**Thema: Taxonomie, Faunistik und Ökologie tropischer Invertebraten**

Oligochaeta, Arthropoda, Araneae, Opiliones,
Isoptera, Orthoptera, Coleoptera und Formicidae

# andrias 13

Staatliches Museum für Naturkunde Karlsruhe 30. 9. 1994

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Dieser Band ist
**Herrn Prof. Dr. Hans-Wilhelm Koepcke**,
einem der Pioniere tropenökologischer Forschung in Südamerika,
zu seinem 80. Geburtstag gewidmet

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LUDWIG BECK, HUBERT HÖFER & MANFRED VERHAAGH

# Tropische Diversität, ihre Aufrechterhaltung und deren Mechanismen

„Mechanismen der Aufrechterhaltung tropischer Diversität“ ist das Thema eines Schwerpunktprogramms der Deutschen Forschungsgemeinschaft, an dem etwa 25 Arbeitsgruppen beteiligt sind. Es ging aus langen, mehrere Jahre währenden Diskussionen hervor, die um die Frage kreisten, wie dem Dilemma des himmelweiten Auseinanderklaffens zwischen der rasant voranschreitenden Zerstörung tropischer Lebensräume, insbesondere der tropischen Regenwälder, und deren Erforschung beizukommen sei. Dabei war allen bewußt, daß „tropische Diversität“ schon auf der Ebene der Struktur alle Dimensionen sprengt – Zahlen zwischen 10 und 80 Mio. Arten stehen zur Diskussion –, von den funktionalen Verknüpfungen zwischen den Gliedern der Ökosysteme ganz zu schweigen.

Angesichts der Aussichtslosigkeit, etwa den Artenbestand auch nur eines einzigen größeren Lebensraumes in überschaubarer Zeit zu erfassen, richtete sich die Hoffnung darauf, auf der höheren Ebene der funktionalen Zusammenhänge die spärlichen Kräfte wirkungsvoller einsetzen zu können und die flächendeckende Vergeblichkeit der Bemühungen mit punktuellen Hoffnungsstrahlen zu erhellen. Zwei Aspekte verstärkten diese Richtung: Zum einen ist es das Streben eines jeden Forschers, gleich welchem Fachgebiet er sich zugehörig betrachtet, über die Feststellung von Vielfalt hinaus zu deren Begründung vorzudringen; zum anderen wäre es sehr schwierig, mit einer offensichtlichen open-end-Veranstaltung, wie sie ein Thema „Tropische Diversität“ für sich genommen darstellte, bei jedweder Förderorganisation zu reüssieren. So entstand die zweifache Eingrenzung dieses Themas in der Formulierung „Mechanismen der Aufrechterhaltung tropischer Diversität“.

Dennoch bleibt der Zugang zu den einzelnen, konkreten Forschungsvorhaben ein induktiver: Die Wahl eines Ausschnitts aus der Vielfalt, das Untersuchen seiner Kontinuität in Raum und Zeit und schließlich das Ergründen der Mechanismen, die diese Kontinuität steuern – das sind die Schritte des Vorgehens, und sie sind methodisch verbunden mit einem Fortschreiten vom Deskriptiven zum Experimentellen. Die beschreibende Erfassung der Glieder gibt dem Abstraktum „Diversität“ die konkrete Grundlage, die dem einzelnen Forscher erst die Wahl seines Untersuchungsgegenstandes ermöglicht.

Aufgabe der naturkundlichen Museen ist die Dokumentation der natürlichen Vielfalt in all ihren Gliedern oder Taxa, also Faunistik und Floristik; sie geht einher mit dem Identifizieren und Beschreiben der Taxa, der Taxonomie, und dem Ordnen der Taxa, der Systematik. Auf unser Thema bezogen bilden Faunistik und Floristik, Taxonomie und Systematik die Grundlage der Erfassung tropischer Diversität.

Die Aufgabe der Museen reicht aber darüber hinaus zur vergleichenden Prüfung der Kontinuität der gefundenen Einheiten in Raum und Zeit: Systematik wird zur Phylogenie, Faunistik und Floristik werden zur beschreibenden Ökologie, beispielsweise zur Vegetationskunde. Für unser Thema heißt dies: Untersuchung der Aufrechterhaltung tropischer Diversität.

Der einzelne Forscher an einem Museum wird sich in der ständigen Konfrontation mit der Vielfalt und ihrer Kontinuität in den verschiedenen Lebensräumen immer wieder angestachelt sehen, nach der Kausalität zu fragen und damit vom Deskriptiven zum Experimentellen überzugehen. Solche „Grenzüberschreitungen“ sind nicht nur zu begrüßen, sondern auch wesentlicher Bestandteil der Forschung an einem Museum: Denn zum einen bringen sie neue Gesichtspunkte und Anregungen auch für die deskriptive Grundlagenarbeit, zum anderen motivieren sie den Wissenschaftler zusätzlich – angesichts der erdrückenden Menge taxonomischer Basisarbeit ein nicht zu unterschätzender Effekt.

Dabei sind freilich der experimentellen Arbeit am Museum enge Grenzen gezogen, und sie bleibt meist Forschungsprojekten mit Drittmittelunterstützung im sächlichen und vor allem personellen Bereich vorbehalten. So ist auch die Beteiligung einer Arbeitsgruppe des Staatlichen Museums für Naturkunde Karlsruhe an der Erforschung von „Mechanismen der Aufrechterhaltung tropischer Diversität“ nur durch die dankenswerte Unterstützung der Deutschen Forschungsgemeinschaft möglich geworden.

Der vorliegende **andrias**-Band soll dokumentieren, daß sich naturkundliche Museen, hier stellvertretend das Karlsruher Museum, über die Schwerpunktförderung hinaus und nicht unerheblich durch sie stimuliert, mit Arbeitskraft und Sachmitteln in der Tropenökologie engagieren und zwar in dem Teil, der ihre ureigene Aufgabe ist, der Erfassung von Diversität. Dies wird im Nachfolgenden durch 13 von insgesamt 18 Aufsätzen belegt, die direkt oder indirekt aus der Arbeitsgruppe des Karlsruher Museums kommen. Darüber hinaus soll dieser Band deutlich machen, daß auch die anderen Arbeitsgruppen, beispielhaft vertreten durch jene der Universitäten Frankfurt, Freiburg, Göttingen und Würzburg sowie des Max Planck-Instituts in Plön deskriptive Basisarbeit leisten als Voraussetzung der Untersuchung von Mechanismen der Aufrechterhaltung tropischer Diversität. Zwischen den verschiedenen Arbeitsgruppen gibt es Querverbindungen, die teilweise zu enger Zusammenarbeit zwischen einzelnen Forschern geführt hat, wie ebenfalls an einigen Aufsätzen des vorliegenden Bandes deutlich wird.

Ökologische Untersuchungen an tropischen Wirbellosen können oft nur dann erfolgreich durchgeführt werden, wenn Ökologen und Taxonomen eng zusammenarbeiten. Schon die Präzisierung ihrer Fragestellungen macht es erforderlich, daß sich Tropenökologen mit Hilfe von Taxonomen und deren Sammlungen an den Museen intensiv in ihre Tiergruppen einarbeiten. Ebenso kann die Beteiligung von Taxonomen an den Feldarbeiten die Qualität derselben erheblich verbessern.

Als besonders wertvoll hat sich bei unseren eigenen Untersuchungen in Südamerika die enge Zusammenarbeit mit Wissenschaftlern, sowohl Taxonomen als auch Ökologen, des jeweiligen Gastlandes erwiesen, die erfreulicherweise im Rahmen des Schwerpunktprogramms durch begleitende Mittel des Bundesministeriums für wirtschaftliche Zusammenarbeit über die Gesellschaft für Technische Zusammenarbeit finanziell unterstützt wurde. Auch dies wird durch eine Reihe der nachfolgenden Aufsätze belegt.

Die Beiträge des vorliegenden **andrias**-Bandes sind sämtlich zoologischen Inhalts und behandeln schwerpunktmäßig zwei Tiergruppen, Spinnen und Ameisen, zwei der wichtigsten Prädatoren-Gruppen terrestrischer Lebensräume der Tropen; darüber hinaus zeigen sie einen geographischen Schwerpunkt der Arbeiten auf, die Neotropen und dort vor allem das Amazonasgebiet. Besonders der geographische Schwerpunkt spiegelt eine lange Tradition deutscher Tropenforschung wider – und eine kleine Tradition der Karlsruher tropenökologischen Arbeitsgruppe. Diese geht zurück auf den Doktorvater des Erstautors, auf FRIEDRICH SCHALLER, der 1956/57 auf seiner ersten großen Forschungsreise in die Tropen mehrere Wochen in Lima zu Gast war bei HANS-WILHELM und MARIA KOEPCKE. Somit ist es kein Zufall. daß wir diesen **andrias**-Band HANS-WILHELM KOEPCKE, nachmalig Professor an der Universität Hamburg, gleichzeitig stellvertretend für seine Ehefrau MARIA KOEPCKE widmen.

Wir möchten damit einen der Pioniere tropenökologischer Forschung ehren, der den Großteil seines Lebens mit der Erforschung tropischer Diversität verbracht hat. Prof. KOEPCKE, geboren am 23. Juni 1914, ging nach dem 2. Weltkrieg zusammen mit seiner Frau, der Ornithologin Dr. MARIA KOEPCKE, nach Peru, wo beide mehr als 20 Jahre als Wissenschaftler am Museo de Historia Natural „Javier Prado“ in Lima tätig waren. Von der Küstenwüste angefangen über die westlichen Andenabhänge bis zum andinen Hochland erforschten sie gemeinsam dieses äußerst vielfältige Land. Ihr Studium tropischer Lebensräume gipfelte 1968 in der Gründung der Regenwald-Forschungsstation „Panguana“ am Río Yuyapichis im Einzugsgebiet des Río Ucayali. Prof. KOEPCKES umfangreiche Forschungen fanden ihren Niederschlag insbesondere in dem zweibändigen Werk „Die Lebensformen“, das bis heute eine Fundgrube der beschreibenden Ökologie geblieben ist.

Mit Prof. KOEPCKE und seiner Forschungsstation Panguana verbindet die Karlsruher Arbeitgsgruppe aber nicht nur die lose historische Verknüpfung einer Begegnung ihrer „wissenschaftlichen Väter“ in Peru, sondern auch die wesentlich engere Beziehung zweier jüngerer Mitarbeiter der Arbeitsgruppe, WERNER HANAGARTH und MANFRED VERHAAGH. Beide, auch Autoren von Aufsätzen dieses Bandes, weilten in den 70er und 80er Jahren jeweils mehr als zwei Jahre lang in Panguana, erster als Doktorand Prof. KOEPCKES, und beide konnten manche seiner Beobachtungen und Anregungen in der eigenen Arbeit aufgreifen.

Abschließend möchten wir noch einmal die Aufmerksamkeit auf die Bedeutung der Sammlungen in den naturkundlichen Museen lenken; diese Sammlungen sind nicht nur unentbehrliche Basis vieler tropenökologischer Arbeiten, sondern stellen angesichts der Zerstörung tropischer Lebensräume auch einzigartige Dokumente derselben dar. Die Museen sind bei der Erfüllung ihrer Aufgabe als Dokumentationszentren auf die Mitarbeit aller Forscher angewiesen, die Beleg- und Begleitmaterial ihrer Untersuchungen den Sammlungen in den Museen zukommen lassen sollten.

Dabei ist der Vorrang der wissenschaftlichen Sammlungen in den tropischen Herkunftsländern mittlerweile eine Selbstverständlichkeit. Gerade die beiden Länder, mit denen das Karlsruher Museum gegenwärtig die intensivsten Beziehungen unterhält, Bolivien und Brasilien, haben in den letzten beiden Jahrzehnten große und gutgeführte Sammlungen aufgebaut, wie beispielweise die Colección Boliviana de Fauna in La Paz und die Sammlungen des Instituto Nacional de Pesquisas da Amazônia in Manaus. Das Karlsruher Museum tauscht mit beiden Sammlungen südamerikanisches Belegmaterial, wobei Holotypen und die Hälfte der Paratypen neu beschriebener Arten stets in den Herkunftsländern archiviert werden. Dieser Austausch von Belegmaterial dient der Erweiterung der Kenntnisse über die naturräumlichen Grundlagen in diesen Ländern und trägt so nicht unerheblich zu einem besseren Verständnis für die Natur und letztlich zu deren Schutz bei.

