults of 23 families (48 %) had a mean body size equal or larger than 2 mm, whereas the mean body length of 22

families (46 %) was between 1.0 and 2.0 mm and that of adults of 3 families only (6 %) was below 1 mm. Almost all individuals of families with a minimum body length larger than 2 mm were singletons, doubletons or tripletons. Exceptions were the Platypodidae and Scarabaeidae with 33 and 25 individuals, respectively. The Scarabaeidae had the largest mean body length. Among the twelve most abundant families only five had a mean body size larger than 2 mm. Even the Staphylinidae achieved only a mean length of 3.0 mm. Nevertheless, in this family the smallest adult specimens were not longer than 0.4 mm, and the largest one measured 42 mm. Carabidae are commonly considered as relatively large predators (THIELE 1977). However, in our study plots, the mean body length of 474 individuals was 1.7 mm, attaining a minimum length of 0.9 mm and a maximum length of 11.5 mm. A high proportion of the ground beetle species is part of the very small Bembidiini (Tachyina and Anillina, ERWIN 1984) with body length ranges of 0.9 to 1.1 mm, or of small Scaritini species (2.0 mm).

The functional position of beetles within the soil fauna table 5 summarizes the biomass data of all considered soil macroarthropods (HÖFER et al. 2000). Among the predators, beetles (adults and larvae) attained a biomass roughly similar (41 - 73 mg/m²) to that of the Araneae (8 - 59 mg/m²) and of Pseudoscorpiones (34 - 62 mg/m²) in the four study plots. The beetles occupied 3 - 4 % of the biomass of the total macroarthropods and 8 - 15 % of that of the predators. In all plots the Chilopoda were the most important predators, attaining high biomasses (168 - 504 mg/m²) and dominances (7 - 37 % of the macroarthropods; 42 - 66 % of

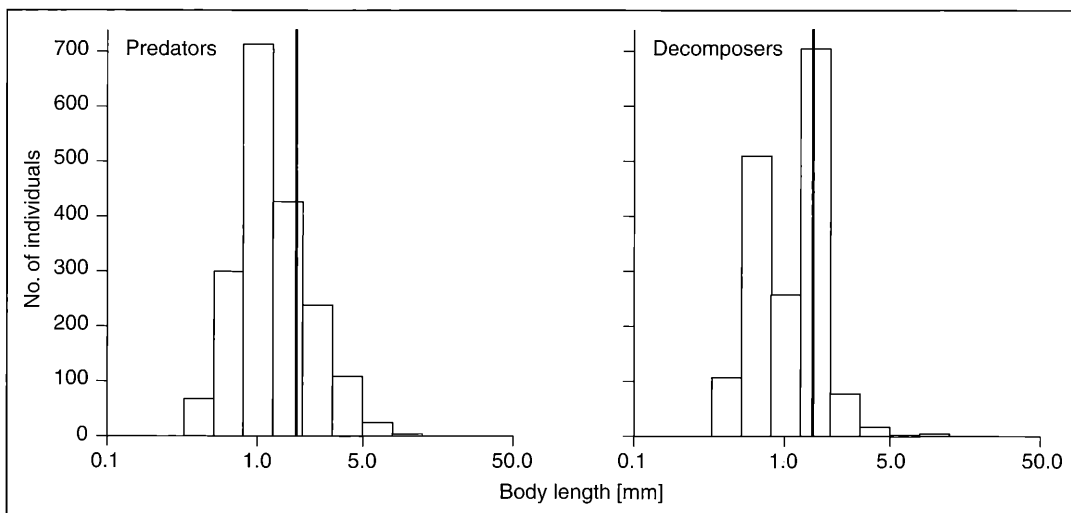


Figure 1. Body length distributions of predatory and decomposer beetle individuals. The mean of the trophic guilds is marked by a vertical line. Note that the body length axis is log₁₀-transformed.

Table 4. Characteristics of the distribution of \log_{10} -transformed body length of predatory and decomposer beetles. N = number of individuals; SD = standard deviation; SE = standard error; K.-S. = probability level for the hypothesis that the distribution of the \log_{10} -transformed data is significantly different from the normal distribution (KOLMOGOROV-SMIRNOV test).

Trophic group	N	Mean	SD	Skewness	SE Skewness	Kurtosis	SE Kurtosis	K.-S.
Predators	1883	0.18	0.25	0.72	0.06	0.47	0.11	< 0.01
Decomposers	1692	0.13	0.24	0.13	0.06	-0.78	0.12	< 0.01

Table 5. Functional position of beetles. Mean biomass of taxonomic groups was calculated among all Berlese samples at four plots. Note that biomass was standardized to mg per m² (Data from HÖFER et al. 2000).

Functional group	Biomass dry weight (mg/ m ²)			
	FLO	SEC	POA	POC
Predators				
Coleoptera (part.)	72.7	60.7	41.4	58.2
Chilopoda	434.2	503.5	183.6	167.5
Formicidae, adults (part.)	145.2	68.5	26.0	62.3
Araneae	58.5	46.8	7.6	40.4
Pseudoscorpionida	62.3	61.6	33.7	55.5
other predators	16.7	16.6	11.9	14.8
Total	789.5	757.7	304.2	398.8
Decomposers				
Coleoptera (part.)	99.4	39.3	67.6	35.0
Isoptera	654.4	306.0	108.7	303.6
Diplopoda	219.6	107.1	247.1	275.9
Isopoda	287.2	33.7	227.0	993.7
Diptera, Larvae	33.5	25.7	64.1	41.6
Formicidae, adults (part.)	22.8	10.4	12.1	8.1
other decomposers	128.3	11.5	19.4	24.7
Total	1445.2	533.7	746.0	1682.6
Herbivores				
Coleoptera (part.)	0.0	0.4	1.3	0.2
Formicidae, adults (part.)	13.2	5.1	4.2	13.2
Rhynchota	43.0	56.4	28.1	75.8
Lepidoptera, larvae	12.1	8.9	20.0	12.9
other herbivores	0.6	1.5	1.3	1.6
Total	69.0	72.3	54.9	103.7
Other groups				
Coleoptera (part.)	3.7	0.3	0.2	1.6
Formicidae, adults (part.)	6.7	3.8	3.6	7.3
Total	10.4	4.1	3.9	8.8
Macrofauna (total)	2314.1	1367.9	1108.9	2193.9

the predators). The ants (Formicidae) had markedly higher biomasses and dominances in the primary forest (145 mg/m²; 18.4 %), than in the other plots (26 - 69 mg/m²; 9 % in POA and SEC, respectively).

The biomass of the decomposer beetles was rather similar compared to that of the predatory beetles (39 - 99 mg/ m², see above). Their contribution to the total biomass was, however, low (2 - 4 % of the macroarthropods; 2 - 9 % of the decomposers) especially when compared to those of termites, Diplopoda and Isopoda (tab. 5). Termites (Isoptera) attained a very high absolute biomass value (654 mg/ m²) and dominance (28 % of the macroarthropods, 45 % of the decomposers) in the primary forest plot (FLO), and medium to high values in the other plots (109 - 306 mg/ m²; 15 - 57 % of the decomposers in the corresponding plots). Other important decomposers in all plots were the Diplopoda and Isopoda whose dominances ranged between 26 and 76 %. In all plots (with exception of the POC plot) decomposer beetles had higher biomasses than decomposer ants and Diptera larvae.

Herbivorous beetles occupied only a small proportion in biomass and dominance, represented by a single family, the Chrysomelidae. Among the other arthropods, the Rhynchota, especially the Homoptera, were the most important herbivores, followed by moth larvae (Lepidoptera) and ants (mainly leaf-cutting species of the genus *Acromyrmex* and *Atta*).

4. Conclusions

Our study indicate that ground dwelling beetles are one of the most diverse taxa of Arthropoda in Amazon forest ecosystems. These results support the findings of ADIS (1982a), ADIS (2000), ADIS & RIBEIRO (1989), DIDHAM et al. (1998b), FRIEBE (1984), SCHUBART & BECK (1968). Ground dwelling beetles are found to be a very diverse group in family richness also in other parts of the tropics (DAMMERMAN 1925, HAMMOND 1990, WILLIAMS 1941) as well as in temperate forests (ELLENBERG et al. 1986, FRIEBE 1983). For example, the latter author found 40 families in soil and litter of a beech forest applying hand sorting and photo electors which is very similar to our findings in the primary forest (36 families). SCHUBART & BECK (1968) applying hand sampling and Berlese extractions recorded in the organic layers of terra firme forests and floodplain forests rather similar numbers (27 and 29, respectively).

The Staphylinidae, Ptiliidae, Pselaphidae, Carabidae and Scydmaenidae were among the most dominant

families. These results support the findings of ADIS (1982), ADIS & RIBEIRO (1989), FRIEBE (1984), DIDHAM (1998), DIDHAM et al. (1998a, 1998b), SCHUBART & BECK (1968), as well as ADIS (2000). Additionally, as in SCHUBART & BECK's samples the xylophagous Scolytidae were dominant in all our four plots, corresponding to the high quantity of dead wood. Of lesser importance but nevertheless among the most dominant families, they mentioned also the Tenebrionidae and Curculionidae. Also among the forest soil beetle fauna of the Barro Colorado Island, Panama, the first four families mentioned above dominated (WILLIAMS 1941). Most other families were uncommon. A very high proportion of the total abundance and biomass may be concentrated on a few families, of which some such as the Staphylinidae are very rich in species (see also DIDHAM et al. 1998a, b).

In total, the biomass of the Berlese beetle fauna was low, although abundance and frequency was high. This might be related to the high proportion of species of very small to small body sizes (see also DIDHAM et al. 1998a). The causes of this phenomenon, which was found also in spiders and Diplopoda (HÖFER et al. 2000), is still unknown. Previous evaluations of the ground beetle fauna in western Amazonia (HANAGARTH 1981) indicated, that the Carabidae assemblages had similar body size ranges compared to that in Central European environments, but the proportion of very small and small species (<3.5 mm) was higher in the tropical site. Applying the macrofauna definition (>2 mm body length) of VAN DER DRIFT (1951) and the Tropical Soil Biology and Fertility Programme (LAVELLE & PASHANASI 1989, ANDERSON & INGRAM 1993) the greatest proportion of the ground dwelling beetles would be part of the mesofauna (<2 mm) (VAN DER DRIFT 1951). Therefore, there are large differences between the abundance of macrofauna collected with handsorting methods (e.g. TAPIA-CORAL et al. 1999, LAVELLE & PASHANASI 1989) and with the Berlese-Tullgren method (e.g. HÖFER et al. 2000) or the similar Kempson method (ADIS 2000). Handsorting methods only take a small spectrum of the beetle fauna. The efficiency of handsorting methods for macrofauna was studied by FRANKE et al. (1988) in a German beech forest. Over 67 % of the important groups of the macrofauna were recorded. The authors applied an efficiency value for the estimation of the total abundance.

The Berlese-Tullgren extraction and the Kempson extraction method may offer the most representative results for beetles of very small and medium body size, but there are doubts if the abundance, species richness and especially the biomass of large species may be approximately realistically estimated. There are indications based on the comparison with results obtained with handsorting methods, pitfall traps and other methods applied in western Amazonia (HANAGARTH 1981) and in a German beech forest (BECK et al.

1998), that the importance of large highly mobile ground species may be underestimated even by handsorting methods (BECK pers. com.). Taking into account the small body size of many species data gained with handsorting methods present only a small spectrum of the beetle fauna. This is shown also by unpublished data of our SHIFT project (HÖFER et al. 2000) and may explain the low abundances of beetles presented in other publications (e.g. TAPIA-CORAL et al. 1999). As in the case of the ants and termites, the abundance and biomass of large beetles is surely underestimated.

In sum, the presented results are a first approach to understand the functional diversity of ground dwelling beetles in Amazon forest systems. Compared to other arthropod taxons, ground-dwelling beetles contribute to a large part of the soil arthropod biodiversity, but may play a minor role as predators and decomposers.

Acknowledgements

The study was conducted as part of the SHIFT program based on a German-Brazilian government agreement. It was financially supported by the German Bundesministerium für Bildung und Forschung (BMBF, grant no. 339675) and the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). The research institution Embrapa Amazônia Ocidental, Manaus, Brazil, logistically supported the study. Thanks are due to the project leaders Prof. Dr. LUDWIG BECK (SMNK) and Dr. LUADIR GASPAROTTO, Embrapa-Amazônia Ocidental, to GESSIENE DO NASCIMENTO PEREIRA and VALDINEZ MONTAIA, who processed the Berlese samples, and to Dipl. Biol. CLAUS WURST (SMNK) for the identification of some beetles.

4. Literature

- ADIS, J. (1982): Zur Besiedlung zentralamazonischer Überschwemmungswälder (Varzea-Gebiet) durch Carabiden (Coleoptera). – Arch. Hydrobiol. **95**: 3-15.
- ADIS, J. (2000): Terrestrial arthropods in soils from inundation forests and deforested floodplains of white water rivers in Central Amazonia. – In: JUNK, W. J., OHLY, J. J., PIEDADE, M. T. F., SOARES, M. G. M. (eds.): The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management: 464-476; Leiden (Backhuys Publishers).
- ADIS, J., MORAES, J. W. DE & RIBEIRO, E. F. (1987a): Vertical distribution and abundance of arthropods in the soil of a neotropical secondary forest during the dry season. – Stud. Neotrop. Fauna Environm., **22** (4): 174-181.
- ADIS, J., MORAES, J. W. DE & GUIMARÃES DE MESQUITA, H. (1987b): Vertical distribution and abundance of arthropods in the soil of a neotropical secondary forest during the rainy season. – Stud. Neotrop. Fauna Environm., **22** (4): 189-197.
- ADIS, J. & RIBEIRO, M. O. A. (1989): Impact of deforestation on soil invertebrates from Central Amazonia inundation forests and their survival strategies to long-term flooding. – Water Quality Bulletin, **14** (2): 88-98 & 104.
- ANDERSON, J. M. & INGRAM, J. (1993): Tropical soil biology and fertility: A handbook of methods. – 2nd. Edition, 221 pp.; Oxford (CAB).

- ARNETT, R. H. (1993): American insects, a handbook of the insects of America north of Mexico. – Gainesville (The Sandhill Crane Press).
- BANDEIRA, A. G. & HARADA, A. Y. (1991): Cupins e Formigas da Amazônia. – In: VAL, A. L., FIGLIUOLO, R. & FELDBERG, E. (eds.): Bases Científicas para Estratégias de Preservação e Desenvolvimento da Amazônia: Fatos e Perspectivas, Vol. 1: 387-395; Manaus, Brazil (Instituto Nacional de Pesquisas da Amazônia, INPA).
- BANDEIRA, A. G. & HARADA, A. Y. (1998): Densidade e distribuição vertical de macroinvertebrados em solos argilosos e arenosos na Amazônia central. – *Acta Amazônica*, **28** (2): 191-204.
- BECK, L. (1963): Zur Ökologie und Taxonomie der neotropischen Bodentiere I. Zur Oribatiden-Fauna Perus. – *Zool. Jb. Syst.*, **90**: 299-392.
- BECK, L. (1972): Der Einfluss der jahresperiodischen Überflutungen auf den Massenwechsel der Bodenarthropoden im zentralamazonischen Regenwaldgebiet. – *Pedobiologia*, **12**: 133-148.
- BECK, L. (1976): Zum Massenwechsel der Makro-Arthropodenfauna des Bodens in Überschwemmungswäldern des zentralen Amazonasgebietes. – *Amazoniana*, **6** (1): 1-20.
- BECK, L., HÖFER, H., MARTIUS, C., GARCIA, M., FRANKLIN, E. & RÖMBKE, J. (1998): Soil fauna and litter decomposition in primary and secondary forests and a polyculture system in Amazonia – study design and methodology. – SHIFT Workshop (Manaus). Proceedings III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998: 463-469; Bonn (BMBF).
- BELL, R. T. (1990): Insecta: Coleoptera, Carabidae, Adults and Larvae. – In: DINDAL, D. L. (ed.) Soil Biology Guide. Chap. 38: 1053-1092; New York, Toronto (John Wiley & Sons).
- BORROR, D. J., LONG, D. M. DE & TRIPLEHORN, C. A. (1981): An introduction to the study of insects. – 5. Edition; Philadelphia (Saunders College Publ.).
- BRASSE, D. (1975): Die Arthropodenfauna von Getreidefeldern auf unterschiedlichen Böden im Braunschweiger Raum. – *Pedobiologia*, **15**: 405-414.
- DAMMERMANN, K. W. (1925): First contribution to a study of the tropical soil and surface fauna. – *Treubia*, **6**: 107-139.
- DECAËNS, T., LAVELLE, P. JIMENEZ JAEN, J. J., ESCOBAR, G. & RIPPSTEIN, G. (1994): Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. – *Eur. J. Soil. Biol.*, **30** (4): 157-168.
- DELVARE, G. & ABERLEN, H. P. (1989): Les insectes D'Afrique et d'Amérique tropicale – clés pour la reconnaissance des familles. – Montpellier, France (Cirad-Gerdat).
- DIDHAM, R.K. (1998) Altered leaf-litter decomposition rates in tropical forest fragments. – *Oecologia*, **116**: 397-406.
- DIDHAM, R. K, HAMMOND, P. M. & LAWTON, J. H. (1998a): Beetle species responses to tropical forest fragmentation. – *Ecol. Monogr.*, **68**: 295-323.
- DIDHAM, R. K., LAWTON, J. H., HAMMOND, P. M. & EGGLETON, P. (1998b): Trophic structure and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. – *Phil. Trans. R. Soc. Lond. B*, **353**: 437-451.
- DRIFT, J. VAN DER (1951): Analysis of the animal community in a beach forest floor. – *Tijdschr. Entomol.*, **94**: 1-118.
- DUNGER, W. (1964): Tiere im Boden. – Neue Brehm-Bücherei, **327**; Wittenberg-Lutherstadt (A. Ziemsen).
- DUNGER, W. & FIEDLER, H. J. (1989): Methoden der Bodenbiologie. – 432 pp.; Stuttgart (G. Fischer-Verlag).
- ELLENBERG, H., MAYER, R. & SCHAUERMANN, J. (1986): Ökosystemforschung – Ergebnisse des Sollingprojektes 1966 – 1986. – 507 pp.; Stuttgart (Ulmer).
- ERWIN, T.L. (1982): Tropical forests: their richness in Coleoptera and other arthropod species. – *Coleopterists Bulletin*, **36**: 74-75.
- ERWIN, T.L. (1984): Small terrestrial ground-beetles of the Amazon Basin (Coleoptera: Bembiidiini: Tachyina and Anillina). – *Amazoniana*, **8** (4): 511-518.
- FAO-UNESCO (1990): Soil Map of the World, Revised Legend: Food and Agriculture Organization of the United Nations, Rome.
- FRANKE, U., FRIEBE, B. & BECK, L. (1988): Methodisches zur Ermittlung der Siedlungsdichte von Bodentieren aus Quadratproben und Barberfallen. – *Pedobiologia*, **32**: 253-264.
- FREUDE, H., HARDE, K. W. & LOHSE, G. A. (1965-1983): Die Käfer Mitteleuropas. – Vol. 1-11; Krefeld (Goecke & Evers).
- FRIEBE, B. (1983): Zur Biologie eines Buchenwaldbodens. 3. Die Käferfauna. – *Carolinea*, **41**: 45-80.
- FRIEBE, B. (1984): Vergleichende Betrachtungen zur Käferbesiedlung von Weisswasser- und Schwarzwasserüberschwemmungswäldern (Várzea, Igapó) Zentral-Amazoniens. – *Biogeographica*, **19**: 101-109.
- HAMMOND, P.M. (1990): Insect abundance and diversity in the Dumoga-Bone National Park, n. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. – In: KNIGHT, W. J. & HOLLOWAY, J. D. (eds.): Insects and the rain forests of the south east Asia (Wallacea): 197-254. London (The Royal Entomological Society)
- HANAGARTH, W. (1981): Vergleichend-ökologische Untersuchungen an epigäischen Arthropoden aus Naturbiotopen und Kulturland im tropischen Regenwald Perus. Ein Beitrag zur Agrarökologie der Tropen. – 240 pp.; Dissertation, Universität Hamburg.
- HARADA, A. Y. & BANDEIRA, A. G. (1994): Estratificação e densidade de invertebrados em solo arenoso sob floresta primária e plantios arbóreos na Amazônia central a estação seca. – *Acta Amazônica* **24** (1/2): 103-118.
- HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rain forest after experiment litter addition in small plots. – *Pedobiologia*, **40**: 570-576.
- HÖFER, H., MARTIUS, C., HANAGARTH, W., GARCIA, M., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2000): Soil fauna and litter decomposition in primary and secondary forests and a mixed culture system in Amazonia. – Final report of SHIFT project ENV 52: 299 pp.; Bonn (BMBF).
- HÖFER, H., HANAGARTH, W., GARCIA, M., MARTIUS, C., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2001): Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. – *Eur. J. Soil Biol.* (in press).
- HOUSE, G. J. & PARMELEE, R. W. (1985): Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. – *Soil Till. Res.*, **5**: 351-360.
- JACOBS, W. & RENNER, M. (1988): Biologie und Ökologie der Insekten. – 690 pp.; Stuttgart (G. Fischer)
- LAVELLE, P. & PASHANASI, B. (1989): Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). – *Pedobiologia*, **33**: 283-291.
- LAVELLE, P., DANGERFIELD, M., FRAGOSO, C., ESCHENBRENNER, V., LOPEZ-HERNANDEZ, D., PASHANASI, B. & BRUSSARD, L. (1994): The relationship between soil macrofauna and tropical soil fertility. – In: WOOMER, P. L. & SWIFT, M. J. (eds.): The Biological Management of Tropical Soil Fertility. TSBF, Wiley-Sayce.
- MARTIUS, C. (1994): Diversity and ecology of termites (Isoptera) in Amazonian forests. – *Pedobiologia*, **38**: 407-428.

NEWTON, A.F. Jr. (1990): Insecta: Coleoptera Staphylinidae, Adults and Larvae. – In: DINDAL, D.L. (eds.): Soil Biology Guide. Chap. 38: 1137-1174; New York, Toronto (John Wiley & Son),.

PREISINGER, H., COELHO, L. F., SIQUEIRA, S. G. DO M. & LIEBERE, R. (1994): Analysis of growth form types and floristic composition of the spontaneous vegetation in an agricultural test area near Manaus, Amazonas, Brazil. – *Angew. Botanik*, **68**: 40-46.

PREISINGER, H., GILVAN, G. C. & COELHO, L. F. (2000): Structural traits of an eight year old secondary forest in the Central Amazon. – Poster, Program and Abstracts, German-Brazilian Workshop on Neotropical Ecosystems, SHIFT-WAVES, Hamburg.

RÖMBKE, J., HÖFER, H., MARTIUS, C., FÖRSTER, B., GARCIA, M., FRANKLIN, E. & BECK, L. (1999): Die Rolle der Bodenfauna beim Streuabbau in Primär- und Sekundärwäldern und einer Holz-Mischkulturfläche in Amazonien (SHIFT Projekt ENV 52): Methodische Überlegungen. – In: OEHLMANN, J. & MARKERT, B. (eds.): Ökotoxikologie: Ökosystemare Ansätze und Methoden: 268-275; Landsberg (ecomede).

SCHAEFER, M. (1974): Auswirkung natürlicher und experimenteller Störungen in Grenzzonen von Ökosystemen untersucht am Beispiel der epigäischen Arthropodenfauna. *Pedobiologia*, **14**: 51-60.

SCHUBART, H. & BECK, L. (1968): Zur Coleopterenfauna amazonischer Böden. – *Amazoniana*, **1** (4): 311-322.

SKATULLA, M., COELHO, L. F., GOTTSBERGER, G., LIEBERE, R. & PREISINGER, H. (2000): Structural traits and regeneration mechanisms in three successional stages of Terra-Firme-forest in the Central Amazon. – Poster, Program and Abstracts, German-Brazilian Workshop on Neotropical Ecosystems, SHIFT-WAVES, Hamburg.

SOUTHWOOD, T. R. E. (1966): *Ecological Methods*. – 391 pp.; London (Chapman and Hall).

TAPIA-CORAL, S. C., LUIZÃO, F. J. & WANDELLI, E. V. (1999): Macrofauna da liteira em sistemas agroflorestais sobre pastagens abandonadas na Amazônia central. – *Acta Amazonica*, **29** (3): 477-495.

THIELE, H. U. (1977): *Carabid Beetles in Their Environments. A Study of Habitat Selection by Adaptations in Physiology and Behaviour*. – 369 pp.; Berlin (Springer-Verlag).

VANICEK, M., ADIS, J. & PAARMANN, W. (1994): Untersuchungen zur Biologie dreier Laufkäferarten (Coleoptera, Carabidae, Harpalini) aus amazonischen Regenwäldern. – *Andrias*, **13**: 161-168.

VOHLAND, K. & SCHROTH, G. (1999): Distribution patterns of the litter macrofauna in agroforestry and monoculture plantations in central Amazonia as affected by plant species and management. – *Appl. Soil Ecol.*, **13**: 57-68.

WILLIAMS, E. C. (1941): An ecological study of the floor fauna of the Panama rain forest. – *Bull. Chicago Acad. Sc.*, **6**: 63-124.

ZAHRADNIK, J. (1985): *Käfer Mittel- und Nordeuropas*. – Hamburg, Berlin (Paul Parey).

Appendix. Body lengths (mm) of litter and soil beetle families, based on 480 Berlese samples from four sites (FLO, SEC, POA and POC).

Trophic group/ taxon	Individuals	Min.	Max.	Mean
Predators				
Carabidae	474	0.9	11.5	1.7
Dytiscidae	6	1.4	3.8	2.1
Histeridae	11	1.8	3.9	2.3
Pselaphidae	215	0.8	3.3	1.5
Scydmaenidae	606	0.4	13.0	1.1
Staphylinidae	566	0.4	42.0	3.0
Decomposers				
Anthicidae	7	1.4	2.1	1.8
Bostrichidae	1	2.3	2.3	2.3
Byrrhidae	8	1.4	1.9	1.7
Ceryllidae	1	1.4	1.4	1.4
Clambidae	1	1.1	1.1	1.1
Colydiidae	29	1.0	6.3	1.7
Corylophidae	11	0.7	1.8	1.2
Cucujidae	6	1.0	1.8	1.4
Curculionidae	31	1.4	5.0	2.9
Elmidae	9	1.1	2.1	1.9
Endomychidae	6	1.1	9.3	2.6
Erotylidae	1	1.2	1.2	1.2
Hydrophilidae	4	1.6	3.4	2.5
Lagriidae	1	0.9	0.9	0.9
Languriidae	2	1.5	2.5	2.0
Lathridiidae	9	1.3	1.5	1.5
Leiodidae	125	0.9	2.3	1.4
Mordellidae	3	1.3	2.8	2.2
Mycetophagidae	1	1.6	1.6	1.6
Nitidulidae	14	1.6	4.3	2.7
Platypodidae	33	2.2	4.3	3.2
Ptiliidae	636	0.5	4.8	0.8
Rhizophagidae	2	1.8	1.8	1.8
Salpingidae	1	1.2	1.2	1.2
Scaphidiidae	6	1.1	2.2	1.7
Scarabaeidae	25	2.1	14.0	4.9
Scolytidae	694	0.7	2.7	2.0
Sphaeridae	1	1.9	1.9	1.9
Tenebrionidae	29	1.2	6.6	2.6
Herbivors				
Chrysomelidae	14	1.4	3.5	2.2
Others				
Aderidae	1	1.9	1.9	1.9
Cholevidae	5	1.8	2.1	1.9
Dasyceridae	1	0.4	0.4	0.4
Euglenidae	1	3.9	3.9	3.9
Heteroceridae	3	2.3	2.6	2.5
Laemophloidae	1	1.8	1.8	1.8
Lyctidae	1	2.3	2.3	2.3
Notiopygidae	1	2.5	2.5	2.5
Scirtidae	2	1.7	2.5	2.1
Silvaniidae	1	2.0	2.0	2.0
Troscidae	1	2.1	2.1	2.1
Unclassified Larvae	22	0.4	3.5	1.1
all families	1655	0.5	38.0	2.7

CHRISTOPHER MARTIUS

Nest architecture of *Nasutitermes* termites in a white water floodplain forest in central Amazonia, and a field key to species (Isoptera, Termitidae)

Dedicated to Prof. LUDWIG BECK honoring his invaluable support of my scientific career

Abstract

The architectural features of the five *Nasutitermes* species occurring in a Neotropical floodplain (várzea) forest on Ilha de Marchantaria in central Amazonia are described: external nest and runway architecture, nest volume, nest height above ground, nesting trees, degree of polycalism). These characteristics are used to build a tentative field key to the nest-building termite species which should be tested for its usefulness for ecological studies of central Amazonian termites.

Author

Dr. Christopher MARTIUS, working group Tropical Ecology, Max-Planck-Institut für Limnologie, Plön, Germany; present address: Center for Development Research, University of Bonn, Walter-Flex-Straße 3, D-53113 Bonn (Germany). e-mail: c.martius@uni-bonn.de

Key words

Termites, *Nasutitermes*, Amazonia, identification key, nest architecture

1. Introduction

Termites are important decomposer organisms in tropical ecosystems. Unlike solitary living decomposers, they are social insects living in colonies found in the soil, within dead wood and in nest mounds above the ground, often attached to trees. Tree-inhabiting makes nest-building termites ideal candidates for the colonization of floodplain forests. Here, termites have a very low diversity but their density is often similar to that in dryland rainforests (MARTIUS 1997; cf. below). Floodplains occupy about 100,000 km² or roughly 2 % of the Amazon basin, the world's largest rainforest area. These "várzea" floodplains, dominated by the white water of the Amazon river, are flooded once a year, the water generally covering the forest floor up to a height of several meters (JUNK 1997). Only a few ground-dwelling species have managed to survive under these conditions, apparently because they developed specific adaptations (MARTIUS 1997). Of the twelve termite species recorded in the várzea of central

Amazonia (MARTIUS 1989, MARTIUS 1997), nine are nest-building species belonging to the family Termitidae, and among these, the most dominant are five wood-feeding species belonging to the genus *Nasutitermes* (BUSTAMANTE & MARTIUS 1998). The *Nasutitermes* community of Ilha de Marchantaria, an island in the Amazon (03°14'17"S / 59°57'09"W) that has served as a case study site for the Max-Planck Work Group on Tropical Ecology (JUNK 1997), has been extensively studied by MARTIUS (1989, 1994a, b, 1997). Here, I present general descriptive data for the nests of these five species and a key to the species of *Nasutitermes* at this study site which should allow their identification in the field.

2. Material and Methods

Ilha de Marchantaria is an island in the Amazon (Solimões) River upstream of the city of Manaus. It is covered by a typical white water floodplain forest (JUNK 1997) that has grown for 20-80 years (WORBES 1986, WORBES et al. 1992). Nests of the local termite assemblage of one 1.4 ha plot on Ilha de Marchantaria (plot P; site description in MARTIUS 1989, 1997) were censused during 1985 and 1986. In total, 151 nests were assessed. Outside this plot, termite nests were sampled on Marchantaria island and elsewhere (Ilha de Careiro, Costa do Marrecão) near the city of Manaus. The censuses included observations of nest structure, external architecture, position on the nesting tree and also measurements of nest size parameters (see below). Termites were collected from the nests and preserved in 70% alcohol. They were identified by WILLIAM SANDS (Natural History Museum London, NHM) in comparison with specimens in the termite collection of NHM. Samples of the identified material were deposited at the museum in London as well as in the Entomological Collection of Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Nomenclature follows CONSTANTINO (1998).

Termite nests were mapped on a plot that measured 280 m along its main axis (E-W), the margins being determined by the margins of the forest. A central line was marked with wooden stakes, and the distance of the forest margin to the central line was measured with a tape. Nest size parameters (height, two diameters, height above ground, gallery width) were recorded and nest volume was calculated (cf. MARTIUS et al. 1994b for formulas used). The trees on which the termite mounds were sitting (nesting trees) were identified on the spot by the botanist LUIS COELHO (Departamento de Botânica,

Table 1. Some structural characteristics of *Nasutitermes* nests in the várzea. "Attachment" indicates how the nest is attached to the tree/liana. "Orientation" gives the cardinal point towards which the nests are directed, and "Gallery width" gives the range and typical values for each species. Difference to total N is based on nests where the attachment point was not discernible from the ground.

	N	Attachment			Laterally attached to tree trunk	Orientation					Gallery width (cm)	
		In branch bifurcation	Branch bifurcation + lianas	Trunk and liana crossing		None	N	S	O	W	Variability	Typical width
<i>N. corniger</i>	92	71	12	1	0	62	20	7	2	1	0.5-10	1-4
<i>N. tatarendae</i>	21	3	14	2	0	13	2	2	3	1	1-5	2-3
<i>N. macrocephalus</i>	27	7	2	8	0	15	9	2	1	0	1-10	2-4
<i>N. surinamensis</i>	5	2	0	0	1	0	4	1	0	0	1-15	² 10
<i>N. ephratae</i>	6	3	0	0	1	1	4	0	0	1	0.5-10	1-5

Table 2. Average nest volume of *Nasutitermes* species of the várzea and average height of the nests above ground in the study site, Ilha de Marchantaria, Central Amazonia (means \pm 99 % confidence interval; data from MARTIUS et al. 1994b).

	All nests	<i>N. corniger</i>	<i>N. macrocephalus</i>	<i>N. surinamensis</i>	<i>N. ephratae</i>	<i>N. tatarendae</i>
n	130	92	6	5	6	21
Volume (l nest ⁻¹)	69.75 \pm 27.84	35.36 \pm 41.40	350.80 \pm 121.52	405.41 \pm 323.92	118.59 \pm 89.97	46.34 \pm 67.85
Height above ground (m)	5.11 \pm 0.50	4.92 \pm 0.58	7.13 \pm 2.03	7.60 \pm 3.12	3.77 \pm 0.99	5.33 \pm 1.24



Figure 1. Surface structure of a nest of *Nasutitermes corniger* ("simple" type).

INPA). Some of the termite species from the várzea are not yet described, the "codes" attributed to them in the key (preliminary morphospecies classifications) are identical to those under which they are deposited in the INPA collection.

3. Results and discussion

3.1 Nest architecture of *Nasutitermes* termites

All *Nasutitermes* nests of the várzea floodplain are arboreal, but they typically differ in architecture, size, and height above ground at which they are attached to trees. Two basic architectural models can be distinguished, the "simple" and the "envelope" type. Nests of *Nasutitermes corniger* and *N. tatarendae* belong to the simple type, where the external nest wall is identical with the outer wall of the outermost single nest chambers. Thus, the surface of these nests is "bumpy" (fig. 1). The termites extend their nest by simply adding new chambers on the top of existing chambers.

In contrast, in the case of *N. ephratae*, *N. macrocephalus* and *N. surinamensis*, the external nest wall is a thin cartonaceous sheet that is only loosely attached to the underlying nest structure. The underlying chambers are open to the external side, and only covered by the sheet. Therefore, parts of this sheet can be removed in large "plaques" from the nest without effort (fig. 2), and the nests of this type exhibit typical "growth zones" (fig. 3). In this nest type, apparently, nest growth is achieved by adding new external chambers under the protective external sheet, or the sheet is opened before along some ridges, the growth zones. Here, the wall is then added to.

The differences between the two groups appear to be species-specific, although deviations from this pattern may be seen in nests that have survived larger external injuries from falling branches, attack by parrots or ants, flooding, etc. (MARTIUS 1989). In most nests, however, these nest characteristics can be used for field identification of the nest-building species. In two species, *N. corniger* and *N. ephratae*, the morphological differences between soldiers are very weak, and identification based on the characteristic nest surface is often more reliable. THORNE (1980) and BECKER (1972) have made similar observations for other species. Therefore, a field key to the species of Ilha de Marchantaria, the studied várzea island, was developed based on nest characteristics (see below).

Other structural characteristics of the nests also show species-specific differences (tab. 1). Generally, nests of *N. ephratae* and *N. surinamensis* are laterally attached to large trees, whereas the nests of *N. corniger*, *N. tatarendae* and *N. macrocephalus* are associated with a bifurcation of branches in smaller trees (fig. 4). The mechanism by which the royal couple selects these bifurcations during nest establishment is not known, but one can speculate that ridges and other bark irregularities or detritus accumulated in such bifurcations provide a better shelter than the plain tree trunk. Also, the bifurcation provides a better mechanical hold for the nest which in these species is often only loosely attached to the stem surface. Additional features are lianas that may run through the nest (tab. 1). Often, nests were found that were not sitting in a bifurcation but on a spot where a liana crossed the unbranched tree trunk. I have listed these cases separately because lianas are abundant and seem to play a role in linking nests together (calies, see below).

Laterally attached nests may actually surround the trunk when they grow to adult size. They are much more firmly attached to the tree surface.

In black water floodplains (igapó, JUNK 1997), *Nasutitermes* nests were found in trees containing central voids in their stems (MARTIUS 1989). However, this was not the case in the várzea, maybe due to the fact that very few such trees were found in the investigated sites.

Galleries

In all species, differences in size were observed in the galleries leading downward and upward from the nest. The galleries leading upward generally consisted only of one runway which was 0.5 to 1.0 cm wide in the smaller species, and up to 2 cm wide in the larger species, whereas the downward leading galleries often consisted of several parallel runways. The latter was the case in *N. surinamensis*, where the parallel runways were over- and undersecting each other in a 10-15 cm wide extension of the nest (tab. 1). Width



Figure 2. Surface structure of a nest of *Nasutitermes ephratae* ("envelope" type).

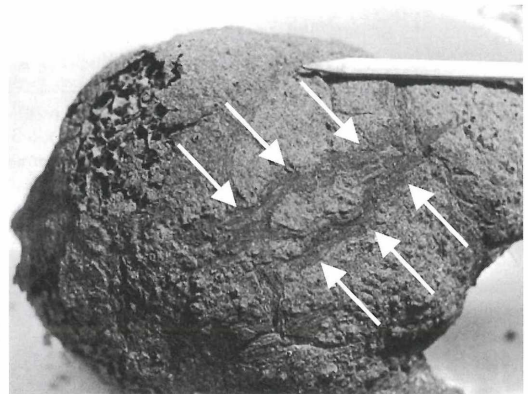


Figure 3. "Growth zone" on surface of a nest of the "envelope" type".

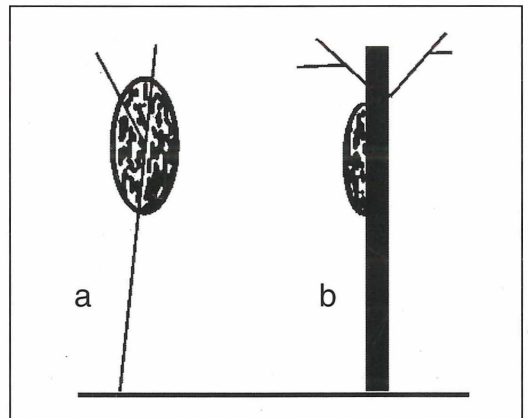


Figure 4. Central (a) and lateral (b) attachment of termite nests to trees.

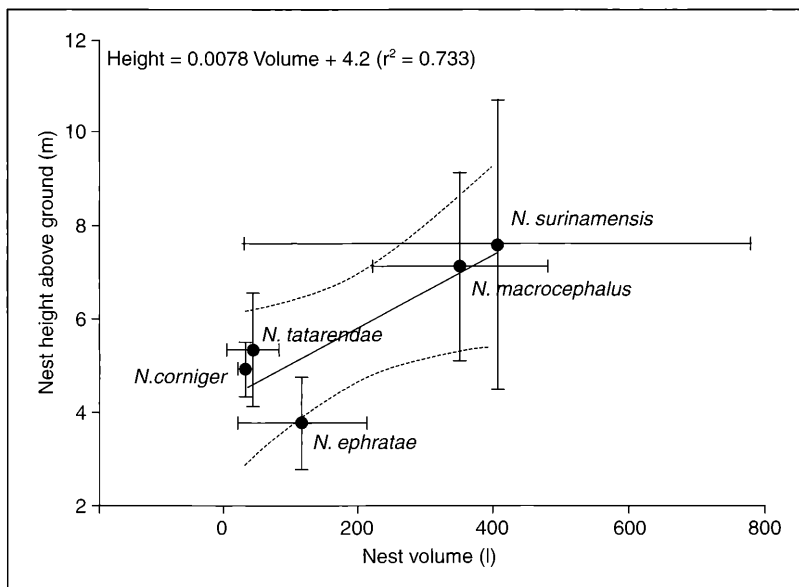


Figure 5. Correlation between average nest volume of each species (l) and the average height above ground in nests of five *Nasutitermes* spp. of the study site, Ilha de Marchantaria.