**andrias, 13:** 7-16, 1 Fig., 1 Colour Plate; Karlsruhe, 30. 9. 1994

JÖRG RÖMBKE & WERNER HANAGARTH

# The present faunistic knowledge on terrestrial Oligochaeta from Bolivia

**Abstract**

An overview on the terrestrial Oligochaeta found in Bolivia is given. The 50 species listed belong to the families Enchytraeidae, Lumbricidae, Glossoscolecidae, Ocnerodrilidae, Octochaetidae, Acanthodrilidae and Megascolecidae. Included in this contribution are informations from ZICSI (in press) who studied 28 species from Bolivia, describing one new genus and six new species. Roughly one half of all terrestrial Oligochaeta known from Bolivia are peregrine species, introduced by man, both from the temperate regions (e.g. lumbricids from Europe) and from other tropical areas (e.g. *Amynthas corticis* from Asia). The other species, mainly Glossoscolecidae, are either widely distributed in tropical South America or seem to be endemic to Bolivia (*Anteoides rosai*, *Andiorrhinus* (*Amazonidrilus*) *bolivianus*, *Andiorrhinus* (*Andiorrhinus*) *montanus*, *Inkadrilus hanagarthi*, *Martiodrilus bolivianus*, *Martiodrilus silvestris*, *Tamayodrilus roembkei*, *Belladrilus* (*Belladrilus*) *vaucheri*). In comparison to better investigated countries like Brazil or Ecuador it can be assumed that today only a very small percentage of the Bolivian oligochaete fauna is known to science.

**Zusammenfassung**

**Der gegenwärtige Kenntnisstand der Verbreitung terrestrischer Oligochäten in Bolivien**

Die bisherigen Kenntnisse über die Verbreitung der terrestrischen Oligochaeten in Bolivien werden zusammengefasst. Die aufgeführten 50 Arten gehören zu den Familien Enchytraeidae, Lumbricidae, Glossoscolecidae, Ocnerodrilidae, Octochaetidae, Acanthodrilidae und Megascolecidae. Aufgenommen wurden auch Nachweise von 28 Arten aus Boliven (einschließlich einer neuen Gattung und sechs neuen Arten), die von ZICSI (im Druck) parallel zusammengestellt wurden. Ungefähr die Hälfte aller bisher aus Bolivien bekannten terrestrischen Oligochaeta sind peregrine, d.h. durch menschliche Aktivitäten eingeführte Arten, und zwar sowohl aus der gemäßigten Zone (z.B. Lumbriciden aus Europa) wie auch aus anderen tropischen Regionen der Welt (z.B. *Amynthas corticis* aus Asien). Von der anderen Hälfte der Arten, meist Glossoscolecidae, sind einige weit im tropischen Südamerika verbreitet, während andere (*Anteoides rosai*, *Andiorrhinus* (*Amazonidrilus*) *bolivianus*, *Andiorrhinus* (*Andiorrhinus*) *montanus*, *Inkadrilus hanagarthi*, *Martiodrilus bolivianus*, *Martiodrilus silvestris*, *Tamayodrilus roembkei*, *Belladrilus* (*Belladrilus*) *vaucheri*) endemisch für Bolivien zu sein scheinen. Im Vergleich zu besser untersuchten Staaten wie Brasilien oder Equador ist anzunehmen, daß bis heute nur ein sehr kleiner Teil der bolivianischen Oligochaetenfauna bekannt ist.

**Resumen**

**El actual conocimiento sobre la distribución de los oligochetos en Bolivia**

Se presenta un sumario de los conocimientos sobre la distribución de los oligochetos en Bolivia. Las 50 especies tratadas, pertenecen a las familias Enchytraeidae, Lumbricidae, Glossoscolecidae, Ocnerodrilidae, Octochaetidae, Acanthodrilidae y Megascolecidae. Se incluyeron también informaciones de ZICSI (en prensa), quién estudió 28 especies de Bolivia, describiendo un nuevo género y seis nuevas especies. Aproximadamente la mitad de todos los oligoquetos terrestres, conocidos de Bolivia son especies peregrinas, introducidas por actividades humanas, tanto de las zonas templadas (p.e. los Lumbricidae desde Europa) como también de otras regiones tropicales del mundo (p.e. *Amynthas corticis* desde Asia). De la otra mitad de las especies, principalmente Glossoscolecidae, varias tienen una distribución amplia en la Sudamérica tropical, mientras que otras (*Anteoides rosai*, *Andiorrhinus* (*Amazonidrilus*) *bolivianus*, *Andiorrhinus* (*Andiorrhinus*) *montanus*, *Inkadrilus hanagarthi*, *Martiodrilus bolivianus*, *Martiodrilus silvestris*, *Tamayodrilus roembkei*, *Belladrilus* (*Belladrilus*) *vaucheri*) paracen ser endémicas de Bolivia. En comparación con otros paises mejor investigados, como son Brasil o Ecuador, se puede suponer, que hasta la fecha se conoce solo una muy pequeña parte de la fauna de oligochetos de Bolivia.

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## 1. Introduction

During the first decades of the 20. century different surveys, mainly by European scientists, were carried out to get a first insight into the earthworm fauna of Bolivia (COGNETTI 1902, CERNOSVITOV 1934, 1935). Unfortunately, nearly no information was gained during the following years. Only recently, the knowledge of the distribution and the taxonomic situation of these important members of the soil biocenosis increased considerably (ZICSI in press). We wish to thank Prof. Dr. ZICSI for the possibility to incorporate these informations from his manuscript in this overview. In his paper the results of own sampling as well as collections from different authors are presented, thus nearly doubling the number of records.

Investigations at limnic sites also added new informations as many oligochaete species, at least those belonging to the enchytraeid and ocnerodrilid families, prefer semi-aquatic habitats. In any case, the differentiation between aquatic and terrestrial species is not easy in other oligochaete families, too. Since the information concerning the distribution of Oligochaeta in Bolivia was never compiled up to now a comprehensive synopsis of the knowledge, including some previously unpublished records, should be of interest.

arbeit leisten als Voraussetzung der Untersuchung von Mechanismen der Aufrechterhaltung tropischer Diversität. Zwischen den verschiedenen Arbeitsgruppen gibt es Querverbindungen, die teilweise zu enger Zusammenarbeit zwischen einzelnen Forschern geführt hat, wie ebenfalls an einigen Aufsätzen des vorliegenden Bandes deutlich wird.

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Als besonders wertvoll hat sich bei unseren eigenen Untersuchungen in Südamerika die enge Zusammenarbeit mit Wissenschaftlern, sowohl Taxonomen als auch Ökologen, des jeweiligen Gastlandes erwiesen, die erfreulicherweise im Rahmen des Schwerpunktprogramms durch begleitende Mittel des Bundesministeriums für wirtschaftliche Zusammenarbeit über die Gesellschaft für Technische Zusammenarbeit finanziell unterstützt wurde. Auch dies wird durch eine Reihe der nachfolgenden Aufsätze belegt.

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**Resumen**

**El actual conocimiento sobre la distribución de los oligochetos en Bolivia**

Se presenta un sumario de los conocimientos sobre la distribución de los oligochetos en Bolivia. Las 50 especies tratadas, pertenecen a las familias Enchytraeidae, Lumbricidae, Glossoscolecidae, Ocnerodrilidae, Octochaetidae, Acanthodrilidae y Megascolecidae. Se incluyeron también informaciones de ZICSI (en prensa), quién estudió 28 especies de Bolivia, describiendo un nuevo género y seis nuevas especies. Aproximadamente la mitad de todos los oligoquetos terrestres, conocidos de Bolivia son especies peregrinas, introducidas por actividades humanas, tanto de las zonas templadas (p.e. los Lumbricidae desde Europa) como también de otras regiones tropicales del mundo (p.e. *Amynthas corticis* desde Asia). De la otra mitad de las especies, principalmente Glossoscolecidae, varias tienen una distribución amplia en la Sudamérica tropical, mientras que otras (*Anteoides rosai*, *Andiorrhinus* (*Amazonidrilus*) *bolivianus*, *Andiorrhinus* (*Andiorrhinus*) *montanus*, *Inkadrilus hanagarthi*, *Martiodrilus bolivianus*, *Martiodrilus silvestris*, *Tamayodrilus roembkei*, *Belladrilus* (*Belladrilus*) *vaucheri*) paracen ser endémicas de Bolivia. En comparación con otros paises mejor investigados, como son Brasil o Ecuador, se puede suponer, que hasta la fecha se conoce solo una muy pequeña parte de la fauna de oligochetos de Bolivia.

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## 1. Introduction

During the first decades of the 20. century different surveys, mainly by European scientists, were carried out to get a first insight into the earthworm fauna of Bolivia (COGNETTI 1902, CERNOSVITOV 1934, 1935). Unfortunately, nearly no information was gained during the following years. Only recently, the knowledge of the distribution and the taxonomic situation of these important members of the soil biocenosis increased considerably (ZICSI in press). We wish to thank Prof. Dr. ZICSI for the possibility to incorporate these informations from his manuscript in this overview. In his paper the results of own sampling as well as collections from different authors are presented, thus nearly doubling the number of records.

Investigations at limnic sites also added new informations as many oligochaete species, at least those belonging to the enchytraeid and ocnerodrilid families, prefer semi-aquatic habitats. In any case, the differentiation between aquatic and terrestrial species is not easy in other oligochaete families, too. Since the information concerning the distribution of Oligochaeta in Bolivia was never compiled up to now a comprehensive synopsis of the knowledge, including some previously unpublished records, should be of interest.

## 2. Material and Methods

Most of the sampling was done using different modifications of handsorting methods. In nearly no case ecological studies like the assessment of density or biomass per area were intended. In fact, up to now no ecological investigations except the study of ERGUETA (1985) in Huaraco were performed. We tried to collect all information from the literature on Bolivian terrestrial Oligochaeta; also, previously unpublished data from sampling surveys done by several persons are included. Species which are with no doubt limnic or marine are not listed (e.g. *Marionina riparia* BRETSCHER, 1899, and other Enchytraeidae from the genus *Lumbricillus*).

Chapter 3 briefly outlines the geographical and ecological division of Bolivia. In chapter 4 all species known from Bolivia are listed (species Nº are the same as in table 1.) First, it is shown whether a species occurs in other South American countries and/or in other continents. Then, each sampling site in Bolivia is described including available ecological informations (see also tab. 1). In some cases taxonomic and distributional

Table 1. Sampling sites of Oligochaeta with altitude (approx.), affiliated political units and gross ecological characterization (see chapter 3). Species Nº refer to species Nº in chapter 4 (Enchy. = Enchytraeidae, Lumbr. = Lumbricidae, Gloss. = Glossoscolecidae, Ocner. = Ocnerodrilidae, Octo. = Octochaetidae, Acan. = Acanthodrilidae, Mega. = Megascolecidae). Nº of sampling sites are the same as in figure 1.

| Nº | Sampling site | altitude | Provincia | Departamento | ecological zone | Enchy. | Lumbr. | Gloss. | Ocner. | Octo. | Acan. | Mega. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. | area of Unduavi | 4650 m | Nor Yungas | La Paz | moist puna | | 6,7,9,10,13 | | | | 49 | |
| 2. | road to Zongo | 4100 m | Murillo | La Paz | moist puna | | 7 | | | | | |
| 3. | Serranía Macho Pelechuco & Serr. de Charazani | 4060 m | Franz Tamayo | La Paz | moist puna | | | 32 | | | | |
| 4. | Unduavi | 3800-3900 m | Nor Yungas | La Paz | yungas-páramo | | | 17,18 | | | | |
| 5. | Huacullani at Lago Titicaca | 3850-3890 m | Ingavi | La Paz | moist puna | | 7 | | | | | |
| 6. | Copacabana (Kusijata) at Lago Titicaca | 3810 m | Manco Capac | La Paz | moist puna | 2,3 | 6,7,8 | 25 | | | | |
| 7. | different sites at Lago Titicaca | 3800-3850 m | | La Paz | moist puna | | 6,10,11,13 | | | | 49 | |
| 8. | Laguna Viscachani Valle de Zongo | 3750 m | Murillo | La Paz | yungas-páramo | 1,3,4 | 7,9,11,12 | | | | | |
| 9. | Rio Pazña affluent of Lago Poopó | 3800-3900 m | Poopó | Oruro | dry puna | | 6 | | | | | |
| 10. | Caiza | 3700-3800 m | Quijarro | Potosí | dry puna | | | 31 | 39 | | | |
| 11. | Huaraco | 3650 m | Aroma | Oruro | dry puna | | 6,7 | | | | | |
| 12. | Chasquipampa | 3600 m | Murillo | La Paz | dry puna | | 5 | | | | | |
| 13. | area of La Paz | 3600 m | Murillo | La Paz | dry puna | | 6,7 | | | | 47,48 | |
| 14. | area of Cambaya Valle de Zongo | 3250 m | Murillo | La Paz | elfin forest | | 7 | | | | | |
| 15. | Cotapata | 2900 m | Nor Yungas | La Paz | elfin forest (Ceja de Montaña) | | | 27 | | | | |
| 16. | Sorata | 2680 m | Larecaja | La Paz | humid mountain forest | | 6 | | | | | |
| 17. | Cambaya Valle de Zongo | 2500 m | Murillo | La Paz | humid mountain forest | | 7,9,10,13 | 26 | | | | 50 |
| 18. | Valle de Zongo | 1150-2000 m | Murillo | La Paz | humid mountain forest | | | | | | | 50 |
| 19. | 15 km E of Tarija | 1860 m | | Tarija | humid mountain forest | | 6,10 | | 33,38 | | | |
| 20. | Mapiri | 610 m | Larecaja | La Paz | tropical rain forest | | | 14 | | 45 | | |
| 21. | between Teoponte and Alcoche | 550 m | Larecaja<br>Nor Yungas | La Paz | tropical rain forest | | | 29 | 38 | | | |
| 22. | Río Quiquibey | 300 m | Ballivan | Beni | tropical rain forest | | | 21,22 | | | | |
| 23. | Guayaramerín | 125 m | Vaca Diez | Beni | tropical rain forest | | | 15,21,22, 24,30 | 34,35,36, 41,42 | 43,44,46 | | |
| 24. | Espíritu | 170 m | Ballivan | Beni | inundation savanna | | | 22,28,30 | | | | |
| 25. | Puerto Suarez | 145 m | Chiquitos | Santa Cruz | inundation savanna (pantanal) | | | | 35 | | | |
| 26. | Aguairenda | 200 m | Gran Chaco(?) | Tarija | chaco woodland | | | 20,23 | 39,40 | | | |
| 27. | Río Pilcomayo | 200 m | Gran Chaco(?) | Tarija | chaco woodland | | | | 37 | | | |