Table 3. Tree species with nests of *Nasutitermes* spp. in the study site, Ilha de Marchantaria and frequency of use by termites. Trees on which several nests were found were counted only once. Importance Value Indices (IVI) of the tree species were determined in a near-by stand (WORBES et al. 1992)

Tree taxon	n	IVI
<i>Laetia corymbulosa</i>	18	35.3
<i>Allophylus amazonicus</i>	16	
<i>Crataeva benthamii</i>	16	56.8
<i>Guarea trichiloides</i>	9	
<i>Casearia aculeata</i>	5	9.5
<i>Zanthoxylum compactum</i>	3	
<i>Tabebuia barbata</i>	3	
<i>Vatairea</i> sp.	3	
<i>Gustavia augusta</i>	2	
<i>Cecropia latiloba</i>	2	17.2
<i>Vitex cymosa</i>	2	23.8
<i>Pithecolobium</i> sp.	2	
<i>Pseudobombax munguba</i>	1	
<i>Astrocaryum jauary</i>	1	
<i>Crescentia amazonica</i>	1	
<i>Crudia amazonica</i>	1	
<i>Cordia</i> sp.	1	
<i>Ficus</i> sp.	1	
<i>Ilex</i> sp.	1	
<i>Luehea</i> sp.	1	24.0
<i>Rheedia</i> sp.	1	
Liana (undet.)	4	
Undet. spp.	13	5.5
Dead tree (undet.)	4	
Sum (140 nests)	111	

and height of the galleries seem to depend on the size of the termites, because galleries of 0.5 cm width were only found in the smaller species, *N. corniger* and *N. ephratae*.

Most (50 - 70 %) of the nests of *N. corniger*, *N. tatarendae* and *N. macrocephalus* were not orientated towards any compass cardinal point ("none" in table 1). Most of the nests of all five species showing an orientation were directed towards the north, but in *N. tatarendae* all cardinal points were equally frequent. Orientation to north may be related with less solar exposure of the nest.

Nest size

Nasutitermes corniger and *N. tatarendae* had small nests (volumes below 50 litres per nest), nests of *N. ephratae* were somewhat larger on average, and *N. macrocephalus* and *N. surinamensis* had very large nests with volumes around 350-400 l (tab. 2). THORNE & NOIROT (1982) recorded values for 129 nests of *N. corniger* in Panama, their largest nest having a volume of 54 l, much below the volumes recorded for the largest nests in the present study (2 nests with a volume of 210 l).

Nest height above ground

Nest height above ground is linearly correlated to nest volume ($R^2 = 0.733$; fig. 5). The nests of *Nasutitermes ephratae* are generally positioned lower in the forest than the other nests; those of *N. surinamensis* and *N. macrocephalus* are highest up in the trees.

Nesting trees

Fifty-nine of the 111 investigated nesting trees belonged to only four species (tab. 3). We did not



Figure 6. Polydomous nest of *Nasutitermes tatarendae*, the parts being linked by galleries on a liana.

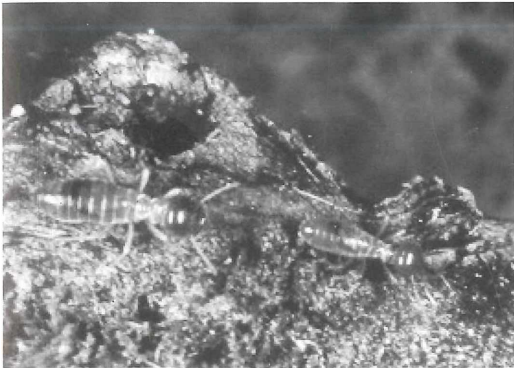


Figure 7. Soldiers and workers of *Nasutitermes macrocephalus*.

assess the tree species density on that site, but the Importance Value Indices (IVI) of the tree species in a near-by stand (WORRES et al. 1992; given in table 3) indicate that although the tree species with the highest IVI, *Crataeva benthamii* and *Laetia corymbulosa* are among the four most termite colonized, the termite distribution on the trees does not totally reflect tree dominance. This may indicate that founding couples actively select trees. The difference between termite occupation on *L. corymbulosa* and *C. benthamii*, for example, could be due to the fact that the former, although less dominant in the stand, has a rougher bark structure, which could facilitate the survival of the royal couple on this tree.

Polycalism

Interactions between the termites of neighboring nests were not observed, but evidence from other studies suggests that a strong intraspecific aggression between termites from different colonies exists (cf. ESENTER 1980, LEVINGS & ADAMS 1984, STUART 1963). Therefore, I assumed nests occurring on the same

tree or on neighboring trees linked with lianas (fig. 6) as belonging to one colony. This is also based on the observation that these nests were always linked with galleries. table 4 lists all nests from one census of the assemblage (June 17, 1985) for which those links could be confirmed. At least 57 of 100 nests were not autonomous but represented parts (calies) of polycalic nests. In *N. corniger* alone, the percentage was higher (43 of 69 nests, 62.3 %) indicating that this species in particular often develops polycalic nests. On average, 3.2 calies belong to one colony (2.9 in *N. corniger*). Most often double nest colonies were observed ($n = 8$), i.e. colonies consisting of two calies occurring on one tree. One colony of *N. tatarendae* consisted of 10 calies on several trees that were connected by one liana; two of the calies were found directly at the point where the liana, making loops, touched itself. This is a much lower number than the 37 nests of *N. corniger* recorded by LEVINGS & ADAMS (1984) and ADAMS & LEVINGS (1987) that belonged to one colony covering 0.8 ha in a mangrove forest in Panama. However, all gallery connections between calies in the mangrove forest with its open canopy were on the ground, making it easier for these authors to document all links between different calies. In the Marchantaria forest

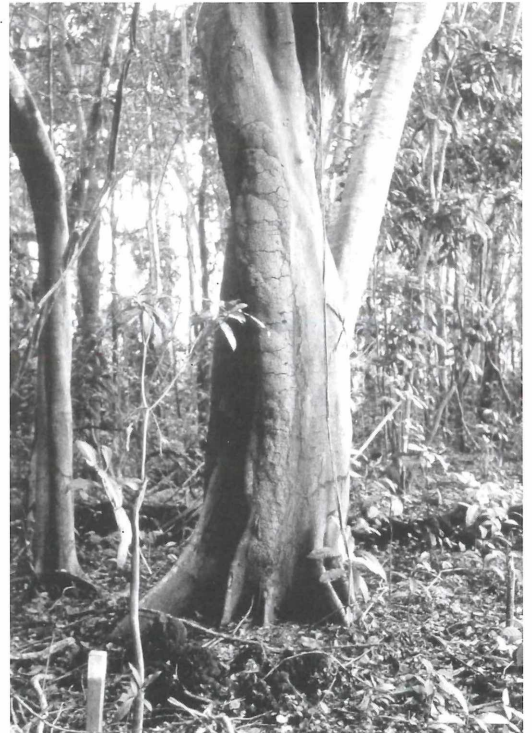


Figure 8. Nest architecture of *Anoplotermes* sp. "A" (cf. MARTIUS 1997).

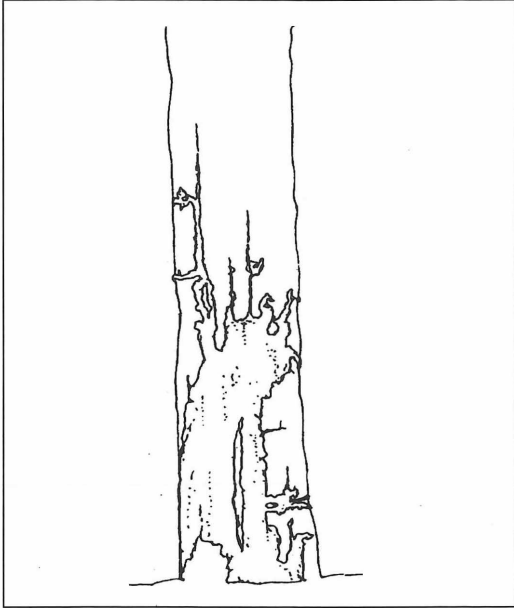


Figure 9. Nest architecture of Apicotermitinae, *Anoplotermes* sp. "D" (cf. MARTIUS 1989).



Figure 10. Habitus of a nest of *Nasutitermes corniger* that has an irregular shape due to attack by ants (*Dolichoderus bispinosus*; cf. MARTIUS 1994b).

where the canopy is closed many such connections occurred in the canopy, and the recorded numbers of calies per colony, based on confirmed connections, are to be considered minimum values. Based on nest mapping, further potential links are possible; e.g. it is possible that the two *N. tatarendae* colonies B and C, or even all 16 calies of this species (B, C, and C') belonged to one colony. If this is the case, this colony would have occupied an area of about 600 m². Much larger assemblages of calies have been observed in *Nasutitermes* species of Papua New Guinea by LEPONCE et al. (1997).

Polycalism seems to be genetically fixed (ROISIN & PASTEELS 1987), and one can hypothesize that this may have several adaptive advantages: The termites may be able to avoid the critical swarming phase through "vegetative budding", a colony separated in different nests may better survive attacks of raiding ants. The species more prone to polycalism, *N. corniger*, is dominant in the studied várzea plots, a pioneer ecosystem with high predatory pressure. Also, it may be an advantage to forage in a large territory from several dispersed nests instead of from one central nest. The larger multi-nest colonies occupy territo-

Table 4. Confirmed and potential polycalism in *Nasutitermes* colonies of the study site, Ilha de Marchantaria (only colonies in which polycalism was observed are listed here)

Species	Colony Code	no. of nests per one colony	
		confirmed	potential maximum colony Size
<i>N. ephratae</i>	A	2	
<i>N. tatarendae</i>	B	10	B+C: 12
<i>N. tatarendae</i>	C	2	
<i>N. tatarendae</i>	C'	4	
<i>N. corniger</i>	D	3	
<i>N. corniger</i>	E	2	
<i>N. corniger</i>	F	2	
<i>N. corniger</i>	G	2	G+H: 5
<i>N. corniger</i>	H	3	
<i>N. corniger</i>	I	3	I+K: 7
<i>N. corniger</i>	K	4	
<i>N. corniger</i>	L	4	
<i>N. corniger</i>	M	2	
<i>N. corniger</i>	N	3	
<i>N. corniger</i>	O	4	
<i>N. corniger</i>	P	2	
<i>N. corniger</i>	Q	4	
<i>N. corniger</i>	R	3	
<i>N. corniger</i>	S	2	
	All		<i>N. corniger</i> only
Sum of Nests	57		43
Sum of Colonies	18		15
Average nest no. per colony	3.17		2.87

ries of up to 600 m² (tab. 4) which corresponds to the territory size controlled by the larger, non-polycalic species like *N. surinamensis* or *N. macrocephalus*.

The construction of secondary nests can, however, also be a reaction to environmental stress as it occurs in a seasonally flooded floodplain. Sometimes, termite nests have been constructed below the high water level of the coming flood, and then, the construction of secondary nests higher up in the tree could be observed in several cases. When the waters cede, the old nest is often re-integrated into the colony system, and the colony has thus won a second nest. Often, the form of these secondary nests built under extreme circumstances differ considerably from the original design. In these cases, identification of the species based on nest characters alone might be misleading to the non-specialist.

3.2 Identification of termite species in the field

The analysis of the *Nasutitermes* assemblage of the várzea floodplain on Ilha de Marchantaria resulted in following findings:

- 1) The dominant species in terms of nest number is *Nasutitermes corniger*, in terms of nest volume *N. macrocephalus* and *N. surinamensis* gain more weight.
- 2) Nest architecture, size and height of the nests above the ground are species-specific characters that are useful for identification of the species in the field. The nests of *Nasutitermes corniger* and *N. tatarendae* are relatively small (about 50 l volume per nest); those of *N. macrocephalus*, *N. surinamensis* and *N. ephratae* are larger (120 - 400 l volume). Only secondary nests built after catastrophic events that destroyed the original nest, are of different, often simpler structure.
- 3) *Nasutitermes corniger* and *N. tatarendae* may form multi-nest (polycalic) colonies that generally consist of 2-3 but may comprise up to 10 or more nests, occupying territories of up to 600 m². This corresponds to the territory size controlled by the larger species, as determined by measurements of total gallery extension.

In the following, a key to the termite species on Ilha de Marchantaria was developed that is based on easily observable external characters and should allow identification of the original nest builder species in the field. Although the species composition in other floodplain forests of Amazonia can be quite different (e.g. in Juruá, CONSTANTINO 1992; cf. also MARTIUS 1994b) the key might be of help in future studies of termite ecology in white water inundation forests in central Amazonia, actually a center of research on the várzea ecosystem (JUNK 1997).

Finally, a few cautionary notes: the termite species found in a nest is not always the one which originally built it (APOLINÁRIO 1993, MARTIUS 1989). Nests and



Figure 11. Surface of a nest of *Nasutitermes macrocephalus* (diameter left to right about 30 cm).

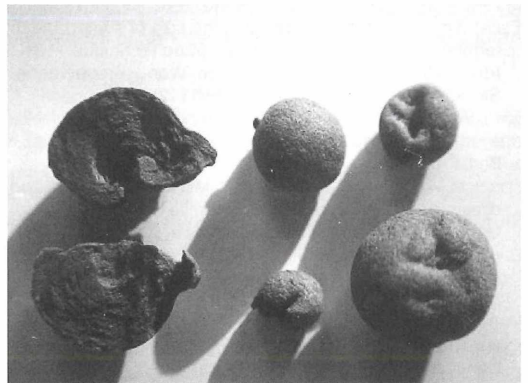


Figure 12. Roundly shaped conglomerates that are typically found in nests of *Nasutitermes macrocephalus* (cf. MARTIUS 1993).

termites should thus be identified separately. Other termites (*Rhinotermes* sp., *Coptotermes* sp.) do not build external nests but live within dead wood (MARTIUS 1997); these are not included to in the key. The following key is based on material collected during an inventory of termites in the years 1985 - 1992 on and around the island Ilha de Marchantaria.

4. Literature

- ADAMS, E. S. & LEVINGS, S. C. (1987): Territory size and population limits in mangrove termites. – *J. Animal Ecol.*, **56** (3): 1069-1081.
- APOLINÁRIO, F. B. (1993): Composição faunística e hábitos de nidificação de térmitas (Insecta: Isoptera) em floresta de terra firme da Amazônia Central. – 72 pp.; Master thesis, INPA/FUA, Manaus.
- BECKER, G. (1972): Termiten im Regenwald des Magdalenenstromtals in Kolumbien. – *Z. Angew. Entomol.*, **70** (2): 120-133.
- BUSTAMANTE, N. C. R. & MARTIUS, C. (1998): Nutritional preference of wood-feeding termites inhabiting floodplain forests of the Amazon river, Brazil. – *Acta Amazonica*, **28** (3): 301-307.
- CONSTANTINO, R. (1992): Abundance and diversity of termites (Insecta: Isoptera) in two sites of primary rain forest in Brazilian Amazonia. – *Biotropica*, **24** (3): 420-430.
- CONSTANTINO, R. (1998): Catalog of the living termites of the New World (Insecta: Isoptera). – *Arq. Zool.*, **35** (2): 135-231.
- ESENTER, G. R. (1980): Estimating the size of subterranean termite colonies by a release-recapture technique. – IRG (International Research Group on Wood Preservation, Stockholm), Document No. IRG/WP/1112: 6 pp.
- JUNK, W. J. (1997): The Central-Amazonian floodplain: ecology of a pulsing system. – *Ecological Studies* **126**: 525 pp.; Berlin (Springer).
- LEPONCE, M., ROISIN, Y. & PASTEELS, J. M. (1997): Structure and dynamics of the arboreal nesting termite community in New Guinea coconut plantations. – *Biotropica*, **29**: 193-203.
- LEVINGS, S.C. & ADAMS, E. S. (1984): Intra- and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. – *J. Animal Ecol.*, **53**: 705-714.
- MARTIUS, C. (1989): Untersuchungen zur Ökologie des Holzabbaus durch Termiten (Isoptera) in zentralamazonischen Überschwemmungswäldern (Várzea). – 285 pp.; Dissertation Univ. Göttingen; Frankfurt (Afra-Verlag).
- MARTIUS, C. (1993): Food provision storing by xylophagous termites in Amazonia (Isoptera: Nasutitermitinae). *Entomol. Gener.*, **17** (4): 269-276.
- MARTIUS, C. (1994a): Diversity and ecology of termites (Isoptera) in Amazonian forests. – *Pedobiologia*, **38**: 407-428.
- MARTIUS, C. (1994b): Termite nests as structural elements of the Amazon floodplain forest. – *Andrias*, **13**: 137-150.
- MARTIUS, C. (1997): The Termites. – In: JUNK, W. J. (ed.): The Central-Amazonian floodplain: ecology of a pulsing system. *Ecological Studies*, **126**: 361-371; Berlin (Springer-Verlag).
- ROISIN, Y. & PASTEELS, J. M. (1987): Caste developmental potentialities in the termite *Nasutitermes novarumhybridarum*. – *Entomologia Experimentalis et Applicata* **44**: 277-287.
- STUART, A. M. (1963): The origin of the trail in the termites *Nasutitermes corniger* (MOTSCHULSKY) and *Zootermopsis nevadensis* (HAGEN), Isoptera. – *Physiol. Zool.*, **36**: 69-84.
- THORNE, B. L. (1980): Differences in nest architecture between the neotropical arboreal termites *Nasutitermes corniger* and *Nasutitermes ephratae* (Isoptera, Termitidae). – *Psyche*, **87**: 235-243.
- THORNE, B. L. & NOIROT, C. (1982): Ergatoid reproductives in *Nasutitermes corniger* (MOTSCHULSKY) (Isoptera: Termitidae). – *Intern. J. Insect Morphol. Embryol.*, **11**: 213-226.
- WORBES, M. (1986): Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. *Scripta Geobotanica*, **17**: 1-112.
- WORBES, M., KLINGE, H., REVILLA, J. & MARTIUS, C. (1992): A contribution to the dynamics, structure and distribution of várzea forest in Central Amazonia. – *J. Veget. Sci.*, **3**, 553-564.

Appendix

Field key to the nest-building termite species of central Amazonian várzea floodplains

1. Nest made of soil matter; long (up to a height of 6 m) "columns" of soil attached to one side of a tree trunk (fig. 8) or shallow soil sheath covering tree trunk entirely up to a height of 12 - 14 m (fig. 9). No termite soldiers (soldierless termites), worker termites are generally small and of dark grey color
 - Nest round or ellipsoid in shape, sometimes very irregularly so, but never as in (1). Nests generally made of "carton" (digested wood) (figs 1 - 3). When disturbed, small orange red- or dark-headed "nasute" soldiers (fig. 7) appear quickly
 - Anoplotermes* (Apicotermitinae) 2
 - Nasutitermes* (Nasutitermitinae) 3
2. Soil nest is a column attached to one side of a tree trunk, being up to 6 m high, 10 - 15 cm deep, 10 - 20 cm wide at breast height, the top of the column often broadening into a wider "head" which reaches beyond the (coming) flood level (nests are rarely found at the beginning of the dry season, termites are subterranean during the dry period and start the epigeal (above-soil) constructions before the coming flood; nests attain highest size shortly before the flood)
 - Soil constructions are shallow (0.5-0.8 cm thick) sheaths of soil which cover the lower parts of a tree trunk up to a height of 12 - 14 m (they probably are covered feeding places of bark-feeding termites which have subterranean nests during the dry season).
 - Anoplotermes* sp. "A" 4
 - Anoplotermes* sp. "D" 5
3. The outer nest wall is a thin cartonaceous coverage which can be easily lifted off the nest in large plaques ("envelope" type; see above; cf. fig. 2); the surface often shows "growth zones" (fig. 3); generally only one and often large nest
 - Nest surface cannot be lifted off as a thin sheet, appearance is "bumpy" ("simple" type; see above; cf. fig. 1) without any growth zones; often several nests on neighboring trees are connected by "galleries" (covered runways). Nests are generally (but not necessarily) small. 6
4. Small to moderately large nests, generally laterally attached to a tree trunk. Termites: small brown-headed nasute soldiers and small workers.
 - Nasutitermes ephratae* (HOLMGREN)
 - Moderately large to large (tab. 2) nests generally built in a branch bifurcation of a tree. Termites: orange- or red-headed nasute soldiers and relatively large workers 5
5. Nest of dark grey to brown color, often connected by a 10 - 15 cm wide "highway" gallery to the ground. External nest surface of the "envelope" type. Termites: Soldier head reddish brown, slender, long pointed nose; workers very large
 - Nasutitermes surinamensis* (HOLMGREN)
 - Nest of a light brown to reddish-brown color, only narrow (3-4 cm) galleries leading to the ground. Surface "envelope" type, as in figure 11. Inside sometimes compact concretions of fecal matter are found which are of lighter color than the surrounding nest material (fig. 12). Nests often on a single tree in the outermost area of the forest where the flood lasts longer. Termites: Soldier head of lighter orange color than *N. surinamensis*, head broadly rounded, nose stout (fig. 7), head covered with numerous bristles (detectable only at a higher magnification), workers smaller than in *N. surinamensis*
 - Nasutitermes macrocephalus* (SILVESTRI)
6. Soldier termites small, soldier head dark chestnut brown, head broadly rounded, nose stout (head very slightly broader and stouter than in *N. ephratae*); small workers. The most common termites found in the várzea forest. Occur often in "polycalic" colonies (colonies with several interconnected nests, fig. 6)
 - Nasutitermes corniger* (MOTSCHULSKY)
 - Soldier termites small, although somewhat larger than those of *N. corniger*; soldier head reddish brown, in shape similar to *N. corniger*; workers smaller than in *N. surinamensis* and *N. macrocephalus*. Rare species, although sometimes occurring in "polycalic" colonies
 - Nasutitermes tatarendae* (HOLMGREN)

ANDREA RUF

Stoffumsatzleistungen in Böden historisch alter und rezenter Laubwälder im niedersächsischen Flachland

Zusammenfassung

In Waldböden sind nicht nur chemische und physikalische Eigenschaften für die Bodenbiözönose wichtig, sondern auch die Dynamik der organischen Streuauflage. Diese kann durch die Erfassung von Variablen aus dem Stickstoff- und Kohlenstoff-Kreislauf charakterisiert werden. Untersucht wurden dazu vier Bodendauerbeobachtungsflächen im Niedersächsischen Flachland, die Probenahme fand vier mal jährlich über zwei Jahre statt (1998 – 2000). Der Abbau von Zellulose und die Stickstoffmineralisationsleistungen wurden ein mal ermittelt. Über Korrelationskoeffizienten wurden die Zusammenhänge zwischen den Variablen, die ein Maß für die Versauerung sind, dem historischen Alter der Wälder und den Endprodukten der Stickstoff-Mineralisation dargestellt. Es ergaben sich keine deutlichen Zusammenhänge zwischen dem Grad an Versauerung und den Abbauleistungen. Der Ammonium-Gehalt war positiv mit der Menge an organischem Material und negativ mit dem mikrobiellen Zelluloseabbau gekoppelt. Es konnte keine Förderung mikrobieller Leistungen durch Ammonium festgestellt werden. Bildung von Nitrat und die höchsten N-Umsatzraten wurden nur in ehemals als Acker genutzten Standorten nachgewiesen. Die Kontinuität des Lebensraums des Waldbodens in den historisch alten Wäldern war ein wichtiger Einflussfaktor für die N-Mineralisation.

Abstract

Decomposition and mineralisation processes in forest soils of two ancient and two recent deciduous woodlands in north-west Germany

The soil fauna community in forest soils is not only determined by soil physical or chemical characteristics but also by the dynamics of the litter layer. Such small-scale dynamic processes can be characterized by variables of the nitrogen and carbon cycle. These were studied in four deciduous forest sites included in the soil monitoring programme of Niedersachsen, Germany. The forests are located in the North-West German lowlands on acid sandy soils. Sampling for soil variables was realized eight times during two years (1998 to 2000). Decomposition of cellulose and N-mineralisation were measured once simultaneously at each site. Correlation coefficients showed the relationships between the variables describing acidification and the historical age of the forests, and the end products of nitrogen mineralisation. There was no detectable influence of pH or Cation - Aluminium ratio to any of the decomposition process variables. The ammonium content was positively correlated with the total weight of soil organic matter and negatively correlated with the microbial decomposition of cellulose. None of the microbial decomposition variables was enhanced by ammonium. Nitrate as the end product of the N-mineralisation could only be detected at those two forests, that have been planted on arable fields 170 years ago. These sites are also characterized by the most efficient N-mineralisation and an elevated $d^{15}N$ value in the mineral soil. That means that the

continuation of undisturbed forest floor conditions in the ancient woodlands had a remarkable influence on nitrogen mineralisation

Autorin

Dr. ANDREA RUF, Universität Bremen, FB 2, UFT, Abteilung Allgemeine und Theoretische Ökologie, Leobenerstr., Postfach 330440, D-28334 Bremen.

Key words

decomposition, mineralisation, nitrification, acidification, eutritification, ancient woodlands, soil monitoring

1. Einleitung

Waldböden stellen einen Lebensraum für Bodentiere und Bodenmikroorganismen dar. Das wichtigste Stratum für Bodenorganismen im Wald ist die organische Auflage. Diese bietet Nahrung, Porenraum, Rückzugsräume zum Schutz vor Räubern, Strukturen zur Ei- und Spermatophorenablage, sie ist gepuffert gegen Temperatur- und Feuchteschwankungen und sie ist in den meisten Wäldern räumlich und zeitlich konstant und vorhersagbar vorhanden. Die organische Auflage ist aber nicht nur Umwelt für Bodenorganismen, sondern sie selbst ist geprägt und bestimmt durch die biotischen Kompartimente im Ökosystem Wald, von den Bäumen, die das Substrat zur Verfügung stellen, bis hin zu der saprophagen Makrofauna (z.B. Regenwürmer und Asseln), die die heruntergefallene Streu zerkleinert und frisst. Die organische Auflage wird auch als Reaktor bezeichnet, da hier die Umsetzungsprozesse von komplexen organischen Verbindungen zu mineralischen Ionen und der Umbau zu Huminstoffen stattfinden. Je effektiver der Stoffabbau geschieht, desto weniger konstant ist der Lebensraum für Bodenorganismen, insbesondere für diejenigen, die ihr ganzes Leben innerhalb der Streuschicht verbringen, wie die Bodenmikroarthropoden. Daher ist die Charakterisierung der Effektivität des Ab- und Umbaus organischer Substanz eine wichtige Eigenschaft des Lebensraums der Bodenmikroarthropoden. Da ein ganzes Gefüge an Umweltvariablen damit verknüpft ist, kann die Stoff- und Abbaudynamik als Schlüsselvariable für das Vorkommen und die Artenzusammensetzung der Bodenmikroarthropoden betrachtet werden.

Die Effektivität des Streuabbaus kann durch den Masseverlust autochthoner Streu in Netzbeuteln gemessen werden, ein anderer Ansatz ist die Messung einzelner Funktionen, z.B. die Ammonifikation, die Stickstoffmineralisation oder der Zelluloseabbau. Netzbeutel mit Streu werden sinnvollerweise über mehrere Jahre exponiert, Methoden, die einzelne Funktionen erfassen, liefern schneller Auskunft über die Stoffumsatzdynamik in Waldböden und erlauben eine differenziertere Aussage. In einer explorativen Phase der Charakterisierung der Abbauprozesse in Waldböden wurde die Stickstoffmineralisierung und der Zelluloseabbau an vier Bodendauerbeobachtungsflächen im Niedersächsischen Flachland untersucht. Ziel war es, erste Einblicke in standortspezifische bodenmikrobiologische Prozesse und Leistungen zu erhalten und Zusammenhänge mit dem Versauerungsgrad und dem historischen Alter der Wälder herauszuarbeiten.

In der Landschaft im Niedersächsischen Flachland herrschen außerhalb der Marschen und Moore sandige Substrate mit sauren Bodenverhältnissen vor. Laubwälder weisen meist Moder- bis Rohhumus als Humusform auf. Bei der inselhaften Verbreitung von Wäldern fällt besonders auf, welche Standorte schon immer bewaldet waren und welche nicht. Die historisch alten Waldstandorte (nach der Definition in WULF & KELM (1994) wurden früher meist als Hudewälder genutzt (d.h. durch Haustiere beweidet) und zeichnen sich durch bizarre, viele Jahrhunderte alte Eichen oder Hainbuchen aus. Dagegen gibt es auch Wälder, die im 19. Jahrhundert auf degenerierten Heiden oder Äckern neu angelegt wurden. Der Vergleich der historisch alten mit den im 19. Jahrhundert angepflanzten Wäldern bietet die Gelegenheit, lange Sukzessionsreihen hinsichtlich der Streu- und Bodenentwicklung zu untersuchen.

Die Stickstoffdynamik wird im Zusammenhang mit der Eutrophierungsproblematik (ABER et al. 1989, BERG et al. 1998) diskutiert. Dabei werden verschiedene Stadien der Stickstoffsättigung unterschieden, die u.a. an der Mineralisationsleistung erkannt werden können. Diese wird aber meist nicht explizit untersucht, sondern lediglich das Sickerwasser im Vergleich zum Traufwasser analysiert (ARBEITSKREIS C, 2000). In einer Langzeitstudie im Solling konnte gezeigt werden, dass sich organisches Material seit 1973 akkumuliert hat (MANDERSCHIED & MATZNER 1996). Parallel zum gesteigerten Eintrag an mineralischen Stickstoffverbindungen lässt sich also auch eine Anreicherung von Kohlenstoff-Verbindungen auf und in dem Waldboden beobachten. Daher schien es sinnvoll, beide Aspekte, den N-Stoffwechsel und den Abbau von Zellulose (C-Stoffwechsel) zu untersuchen.

Die Mineralisierung von organischen Stickstoffverbindungen verläuft über mehrere Stufen. Es sind verschiedene Enzyme unterschiedlicher Mikroorganismen beteiligt. Die ersten Abbauschritte der organi-

schen Stickstoffverbindungen sind unspezifisch und können von einer ganzen Reihe von Mikroorganismen geleistet werden. Spezifisch und kritisch zugleich ist die Oxidation von Ammonium zu Nitrit und weiter zu Nitrat. Ammonium ist ein positiv geladenes Ion und bindet sehr gut an Huminstoffe, Tonminerale und andere organische Verbindungen. Es ist daher im Boden wenig mobil und wird im Sickerwasser nur in geringen Konzentrationen gefunden. Ammonium kann von Pflanzenwurzeln aufgenommen werden und dient als N-Quelle. Beim Eintrag von N-Verbindungen über die Luft stellt Ammonium den größten Anteil (BMELF 1997). Auch Nitrat kann von Pflanzenwurzeln aufgenommen werden, es ist aber als negativ geladenes Ion mobil in der Bodenlösung und wird leicht ausgewaschen. Die Oxidation von Ammonium zu Nitrat wird von Bakterien geleistet, die pH-Wert abhängig sind und bei niedrigen pH-Werten nicht mehr arbeiten können. Daneben gibt es aber auch eine pH-Wert unabhängige Nitrifikation, die von autotrophen und/oder heterotrophen Mikroorganismen durchgeführt wird. Welche Arten dabei beteiligt sind, ist noch nicht geklärt. In sauren Waldböden stellt sich daher die Frage, ob Nitrifikation stattfindet oder ob die Mineralisation beim Ammonium stehenbleibt und welche anderen Lebensraumeigenschaften damit gekoppelt sind.

2. Material und Methoden

2.1 Standorte

Untersucht wurden vier Standorte im Niedersächsischen Flachland, die auch im Boden-Dauerbeobachtungsprogramm des Landes enthalten sind. Es waren die Standorte Ihlow bei Aurich (IHEI, BDF-14), Ehrhorn in der Hohen Heide (EHEI, BDF-2), Lüss in der Süddeide (LSBU, BDF-3) und Góhrde (GDEI, BDF-13). Auf allen Standorten stehen relativ naturnahe Laubwälder. Zwei der untersuchten Wälder, Lüss und Góhrde, sind historisch alt im Sinne von WULF & KELM (1994), die anderen zwei wurden noch am Ende des 18. Jahrhunderts als Acker genutzt und später aufgeforstet (Ihlow und Ehrhorn). Die wichtigsten Eigenschaften sind in Abbildung 1 und Tabelle 1 dargestellt.

2.2 Probennahmen

Die Probennahme erfolgte achtmal in einem Zeitraum von annähernd zwei Jahren. Beginn der Untersuchung war im April 1998 und Ende im Januar 2000. Proben wurden in ca. drei-monatigem Abstand an jedem Standort nacheinander entnommen. Für jeden Standort gibt es also Proben aus jeder Jahreszeit aus zwei aufeinanderfolgenden Jahren.

Die organische Auflage der Wälder wurde mit Hilfe eines quadratischen Stahl-Stechrahmens mit 25 cm Kantenlänge beprobt. Die Horizonte L, O₁, O₂ wurden getrennt eingesammelt. Der darunterliegende Mineralboden wurde in der gleichen Fläche mit einem zylindrischen Schlagbohrer mit einem Durchmesser von 7,3 cm beprobt. Dabei wurden zwei Tiefen unterschieden: 0-4 cm und 4-8 cm. Pro 25 x 25 cm² Fläche wurde der Mineralboden zweimal beprobt. Pro Termin und Stand-

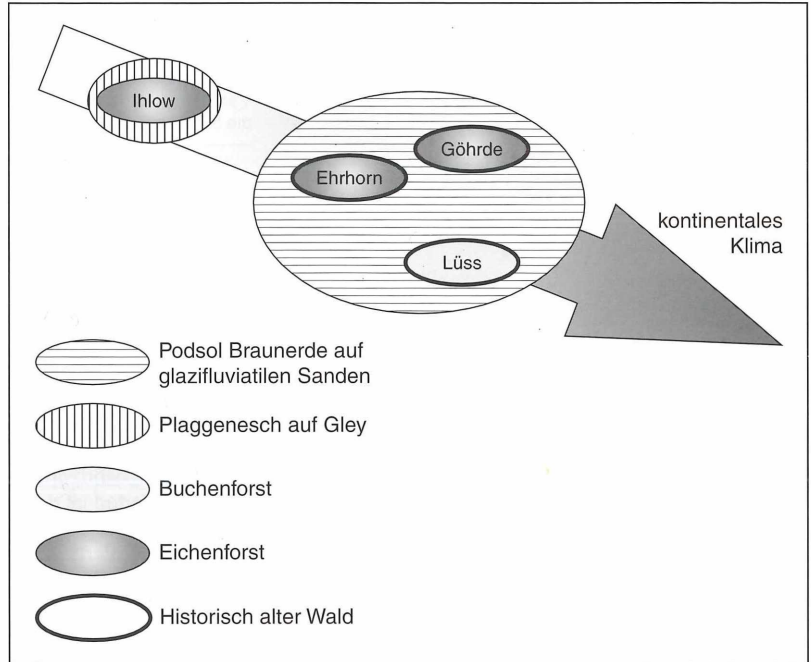


Abbildung 1. Schematische Darstellung der geographischen Lage und der wichtigsten Unterschiede bzw. Gemeinsamkeiten der untersuchten vier Waldstandorte.

Tabelle 1. Wichtige Standorteigenschaften der untersuchten Wälder nach Angaben der Niedersächsischen Forstlichen Versuchsanstalt (NFVA), Göttingen

	Höhe über NN [m]	dominante Baumart	Bestandesalter	Nutzung um 1790	Humusform
Ihlow	3	Stieleiche	145 Jahre	Acker	rohhumusartiger Moder (2)
Ehrhorn	109	Traubeneiche	120 Jahre	Acker	typischer Moder (1)
Lüss	115	Buche	120 Jahre	Wald	Moder – Rohhumus (3)
Gohrde	97	Traubeneiche	110 Jahre	Wald	Möder – Rohhumus (3)

ort wurden vier Proben aus der Streu und entsprechend 8 Proben aus dem Mineralboden entnommen.

Im Labor wurde das Frischgewicht bestimmt, dann die Proben luftgetrocknet und ein Aliquot bei 105°C getrocknet. Die organischen Proben wurden in einer Mühle zerkleinert, die mineralischen durch ein Sieb mit 1 mm Maschenweite gesiebt. Der Gehalt an organischer Substanz wurde durch Veraschen bei 500°C und der pH-Wert in 0,1 molarer CaCl₂ Lösung mit einer Elektrode bestimmt.

2.3 Bestimmung der mikrobiellen Leistung

Zelluloseabbau

Ein rundes Filterpapier (Trockenmasse 323 mg, ³ 70 mm, Schleicher & Schuell, 589², Weißband) wurde in Gaze verschiedener Maschenweite eingeschlossen und im Freiland in der oberen F-Schicht exponiert. Die groben Beutel hatten eine Maschenweite von ca. 0,5 cm, die feinen eine Maschenweite von 25 µm. Alle Beutel verblieben drei Monate lang am Standort, die groben von Juli bis Oktober 1999, die feinen von Oktober 99 bis Januar 2000. Nach der Entnahme im Frei-

land wurde die übriggebliebene Zellulose aus den Netzbeuteln bei 105°C getrocknet und bei 500°C verascht. Damit wurde das aschefreie Trockengewicht bestimmt und aus der Expositionsdauer der tägliche Masseverlust der Zellulose errechnet.

N-Mineralisierung

Die Stickstoffmineralisierung wurde im aeroben Brutversuch nach BECK (1983), abgewandelt in Anlehnung an die Referenzmethode der eidgenössischen Forschungsanstalten (B-NM-BA), gemessen. Es wurden die beiden Horizonte der organischen Auflage, O₁ und O₂, sowie der obere Mineralboden untersucht. Die Einwaage naturfeuchten Bodens war 5 g (O₁), 7 g (O₂) und 10 g (Mineralboden). Im weiteren Verlauf wurde entsprechend der schweizerischen Anleitung verfahren. Die Inkubation wurde abweichend davon bei 15°C im Kühlraum durchgeführt.

Nitrat und Ammonium Konzentrationen wurden im 2M KCl Extrakt mit HPLC gemessen.

Die Menge an ¹⁵N Isotopen wurde im oberen Mineralboden (0 – 4 cm) mit Hilfe eines Massenspektrometers bestimmt. d¹⁵N gibt den Unterschied im Anteil des schwereren Stickstoffisotops

Tabelle 2. Übersicht über die gemessenen und die von der Niedersächsischen Forstlichen Versuchsanstalt (NFVA) erhaltenen Variablen.

	eigene Messungen	NFVA
Humusform		X
pH-Wert in CaCl ₂	X	X
C/N Verhältnis		X
Menge org. Substanz (kg / ha)	X	
Gehalt an org. Substanz (kg / ha)	X	
Nitrifizierungsgrad (NO ₃ / N _{min} tot) [%]	X	
Gehalt NH ₄ (mg / kg TG)	X	
Gehalt NO ₃ (mg / kg TG)	X	
BC / AI (0-10 cm)		X
Abbau feine NB, mg / d	X	
Abbau grobe NB, mg / d	X	
Nitrifizierungsgrad der Mineralisation [%]	X	
N-Mineralisation mg N / d / kg TG	X	
d ¹⁵ N (in 0 – 4 cm)	X	

tops (¹⁵N) am gesamten Stickstoff der Probe zu einem Luftstandard an.