remarks are added. At the end of the species list of each family, the biogeographic situation of the family is briefly outlined. A general discussion is given in chapter 5.

## 3. Geographical division of Bolivia

Geographically, Bolivia can be divided into four main regions: the Andes, the Amazon lowland, the Gran Chaco, and the Cerrados. These regions can be concisely characterized as follows (for a detailed description see KILLEEN et al. 1993):

The Bolivian Andes are very heterogenous concerning climate and soil types, and therefore in their ecology. The upland in its western part (2500 - 4000 m above sea level), called Altiplano, is mainly a grassland with a mean annual temperature of 10 °C or less and an average precipitation between 600 and 1000 mm/y in

Figure 1. Map of Bolivia, indicating the limits of „departamentos" and the sampling sites of Oligochaeta. Nº of sampling sites are the same as in table 1. The Andean region is marked grey.

the north (moist Puna) and 400 mm/y or less in the south (dry Puna). Between the Altiplano and the eastern edge of the Andes dry valleys are situated (500 - 3300 m above sea level), with different deciduous forests and arid plant associations. Altiplano as well as Andean valleys are influenced by man since thousands of years, and different plants and animals from other continents have been introduced by the European colonizers.

The eastern slopes of the Andes are mainly covered with humid mountain forests (Yungas). Climate is very moist (mean precipitation 2000 - 3500 mm/y; in extreme cases up to 6000 mm/y) and warm (mean annual temperature 17 - 24 °C). Above the Yungas, between 2700 - 3500 m, follows the „Ceja de la Montaña“ densely covered with foggy Elfin forest. This region often lies in clouds, and temperatures only rise to 10 - 14 °C. The vegetation belt between Elfin forest and moist puna is called „Yungas-Páramo“ in Bolivia, to distinguish it from the Colombian-Ecuadorian Páramos. The soils of the eastern Andean slope are relatively poor in nutrients, despite the fact that they are not much weathered. Colonization by European settlers started only 50 years ago except in Valle de Zongo, a valley close to the capital La Paz, that has been used for a long time past to gather fire-wood.

The north of the Bolivian Amazon lowlands is covered with true lowland tropical rain forest and characterized by high temperatures (26 - 27 °C) and rainfall (1800-2000 mm/y) with 1 to 3 arid months. Further in the south, separated by a large area of cerrados and savannas, grow the humid forests of the Beni plain. This region is also very warm, but the precipitation decreases from the Andes to the Brazilian border (from >2000 to 1500 mm). The Beni forests adjoin in the east the humid forests of the Brazilian Precambrian shield, and in the southeast the drier Chiquitanian semi-decidous forests, both interspersed with Campos cerrados. The soils of this whole area are mostly very old, weathered and acidic, and concretions of ferric oxides (laterites) can often be found.

The centre of the Beni plain is dominated by savannas of which the northern part is similar to the Campos cerrados. The southern part is a vast inundation area (>80.000 km$^2$) which is flooded for several months every year. The soils are much younger and more heterogenous than in the other regions of the Beni department. In some places even alkaline subsoils were found but the upper soil layers show neutral or slightly acidic reactions because of the high precipitation. In both parts of the Beni savannas earthworms play an important role in the formation of the soil micro-relief (see chapter 4: species № 23: *Enantiodrilus borellii* and plate 1 a, b). Large parts of the central Beni are now used as extensive pastures for cattle.

The southern lowlands of Bolivia are called the „Gran Chaco“ Climate is warm (22 26 °C) but not very moist (mean 500 - 1000 mm/y). The dry Chaco forest grows partly on sodium-rich, alkaline soils. European influence is partly still very young in this region. In the southeastern parts of Bolivia the Pantanal - an inundation area similar to the Beni savannas - reaches into the country.

## 4. Faunistic data

### Enchytraeidae

#### 1. *Buchholzia appendiculata* (Buchholz, 1862)

Distribution: Europe
Site: Laguna Viscachani, Valle de Zongo, Prov. Murillo, Dpto. La Paz; close to or in a small river (Martinez-Ansemil & Giani 1986).

Remarks: The sampling site „lago pequeño de Viscachuni“ in Martinez-Ansemil & Giani (1986) is identical with the little lake called „Laguna Viscachani“ in this paper.

#### 2. *Enchytraeus buchholzi* Vejdovsky, 1879

Distribution: Argentina, Brazil, Venezuela, worldwide
Site: Uruni Bay, Lago Titicaca, Dpto. La Paz; at a depth of 1.3 m (Cernosvitov 1939).

Remarks: Both the determination, based on a single macerated specimen, and the sampling site (belonging to Peru or Bolivia?) are doubtful; we did not find a place with this name on maps at the Lago Titicaca, but there is an „Estancia Uruna“, about 10 km from Tiquina on the way to Copacabana at Lago Titicaca (3812 m), Prov. Manco Capac, Dpto. La Paz. However, this cosmopolitan species (group of species?) seems to be common in many areas of South America where it has been introduced by man.

#### 3. *Fridericia* sp.

Distribution: Worldwide
Site: Laguna Viscachani, Valle de Zongo, Prov. Murillo, Dpto. La Paz; close to or in a small river (Martinez-Ansemil & Giani 1986).
Site: Copacabana (3812 m), Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; close to a small road near a village, under stones (leg. W. Hanagarth, February 3, 1985).

#### 4. *Henlea perpusilla* Friend, 1911

Distribution: Europe
Site: Close to the Laguna Viscachani, Valle de Zongo, Prov. Murillo, Dpto. La Paz (Martinez-Ansemil & Giani 1986).

Without doubt the species shown here (fig. 1, tab. 1) represent only a negligible percentage of the enchytraeid fauna of Bolivia. The species ***Hemienchytraeus***

***stephensoni* (Cognetti, 1927)**, probably very common in tropical South America, was described from the Peruvian lake Laguna Lagunilla by Cernosvitov (1939), and was wrongly counted for Bolivia by Dozsa-Farkas (1989). The worms described as *H. stephensoni* seem to belong to a group of at least four closely related species (Christoffersen 1979, Dozsa-Farkas 1989).

With the exception of *H. stephensoni* the other species are typically found in disturbed soils, e.g. at ruderal places, where they quickly spread partly due to their mode of reproduction: parthenogenesis or fragmentation. In addition to these introduced or pantropical species it can be expected that other genera (e.g. *Achaeta, Marionina* and *Guaranidrilus*) are common in this country, especially as there is some evidence that the Enchytraeidae might have been arisen in South America or a continuous southern land mass (Coates 1989).

## Lumbricidae

### 5. *Aporrectodea* sp.

Distribution: Worldwide
Site: Chasquipampa (3.600 m), Prov. Murillo, Dpto. La Paz (leg. W. Hanagarth, February 10, 1985).

### 6. *Aporrectodea caliginosa* (Savigny, 1826)

Distribution: Bolivia, Argentina, Brazil, Chile, Ecuador, French Guayana, Paraguay, Peru, Uruguay, worldwide
Site: Sorata, Prov. Larecaja, Dpto. La Paz (Michaelsen 1902).
Site: Near the Río Pazña, affluent of the Lago Poopó, Prov. Poopó, Dpto. Oruro (Cernosvitov 1934, 1935).
Site: Close to the Río Bamba, Dpto. (?) (Cernosvitov 1934, 1935).

Remarks: We did not find any Río Bamba in Bolivia, but rivers with this name exist in Peru and Ecuador.

Site: Huaraco (3650 m), Prov. Aroma, Dpto. La Paz; in dry puna (leg. W. Hanagarth, July, 1983).

Remarks: During an ecological study at five different sites (November 1982 - October 1983; Ergueta 1985) which were characterized by their plant cover more than 95% of all Oligochaeta belonged to this species. The biomass of *A. caliginosa* per square meter varied strongly between the different plant formations (characterized by *Parastrefia lepidophyla*, *Baccharis incarum*, *Stipa ichu*, *Trifolium amabile* and *Medicago sativa*). Few earthworms were found in Quinoa-fields, and none in soil without plant cover. The abundance of this endogeic species fluctuated considerably during the course of the year; approximately 40% were living at 10 - 20 and at 20 - 30 cm depth, respectively.

Site: Kusijata near Copacabana (3812 m), Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; especially close to paths and irrigation channels in moist puna (leg. W. Hanagarth, July 10, 1991).
Site: Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; in moist puna (leg. W. Hanagarth, 1980).
Site: Different localities close to La Paz (3.600 m), Prov. Murillo, Dpto. La Paz (Zicsi in press = *Allolobophora caliginosa trapezoides*).
Site: Unduavi (4654 m), Prov. Nor Yungas, Dpto. La Paz (Zicsi in press = *Allolobophora caliginosa trapezoides*).
Site: 15 km from Tarija to Entre Ríos, Dpto. Tarija (Zicsi in press = *Allolobophora caliginosa trapezoides*).

### 7. *Aporrectodea rosea* (Savigny, 1826)

Distribution: Bolivia, Argentina, Brazil, Chile, Columbia, Ecuador, Peru, Uruguay, worldwide
Site: area of Cambaya (2500 - 3250 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; four sites in mountain and elfin forest (Righi & Römbke 1987).
Site: Close to the road to Zongo (4.100 m), Prov. Murillo, Dpto. La Paz; moist place adjacent to a creek in moist puna (leg. W. Hanagarth, February 23, 1980).
Site: Laguna Viscachani (3750 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; 10 - 50 m from the shore line (leg. J. Römbke, March 19, 1985).
Site: Kusijata near Copacabana (3812 m), Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; especially close to paths and irrigation channels in moist puna (leg. W. Hanagarth, July 10, 1991).
Site: Huacullani, Lago Titicaca (3.850 - 3.890 m), Prov. Ingavi, Dpto. La Paz; in moist puna (leg. W. Hanagarth, February 10, 1980).
Site: Huaraco (3.650 m), direction to Oruro, Prov. Aroma, Dpto. La Paz; moist sites in the dry puna (leg. W. Hanagarth, April 27, 1980).
Site: Different localities close to La Paz (3.600 m), Prov. Murillo, Dpto. La Paz (Zicsi in press = *Allolobophora rosea*).
Site: Unduavi (4654 m), Prov. Nor Yungas, Dpto. La Paz (Zicsi in press = *Allolobophora* rosea).

### 8. *Dendrobaena* sp.

Site: Copacabana (3812 m), Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; in moist puna close to a small road near a village, under stones (leg. W. Hanagarth, February 3, 1985).

### 9. *Dendrobaena octaedra* (Savigny, 1826)

Distribution: Bolivia, Chile, Columbia, Ecuador, worldwide
Site: Cambaya (2500 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; in humid mountain forest (leg. J. Römbke, March 19, 1985).
Site: Laguna Viscachani (3750 m), Prov. Murillo, Dpto. La Paz; 10 - 50 m from the shore line (leg. J. Römbke, March 19, 1985).
Site: Unduavi (4654 m), Prov. Nor Yungas, Dpto. La Paz (Zicsi in press).

### 10. *Dendrodrilus rubidus* (Savigny, 1826)

Distribution: Bolivia, Argentina, Brazil, Chile, Columbia, Uruguay, worldwide

Site: Cambaya (2500 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; in humid mountain forest (leg. J. RÖMBKE, March 19, 1985).
Site: Unduavi (4654 m), Prov. Murillo, Dpto. La Paz (ZICSI in press).
Site: Lago Titicaca, Dpto. La Paz (ZICSI in press).
Site: 15 km from Tarija to Entre Ríos, Dpto. Tarija (ZICSI in press).

### 11. *Eiseniella tetraeda* (SAVIGNY, 1826)

Distribution: Bolivia, Argentina, Chile, Ecuador, Peru, worldwide
Site: Laguna Viscachani (3750 m), Prov. Murillo, Dpto. La Paz; 10 - 50 m from the shore line (leg. J. RÖMBKE, March 19, 1985).
Site: Lago Titicaca, Dpto. La Paz (CERNOSVITOV 1939).
Site: Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; in moist puna (leg. W. HANAGARTH, 1980).

Remarks: It seems that most of the sampling sites in the Titicaca basin mentioned by CERNOSVITOV (1939) are located in Peru. However, it is evident that this species is common in the whole area.

### 12. *Lumbricus rubellus* (SAVIGNY, 1826)

Distribution: Bolivia, worldwide
Site: Laguna Viscachani (3750 m), Prov. Murillo, Dpto. La Paz; 10 - 50 m from the shore line (leg. J. RÖMBKE, March 19, 1985).

### 13. *Octolasion tyrtaeum* (SAVIGNY, 1826)

Distribution: Bolivia, Argentina, Brazil, Chile, Ecuador, Peru, Uruguay, worldwide
Site: Cambaya (2500 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; in humid mountain forest (RIGHI & RÖMBKE 1987).
Site: Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; in moist puna (leg. W. HANAGARTH, 1980).
Site: Unduavi (4654 m), Prov. Nor Yungas, Dpto. La Paz (ZICSI in press = *Octolasion lacteum*).

All Lumbricidae found in Bolivia belong to the group of approximately 20 species, mainly of central European origin, which were widely distributed by man during the last five centuries (LEE 1985). Except *L. rubellus* all were found many times in other South American countries. Out of this group *A. caliginosa* seems to be the most successful one, maybe due to its relatively long individual and reproductive lifespan rather than due to a quick reproduction (BENGTSSON et al. 1979). Another explanation for its broad ecological tolerance might be the fact that the same name is used for a group of closely related species with different ecological demands. Looking at the distribution map (fig. 1, tab. 1), it seems that Lumbricidae were introduced by early European settlers into central and southern Andine areas suitable for agriculture where they reach very high dominance values (close to 100%).

## Glossoscolecidae

### 14. *Andiorrhinus (Andiorrhinus)* sp.

Distribution: South America
Site: Mapiri, Prov. Larecaja, Dpto. La Paz (ZICSI in press).

### 15. *Andiorrhinus (Amazonidrilus) bolivianus* ZICSI, in press

Distribution: Bolivia
Site: Guayaramerín (Estancia Esperanza), Prov. Vaca Diez, Dpto. Beni (ZICSI in press).

### 16. *Andiorrhinus (Amazonidrilus) holmgreni* MICHAELSEN, 1918

Distribution: Bolivia, Brazil
Site: Site of original description not known.

Remarks: Mentioned for Bolivia by RIGHI (1971) and RIGHI (1990); in the former case as *A. paraguayensis holmgreni*.

### 17. *Andiorrhinus (Amazonidrilus)* c.f. *holmgreni* MICHAELSEN, 1918

Distribution: Bolivia, Brazil
Site: Unduavi (3800 m), Prov. Nor Yungas, Dpto. La Paz (ZICSI in press).

Remarks: According to ZICSI (in press) the taxonomic relationships between *A. (A.) holmgreni, A. (A.)* c.f. *holmgreni, A. (A.) evelinae* and *A. (A.) paraguayensis* are not yet clear.

### 18. *Andiorrhinus (Andiorrhinus) montanus* ZICSI, in press.

Distribution: Bolivia
Site: Unduavi (3.900 m), Prov. Nor Yungas, Dpto. La Paz (ZICSI in press).

### 19. *Andiorrhinus (Andiorrhinus) salvadori* COGNETTI, 1908

Distribution: Bolivia, Brazil, Paraguay, Venezuela
Site: Site of original description not known.

Remarks: Mentioned for Bolivia by CORDERO (1945), OMODEO (1954) and RIGHI (1990).

### 20. *Anteoides rosae* COGNETTI, 1902

Distribution: Bolivia, Argentina
Site: Aguairenda, Prov. Gran Chaco (?), Dept. Tarija (COGNETTI 1902).

### 21. *Diaguita* sp.

Distribution: Bolivia

Site: Río Quiquibey (300 m), Prov. Ballivan, Dpto. Beni; in tropical rain forest (leg. W. HANAGARTH, March 9, 1982).
Site: Guayaramerín (Nicolas Suarez Island), Prov. Vaca Diez, Dpto. Beni (ZICSI in press).

Remarks: All specimens of this genus sampled in Bolivia up to now were juvenile; thus it was not possible to determine the species.

### 22. *Enantiodrilus borellii* (COGNETTI, 1902)

Distribution: Bolivia, Argentina, Brazil
Site: Different localities (Río Urioste, Espíritu viejo) close to Espíritu (170 m), Prov. Ballivian, Dpto. Beni; in inundation savanna and pastures (leg. W. HANAGARTH, May 10, 1985).
Site: Different localities (Estancia Esperanza, Nicolas Suarez Island) close to Guayaramerín, Prov. Vaca Diez, Dpto. Beni; forest adjacent to the Río Mamoré (ZICSI in press).
Site: Río Quiquibey (300 m), Prov. Ballivan, Dpto. Beni; in tropical rain forest (leg. W. HANAGARTH, March 10, 1982).

Remarks: This is a taxonomically very interesting species since it is relatively isolated within the Glossoscolecidae. It seems to be the most abundant species in the inundation savannas of the Dpto. Beni where the worms are very important for the micro-relief of the soil surface. When the area is about to be flooded, the worms flee the water saturated soil and concentrate on bunches of grass where they deposit their casts. By the time they build in this way 20 - 40 cm high small soil towers („sartenejales“) which rise above the water level (HANAGARTH 1993). Similar worm shaped micro-reliefs are also known from Colombia („zurales“, GOOSEN 1971) and Venezuela („lombricales“, SARMIENTO 1984). The „sartenejales“ can cover wide areas and are then very characteristic for the whole landscape (plate 1 a, b).

### 23. *Glossodrilus peregrinus* (MICHAELSEN, 1897)

Distribution: Bolivia, Caribbean Area
Site: Aguairenda, Prov. Gran Chaco (?), Dept. Tarija (COGNETTI 1902 = *Glossoscolex peregrinus*)

Remarks: The species, originally described as *Tykonos peregrinus* by MICHAELSEN and later named *Andioscolex peregrinus*, is now placed into the genus *Glossodrilus* (RIGHI 1975).

### 24. *Goiascolex vanzolinii* RIGHI, 1984

Distribution: Bolivia, Brazil
Site: Guayaramerín (Nueva Cuba), Prov. Vaca Diez, Dpto. Beni (ZICSI in press).

### 25. *Inkadrilus hanagarthi* ZICSI, in press

Distribution: Bolivia
Site: Kusijata near Copacabana (3812 m), Lago Titicaca, Prov. Manco Capac, Dpto. La Paz; at a depth of 30 cm (ZICSI in press).

Remarks: For the first time since 1900 a specimen of the genus *Inkadrilus* was re-discovered. Other, closely related species of this genus were described from Colombia and Peru (MICHAELSEN 1935).

### 26. *Martiodrilus bolivianus* RIGHI & RÖMBKE, 1987

Distribution: Bolivia
Site: Cambaya (2500 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; in humid mountain forest (RIGHI & RÖMBKE 1987).

### 27. *Martiodrilus silvestris* ZICSI, in press

Distribution: Bolivia
Site: Cotapata (2900 m), Prov. Nor Yungas, Dpto. La Paz; natural forest (Ceja de Montaña), in the root layer of the soil (ZICSI in press).

### 28. *Periscolex* sp.

Distribution: South America
Site: Espíritu (Río Yacuma), Prov. Ballivian, Dpto. Beni (ZICSI in press).
Remarks: The specimens were so softened that it was not possible to determine the species.

### 29. *Periscolex yuya* RIGHI & RÖMBKE, 1987

Distribution: Bolivia, Peru
Site: Between Teoponte, Prov. Larecaja, and Alcoche (550 m), Prov. Nor Yungas, Dpto. La Paz (ZICSI 1992).

### 30. *Pontoscolex corethrurus* (MÜLLER, 1857)
(plate 1 c)

Distribution: Bolivia, Argentina, Brazil, British Guayana, Chile, Ecuador, French Guayana, Peru, Paraguay, Suriname, Venezuela, worldwide
Site: Espíritu (170 m), Prov. Ballivian, Dpto. Beni; in forest island in inundation savanna (leg. T BECK & W. HANAGARTH, March 3, 1993).
Site: Different localities (Nicolas Suarez Island) close to Guayaramerín, Prov. Vaca Diez, Dpto. Beni; plantation adjacent to the Río Mamoré (ZICSI in press).

### 31. *Rhinodrilus parvus* (ROSA, 1895)

Distribution: Bolivia, Argentina
Site: Caiza, Prov. Quijarro, Dpto. Potosí (COGNETTI 1902)

### 32. *Tamayodrilus roembkei* ZICSI, in press

Distribution: Bolivia
Site: Serranía Macho Pelechuco and Serranía de Charazani (4060 m), Prov. Franz Tamayo, Dpto. La Paz (ZICSI in press).

Glossoscolecidae were found in Bolivia in the Andes as well as in the Amazonian lowland of the Beni Department (fig. 1, tab. 1). The absence of records in vast areas in the south and east of Bolivia can be explained simply by the fact that no one sampled there since in adjacent Brazilian provinces many species were described (Righi 1990). *P. corethrurus*, coming originally from the Guayana Plateau in northern South America (Righi 1984), is the only peregrine species of this family, living pantropically today. All other species are restricted to Central and South America. At the moment it is not possible to assess the true size of their geographical range. Up to now seven species (*Anteoides rosai, Andiorrhinus (Amazonidrilus) bolivianus, Andiorrhinus (Andiorrhinus) montanus, Inkadrilus hanagarthi, Martiodrilus bolivianus, Martiodrilus silvestris, Tamayodrilus roembkei*) seem to be endemic to Bolivia.

## Ocnerodrilidae

### 33. *Belladrilus (Belladrilus) vaucheri* Zicsi, in press

Distribution: Bolivia
Site: 15 km from Tarija to Entre Ríos, Prov. Gran Chaco (?), Dpto. Tarija (Zicsi in press).

### 34. *Eukerria asuncionis* (Rosa, 1895)

Distribution: Bolivia, Argentina, Paraguay
Site: Guayaramerín, Prov. Vaca Diez, Dpto. Beni; plantation adjacent to the Río Mamoré (Zicsi in press).

### 35. *Eukerria eiseniana* (Rosa, 1895)

Distribution: Bolivia, Argentina, Brazil, Paraguay
Site: Puerto Suarez, Prov. Chiquitos, Dpto. Santa Cruz (Righi 1990).
Site: Guayaramerín, Prov. Vaca Diez, Dpto. Beni; park, garden (Zicsi in press).

### 36. *Eukerria garmani* (Rosa, 1895)

Distribution: Bolivia, Brazil, Paraguay
Site: Guayaramerín, Prov. Vaca Diez, Dpto. Beni; park, garden (Zicsi in press).

### 37. *Eukerria halophila* (Beddard, 1892)

Distribution: Bolivia, Argentina
Site: Tributaries of the Río Pilcomayo, Prov. Gran Chaco (?), Dpto. Tarija; in exceedingly salt and bitter water (Cognetti 1905).

### 38. *Eukerria saltensis* (Beddard, 1896)

Distribution: Bolivia, Argentina, Brazil, Chile
Site: Between Teoponte, Prov. Larecaja, and Alcoche (550 m), Prov. Nor Yungas, Dpto. La Paz (Zicsi in press).
Site: 15 km outside of Tarija, Prov. Gran Chaco (?), Dpto. Tarija (Zicsi in press).