Da alle vier Flächen im Dauerbeobachtungsprogramm in Niedersachsen enthalten sind, führte die Niedersächsische Forstliche Versuchsanstalt (im Folgenden: NFVA) ausführliche Untersuchungen und Analysen dazu durch. Einige Variablen konnten so mit meinen Messungen verglichen werden, andere konnten in die Auswertung mit aufgenommen werden. Eine Übersicht über die selbst erhobenen und die von der NFVA übernommenen Variablen gibt Tabelle 2.

Statistik

Signifikanz-Tests und die Berechnung der Korrelationen wurden mit dem Programm SPSS für Windows Version 9.0 durchgeführt.

3. Ergebnisse

3.1 Standorteigenschaften

Menge an organischer Substanz in den Horizonten
Aus Abbildung 2 wird deutlich, dass sich die Standorte in der Verteilung der organischen Substanz im Bodenprofil unterscheiden. Während Ehrhorn und Göhrde eine geringe Auflage aufweisen und v.a. in Göhrde eine Anreicherung von organischer Substanz im Mineralboden messbar ist, sind die Verhältnisse in Ihlow und Lüss umgekehrt. Hier ist die meiste organische Substanz in der Auflage vorhanden und im Verhältnis dazu deutlich weniger im Mineralboden. Ehrhorn zeigt insgesamt die geringsten Menge an organischer Substanz, gefolgt von Lüss und Ihlow.

Tabelle 3. Angaben über die räumliche und zeitliche Variabilität des pH-Wertes im O₁-Horizont. Die Variabilität des pH-Wertes im O₁ Horizont war am höchsten im Vergleich zu den anderen Horizonten der organischen Auflage. Angabe des Variationskoeffizienten in %, für die räumliche Variabilität ist die Spanne über alle Probenstermine angegeben.

	zeitliche Variabilität Variationskoeffizient n = 8	räumliche Variabilität Variationskoeffizient n = 4	Median VK
Ehrhorn	9	2 – 7	5
Ihlow	8	2 – 5	3
Lüss	9	3 – 6	5
Göhrde	5	1 – 5	3

pH-Werte

Die gemessenen pH-Werte weisen alle vier Standorte als sehr sauer aus (Abb. 3). Der niedrigste Mittelwert wurde im O_n-Horizont in Lüss mit 2,7 gemessen. An allen Standorten ist der O_n-Horizont der sauerste, gefolgt vom oberen Mineralboden. Weiter nach unten steigt der pH-Wert wieder leicht an. Die größten Unterschiede in der Horizontabfolge waren in Lüss zu verzeichnen, hier lag der Mittelwert der L-Schicht bei 4,5, die Differenz zum niedrigsten Wert im O_n Horizont betrug 1,8 pH-Wert Einheiten. Göhrde zeigte den ausgeglichsten Verlauf, selbst in der obersten Streuschicht betrug der pH-Wert nur 3,8 und er sank im gesamten Profil nicht unter 3,0. Auffallend ist die geringe Spanne des Konfidenzintervalls, die die relativ geringe Schwankung des pH-Wertes in der Zeit dokumentiert. Die geringsten Schwankungen zeigten die Mineralbodenhorizonte, während die O₁-Schicht am stärksten variabel war. Die Variationskoeffizienten zwischen 5 und 9 % in diesem Horizont bei allen Standorten sind allerdings auch nicht sehr hoch (Tab. 3). Auch die räumliche Variabilität des pH-Wertes zu einem Probenzeitpunkt ist gering, die Variationskoeffizienten schwanken lediglich zwischen 1 und 10 %, wobei die höchste Variabilität im Mineralboden zu messen war. In der organischen Auflage war die höchste räumliche Variabilität im O₁-Horizont, sie lag hier zwischen 1 und 7 % (Tab. 3).

Gehalt an Stickstoffverbindungen im Boden

An allen Standorten bis auf Ihlow war die höchste Konzentration von mineralischen Stickstoffverbindungen im O₁-Horizont der organischen Auflage, in Ihlow war die höchste Konzentration im O_n Horizont (Abb. 4)

An den beiden Standorten Göhrde und Lüss konnte kein Nitrat nachgewiesen werden. In Ihlow und Ehrhorn lag der Anteil von Nitrat an der Gesamtmenge mineralischen Stickstoffs dagegen über 50% (Tab. 4). In Ihlow war insgesamt die höchste Konzentration an mineralischem Stickstoff zu messen, am Standort Göhrde die niedrigste, Lüss und Ehrhorn lagen dazwischen.

Abbildung 2. Menge an organischer Substanz in den unterschiedenen Horizonten bzw. Schichten des Mineralbodens. Angegeben sind die Mittelwerte über alle 8 Probenstermine.

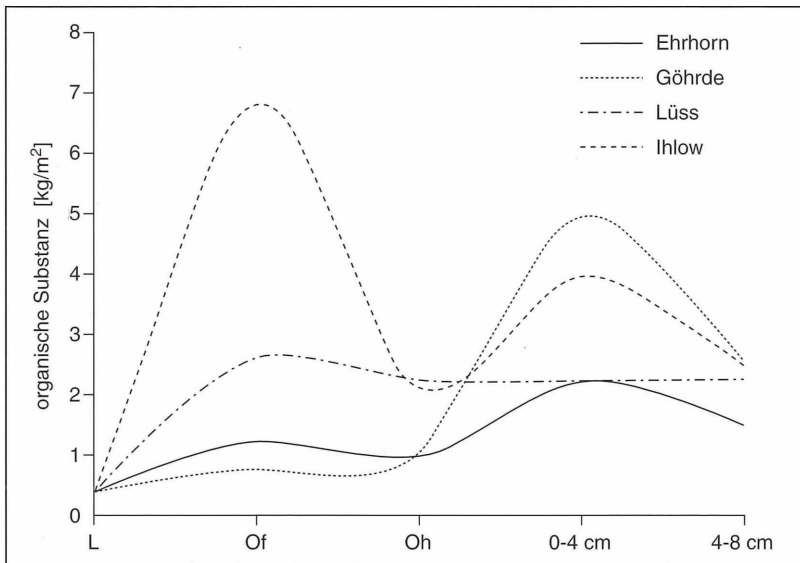


Abbildung 3. Die pH-Werte gemessen in CaCl₂ als Mittelwerte über 4 bzw. 8 Proben je Probenahme, gemittelt über 8 Termine in zwei Jahren. Die Fehlerbalken geben das 95% Konfidenzintervall über die 8 Probenahme-Termine an.

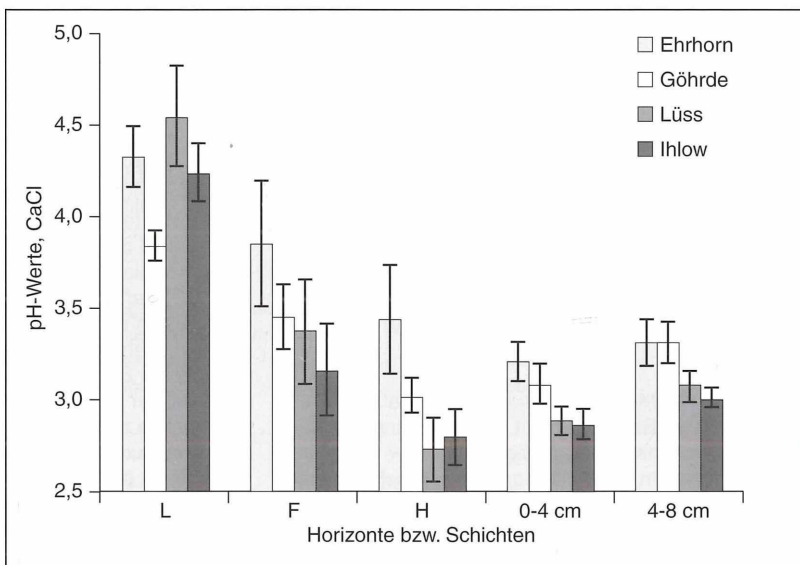


Tabelle 4. Gehalt an mineralischen Stickstoffverbindungen als Mittel aus allen untersuchten Horizonten. Angabe in mg pro kg Trockengewicht (ppm).

	NH ₄	NO ₃	Nitrifizierungsgrad [%]
Ehrhorn	6,8	9,9	59,3
Ihlow	36,1	47,2	56,7
Lüss	18,9	0	0
Göhrde	11,0	0	0

Tabelle 5. Menge von mineralischen Stickstoffverbindungen, die während einer 4 wöchigen Inkubationszeit im Labor bei 15°C gebildet wurde, getrennt nach Horizonten. Angabe in mg pro kg Trockengewicht (ppm), die Summe über den gesamten untersuchten Horizont ist in mg pro m² angegeben.

	O _i	O _h	0-4 cm	insgesamt [mg/m ²]
Ehrhorn	11,5	2,1	0,2	49,3
Ihlow	11,2	2,5	0,3	120,3
Lüss	3,6	0,7	-0,4	-1,1
Göhrde	4,9	2,0	0,1	16,0

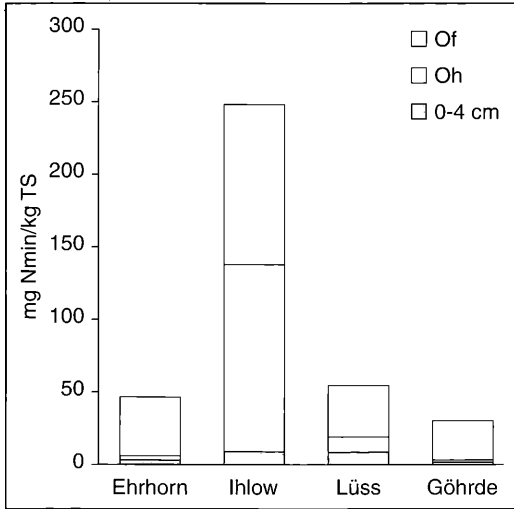


Abbildung 4. Gehalte an den mineralischen Stickstoffverbindungen Ammonium und Nitrat in den unterschiedenen Horizonten bzw. Bodenschichten.

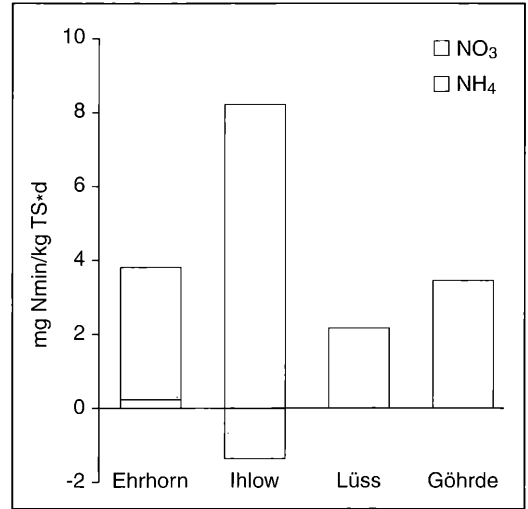


Abbildung 5. Menge von mineralischen Stickstoffverbindungen, die während einer vierwöchigen Inkubationszeit im Labor bei 15°C gebildet wurde als Mittelwert aus der organischen Auflage, getrennt nach Verbindungen. Angabe in mg pro kg Trockengewicht (ppm) pro Tag.

3.2 Umsatzleistungen

Stickstoffmineralisierung

In Ehrhorn und Ihlow war die Mineralisierungsleistung mehr als doppelt so hoch wie in Göhrde und Lüss (Abb. 5). Die Stickstoffmineralisierung pro Gramm Boden war an allen Standorten im Of-Horizont am höchsten (Tab. 5). Wegen der größeren Masse der organischen Auflage in Ihlow ist die tatsächliche Menge an Stickstoffverbindungen hier auch gegenüber Ehrhorn deutlich erhöht.

Zelluloseabbau

Der Beitrag der Makrofauna zum Zelluloseabbau war an den meisten Standorten mit der angewandten Methode nicht nachweisbar. Lediglich in Ihlow wurde in den Netzbeuteln mit der groben Maschenweite während des Sommers mehr Zellulose pro Tag abgebaut, als in den Netzbeuteln mit der feinen Maschenweite im Herbst und Winter (Tab. 6). An den anderen drei Standorten war die Abbauleistung in den Netzbeuteln mit der feinen Maschenweite sogar höher bzw. in Lüss war kein Unterschied zu erkennen. Der mikrobielle Zelluloseabbau war in Ehrhorn am höchsten (2,7 mg/d) und in Ihlow am niedrigsten (1,4 mg/d), die beiden anderen Standorte unterschieden sich kaum voneinander und hatten eine mittlere Abbauleistung (2,2 mg/d).

Die Übersicht in Tabelle 6 stellt die wesentlichen Eigenschaften der vier Standorte gegenüber. Deutlich werden die Gemeinsamkeiten im niedrigen pH-Wert und im sehr ungünstigen BC / AI Verhältnis. Aber auch Unterschiede in vielen Variablen, v.a. denen des N-

Stoffwechsels sind evident. Im C/N Verhältnis fällt vor allem Lüss auf, hier ist es sehr weit, günstig für mikrobiellen Abbau ist es dagegen in Ehrhorn und auch noch in Göhrde. Der Zusammenhang zwischen den Variablen wurde mit Hilfe einer Korrelationsanalyse ausgearbeitet. Die Ergebnisse sind in Tabelle 7 und Abbildung 6 dargestellt.

Keine Korrelationen bestehen zwischen dem pH-Wert, dem C/N Verhältnis und dem Zellulose-Abbau in den Netzbeuteln mit der groben Maschenweite und anderen Variablen. Ein wichtiger Faktor ist die Menge an organischer Substanz im gesamten untersuchten Profil. Diese war sehr eng mit der Abbauleistung in den feinen Netzbeuteln und mit dem Gehalt an Ammonium-Ionen korreliert. Auch die Menge an organischer Substanz in der Auflage hängt mit den Ammonium-Ionen und mit dem Gesamtgehalt an mineralischen N-Verbindungen eng zusammen. Es besteht eine deutliche Korrelation zwischen dem Gehalt an Ammonium-Ionen und dem mikrobiellen Abbau von Zellulose (Abbau in den Netzbeuteln mit der feinen Maschenweite), je mehr Ammonium vorhanden ist, desto langsamer verläuft der Abbau. Hohe Ammonium-Konzentrationen weisen demnach auf einen stagnierenden Abbau organischer Substanz (insbesondere Zellulose) hin. Einen zweiten Faktorenkomplex stellt die N-Mineralisierung, die Nitrifikationsrate, der Gehalt an Nitrat, das Alter und der Anteil an $d^{15}N$ dar. Die Bildung und der Gehalt an Nitrat (der Nitrifizierungsgrad) war mit der Mineralisationsrate verknüpft, so dass Nitrat eher als Indikator für die Intensität des Stickstoff-Stoffwechsels dienen kann.

Tabelle 6. Abbauleistung für Zellulose, N-Verbindungen, Variablen des N-Metabolismus und Versauerungszeiger an den vier Standorten. Die Gehalte an N-Verbindungen sind die Mittel über alle Horizonte, "BC" ist die Summe aller basischen Kationen an den Austauschern, "Al" die Aluminium-Belegung der Austauscher, "NB" steht für Netzbeutel.

	Ihlow	Göhrde	Lüss	Ehrhorn
Abbau feine NB, mg / d	1,42	2,23	2,22	2,71
Abbau grobe NB, mg / d	2,44	0,41	2,17	2,19
Humusform, NFVA	2,00	3,00	3,00	1,00
pH-Wert (0-10 cm), CaCl ₂ , NFVA	3,12	3,27	3,02	3,23
C/N (0-5 cm), NFVA	19,50	18,20	28,90	16,20
BC / Al (0-10 cm), NFVA	0,40	0,14	0,23	0,47
Menge org. Substanz (kg / ha)	15,70	9,60	9,70	6,10
Menge org. Subst. in der Auflage (kg / ha)	9,30	2,20	5,20	2,40
Nitrifizierungsgrad (NO ₃ / Nmin tot) [%]	56,70	0	0	59,30
Gehalt NH ₄ (mg / kg TG)	36,10	11,00	18,90	6,80
Gehalt NO ₃ (mg / kg TG)	47,20	0	0	9,90
Nitrifizierungsgrad der Mineralisation [%]	100,00	0	0	95,60
N-Mineralisation mg N / d / kg TG	4,90	2,30	1,30	4,60
d ¹⁵ N (in 0 – 4 cm)	5,30	0,40	2,20	2,20

Tabelle 7 Pearsons Korrelationskoeffizienten der angegebenen Variablen (aus Tab. 6). Es sind nur die Paare mit einer Irrtumswahrscheinlichkeit unter 0,05 angegeben ($p < 0,05$).

Variable 1	Variable 2	Pearsons Korrelationskoeffizient	p
Abbau feine NB	Menge an org. Substanz	-1,000	0,000
Abbau feine NB	Gehalt NH ₄	-0,962	0,038
Alter	Nitrifizierungsgrad	-1,000	0,000
Alter	Nitrifizierungsgrad der Mineralisation	-0,999	0,001
Alter	N-Mineralisation	-0,970	0,030
Gehalt N _{min}	Menge an org. Substanz in d. Auflage	0,980	0,020
Gehalt NH ₄	Menge an org. Substanz	0,964	0,036
Gehalt NO ₃	Gehalt N _{min}	0,979	0,021
Nitrifizierungsgrad	Nitrifizierungsgrad der Mineralisation	0,972	0,028
N-Mineralisation	Nitrifizierungsgrad der Mineralisation	0,972	0,028
N-Mineralisation	Nitrifizierungsgrad	0,967	0,033
BC / Al	Nitrifizierungsgrad	0,957	0,043
BC / Al	Alter	-0,952	0,048

Das Verhältnis basischer Kationen (BC) zu Aluminium-Ionen hängt andeutungsweise mit dem Nitrifizierungsgrad und der Humusform zusammen. Je niedriger das Verhältnis, desto mehr tendiert die Humusform in Richtung Rohhumus (Korrelation: -0,941, $p = 0,059$) und desto niedriger ist der Nitrifizierungsgrad (Abb. 6). Der pH-Wert ist mit keiner dieser Variablen korreliert.

Die beiden historisch alten Waldstandorte unterscheiden sich von den anderen beiden hauptsächlich durch den Nitrifizierungsgrad und zwar sowohl den der Mineralisation als auch der extrahierbaren mineralischen N-Verbindungen in der Of-Schicht, aber auch in der N-Mineralisation (Abb. 6) und im Verhältnis basischer Kationen zu Aluminium-Ionen (Tab. 7). Die alten Waldstandorte weisen kein Nitrat auf, haben geringere Mineralisationsraten und ein ungünstigeres BC/Al Verhältnis.

4. Diskussion

Die gefundenen Umsatzprozesse in den vier untersuchten Wäldern zeigen, dass die beiden mineralischen Stickstoffverbindungen (NH₄ und NO₃) für verschiedene Abbauprozesse stehen. Ammonium ist ein Indikator für einen stagnierenden Abbau bzw. für eine Anreicherung organischer Substanz, während Nitrat für die Intensität des Stickstoff-Stoffwechsels steht. Dabei sind die Ausgangsgehalte in der Auflage eng an die tatsächlich gemessene Mineralisierungsleistung geknüpft. An Standorten, an denen viel Nitrat in der Auflage nachgewiesen werden konnte, wird auch entsprechend viel Nitrat gebildet, ähnliches gilt für Ammonium. Die mineralischen Stickstoffverbindungen können also autochthon gebildet werden und es liegt kein

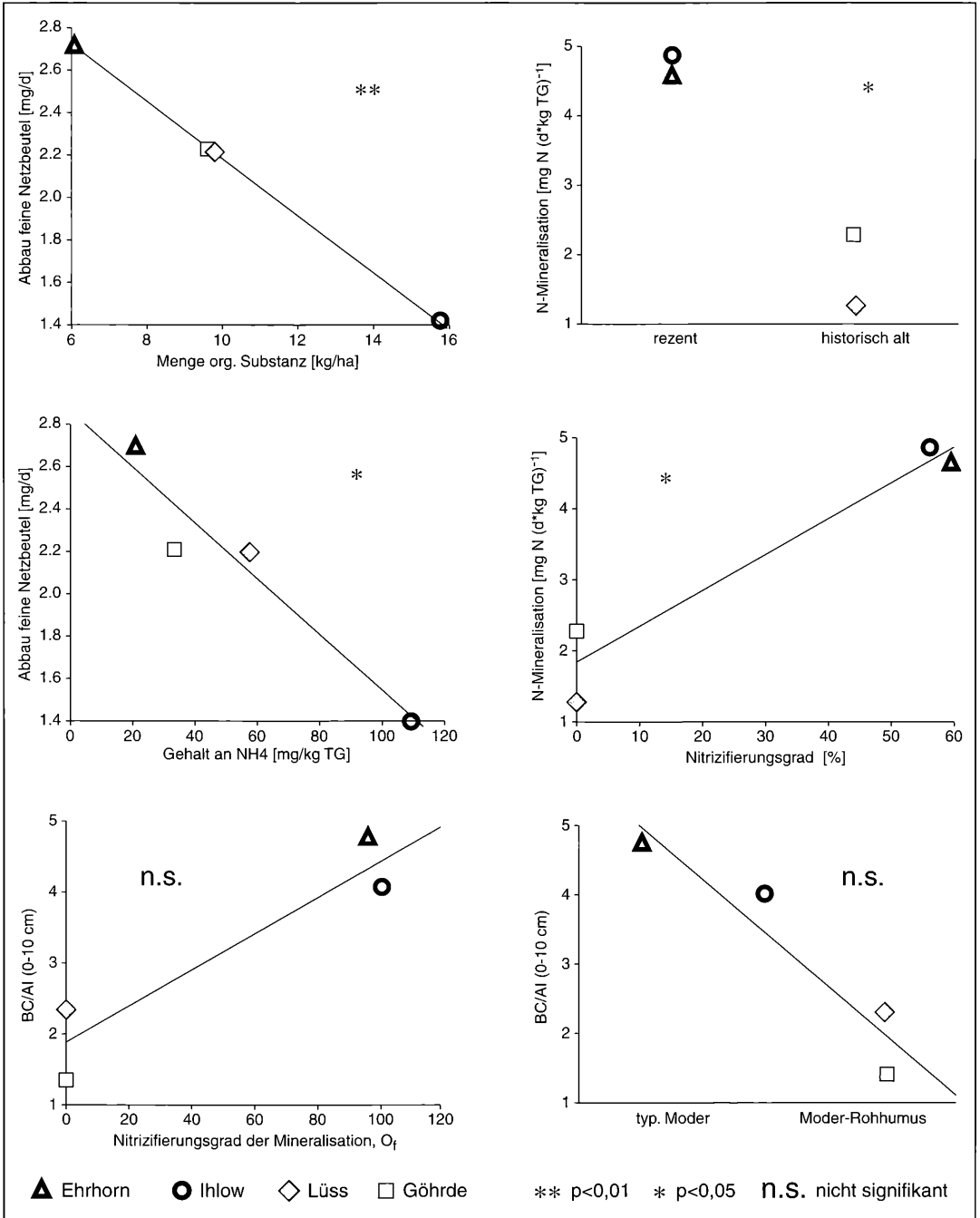


Abbildung 6. Ausgewählte Korrelationen zwischen verschiedenen Variablen der vier untersuchten Standorte. Angaben aus Tabelle, Korrelationskoeffizienten siehe Tabelle.

Hinweis auf einen wesentlichen Eintrag von aussen vor.

Die organische Auflage, der Humus eines Waldbodens wird von Seiten der Forstwirtschaft als Speicher und Quelle für Nährstoffe, besonders N-Verbindungen, angesehen (MANDERSCHIED & MATZNER 1996). Ein Austrag durch das Sickerwasser findet nur in Form von Nitrat statt. Die Nitratgehalte im Sickerwasser zeigen jedoch eine sehr große Schwankung zwischen den Jahren. Dafür wird die Variabilität biologischer Prozesse verantwortlich gemacht. Häufig wird vermutet, dass die Mineralisationsleistung an den Versauerungsgrad eines Bodens geknüpft ist (MANDERSCHIED & MATZNER 1996, KLEMEDTSSON et al. 1999). BERG et al. (1997) finden im Mittel höhere Nitrifikationsraten bei pH-Werten über 4,2 als in saureren Böden, jedoch sind die Schwankungen zwischen den Standorten so groß, dass keine Vorhersage über die tatsächlichen Nitrifikationsraten auf Grund des pH-Wertes möglich sind.

In den Nordwestdeutschen Wäldern war jedoch keine Variable, mit der der Versauerungsgrad gemessen werden kann, mit der N-Mineralisation gekoppelt. Lediglich der Nitrifizierungsgrad der Mineralisation hängt mit dem BC/Al Verhältnis zusammen. Der pH-Wert war in allen untersuchten Wäldern so niedrig, dass er die Unterschiede in der Mineralisationsleistung nicht erklären kann. Alle befinden sich im Aluminium-Puffer Bereich (ULRICH 1981), so dass in diesem Bereich offensichtlich keine Zusammenhänge mit dem pH-Wert bestehen.

KRIEBITZSCH (1978) untersuchte ebenfalls saure Wälder im nordwestdeutschen Flachland. Auch in dieser sehr ausführlichen Arbeit werden keine Zusammenhänge zwischen dem pH-Wert und der N-Mineralisation gefunden. Allerdings wird ein Zusammenhang zwischen C/N Verhältnis und Mineralisationsleistung nachgewiesen, der bei den lediglich vier untersuchten Wäldern nicht bestätigt werden konnte. KRIEBITZSCH (1978) interessierte sich für die Bedingungen, unter denen Nitrat gebildet wird. Auch er findet Nitratbildung in sehr sauren Böden und vermutet, dass dies ein Merkmal für ungestörte, natürliche Waldböden sei. Auf den vier Bodendauerbeobachtungsflächen wird nur in den historisch alten Wäldern kein Nitrat gebildet, während auf den ehemals gestörten Böden Nitrat produziert wird. Das widerspricht KRIEBITZSCH's Vermutung und könnte ein Hinweis auf eine frühere (Über-) Nutzung dieser Standorte sein (z.B. durch Waldweide oder Laubharken) oder ein Hinweis auf den engen N-Kreislauf in den historisch alten Waldböden.

Nach KLEMEDTSSON et al. (1999) könnte die Nitrifikation ebenfalls durch hohe Ammonium-Gehalte gehemmt sein. Das konnte in keinem der Wälder nachgewiesen werden. Viel Ammonium hemmt dagegen den Zelluloseabbau und wird in hohen Konzentrationen in den mächtigen Streuauflagen gefunden. In diesen ist wie-

derum die N-Mineralisation und der Nitrifizierungsgrad der Mineralisation höher. Es ist hier also eher der gegenläufige Prozess festzustellen, dass Ammonium keinen Einfluss auf die Bildung von Nitrat hat und sowohl die Ammonium-Gehalte als auch die Nitrifikationsrate in den mächtigen Streuauflagen höher sind. Einen ähnlichen Zusammenhang zeigen auch DE BOER et al. (1989) auf. Sie stellen hohe Nitrifikationsleistungen bei hohen Gehalten von mineralischen N-Verbindungen (vor allem NH_4) fest und sehr niedrige bei geringen Gehalten von N-Verbindungen. VITOUSEK et al. (1982) geben als Grenzwert, ab dem Nitrifikation einsetzen kann, 60 – 90 ppm N_{min} an. BLEW & PARKINSON (1993) konnten bestätigen, dass bei N_{min} Gehalten unter diesem Grenzwert in dem von ihnen untersuchten Wald in Kanada keine Nitrifikation stattfindet. Die Ergebnisse aus Ehrhorn widersprechen allerdings diesem Grenzwert, hier konnte Nitrifikation nachgewiesen werden, obwohl N_{min} kleiner als 50 ppm war. Die Nitrifikation scheint also noch von anderen Faktoren abhängig zu sein.

Welche Bedeutung haben die erhöhten Einträge von mineralischen Stickstoffverbindungen über die Luft und das Regenwasser? ABER et al. (1989) unterscheiden verschiedene Stufen der Reaktion von Waldböden auf diese N-Einträge. Unter N-Mangelbedingungen sollte in einem Moderhumus weniger als 50 % der gebildeten mineralischen N-Verbindungen Nitrat sein. Das trifft für die beiden Wälder Ihlow und Ehrhorn nicht zu. Zudem sollte bei pH-Werten niedriger als 4,2 keine Nitrifikation stattfinden, auch das trifft für Ehrhorn und Ihlow nicht zu. Ob das jedoch als Anzeichen einer N-Sättigung zu interpretieren ist, kann nicht entschieden werden. Unter N-Sättigungsbedingungen sollte sich der N-Anteil in den Blättern erhöhen. Ihlow hatte zwar das engste C/N Verhältnis in der L-Schicht, wurde jedoch von Göhrde sehr dicht gefolgt, wo keinerlei Nitrat nachgewiesen werden konnte. Dies ließ sich auch durch eine Nachuntersuchung bestätigen (LAMPE mündl.). Zudem sollte ein höherer Ammonium Gehalt zu höheren Nitrifikationsraten führen. Eine messbare Nitrifikation konnte nur in Ihlow und in Ehrhorn ermittelt werden. Ihlow hatte gleichzeitig auch die höchsten Ammonium-Gehalte, was der Vermutung entsprechen würde, Ehrhorn hatte jedoch die niedrigsten Ammonium-Gehalte bei vergleichbarer Nitrifikationsrate. Es gibt also keinen eindeutigen Hinweis für eine Steigerung der Nitrifikation mit dem Ammoniumgehalt.

Welche Rolle könnte das Alter der ungestörten Bodenentwicklung spielen? LEBRET et al. (2000) untersuchten Sukzessionsreihen unterschiedlich alter Wälder hinsichtlich ihrer Mikroorganismenzönose. Dabei wird deutlich, dass (entgegen der Anschauung) weder die Anreicherung von organischer Substanz, noch die Etablierung einer diversen Mikroorganismenzönose nach 90 Jahren abgeschlossen ist. MERILÄ & SMOLAN-

Tabelle 6. Vergleich der $\delta^{15}\text{N}$ -Werte aus dem oberen Mineralboden aus verschiedenen Untersuchungen.

	Koerner 1999	Jussy 1998	Ihlow	Göhrde	Lüss	Ehrhorn
historisch alter Wald	0,03	-0,32		0,4	2,2	
Ehemalige Weide	1,38					
ehemaliger Acker	1,63	1,69	5,3			2,2
Ehemalige Wiese	2,53					
ehemaliger Garten	3,82					

DER (2000) fanden in einem Pionierstadium mit Esche und Eberesche sehr hohe Nitrifizierungsraten, bei allen anderen Wäldern trat ausschliesslich Ammonium als Endprodukt der N-Mineralisierung auf. Es gibt also Hinweise darauf, dass die Etablierung einer waldbodentypischen Mikroorganismenzönose mindestens Jahrzehnte dauert und dass die Nitratbildung eine Erscheinung der früheren Sukzessionsphasen ist. Das spiegelt sich genau in den vier untersuchten norddeutschen Wäldern wider, hier allerdings in einem Zeitraum von 170 Jahren.

Der Gehalt an dem schwereren Stickstoff-Isotop ^{15}N wird von KOERNER et al. (1999) als Indikator für historisch alte Wälder angesehen, während HÖGBERG (1990) einen erhöhten Wert als Indikator für N Verluste bzw. geringe Werte als Zeichen für einen eng geschlossenen N-Kreislauf betrachtet. HÖGBERG betrachtet jedoch das ^{15}N Verhältnis in einer Pflanze, während KOERNER auch im Boden misst. Jedoch sollte sich das Verhältnis nicht ändern, lediglich die absolute Höhe des Wertes. Im Vergleich mit den Werten aus dem Elsass (KOERNER 1999, JUSSY 1998) in Tabelle 6 wird deutlich, dass lediglich Lüss nicht in das Bild passt und der Wert für Ihlow viel zu hoch ist. Zusammen mit den hohen Nitrat-Gehalten an dem Standort könnte man hier einen N-Verlust durch Auswaschung vermuten. Der $\delta^{15}\text{N}$ -Wert eignet sich nur bedingt als Indikator für historisch alte Wälder, er ist jedoch erhöht an Standorten, die ehemals anders genutzt waren. Gleichzeitig treten erhöhte Werte an den beiden Standorten mit Nitrifikation auf, wie auch KOBA et al. (1998) in ihren Untersuchungen zeigen konnten. Allerdings zeigt Lüss auch ohne Nitrifikation relativ hohe $\delta^{15}\text{N}$ -Werte.

Der Abbau und die Mineralisation von organischem Material, der Laubstreu auf dem Waldboden ist kaum von den Bodenbedingungen beeinflusst. Jedenfalls nicht in dem Spektrum von Standorteigenschaften, das in den vier Bodendauerbeobachtungsflächen im Niedersächsischen Flachland repräsentiert ist. Bei den vorgegebenen Bedingungen sind die Abbauvariablen untereinander korreliert, wobei die Menge an organischer Substanz in der Auflage und der Nitrifizierungsgrad der Mineralisation die wichtigsten Eigenschaften sind. Wesentliche Unterschiede hängen jedoch mit dem Alter der Standorte zusammen, ob sie

historisch alte Wälder sind oder neu angepflanzte (jünger als 200 Jahre). Dieser Aspekt wird in der Literatur jedoch nicht diskutiert, die Erforschung der Bedeutung der Lebensraum-Kontinuität über viele Jahrhunderte für Bodenorganismen steht erst am Anfang. Nach den vorliegenden Ergebnissen unterscheiden sich die Leistungen der Mikroorganismen in historisch alten Wäldern von denen in rezenten.

Danksagung

Die Informationen zu den Bodendauerbeobachtungsflächen hat freundlicherweise die Niedersächsische Forstliche Versuchsanstalt Göttingen zur Verfügung gestellt. Besonderer Dank gilt HENNING MEESENBURG und KARL-JOSEF MEIWES für die unkomplizierte Unterstützung mit Kartenmaterial und Wertetabellen. Die Leiter der zuständigen Forstämter haben die Arbeit ebenfalls unterstützt, dafür sei auch ihnen ganz herzlich gedankt. HEIDI KRIETE führte die Mineralisations-Versuche und N-Messungen im Labor durch, ELKE LAMPE stand für Rückfragen und Diskussion der Ergebnisse zur Verfügung, MONIKA SEGL übernahm die Organisation der Messung der N-Isotope. Die FNK der Universität Bremen fördert die bodenbiologischen Arbeiten an den Dauerbeobachtungsflächen im Forst. LUDWIG BECK hat mich durch sein andauerndes Bemühen um Verständnis von ökologischen Prozessen von Waldböden, das auf einer unvergleichlich reichen Anschauung beruht, ange-regt, auch Stoffumsatzprozesse in bodenbiologische Arbeiten mit einzubeziehen. Ihm sei besonders für die vielen Gespräche und Diskussionen am Binokular, am Rechner und besonders auf Exkursionen und bei Probenahmen vor Ort gedankt.

5. Literatur

- ABER, J. D., NADELHOFFER, K.J., STEUDLER, P. & MELILO, J. M. (1989): Nitrogen saturation in northern forest ecosystems. – *Bioscience*, **39**: 378-386.
- ARBEITSKREIS C DER BUND-LÄNDER ARBEITSGRUPPE LEVEL II (2000): Kennwerte zur Charakterisierung des ökochemischen Bodenzustandes und des Gefährdungspotentials durch Bodenversauerung und Stickstoffsättigung an Level II-Waldökosystem-Dauerbeobachtungsflächen. – 176 pp.: Bonn (Hrsg.: Bundesministerium für Ernährung, Landwirtschaft und Forsten).
- BECK, T. (1983): Die N-Mineralisation von Böden im Laborbrutversuch. – *Z. Pflanzenernähr. Bodenkd.*, **146**: 243-252.
- BERG, M. P., VERHOEF, H. A., BOLGER, T., ANDERSON, J. M., BEESE, F., COUTEAUX, M. M., INESON, P., MCCARTHY, F., PALKA, L., RAUBUCH, M., SPLATT, P. & WILLISON, T. (1997): Effec-

- ts of air pollutant-temperature interactions on mineral N-dynamics and cation leaching in replicate forest soil transplantation experiments. – *Biogeochem.*, **39**: 295-326.
- BERG, M. P., KNIESE, J. P. & VERHOEF, H. A. (1998): Dynamics and stratification of bacteria and fungi in the organic layer of a Scots pine forest. – *Biol. Fert. Soils*, **26**: 313-322.
- BLEW, R. D. & PARKINSON, D. (1993): Nitrification and denitrification in a white spruce forest in southwest Alberta, Canada. – *Can. J. For. Res.*, **23**: 1715-1719.
- BMELF, Bundesministerium für Ernährung, Landwirtschaft und Forsten (Hrsg.) (1997): Dauerbeobachtungsflächen zur Umweltkontrolle im Wald, Level II. – 148 pp.; Bonn.
- DEBOER, W., KLEIN GUNNEWIEK, P. J. A., TROELSTRA, S. R. & LAANBROEK, H. J. (1989): Two types of chemolithotrophic nitrification in acid heathland humus. – *Plant and Soil*, **119**: 229-235.
- HÖGBERG, P. (1990): Forests losing large quantities of Nitrogen have elevated $^{15}\text{N}/^{14}\text{N}$ ratios. – *Oecologia*, **84**: 229-231.
- JUSSY, J.H. (1998): Minéralisation, nitrification et prélèvement d'azote dans différents peuplements forestiers sur sol acide. – PhD thesis, Université de Nancy.
- KLEMEDTSSON, L., JIANG, Q., KASIMIR KLEMEDTSSON, A. & BAKKEN, L. (1999): Autotrophic ammonium-oxidising bacteria in Swedish mor humus. – *Soil Biol. Biochem.*, **31**: 839-847.
- KOBA, K., TOKUCHI, N., YOSHIOKA, T., HOBBI, E. A. & IWATSUBO, G. (1998): Natural abundance of nitrogen-15 in a forest soil. – *J. Soil Sci. Soc. America*, **62** (3): 778-781.
- KOERNER, W. (1999): Impactes des anciennes utilisations agricoles sur la fertilité du milieu forestier actuel. – PhD thesis, Université de Paris.
- KOERNER, W., DAMBRINE, E., DUPOUEY, J. L. & BENOIT, M. (1999): $\delta^{15}\text{N}$ of forest soil and understory vegetation reflect the former agricultural land use. – *Oecologia*, **121**: 421-425.
- KRIEBITZSCH, W.-U. (1978): Stickstoffnachlieferung in sauren Wäldern Nordwestdeutschlands. – *Scripta Geobotanica*, **14**: 1-66.
- LEBRET, M. N., PAREKH, R. & FORGEARD, F. (2000): Functional diversity of soil bacteria communities in a chronosequence of declining lowland beech. – *Eurosoils 2000: Abstracts*.
- MANDERSCHIED, B. & MATZNER, E. (1996): Spatial and temporal variability of soil solution chemistry and ion fluxes through the soil of a mature Norway spruce (*Picea abies* (L.) KARST.) stand. – *Biogeochem.*, **30**: 99-114.
- MERILÄ, P. & SMOLANDER, A. (2000): Nitrogen transformations along a primary succession transect on the land-uplift coast (Western Finland). – *Eurosoils 2000: Abstracts*.
- ULRICH, B. (1981): Ökologische Gruppierung von Böden nach ihrem chemischen Bodenzustand. – *Z. Pflanzenernähr. Bodenkd.*, **144**: 289-305.
- VITOUSEK, P. M., GOSZ, J. R., GRIER, C. C., MELILLO, J. M. & REINERS, W. A. (1982): A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecol. Monogr.*, **52** (2): 155-177.
- WULF, M. & KELM, H. - J. (1994): Zur Bedeutung "historisch alter Wälder" für den Naturschutz – Untersuchungen naturnaher Wälder im Elbe-Weser Dreieck. – *NNA-Berichte*, **7** (3): 15-49.

BERNHARD FÖRSTER

Streuabbau unter chemischem Stress: Potentielle Wirkung von Chemikalien am Beispiel des Fungizids Carbendazim

Zusammenfassung

Die Wirkung des Fungizids Carbendazim auf den Streuabbau wurde am Beispiel des Abbaus von Heu, Buchenlaubstreu und Cellulose untersucht. Carbendazim wurde in Labor-, Mikrokosmos- sowie in Freilandexperimenten in Konzentrationen zwischen der maximalen praxis-üblichen und der 100-fachen Dosis eingesetzt. Bei allen drei untersuchten Substraten bewirkte Carbendazim einen verzögerten Abbau, der im Wesentlichen auf die toxische Wirkung von Carbendazim auf Lumbriciden zurückzuführen war. Die Effekte auf den mikrobiellen Streuabbau waren weniger deutlich und quantitativ nur nachweisbar, wenn keine Regenwürmer am Streuabbau beteiligt waren. Mikroorganismen und Mesofauna konnten die fehlende Abbauleistung der Regenwürmer im betrachteten Zeitraum quantitativ nicht kompensieren.

Abstract

Litter decomposition influenced by chemical stress: Effects of the fungicide carbendazim

The impact of the fungicide carbendazim on the breakdown of organic matter was assessed by investigating the effects of carbendazim on the decomposition of hay, beech leaf litter and pure cellulose. Carbendazim was applied in laboratory, semi-field and field tests at concentration rates between the highest recommended application rate and the 100fold dosage. Carbendazim led to a reduced decomposition rate of all three substrates which was mainly caused by the toxic effect of Carbendazim on earthworms. Effects on the microbial litter decomposition appeared to be small and were detectable only if no earthworms were involved in the decomposition. Microorganisms and mesofauna could not compensate the falling feeding activity of earthworms within the experimental period.

Author

Dr. BERNHARD FÖRSTER, ECT Oekotoxikologie GmbH, Böttgerstr. 2-14, D-65439 Flörsheim am Main.

Key words

litter decomposition, fungicides, Carbendazim, earthworms, microbial respiration

1. Einleitung

Die Dekomposition von organischem Material durch Bodenorganismen stellt eine zentrale Funktion im Stoffkreislauf terrestrischer Ökosysteme dar (ALBERTI et al. 1996; BECK 2000). Als ein hoch integrierender Prozess unterliegt der Streuabbau zahlreichen Einflussfaktoren. Neben der Substratmenge und -qualität (C/N-Verhältnis,

Phenol- und Ligningehalt) bestimmen Klima (Niederschlagverteilung, Temperatur) und Bodeneigenschaften (pH, Porenraum, Wasserregime) die Abbaugeschwindigkeit der organischen Substanz (SWIFT et al. 1979).

Von herausragender Bedeutung ist jedoch der Einfluss der Bodenorganismen (BECK et al. 1988; CADISCH & GILLER 1997). Der Streuabbau resultiert aus einer komplexen Wechselbeziehung zwischen den Bodenorganismen von denen nach Biomasse und Anzahl die Pilze und Bakterien den überwiegenden Teil bilden. Ihre besondere Bedeutung liegt im Abbau und der Mineralisierung komplexer organischer Substanzen und in der damit verbundenen Freisetzung pflanzenverfügbarer Nährstoffe. Die Bodenfauna hat vor allem steuernde Funktionen. Ihre Fraßaktivität bewirkt sowohl einen teilweisen chemischen Aufschluss sowie die mechanische Zerkleinerung der Streu (Pelletierung) und damit eine Vergrößerung der Oberfläche, die von Mikroorganismen besiedelt werden kann. Infolge der Einarbeitung der Streu in den Boden, besonders durch Regenwürmer, gelangt das organische Material in ein für den Abbau günstiges Milieu (CORTEZ & BOUCHE 1998). Durch das Abweiden von Bakterien und Pilzhyphe regt die Bodenfauna das Wachstum der Mikroflora an (CADISCH & GILLER 1997).

Der Boden erweist sich auch als eine Senke für eine Vielzahl anthropogener Chemikalien (RÖMBKE & MOLT-MANN 1996). Sie gelangen entweder direkt (z.B. Agrochemikalien) oder indirekt in den Boden und stellen damit eine potenzielle Gefahr für zahlreiche ökosystemare Strukturen und Funktionen des Streuabbaus im terrestrischen Ökosystem dar.

Im Rahmen der Zulassung von Pflanzenschutzmitteln ist neuerdings für persistente Stoffe auch die Prüfung der Wirkung auf den Streuabbau erforderlich (KULA & RÖMBKE 1998). In den dazu durchgeführten Streuabbautests im Freiland wird das Fungizid Carbendazim als toxische Referenzsubstanz eingesetzt. Der Sinn einer toxischen Referenzsubstanz in ökotoxikologischen Tests ist es, eine möglichst deutliche und reproduzierbare Hemmung des betrachteten Endpunktes zu bewirken, hier also des Streuabbaus, um die Sensibilität des Testsystems zu dokumentieren. Die Wirkung einer zu prüfenden chemischen Substanz kann dann im Vergleich zur unbelasteten Kontrolle einerseits sowie zur Wirkung der toxischen Referenzsubstanz andererseits bewertet werden.

In der vorliegenden Arbeit wird die Wirkung des Fungizids Carbendazim auf den Abbau von Heu, Buchenlaubstreu und Cellulose in Labor-, Mikrokosmos- und Freilandversuchen untersucht. Die Ergebnisse werden vor dem Hintergrund der Eignung von Carbendazim als Referenzsubstanz für Streuabbauuntersuchungen diskutiert.

2. Material und Methoden

2.1 Chemischer Stressor

Carbendazim wurde in der Formulierung Derosal® (aktiver Wirkstoff Carbendazim, 360 g/l) verwendet. Aufgrund seiner fungiziden Wirkung wird Carbendazim in der Landwirtschaft gegen verschiedene Pilzkrankungen (z.B. im Getreide) eingesetzt. Carbendazim wirkt bereits bei niedrigen Konzentrationen toxisch auf Lumbriciden (LOFS-HOLMIN 1981, KULA 1994, RÖMBKE & FEDERSCHMIDT 1995). Die Wirkung auf andere Gruppen der Bodenfauna sowie der Bodenmikroflora ist weniger eindeutig (WAINWRIGHT 1977, KROGH 1991, MARTIKAINEN et al. 1998). In den hier beschriebenen Experimenten wurde Carbendazim in Konzentrationen verwendet, die der empfohlenen Aufwandsmenge von 0,18 kg aktiver Wirkstoff pro Hektar entsprach (C1) sowie den Konzentrationen 0,36 kg/ha (C2), 1,08 kg/ha (C6), 1,8 kg/ha (C10) und 18,0 kg/ha (C100).

2.2 Organische Substanz

Die Wirkung auf den Streuabbau wurde am Beispiel von Buchen-Falllaub (*Fagus sylvatica*), Heu (Talglatthaferwiese) sowie Cellulose untersucht. Das Laub und das Heu wurden an den jeweiligen Versuchsstandorten gewonnen und luftgetrocknet. Cellulose wurde als Filterpapier (Faltenfilter ϕ 70 cm, Schleicher & Schuell 595½) sowie als Carboxymethylcellulose-Pulver eingesetzt.

2.3 Messung des Streuabbaus

Der Streuabbau wurde über den Masseverlust auf Basis des aschefreien Trockengewichts bestimmt. Dazu wurden die Proben zunächst von Hand von anhaftenden Bodenpartikeln befreit und anschließend für 4-5 Stunden bei 560° C verascht. Zur Messung des Streuabbaus durch Mikroorganismen wurde die Basalatmung (CO_2 -Produktion) der Streu mit Hilfe einer automatischen Bodenatmungsmessanlage mit Infrarot Gasanalyse im kontinuierlichen Durchfluss bestimmt (FÖRSTER et al. 1995).

2.4 Versuchsplanung

Laborversuch (Nr. 1 und 4)

Zur Erfassung der Wirkung von Carbendazim auf die Mikroorganismen der Streumaterialien wurden Aliquots von 80 g Buchenlaubstreu (Versuch Nr. 1) bzw. 120 g Heu (Versuch Nr. 4) separat in 1,5 L Einmachgläser eingewogen und mit Carbendazim entsprechend der Dosis C1 und C100 gleichmäßig kontaminiert. Die Streu war eine Woche zuvor auf einen Wassergehalt von ca. 90 % der maximalen Wasserhaltekapazität eingestellt und danach bei 22°C im Dauerdunkel bebrütet worden. Nach Ansetzen des Versuchs wurden die Versuchsgefäße im Dunkeln bei 22°C inkubiert und die Basalatmung an Aliquots von 1 g (TS) nach 1, 4 und 8 Wochen bestimmt.

Laborversuch (Nr. 7a)

Aliquots von je 200 g feldfrischem Wiesenboden wurden gesiebt (2 mm), mit 4 mg bzw. 22 mg Cellulosepulver pro Gramm Boden vermischt und bei 22°C für 2 Wochen inkubiert. Die CO_2 -Produktion wurde nach einer und nach zwei Wochen bestimmt.

Laborversuch (Nr. 7b)

Aliquots von je 200 g feldfrischem Wiesenboden wurden gesiebt (2 mm), in 12 Glasgefäße (Volumen 0,3 l) eingewogen und je 3 Regenwürmer (*Eisenia fetida*) zugesetzt. In 4 Versuchsgefäßen wurde der Boden mit Carbendazim entsprechend der Dosis C2 kontaminiert. Cellulosepapier wurde im Boden für 6 Wochen bei 20°C im Dauerdunkel inkubiert.

Mikrokosmos (Nr. 2 und 5)

Aliquots von 2,0 kg feldfrischem Wiesenboden (Versuch Nr. 2) bzw. Buchenwaldboden (Versuch Nr. 5) wurden gesiebt (2 mm), in PVC-Rohre (h = 30 cm, d = 10 cm) gefüllt und je 5 Regenwürmer zugesetzt (*Lumbricus terrestris*). Heu bzw. Buchenlaub wurde in Netzbeuteln (5 mm Maschenweite) auf die Bodenoberfläche gelegt und mit Carbendazim in der Dosierung C10 in einer wässrigen Lösung auf die Streu appliziert. Die Mikrokosmen wurden bei 10°C für 4 Wochen im Dauerdunkel inkubiert.

Mesokosmos (Nr. 8a und b)

Die Mesokosmen bestanden aus intakten Bodenkernen mit einem Durchmesser von 17,5 cm und einer Höhe 40 cm (Abb. 1). Je 10 Bodenkern wurden auf einem Wiesenstandort (Versuch Nr. 8a) bzw. einem Ackerstandort (Versuch Nr. 8b) unter Beibehaltung der natürlichen Bodenstruktur und Bodenorganismen gewonnen und im Labor bei einer Bodentemperatur von 12-14°C aufbewahrt. Auf die Bodenoberfläche von je 4 Mesokosmen wurde Carbendazim entsprechend der Dosis C6 appliziert, je 6 Mesokosmen blieben unbehandelt und dienen als Kontrolle. Zur Erfassung des Streuabbaus wurde im Wiesen-Mesokosmos Cellulosepapier in den Oberboden vertikal eingesteckt bzw. im Acker-Mesokosmos auf die Bodenoberfläche gelegt und jeweils für 8 bzw. 12 Wochen inkubiert. Das Filterpapier für die kontaminierten Mesokosmen war durch Eintauchen in eine verdünnte Carbendazimlösung behandelt worden (entsprechend der Dosis bei Applikation auf die Papierfläche), während das Filterpapier für die Kontrollen in Wasser getaucht wurde.

Feldstudie (Nr. 3a)

Auf einer Wiese wurde je eine Parzelle von 100 m² Größe zweimalig im Abstand von 8 Wochen mit Carbendazim in der Dosis C1 bzw. C10 besprüht, eine dritte Parzelle diente als unbelastete Kontrolle. Je 4 g Heu wurde in Netzbeuteln mit einer Größe von 10 x 20 cm und einer Maschenweite von 5 mm auf der Bodenoberfläche für 28 Wochen exponiert.

Feldstudie (Nr. 3b und 3c)

Je 15 Netzbeutel mit einer Größe von 10 x 10 cm und einer Maschenweite von 5 mm wurden mit 4 g Heu befüllt und auf der Bodenoberfläche einer Wiese ausgelegt (Versuch Nr. 3b) bzw. in 5 cm Tiefe eingegraben (Versuch 3c). Nach 8 Wochen wurde der Gewichtsverlust ermittelt.

Feldstudie (Nr. 6)

In einem Eichen-Hainbuchenwald wurde ein Fläche von 240 m² Größe zweimalig im Abstand von 8 Wochen mit Carbendazim in der Dosis C1 besprüht, die benachbarte Fläche diente als unbelastete Kontrolle. Auf der Bodenoberfläche wurde Buchenlaubstreu in Netzbeuteln (Größe 20 x 30 cm, Maschenweite 10 mm) für 28 Wochen exponiert.

Feldstudie (Nr. 9)

Parallel zur Mesokosmos-Studie (Versuch Nr. 8a) wurde die Wirkung von Carbendazim am Entnahmestandort der Bodenkerne in einer Feldstudie untersucht. Dazu wurden 4 Parzellen von je 25 m² Größe mit Carbendazim in der Dosis C6 besprüht, weitere 6 Parzellen dienten als unbehandelte Kontrollen. Zur Bestimmung des Streuabbaus wurde Cellulosepapier für 4 bzw. 8 Wochen im Boden exponiert.

Feldstudie (Nr. 10)

Ein Jahr nach Applikation der Chemikalie im Feld wurde auf den Parzellen der Feldstudie (Versuch Nr. 9) erneut Cellulosepapier zur Erfassung des Abbaus ausgebracht. Das Filterpapier wurde dazu in Streifen von 2 mm Breite geschnitten und in Netzbeuteln mit 5 mm Maschenweite für 8 Wochen auf der Bodenoberfläche ausgelegt. Damit sollte geprüft werden, ob der im Vorjahr beobachtete Effekt durch Carbendazim anhält oder eine Erholung eingetreten war.

3. Ergebnisse und Diskussion

3.1 Abbau von Heu

Aufgrund seines N-Gehaltes stellt Heu ein attraktives Substrat für zahlreiche streuabbauende Organismen dar und unterliegt einem raschen Abbau (EDER et al. 1992). Dies spiegelt sich auch in der hohen mikrobiellen Atmungsaktivität der Streu im Laborversuch wider, die jedoch mit zunehmender Inkubationszeit der Streu abnimmt (Tab. 1). Der Grund dafür dürfte in der Abnahme an leicht verwertbaren Stoffen liegen, z.B. Aminosackern. Die Abnahme der Atmungsaktivität wurde auch bei Heu beobachtet, das in Netzbeuteln im Freiland exponiert war (FÖRSTER et al. 1992). AERTS & DE CALUWE (1997) fanden dagegen die Respirationsraten von Pflan-

zenstreu (*Carex*-Arten) im Labor mit dem Gewichtsverlust der Streu unter Feldbedingungen positiv korreliert. Im Feldversuch mit Expositionsbeginn im September (Versuch 3a) wurde auf der Bodenoberfläche exponiertes Heu in 28 Wochen zu 67 % abgebaut, während es bei einem Expositionsbeginn im Juni (Versuch 3b und 3c) bereits nach 8 Wochen nahezu vollständig abgebaut war (Tab. 2). Dabei hatte die Position der Netzbeutel, ob auf der Bodenoberfläche oder im Boden exponiert, offenbar wenig Einfluss auf die Abbaugeschwindigkeit. Auch CURRY (1969) fand in seiner Untersuchung keine unterschiedlichen Abbauraten von Wiesenstreu in oberirdisch exponierten oder eingegrabenen Netzbeuteln. Entscheidend ist jedoch die Feuchtigkeit. In der Regel wird Wiesenstreu im Boden schneller abgebaut (STEMMER et al. 1999). Auf der Bodenoberfläche trocknet die Streu schneller aus, wodurch sich der Abbau verzögert (MAGID et al. 1999). Der Abbau im Feldversuch (Versuch Nr. 3b und 3c) war offenbar durch die feuchtwarme Witterung und eine in der Folge sehr aktive Bodenfauna und -mikroflora während der Exposition begünstigt. Die quantitative Bedeutung von Regenwürmern für den Streuabbau zeigt sich deutlich im Mikrokosmosexperiment, wo innerhalb von 4 Wochen mehr als 50 % der Streu abgebaut wurden (Tab. 2). Netzbeutel mit einer Maschenweite von 20 µm wiesen im gleichen Zeitraum lediglich einen Abbau von 19 % auf (FÖRSTER et al. 1996). Auch EDER et al. (1992) konnten zeigen, dass Wiesenstreu in feinmaschigen Netzbeuteln, die den Zugang der Makrofauna verhindern, deutlich langsamer abgebaut wurde als in grobmaschigen Beuteln. Regenwürmer haben jedoch auch einen qualitativen Einfluss auf den Abbau, da sie bevorzugt die N-reichen Bestandteile der Streu fressen (HENDRIKSEN 1990, JUDAS 1993). Die in den Netzbeuteln zurückbleibende Streu bestand daher überwiegend aus N-armen Material (FÖRSTER et al. 1996).

Carbendazim gilt als wenig wirksam für die Mehrzahl der Bodenmikroorganismen (PEEPLES 1974; WAINWRIGHT 1977). Grundsätzlich kann jedoch eine Beeinträchtigung des Streuabbaus über die Wirkung auf Mikroorganismen nicht ausgeschlossen werden, wie TORSTENSSON & WESSÉN (1984) am Beispiel von Weizenstrohabbau unter Laborbedingungen zeigen konnten. Sie beobachteten u.a., dass Carbendazim das Artenspektrum der strohbesiedelnden Pilze veränderte. Für Mykorrhizapilze konnten SCHWEIGER & JAKOBSEN (1998) zeigen, dass Carbendazim die Phosphoraufnahme über die Hyphen bereits ab sehr geringen Konzentrationen hemmt.

Im hier beschriebenen Laborversuch Nr.1 zeigte sich bei Konzentration C1 eine gegenüber der Kontrolle erhöhte Besiedlung der Streu mit Basidiomyceten sowie eine leicht reduzierte mikrobielle Atmung (Tab. 3). Bei der 100-fachen Dosis war kein Unterschied zur Kontrolle zu erkennen. Es kann nicht ausgeschlossen werden, dass Effekte von Carbendazim auf die mikrobielle

Tabelle 1. Mikrobieller Abbau (Basalatmung) von Heu, Buchenlaubstreu und Cellulose im Laborversuch (ohne Carbendazim).

Vers. Nr	Organisches Material	Dauer [Wochen]	Replikate [n]	Mittelwert* ± Stabw
1	Heu	1	1	692
1	Heu	4	1	325
1	Heu	8	1	231
4	Buchenlaub	1	3	27,4 ± 2,3
4	Buchenlaub	4	3	28,2 ± 3,2
4	Buchenlaub	8	3	27,8 ± 3,0
7a	Boden+Cellulose 4 ^a	1	1	2,75**
7a	Boden+Cellulose 4 ^a	2	1	2,69
7a	Boden+Cellulose 22 ^b	1	1	3,09
7a	Boden+Cellulose 22 ^b	2	1	2,92

Angaben der Basalatmung in µL CO₂ h⁻¹ g⁻¹ TM;

** Die Basalatmung des Bodens ohne Cellulosezusatz betrug nach 1 Woche bzw. nach 2 Wochen 1,85 bzw. 1,78 µL CO₂ h⁻¹ g⁻¹ TM.

^a 4 mg Cellulose/g Boden,

^b 22 mg Cellulose/g Boden

Atmung der Streu durch eine erhöhte CO_2 -Produktion infolge der Besiedlung mit Basidiomyceten maskiert wurden. ROBINSON et al. (1993) haben solche Steigerungen der Respiration durch synergistische Interaktionen von Stroh-besiedelnden Pilzen beschrieben. Auffällig war eine deutlich dunklere Färbung der Streu in den drei unbelasteten Kontrollen, deren Ursache nicht geklärt werden konnte.

Insgesamt sind die unter Laborbedingungen gefundenen Effekte auf die Mikroflora nicht ausreichend, die deutlichen Effekte auf den Streuabbau im Mikrokosmos sowie im Freiland zu erklären. Die Wirkung von Carbendazim auf den Abbau von Heu wird daher im Wesentlichen auf die toxische Wirkung auf Regenwürmer zurückgeführt. Waren Lumbriciden am Streuabbau beteiligt, so war deren quantitativer Beitrag zum Abbau stets so hoch, dass sich mögliche Wirkungen auf die Abbauleistung der Mikroorganismen in der Regel nicht quantifizieren ließen.

3.2 Abbau von Buchenlaub

Die Basalatmung der Buchenlaubstreu war im gesamten Untersuchungszeitraum nahezu gleich und deutlich geringer als beim Heu (Tab. 1). Eine Abnahme der Atmungsaktivität wie beim Heu wurde hier nicht beobachtet. Dies deutet auf eine gleichbleibende mikrobielle Aktivität hin. Der mikrobielle Abbau von Buchenlaub unter Laborbedingungen ist jedoch gering. Während der 8-wöchigen Inkubation im Laborexperiment Nr. 4 wurden pro Gramm Buchenlaub insgesamt etwa 18,8 mg CO_2 -C freigesetzt. Bezogen auf den Kohlenstoffgehalt der Laubstreu zu Beginn des Experiments von 46,8 % (FÖRSTER et al. 1996) entspricht das einem Abbau von 3,8 % innerhalb von 8 Wochen. ZIEGLER (1990) errechnete eine theoretische Halbwertszeit für den mikrobiellen Abbau von Buchenlaub unter Laborbedingungen von 533 Tagen.

Im Mikrokosmos wurden im Zeitraum in 4 Wochen 37,7 % der Buchenstreu abgebaut (Tab. 2). Es ist anzunehmen, dass dieser Abbau im Wesentlichen von den im Mikrokosmos vorhandenen Lumbriciden (*Lumbricus terrestris* L.) verursacht wurde. Unter Feldbedingungen war der Abbau deutlich geringer als in den dauerfeuchten Versuchsansätzen im Labor und Mikrokosmos. Als Ursache wird die kalte und z. T. sehr trockene Witterung während der Exposition der Netzbeutel im Feld und eine in der Folge reduzierte Fraßaktivität der Makrofauna vermutet.

Die Wirkung von Carbendazim auf den Abbau von Buchenlaubstreu zeigt im Laborversuch ein heterogenes Bild. Während bei der Dosis C1 eine reduzierte mikrobielle Aktivität gemessen wurde, war bei der 100-fach erhöhten Dosis eine starke Zunahme zu verzeichnen. Der beobachtete Effekt von Carbendazim steht in Widerspruch zu Ergebnissen von VINK & VAN STRAALEN (1999), die bei dem Carbendazim-verwandten Wirkstoff Benomyl nur geringe Effekte auf die Basalatmung von Laubstreu fanden. Andererseits ist eine Zunahme der mikrobiellen Atmung nach Einwirkung von Chemikalien bekannt. So fanden z. B. DUMPERT & SCHÖNBORN (1990) bei Untersuchungen zur Auswirkung zweier Umweltchemikalien im Stadtwald Ettlingen (RÖMBKE 2001) eine erhöhte Basalatmung von Buchenlaubstreu nach Applikation von PCP sowie 2,4,5-T im Freiland. Ein Ansteigen der Basalatmung kann durch eine gesteigerte Aktivität oder eine größere Biomasse der Mikroflora verursacht sein. Da sich die mikrobielle Biomasse im Versuch mit der 100-fachen Dosis Carbendazim gegenüber der Kontrolle ebenfalls als deutlich erhöht erwies (FÖRSTER 1994) ist anzunehmen, dass zumindest Teile der Mikroflora den Wirkstoff oder Verbindungen der Formulierung als Substrat nutzen konnten. Dies gilt insbesondere für Stickstoffverbindungen.

Tabelle 2. Gewichtsverlust von Heu, Buchenlaub und Cellulosepapier nach Exposition im Boden in Labor-, Mikrokosmos- und Feldstudien (Kontrollen zu den Versuchen Nr. 1 – 10). Angaben des Abbaus in % vom Initialgewicht als Mittelwert \pm Standardabweichung (Stabw).

Versuch Nr.	Test System Typ	Organisches Material	Dauer [Wochen]	Replikate [n]	Mittelwert \pm Stabw
2	Mikrokosmos	Heu	4	4	52,3 \pm 3,7
3a	Feld (Wiese)	Heu	28	8	67,0 \pm 5,0
3b	Feld (Wiese)	Heu	8	15	91,5 \pm 8,4
3c	Feld (Wiese)	Heu	8	15	74,0 \pm 6,4
5	Mikrokosmos	Buchenlaub	4	4	37,7 \pm 3,6
6	Feld (Wald)	Buchenlaub	28	6	20,4 \pm 7,0
7b	Labor	Cellulose	6	8	28,8 \pm 5,3
8*	Mesokosmos (Wiese)	Cellulose	8	6	100
8b	Mesokosmos (Acker)	Cellulose	12	6	27,7 \pm 3,0
9a	Feld (Wiese)	Cellulose	4	6	21,9 \pm 14,2
9b	Feld (Wiese)	Cellulose	8	6	100
10	Feld (Wiese)	Cellulose	8	6	36,7 \pm 12,2

Tabelle 3. Wirkung von Carbendazim auf die mikrobielle Mineralisierung (Basalatmung) und den Abbau von Heu im Labor-, Mikrokosmos- und Feldversuch.

Versuch Nr.	1		2	3	
Testsystem	Labortest		Mikrokosmos	Freiland	
Boden	ohne		homogen	natürlich	
Vegetation	ohne		ohne	Wiese	
Exposition der Streu	n.a.		auf dem Boden	auf dem Boden	
Kontaminiert	Heu		Heu	Boden + Heu	
Dauer [Wochen]	4		4	28	
Endpunkt	Basalatmung		Abbau	Abbau	
Dosis	C1	C100	C10	C1 ^a	C10 ^a
Messwert [% Kontrolle]	78,7	98,6	34,0	87,6	74,0

^a Applikation von Carbendazim 3-mal im Abstand von je 8 Wochen; = nicht anwendbar; Dosis: C1 = 0,180 kg/ha; C10 = 1,80 kg/ha; C100 = 18,0 kg/ha.

gen, da der Gesamtstickstoffgehalt der Buchenstreu gering und damit für das Wachstum der Biomasse limitierend war. Ein vergleichbares Phänomen beschrieb bereits VAN FAASSEN (1973), der mit steigender Konzentration von Benomyl eine Zunahme der Bakterienpopulation beobachtete

Im Mikrokosmos führte die Kontamination der Buchenstreu mit Carbendazim zu einem um über 70 % reduzierten Abbau (Tab. 4). Auch für die Buchenlaubstreu gilt, daß quantitative Effekte auf die Abbauleistung der Mikroflora im Untersuchungszeitraum nicht erfasst werden konnten, da sie gegenüber der Fraßaktivität der Regenwürmer zu gering war. BLAIR et al. (1989) konnten beobachten, daß der Abbau von Laubstreu in einem Mikrokosmosversuch trotz deutlich erhöhter mikrobieller Atmung durch Naphthalin nicht zunahm. Dies würde eine mikrobielle Atmung auf Kosten der eigenen Biomasse bedeuten.

Trotz des insgesamt geringen Abbaus zeigte sich auch unter Feldbedingungen ein hemmender Effekt der Versuchsschemikalie von ca. 40 % (Tab. 4). Auch hier ist, wie im Mikrokosmos, die Wirkung der Chemikalie auf die Lumbriciden als Ursache anzunehmen.

3.3 Abbau von Cellulose

Cellulose wurde in der Vergangenheit vielfach zur Erfassung des Streuabbaupotenzials und der mikrobiellen Aktivität im Boden eingesetzt (SØRENSEN 1983, BEYER et al. 1992, MEYER et al. 1998, KURKA et al. 2001). Obwohl reine Cellulose in der Natur nicht vorkommt wird sie im Boden mikrobiell abgebaut. Dies galt auch für den hier verwendeten Boden, wie sich in der erhöhten Basalatmung im Laborversuch nach Zugabe von 4 mg bzw. 22 mg pulverisierter Cellulose pro Gramm Boden um über 50 % nach 7 bzw. 14 Tagen zeigt (Tab. 1). ALBERTI et al. (1996) fanden ebenfalls eine erhöhte mikrobielle Aktivität (O₂-Aufnahme) von Bodenproben nach Zugabe von Cellulosepulver.

Im Boden exponiertes Cellulosepapier wurde sowohl im Freiland- als auch im Mesokosmos-Versuch innerhalb von 8 Wochen vollständig abgebaut. Nach der halben Expositionszeit (4 Wochen) waren jedoch im Freiland noch fast 80 % der ausgebrachten Cellulose vorhanden (Tab. 2). Die Tatsache, dass die Cellulose gegen Ende der 8-wöchigen Exposition im Feld verstärkt abgebaut wurde, lässt vermuten, dass sie für Lumbriciden erst dann als Substrat attraktiv war, als

Tabelle 4. Wirkung von Carbendazim auf die mikrobielle Mineralisierung (Basalatmung) und den Abbau von Buchenlaubstreu im Labor-, Mikrokosmos- und Feldversuch.

Versuch Nr.	4		5	6	
Testsystem	Labortest		Mikrokosmos	Freiland	
Boden	ohne		homogen	natürlich	
Vegetation	ohne		ohne	ohne	
Exposition der Streu	n.a.		auf dem Boden	auf dem Boden	
Kontaminiert	Buchenlaubstreu		Buchenlaubstreu	Boden + Streu	
Dauer [Wochen]	4		4	28	
Endpunkt	Basalatmung		Abbau	Abbau	
Dosis	C1	C100	C10	C1 ^a	
Messwert [% Kontrolle]	69,1	164,4	23,6	57,4	

^a Applikation von Carbendazim wurde im Abstand von 8 Wochen einmal wiederholt; n.a. = nicht anwendbar.

Tabelle 5. Wirkung von Carbendazim auf den Abbau von Cellulosepapier im Labor-, Mesokosmos- und Feldversuch.

Versuch Nr.	7	8		9		10
Testsystem	Labortest	Mesokosmos		Freiland		Freiland
Boden	homogen	intakter Bodenkern		natürlich		natürlich
Vegetation	ohne	Wiese	Acker	Wiese		Wiese
Exposition der Cellulose	auf dem Boden	im Boden	auf dem Boden	im Boden		auf dem Boden
Kontaminiert	Boden	Boden und Cellulose		Boden und Cellulose		Boden
Endpunkt	Abbau	Abbau		Abbau		Abbau
Dauer [Wochen]	6	8	12	4	8	8 (>1 Jahr) ^a
Dosis	C2	C6	C6	C6	C6	C6
Messwert [% Kontrolle]	710	70,2	46,0	36,4	66,0	59,5

^a Ausbringung der Netzbeutel ein Jahr nach Applikation von Carbendazim.

sie von Mikroorganismen besiedelt war. Bereits WRIGHT (1972) konnte beobachten, dass mit Bakterien beimpfte Cellulose die Fraßrate von Regenwürmern um über 60 % steigerte.

Auch die Bodenmesofauna ist am Celluloseabbau beteiligt, wie u. a. von SIEDENTOP (1995) für Collembolen gezeigt werden konnte. Es ist jedoch davon auszugehen, dass der quantitative Anteil der Mikroorganismen und der Mesofauna am Abbau im Vergleich zu dem der Lumbriciden gering ist. Die Ergebnisse aus dem Acker-Mesokosmos, in dem der Celluloseabbau aufgrund fehlender Regenwürmer ausschließlich durch die Aktivität der Mikroorganismen und der Mesofauna verursacht wurde, bekräftigen diese Annahme. Hier war der Abbau trotz längerer Expositionszeit deutlich geringer als im Wiesen-Mesokosmos. Carbendazim bewirkte sowohl im Labortest als auch im Mesokosmos und im Freiland eine Reduktion des Celluloseabbaus (Tab. 5). Die deutliche Wirkung in Testsystemen ohne Lumbriciden zeigt, dass Carbendazim offenbar die cellulolytische Mikroflora beeinträchtigen kann. Eine Wirkung von Carbendazim auf cellulolytische Mikroorganismen wurde von verschiedenen Autoren berichtet (DOMSCH 1992). Andererseits hatte nach VAN FAASSEN (1973) Benomyl in einer Konzentration von 200 mg/kg keinen Einfluss auf die Bodenatmung eines Bodens, der für 14 Tage mit Cellulose als Substrat inkubiert war. Auch bei den Versuchen mit Cellulose als Abbausubstrat wurde deutlich, welche entscheidende Rolle den Lumbriciden beim Streuabbau zukommt. Im Feldversuch Nr. 10 zeigte sich noch ein Jahr nach Applikation der Chemikalie ein signifikanter Effekt auf den Celluloseabbau. Offensichtlich hatte sich die Lumbricidenzönose auf den mit Carbendazim behandelten Parzellen im Zeitraum von 12 Monaten nach Applikation noch nicht wieder auf den Stand vor Applikation bzw. der unbehandelten Kontrollparzellen erholt. Dies gilt insbesondere für die Art *Lumbricus terrestris*, die bevorzugt Streu von der Bodenoberfläche in ihre Wohnröhre zieht.

3.4 Carbendazim als toxische Referenzsubstanz

Eine als toxische Referenzsubstanz für Streuabbauuntersuchungen geeignete Chemikalie sollte eine möglichst breite Wirkung auf die am Dekompositionsprozess beteiligten Bodenorganismen aufweisen. Wenngleich die Regenwürmer an zahlreichen Standorten aufgrund ihrer Abundanz, Biomasse sowie ihrer Fraßaktivität den größten quantitativen Einfluss auf den Streuabbau im Boden haben, sollte eine toxische Referenzsubstanz auch auf die anderen Bodenorganismen wirken. Bei den hier untersuchten drei Substraten bewirkte Carbendazim in allen Testsystemen eine Reduktion des Abbaus gegenüber der Kontrolle, wenn Regenwürmer am Abbau beteiligt waren. Dies deckt sich mit den Erwartungen aufgrund der in der Literatur beschriebenen Toxizität von Carbendazim auf Regenwürmer. Die Mikroflora zeigte im Laborversuch eine uneinheitliche Reaktion auf Carbendazim. Insgesamt erschien die Wirkung von Carbendazim auf die Bodenmikroflora auch bei sehr hohen Konzentrationen gering. Da der quantitative Beitrag der Mikroorganismen zum Masseverlust klein ist, konnten mögliche Wirkungen auf die mikrobielle Dekomposition im Mesokosmos sowie im Feld vom Beitrag der Regenwürmer überdeckt werden, so dass sie über den Endpunkt Masseverlust nicht zu quantifizieren waren. Vor diesem Hintergrund erscheint Carbendazim für Untersuchungen des Streuabbaugeschehens an solchen Standorten geeignet, an denen die Aktivität der Regenwurmfauna den Streuabbau dominiert. Für andere Standorte scheint eine Prognose des Streuabbaus unter Carbendazimeinfluss aufgrund der unklaren Effekte auf andere Gruppen der Bodenmakrofauna sowie der Bodenmesofauna (KROGH 1991, MARTIKAINEN et al. 1998) gegenwärtig nicht möglich.

Danksagung

Ich danke allen Personen, die durch ihre vielfältige Unterstützung zum Entstehen der vorliegenden Arbeit beigetragen haben. Stellvertretend seien Dr. JÖRG RÖMBKE, Dr. THOMAS KNACKER, HANS SCHALLNAB, GERRIT NENTWIG und Dr. MONIKA EDER genannt.

Mein besonderer Dank gilt Prof. Dr. LUDWIG BECK, dessen wertvolle Anregungen und hilfreichen Diskussionen meine Arbeit über Jahre begleitet haben.

Teile der hier dargestellten Arbeiten wurden vom BMBF (Projekt Nr. 0339302B) sowie von der EU (Projekt Nr. ENV4-CT97-0470) finanziell unterstützt.

4. Literatur

- AERTS, R. & DE CALUWE, H. (1997): Initial litter respiration as indicator for long-term leaf litter decomposition of *Carex* species. – *Oikos*, **80**: 353-361.
- ALBERTI, G., HAUK, B., KÖHLER, H.-R. & STORCH, V. (1996): Dekomposition: qualitative und quantitative Aspekte und deren Beeinflussung durch geogene und anthropogene Belastungsfaktoren. – 1. Auflage, 490 S.; Landsberg (ecomod).
- BECK, L. (2000): Streuabbau und Bodenfauna in Wäldern gemäßigter und tropischer Breiten. – *Carolinea*, **58**: 243-256.
- BECK, L., DUMPERT, K., FRANKE, U., MITTMANN, H., RÖMBKE, J. & SCHÖNBORN, W. (1988): Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien. – *Jülich Spezial*, **439**: 548-702.
- BLAIR, J. M., CROSSLEY, D. A. & RIDERS, S. (1989): Effects of naphthalene on microbial activity and nitrogen pools in soil-litter microcosms. – *Soil Biol Biochem*, **21**: 507-510.
- BEYER, L., BLUME H.-P., FRIEDRICH, F. & VOGT, J. (1992): Der durchschnittliche Abbau vergrabener Zellulose in typischen Acker- und Waldböden der Norddeutschen Tiefebene. – *Pedobiologia*, **36**: 11-20.
- CADISCH, G. & GILLER, K. E. (1997): Driven by nature: Plant litter quality and decomposition. – 409 S.; Wallingford (CAB International).
- CORTEZ, J. & BOUCHÉ, M. B. (1998): Field decomposition of leaf litters: Earthworm-Microorganism interactions – the ploughing-in effect. – *Soil Biol. Biochem.*, **30**(6): 795-804.
- CURRY, J. P. (1969): The decomposition of organic matter in soil, Part I. The role of the fauna in decaying grassland herbage. – *Soil Biol. Biochem.*, **1**: 253-258.
- DOMSCH, K. H. (1992): Pestizide im Boden. Mikrobieller Abbau und Nebenwirkungen auf Mikroorganismen. – Weinheim, New York (VCH).
- DUMPERT, K. & SCHÖNBORN, W. (1990): Effects of pentachlorophenol and 2,4,5-trichlorophenoxyacetic acid on the microflora of the soil in a beech wood. – *Biol. Fertil. Soils*, **9**: 292-300.
- EDER, M., KNACKER, T. & FÖRSTER, B. (1992): Bodenbiologische Untersuchungen an einer Streuobstwiese: Dekompositionsraten und Carboxymethylcellulase-Aktivität. – *Verh. Ges. Ökol.*, **21**: 53-57
- FÖRSTER, B. (1994): Untersuchungen zur Rolle der Mikroorganismen im Dekompositionsprozeß eines Wiesen- und eines Waldökosystems unter dem Einfluß des Fungizids Carben-dazim. – 193 S.; Dissertation, J.-W.-Goethe-Universität Frankfurt/Main.
- FÖRSTER, B., SCHALLNAB, H. & EDER, M. (1992): Bodenbiologische Untersuchungen an zwei Ökosystemen - Natürliche Variabilität am Beispiel von Bodeneigenschaften und Bodenmikroflora. – *Verh. Ges. Ökol.*, **21**: 65-69.
- FÖRSTER, B., RÖMBKE, J., KNACKER, T. & MORGAN, E. (1995): Microcosm study of the interactions between microorganisms and enchytraeid worms in grassland soil and litter. – *Eur. J. Soil Biol.*, **31**: 21-27.
- FÖRSTER, B., EDER, M., MORGAN, E. & KNACKER, T. (1996): A microcosm study of the effects of chemical stress, earthworms, and microorganisms and their interactions upon litter decomposition. – *Eur. J. Soil Biol.*, **32**: 25-33.
- GILLER, K. E. & CADISCH, G. (1997): Driven by nature: a sense of arrival or departure? – In: CADISCH, G. & GILLER, K. E. (eds.): *Driven by nature: Plant litter quality and decomposition*: 393-399; Wallingford (CAB International).
- HENDRIKSEN, N. B. (1990): Leaf litter selection by detritivore and geophagous earthworms. – *Biol. Fertility Soils*, **10**: 17-21.
- JUDAS, M. (1993): Indifferente Bodenwühler oder selektive Feinschmecker? Strategie der Nahrungsaufnahme bei Regenwürmern. – *Mitt. Dt. Bodenkundl. Ges.*, **69**: 167-170.
- KROGH, P. H. (1991): Perturbation of the soil microarthropod community with the pesticides benomyl and isofenphos. – *Pedobiologia*, **35**: 71-88.
- KULA, C. (1994) A prolonged laboratory test on sublethal effects of pesticides on *Eisenia fetida*. – In: DONKER, M.H., EIJ-SACKERS, H. & HEIMBACH, F. (eds.): *Ecotoxicology of soil organisms*: 257-262; London (Lewis Publishers).
- KULA, C. & RÖMBKE, J. (1998): Evaluation of soil ecotoxicity tests with functional endpoints for the risk assessment of plant protection products. – *ESPR-Environ. Sci. & Pollut. Res.*, **5** (1): 55-60.
- KURKA, A.M., STARR, M., KARSISTO, M. & SALKINOJA-SALONEN, M. (2001): Relationship between decomposition of cellulose stripes and chemical properties of humus layer in natural boreal forests. – *Plant and Soil*, **229**: 137-146.
- LOFS-HOLMIN, A. (1981): Influence in field experiments of benomyl and carbendazim on earthworms (Lumbricidae) in relation to soil texture. – *Swedish J. agric. Res.*, **11**: 141-147
- MAGID, J., KJERGAARD, C., GORISSEN, A. & KUIKMAN, P. J. (1999): Drying and rewetting of a loamy sand soil did not increase the turnover of native organic matter, but retarded the decomposition of added ¹⁴C-labelled plant material. – *Soil Biol. Biochem.*, **37**: 595-602.
- MARTIKAINEN, E., HAIMI, J. & AHTIAINEN, J. (1998): Effects of dimethoate and benomyl on soil organisms and soil processes - a microcosm study. – *Appl. Soil Ecol.*, **9**: 381-387
- MASON, C. F. (1976): *Decomposition*. – *Studies in Biology no. 74*; London (Edward Arnold).
- MEYER, M. C., PASCHKE, M. W., MCLENDON, T. & PRICE, D. (1998): Decreases in soil microbial function and functional diversity in response to depleted uranium. – *J. Environm. Qual.*, **27**: 1306-1311.
- PEEPLES, J. L. (1974): Microbial activity in benomyl-treated soils. – *Phytopathology*, **64**: 857-860.
- ROBINSON, C. H., DIGHTON, J., FRANKLAND, J. C. & COWARD, P. A. (1993): Nutrient and carbon dioxide release by interacting species of straw-decomposing fungi. – *Plant and Soil*, **151**: 139-142.
- RÖMBKE, J. (2001): Auswirkungen zweier Umweltchemikalien auf die Enchytraeen eines Moderbuchenwaldes, – *Andrias*, **15**: 205-218.
- RÖMBKE, J. & FEDERSCHMIDT, A. (1995): Effects of the fungicide Carbendazim on Enchytraeidae in laboratory and field tests. – *Newsletter on Enchytraeidae*, **4**: 79-96.