### 39. *Eukerria subandina* (Rosa, 1895)

Distribution: Bolivia, Argentina, Brazil
Site: Caiza, Prov. Quijarro, Dpto. Potosí (Cognetti 1902 = *Kerria subandina*).
Site: Aguairenda, Prov. Gran Chaco (?), Prov. Tarija (Cognetti 1902 = *Kerria subandina*).

### 40. *Ilyogenia paraguayensis* (Rosa, 1895)

Distribution: Bolivia, Argentina, Paraguay
Site: Aguairenda, Prov. Gran Chaco (?), Prov. Tarija (Cognetti 1902 = *Ocnerodrilus (Ilyogenia) parguayensis*).

### 41. *Ilyogenia tuberculatus* Eisen, 1900

Distribution: Bolivia, Guatemala
Site: Nueva Cuba close to Guayaramerín, Prov. Vaca Diez, Dpto. Beni; park (Zicsi in press).

### 42. *Ocnerodrilus occidentalis* Eisen, 1878

Distribution: Bolivia, Argentina, Brazil, worldwide
Site: Different localities close to Guayaramerín, Prov. Vaca Diez, Dpto. Beni (Zicsi in press).

The ocnerodrilids are included here since they, usually found in more or less limnic habitats, can also live in very moist soils (fig. 1, tab. 1). With the exception of *B. vaucheri* and, partly, the *Ilyogenia* species, they seem to be very common in wide areas of South America. Especially *O. occidentalis*, probably originally from Central America, is now found pantropical, sometimes even in temperate regions (Lee 1985). It can be expected that species of this family are inhabitants of all very moist soils in Bolivia.

## Octochaetidae

### 43. *Dichogaster affinis* (Michaelsen, 1890)

Distribution: Bolivia, Argentina, Brazil, Chile, Columbia, Ecuador, Paraguay, Peru
Site: Guayaramerín, Prov. Vaca Diez, Dpto. Beni; park (Zicsi in press).

Remarks: Mentioned for north Bolivia by Csuzdi & Zicsi (1991).

### 44. *Dichogaster bolaui* (Michaelsen, 1891)

Distribution: Bolivia, Argentina, Brazil, Chile, Columbia, Ecuador, French Guayana, Paraguay, Venezuela, worldwide
Site: Guayaramerín, Prov. Vaca Diez, Dpto. Beni (Csuzdi & Zicsi 1991).
Site: Urucum, 18 km southeast of Corumba (Cognetti 1905).

Remarks: This locality is situated in the Brazilian pantanal. Cognetti (1905) cites the place in the same paper once for Bolivia (p. 42) and once for Brazil (p. 55).

### 45. *Dichogaster modigliani* (Rosa, 1896)

Distribution: Bolivia, Brazil, Columbia, Ecuador, French Guayana, Peru, Venezuela, worldwide
Site: Mapiri, Prov. Larecaja, Dpto. La Paz; in a forest (Zicsi in press).

Remarks: Mentioned for north Bolivia by CSUZDI & ZICSI (1991).

### 46. *Dichogaster saliens* (BEDDARD, 1892)

Distribution: Bolivia, Argentina, Brazil, Ecuador, Paraguay, Peru, worldwide
Site: Different localities (Nicolas Suarez Island) close to Guayaramerín, Prov. Vaca Diez, Dpto. Beni (ZICSI in press).

Remarks: Mentioned for north Bolivia by CSUZDI & ZICSI (1991).

All Octochaetidae reported from Bolivia up to now, especially *D. bolaui*, belong to a group of peregrine species which are pantropically (and partly in temperate regions, too) distributed today (fig. 1, tab. 1). Probably, they originate from West Africa (LEE 1985).

## Acanthodrilidae

### 47. *Microscolex dubius* (FLETCHER, 1887)

Distribution: Bolivia, Argentina, Brazil, Chile, Paraguay, Uruguay, worldwide
Site: La Paz (3.600 m), Prov. Murillo, Dpto. La Paz (ZICSI in press).

### 48. *Microscolex phosphoreus* (ANT. DÜGES, 1837)

Distribution: Bolivia, Argentina, Chile, Ecuador, Paraguay, worldwide
Site: La Paz (3.600 m), Prov. Murillo, Dpto. La Paz (ZICSI in press).

### 49. *Yagansia peruana* CERNOSVITOV, 1939

Distribution: Bolivia, Peru
Site: Between Unduavi and Cota (4.654 m), Prov. Nor Yungas, Dpto. La Paz (ZICSI in press).
Site: Different localities at Lago Titicaca (3.800 - 3.850 m), Dpto. La Paz; e.g. under stones at the shoreline (ZICSI in press).

*Y peruana* belongs to a genus of which the distribution center seems to be Chile (ZICSI 1989), whereas the other acanthodrilids found in Bolivia (fig. 1, tab. 1) are truely peregrine species. The two *Microscolex* species, probably originating from southern South America (Patagonia ?), are now established by human activities throughout the southern temperate zone and also in North America and in Europe, mainly in agricultural and pastoral areas (LEE 1985).

## Megascolecidae

### 50. *Amynthas corticis* (KINBERG, 1867)

Distribution: Bolivia, Brazil, worldwide
Site: Cambaya (2500 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz; in humid mountain forest (RIGHI & RÖMBKE 1987 = *Amynthas diffringens*).
Site: Valle de Zongo (2000 m), Prov. Murillo, Dpto. La Paz; open sandy area in humid mountain forest (leg. L. BECK, August 5, 1993).
Site: Estación Cahua (= Calwa, 1150 m), Valle de Zongo, Prov. Murillo, Dpto. La Paz (ZICSI in press).

Remarks: According to EASTON (1982), *Amynthas diffringens* (BAIRD, 1869) is a synonym of this species. This striking species, probably coming from Southeastern Asia, belongs to the „Pheretima“-group which is peregrine in tropical areas (EASTON 1979). Up to now, *A. corticis* seems to be restricted to humid mountain forests close to La Paz (fig. 1, tab. 1), where it is usually found at the edge of natural forests, especially abundant close to or beneath dung pats of horses. Probably, it has been introduced but in recent times.

## 5. Discussion

The terrestrial oligochaete fauna of Bolivia is composed of four different groups:
A. – widely distributed species of European origin, probably introduced by early settlers;
B. – species originated from tropical regions of Central America or Asia, and with a pantropical distribution today due to human activities;
C. – species found in at least two South American countries;
D. – species endemic to Bolivia.
From the 50 species (including those which were not determinable to the species level) listed here 13 (26%) belong to group A, 9 (18%) to group B, 20 (40%) to group C, and 8 (16%) to group D, respectively. Thus, nearly half of all earthworms found in Bolivia up to now were introduced by man during the last centuries. Very probably, this ratio will change in favor to South American species when more sampling has been done.
Regarding the geographical distribution (fig. 1, tab. 1) it seems to be evident, even with such a limited number of data, that the introduced lumbricid species are common in the Andes, especially in agricultural areas, whereas the pantropical species live in all not too cold (Alpine regions) parts of Bolivia. Despite the fact that the ways of dispersal and, at least partly, the reasons for their advantages compared to non-peregrine species are known (LEE 1985), it is still a matter of debate whether they have displaced native species or whether they mainly inhabited areas formerly free of earthworms. Species of the family Glossoscolecidae can be found in both parts of the country. Our knowledge on the distribution of these worms is yet to small to decide how many of them are really endemic to Bolivia. However, most of them seem to be distributed in a wide range of tropical areas in South America, including at least western Brazil, Paraguay and northern Argentina.
The geographical distribution of terrestrial Oligochaeta in Bolivia is far from being well investigated. The sites

listed here show mainly where some early investigators and modern scientists made their collections, most of them not regarding earthworms as their main point of interest. In fact, the distribution maps (fig. 1, tab. 1) show clearly which areas are relatively easy to reach (e.g. surroundings of La Paz, Valle de Río Zongo) whereas whole departments, in the Andes (e.g. Oruro, Potosí) as well as in the lowlands (e.g. Pando, Santa Cruz) of Bolivia have never been studied.
Therefore, and in comparison to better investigated countries like Brazil or Ecuador, it can be assumed that only a very small percentage of the Bolivian oligochaete fauna is known to science today. For example, in the adjacent Brazilian states of Mato Grosso and Rondônia RIGHI (1990) found 45 species belonging to the families Glossoscolecidae, Ocnerodrilidae, Octochaetidae and Acanthodrilidae, excluding introduced Lumbricidae and Megascolecidae, in comparison to 29 species described here from a comparable area of Bolivia. Since in this country the percentage of natural biotopes is quickly decreasing (e.g. by agriculture), the investigation of these ecologically very important organisms should be promoted in the future.

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Plate 1. a) Earthworm-termites-Sartenejal of North Beni inundation savanna: Earthworm mounds between the grass; trees and bushes grow on decayed termites mounds.

b) Earthworm-Sartenejal south of Río Yata, South Beni: Mounds are about 30 cm high; during the rainy season the area is inundated by backwater leaving only the upper parts of the mounds uncovered.

c) *Pontoscolex corethrurus* (Glossoscolecidae).

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CHRISTOPHER MARTIUS, HUBERT HÖFER, MANFRED VERHAAGH, JOACHIM ADIS & VOLKER MAHNERT

# Terrestrial arthropods colonizing an abandoned termite nest in a floodplain forest of the Amazon River during the flood

### Abstract

Terrestrial arthropods were identified as secondary colonizers of an abandoned termite nest (*Nasutitermes tatarendae*) at the beginning of the inundation period in a floodplain forest influenced by whitewater in central Amazonia. About 50 individuals of non-termite meso- and macrofauna were recorded per liter of nest volume, mainly terrestrial Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae, and Formicidae. Apparently, abandoned termite nests could be important for the survival of the soil-fauna which migrates to the canopy during the flood period.

### Kurzfassung

**Terrestrische Arthropoden als Besiedler eines verlassenen Termitennests in einem Überschwemmungswald während der Überflutungsphase**

In einem várzea-Wald Zentralamazoniens wurden zu Beginn der Überschwemmungsphase terrestrische Arthropoden als Sekundärbesiedler eines verlassenen Termitennestes (*Nasutitermes tatarendae*) identifiziert. Etwa 50 Individuen der Meso- und Makrofauna (keine Termiten) wurden pro Liter Nestvolumen registriert, überwiegend terrestrische Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae und Formicidae. Verlassene Termitennester können offensichtlich für das Überleben der Bodenfauna, die während der Flutphase in die Baumkronen wandert, wichtig sein.

### Resumo

**Colonização por artrópodos terrestres de um ninho abandonado de cupim no início do período da enchente numa floresta de várzea**

Artrópodos terrestres foram identificados como colonizadores secundários de um ninho abandonado de cupim (*Nasutitermes tatarendae*) no início do período da enchente numa floresta de várzea da Amazônia Central. Aproximadamente 50 indivíduos de meso- e macrofauna (não cupins) foram achados no volume de um litro de ninho, sobretudo Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae, e Formicidae. Evidentamente ninhos abandonados de cupins podem ser importantes para a sobrevivência da fauna de solo que migra ao dossel da floresta durante a inundação.

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## Introduction

Survival strategies of soil arthropods in the periodically inundated floodplain forests (várzea) along the Solimões-Amazon River have long been in the focus of research (IRMLER 1981, ADIS 1992). Migration to tree canopies is one possibility for soil species to survive flooding. Termites represent a considerable part of the várzea fauna (MARTIUS 1989), and a great part of their arboreal nests is abandoned (MARTIUS 1994). However, the question whether these nests are „refugia“ for the migrating soil fauna has never been analysed.

To get an insight into this problem we present here some data gathered during field studies on termite colonization (MARTIUS 1989) of Ilha de Marchantaria, an island in the river Amazon near Manaus, Brazil (fig. 1), and a typical várzea (= white water floodplain forest fig. 2) site (JUNK 1984).

The fauna of an abandoned termite nest of *Nasutitermes tatarendae* was determined. The nest was located on a tree which base had been flooded the day before sampling. Its lower half (with a volume of more than 80 liters) was cut from the tree with a chain saw, then transported in an aluminium container to the laboratory, split into small fractions of approx. 5-10 dm$^3$ each, and extracted by heat in a Tullgren Funnel. Specimens were separated to orders, stored in alcohol, and identified. Additionally, nine abandoned arboreal *Nasutitermes* nests (mostly *N. corniger*) which were found on the forest floor during the low-water period were screened for associated fauna.

## Secondary colonizers of the abandoned nest of *Nasutitermes tatarendae*

Table 1 shows the arthropods which we found in the abandoned termite nest of *Nasutitermes tatarendae.* No termites, not even of other species, were found in this nest. Due to the sampling procedure, the small mesofauna (usually <1mm, e.g. Acari and Collembola) has not been quantitatively assessed, and its presence is only assigned with an „x“ in table 1. Animals of size classes usually ≥1 mm (larger meso- and macrofauna) have been quantitatively assessed.

At least 77 different arthropod taxa were registered in this single abandoned nest. With a total of 4054 individuals of the fauna with a size of ≥1 mm the nest contained a high density of arthropods (corresponding to about 50 individuals per liter of nest volume). We clas-

Figure 1. Aerial view of Ilha de Marchantaria during high water level; Photo: J. ADIS.

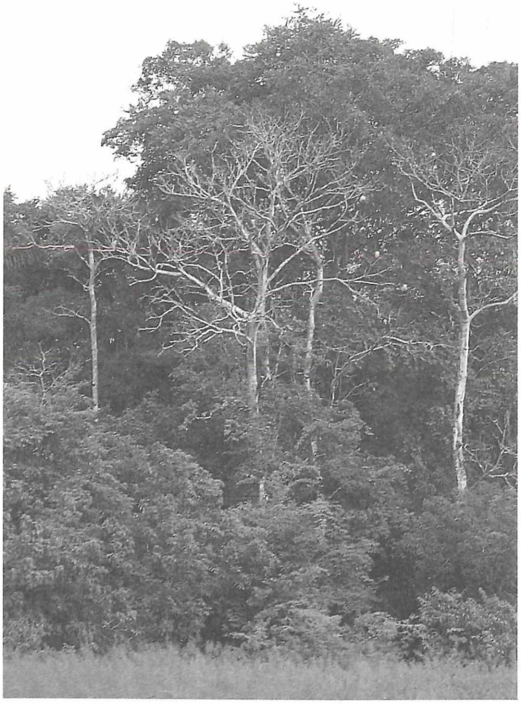

Figure 2. Edge of the study site in the várzea forest on Ilha de Marchantaria, where the termite nest has been found; Photo: H. Höfer.

Table 1. Arthropods found in an abandoned nest of *Nasutitermes tatarendae*. x = no quantitative assessment; n = not determined.

| Taxa | Number of Individuals | Number of Species |
|---|---|---|
| Chelicerata - Arachnida | | |
| Araneae | 156 | 11 |
| Pseudoscorpiones | 1 | 1 |
| Opiliones | | |
| sp. 1 ad. | 22 | 1 |
| sp. 2 ad. | 17 | 1 |
| sp. 3 ad. | 18 | 1 |
| juv. | 412 | |
| Acari | x | ? |
| Crustacea, Chilopoda, Diplopoda | | |
| Isopoda | | |
| *Dubioniscus* sp. (Eubelidae) | 159 | 1 |
| *Prosekia* sp. (Philosciidae) | 158 | 1 |
| Chilopoda - Scolopendromorpha | 72 | n |
| Diplopoda - Polydesmida (juv. & adults) | 185 | 2 |
| Insecta | | |
| Collembola | x | ? |
| Orthoptera - Blattodea | 104 | n |
| Dermaptera | 2 | n |
| Homoptera - Stenorrhyncha | 8 | n |
| Coleoptera | | |
| unident. larvae | 7 | n |
| Carabidae | 26 | 10 |
| Elateridae | 3 | n |
| Staphylinidae | 370 | n |
| Pselaphidae | 3 | n |
| Tenebrionidae | 27 | 3 |
| Scarabaeidae | x | n |
| Scolytidae | 7 | n |
| Colydiidae | 16 | 1 |
| Histeridae sp. 1 | 5 | 1 |
| sp. 2 | 12 | 1 |
| sp. 3 | 1 | 1 |
| Scydmaenidae | 13 | 1 |
| Scaphidiidae sp. 1 | 3 | 1 |
| sp. 2 | 3 | 1 |
| sp. 3 | 1 | 1 |
| Leptodiridae | 1 | 1 |
| others (small mesofauna) | 64 | 7 |
| Hymenoptera | | |
| Formicidae (det. M. VERHAAGH) | | |
| Ponerinae | 782 | 1 |
| *Pachycondyla constricta* | | |
| workers (735) | | |
| alates (13) | | |
| pupae (34) | | |
| Myrmicinae | 86 | 4 |
| *Solenopsis (Diploropthrum)* sp. | | |
| *Cyphomyrmex rimosus* | | |
| *Pheidole* sp. | | |
| *Crematogaster* sp. (*limata*-group) | | |
| Formicinae | 1291 | 2 |
| *Paratrechina* sp. | | |
| *Camponotus* sp. | | |
| Dolichoderinae | 1 | 1 |
| *Tapinoma melanocephalum* | | |
| Bethylidae | 7 | 4 |
| unident. Hymenoptera | 8 | 4 |
| sum | >4054 | >77 |

sify them mostly as opportunistic users of the nest structure (facultative „termitariophiles"; ARAUJO 1970). It was particularly striking how many large scolopenders were extracted. This shows the extension of the internal surface area of the chambers in termite nests (cf. MARTIUS 1994).

Spider species are listed in table 2. All spider species, collected in the abandoned termite nest, have already been collected in the same várzea forest during an ecological survey of the spider fauna (HÖFER unpubl.). Most of them can be considered ground living species. The oonopid species, *Anapistula* sp. and *Theotima* cf. *minutissima* (PETRUNKEVITCH), are tiny spiders dominant in leaf litter samples, pitfall traps and ground-photoeclectors taken in blackwater and whitewater inundation forests during the non-inundated period (HÖFER 1990). When these forests are being flooded (February-April) these spiders migrate into the trunk region, where they have been collected in arboreal funnel traps. The same is true for *Tricongius amazonicus* PLATNICK & HÖFER, 1990, a small sized (≈3 mm) gnaphosid species. The juveniles migrate to the trunks, where they become adult. Adult spiders return to the ground when the water has receded from the forest (September) and reproduce there (PLATNICK & HÖFER 1990). Thereafter the spiderlings of the new generation spread out on the newly emerged ground.

*Orthobula* sp. and *Diestus* sp. are medium sized spiders which were only rarely captured in traps during our studies in inundation forests. It seems possible that they live permanently in higher strata.

*Ctenus* spp. are the most conspicuous large ground living spiders (>10 mm) in all central Amazon forests. In inundation forests they avoid being flooded by vertical or horizontal movements away from the rising water. Consequently they also appear in arboreal funnel traps during inundation.

A wide variety of beetles was found in the nest, many of them very small. Although Staphylinidae are among the most abundant groups (tab. 1), no termitophilous species (KISTNER 1969) were present among them, probably because these species only live in inhabited termite colonies.

Among the ants the ponerine *Pachycondyla* (=*Mesoponera*) *constricta* (MAYR, 1883) was present with wor-

Table 2. Spiders (Arachnida) collected in the abandoned nest of *Nasutitermes tatarendae* in the várzea forest (det. H. HÖFER).

| Family | Genus/Species | Number of Individuals |
|---|---|---|
| Spiders <2 mm body length: | | |
| Oonopidae | | |
| Gamasomorphinae | | 3 |
| Oonopinae | | 2 |
| | | 116 juv. |
| Symphytognathidae | *Anapistula* sp. | 2 |
| Ochyroceratidae | *Theotima* cf.*minutissima* | 2 juv. |
| Salticidae | | 1 juv. |
| Spiders >2 mm body length: | | |
| Gnaphosidae | *Tricongius amazonicus* | 15 juv. |
| Corinnidae | *Orthobula* sp. | 2 |
| Corinnidae | *Diestus* sp. | 2 |
| Ctenidae | *Ctenus* sp. 1 | 3 juv. |
| | *Ctenus* sp. 2 | 7 juv. |
| n. det. | | 1 juv. |
| Total number of individuals | | 156 |
| Total number of species | | 11 |

kers, sexual castes and brood. During an ant survey in Amazonian Peru (VERHAAGH unpubl.), *P. constricta* nests were normally found in soil or rotting wood of advanced state, and in one case in the earth mound of a soil living termite species. The ant (≈8 mm) lives in different forest types as well as in open, man – made habitats, and the nests may contain several hundred up to probably more than thousand workers. Activity is mostly on the ground, and partly hypogeic in litter and soil cavities. We therefore conclude that a whole colony of *P. constricta* moved from the ground into the termite nest, carrying the pupae to the refuge, and possibly other brood as well, which died during the extraction process.

The little (≈3 mm) attine (leafcutting ants and other fungus growers) *Cyphomyrmex rimosus* (SPINOLA, 1853) does not cut leaves but cultivates its fungi on different organic material, mainly insect feces and parts of insect corpses. It can be found active on the ground and in the vegetation, and nests are located in soil, or rotting wood, sometimes high on trees (VERHAAGH, unpubl.). Therefore, workers from the termite nest did not necessarily come from the ground. We did not find any brood, but there might have been brood together with more workers in the upper part of the termite nest which was not examined. The same is true for the the myrmicine ants *Solenopsis* (*Diploropthrum*) sp. and *Pheidole* sp., and the formicine *Camponotus* sp. In all these genera, species exist which nest on the ground as well as on trees, in dead wood or epiphyte humus.

The only dolichoderine species, *Tapinoma melanocephalum* (FABRICIUS, 1793), is a tramp species (≈1,5 mm) with a wide distribution in the neotropics and other tropical regions (KEMPF 1972). It nests in small cavities of any types in all vegetation strata and the single worker certainly did not belong to a nest on the ground; the same we conclude for the single worker of the arboricolous *Crematogaster* sp. (*limata* group).

Most ants found in the termite nest were workers of the formicine *Paratrechina* sp. (≈2,5 mm). 1285 of 1291 formicine ants belonged to this species. *Paratrechina* species in Amazonia nest e.g. in rotten wood, in plant cavities, and in detritus nests which they construct on undersides of leaves (VERHAAGH unpubl.). In general, they are very mobile ants ready to leave their nests at the slightest disturbance. This makes it probable that the workers caught are part of a colony that fled the rising water.

Only one arboricolous pseudoscorpion was found in this mound, but additional species (all arboricolous; MAHNERT & ADIS 1985) were found in other abandoned termite nests, and in dead wood colonized by termites (tab. 3).

## Abandoned nests on the ground

Typical secondary colonizers found in abandoned termite nests on the ground are mostly terricolous spiders, harvestmen, isopods, cockroaches, and ants (tab. 4). Generally, the nests contained only few specimens of these groups, and were thus much less populated than the *N. tatarendae* nest described before.

Table 3. Pseudoscorpions collected in association with termites in the várzea forest (det. V. MAHNERT); P, D, T = Proto-, Deuto-, Tritonymphe.

| Date | Termite Species | Pseudoscorpion Species & Numbers | |
|---|---|---|---|
| 22.04.86 | *Nasutitermes tatarendae* | *Dolichowithius* (?) sp. | 1P |
| 10.12.85 | *N. macrocephalus* | *Parawithius* sp. | 1D |
| 11.03.86 | *Nasutitermes corniger* | *Lustrochernes intermedius* | 1 |
| 28.01.87 | *Anoplotermes* sp. A(?) | *Pachychernes baileyi* | 1T |
| 14.02.85 | termites in dead wood | *Lustrochernes intermedius* | 1 |

Table 4. Presence of secondary fauna in dead arboreal termite nests (mostly of *Nasutitermes corniger*) fallen to the ground. 1= Araneae; 2= Opiliones; 3= Isopoda; 4= Blattodea; 5= Formicidae.

| Nest No. | Date | Conditions | 1 | 2 | 3 | 4 | 5 | Others |
|---|---|---|---|---|---|---|---|---|
| 75-1 | 1.4.86 | dry | X | X | X | X | X | |
| 98-13 | | moist | X | X | X | X | | |
| 118-6 | | fresh, dry | | | X | X | | |
| 197-5 | | ++ dry | | | | | | |
| 197-7 | | ++ dry | | | | | | |
| 109-15 | 2.4.86 | | X | X | X | | | |
| 242-2 | | | X | X | | | | |
| 52-4 | 10.3.86 | moist, fungus | X | X | X | X | X | X* |
| 206-9 | 22.3.86 | moist, fungus | X | X | X | X | X | X** |

*= Oligochaeta, Pseudoscorpiones (cf. tab. 3), Chilopoda, Coleoptera; **= Acari, Staphylinidae

Abandoned termite nests on the ground generally show a higher moisture content than those which are still attached to the trees. Secondary colonization is compartmentalized, which means that some nest parts are occupied and others are not. This is in part due to stochastic processes (who comes first occupies the place and defends it against other immigrants), and in part related to differences in moisture which determine suitability of the nest parts for the different species (the top region of the nests is dry and hard, and the side which is in contact with the ground is moist and rot). In some nests, the activity of the decomposers (mainly isopods) results in a complete filling of the former nest chambers with detritus (for example feces of digested termite nests), which makes further colonization by larger faunal elements almost impossible.