- RÖMBKE, J. & MOLTSMANN, J. F. (1996): Applied Ecotoxicology. – 1. Aufl., 282 S.; London (Lewis Publishers).
- SCHWEIGER, P. F. & JAKOBSEN, I. (1998): Dose-response relationships between four pesticides and phosphorous uptake by hyphae of arbuscular mycorrhizas. – Soil Biol. Biochem., **30** (10/11): 1415-1422.
- SIEDENTOP, S. (1995): A litterbag-test for the assessment of side effects of pesticides on soil mesofauna. – Acta Zool. Fennica, **196**: 357-360.
- SØRENSEN, L. H. (1983): Size and persistence of the microbial biomass formed during the humification of glucose, hemicellulose, cellulose, and straw in soils containing different amounts of clay. – Plant and Soil, **75**: 121-130.
- STEMMER, M., VON LÜTZOW, M., KANDELER, E., PICHLMAYER, F. & GERZABEK, M. H. (1999): The effect of maize straw placement on mineralization of C and N in soil particle size fractions. – Eur. J. Soil Sci., **50**: 73-85.
- SWIFT, M. J., HEAL, W. & ANDERSON, J. M. (1979): Decomposition in Terrestrial Ecosystems. – London (Blackwell).
- TORSTENSSON, L. & WESSÉN, B. (1984): Interactions between the fungicide benomyl and soil microorganisms. – Soil Biol. Biochem., **16**: 445-452.
- WAINWRIGHT, M. (1977): Effects of fungicides on the microbiology and biochemistry of soils - a review. – Zeitschr. Pflanzenern. Bodenk., **140**: 587-603.
- WRIGHT, M.A. (1972): Factors governing ingestion by the earthworm *Lumbricus terrestris* (L.), with special reference to apple leaves. – Ann. Appl. Biol., **70**: 175-188.
- VAN FAASSEN, H. G. (1973): Effect of the fungicide benomyl on some metabolic processes, and on numbers of bacteria and actinomycetes in the soil. – Soil Biol. Biochem., **6**: 131-133.
- VINK, K. & VAN STRAALLEN, N. M. (1999): Effects of benomyl and diazinon on isopod-mediated leaf litter decomposition in microcosms. – Pedobiologia, **43**: 345-359.
- ZIEGLER, F. (1990): Zum Einfluß von Regenwürmern (*Eisenia fetida*, Lumbricidae) und mineralischer Substanz auf die Zersetzung von Buchenstreu (*Fagus sylvatica*) und Gerstenstroh (*Hordeum vulgare*) im Modellversuch. – Bayreuther Bodenkundl. Ber., **13**; Bayreuth (Selbstverlag, Lehrstuhl Bodenkunde und Bodengeographie der Universität Bayreuth).

HARTMUT GREVEN, ULRICH RÜTHER & JOCHEN D'HAESE

Cadmium accumulation and metallothioneins in some members of the soil fauna

Dedicated to Prof. Dr. LUDWIG BECK on the occasion of his 65th birthday and retirement

Abstract

The oligochaetes *Dendrodrilus rubidus* (intestine/chloragog), *Cognettia sphagnetorum* (whole specimens), and the gastropod *Arion subfuscus* (midgut gland) collected in the Egge Mountains (North Rhine-Westphalia, Germany) accumulated cadmium (Cd) above the level of that soil horizon they preferably live in. Cd was also detected in the fat body and ovarioles of several carabid species (*Carabus problematicus*, *Abax parallelipedus*, *Pterostichus oblongopunctatus*). Seasonal variations were apparently dependent on the activity and reproduction of the species investigated. In some tissues of field collected *Carabus problematicus* (intestine, fat body, ovarioles) and of experimentally Cd-stressed *Lumbricus terrestris* (intestine/chloragog), *Enchytraeus albidus* (whole specimens), *Arion subfuscus* (midgut gland), but also in control tissues metallothioneins (MTs) could be detected. These proteins had a low molecular mass (6 to 11 kDa), a high Cd-binding capacity, a considerable amount of cysteine and a higher extinction at 254 nm compared to 280 nm. Cd-stress induced an additional synthesis of these proteins, which was roughly estimated using the cysteine content of the crude MT-fraction.

Kurzfassung

Cadmium-Akkumulation und Metallothioneine in einigen Bodenorganismen

Im Eggegebirge (Nordrhein Westfalen, Deutschland) gesammelte Oligochaeten *Dendrodrilus rubidus* (Darm-Chloragog-Gewebe), *Cognettia sphagnetorum* (ganze Tiere) sowie die Nacktschnecke *Arion subfuscus* (Mitteldarmdrüse) wiesen in den untersuchten Geweben Cadmium (Cd)-Gehalte auf, die höher als der von ihnen bevorzugte Bodenhorizont waren. Auch im Fettkörper und in den Ovariole verschiedener Carabiden-Arten (*Carabus problematicus*, *Abax parallelipedus*, *Pterostichus oblongopunctatus*) war Cd nachzuweisen. Schwankungen des Cd-Gehalts im Verlaufe eines Jahres hingen offenbar mit der Aktivität und der Fortpflanzung der jeweiligen Organismen zusammen. In den Oligochaeten *Lumbricus terrestris* (Darm-Chloragog-Gewebe), *Enchytraeus albidus* (ganze Tiere) sowie in *Arion subfuscus* (Mitteldarmdrüse) und *Carabus problematicus* (Darm, Fettkörper, Ovariole) waren in den untersuchten Organen vor und vor allem nach experimentell verursachtem Cd-Stress Metallothioneine nachzuweisen, die sich durch relativ niedrige Molekularmassen (6 bis 11 kDa), eine hohe Fähigkeit Cd zu binden, beträchtlichen Cysteingehalt sowie durch eine Erhöhung der Extinktion bei 254 nm im Vergleich zu 280 nm auszeichneten. Cd-Stress führte zu einer deutlich erhöhten Synthese dieser Proteine, die in erster Annäherung durch die Bestimmung des Cysteingehalts abgeschätzt werden konnte.

Authors

Dr. HARTMUT GREVEN, Dr. ULRICH RÜTHER, Dr. JOCHEN D'HAESE, Institut für Zoomorphologie und Zellbiologie der Heinrich Heine Universität Düsseldorf, Universitätsstr. 1, D-40225 Düsseldorf, Germany; e-mail: grevenh@uni-duesseldorf.de.

Key words

Soil fauna, ecotoxicology, cadmium, metallothionein

1. Introduction

The capacity of many soil organisms to take up and store heavy metals, often above substrate level, is well documented and has been used to estimate heavy metal pollution in the field and to assess ecotoxicological risk (summarised by MARTIN & COUGHTREY 1982; see also MORGAN & MORGAN 1990, WEIGMANN 1991 etc.; for a more dynamic approach considering substrate and time see PEIJNENBURG et al. 1999 a,b, CONNOR & LANNO 2000).

Especially Cadmium(Cd) stress leads to the expression of a variety of proteins with a high binding capacity for Cd and certain other heavy metals. They belong to the metallothionein (MT) protein family (for terrestrial invertebrates see reviews by POSTHUMA & VAN STRAALEN 1993, DALLINGER 1996 and DALLINGER et al. 2000). MTs are characterised by a low molecular mass (6-7 kDa), a high cysteine content (in vertebrates up to 33%), no significant amount of aromatic amino acids, and a selective capacity to bind metal ions such as copper, zinc, mercury and cadmium. Among invertebrates MTs are of considerable heterogeneity. In both, invertebrates and vertebrates MTs are expressed not only after heavy metal stress, but also under normal physiological conditions (summarised e.g. by RIORDAN & VALLEE 1991; regulation of MT gene expression is reviewed by GHOSAL & JACOB 2001).

Some years ago we studied the distribution of heavy metals (Cd, Pb, Zn) in the soil horizons and in some members of the soil macro- and mesofauna throughout the year in three beech forests along a height and deposition gradient in the Egge Mountains, North Rhine Westphalia, Germany. At that these forests were moderately polluted by Cd (RÜTHER & GREVEN 1988, 1992; for a detailed characterisation of this area see GERDSMEIER & GREVEN 1991).

In the first part of the present paper we broaden knowledge of the investigation site in the Egge Moun-

tains focusing on the distribution and accumulation of cadmium in some members of its soil fauna and the soil horizons they live in. In the second more detailed part we show that the Cd content of field captured animals and those exposed experimentally to Cd is correlated with the presence of MTs.

2. Material and methods

2.1 Field data

Various soil organisms (the oligochaetes *Dendrodrilus rubidus* and *Cognettia sphagnetorum*, the arionid slug *Arion subfuscus*, and the carabids *Carabus problematicus*, *Abax parallelipedus*, *Pterostichus oblongopunctatus*) were collected monthly from April to May to November 1986 and in March and April 1987 in three beech forests (I, II, III) in the Egge Mountains (see 3.1.)

Three to five specimens (>30 in *C. sphagnetorum*) and the specimens of *D. rubidus* were kept on moist filter paper to empty their gut. The Cd-content of the intestine/chloragoc (*D. rubidus*), whole worms (*C. sphagnetorum*), the midgut gland (*A. subfuscus*) and the fat body and/or ovarioles (carabids; ovarioles were excised only in July and August) was determined by AAS. Cd-content was referred to dry mass (see 2.5.). Concentration factors were calculated for the oligochaetes and *A. subfuscus* using the total Cd-content (mean value of data collected during the entire period of investigation) of the soil horizon these animals prefer and for *C. problematicus* the preferred prey (intestine/chloragoc of *D. rubidus*) as reference (see MARTIN & COUGHTRY 1992). The WILCOXON, MANN & WHITNEY U-test (SACHS 1984) was used to determine the significance of differences.

2.2 Experimental animals and application of Cd

Lumbricus terrestris were obtained from a fishing supply shop. Fifteen specimens were kept without food in aerated artificial pond water (DIETZ & ALVARADO 1970) plus 1 µg/ml Cd applied as Cd(PO₄)₂ for three days at 4°C. Controls were run with 15 specimens kept in water without Cd. Each of ca. 10 g *Enchytraeus albidus* obtained from a pet shop were kept similarly, but in water supplemented with only 0.25 µg/ml Cd, because pilot experiments had shown that at Cd concentrations of 1 mg/ml a considerable amount of the animals died after two days.

15 *Arion subfuscus* collected in the field were loaded with Cd by injecting 0.2 ml of a 0.6% NaCl solution containing 0.5 µg Cd/ml (applied as Cd(PO₄)₂) or without Cd into the body cavity. Injection of Cd allowed a more controlled contamination than feeding. After three days the midgut gland was dissected and prepared for Cd-determination.

Intestine/chloragoc tissue and body wall (*L. terrestris*), whole *E. albidus*, the midgut gland (*A. subfuscus*) and ovarioles, intestine as well as the fat body (*C. problematicus*, captured in the Egge mountains (3.1.) and not experimentally exposed to Cd) were subjected to AAS (2.5.) and the procedures for the isolation of crude MT-fractions (2.3.).

2.3 Isolation of MTs

A cytosolic fraction enriched in MTs (crude MT-fraction) was prepared according to the method of BÜHLER & KÄGI (1974) and WINGE & BROUWER (1986) with some modifications. All steps of the preparation procedure were carried out on ice or at 4°C. Whole organisms or tissues were thoroughly homoge-

nized in three volumes (mass/vol) of extraction buffer (0.1 mol/l Tris-HCl, pH 8.0, or 0.1 mol/l potassium-phosphate buffer, pH 7.0, each supplemented with 1 mmol/l PMSF and 5 mmol/l 2-mercaptoethanol). Insoluble material was removed by centrifugation at 45,000 g for 20 min as the first pellet (pe). The supernatant was clarified by centrifugation at 170,000 g for 2 h (2. pe) and then incubated at 65°C in a water bath for 8 min. The denatured and precipitated material was removed by centrifugation (3,000 g for 10 min; 3. pe). Non-MT-proteins were subsequently precipitated by the addition of ethanol-chloroform to the supernatant (1.2 vol ethanol and 0.1 vol chloroform, -20°C) and removed by centrifugation (3,000 g for 20 min; 4. pe). MT- proteins were precipitated by further addition of 2 vol ethanol (-20°C). After overnight standing the precipitate was collected by centrifugation at 3,000 g for 20 min and resuspended in a small volume of extraction buffer. The solution was clarified by a final 2 h centrifugation at 20,000 g. Separation of proteins of the crude MT-fraction was achieved by gel filtration on a calibrated Superose 12 column (Amersham-Pharmacia) in gel filtration buffer (0.1 mol/l KCl, 10 mmol/l Tris-HCl pH 8.0, 5 mmol/l Cd(PO₄)₂ and 5 mmol/l CaCl₂). The elution was monitored at 280 nm and 254 nm as MT-polypeptide-Cd complexes show a 250 nm UV absorption maximum due to Cd thiolate coordination.

2.4 Electrophoresis

Electrophoresis on 0.75-mm-thick polyacrylamide slab gels in the presence of sodium dodecylsulfate was performed according to LAEMMLI (1970) with minor modifications.

2.5 Atomic absorption spectroscopy (AAS)

For Cd measurement samples were dried (36-60 h at 105 °C), weighed, digested with conc. HNO₃ at 180°C for 3 to 4 h and analysed by atomic absorption spectroscopy (Perkin Elmer, model PE400 equipped with a graphite furnace, Perkin Elmer, model HGA 76). Cd and Calcium (Ca) concentrations in supernatants and fractions derived from gel filtration were measured directly.

2.6 Protein and cysteine determination

Protein concentrations were determined by the method of BRADFORD (1976) using bovine serum albumin as a standard. Cysteine content of the MT-fraction was inferred from the extinction on 5,5'-dithiobis-(2-nitrobenzoic acid) (DTNB) binding according to a modified method of ELLMAN (1959). DTNB to a final concentration of 10 mmol/l was added to the samples in extraction or gel filtration buffer (see above) and extinction at 412 nm read after 30 min. L-cysteine was used as a standard.

3. Results

3.1 Area of investigation

The site of investigation in the Egge Mountains included three beech forests along a height gradient and has been described repeatedly (e.g. GERDSMEIER & GREVEN 1991). Cd contamination of its soil horizons was determined bimonthly by RÜTHER & GREVEN (1992). Therefore only the most important data (forest community, height above sea level, soil, variation and mean values of total Cd-content of the O₁ and O_h horizon during the period of investigation) will be summarized herein:

I: Luzulo-Fagetum; 320 m; loamy sand; O_i 0.47 – 2.04 (0.91 ± 0.37 , O_h 0.27 – 0.67 (0.44 ± 0.11) mg/kg/dm.

II: Melico-Fagetum; 360 m; silty loam; O_i 0.54 – 2.12 (1.04 ± 0.44), O_h 0.3 – 1.05 (0.53 ± 0.17) mg/kg/dm.

III: Melico-Fagetum (Asperulo-Fagetum); 410 m; stony and loamy sand; O_i 0.6 – 2.27 (1.00 ± 0.40), O_h 0.45 – 1.05 (0.67 ± 0.16) mg/kg/dm.

3.2 Cd content of selected animals

Dendrodriulus rubidus (Oligochaeta): Cd content of the intestine/chloragog varied from 3.9 to 6.56 (I), from 3.5 to 7.2 (II), and from 3.4 to 6.2 (III) $\mu\text{g/g/dm}$ on average. Pooled data of the entire investigation period did not show significant differences in the Cd-content of worms of the three forests. Compared to May the Cd-content increased significantly in June (pooled data from I, II and III) (fig. 1 a). Concentration factors related to the O_h horizon ranged from 4.6 to 17.0.

Cognettia sphagnetorum (Oligochaeta): Cd-content of whole worms varied from 6.0 to 15.3 (I), from 6.1 to 15.0 (II), and from 7.0 to 17.0 (III) $\mu\text{g/g/dm}$. Pooled data reveal that the Cd-content of worms in the forests II and III was higher than in forest I ($p < 0.25$ and $p < 0.05$). Monthly variations were not significant. Concentration factors related to the O_i horizon ranged from 2.8 to 6.7

Arion subfuscus (Gastropoda): Cd-content of the midgut gland varied from 6.4 to 10.5 (I), from 5.0 to 12.0 (II), and from 7.2 to 10.25 (III) $\mu\text{g/g/dm}$. Significant differences between the specimens of the three forests could not be detected. The Cd-content decreased in June and November and increased in September ($p < 0.01$) (fig. 1 b). Concentration factors related to the O_i horizon ranged from 2.8 to 4.6.

Carabus problematicus (Coleoptera): Cd-content of the female fat body varied from 0.47 to 0.72 (I), from 0.50 to 0.84 (II), and from 0.6 to 0.87 (III) $\mu\text{g/g/dm}$. Specimens of forest III contained more Cd than those in forest I ($p < 0.05$). The Cd-content decreased in July and increased in September ($p < 0.01$) (fig. 1 c). Ovarioles prepared in July and August contained 0.66 ± 0.15 , the intestine 0.22 ± 0.16 , and the fat body 0.61 ± 0.17 $\mu\text{g Cd/g/dm}$. The tentatively determined concentration factors related to the mean Cd content

of the intestine/chloragog tissue of *D. rubidus* varied from 0.16 to 0.40.

Abax parallelipedus (Coleoptera): Cd-content of the female fat body varied from 0.75 to 1.5 (I), from 0.9 to 1.8 (II), and from 0.9 to 1.8 (III) $\mu\text{g/g/dm}$. Compared to forest I Cd-content was higher in specimens of forest III ($p < 0.05$). The Cd-content decreased in June and July ($p < 0.01$ and < 0.025) and increased in August and March ($p < 0.01$) (fig. 1 d). Ovarioles analysed in July and August contained 0.38 ± 0.11 $\mu\text{g Cd/g/dm}$.

Pterostichus oblongopunctatus (Coleoptera): Cd-content of the fat body (males and females) varied from 0.4 to 0.88 (I), from 0.42 to 1.1 (II), and from 0.4 to 0.9 (III) $\mu\text{g/g/dm}$. Specimens of forest II had a significantly higher Cd-content than those of forest I ($p < 0.05$). The Cd-content decreased in July and October ($p < 0.01$ and < 0.025) (fig. 1 e).

3.3 Lumbricus terrestris and Enchytraeus albidus (Oligochaeta)

The data of the distribution of Cd in fresh tissue and in subcellular fractions of *L. terrestris* after a 3-day Cd-exposure are summarised in table 1. Despite the increase in Cd content after exposure there is only little change in the percentage distribution of Cd between the various fractions of the Cd-treated and the control samples. Values given for the different preparation steps do not reach 100% because up to 20% of Cd is lost during the procedure. The pellets of the intestine/chloragog sample after the first and second centrifugation that contained the cell debris, mitochondria and nuclei (1. pe) and the microsomal fraction (2. pe) comprised about 25% of the Cd in the starting material. Nearly 50% of the Cd was found in the crude MT-fraction. On the contrary, in the case of the body wall samples less than 30% of the Cd was in the crude MT-fraction and up to 50% in the first two pellets (particle fraction). The six fold increase in the Cd content after Cd exposure was reflected by a threefold increase in the amount of cysteine determined in the MT-fraction. In the body wall a comparable increase in the Cd-content leads only to a duplication of the measurable cysteine (tab. 1).

Table 1. Cadmium balance in % of the initial content of the different fractions obtained during isolation of MT and cysteine content of the crude fraction (MT) from the intestine/chloragog complex and the body wall of *Lumbricus terrestris* exposed 72 h to 1mg Cd/ml. 1. pe pellet after the first centrifugation (45,000 g), 2. pe after the second centrifugation (17,000 g), 3. pe after heat denaturation, 4 pe after chloroform/ethanol-precipitation, MT crude fraction of water soluble proteins, cys cysteine content of the crude fraction, wm wet mass. During the preparation up to 20% of Cd is lost.

	Initial Cd-content (100%) $\mu\text{g/g wm}$	1. pe %	2. pe %	3. pe %	4. pe %	MT %	Cys ng
intestine/chloragog control	0.67	16.2	8.4	6.5	10.2	44.4	131
intestine/chloragog cadmium	3.9	14.8	6.7	6.1	7.7	48.5	389
body wall-control	0.58	31.4	7.6	8.5	6.9	29.2	99
body wall-cadmium	3.14	38.5	10.00	7.2	8.5	26.4	172

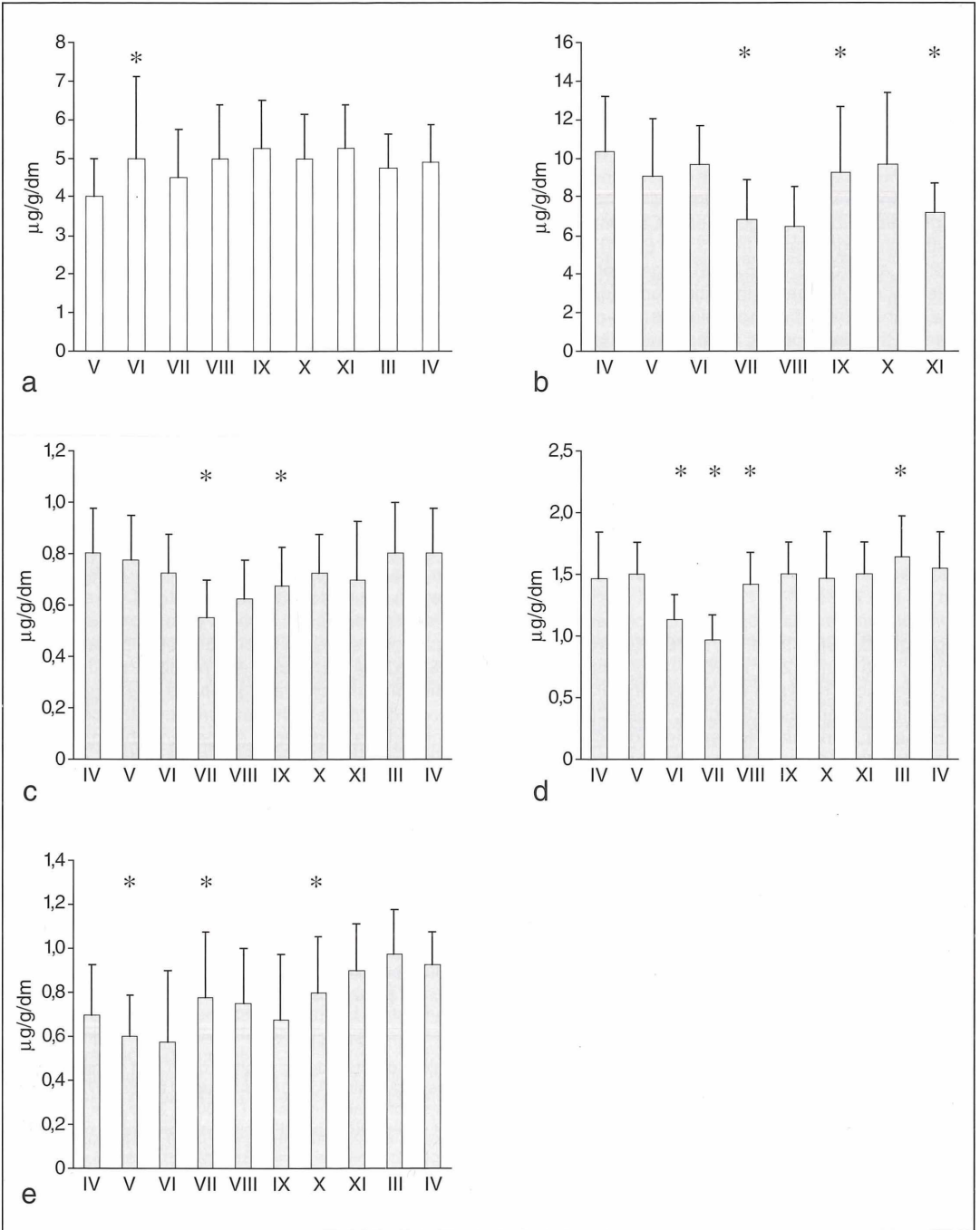


Figure 1. Mean Cd-content (µg/g/dm) of various tissues of several soil organisms during the investigation period (abscissa: months). Data were pooled from the three beech forests. a) Intestine/chloragog tissue of *Dendrodrilus rubidus*, b) midgut gland of *Arion subfuscus*, c) fat body of *Carabus problematicus*, d) *Pterostichus oblongopunctatus*, and e) *Abax parallelipedus*. * Significantly different.

Table 2. Cadmium balance in % of the initial content of the different fractions obtained during isolation of MT and cysteine content of the crude fraction (MT) from specimens of *Enchytraeus albidus* after 24 h exposure to 0.25 µg Cd/ml. For further explanation see legend of table 1.

	Initial Cd-content (100%) µg/g wm	1. pe %	2. pe %	3. pe %	4. pe %	MT %	Cys ng
control	0.04	20.4	19.4	9.7	2.4	31.6	260
cadmium	27.0	13.4	16.3	12.9	3.3	38.2	1141

Table 3. Cadmium balance in % of the initial content of the different fractions obtained during isolation of MT and cystein content of the crude fraction (MT) of the midgut gland of *Arion subfuscus* 48 h after injection of 0.2 ml 0.6% NaCl solution plus 0.5 µg Cd/ml. For further explanation see legend of table 1.

	Initial Cd-content (100%) µg/g wm	1. pe %	2. pe %	3. pe %	4. pe %	MT %
midgut glandcontrol	16.25	18.4	16.3	6.0	6.4	43.8
midgut glandcadmium	23.14	20.1	15.2	6.8	5.5	48.8

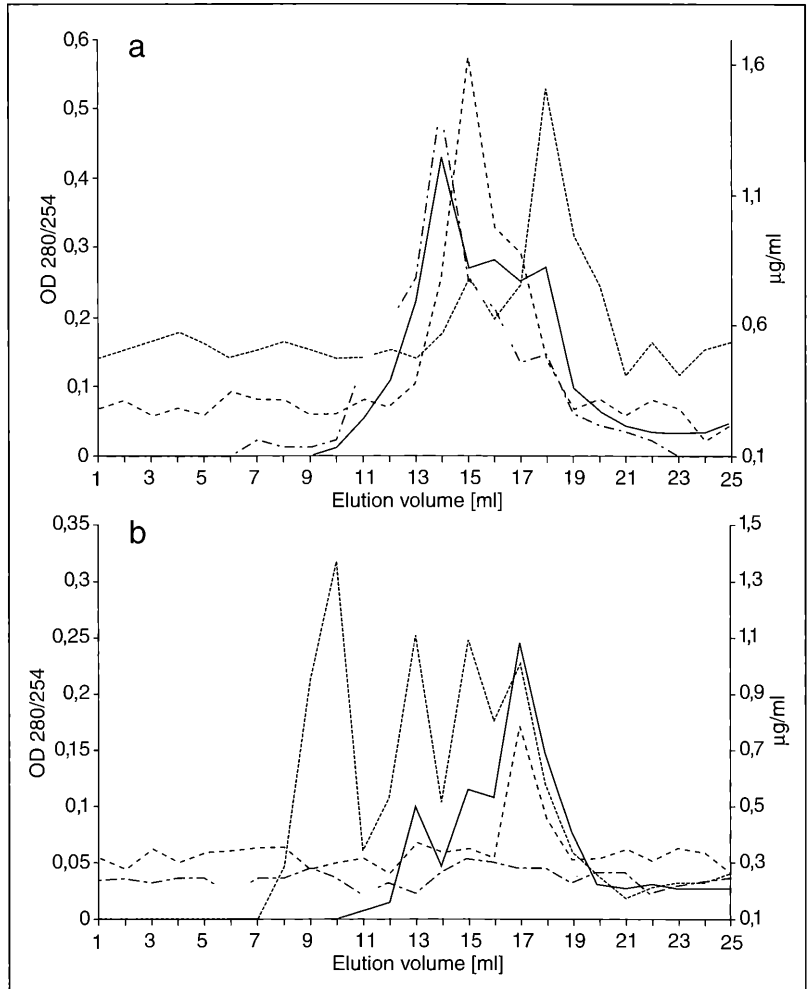


Figure 2. Gelfiltration of the MT-enriched fractions isolated a) from the body wall and b) the intestine/chloragogen tissue of *Lumbricus terrestris* exposed to Cd (see table 2). For each eluted fraction of 1 ml the extinction of 1 ml was determined at 280 nm and 254 nm (left ordinate) as well as the Ca- and Cd-content (µg/ml; right ordinate).

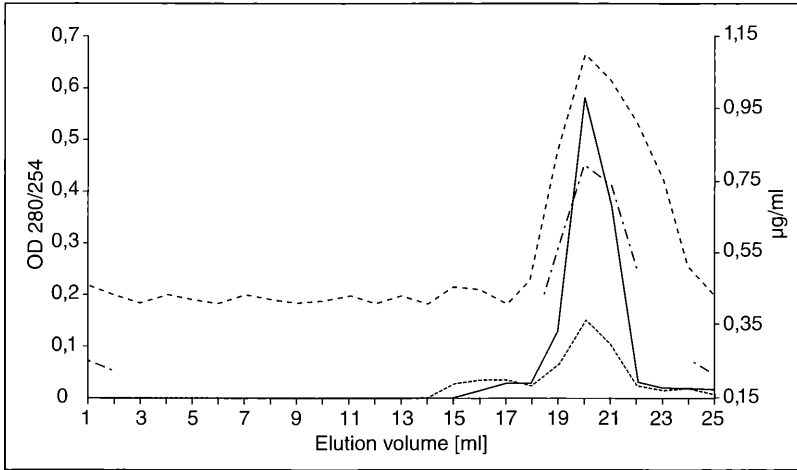


Figure 3. Gelfiltration of the MT-enriched fractions isolated from whole *Enchytraeus albidus* exposed to Cd (see table 3). For further explanation see figure 1.

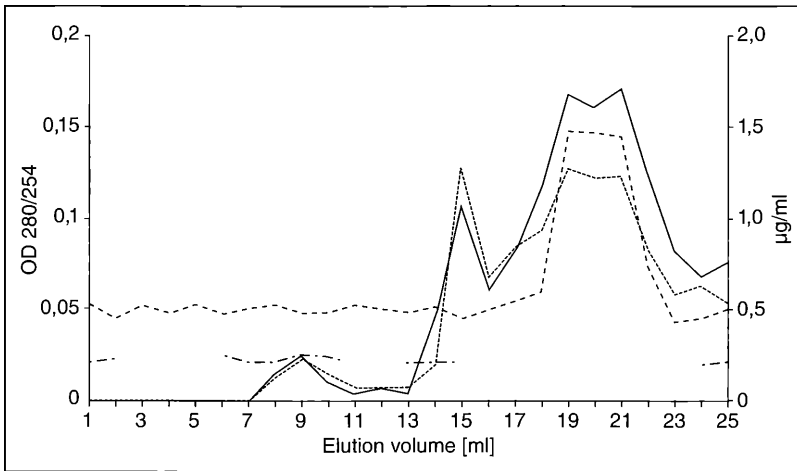


Figure 4. Gelfiltration of the MT-enriched fractions isolated from the midgut gland of *Arion subfuscus* injected with Cd containing NaCl solution (see table 4). For further explanation see figure 1.

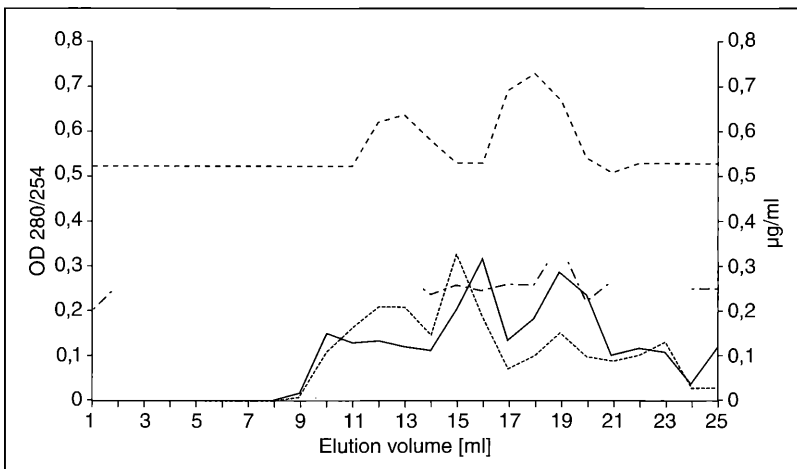


Figure 5. Gelfiltration of the MT-enriched fractions isolated from ovarioles of *Carabus problematicus* captured in the field. For further explanation see figure 1.

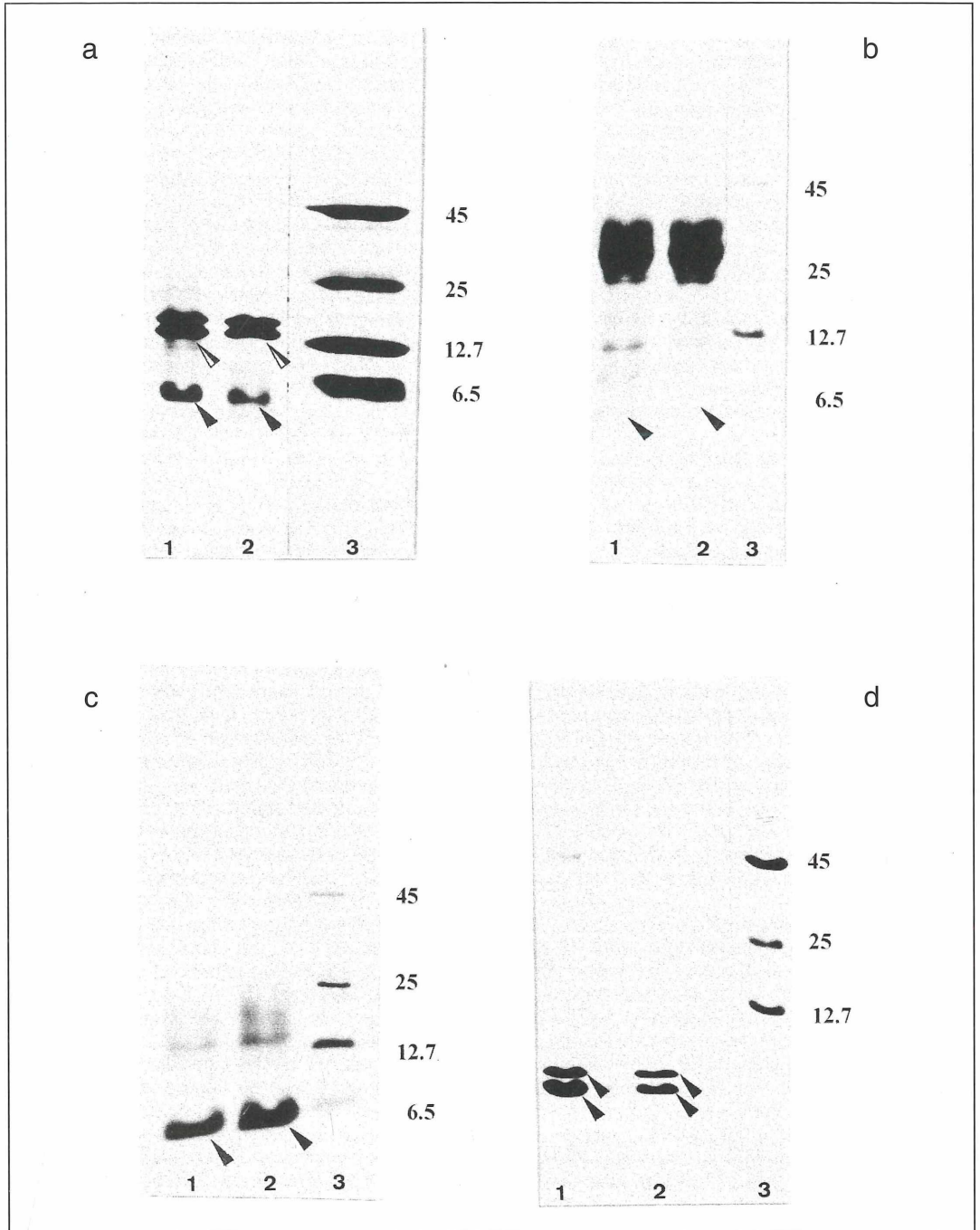


Figure 6. SDS-PAGE of the crude fractions prepared from Cd-exposed (1) and control organisms (2). Crude fraction from a) the body wall and b) the intestine/chloragogen tissue of *Lumbricus terrestris*, from c) whole specimens of *Enchytraeus albidus*, and d) the midgut gland of *Arion subfuscus*. Low molecular mass metal binding proteins are marked by arrowheads; Ca-binding proteins by black and white arrowheads; 3 standard in kDa. Note increase in MT protein after Cd-exposure in a and b.