## Conclusion

Termitaria in general offer a suitable habitat for a wide variety of arthropods (ARAUJO 1970, WILSON 1971). They seem to be important hiding places for many of the principally nocturnal spider species even in non-inundated forests (MARTIUS & HÖFER pers. obs.). Ants, too, have often been recorded from inhabited or abandoned termitaria all over the tropics (WHEELER 1936) but in most cases their relationships to the termites and the significance of the termitarium as nesting habitat remained obscure.

In the case of the reported nest, the base of the tree on which this nest was located was flooded the day before it was sampled. Therefore we conclude that the arthropods recorded in that nest belong in large part to the soil fauna which was driven up the trunk by the flood. In fact, the abandoned termite nests on the ground contained much less animals.

Survival strategies of the soil fauna in the floodplains include migration to the trunk and canopy of trees due to the rising water (ADIS 1992). The high number of arthropods found indicates that abandoned termite nests on tree trunks above the highest water level are important temporal refuges for the survival of soil arthropods during the flood period in inundation forests. Although the internal surface of termite nests is small in relation to the surface existing in the tree canopy (MARTIUS 1994), abandoned termite nests could be highly attractive to the soil fauna due to their elevated moisture and many small cavities.

Alternatively, the high catches can be explained by a „trap“ effect of the nest: Arthropods on their way into the upper trunk region which would hide under loose bark, in fresh water sponges on the trunk or disperse into the canopy, are gathered in the nest and will disperse into the canopy only during the following days. Due to the presence of many predators (e.g. most of the ants, the spiders and the centipeds), a considerable mutual predation pressure is likely to be exerted within the nest. In this scenario, the nest „catalyzes“ predatorial interactions between the fauna which is only „accidentally“ agglomerated in the nest. Thus, the nest could lower the density of the migrating fauna instead of enhancing survival. Probably, both processes will occur.

Further comparative studies of the migration processes in relation to the colonization of termite nests by arthropods in the várzea are necessary for a better understanding of the function of abandoned termite nests for migrating soil fauna.

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ANDREAS FLOREN & K. EDUARD LINSENMAIR

# Zur Diversität und Wiederbesiedlungsdynamik von Arthropoden auf drei Baumarten in einem Regenwald in Sabah, Malaysia

**Kurzfassung**

Mit Hilfe einer weiterentwickelten Kronenbenebelungsmethode untersuchen wir die Zusammensetzung von Arthropodengemeinschaften einiger ausgewählter Baumarten eines Tieflandregenwaldes in Sabah, Malaysia. Neben der Erfassung der Diversitäten von Arthropodenzönosen auf verschiedenen Baumarten stehen dabei Fragen zur Wiederbesiedlungsdynamik der behandelten Bäume im Vordergrund. Bei den 10 bislang benebelten Bäumen erwiesen sich die Ameisen mit einem mittleren Anteil von 60% der Gesamtfangzahlen pro Baum (bei mehr als 45000 ausgezählten Arthropoden ohne Berücksichtigung von 13400 Termiten aus einem Baumnest) als die dominante Tiergruppe. Maximal wurden bis zu 61 Ameisenarten auf einem Baum gefunden. Alle anderen Arthropodengruppen waren im Schnitt mit weniger als 10% der Gesamtindividuenzahl pro Baum vertreten. Die dreimalige Benebelung eines Baumes im Abstand von jeweils 9 Tagen ließ die Fangzahlen der meisten Arthropodengruppen stark sinken. Die Dipterenzahlen blieben weitgehend konstant, während die Fangzahlen der Hymenopteren (ohne Formiciden) und besonders der Coleopteren bei der 2. Benebelung stark zunahmen, bei der 3. Benebelung jedoch unter die Anfangswerte sanken. Mögliche Gründe für die Zusammensetzung der Zönosen werden diskutiert.

**Abstract**

**About the diversity and re-colonization dynamics of arthropods on three tree species in a lowland rain forest in Sabah, Malaysia**

An improved method of insecticidal fogging is used to study arthropod communities of the crowns of three tree species in a lowland rainforest in Sabah, Malaysia. Beside the diversities of arthropod groups on different tree species the recolonisation dynamics of fogged trees are investigated. Formicidae were dominant on all 10 trees so far fogged, with 60% of the total counts per tree on the average (>45000 counted arthropods not considering 13400 termites of a single tree nest). Highest number of ant species was 61 for one single tree. All other groups of arthropods averaged less than 10% of the samples. Triple fogging of one tree resulted in a decrease of captures in most arthropod groups. Numbers of Diptera remained nearly constant, those of Hymenoptera (without Formicidae) and, especially, of Coleoptera strongly increased at the second fogging, and then decreased at the third fogging below the primary counts. Possible reasons for the composition of the coenoses are discussed.

Mit Unterstützung der Deutschen Forschungsgemeinschaft im Rahmen des Schwerpunktprogramms „Mechanismen der Aufrechterhaltung tropischer Diversität“

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## 1. Einleitung

Seitdem Naturforscher die Tropen erkunden, stoßen sie immer wieder auf einen fundamentalen Unterschied im Vergleich zu den Lebensräumen der gemäßigten Breiten: auf die extreme floristische und faunistische Diversität tropischer Ökosysteme, die am ausgeprägtesten in den dauerfeuchten, immergrünen Tieflandregenwäldern ist. Die in diesen Wäldern mit sehr vielen Arten vertretenen Phanerophyten bilden ein vielfältiges Mosaik von Habitaten und beherbergen eine noch unüberschaubare Vielfalt von Arthropoden, für deren Gesamtzahl wir nicht einmal fundierte Schätzwerte angeben können. Die Entwicklung neuer methodischer Ansätze ermöglicht es nun, auch die Arthropodenzönosen der bis dahin unerreichbaren Kronenschicht, die als artenreichste Lebensgemeinschaften überhaupt angesehen werden, quantitativ zu erfassen (ERWIN 1989). Nach wie vor stellt diese Artenmannigfaltigkeit eines der zentralen Probleme der Tropenforschung dar (vgl. STORK 1988). Während die Untersuchungen zum Verständnis von Ökosystemen der gemäßigten Breiten zur Entwicklung deterministischer Nischenmodelle führten, wurde während der letzten Jahre immer deutlicher, daß sich diese Modelle nicht ohne weiteres auf tropische Ökosysteme übertragen lassen (LINSENMAIR 1990, TERBORGH 1993). Stattdessen bieten stochastische Modelle plausible Erklärungen für die Koexistenz sehr vieler Arten mit weitgehender Nischenäquivalenz an (CHESSON & CASE 1986). Im Gegensatz zu den deterministischen Nischentheorien gehen sie nicht davon aus, daß die Lebensgemeinschaften einen definierten Gleichgewichtszustand besitzen, auf den die Entwicklung des Systems zusteuert und der es nur einer relativ geringen Anzahl von Arten ermöglicht, in einem Klimaxzustand zu koexistieren.

Zur Klärung der Struktur haben wir begonnen, die Arthropodenzönosen in den Kronen einiger weniger Baumarten in einem Tieflandregenwald auf Borneo (Sabah, Malaysia) zu untersuchen. Das Gebiet liegt

auf etwa 6° N im Kinabalu Nationalpark und wird auf Grund seiner hohen Diversität sowie seines hohen Endemismusgrades als 'Hot Spot Region' innerhalb tropischer Waldsysteme bezeichnet (MYERS 1988).
Für unsere Arbeit stehen folgende Aspekte im Vordergrund:

1. Erfassung und Vergleich der Alpha- und Beta-Diversitäten von Arthropodenzönosen gleicher und verschiedener Baumarten.
   (Unter Alphadiversität versteht man den Artenreichtum eines Habitates, die Betadiversität hingegen beschreibt die Unterschiede zwischen zwei vergleichbaren Habitaten).
2. Besondere Aufmerksamkeit widmen wir den Ameisen und speziell der Frage, welche Rolle sie als hochmobile und bedeutendste Prädatorengruppe in den Baumkronen spielen. Sind sie strukturierende Elemente für die Arthropodengemeinschaften?
3. Welchen Mustern folgt die Wiederbesiedlungsdynamik? Konvergieren die Arthropodengemeinschaften auf einen bestimmten Klimaxzustand hin? Wie wirken sich Unterschiede in der Mobilität und im Generalisten-Spezialisten-Verhältnis auf die Strukturierung der Zönosen bei der Wiederbesiedlung aus?
4. Inwieweit lassen sich aus diesen Analysen Einflüsse deterministischer bzw. stochastischer Prozesse erkennen?

## 2. Material und Methoden

Voraussetzung für die Bearbeitung dieser Fragestellungen ist, den Arthropodenbesatz einzelner Bäume quantitativ und selektiv abfangen zu können. Aus diesem Grunde untersuchen wir mit bis zu 30 m Höhe nur relativ kleine Bäume des unteren Kronenstratums. Methodisch wurde dies durch die Entwicklung der selektiven Kronenbenebelung möglich: Um zu garantieren, daß während der Benebelung nur Arthropoden des Probebaumes und nicht auch der darüberliegenden Strata erfaßt werden, wird über dem zu benebelnden Baum ein ca. 100 $m^2$ großes Stoffdach aufgespannt. Da zwischen den ausgewählten Baumkronen und der oberen Kronenschicht gewöhnlich 10-15 m Distanz liegen, ist der Dachaufbau ohne größere Störung möglich (Taf. 1a – c).
Die Benebelungen fanden jeweils morgens zwischen sechs und sieben Uhr statt, wenn es weitestgehend windstill war. Genebelt wurde zehn Minuten lang mit einer 2% Pyrethrumlösung, appliziert mit einem hochraffinierten technischen Weißöl als Trägersubstanz. Es handelt sich hierbei um natürliches Pyrethrum, das selektiv auf Arthropoden wirkt und bereits nach wenigen Stunden völlig abgebaut ist. Auch das als Trägersubstanz verwandte Weißöl ist biologisch völlig abbaubar und seine Benutzung in jeder Hinsicht dem des bislang benutzten Dieselöls vorzuziehen. Die herabfallenden Arthropoden wurden in 1 m Höhe über dem Boden in aufgehängten Trichtern aufgefangen. Die gesamte Fangfläche betrug 23 $m^2$ pro Baum und deckte mindestens 80% der Kronenprojektionsfläche ab. Der Versuch war nach drei Stunden beendet, wenn keine Tiere mehr in die Fangtrichter fielen. Anschließend wurden die Tiere in 80% Alkohol aufbewahrt und später im Labor präpariert und sortiert.
Die Effektivität der Benebelungen wurde mehrfach überprüft. Bei der visuellen Kontrolle der Baumkronen (Kletterausrüstung) konnten kaum noch Arthropoden festgestellt werden. Auffällig war, daß selbst Ameisen nicht mehr zu beobachten waren, obwohl sie nicht quantitativ zu eliminieren waren (s. 4.2). Das über der Baumkrone aufgespannte Dach erwies sich als sehr wirksam, da hierauf eine Vielzahl von Arthropoden lag, die aus den oberen Kronenschichten herabgefallen waren und so nicht in die Fangtrichter gelangen konnten.
Durch dreimaliges Schütteln der Baumkrone nach der Benebelung ließen sich ca. 5% mehr Tiere gegenüber den direkt heruntergefallenen einsammeln. Davon waren wiederum 40-50% Ameisen. Die hier vorgestellten Ergebnisse wurden ohne Schütteln der Bäume gewonnen.
Für die Untersuchungen wurden zwei Euphorbiaceae, *Aporusa lagenocarpa* und *Aporusa subcaudata*, sowie eine Polygalaceae, *Xantophyllum affine*, gewählt. Alle drei Baumarten sind typisch für den primären Tieflandregenwald im Untersuchungsgebiet. *Aporusa lagenocarpa* tritt geklumpt in Gruppen von bis zu 50 Bäumen auf, ist insgesamt aber ein seltener Baum.
Während der ersten Freilandphase (Februar bis Juli 1992) wurden zehn Bäume je einmal benebelt. Eine *A. subcaudata* wurde insgesamt dreimal im Abstand von jeweils neun Tagen benebelt.