By gel filtration of the crude MT-fraction of the body wall of the Cd-exposed animals (fig. 2 a) separate peaks were obtained for proteins with high Ca- and Cd-binding. The Ca-binding fraction with a calculated binding capacity of 2.3 mol Ca/mol protein eluted first and corresponded to a molecular mass of about 20 kDa. Cd-binding was comparable low (0.8 mol/mol protein). The Cd-binding fraction contained proteins with a molecular mass of around 10 kDa according to the elution profile. 3.6 mol Cd were bound per mol of protein of this fraction; no Ca-binding could be detected. The molecular masses calculated from SDS-PAGE of the fractions were 18 and 21 kDa (two bands) for the Ca- and 6 kDa for the Cd-binding fraction (fig. 6 a). By gel filtration of the intestine/chloragoc fraction a clear Cd-binding peak was obtained, but in contrast to the body wall fraction no Ca-binding peak. The Cd fraction corresponded to the body wall fraction with a binding capacity of 3.4 mol/mol protein and the same molecular mass (fig. 2 b, 6 b). The elution profile at 280 nm (fig. 2 b) revealed a considerable amount of non-MT proteins (see also fig. 6 b).

Distribution of Cd in the various fractions of the *E. albidus*-samples with and without Cd exposure is shown in table 2. The basal Cd-content of the control samples was rather low (approx. 0.04 µg/g wet mass (wm)), about one tenth of that found in *L. terrestris* samples. 30-40% of the Cd was present in the sedimentable fraction as well as in the soluble crude MT-fraction. After exposure the Cd increased manifold to nearly 27 µg/g wm accompanied by a four- to fivefold increase in cysteine content of the crude Mt-fraction. Gel filtration shows a single peak with a high extinction ratio between 254 and 280 nm (fig. 3). Peak fractions revealed high binding capacities for Cd as well as for Ca. Binding capacity for Cd was 4.8 mol/mol protein and for Ca 0.6 mol/mol protein. SDS Page of the crude fractions reveals a single band (6 kDa) in both, the control and the probe (fig. 6 c).

3.4 *Arion subfuscus* (Gastropoda)

Distribution of Cd in the various fractions of the midgut gland is shown in table 3. The basal Cd content of the control samples collected in the field was remarkable high (16 µg/g wm). 35% of the Cd was present in the first and second pellet of Cd-loaded as well as of the control animals. In the crude MT-fraction it amounted to 45%. Only a 1.5 fold increase was seen in loaded specimens. The strong colour of the fraction prevented cysteine determination.

Gel filtration of the crude MT-fraction showed fractions with high Cd-binding and an increased extinction at 254 nm compared to 280 nm. The protein peak apparently consisted of two different proteins (fig. 3) with only slight differences in molecular mass (approx. 6.5 kDa) also seen in the SDS-PAGE (fig. 6 d). Cd-binding capacity of the combined fraction amounted to 2.7 µg/mol protein; no Ca-binding occurred.

3.5 *Carabus problematicus*-females (Coleoptera)

Gel filtration of the crude MT-fraction of the intestine, fat body and ovarioles of field-captured, not exposed beetles (see 3.1.2.) revealed the presence of two Cd-binding proteins in the three organs, a high molecular mass protein of about 80-100 kDa and a low molecular mass protein of about 5-6 kDa. Binding capacities for the high molecular mass protein fraction were as follows: 0.4 mol Cd and 0.2 mol Ca/mol protein in the intestine, 0.8 mol Cd in the fat body and 1.4 mol Cd in the ovarioles (fig. 5). Remarkably, the fractions from the fat body and the ovarioles did not bind any measurable Ca. For the low molecular mass protein fractions, binding capacities of 2.5 mol Cd and 0.5 mol Ca/mol protein were determined for the intestine fraction, 2 mol Cd and 0.2 mol Ca/mol protein for the fat body, and 1.2 mol Cd and 0.45 mol Ca/mol protein for the ovariole fraction. Samples were too small to allow determination of cysteine content and Cd balance.

4. Discussion

Cd-concentration factors estimated in this study give only a rough imagination as knowledge on habits, uptake mechanisms, exposure routes, and food of many soil organisms including variations of local edaphic factors are often not sufficiently known. For calculations we used the total Cd-content of the soil horizon the respective animals prefer and in one case the putative main prey as reference (e.g. MARTIN & COUGHTREY 1982, FANGMEIER et al. 1986, HUNTER et al. 1987). However, soil quality criteria that are based on total concentrations are said to be unlikely to be predictive of adverse biological effect. Water- or neutral salt extractable metal concentrations are obviously better related to uptake and effects of metals (e.g. JANSSEN et al. 1996, PEIJENBURG et al. 1999 a,b, CONDER & LANNO 2000). Thus, our calculations based on total Cd-content demonstrate simply the capacity of the oligochaete- and gastropod-species examined herein to accumulate Cd above substrate level. Differences in the Cd-content perhaps due to the height and deposition gradient (GREVEN & GERDSMEIER 1991, RÜTHER & GREVEN 1992) are suggested only in the enchytraeid-species and the carabids.

Cd-concentration factors of *Dendrodrilus rubidus* are in the range of those shown for other lumbricids (e.g. IRELAND 1983, FANGMEIER et al. 1986, MORGAN & MORGAN 1990), but may be even higher (BREWER & BARRETT 1995). Cd is accumulated in lumbricids and detoxified in the intestine/chloragoc tissue (e.g. IRELAND & RICHARDS 1981), and here primarily within the posterior alimentary canal (MORGAN & MORGAN 1990, MORGAN et al. 1993). As shown herein, Cd is also present in considerable amounts in the body wall. Metal uptake in earthworms and enchytraeids appears simi-

lar suggesting similarity of metal uptake routes within oligochaetes in general (PEIJNENBURG et al. 1999 b). Although single organs of enchytraeids were not examined by us, the intestine/chloragog tissue is probably the most important heavy metal binding organ as in lumbricids. The vast literature on oligochaetes approaching the problem of metal accumulation and ecotoxicological risk assessment will only be touched herein. Several soil parameters such as pH and clay determine uptake rate constants and bioaccumulation factors. Steady state concentrations of Cd appear to be predictable on the basis of the Cd concentration in the pore water and pH in *Enchytraeus crypticus* (PEIJNENBURG et al. 1999 a) and by the CaCl_2 -extractable amount of Cd in the soil in *Eisenia andrei* (PEIJNENBURG et al. 1999 b). Steady state conditions rather than concentrations measured in a short-term bioassay should be used for interpreting test results (PEIJNENBURG et al. 1999 b) Furthermore, there is evidence that accumulation of Cd may continue for the life span of earthworms (SHEPPARD et al. 1997). It has been demonstrated that *Enchytraeus buchholzi* (species determination doubtful) exposed to different Cd-concentrations in agar and aquatic test media (e.g. RÜTHER & GREVEN 1990, WILLUHN et al. 1994 a,b, 1996) seem to accumulate Cd extremely far above substrate level. In the present study this is confirmed for field-captured *Cognettia sphagnetorum* (see 3.1.2) and cultivated *Enchytraeus albidus* (perhaps more than 500, see tab. 2), depending on the concentrations and on true bioavailability (PEIJNENBURG et al. 1999 b). Differences in concentration factors may be explained by earthworm ecology and activity (e.g. MORGAN & MORGAN 1993)

In snails and slugs the midgut gland is the main storage organ for Cd (e.g. IRELAND 1981, summarised by MARTIN & COUGHTREY 1982). Concentration factors calculated for *Arion subfuscus* lie in the range known for a variety of other slugs (MARTIN & COUGHTREY 1982). Generally large variability in metal levels have been reported, in part caused by interactions of various seasonal changes such as climate, food availability etc. (e.g. *Deroceras reticulatum*: GREVILLE & MORGAN 1989). Decrease in Cd-content in July might be connected to the relative high temperature and low rainfall (on average) measured in this month (RÜTHER & GREVEN 1988). More even climatic conditions led to a continuous increase of the wet mass of whole animals and the midgut gland that positively correlated with the Cd content (IRELAND 1984).

Carabids have been characterised as poor accumulators of heavy metal which may be due to effective detoxification and excretion (HOPKIN 1989, KRAMARZ 1999). Cd-concentrations in *Poecilus cupreus* from a laboratory culture fed with Cd-treated housefly larvae increased about thirty times (analysis of whole animals) but eliminated excess metal quickly after switch-

ing to non polluted food (KRAMARZ 1999). However, distribution and accumulation in different tissues appear poorly documented in beetles and tissues other than the fat body and the ovarioles, e.g. the cuticle (VOGEL 1988), may incorporate significant amounts of heavy metals. Furthermore, calculations of concentration factors on the basis of the Cd-content of the intestine/chloragog tissue of *D. rubidus* may be highly questionable. Fat body, intestine and ovarioles of the carabids investigated contained significant amount of Cd, but a remarkable high accumulation was not observed. A relative low accumulation was observed in other studies in which heavy metal content of whole beetles was analysed (ZÖTTL 1985, HUNTER et al. 1987).

It might be speculated that the significant decrease of Cd (and Pb and Zn, unpublished) in the fat body in females of the autumn breeder *Carabus problematicus* and in females of *Abax parallelepipedus* in June/July reflect a transport to the ovary during vitellogenesis, but more detailed studies are necessary. Differences in the Cd-content of carabids (whole individuals) could be assigned to different activities including feeding during a year (HUNTER et al. 1987).

In brief, Cd was found in all organisms investigated by us. At the time of investigation (1986/1987) the Egge Mountains apparently were moderately polluted by Cd. However, concentrations measured in the O_h (and O_i) horizon were somewhat elevated in the uppermost beech forest (RÜTHER & GREVEN 1992). Primary and secondary decomposers (lumbricids, enchytraeids, arionids) accumulated Cd above substrate level. The carabids that are mostly second-order consumers did not significantly accumulate Cd. These findings are in agreement with the view that an accumulation of metals at a lower trophic level does not necessarily result in biomagnification in the next trophic level (e.g. VAN STRAALEN 1987, HOPKIN 1989, LASKOWSKI 1991, KRAMARZ 1999).

The Cd-binding proteins isolated and described in the present paper meet the criteria for MTs, i.e. low molecular mass, high cysteine content and strong Cd-binding. MTs of a variety of terrestrial invertebrates are well known including their primary structure (DALLINGER et al. 2000). A considerable heterogeneity apparently exists among the various invertebrate MTs, though differences may also be found as a consequence of the different methods used. It is known that the rod-shaped structure of the MTs leads to a higher apparent molecular mass in gel filtration and that the high content of cysteine can cause abnormal mobility in electrophoresis. In earthworms MTs and other metal binding proteins have been isolated and characterised (for review see SCOTT-FORDSMAN & WEEKS 2000). In this taxon MTs with molecular masses between 6 and 27 kDa have been described (e.g. *Eisenia foetida* 6-7 kDa: SUZUKI et al. 1980, YAMAMURA et al. 1981; *Lumbr-*

cus terrestris 6-9 kDa: the present paper; see also RAMSEIER et al. 1990; *Dendrodilus rubidus*: 27.5 kDa, *Lumbricus rubellus*: two isoforms 24 and 27 kDa: MORGAN et al. 1989; *Dendrobaena octaedra*: two isoforms 6.5 and 13.5 kDa: BENGTTSSON et al. 1992). STÜRZENBAUM et al. (1998) isolated and sequenced the two MT isoforms of *L. rubellus* and GRUBER et al. (2000) characterised the Cd-MT in *Eisenia foetida* and discussed the creation of MT variants by posttranslational processing. A cysteine-free, Cd-binding, soluble protein with a high level of aromatic amino acids and a molecular mass of 14 kDa was isolated from *Allolobophora caliginosa* (NEYMEDDINE et al. 1992). The MT identified in the body wall of *L. terrestris* appears to be identical with that isolated from the intestine/chloragoc complex as indicated by their identical mobility in the SDS-PAGE and their capacity to bind Cd. In addition, both MTs lack Ca-binding. Presence in this tissue is noteworthy, as MTs in lumbricids were detected to our knowledge to date in white worms only, or in the intestine/chloragoc complex (see literature cited above). A second protein of the body wall of 15 to 20 kDa with a weak binding capacity for Cd even in the presence of Ca is known as a soluble Ca-binding protein (HUCH et al. 1988). The toxic effect of Cd might in part be caused by its binding to Ca-binding proteins, thereby changing the Ca signal.

In *E. albidus* a large amount of the accumulated Cd was bound to a low molecular protein (6-8 kDa). Binding of Cd (up to 4.8 mol/mol protein) was stronger than in *L. terrestris* and a strong binding of Ca could also be observed. Interestingly in *E. buchholzi* Cd specifically induces a gene (CRP-gene) that encodes a cysteine-rich, but non-MT 25-kDa protein (WILLUHN et al. 1994 a,b).

MTs have been repeatedly demonstrated in terrestrial gastropods (e.g. IRELAND 1981, DALLINGER & WIESER 1984, DALLINGER et al. 1989, 2000). IRELAND (1981) described a 9 kDa Cd-binding protein (calculated by gel filtration) and three other Zn-binding proteins in the midgut gland of the slug *Arion ater*. DALLINGER et al. (1989) showed a strictly inducible 10 kDa MT in *A. lusitanicus* which could not be detected without Cd exposure. We found two soluble, Cd-binding fractions (7 and 9 kDa, SDS-PAGE) in the midgut gland of *A. subfuscus* before and after Cd-loading. Approximately 50% of Cd were found in the particle-free cytosolic supernatant, whereas IRELAND (1981) found even >80% of the Cd in these fraction in *A. ater*. These differences cannot be explained at the moment. In the related *A. rufus* we found a MT with a molecular mass of 10 kDa, a higher Cd-binding capacity as the proteins of *A. subfuscus* and a considerable Ca-binding capacity (unpublished).

There are many studies on insect MTs (e.g. EVERAD & SWAIN 1983, KASAI et al. 1993). Accumulation of Cd was described to occur mainly by the digestive tract

(95%) in the larvae of *Sarcophaga peregrina* (AOKI et al. 1984). The molecular mass was estimated by gel filtration to be about 8 kDa. Unusually low molecular mass was described for the MT from *Orchesella cincta* 3 and 4 kDa (HENSBERGER et al. 2000). As in lumbricids posttranslational processing is discussed (HENSBERGER et al. 1999). In *Drosophila melanogaster* two genes for MT exist (MOKDAD et al. 1987). Interestingly, a duplication of the MT-Gen is found in natural populations of *Drosophila melanogaster* and is accompanied by increased metal tolerance.

We could demonstrate in the field-captured *Carabus problematicus* a low molecular protein in the intestine, in the fat body and the ovarioles. Molecular masses as well as Cd- and Ca-binding capacities were similar in the three tissues and, thus, they are probably identical. The high molecular mass protein that binds Cd may belong to a group of Cd-binding non-MTs. Such proteins have been detected in several invertebrates and vertebrates (STONE & OVERNELL 1985).

It should be emphasised that MTs could be detected not only in the Cd-stressed animals, but also in the "controls", i.e. in non-exposed *E. albidus* and *L. terrestris* from a commercial dealer, as well as in *A. subfuscus* and *C. problematicus* from the field. Past of both groups of experimental animals was unknown to us. Cd-binding proteins were detected even in *Dendrobaena octaedra* of unpolluted soils (BENGTTSSON et al. 1992). MTs, thus, might be induced in these specimens by stress other than heavy metal exposure or even might reflect the physiological level (e.g. TALBOT & MAGGEE 1978; see also GHOSAL & JACOB 2001). To our knowledge, this aspect has not been investigated in detail in the invertebrates examined. However, additional expression of MT is inducible by heavy metal exposure. Therefore, MTs as well as the above mentioned obviously very sensitive and specific CRP-gene (WILLUHN et al. 1994 a,b, 1996) have been used or suggested as biomarkers in the aquatic and terrestrial environment (e.g. COSSON 2000, DALLINGER et al. 2000). Nevertheless several limitations and pitfalls of these procedures were discussed such as species related variation of MTs, fluctuations of MT levels with seasons, lack of common methods to prepare and analyse the samples, possible effects of mixtures of heavy metals, etc. (e.g. COSSON 2000). A reliable standardised method based on MTs or metal binding non-MT proteins involving soil organisms apparently has not been established so far.

Acknowledgement

We are indebted to the "Gesamtverband des Deutschen Steinkohlenbergbaus, Essen" for financial support and Mr. M. BRENNER, Düsseldorf for preparing the figures.

5. Literature

- AOKI, Y., SUZUKI, K.T. & KUBOTA, K. (1984): Accumulation of cadmium and induction of its binding protein in the digestive tract of fleshfly (*Sarcophaga peregrina*) larvae. – *Comp. Biochem. Physiol.*, **77 C**: 279-282.
- BENGTSSON, G., EK, H. & RUNDGRÉN, S. (1992): Evolutionary response of earthworms to long-term metal exposure. – *Oikos*, **63**: 289-297
- BRADFORD, M. M. (1976): A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. – *Anal. Biochem.*, **72**: 248-255.
- BREWER, S. R. & BARRETT, G. W. S. (1995): Heavy metal concentrations in earthworms following long-term nutrient enrichment. – *Bull. Environ. Contam. Toxicol.*, **54**: 120-127
- BÜHLER, R. H. O. & KÁGI, J. H. R. (1974): Human hepatic metallothioneins. – *FEBS Letters*, **39**: 229-234.
- CONDER, J. M. & LANNO, R. P. (2000): Evaluation of surrogate measures of cadmium, lead and zinc bioavailability to *Eisenia fetida*. – *Chemosphere*, **41**: 1659-1668.
- COSSON, R. P. (2000): Bivalve metallothionein as a biomarker of aquatic ecosystem pollution by trace metals: Limits and perspectives. – *Cell Mol. Biol.*, **46**: 295-305.
- DALLINGER, R. (1996): Metallothionein research in terrestrial invertebrates: Synopsis and perspectives. – *Comp. Biochem. Physiol.*, **113 C**: 125-133.
- DALLINGER, R. & WIESER, W. (1984): Molecular fractionation of Zn, Cu, Cd and Pb in the midgut gland of *Helix pomatia* L. *Comp. Biochem. Physiol.*, **79 C**: 125-129.
- DALLINGER, R., JANSSEN, H. - H., BAUER-HILTY, A. & BERGER, B. (1989): Characterization of an inducible cadmium-binding protein of metal exposed slugs (Arionidae, Mollusca). – *Comp. Biochem. Physiol.*, **92 C**: 355-360.
- DALLINGER, R., BERGER, B., GRUBER, C., HUNZIKER, P. & STÜRZENBAUM, S. (2000): Metallothioneins in terrestrial invertebrates: Structural aspects, biological significance and implications for their use as biomarkers. – *Cell. Mol. Biol.*, **46**: 331-346.
- DIETZ, T. H. & ALVARADO, R. H. (1970): Osmotic and ionic regulation in *Lumbricus terrestris*. – *Biol. Bull.*, **138**: 247-261.
- ELLMAN, T. (1959): Tissue sulfhydryl groups. – *Arch. Biochem. Biophys.*, **82**: 70-77.
- EVERAD, L. N. & SWAIN, R. (1983): Isolation, characterization and induction of metallothionein in the stonefly *Eustenia spectabilis* following exposure to cadmium. – *Comp. Biochem. Physiol.*, **75 C**: 275-280.
- FANGMEIER, A., STEUBING, L. & GNITKE, J. (1986): Analyse der Schadstoffbelastung verschiedener Kompartimente eines Waldökosystems. – *Verh. Ges. Ökol.*, **14**: 269-278.
- GERDSMEIER, J. & GREVEN, H. (1991): Abundanz und Dominanz einiger Kleinarthropoden in Buchenwäldern des Eggegebirges, Nordrhein-Westfalen. – *Acta Biol. Benrodis*, **3**: 1-26.
- GHOSAL, K. & JACOB, S. T. (2001): Regulation of metallothionein gene expression. – *Prog. Nucleic Ac. Res. Mol. Biol.*, **66**: 357-384.
- GREVILLE, R. W. & MORGAN, A. J. (1989): seasonal changes in metal levels (Cu, Pb, Cd, Zn und Ca) within the Grey Field Slug, *Deroceras reticulatum*, living in a highly polluted habitat. – *Environ. Pollut.*, **59**: 287-303.
- GRUBER, C., STÜRZENBAUM, S., GEHRIG, P., SAC, R., HUNZIKER, P., BERGER, B. & DALLINGER, R. (2000): Isolation and characterization of a self-sufficient domain protein (Cd)-metalothionein from *Eisenia foetida*. – *Eur. J. Biochem.*, **267**: 573-582.
- HENSBERGER, P. J., DONKER, M. H., VAN VELZEN, M. J. M., ROELOFS, D., VAN DER SCHORS, R. C., HUNZIKER, P. E. & VAN STRAALLEN, N. M. (1999): Primary structure of a cadmium-induced metallothionein from the insect *Orchesella cincta* (Collembola). – *Eur. J. Biochem.*, **259**: 197-203.
- HENSBERGER, P. J., VAN VELZEN, M. J. M., NUGROHO, R. A., DONKER, M. H. & VAN STRAALLEN, N. M. (2000): Metallothionein bound cadmium in the gut of the insect *Orchesella cincta* (Collembola) in relation to dietary cadmium exposure. – *Comp. Biochem. Physiol.*, **125**: 17-24.
- HOPKIN, S. P. (1989): *Ecophysiology of Metals in Invertebrates*. – London, New York (Elsevier Applied Science).
- HUCH, R., D'HAESE, J. & GERDAY, C. (1988): A soluble calcium-binding protein from the terrestrial annelid *Lumbricus terrestris* L. – *J. Comp. Physiol. B*, **158**: 325-334.
- HUNTER, B. A., JOHNSON, M. S. & THOMPSON, D. J. (1987): Ecotoxicology of copper and cadmium in a contaminated grassland ecosystem. II. Invertebrates. – *J. Appl. Ecol.*, **24**: 587-599.
- IRELAND, M. P. (1981): Uptake and distribution of cadmium in the terrestrial slug *Arion ater* (L.). – *Comp. Biochem. Physiol.*, **68 A**: 37-41.
- IRELAND, M. P. (1983): Heavy metal uptake and tissue distribution in earthworms. – In: SATCHELL, J. E. (ed.): *Earthworm ecology. From Darwin to vermiculture*: 247-265; New York (Chapman and Hall).
- IRELAND, M. P. (1984): Seasonal changes in zinc, manganese, magnesium, copper and calcium content in the digestive gland of the slug *Arion ater* L. – *Comp. Biochem. Physiol.*, **78 A**: 855-858.
- IRELAND, M. P. & RICHARDS, K. S. (1981): Metal content after exposure to cadmium of two species of earthworms of known differing calcium metabolite activity. – *Environ. Pollut.*, **26 A**: 69-78.
- KASAI, T., WATANABE, T., INOUE, K., & HASEGAWA, T. (1993): Purification and some properties of metal binding proteins in housefly larvae (*Musca domestica*). – *Biosci. Biotech. Biochem.*, **57**: 1873-1876.
- KRAMARZ, P. (1999): The dynamics of accumulation and decontamination of cadmium and zinc in carnivorous invertebrates. 1. *Poecilus cupreus* L. – *Bull. Environ. Cont. Toxicol.*, **63**: 531-537
- LÄMMLI, U. K. (1970): Cleavage of structural proteins during the assembly of the head of bacteriophage T4. – *Nature*, **227**: 680-685.
- LASKOWSKI, R. (1991): Are the top carnivores endangered by biomagnification? – *Oikos*, **60**: 387-390.
- MARTIN, M. H. & COUGHTREY, P. J. (1982): *Biomonitoring of Heavy Metal Pollution. Land and Air*. – London, New York (Applied Sci. Publ.).
- MOKDAD, R., DEBEC, A. & WEGNEZ, M. (1987): Metallothionein genes in *Drosophila melanogaster* constitute a dual system. – *Proc. Natl. Acad. Sci USA*, **84**: 2658-2662.
- MORGAN, J. E. & MORGAN, A. J. (1990): The distribution of cadmium, copper, lead, zinc and calcium in the tissues of the earthworm *Lumbricus rubellus* sampled from an uncontaminated and four polluted soils. – *Oecologia*, **84**: 559-566.
- MORGAN, A. J., MORGAN, J. E., TURNER, M., WINTERS, C. & YANNOOD, A. (1993): Metal relationships of earthworm. – In: DALLINGER, R. & RAINBOW, P. (eds.): *Ecotoxicology of Metals in Invertebrates*: 333-358; Boca Raton, FL (Lewis).
- MORGAN, J. E. & MORGAN, A. J. (1993): Seasonal changes in the tissue metal (Cd, Zn, and Pb) concentrations in two

- ecophysiologically dissimilar earthworm species: Pollution-monitoring implications. – *Environ. Poll.*, **82**: 1-7.
- MORGAN, J. E., NOREY, C. G., MORGAN, A. J. & KAY, J. (1989): A comparison of the cadmium-binding proteins isolated from the posterior alimentary canal of the earthworm *Dendrodrilus rubidus* and *Lumbricus rubellus*. – *Comp. Biochem. Physiol.*, **92 C**: 15-21.
- NEYMEDDINE, A., SAUTIERE, P., DHAINAUT-COURTOIS, N. & BAERT, J. - L. (1992): Isolation and characterization of a Cd-binding protein from *Allolobophora caliginosa* (Annelida, Oligochaeta): Distinction from metallothionein. – *Comp. Biochem. Physiol.*, **101 C**: 601-605.
- PEIJNENBURG, W. J. G. M., POSTHUMA, L., ZWEERS, P. G. P. C., BAERSELMAN, R., DE GROOT, A. C., VAN VEEN, R. P. M. & JAGER, T. (1999a): Prediction of metal bioavailability in Dutch field soils for the oligochaete *Enchytraeus crypticus*. – *Ecotoxicol. Environ. Saf.*, **43**: 170-186.
- PEIJNENBURG, W. J. G. M., BAERSELMAN, R., DE GROOT, A. C., JAGER, T., POSTHUMA, L. & VAN VEEN, R. P. M. (1999b): Relating environmental availability to bioavailability: Soil type-dependent metal accumulation in the oligochaete *Eisenia andrei*. – *Ecotoxicol. Environ. Saf.*, **44**: 294-310.
- POSTHUMA, L. & VAN STRAALLEN, N. M. (1993): Heavy metal adaptation in terrestrial invertebrates: A review of occurrence, genetics, physiology and ecological consequences. *Comp. Biochem. Physiol.*, **106 C**: 11-38.
- RAMSEIER, S., DESHUSSES, J. & HAERDI, W. (1990): Cadmium speciation studies in the intestine of *Lumbricus terrestris* by electrophoresis of metal protein complexes. – *Mol. Cell. Biochem.*, **97**: 137-144.
- RIORDAN, J. & VALLEE, B. L. (1991): *Methods in Enzymology*. Vol. 205. Metallobiochemistry. Part B. Metallothionein and related molecules. New York, London (Academic Press).
- RÜTHER, U. & GREVEN, H. (1988): Jahreszeitliche Schwankungen im Schwermetallgehalt der Mitteldarmdrüse von *Arion subfuscus* DRAP. (Gastropoda, Arionidae). – *Verh. Dtsch. Zool. Ges.*, **81**: 328.
- RÜTHER, U. & GREVEN, H. (1990): The effect of heavy metals on enchytraeids. I. Uptake from an artificial substrate and influence on food preference. – *Acta Biol. Benrodis*, **2**: 125-131.
- RÜTHER, U. & GREVEN, H. (1992): Cadmium, Blei und Zink im Boden dreier Buchenwälder des Eggegebirges. – *Decheniana*, **145**: 341-349.
- SACHS, L. (1984): *Angewandte Statistik*. – Berlin, Heidelberg (Springer).
- SCOTT-FORTSMAND, J. J. & WEEKS, J. M. (2000): Biomarkers in earthworms. – *Rev. Environ. Contam. Toxicol.*, **165**: 117-159.
- SHEPPARD, S., EVENDEN, W. G. & CORNWELL, T. C. (1997): depuration and uptake kinetics of I, Cs, Mn, Zn and Cd by the earthworm (*Lumbricus terrestris*) in radiotracer-spiked litter. – *Environ. Toxicol. Chem.*, **16**: 2106-2112.
- STONE, H. & OVERNELL, J. (1985): Non metallothionein cadmium binding proteins. – *Comp. Biochem. Physiol.*, **80 C**: 9-14.
- STÜRZENBAUM, S. R., KILLE, P. & MORGAN, A. J. (1998): The identification, cloning and characterization of earthworm metallothionein. – *FEBS Letters*, **431**: 437-442.
- SUZUKI, K. T., YAMAMURA, M. & MORI, T. (1980): Cadmium-binding proteins induced in the earthworm. – *Arch. Environ. Contam. Toxicol.*, **9**: 415-424.
- TALBOT, V. & MAGEE, R. J. (1978): Naturally occurring heavy metal-binding proteins in invertebrates. – *Arch. Environ. Contam. Toxicol.*, **7**: 73-81.
- VAN STRAALLEN, N. M. (1987): Turnover of accumulating substances in populations with weight-structure. – *Ecol. Modell.*, **36**: 195-209.
- VOGEL, W.R. (1988): Zur Aufnahme und Auswirkung der Schwermetalle Zink und Cadmium beim Mehlkäfer *Tenebrio molitor* L. (Col., Tenebrionidae) unter Berücksichtigung möglicher Wechselwirkungen. – *Zool. Anz.*, **220**: 25-32.
- WEIGMANN, G. (1991): Heavy metal levels in earthworms of a forest ecosystem influenced by traffic and air pollution. – *Water, Air, Soil Pollut.*, **57-58**: 655-663.
- WILLUHN, J., OTTO, A., SCHMITT-WREDE, H. E. & WUNDERLICH, F. (1996): Earthworm gene as indicator of bioefficacious cadmium. – *Bioch. Biophys. Res. Comm.*, **220**: 581-585.
- WILLUHN, J., SCHMITT-WREDE, H. P., GREVEN, H. & WUNDERLICH, F. (1994a): Cadmium-induced mRNA encoding a nonmetallothionein 33-kDa protein in *Enchytraeus buchholzi* (Oligochaeta). – *Ecotoxicol. Environ. Saf.*, **29**: 93-100.
- WILLUHN, J., SCHMITT-WREDE, H. P., GREVEN, H. & WUNDERLICH, F. (1994b): cDNA cloning of a Cadmium-inducible mRNA encoding a novel Cysteine-rich, non-metallothionein 25-kDa Protein in an enchytraeid earthworm. – *J. Biol. Chem.*, **269**: 24688-24691.
- WINGE, D. R. & BROUWER, M. (1986): Techniques and problems in metal-binding protein chemistry and implications for proteins in nonmammalian organisms. – *Health Perspect.*, **65**: 211-214.
- YAMAMURA, M., MORI, T. & SUZUKI, K. T. (1981): Metallothionein induced in the earthworm. – *Experientia*, **37**: 1187-1189.
- ZÖTTL, H. W. (1985): Heavy metal levels and cycling in forest ecosystems. – *Experientia*, **41**: 1104-1113.
- ZÖTTL, H. W. & LAMPARSKI, F. (1981): Schwermetalle (Pb, Cd) in der Bodenmakrofauna des Südschwarzwaldes.- *Mitt. Dtsch. Bodenkundl. Ges.*, **32**: 509-518.

JÖRG RÖMBKE

Auswirkungen zweier Umweltchemikalien auf die Enchytraeen eines Moderbuchenwalds

Zusammenfassung

Während eines Zeitraums von 5 Jahren (1981 - 1985) wurden Abundanz, Biomasse, Vertikalverteilung und Altersstadienverteilung der Enchytraeen eines Moderbuchenwalds im nördlichen Schwarzwald (Stadtwald Ettlingen) mittels Aufschlammung erfasst (= Standardprogramm). Durchschnittlich leben an diesem Standort 46.000 Ind/m² mit einer Biomasse von 1,31 g Trockengewicht (= 8,80 g Frischgewicht) pro m². Die Populationsdynamik der Tiere verläuft, insbesondere bei der Biomasse, sehr regelmäßig mit Sommerminima und Wintermaxima und wird im Allgemeinen nur durch extreme klimatische Umstände verändert.

Parallel zum Standardprogramm wurden auf unmittelbar benachbarten Flächen im Stadtwald Ettlingen im Rahmen des Chemikalienprogramms zwei Umweltchemikalien (PCP, 2,4,5-T) in jeweils 2 Konzentrationen (1 bzw. 5 g/m²) zweimonatlich für 2 Jahre (1982 - 83) ausgebracht. Während dieser Zeit sowie in der ebenfalls zweijährigen Erholungsphase (1984 - 85) wurden die Auswirkungen der Chemikalien auf die Populationsdynamik der Enchytraeen untersucht.

In der Applikationsphase wurde die Zahl der Enchytraeen durch die Chemikalien stark reduziert. Die Wirkung trat dabei konzentrationsabhängig und schichtspezifisch auf. Außerdem beeinflussten die beiden Stoffe die Altersverteilung der Enchytraeen. Gewöhnungseffekte waren mit Ausnahme auf der 2,4,5-T(1)-Fläche nicht feststellbar. Wichtigster Faktor bei der Erklärung der Wirkung der Chemikalien ist ihr geochemisches Verhalten (Löslichkeit, Adsorption, Akkumulation) im Boden. Bis auf die Fläche mit der hohen PCP-Konzentration hatten sich Abundanz und Biomasse zwei Jahre nach Ende der Applikation weitgehend der Kontrolle wieder angeglichen. Dabei traten teilweise erhebliche Überschussreaktionen (mehrere hundert Prozent!) über Kontrollniveau auf, deren Höhe mit der vorhergehenden Wirkung umgekehrt korreliert war. Diese Zunahme ist eine Reaktion der Enchytraeenzönose auf den durch die Chemikalien bedingten Abbaurückstand der Streu, wie sie in ähnlicher Form in anderen Belastungssituationen auch gefunden wurde. Abschätzungen der energetischen Parameter (z.B. Respiration) der Enchytraeenzönose legen nahe, dass die gefundenen Beeinträchtigungen sich auch auf der Ebene ökosystemarer Funktionen (speziell des Streuabbaus) niederschlagen können. Die differenzierte Reaktion der Enchytraeen des Stadtwalds Ettlingen nach Applikation zweier Umweltchemikalien sowie Erfahrungen aus der Literatur belegen ihre Eignung als Monitororganismen in ökotoxikologischen Freilandstudien.

Abstract

Effects of two environmental chemicals on the enchytraeids of a mor beech wood forest

During a period of five years (1981 - 1985) abundance, biomass, vertical distribution and age class distribution of enchytraeids living in a mor soil of a beech wood forest (Stadtwald Ettlingen) were determined using a floating technique (= standard program). On average, 46.000 Ind/m² with a biomass of 1.31 g dry weight (= 8.80 g fresh weight) pro m² were

found. The population dynamics of these animals is quite regular (especially the biomass), showing minima in summer and maxima in winter. Usually this pattern is influenced only by extreme climatic conditions.

In parallel to the standard program two environmental chemicals (PCP, 2,4,5-T) in two concentrations (1 and 5 g/m²) were applied at two sites close by the standard plot in the same forest bimonthly for two years (1982 - 83). During this time and during the recovery period (1984 - 85) as well the effects of the chemicals on the population dynamics of the enchytraeids were investigated.

In the application period, the number of enchytraeids decreased considerably. These effects depend on the concentration and the litter layer, respectively. In addition, both chemicals influenced the age class distribution of the worms. Except on the 2,4,5-T(1)-plot no accustoming of the enchytraeid coenosis was detectable. The effects of the chemicals can be explained best by considering their fate in soil (i.e. solubility, adsorption, accumulation).

Abundance and biomass of the enchytraeids were more or less similar on all plots two years after the end of the application period (except on the PCP(5)-plot). Partly extreme surplus reactions (several hundred percent above control level) were observed. The intensity of these reactions was negatively correlated with the intensity of the effects observed beforehand. This increase in enchytraeid number and biomass is caused by the high amount of litter accumulated during the application period. Such a reaction pattern is known from other field studies with enchytraeids. Estimations of enchytraeid energetic parameter (e.g. the respiration) seem to indicate that effects on the worms are responsible for functional changes on an ecosystem level (especially decomposition of litter). The differentiated reaction of the enchytraeids in the "Stadtwald Ettlingen" after application of two environmental chemicals as well as data from literature proof their usefulness as monitoring organisms in ecotoxicological field studies.

Autor

Dr. JÖRG RÖMBKE, ECT Oekotoxikologie GmbH, Böttgerstr. 2-14, D-65439 Flörsheim am Main.

Key words

Ecotoxicology, environmental chemicals, mesofauna, Enchytraeidae, beech forest

1. Einleitung

Die vorliegende Arbeit ist Teil eines Projekts, das zwischen 1976 und 1985 durch Prof. BECK und seine Arbeitsgruppe am Staatlichen Museum für Naturkunde Karlsruhe in einem Moderbuchenwald im nördlichen Schwarzwaldvorland durchgeführt wurde (BECK et al. 1988). Zentrales Thema dieser Untersuchungen war

die Frage nach der Rolle der Bodenfauna beim Abbau der Laubstreu und dessen Beeinträchtigung durch Chemikalien. In diesem Beitrag wird dem zweiten Aspekt am Beispiel der Tiergruppe der Enchytraeen in toto (d.h. ohne Artauftrennung) nachgegangen. Enchytraeen dürften mit Ausnahme von reinen Wüstengebieten in allen Landökosystemen vorkommen. Sie bevorzugen feuchte, oft saure Böden (DIDDEN 1993). Ob diese Vorliebe auf physiologischen Mechanismen oder auf einer im Vergleich zu anderen Bodentieren, speziell Regenwürmern, geringeren Konkurrenzstärke beruht, ist gegenwärtig nicht entscheidbar. Innerhalb der Zönose "Buchenwaldboden" gehören Enchytraeen zur Saprophyten-Nahrungskette, die sich hauptsächlich vom Bestandesabfall der Buche ernährt, wobei kaum zwischen toter organischer Substanz und Mikroorganismen unterschieden wird (SWIFT et al. 1979). Daher können sie sowohl als Makro- wie Mikrophytophage bzw. als Mycetophage (Pilzfresser) wie Bacteriovore (Bakterienfresser) bezeichnet werden. Trotz der großen Zahl von Räubern (speziell Arthropoden) und Parasiten dürfte die Populationsdynamik der Enchytraeen weitgehend durch das Klima und das Futterangebot (Konkurrenzdruck) reguliert werden (NIELSEN 1955). Die Tiere sind im Boden aggregiert verteilt, was primär durch Umweltfaktoren wie die Nahrungsverfügbarkeit bewirkt wird (CHALUPSKY & LEPS 1985). Sie besiedeln im allgemeinen die obersten Bodenschichten (bis ca. 20 cm Tiefe), wobei viele Arten deutliche Schichtpräferenzen zeigen (O'CONNOR 1967). Enchytraeen wurden bisher trotz weiter Verbreitung und häufigem Vorkommen aufgrund schwieriger Taxonomie nur selten als Monitororganismen benutzt. Wenn dies aber geschah, erwiesen sich die Tiere, unabhängig von der Art der Belastung (Chemikalien, Versauerung etc.), als empfindlich gegenüber anthropogenen Stressfaktoren (DIDDEN & RÖMBKE 2000). Außerdem werden Enchytraeen als Testorganismen in ökotoxikologischen Labortests verwendet (RÖMBKE & MOSER 2000). Internationale Richtlinien zur Testdurchführung liegen vor (z.B. OECD 2000).

Im Mittelpunkt dieser Untersuchung stand daher die Frage, ob die Enchytraeen eines Moderbuchenwalds deutlich und zugleich differenziert auf anthropogene Stressfaktoren reagieren. Dazu wurde ein Standort ausgewählt, in dem 4 Jahre lang die Rolle der Bodenfauna beim Streuabbau untersucht wurde, bevor parallel zu diesem Standardprogramm (1978 – 1981) für weitere 4 Jahre die Auswirkungen zweier modellhaft ausgewählter Umweltchemikalien auf die Bodenbiozönose im sogenannten Chemikalienprogramm (1982 – 1985) studiert wurden.

In dieser Arbeit soll dabei auf die folgenden Fragen eingegangen werden:

- Wie reagiert die Enchytraeenzönose auf die beiden Chemikalien (jeweils in zwei Konzentrationen) während und vor allem nach deren Applikation?

- Bewirken die Chemikalien eine Änderung der Tiefenverteilung der Würmer?

- Gibt es eine unterschiedliche Empfindlichkeit der verschiedenen Altersstadien (juvenil, subadult, adult)?

Diese Informationen werden abschließend dahingehend diskutiert, ob Auswirkungen der Chemikalien auf die Enchytraeenzönose sich auch auf der funktionellen Ebene des Ökosystems Boden, speziell beim Abbau organischen Materials, niederschlagen können. Dabei ist schon hier darauf hinzuweisen, dass dieser Punkt umfassend nur in einem größeren Rahmen (d.h. unter Nutzung aller in dem Projekt erhobenen Daten aus Mikrobiologie, Zoologie und Ökologie) bearbeitet werden kann (vgl. BECK et al. 1988).

2. Material und Methoden

2.1 Untersuchungsgebiet

Das Untersuchungsgebiet "Stadtwald Ettlingen" liegt am Nordwestrand des Schwarzwalds, ca. 15 km südlich von Karlsruhe, auf der Südwestseite des Breitenbachtals zwischen den Ortschaften Schluttenbach und Ettlingenweiher (Topographische Karte 7016, Karlsruhe-Süd) in 310-340 m Höhe ü.NN. (Hangneigung 10 - 15°). Pflanzensoziologisch ist das Gebiet ein Hainsimonsbuchenwald (Luzulo-Fagetum). Die bei Versuchsbeginn (1976) 136-jährigen Rotbuchen (*Fagus sylvatica* L.) lassen durch ihre ungestuften, geschlossenen Kronen weder eine Strauch- noch eine Krautschicht aufkommen (Abb. 1).

Der Untergrund besteht aus Gesteinen des Buntsandstein-Hauptkonglomerats (smc₂). Der Boden ist eine steinige, tiefgründige, oligotrophe Braunerde. Unter der organischen Auflage (bestehend aus einer insgesamt mehrere Zentimeter dicken L-, F- und H-Schicht) beginnt der gut durchwurzelte Mineralboden mit einem ca. 10 cm starken A_h-Horizont, dem sich ein 60 - 90 cm mächtiger, stark steiniger Bv-Horizont anschließt. Der pH-Wert des Auflagehorizonts beträgt 3,8 - 4,7 (H₂O), der des Mineralbodens 3,1 - 4,2 (CaCl₂).

Im nördlichen Schwarzwald ist im Vergleich zu anderen deutschen Mittelgebirgen die Niederschlagsmenge hoch: Der Durchschnitt der Jahre 1979 - 1985 betrug 1017 mm (BECK & MITTMANN 1982). Auffallend ist der Verlauf des Jahres 1983: Nach einem sehr nassen Frühjahr folgte ein sehr warmer und trockener Sommer. Die Lufttemperatur in 50 cm Höhe erreichte durchschnittlich 8,3°C in den Jahren 1979 bis 1985.

2.2 Probennahme und -aufarbeitung

Die Erfassung der Enchytraeen erfolgte mittels Aufschlämmung (QA). Alle 8 Wochen (jeweils in den geraden Monaten 1978 bis 1985) sowie einmalig im August 1987 wurden 20 g Material (Frischgewicht) aus der L-, F- und H-Schicht jeder Versuchsfläche ins Labor verbracht und mit Formol (4 %) fixiert. Proben des Mineralbodens wurden nicht genommen, da dort ihre Anzahl vernachlässigbar war. Die so entstandene Aufschlämmung wurde dann sukzessive auf ca. 2 l weiter verdünnt und bei 10-facher Vergrößerung unter dem Binokular durchmustert. Die durch die Fixierung opak-weiß gefärbten Tiere können nur schwer mit großen Nematoden der Gattungen *Priochulus* und *Eudorylaimus* (ZELL, pers. Mittl.) verwechselt werden. Nach Formolfixierung wurden die Enchytraeen einzeln (ca. 40.000 Exemplare) in Lactophenol aufgehellt und als Dauerpräparat in Polyvinylactophenol (PVLV) einge-



Abbildung 1. Das Untersuchungsgebiet im Stadtwald Ettlingen.

bettet. Die Dauerpräparate sind in der Zoologischen Sammlung des Staatlichen Museum für Naturkunde Karlsruhe (SMNK) hinterlegt. Die Bestimmung erfolgte nach NIELSEN & CHRISTENSEN (1959, 1961).

Von jeder der dominanten Arten wurden, aufgeteilt nach Altersstadien, repräsentative Mengen von Tieren mit einem halbautomatischen Bildanalysegerät (System Videoplan) vermessen. Dabei wurden sowohl taxonomische Merkmale (Borstenverteilung, Segmentzahl) als auch Kennwerte der Biomasseberechnung (Länge, Durchmesser, Volumen) aufgenommen (RÖMBKE & KREYSCH 1988). Das Volumen des einzelnen Tieres wurde mit einem mittleren Dichtefaktor von 1,051 multipliziert (ABRAHAMSEN 1973). Zur besseren Vergleichbarkeit wurden diese Werte auf Trockengewicht umgerechnet (Faktor 0,149 nach AXELSSON et al. 1984). Nach Multiplikation mit den jeweiligen Fangzahlen war damit die Gesamtbiomasse abschätzbar.

Da im Laufe des Jahres die Dicke der einzelnen Schichten in Abhängigkeit vom Laubfall wechselt, wurden die Rohdaten auf einen Quadratmeter umgerechnet, wozu ein Faktor aus dem durchschnittlichen Trockengewicht jeder Schicht, gemittelt aus 8 Jahren, verwendet wurde. In der graphischen Darstellung sind die Ergebnisse als "Gewichtetes Gleitendes Mittel" (O'CONNOR 1971) aufgetragen. Dabei wurde folgende Formel benutzt (A - Abundanz pro m^2 , M - Einzelmonat, GGM - Gemittelte Abundanz): $A_{GGM} = (A(M * 2) + A(M - 1) + A(M + 1)) / 4$. Aufgrund des Probenahmedesigns (keine Replikate) entfällt eine statistische Auswertung. Abweichungen innerhalb eines „Normalbereich“ um die jeweiligen Kontrollwerte (67 - 150 % = Faktor 1,5) herum werden als zufällig angesehen. Darüber hinaus gehende Unterschiede werden im Einzelfall biologisch diskutiert. Zur besseren Übersichtlichkeit wird die Wirkung bei-

der Chemikalien sowohl in Absolutzahlen als auch in Prozent der Kontrolle dargestellt. Aus dem gleichen Grund werden bei der Auswertung mehrfach die Jahressummen des Applikationszeitraums 1982 - 1983 und des Erholungszeitraums 1984 - 1985 gebildet.

3. Charakterisierung der Chemikalien

PCP und 2,4,5-T wurden als prinzipiell austauschbare Belastungsfaktoren für das zu betrachtende Ökosystem ausgesucht. Sie gehören zu einer Gruppe von Ende der achtziger Jahre verbotenen Umweltchemikalien, die vom BMFT nach verschiedenen Kriterien als besonders geeignete Referenzsubstanzen für ökotoxikologische Untersuchungen angesehen wurden (SCHEELE 1980). Zur besseren Einschätzung der Versuchsergebnisse sollen im Folgenden kurz ihre wichtigsten physiko-chemischen und toxikologischen Eigenschaften vorgestellt werden.

3.1 PCP = Pentachlorphenol (C_6HCl_5O)

Verwendung: Fungizid, Konservierungsmittel; selten: Insektizid, Herbizid (Dritte Welt)
 Löslichkeit: 0,14 g (2,2 g) pro 100 ml Wasser; Angaben in Klammern als Natriumsalz
 Ausbringungsmenge: In Deutschland nur indirekt über Holzkonservierung etc.



Abbildung 2. Ausbringung der Chemikalien auf der Versuchsfläche.

Sowohl PCP als auch Na-PCP sind Konservierungsmittel mit einem breiten fungiziden und bakteriziden Wirkungsspektrum. Genutzt wurden beide Stoffe hauptsächlich für den Holzschutz, weniger in der Textil- und Lederkonservierung. Aufgrund toxikologischer Kriterien (z.B. Mutagenität) wurde die Produktion in der BRD 1985 eingestellt. Die Wirkung von PCP (zumindest bei Mikroorganismen) scheint in einer Hemmung der membrangebundenen ATPase sowie der oxidativen Phosphorylierung zu bestehen. In fast allen Umweltkompartimenten lassen sich PCP-Spuren nachweisen, wobei oftmals unklar ist, ob PCP selbst oder Metabolite aus anderen chlorierten organischen Stoffen im Einzelfall vorliegen (RIPPEN 1995).

In sauren Böden wird PCP schon in den obersten Schichten stark adsorbiert (vor allem an Humus; SALMINEN & HAIMI 1997), aber bei hohen Niederschlagsmengen wieder desorbiert. Unter neutralen oder basischen Bedingungen ist die Beweglichkeit weitaus größer, so dass es zu einer Versickerung ins Grundwasser kommen kann, wo ein Abbau von PCP sehr unwahrscheinlich ist. Die organische Substanz des Bodens dient dabei als reversibler Speicher. In einem terrestrischen Modellökosystem waren nach 20 Tagen 51 % des applizierten PCP's bzw. seiner Abbauprodukte verdunstet, 48 % verblieben im Boden und 1 % gelangte in die Bodentiere (LU et al. 1978). In den oberen Bodenschichten kann PCP photolytisch abgebaut

werden, wobei bis zur vollständigen Mineralisierung viele chlorierte Zwischenprodukte entstehen. Auf das gesamte Bodenprofil bezogen werden PCP wie Na-PCP überwiegend von Mikroorganismen metabolisiert (oft nach längerer Adaptationsperiode). Je nach mikrobieller Aktivität (temperatur- und feuchteabhängig) wurden im Freiland Halbwertszeiten zwischen 14 und 120 Tagen gefunden. (CROSBY 1981). Trotz dieses im Vergleich zu anderen Umweltchemikalien schnellen Abbaus wird PCP als biologisch schwer abbaubar eingestuft, weil der mikrobielle Abbau mit der fungiziden und bakteriziden Wirkung konkurriert.

3.2 2,4,5-T = 2,4,5-Trichlorphenoxyessigsäure ($C_6H_5Cl_3O_3$)

Verwendung: Selektives Herbizid

Löslichkeit: 0,25 g/l (bei 20 °C)

Anwendungskonzentrationen (LITZ & BLUME 1985):

Getreidebau 0,3 – 0,9 g/m²; Forst, Bahnböschungen ca. 0,6 g/m² (punktuell bis 20 g/m²)

Die herbizide Wirkung von 2,4,5-T beruht auf der Ähnlichkeit zu bestimmten Hormonen (Auxine, z.B. Indol-essigsäure) von dicotylen Pflanzen. Die Chemikalie stört die Wachstumsregulation sowie, in hohen Konzentrationen, die oxydative Phosphorylierung der Zellen. Die Chemikalie wurde in der Forstwirtschaft zur Unterholz-, Weichholz- und Kräuterbekämpfung in Kiefernschonungen und an Wegrändern benützt

(BERGMANN 1981). In der BRD war der wichtigste Anwendungsbereich, nach der weitgehenden Beschränkung des großflächigen Einsatzes, die Freihaltung der Gleiskörper der Bahn. Trotz vielfältiger Untersuchungen gibt es bis heute keine eindeutige Einschätzung der Toxizität von 2,4,5-T. Aufgrund einiger Studien, meist im Zusammenhang mit seinem Einsatz in Vietnam als Teil des Entlaubungsmittels "Agent Orange" (Ausbringung zusammen mit 2,4 D im Verhältnis 50:50 in einer Konzentration von 2,9 g/m²) wurde die Verwendung der Chemikalie in Italien 1970, den USA 1985 und Deutschland 1997 beschränkt bzw. verboten (RIPPEN 1999).

Im Boden kann 2,4,5-T unter günstigen Umständen innerhalb von 1 - 2 Wochen mikrobiell abgebaut werden. In einer Untersuchung des Verhaltens von 2,4,5-T in 10 deutschen Weide- und Waldböden fanden LITZ & BLUME (1985) große Unterschiede in der Abbaurate in Abhängigkeit von den Standortverhältnissen, insbesondere von der Bindungsintensität durch Huminstoffe sowie der Temperatur: Im Winter (4 - 7°C) werden 50 % des Herbizids in 40 - 220 Tagen, im Sommer (13 - 18°C) dagegen in 8 - 46 Tagen eliminiert. In der warmen Jahreszeit spielt neben dem mikrobiellen Abbau auch die Verdampfung eine nennenswerte Rolle.

3.3 Ausbringung

Für jede der beiden auszubringenden Chemikalien wurde auf der Versuchsfläche ein Gebiet von 10 x 20 m abgezaunt. Jeweils die Hälfte dieser Fläche wurde mit einer Konzentration von 1 g/m² (= PCP(1) und 2,4,5-T(1)) bzw. mit 5 g/m² (= PCP(5) und 2,4,5-T(5))

in zweimonatigem Abstand insgesamt achtmal besprüht (= Applikationsphase 1982 - 1983 im Gegensatz zur Erholungsphase 1984 - 1985). Zur Kontrolle der ausgebrachten Mengen wurde in den Jahren 1982

1983 jeweils eine Probe aus der L-Schicht direkt vor bzw. nach der Applikation aus jeder Chemikalienparzelle entnommen (ZIETZ et al. 1987). Um einen Eindruck von der Verteilung der ausgebrachten Chemikalien zu bekommen, wurden an fünf Probenahmeterminen auch Proben aus der F- und H-Schicht untersucht.

Im ersten Versuchsjahr wurde die reine Wirksubstanz benutzt, im zweiten dagegen die jeweiligen Salze (Natrium-PCP bzw. Diethylamin-2,4,5-T). Diese Umstellung erfolgte teils aus finanziellen Gründen, teils aus praktischen Erwägungen: Die Chemikalien sind als Salz leichter löslich und daher weitaus einfacher auszubringen. Beide Chemikalien wurden einen Tag vor der Applikation in Isopropanol vorgelöst (40 g pro 0,3 l Alkohol) und kurz vor der Ausbringung mit Wasser im Verhältnis 1:12,5 vermischt. Die Besprühung erfolgte mit einer Motorrückenspritze entsprechend den Ausbringungsvorschriften des "Deutschen Pflanzenschutzdienstes" (Abb. 2). Aufgrund der schwierigen Geländebeschaffenheit war eine gleichmäßige Verteilung schwierig. Nach der Ausbringung wurden die Parzellen mit Wasser besprüht, um die Chemikalien besser in die Streuschicht einzuwaschen.

3.4 Rückstandsanalytik

Beide Chemikalien wurden mittels HPLC bestimmt (für Details siehe ZIETZ et al. 1987): Die Wiederfindungsrate betrug für PCP 57 % ± 5,2 %, für 2,4,5-T

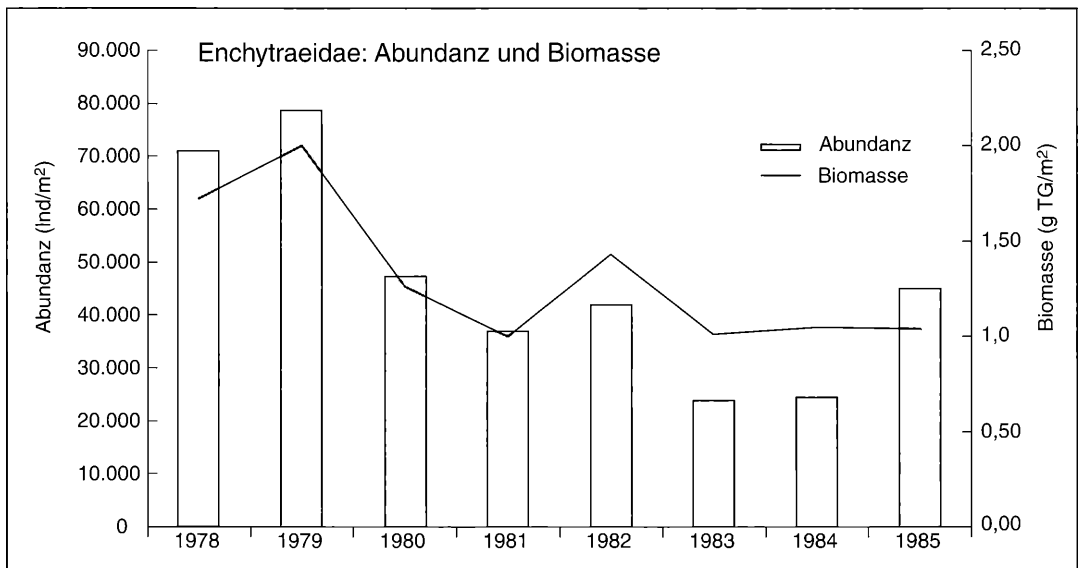


Abbildung 3. Durchschnittliche Abundanz bzw. Biomasse der Enchytraeen 1978 - 1985 im Versuchsgebiet Stadtwald Ettlingen.

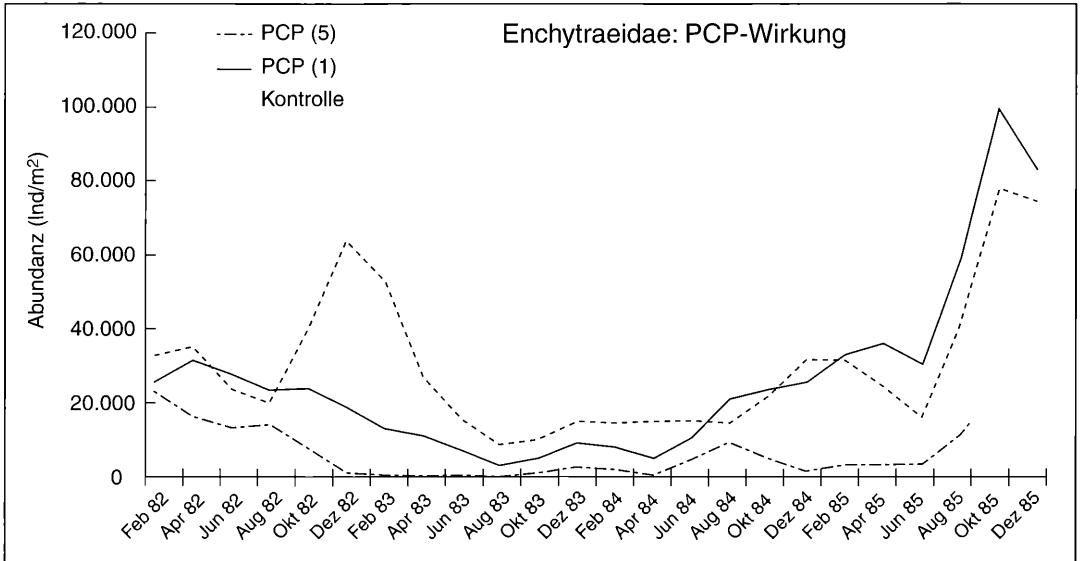


Abbildung 4. Wirkung von PCP auf die Enchytraeen im Stadtwald Ettlingen (Absolutzahlen).

66 % \pm 3,9 %. Für PCP fanden SALMINEN & HAIMI (1997) praktisch identische Raten (ca. 50 %) in einem finnischen Waldboden. Die Nachweisgrenze lag bei 0,1 mg pro kg Streu. Bei PCP wurden die Sollwerte von 1 bzw. 5 g/m² direkt nach der Applikation im Durchschnitt erreicht, bei 2,4,5-T dagegen nur in der Hälfte aller Fälle. PCP wurde daher aufgrund seines langsamen Abbaus im Versuchszeitraum akkumuliert (besonders deutlich auf PCP(5)), 2,4,5-T dagegen nicht. Das heißt, dass PCP permanent in hohen, während der Applikationsphase langsam steigenden Konzentrationen vorhanden war, während die durchschnittliche Konzentration von 2,4,5-T direkt nach jeder Ausbringung nur 50 % des Sollwerts erreicht, später meist sogar unter 10 % lag (Tab. 1). Aufgrund der hohen Variabilität der Werte werden in dieser Arbeit alle Ergebnisse auf die jeweilige Nominalkonzentration (= Sollwerte) bezogen.

Tabelle 1. Durchschnittliche Konzentration von PCP und 2,4,5-T in der L-Schicht direkt vor und nach jeder Applikation pro m² sowie während der Applikationsphase pro kg Trockensubstanz (Abschätzung).

	PCP(5)	PCP(1)	2,4,5-T(5)	2,4,5-T(1)
Sollwerte (g/m ²)	5	1	5	1
vor Appl. (g/m ²)	2,85 \pm 2,0	0,43 \pm 0,3	0,23 \pm 0,2	0,03 \pm 0,1
nach Appl. (g/m ²)	8,71 \pm 2,8	1,20 \pm 0,7	2,23 \pm 1,7	0,49 \pm 0,5
währ. Appl. (g/kg TG)	11,26 \pm 7,5	1,57 \pm 1,4	3,48 \pm 6,3	0,49 \pm 0,8

Vier Monate nach der letzten Applikation Ende 1983 war 2,4,5-T auf beiden Parzellen kaum mehr nachweisbar: Durchschnittlich wurden bei dieser letzten Probennahme 0,03 g/m² in der L-Schicht, 0,014 g/m² in der F-Schicht und 0,007 g/m² in der H-Schicht gefunden. Auf der PCP(1)-Fläche wurden 2 Monate nach der letzten Ausbringung noch Werte in der erwarteten Größenordnung festgestellt: 0,6, 0,2 bzw. 0,07 g/m² in der L-, F- und H-Schicht. Dagegen wurden auf der PCP(5)-Fläche nach über einem Jahr der Erholung immer noch 0,9 g/m² in der L-Schicht, 0,6 g/m² in der F-Schicht und 0,35 g/m² in der H-Schicht gemessen. Besonders überrascht dabei die relativ hohe PCP-Konzentration in der L-Schicht, deren Laub überwiegend 10 Monate nach der letzten Applikation vom Baum gefallen ist. Das hier nachgewiesene PCP dürfte überwiegend aus der oberen F-Schicht stammen und entweder durch kapillaren Wassertransport oder tierische Aktivität nach oben gelangen. Der Abbau erfolgte in den am schnellsten in der L-, am langsamsten in der H-Schicht, wofür neben der unterschiedlichen Intensität des mikrobiellen Anteils der an der Bodenoberfläche zusätzlich wirksame photolytische Abbau verantwortlich sein dürfte. Offenbar wird der mikrobielle Abbau von PCP ab einer bestimmten Konzentration überproportional gehemmt. Toxische Wirkungen auf die Mikroflora von Waldböden wurden im Bereich von 200 – 500 mg/kg gefunden (SALMINEN et al. 1995; ZELLES et al. 1998) – Konzentrationen, die in der L-Schicht der PCP(5)-Fläche während der gesamten Applikationsphase und auf PCP(1) zumindest mehrfach überschritten wurden (Tab. 1).

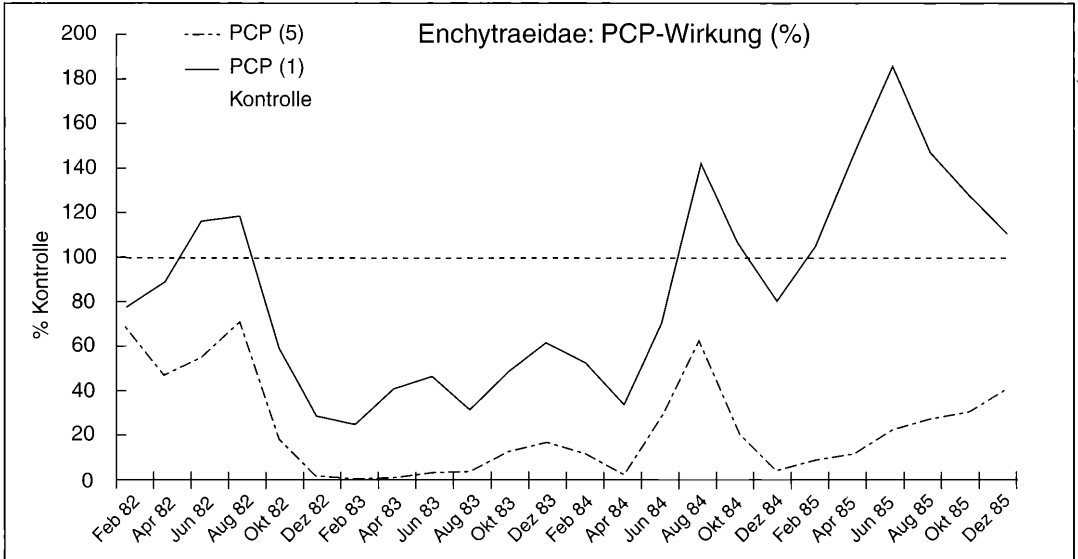


Abbildung 5. Wirkung von PCP auf die Enchytraeen im Stadtwald Ettlingen (relativ zur Kontrolle).

4. Ergebnisse

4.1 Populationsdynamik ohne Chemikalienbelastung

Bevor auf die Auswirkungen der Chemikalien eingegangen wird, ist kurz die langjährige Populationsdynamik der Enchytraeen auf der Kontrollfläche im Jahresdurchschnitt darzustellen, um einen Eindruck von der natürlichen Variabilität des Auftretens dieser Tiergruppe am Standort „Stadtwald Ettlingen“ zu bekommen (Römbke 1989). Demnach war in den ersten beiden Jahren (1978/79) die Zahl der Tiere sehr hoch (Abb. 3). Dann hielt sich die Dichte der Tiere für 3 Jahre auf einem mittleren Niveau, bevor es 1983 zu einem drastischen Einbruch kam. Erst 1985 wurde wieder eine Zahl im Jahresdurchschnitt erreicht, die in etwa dem langjährigen Mittel von 46.000 Tieren pro m² entspricht. Die Biomasse lag zu Versuchsbeginn ebenfalls sehr hoch (1,6 – 1,9 g TG/m²), schwankte seit 1980 aber nur noch wenig zwischen 1,0 (1981) und 1,4 (1982) g TG/m². Der bei der Dichte beobachtete Einbruch 1983/84 samt folgender Erholung ist bei der Biomasse kaum ausgeprägt.

Die Zahl der Enchytraeiden schwankt im Jahresverlauf sehr stark: Das absolute Minimum lag bei 352 Tieren/m² (August 1983), das absolute Maximum bei 145.280 pro m² (Februar 1979). Dabei wurden Maxima im Winter (Oktober bis Februar) erreicht, während die Minima fast immer im Sommer (Juni - August) lagen. Die Biomasseentwicklung verlief, wie sich schon beim Vergleich der Jahresmittelwerte andeutete, regelmäßiger. Unabhängig vom absoluten Niveau lag das Maximum mit einer Ausnahme (Februar 1979) im-

mer im Dezember, das Minimum im Juni/August. Wie bei der Abundanzentwicklung ist das absolute Minimum (0,14 g FG/m²) im August 1983 zu konstatieren. Die sich anschließende Erholungsphase ist nicht am Verlauf der Biomassekurve, sondern nur an ihrem absoluten Niveau erkennbar: Das Wintermaximum 1983/84 fiel z.B. um 30 - 50 % niedriger aus als gewöhnlich.

4.2 Effekte der Chemikalien

Im Folgenden werden nur Trends der Chemikalienwirkung diskutiert, da aufgrund des Probenahmedesigns einzelne Abweichungen nicht von Zufallsschwankungen unterscheidbar sind.

4.2.1 Wirkung auf die Populationsdynamik

Die Auswirkung von PCP bzw. 2,4,5-T auf die Gesamtpopulation der Enchytraeen ist als drastisch, aber differenziert zu bezeichnen (Abb. 4 - 7). Im großen und ganzen folgen die Enchytraeen auf den Versuchsflächen dem von der Kontrollfläche bekannten Zyklus mit Wintermaximum und Sommerminimum, wobei es zu vielfältigen Verschiebungen, sowohl durch die Chemikalien als auch durch außergewöhnliche Witterungsumstände bedingt, kommen kann. Insbesondere von Mitte 1983 bis Mitte 1984 ist der Verlauf bei einem auf allen Flächen sehr niedrigem Niveau ungewöhnlich, da das Wintermaximum 1983/84 mit Ausnahme der schwachen Biomasse-Ausprägung auf der Kontrollfläche völlig ausgefallen ist.

Gegenüber der Kontrolle sind Zahl und Biomasse der Tiere auf der Fläche PCP(5) bis zum Ende des Versuchszeitraums sehr stark herabgesetzt (Abb. 4 & 5).

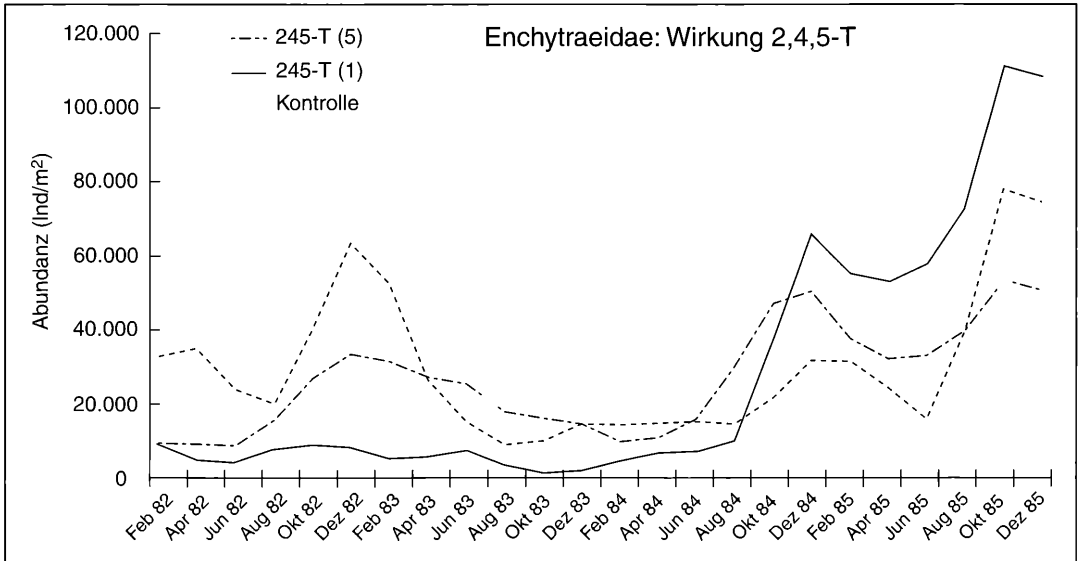


Abbildung 6. Wirkung von 2,4,5-T auf die Enchytraeen im Stadtwald Ettlingen (Absolutzahlen).

Auffallend ist dabei, dass die Wirkung bei der Abundanz erst im Spätsommer 1982, d.h. nach 4 Applikationsterminen, deutlich wird, während die Biomasse kontinuierlich von Beginn an abfällt. Die niedrigere PCP-Konzentration führt von Beginn an zu einer langsamen Reduzierung der Würmer, doch beginnt die Erholung schon ab dem Frühjahr 1984.

Die Tiere auf den beiden 2,4,5-T-Flächen (Abb. 6 & 7) reagieren sofort auf die Applikation mit einem Rückgang auf ca. 30 % der Kontrolle. Dieser Effekt hält bei 2,4,5-T(1) aber nur ein halbes Jahr an, denn im April 1983, d.h. noch unter Belastung, wird der Kontrollwert erstmals überschritten (bei der Biomasse schon im Herbst 1982). Die hohe 2,4,5-T-Konzentration führt bis zum Ende der Applikationsphase zu einer durchgängigen Verringerung der Enchytraeendichte um ca. 70 %. Ihre Anzahl ist dabei praktisch konstant, beginnend direkt nach der Ausbringung bis 4 Monate nach der letzten Ausbringung.

In der Erholungsphase übertrifft die Anzahl der Würmer auf allen Chemikalienflächen mit Ausnahme von PCP(5) diejenige der Kontrolle. Überschussreaktionen im Vergleich zur Kontrolle sind dabei meistens im Sommer bei geringen Absolutwerten festzustellen. Bemerkenswert ist die explosionsartige Zunahme der Tiere auf den 2,4,5-T-Flächen im Sommer 1984. Nach einem teils unterdurchschnittlichen (PCP(1), Kontrolle), teils deutlichem (2,4,5-T(1), 2,4,5-T(5)) winterlichen Maximum 1984/85 deutet sich auf diesen Flächen ein Sommerminimum nur an. Im weiteren Verlauf 1985 können die Würmer auf den Flächen PCP(1) und 2,4,5-T(5) Rekorddichten erreichen, die die ebenfalls hohe Kontrolldichte noch etwas übersteigen.

Tabelle 2. Jahressummen der Anzahl bzw. Biomasse der Enchytraeidae in Prozent der Kontrolle, sowie nach Phasen zusammengefasst.

Abundanz					
Jahr bzw. Phase	PCP(5)	PCP(1)	2,4,5-T(5)	2,4,5-T(1)	Kontr.
1982	34,2	68,5	20,5	44,6	100
1983	4,7	38,6	18,9	108,5	100
Applikation	23,6	57,7	19,9	67,7	100
1984	17,2	74,9	168,1	145,6	100
1985	30,0	130,9	169,2	92,9	100
Erholung	26,0	113,4	168,9	109,4	100
Biomasse					
Jahr bzw. Phase	PCP(5)	PCP(1)	2,4,5-T(5)	2,4,5-T(1)	Kontr.
1982	28,1	72,3	18,9	50,7	100
1983	6,1	70,7	42,7	319,5	100
Applikation	22,0	71,9	25,5	125,2	100
1984	11,1	58,5	222,8	150,0	100
1985	33,0	177,1	247,6	91,3	100
Erholung	24,3	130,1	237,8	114,5	100

Betrachtet man die Jahressummen der Abundanz bzw. Biomasse (Tab. 2), so werden diese in der Applikationsphase durch die hohen Konzentrationen deutlich reduziert, während von den niedrigen Konzentrationen 2,4,5-T im ersten und PCP im zweiten Jahr wirken. In der Erholungsphase zeigen sich mit Ausnahme von PCP(5) Überschussreaktionen, deren Ausprägung im umgekehrten Verhältnis zur vorherigen Schädigung steht.

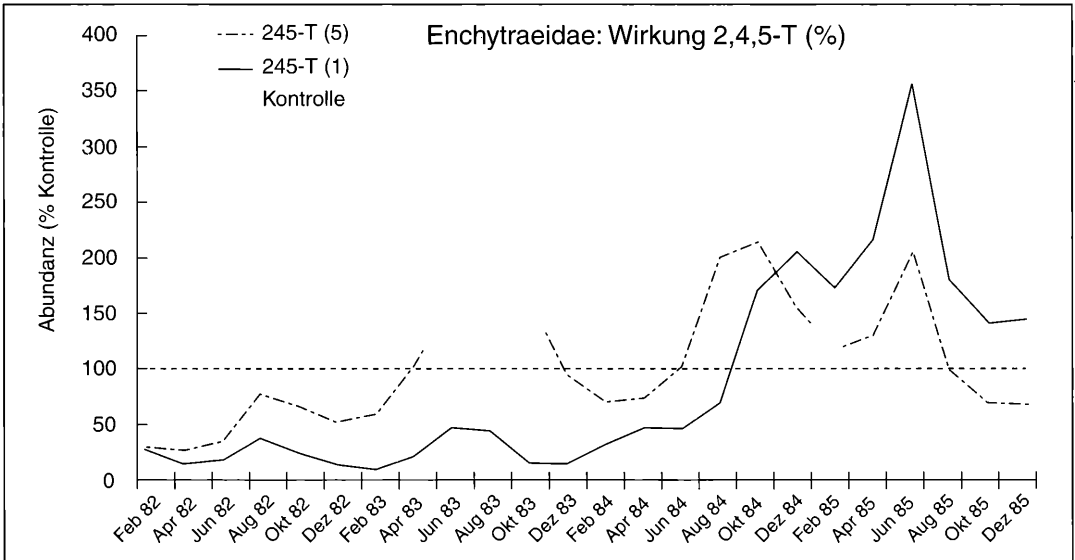


Abbildung 7 Wirkung von 2,4,5-T auf die Enchytraeen im Stadtwald Ettlingen (relativ zur Kontrolle).

Bei der zwei Jahre nach Beendigung der Erholungsphase im August 1987 genommenen einmaligen Probenreihe auf allen fünf Versuchsflächen lag die Abundanz der Enchytraeen auf den vier Chemikalienflächen zwischen 70 % und 110 % der Kontrolle; d.h. es gab keinen Hinweis auf eine noch anhaltende Chemikalienwirkung.

4.2.2 Wirkung auf die Tiefenverteilung

Bei einer getrennten Betrachtung der Streuschichten lassen sich die Jahressummen der Enchytraeen auf den vier Chemikalienflächen (in Prozent der Kontrolle) vergleichen (Tab. 3). Dabei zeigten sich die je nach Schicht unterschiedliche Wirkung der beiden Chemikalien. PCP reduziert demnach nur in der L-Schicht die Anzahl der Enchytraeen sofort, während es in den tieferen Schichten erst im 2. Jahr der Applikationsphase drastisch wirkt (Ausnahme aus unbekanntem Grund: PCP(1) in der F-Schicht). 1985 ist auf PCP(1) in allen 3 Schichten, auf PCP(5) nur in der L- (teilweise) und F-Schicht, eine Erholung zu konstatieren. 2,4,5-T wirkt, selbst in der L-Schicht, weniger drastisch als PCP. Dafür tritt die Wirkung, vor allem in der H-Schicht, sofort ein. In der F-Schicht ist eine Erholung bei der niedrigen Konzentration noch im Jahr 1982, bei der hohen Konzentration erst ab 1984 zu verzeichnen. Auffallend ist, dass 1985 nur in der H-Schicht von 2,4,5-T(1) die sonst auf beiden Flächen in allen Schichten auftretende Überschussreaktion fehlt. Beide Chemikalien wirken demnach 1985 in der H-Schicht stärker als in der F-Schicht.

4.2.3 Wirkung auf die Altersstruktur

Die Verteilung der Würmer auf die einzelnen Altersstadien auf der Kontrollfläche war im Versuchszeitraum weitgehend konstant (72 17 11 %; Tab. 4). Auf der Fläche PCP(5) werden in der Applikationsphase juvenile Tiere relativ stärker beeinträchtigt als subadulte oder adulte Individuen. Auf den anderen drei Chemikalienflächen wurden dagegen die älteren Stadien mehr geschädigt als die Jungtiere. In der Erholungsphase reagieren die Tiere auf jeder Fläche unterschiedlich. Auf PCP(5) fallen bei Anstieg des Juvenil- und des Subadulti-Anteils die Adulti weitgehend aus, bei PCP(1) ändert sich wenig und auf den 2,4,5-T-Flächen ist bei anhaltend geringer Adultzahl aber steigendem Subadultanteil eine beginnende Angleichung an die Kontrolle zu beobachten. Mit Ausnahme der hohen PCP-Konzentration wirken demnach die Chemikalien in der Applikationsphase verstärkt auf ältere Stadien. In der Erholungsphase ist der niedrige Adultanteil eher durch das Ausfallen der vorangegangenen Generationen zu erklären.

4.2.4 Wirkungen auf energetische Parameter

Um die durch die Beeinträchtigung der Enchytraeen-zönose mittelbar auf der Ebene des Bodenökosystems entstehenden Effekte einschätzen zu können, wurde versucht, die Veränderungen auf energetischer Ebene zu quantifizieren. Dazu wurden auf der Grundlage der gemessenen Abundanz- und Biomassewerte sowie unter Bezug auf Umrechnungsfaktoren aus der Literatur (z.B. PETERSEN & LUXTON 1982; für Einzelheiten siehe RÖMBKE 1991) Respiration, Produktion und Konsumtion (jeweils in $\text{kJ/m}^2 \cdot \text{y}$) der Enchytraeen auf

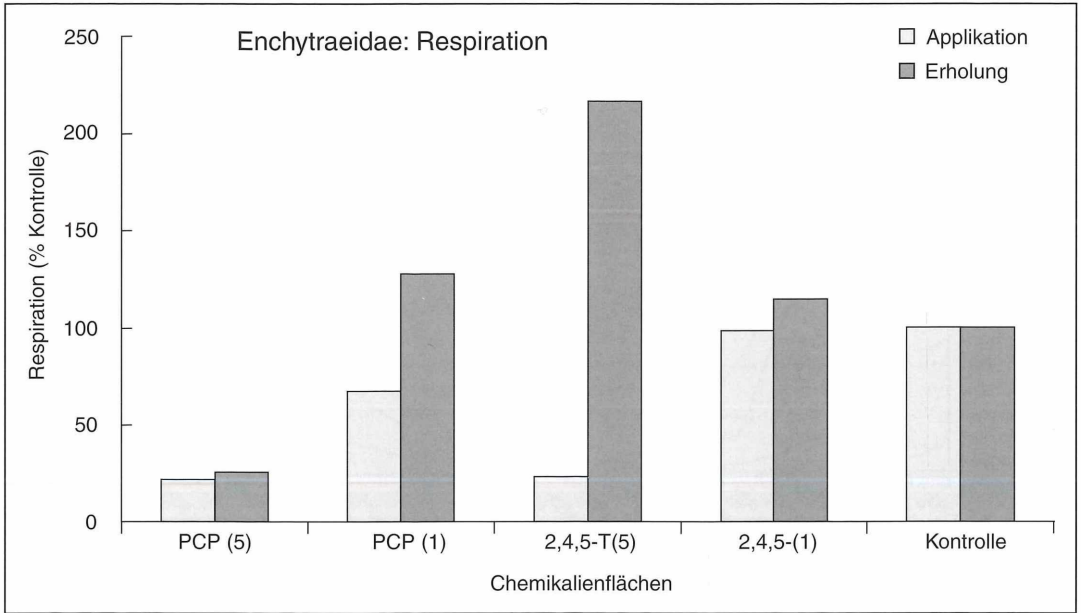


Abbildung 8. Anteil der energetischen Parameter auf den Chemikalienflächen im Vergleich zur Kontrolle des Standardprogramms.

Tabelle 3. Jahressummen der Enchytraeidae in % der Kontrolle nach Schichten getrennt.

	PCP(5)	PCP(1)	2,4,5-T(5)	2,4,5-T(1)	Kontr.
L-Schicht					
1982	0,0	5,5	16,1	28,8	100
1983	0,0	19,6	18,0	37,4	100
1984	3,8	55,8	216,0	317,6	100
1985	57,4	111,4	225,3	411,1	100
F-Schicht					
1982	45,4	108,5	55,9	96,0	100
1983	5,5	75,6	32,2	216,5	100
1984	8,1	73,1	145,7	158,2	100
1985	77,6	214,6	230,1	170,2	100
H-Schicht					
1982	32,1	57,2	7,1	25,8	100
1983	4,4	13,5	9,4	30,5	100
1984	32,5	79,5	96,0	108,4	100
1985	14,6	104,5	149,3	65,2	100

den Chemikalienflächen (zusammengefasst nach Applikations- und Erholungsphase) abgeschätzt und in Bezug zu den Werten der Kontrolle gesetzt.

Am Beispiel der Respiration (Abb. 8) wird deutlich, dass die Effekte der Chemikalien – bedingt durch die einfachen Abschätzungsmethoden – sehr denen bei Abundanz und Biomasse ähneln. In der Erholungsphase ist auf PCP(5) nach dem vorhergehenden starken Rückgang nur eine minimale Zunahme festzustellen. Auf den drei anderen Flächen kommen im umgekehrten Ver-

Tabelle 4. Anteil der drei Altersstadien in % der Gesamtzahl jeder Fläche während der Applikations- und Erholungsphase.

Stadium	PCP(5)	PCP(1)	2,4,5-T(5)	2,4,5-T(1)	Kontr.
Applikation					
Juvenil	58,0	80,9	89,4	84,4	71,5
Subadult	14,3	10,4	4,8	7,8	15,9
Adult	27,7	8,8	5,8	7,8	12,6
Erholung					
Juvenil	77,2	82,5	82,8	80,9	72,9
Subadult	18,1	10,7	13,1	14,2	17,3
Adult	4,7	6,8	4,1	4,9	9,8

hältnis zur vorherigen Schädigung Überschussreaktionen vor. Für 2,4,5-T(1) und PCP(1) liegen die Werte noch im Rahmen der normalen Schwankungsbreite, aber auf 2,4,5-T(5) wird die Kontrolle um mehr als den Faktor 2 übertroffen. Während auf der Kontrollfläche die Respiration der Enchytraeen durchschnittlich bei ca. 4 % des Feinstreueintrags von 10.894 kJ/m²*y liegt (BECK & MITTMANN 1982), würde sie demnach auf den Chemikalienflächen in der Applikationsphase auf 1 % (PCP(5), 2,4,5-T(5)) bzw. 2,5 % (PCP(1)) absinken. In der Erholungsphase steigt der Anteil der Enchytraeen erheblich: Von 4,6 % (2,4,5-T(1)) über 5,2 % (PCP(1)) bis zu 8,8 % (2,4,5-T(5)), während es auf PCP(5) bei 1 % bleibt. Entsprechend hoch liegen die Extremwerte bei der Konsumption. Auf 2,4,5-T(5) könnten demnach (zumindest kurzfristig) bis zu 32 % der gesamten Feinstreu von den Enchytraeen gefressen werden.

5. Diskussion

5.1 Wirkung von Pentachlorphenol

PCP ist eine für Oligochaeten hochtoxische Substanz und wird u.a. deshalb als "umweltgefährlicher" Stoff eingeschätzt (RUDOLPH & BOJE 1986). In Laborversuchen mit der Spezies *Enchytraeus albidus* wurden LC_{50} -Werte von 33 - 204 mg/kg TG in verschiedenen Bodensubstraten gefunden (RÖMBKE & KNACKER 1989). SALMINEN et al. (1995) bestimmten in einem nicht-standardisierten Labortest eine hohe Toxizität von PCP auf die auch im Stadtwald Ettlingen dominante Art *Cognettia sphagnetorum* (geschätzte LC_{50} : 154 mg/kg).

PCP wirkt äußerst toxisch auf die Enchytraeen des Stadtwalds Ettlingen. Während der Applikationsphase werden in der L-Schicht alle Würmer abgetötet (oder vertrieben – bei der auch dominanten Art *C. sphagnetorum* wurden Vermeidungsreaktionen auf PCP-kontaminierte Streu nachgewiesen (SALMINEN & SULKAVA 1996)). In den tieferen Schichten treten ähnlich drastische Wirkungen 6 - 8 Monate später ein, wobei die höhere Konzentration immer stärker und, in der H-Schicht, auch früher wirkt als die niedrige Konzentration. Diese Verzögerung ist primär durch die Adsorption des PCP am Humus und die daraus resultierende langsame Tiefenverlagerung der Chemikalie zu erklären (SALMINEN & HAIMI 1997). Nimmt man aufgrund der Labortestergebnisse einen Bereich von ca. 30 - 200 mg/kg Substrat an, in dem PCP eine Halbierung der Enchytraeenabundanz bewirkt, so werden diese Werte auf PCP(5) in allen Schichten bis einschließlich 1984 weit überschritten. Erst 1985 können die aktuellen Konzentrationen in diese Größenordnung absinken, was im Einklang mit der Ende 1985 beginnenden Erholung der Enchytraeenzönose steht. Im Applikationszeitraum liegt die Chemikalienkonzentration auf PCP(1) nur in der L-Schicht wesentlich oberhalb der LC_{50} -Werte. In den tieferen Schichten ist eher eine etwa fünfzigprozentige Reduktion der Zahl der Enchytraeen zu erwarten, was sehr gut mit dem gefundenen Wert von 58 % übereinstimmt. Studien an finnischen Waldstandorten, die durch den langjährigen Gebrauch von Natrium-PCP-haltigen Holzschutzmitteln kontaminiert wurden, bestätigten die starke Wirkung dieser Substanz auf Enchytraeen (SALMINEN et al. 1995, SALMINEN & HAIMI 1997). Bei einer Nominalkonzentration von 50 mg/kg war die Anzahl der Tiere 15 Wochen nach Applikation um mehr als die Hälfte reduziert, während nach insgesamt 49 Wochen kein Unterschied der Abundanz zur Kontrolle feststellbar war.

Das Fehlen einer höheren Empfindlichkeit jüngerer Enchytraeen gegenüber PCP steht im Gegensatz zur generellen Erwartung, nach der juvenile Tiere gegenüber Umweltchemikalien anfälliger sind als ältere Tiere (WEBER 1953). Allerdings zeigen die Erfahrungen mit *E. albidus* im Labortest, dass die Stadien der Entwick-

lung bis zum Schlüpfvorgang am empfindlichsten sind. Wenn ein Wurm diese Phase überstanden hat, ist mit Sensitivitätsunterschieden im weiteren Verlauf der Entwicklung kaum mehr zu rechnen. Hinweise auf eine Gewöhnung an PCP wurden nicht gefunden. Die im Sommer 1987, also 3,5 Jahre nach Beendigung der Applikation durchgeführte einmalige Probennahme auf allen Versuchsflächen zeigte keine Unterschiede mehr zwischen PCP- und Kontrollflächen.

Für den Beginn der Erholung ist neben dem Rückgang der PCP-Konzentration die differenzierte Reaktion der PCP-abbauenden Mikroflora verantwortlich. Auf PCP(5) ist sie offenbar so extrem geschädigt, dass erst ein Jahr nach Ende der Applikation eine Erholung der Mikroorganismen beginnt, wahrscheinlich bei drastisch verändertem Dominanz-, vielleicht auch Artenspektrum (SCHÖNBORN & DUMPERT 1986). Trotz der nachgewiesenen Schädigung der Mikroflora ist eine Nahrungsverknappung als primäre Ursache der Chemikalienwirkung bei den Würmern zur Deutung der Effekte nicht notwendig, da sich Zeitverlauf und Intensität hinreichend durch direkte toxische Effekte erklären lassen (was auch die Ergebnisse der Laborversuche nahe legen DIDDEN & RÖMBKE 2000).

5.2 Wirkung von 2,4,5-T

Nach den bisher veröffentlichten Untersuchungen ist 2,4,5-T für Oligochaeten wenig toxisch (ADEMA et al. 1984). Im Labortest mit *E. albidus* wurden LC_{50} -Werte zwischen 2400 und 14400 mg/kg gemessen (RÖMBKE & KNACKER 1989). Überraschend ist, dass die auf 2,4,5-T getesteten Arten des Stadtwalds Ettlingen eine deutlich höhere Empfindlichkeit zeigten (LC_{50} -Werte zwischen 100 und 500 mg/kg), was für unterschiedliche physiologische Wirkmechanismen spricht. Bisher wurden Wirkungen von 2,4,5-T meist auf Verunreinigungen wie TCDD zurückgeführt (RIPPEN 1999), so dass die Ergebnisse aus dem Stadtwald Ettlingen, nach denen auch reines 2,4,5-T bei Enchytraeen Schädigungen hervorrufen kann, die ökotoxikologische Beurteilung dieser Chemikalie modifizieren.

2,4,5-T in hoher Konzentration reduziert Zahl und Biomasse der Enchytraeen während der Applikationsphase deutlich. Nach den durch Labortests bekannten LC_{50} -Werten wäre ein fünfzigprozentiger Rückgang der Tiere zwischen 100 - 500 mg 2,4,5-T pro kg TG zu erwarten. Diese Größenordnung wird auf den 2,4,5-T-Flächen nur in der L-Schicht der Applikationsphase erreicht (2,4,5-T(1)) bzw. überschritten (2,4,5-T(5)), während in den tieferen Schichten deutlich geringere Werte bei den 5 stichprobenartigen Messungen gefunden wurden, die keine Beeinträchtigung der Tiere hervorrufen sollten. Trotzdem kommt es auf der 2,4,5-T(5)-Fläche auch in den beiden tieferen Schichten 1983 zu eindeutigen Wirkungen. Dies ist wahrscheinlich durch die erhebliche Tiefenverlagerung der Chemikalie zu erklären, die mit den relativ wenigen rück-

standsanalytischen Probennahmen nicht erfasst wurde. In der F-Schicht ist eine Wirkung der niedrigen 2,4,5-T-Konzentration weder in der Belastungs- noch dem größten Teil der Erholungsphase nachweisbar, während in der H-Schicht die Zahl der Tiere in der gesamten Applikationsphase stark erniedrigt ist. Aus ungeklärten Gründen sinkt die Zahl der Enchytraeen Ende 1985 sogar unter die der Kontrolle.

Insgesamt zeigt sich auf der 2,4,5-T(1)-Fläche das Bild einer nur kurz beeinträchtigten Population, die sich, trotz weiter anhaltender Chemikalienausbringung, bald wieder erholt. Offenbar liegt hier eine Gewöhnung der Tiere an den Stressfaktor vor. In dieser Gesamtdarstellung wird aber die unterschiedliche Reaktion in den einzelnen Schichten überdeckt. Nach dem warmen und trockenen Sommer 1983, durch den die Zahl der Tiere auf allen Versuchsflächen stark zurückgeht, erweist sich die Erholung in der L-Schicht als labil, denn sie ist gegenüber der Kontrolle um ca. ein halbes Jahr verzögert. An anderen Standorten kann die Wirkung einer Chemikalie durch Trockenheit sogar maskiert werden, da letztere die Tiere in tiefere Bodenschichten treibt, wo sie der Chemikalie nicht direkt ausgesetzt sind (MARTIKAINEN 1998).

Auch wenn der Zeitverlauf auf beiden Flächen ähnlich ist, so wirkt die hohe Konzentration doch wesentlich toxischer. Hinweise auf eine Gewöhnung der Enchytraeen fehlen auf 2,4,5-T(5). Es bleibt der Widerspruch, dass trotz ähnlicher Chemikalienkonzentrationen die Tiere in der F-Schicht 1982/83 weniger als in der H-Schicht reagieren. Die wahrscheinlichste Erklärung ist, dass diese Chemikalie artspezifisch wirkt, was sowohl durch Netzbeutelversuche (RÖMBKE 1994) als auch durch die Ergebnisse der Labortests nahegelegt wird. Unterschiedliche Auswirkungen einer Chemikalie auf verschiedene Enchytraeenarten (selbst innerhalb einer Gattung) fanden auch BETHGE-BEILFUSS & WESTHEIDE (1987) am Beispiel mehrerer Pestizide und *Enchytraeus*-Species. Vielleicht beruht dies auf der jeweiligen Ausbildung pestizid-abbauender Enzyme (z.B. Glutathion-S-transferase), wie sie z.B. in *E. albidus* nachgewiesen wurde (STENERSSEN & OIEN 1981). Die Notwendigkeit des "Anwerfens" solcher vielleicht nur fakultativ vorhandener Enzymkomplexe könnte zugleich eine Erklärung für die zuerst deutliche, aber schon nach wenigen Monaten beendete Wirkung auf der Fläche 2,4,5-T(1) sein.

5.3 Beurteilung der Chemikalienwirkung

Die trotz der drastischen Chemikalienwirkung auf allen Versuchsflächen (mit Ausnahme von PCP(5)) nach Abklingen der aktuellen, extrem hohen Belastung zu beobachtende schnelle Erholung der Enchytraeenzönose ist durch die kurzen Generationszeiten der meisten Arten erklärbar. Die schnelle Vermehrung sichert diesen Enchytraeenarten in der Erholungsphase einen Vorsprung gegenüber anderen saprophagen Tiergrup-

pen, die fast alle längere Generationszeiten haben (BECK et al. 1988). Dementsprechend ist bei der Biomasse der Enchytraeen, die weitgehend von großkörperigen Tieren mit univoltinen Lebenszyklus abhängt (*Mesenchytraeus glandulosus*), eine verspätete Erholungsreaktion zu beobachten.

FLETCHER & FREEDMAN (1986) konnten keine Auswirkungen von 2,4,5-T auf die Dekomposition eines Waldstreu-Gemischs bei einer Konzentration von 0,67 g/m² finden. Dagegen wird der Abbau der Laubstreu im Stadtwald Ettlingen bei ähnlichen Konzentration (2,4,5-T(1)) etwa ein halbes Jahr verzögert, während es auf 2,4,5-T(5) ca. 1,5 Jahre sind (die entsprechenden Werte für PCP(1) und PCP(5) betragen 1,5 und 2 Jahre, BECK et al. 1988). Dadurch kommt es zur Akkumulation organischen Materials, das nach Abklingen der Belastung von den Enchytraeen genutzt werden kann, zumindest solange, wie nicht andere Faktoren (z.B. andere abiotische Eigenschaften der im Verlauf des Abbauprozesses in tiefere Schichten abgesunkenen Streu) dem entgegenstehen.

Demzufolge sind, genau spiegelbildlich zum Grad der vorherigen Belastung, aber direkt korreliert mit der verfügbaren Nahrungsmenge, Überschussreaktionen bei Abundanz und Biomasse der Enchytraeen zu beobachten. Da nicht nur die Ausprägung, sondern auch die Dauer der Kompensation vom Abbaurückstand abhängt, reichte die Länge des Versuchszeitraums bei PCP(5), teilweise auch bei 2,4,5-T(5) nicht aus, um eine vollständige Wiederangleichung an die Kontrolle festzustellen. Bestes Beispiel für diese Reaktion ist die Biomasseentwicklung, doch lässt sich ein ähnliches Verhältnis auch bei den Abundanzzahlen feststellen. Für die Fläche PCP(5) wäre demnach für den Zeitraum 1986/87 eine noch ausgeprägtere Überschussreaktion als auf den anderen Versuchsflächen zu erwarten. Diese Erwartung konnte bei der einmaligen Probennahme im August 1987 nicht bestätigt werden. Es muss offen bleiben, ob der dabei festgestellte Gleichstand bei den Abundanzzahlen den Beginn oder das Ende einer Überschussreaktion markiert. Selbst das Fehlen einer solchen Reaktion, bedingt durch eine zu tiefgehende Schädigung der Enchytraeenzönose, ist möglich.

Solche abgestuften Überschussreaktionen stellen offenbar die normale Reaktion von Enchytraeen auf eine einmalige Belastung (als solche kann die gesamte Applikationsphase aufgefaßt werden) dar. Die Belastung kann dabei eine Chemikalie (DIDDEN & RÖMBKE 2000) oder eine Biotopveränderung (z. B. ein Kahlschlag, sein (LUNDKVIST 1983); auch natürliche Stressfaktoren wie Trockenheit können solche Reaktionen auslösen (MARTIKAINEN 1998). In allen Fällen war eine verbesserte Nahrungsversorgung der Grund für die Massentwicklung der Enchytraeen. Voraussetzung dafür dürften immer günstige Bedingungen für die Mikroflora sein (LOHM et al. 1977), während der Beitrag geringeren Konkurrenzdrucks, z.B. von Collembolen, schwer

einzuschätzen ist. Der Ausfall von Räubern spielt offenbar nur auf einer mit Insektiziden behandelten Ackerfläche eine Rolle (WAY & SCOPES 1968).

Aufgrund dieser Kompensationsreaktionen und unter Berücksichtigung der wichtigen Rolle der Enchytraeen (quantitativ und qualitativ) bei der Dekomposition des Bestandesabfalls wurde von WAY & SCOPES (1968) der Schluss gezogen, dass eine Belastung als tolerabel anzusehen ist, wenn der Streuabbau (primär die Regulation der Mikroflora) insgesamt nicht beeinträchtigt wird. Wie die Abschätzung der energetischen Parameter der Enchytraeen auf den Chemikalienflächen zeigt, wird mit Ausnahme von PCP(5) der Rückstand aus der Applikationsphase in den ersten 2 Jahren nach Ende der Applikation aufgrund der Überschussreaktionen kompensiert, teilweise sogar übertroffen.

Auswirkungen der Chemikalien auf funktionaler Ebene (z.B. als Defizit in der Nährstoffversorgung der Bäume aufgrund einer Verzögerung des Streuabbaus) sind nicht leicht quantifizierbar. Auch ist unklar, ab welcher Dauer eine solche Beeinträchtigung messbare Veränderungen des Nährstoffzyklus verursachen kann. Allerdings fanden SALMINEN et al. (1995) in Mikrokosmosversuchen, dass die Regulation der Mikroorganismen durch Enchytraeen (und speziell Nematoden) vor allem zu Beginn des Dekompositionsprozesses durch Chemikalien wie PCP so beeinflusst werden kann, dass langfristig Auswirkungen auf den Nährstoffhaushalt des Waldbodens nicht auszuschließen sind. Chemikalien, die potenziell solch drastische Wirkungen auf das Gesamtsystem hervorrufen können, dürfen nicht in die Umwelt gelangen und sind damit als nicht tolerierbar anzusehen.

Bei der Beurteilung der Tolerierbarkeit einer nach zwei Jahren wieder weitgehend ausgeglichenen Wirkung sind demnach zwei Kriterien anzulegen: Ausmaß und Nachhaltigkeit (DOMSCH et al. 1983), wobei diese nicht nur auf der Ebene der Funktion einer Tiergruppe oder des Gesamtsystems, sondern auch für die jeweilige Struktur (Artenspektrum und Dominanzgefüge) zu gelten haben (BECK et al. 1988). Das heißt, selbst wenn die Enchytraeen den Leistungsrückstand auf den Versuchflächen vollständig aufgeholt haben, ist es nicht gleichgültig, ob diese Funktion von wenigen Arten oder der natürlicherweise an diesem Standort vorkommenden Zönose erbracht wurde. Wie an anderer Stelle gezeigt wurde (RÖMBKE 1994), wird die normale Artenzahl (Kontrollfläche: ca. 10) während der Applikationsphase stark reduziert (häufig tritt nur noch *C. sphaagnetorum* auf), so dass auch dieses Ergebnis für eine Nicht-Tolerierbarkeit des Einsatzes solch toxischer Umweltchemikalien spricht.

Abschließend ist die praktische Frage zu beantworten, ob Enchytraeen aufgrund der vorliegenden Untersuchung für ein Biomonitoring nutzbar sind. Ihre differenzierte Reaktion im Freiland bestätigt die grundsätzliche Eignung für diesen Zweck. Neben einer Reihe von Ar-

beiten, in denen die Würmer ähnlich wie im Stadtwald Ettlungen reagieren (z.B. KITAZAWA & KITAZAWA 1980; PIRHONEN & HUHTA 1984; MOSER et al. 1999) gibt es einige wenige Beispiele, in denen ihr Auftreten nicht mit anthropogenen Belastungsfaktoren korrelierbar war. Neben methodischen Gründen, z.B. unzureichenden Extraktionsverfahren (McCOLL 1984) kommen für solche Fälle belastungsspezifische Gründe in Frage (MILLS & ALLEY 1973). Als einzige Einschränkung gegen eine verstärkte Nutzung der Enchytraeen für Monitoringzwecke bleibt demnach der geringe Wissensstand bezüglich Taxonomie und Ökologie der einzelnen Arten (BENGTSSON & RUNDGREN 1984). Die vorliegende Arbeit soll daher ein Beitrag zur Verbesserung der ökologischen Kenntnisse über Enchytraeen sein, um die weitergehende Nutzung dieser auf den ersten Blick so einheitlichen und unscheinbaren Tiergruppe zu ermöglichen.

Danksagung

Ich danke in besonderer Weise Herrn Prof. LUDWIG BECK für die langjährige Unterstützung meiner wissenschaftlichen Arbeit und die durch ihn aufgebaute außerordentlich erfolgreiche Kooperation zwischen dem Naturkundemuseum Karlsruhe und der Firma ECT Oekotoxikologie GmbH. Besonders wertvoll ist mir die Erinnerung an viele gemeinsame Exkursionen und Tagungsauftritte und die uns verbindende Freundschaft.

6. Literatur

- ABRAHAMSEN, G. (1973): Studies on body-volume, body-surface area, density and live weight of Enchytraeidae (Oligochaeta). – *Pedobiologia*, **13**: 6-15.
- ADEMA, D. M., BARUG, D. & VONK, J. W. (1984): Comparison of the effects of several chemicals on microorganisms, higher plants and earthworms. – In: *Actes Symp. Int. "Ecotoxicologie terrestre"*: 199-214; Les Arcs.
- AXELSSON, B., LOHM, U. & PERSSON, T. (1984): Enchytraeids, lumbricids and soil arthropods in a northern deciduous woodland - a quantitative study. – *Holarctic Ecology*, **7**: 91-103.
- BECK, L. & MITTMANN, H.-W. (1982): Zur Biologie eines Buchenwaldbodens. 2. Klima, Streuproduktion und Bodendestruktion. – *Carolina*, **40**: 65-90.
- BECK, L., DUMPERT, K., FRANKE, U., MITTMANN, H.-W., RÖMBKE, J. & SCHÖNBORN, W. (1988): Vergleichende ökologische Untersuchungen in einem Buchenwald nach Einwirkung von Umweltchemikalien. – *Jülich Spezial*, **439**: 548-702.
- BENGTSSON, G. & RUNDGREN, S. (1982): Population density and species number of enchytraeids in coniferous forest soils polluted by a brass mill. – *Pedobiologia*, **24**: 211-218.
- BERGMANN, J.H. (1981): Herbizide in der Forstwirtschaft. – Berlin (VEB Deutsch. Landwirtschaftsverl.).
- BETHGE-BEILFUSS, D. & WESTHEIDE, W. (1986): Subletale Schädigungen terrestrischer Enchytraeiden (Oligochaeta, Annelida) durch Pflanzenbehandlungsmittel. – *Verh. Ges. Ökol.*, **16**: 417-422.
- CHALUPSKY, J. & LEPS, J. (1985): The spatial pattern of Enchytraeidae (Oligochaeta). – *Oecologia*, **68**: 153-157.
- CROSBY, D. G. (1981): Environmental chemistry of Pentachlorophenol. – *Pure Appl. Chem.*, **53**: 1051-1080.

- DIDDEN, W. A. M. (1993): Ecology of terrestrial Enchytraeidae. – *Pedobiologia*, **37**: 2-29.
- DIDDEN, W. A. M. & RÖMBKE, J. (2000): Enchytraeids as indicator organisms for chemical stress in terrestrial ecosystems. – *Ecotox. Envir. Safety* (im Druck).
- DOMSCH, K.H., JAGNOW, G. & ANDERSON, T.H. (1983): An ecological concept for the assessment of side-effects of agro-chemicals on soil microorganisms. – *Residue Review*, **86**: 65-105.
- FLETCHER, K. & FREEDMAN, B. (1986): Effects of the herbicides Glyphosate, 2,4,5-Trichlorophenoxyacetic acid, and 2,4-Dichlorophenoxyacetic acid on forest litter decomposition. – *Can. J. Forest Res.*, **16**: 6-9.
- KITAZAWA, Y. & KITAZAWA, T. (1980): Influence of application of a fungicide, an insecticide, and a compost upon soil biotic community. – *Proc. VII Int. Coll. Soil Zool.*: 94-108.
- LITZ, N. & BLUME, H.-P. (1985): The behavior of the herbicide 2,4,5-T in German soils under arable land and forest. *Zeit. Pflanzenern. Bodenkd.*, **148**: 289-305.
- LOHM, U., LUNDKVIST, H., PERSSON, T. & WIRÉN, A. (1977): Effects of nitrogen fertilization on the abundance of enchytraeids and microarthropods in Scots pine forests. – *Studia forestalia Suecia*, **140**: 5-23.
- LU, P.-Y., METCALF, R. I. & COLE, L. K. (1978): The environmental fate of ¹⁴C-Pentachlorophenol in laboratory model ecosystems. – In: RANGA, RAO, K. (Ed.) *Pentachlorophenol. Chemistry, Pharmacology, and Environmental Toxicology*: 58-68; London/New York (Plenum Press).
- LUNDKVIST, H. (1983): Effects of clear-cutting on the Enchytraeids in a Scots Pine forest soil in central Sweden. – *J. Appl. Ecol.*, **20**: 873-886.
- MARTIKAINEN, E. (1998): Environmental Factors Influencing Effects of Chemicals on Soil Animals. *Studies at Population and Community Levels*. – 121 S.; Dissertation, University Jyväskylä, Finland.
- MCCOLL, H. P. (1984): Nematicides and field population of Enchytraeids and Earthworms. – *Soil Biol. Biochem.*, **16**: 139-144.
- MILLS, J. T. & ALLEY, B. P. (1973): Interactions between biotic components in soils and their modification by management practices in Canada: A review. – *Can. J. Plant Sci.*, **53**: 425-441.
- MOSER, T., FÖRSTER, B. & RÖMBKE, J. (1999): Overview on the use of Enchytraeidae in Terrestrial Model Ecosystems (or „microcosm“) investigations. – *Newsletter on Enchytraeidae*, **6**: 111-116.
- NIELSEN, C. O. (1955): Studies on Enchytraeidae 5. Factors causing seasonal fluctuations in numbers. – *Oikos*, **6**: 153-169.
- NIELSEN, C. O. & CHRISTENSEN, B. (1959): The Enchytraeidae, critical revision and taxonomy of European species. – *Natura Jutlandica*, **8-9**: 1-160.
- NIELSEN, C. O. & CHRISTENSEN, B. (1961): The Enchytraeidae, critical revision and taxonomy of European species. Supplement 1. – *Natura Jutlandica*, **10**: 1-23.
- O'CONNOR, F. B. (1967): The Enchytraeidae. – In: BURGESS, A. & RAW, F. (Ed.). *Soil Biology*: 212-257; London, New York.
- O'CONNOR, F. B. (1971): The enchytraeids. – In: PHILLIPSON, J. (Ed.). *Methods of study in quantitative soil ecology*: 83-106; Oxford (IBP Handbook, Blackwell).
- OECD (Organisation for Economic Development) (2000): OECD-Guideline for Testing of Chemicals Proposal for a new guideline No. 220. *Enchytraeidae Reproduction Test*. Paris.
- PETERSEN, H. & LUXTON, M. (1982): A comparative analysis of soil fauna populations and their role in decomposition processes. – *Oikos*, **39**: 287-388.
- PIRHONEN, R. & HUHTA, V. (1984): Petroleum fractions in soil: Effects on populations of Nematoda, Enchytraeidae and Microarthropoda. – *Soil Biol. Biochem.*, **16**: 347-350.
- RIPPEN, G. (1995): *Handbuch der Umweltchemikalien*. – 27 Erg.Lfg., 67 S.; Landsberg (Ecomed).
- RIPPEN, G. (1999): *Handbuch der Umweltchemikalien*. – 47 Erg.Lfg., 18 S.; Landsberg (Ecomed).
- RÖMBKE, J. & KREYSCH, H.-G. (1988): Nutzung eines halbautomatischen Bildauswertegerätes zur Erfassung biometrischer Kenndaten von Enchytraeiden (Oligochaeta). – *Pedobiologia*, **32**: 267-271.
- RÖMBKE, J. (1989): Zur Biologie eines Buchenwaldbodens. 12. Die Enchytraeidae. – *Carolinea*, **47**: 55-92.
- RÖMBKE, J. & KNACKER, T. (1989): Aquatic toxicity test for enchytraeids. – *Hydrobiologia*, **180**: 235-242.
- RÖMBKE, J. (1991): Estimates of the Enchytraeidae (Oligochaeta, Annelida) contribution to energy flow in the soil system of an acid beech wood forest. – *Biol. Fert. Soils*, **11**: 255-260.
- RÖMBKE, J. (1994): Die Auswirkungen von Umweltchemikalien auf die Enchytraeidae (Oligochaeta) eines Moder-Buchenwaldbodens. – *Mitt. Hamburg. Zool. Mus. Inst.*, **89** Ergbd. 2: 187-197.
- RÖMBKE, J. & MOSER, T. (2000): *Enchytraeid Reproduction Test (ERT): Description of the method and results of a ring-test* (in prep.).
- RUDDOLPH, P. & BOJE, R. (1986): *Ökotoxikologie*. – 105 S.; Landsberg (Ecomed).
- SALMINEN, J. & SILKAVA, P. (1996): Distribution of soil animals in patchily contaminated soil. – *Soil Biol. Biochem.*, **28**: 1349-1355.
- SALMINEN, J., HAIMI, J., SIRONEN, A. & AHTIAINEN, J. (1995): Effects of Pentachlorophenol and Biotic Interactions on Soil Fauna and Decomposition in Humus Soil. – *Ecotox. Envir. Safety*, **31**: 250-257
- SALMINEN, J. & HAIMI, J. (1997): Effects of pentachlorophenol on soil organisms and decomposition in forest soil. – *J. Appl. Ecol.*, **34**: 101-110.
- SCHÉELE, B. (1980): Reference chemicals as aids in evaluating a research programme - selecting aims and criteria. – *Chemosphere*, **9**: 293-309.
- SCHÖNBORN, W. & DUMPERT, K. (1986): Zur Biologie eines Buchenwaldbodens. 8. Die Mikroflora. *Carolinea*, **44**: 129-138.
- STENERSEN, J. & OIEN, N. (1981): Glutathione-S-transferases in earthworms (Lumbricidae). Substrate specificity tissue and species distribution and molecular weight. – *Comp. Biochem. Physiol.*, **69 C**: 243-252.
- SWIFT, M. J., HEAL, O. W., & ANDERSON, J. M. (1979): Decomposition in terrestrial ecosystems. – *Studies in Ecology*, **5**, 372 S.; Oxford (Blackwell)
- WAY, M. Y. & SCOPES, N. E. A. (1968): Studies on the persistence and effects on soil fauna of some soil-applied systemic insecticides. – *Ann. Appl. Biol.*, **62**: 199-214.
- WEBER, G. (1953): Die Makrofauna leichter und schwerer Ackerböden und ihre Beeinflussung durch Pflanzenschutzmittel. – *Zeit. Pflanzenern. Bodenkd.*, **61**: 107-118.
- ZELLES, L., EL-KABBANY, S., SCHEUNERT, I. & KÖRTE, F. (1989): Effects of pentachlorophenol-¹⁴C and HgCl₂ on the microflora of various soils in comparison to biodegradation and volatilization. – *Chemosphere*, **19**: 1721-1727
- ZIETZ, E., DUMPERT, K. & J. RÖMBKE (1987): Effects of Pentachlorophenol and 2,4,5-Trichlorophenol on a soil ecosystem. I. Application and residue analysis. – *Science Total Environm.*, **61**: 153-165.

Publikationen des Staatlichen Museums für Naturkunde Karlsruhe

andrias

unregelmäßig erscheinende Einzelbände zu Themen aus naturkundlichen Forschungsgebieten

- | | |
|---|---------|
| 1. Taxonomie und Phylogenie von Arthropoden. – 102 S., 37 Abb.; 1981 | DM 34,- |
| 2. Vegetationskunde und Lichenologie. – 64 S., 17 Abb.; 1983 | DM 28,- |
| 3. Morphologie und Taxonomie von Insekten. – 104 S., 172 Abb.; 1983 | DM 40,- |
| 4. Fossilfundstätte Messel. – 171 S., 49 Abb., 17 Taf.; 1985 | DM 60,- |
| 5. Taxonomie und Phylogenie von Arthropoden. – 224 S., 114 Abb.; 1986 | DM 65,- |
| 6. Fossilfundstätte Höwenegg. – 128 S., 96 Abb., 6 Taf., 1 Falttaf.; 1989 | DM 56,- |
| 7. Taxonomie und Phylogenie von Arthropoden. – 172 S., 79 Abb.; 1990 | DM 52,- |
| 8. Fossilfundstätte Höwenegg. – 64 S., 30 Abb.; 1991 | DM 28,- |
| 9. Taxonomie und Phylogenie von Arthropoden. – 210 S., 127 Abb.; 1992 | DM 60,- |
| 10. Fossilfundstätte Höwenegg. – 230 S., 192 Abb.; 1997 | DM 80,- |
| 11. Taxonomie und Phylogenie von Nematoden. – 90 S., 24 Abb., 81 Taf.; 1993 | DM 52,- |
| 12. Taxonomie und Phylogenie von Arthropoden. – 94 S., 48 Abb.; 1994 | DM 30,- |
| 13. Taxonomie und Ökologie tropischer Invertebraten. –
224 S., 82 Abb., 16 Farbtaf.; 1994 | DM 70,- |
| 14. Taxonomie, Verbreitung und Ökologie von Spinnen. –
279 S., 2 Abb., 124 Kart., 118 Taf.; 1999 | DM 70,- |
| 15. Festband zu Ehren von Prof. Dr. LUDWIG BECK. –
218 S., 88 Abb., 10 Farbtaf.; 2001 | DM 70,- |

carolinea

setzt mit Band 40 die von 1936 bis 1980 mit 39 Bänden erschienenen „Beiträge zur naturkundlichen Forschung in Südwestdeutschland“ fort. Jahresbände mit naturkundlichen Arbeiten und Mitteilungen aus dem südwestdeutschen Raum sowie aus dem Museum am Friedrichsplatz, dem Naturwissenschaftlichen Verein Karlsruhe und der Bezirksstelle für Naturschutz und Landschaftspflege Karlsruhe in allgemeinverständlicher Form.

letzter Band:

- | | |
|--|---------|
| Band 58: 278 S., 101 Abb., 16 Farbtaf.; 2000 | DM 80,- |
|--|---------|

carolinea, Beihefte

Monografische Arbeiten, Kataloge, Themenbände etc., in unregelmäßiger Folge

- | | |
|--|---------|
| 5. U. FRANKE: Katalog zur Sammlung limnischer Copepoden von Prof. Dr. F. KIEFER –
433 S., 2 Abb.; 1989 | DM 36,- |
| 6. R. WOLF & F.-G. LINK: Der Füllmenbacher Hofberg – ein Rest historischer
Weinberglandschaft im westlichen Stromberg – 84 S., 35 Abb.; 1990 | DM 20,- |
| 7. Gesamtverzeichnis der Aufsätze der Publikationsreihen des Naturkundemuseums
und des Naturwissenschaftlichen Vereins in Karlsruhe 1864 - 1993; in Vorbereitung | |
| 8. E. FREY & B. HERKNER (Eds.): Artbegriff versus Evolutionstheorie? – 86 S., 3 Abb;
1993 | DM 15,- |
| 9. P. HAVELKA: Auswilderung, Gefangenschaftsvermehrung und Erhaltung bedrohter
Tierarten – eine Aufgabe des Naturschutzes. – 64 S., 75 Abb; 1995 | DM 20,- |
| 10. R. HECKMANN: Katalog der Wanzen aus Baden-Württemberg in der Sammlung
des Staatlichen Museums für Naturkunde Karlsruhe (Insecta, Heteroptera). –
146 S., 25 Karten; 1996 | DM 25,- |
| 11. D. HAAS, P. HAVELKA & H.-W. MITTMANN: Neusiedler in menschlichen Siedlungen:
Wasservogel auf städtischen Gewässern. – 84 S., 137 Farbb.; 1998 | DM 10,- |
| 12. M. R. SCHEURIG, H.-W. MITTMANN & P. HAVELKA: Brutvogel-Monitoring
Baden-Württemberg 1992-1998. – 203 S., 12 Abb.; 1998 | DM 10,- |
| 13. B. HERKNER: Über die evolutionäre Entstehung des tetrapoden Lokomotions-
apparates der Landwirbeltiere. – 353 S., 105 Abb.; 1999 | DM 30,- |
| 14. M. R. SCHEURIG, P. HAVELKA & H.-W. MITTMANN: Brutvogel-Monitoring
Baden-Württemberg 1992-1999. – 151 S., 24 Abb.; 1999 | DM 10,- |

Bestellungen an das Staatliche Museum für Naturkunde Karlsruhe – Bibliothek –, Postfach 6209, D-76042 Karlsruhe.

Zu den angegebenen Preisen wird bei Versand ein Betrag von DM 3,50 für Porto und Verpackung in Rechnung gestellt. Bestellungen unter DM 20,- nur gegen Vorkasse.

Mitglieder des Naturwissenschaftlichen Vereins Karlsruhe e. V. erhalten auf die Zeitschriften andrias und carolinea, auf die Beihefte und auf ältere Bände der „Beiträge“ einen Rabatt von 30%.