## 3. Ergebnisse

Insgesamt wurden bei den 10 Erstbenebelungen mehr als 59000 Arthropoden gesammelt. Läßt man ein mit 13400 Individuen sehr volkreiches Kartonnest einer *Nasutitermes*-Art auf einem der Probebäume unberücksichtigt - denn ein Einfluß dieser Termiten auf die Zusammensetzung der Zönosen war nach dem Vergleich aller Bäume untereinander nicht erkennbar - ergab dies im Durchschnitt 3-4000 Individuen pro Baum. Auf Ordnungsniveau zeigte sich in allen Fällen eine typische Zusammensetzung der von den Bäumen herabgefallenen Arthropodenfauna: Die Formicidae stellten auf jedem Baum die dominante Tiergruppe. Gewöhnlich fanden sich 30-40 Ameisenarten pro Baum, wobei meist eine Art eudominant war. 70-80% der Arten traten mit weniger als zehn Individuen auf, und 40% aller Individuen waren Einzeltiere. Maximal haben wir aus der Krone eines Baumes 61 Ameisenarten nachweisen können.
Auch die meisten anderen Arthropodengruppen waren auf den einzelnen Bäumen abundanzmäßig immer in ähnlichen Größenordnungen vertreten, so die regelmäßig in größeren Quantitäten auftretenden Coleopteren, Dipteren, Hymenopteren (ohne Formiciden), Homopteren und Arachniden.
Die Coleopteren wurden von jedem Baum mit einem mehr oder weniger konstanten Anteil von 5% der Gesamtindividuenzahl gesammelt. Die Aufarbeitung des Materials ist noch in vollem Gange, es zeigt sich jedoch, daß die abundanzmäßig mit Abstand dominierende Familie die der Chrysomelidae war, die bis zu

50% aller Käfer einer Gemeinschaft ausmachen konnte. Innerhalb der Chrysomeliden war die Gattung *Monolepta* aus der Unterfamilie Galerucinae mit besonders vielen Arten vertreten. Weitere zahlenmäßig bedeutende Familien waren die Curculionidae, Staphylinidae und auf manchen Bäumen die Cantharidae. Allerdings traten auf einzelnen Bäumen immer wieder neue, ansonsten nur mit wenigen Individuen vertretene Familien in größeren Abundanzen auf, so daß die Verteilungsmuster der Käferfamilien von Baum zu Baum relativ stark variierten. Eine erste Durchsicht zeigt, daß nur wenige Arten mit mehr als 20 Individuen vertreten waren.

Die Heteropteren spielten zahlenmäßig eine nur untergeordnete Rolle. Während auf *Xantophyllum* nur wenige Individuen gefangen wurden, traten auf *Aporusa* vor allem äußerlich sehr ähnliche Netzwanzen (Tingidae, vermutlich der Gattung *Physatocheila*) in Erscheinung.

Auffällig war die taxonomische Zusammensetzung der Orthopteren-Fauna, da beinahe ausschließlich Ensifera (meist Tettigonidae) gefangen wurden. Von den 824 gesammelten Tieren gehörten lediglich sechs zu den Caelifera. Ungefähr 80% aller gefangenen Orthopteren - und auch der Homopteren - waren Nymphen.

Von weiteren Arthropodengruppen fanden sich pro Baum meist nur wenige Individuen in den Fanggefäßen. Lediglich die Psocopteren, Thysanopteren, Acarinen und Collembolen zeigten im Vergleich der Bäume große Abundanzschwankungen. Tabelle 1 gibt eine Übersicht der absoluten Fangzahlen und prozentualen Anteile der einzelnen Arthropodengruppen von allen 10 Bäumen.

Bisher wurde ein Baum (*Aporusa subcaudata*) dreimal nacheinander benebelt, jeweils im Abstand von neun Tagen (Tab. 2). Nach dem ersten Benebelungsversuch ergab sich dabei das typische Bild der Zönosenzusammensetzung, wie es sich uns nach allen Erstbenebelungen geboten hatte.

Bei der zweiten und dritten Benebelung lagen die absoluten Individuenzahlen bei fast allen Tiergruppen jeweils niedriger als bei der vorausgegangenen Benebelung. Auch die Gesamtindividuenzahlen verringerten sich stark und zwar auf 78,6% bzw. 38,1% der Werte für die Erstbenebelung. Die bemerkenswertesten Ausnahmen von diesem Schema waren bei den Coleopteren, Dipteren und Hymenopteren (ohne Formicidae) zu finden. Während die Zahl der Dipteren in allen drei Aufsammlungen relativ konstant blieb (maximal 20% Abweichung), nahmen Hymenopteren (ohne Formicidae) und Coleopteren in der Ausbeute der zweiten Benebelung zu und der dritten stark ab. Besonders auffallend waren mit 349% bzw. 34% (bezogen auf den Wert bei der Erstbenebelung) die Schwankungen bei den Coleopteren.

Tabelle 1. Absolute Anzahl, mittlerer prozentualer Anteil und Standardabweichung der Dominanzwerte (SD) der Arthropoden aller 10 erstmals benebelter Bäume, nach Ordnungen getrennt (Berechnung der Werte ohne Berücksichtigung der 13400 von einem Baum gesammelten Termiten); andere Hymenoptera = ohne Formicidae.

| | Absolut | % | SD |
|---|---|---|---|
| Formicidae | 26329 | 60,02 | 13,72 |
| Thysanoptera | 3754 | 6,19 | 7,70 |
| Diptera | 2399 | 4,72 | 2,16 |
| Arachnida | 2265 | 4,61 | 2,03 |
| Coleoptera | 2121 | 4,74 | 2,16 |
| Homoptera | 1793 | 3,75 | 2,04 |
| Andere Hymenoptera | 1213 | 2,61 | 0,75 |
| Heteroptera | 1197 | 2,22 | 2,01 |
| Collembola | 1010 | 1,61 | 2,50 |
| Orthoptera | 831 | 1,47 | 1,07 |
| Andere Arthropoda | 793 | 1,77 | 1,57 |
| Psocoptera | 540 | 1,43 | 1,12 |
| Blattodea | 488 | 1,08 | 0,63 |
| Lepidoptera Larven | 453 | 1,03 | 1,24 |
| Andere Larven | 318 | 1,01 | 1,45 |
| Dermaptera | 170 | 0,41 | 0,26 |
| Lepidoptera | 67 | 0,25 | 0,33 |
| Summe gesamt | 45741 | | |

## 4. Diskussion

### 4.1 Vergleich der erstmals benebelten Bäume

Bei dem Vergleich der Arthropodenzönosen auf den verschiedenen Probebäumen zeigte sich eine verblüffende Regelmäßigkeit bezüglich der absoluten Individuenzahlen der einzelnen Arthropodengruppen. Die Formiciden waren immer mit vielen Arten in der Kronenregion vertreten und zahlenmäßig so dominant, daß sie als ein wichtiger strukturierender Faktor der Zönose vermutet werden können. Es ließen sich aber keine 'Mosaike' dominanter Arten erkennen, wie sie in der Literatur, vornehmlich nach Untersuchungen in Plantagen, beschrieben wurden (JACKSON 1984, MAJER & CAMER-PESCI 1991). Von vielen der in höheren Abundanzen aufgetretenen Arten wissen wir, daß sie tatsächlich in dem benebelten Baum nisteten, da wir meist vor der Benebelung Köder ausgelegt hatten. Durch das Sammeln am Köder allein läßt sich jedoch nur ein Bruchteil der seltenen Arten aus der Krone eines Baumes erfassen.

Beinahe 70% der Ameisenarten jedes Baumes haben wir nur in geringen Abundanzen gefunden, so daß wir vermuten, daß ein Großteil von ihnen nicht auf diesen Bäumen nistete sondern sich nur zufällig, z.B. zur Nahrungssuche, dort befand.

Auch nach Erstellung einer Gesamtartenliste der Ameisen aller untersuchten Bäume (FLOREN in Vorb.)

Tabelle 2. Absolute Individuenzahlen und mittlere prozentuale Anteile der Arthropodengruppen bei dreimaliger Benebelung einer *Aporusa subcaudata* im Abstand von jeweils neun Tagen; andere Hymenoptera = ohne Formicidae.

| | 1.Benebelung | | 2.Benebelung | | 3.Benebelung | |
|---|---|---|---|---|---|---|
| | n | % | n | % | n | % |
| Formicidae | 3530 | 50,65 | 2064 | 37,66 | 1266 | 47,72 |
| Collembola | 598 | 8,58 | 190 | 3,47 | 129 | 4,86 |
| Arachnida | 539 | 7,73 | 157 | 2,86 | 151 | 5,69 |
| Coleoptera | 531 | 7,62 | 1854 | 33,83 | 179 | 6,75 |
| Diptera | 372 | 5,34 | 319 | 5,82 | 395 | 14,89 |
| Homoptera | 369 | 5,29 | 248 | 4,53 | 181 | 6,82 |
| Orthoptera | 238 | 3,42 | 82 | 1,50 | 40 | 1,51 |
| Heteroptera | 207 | 2,97 | 94 | 1,72 | 60 | 2,26 |
| Andere Hymenoptera | 185 | 2,65 | 242 | 4,42 | 96 | 3,62 |
| Andere Arthropoda | 175 | 2,51 | 44 | 0,80 | 35 | 1,32 |
| Blattodea | 74 | 1,06 | 37 | 0,68 | 21 | 0,79 |
| Psocoptera | 50 | 0,72 | 27 | 0,49 | 18 | 0,68 |
| Lepidoptera Larven | 46 | 0,66 | 38 | 0,69 | 19 | 0,72 |
| Dermaptera | 18 | 0,26 | 11 | 0,20 | 11 | 0,41 |
| Andere Larven | 15 | 0,22 | 37 | 0,68 | 6 | 0,23 |
| Lepidoptera | 13 | 0,19 | 18 | 0,33 | 9 | 0,34 |
| Thysanoptera | 9 | 0,13 | 18 | 0,33 | 37 | 1,39 |
| Summe | 6969 | | 5480 | | 2653 | |

ist ein sehr hoher Anteil seltener Arten zu erkennen, so daß wir annehmen müssen, daß noch etliche zusätzliche Arten in den Baumkronen vorkommen.

Unter den anderen Arthopoden traten nur die auf den *Aporusa* spp. gefangenen Netzwanzen mit bis zu mehreren hundert, äußerlich kaum unterscheidbaren Individuen auf. Ob es sich bei ihnen um eine Art oder einen Artenkomplex handelt, muß die genauere taxonomische Untersuchung erst noch zeigen.

Bei den Homopteren fanden sich keine zahlenmäßig sehr stark vertretenen Gruppen, auch keine großen Aphidenpopulationen, wie sie von Wäldern gemäßigter Breiten bekannt sind. Das Gleiche gilt mit ca. 30 Individuen pro Baum für die Lepidopterenlarven. Unverstanden ist bislang, warum wir beinahe ausschließlich Langfühlerschrecken und nur vereinzelt Kurzfühlerschrecken gefangen haben. RIEDE (1993) fand in südamerikanischen Wäldern genau umgekehrte Verhältnisse.

Von der weitgehenden Übereinstimmung in der numerischen Zusammensetzung der Arthropodengemeinschaften, wie sie auf allen Bäumen gefunden wurde, wichen lediglich die Acarinen, Collembolen, Psocopteren und Thysanopteren ab, die im Vergleich große Abundanzschwankungen zeigten. Für die Thysanopteren könnte hierfür ein saisonaler Effekt verantwortlich sein: Mehrere der Probebäume standen zur Zeit der Benebelung in Blüte, jedoch waren Thysanopteren nicht auf allen blühenden Bäumen mit hohen Individuenzahlen vertreten. Eventuell lassen sich die Abundanzschwankungen der Collembolen auf Wanderungsbewegungen zurückführen (BOWDEN et al. 1976). Natürlich hat auch die Benebelungsmethode ihre Grenzen, und für viele der Kleinarthropoden ist die Kronenbenebelung sicher nicht die optimale Fangmethode. Insgesamt können wir aber nach unseren Erfahrungen davon ausgehen, daß sich durch die von uns angewandte Methode die Arthropodengemeinschaften der Baumkronen bis auf die im Holz lebenden Tiere (s. 4.2) beinahe vollständig erfassen lassen.

### 4.2 Die Wiederbenebelungsversuche

Aus den hier vorgestellten Daten der Wiederbenebelungsversuche lassen sich erste Einblicke in die Dynamik der kurzfristigen Wiederbesiedlung gewinnen. Es zeigte sich, daß die Ameisen alleine durch die Benebelungen nicht von den Bäumen eliminierbar waren, da die hochabundanten Arten (vor allem der Gattungen *Plagiolepis*, *Dolichoderus* und *Crematogaster*) ihre Nester im Stammbereich hatten, in denen sie vor dem Insektizid geschützt waren. Ihre zahlenmäßige Dezimierung ist aber so groß, daß ein Effekt auf die anderen Arthropodengruppen durchaus möglich erscheint, wenn ihnen, wie vermutet, bei der Strukturierung der Zönosen eine Schlüsselrolle zukommt. Ob ihre Verringerung eine Ursache für den nur bei den Coleopteren beobachteten, steilen zahlenmäßigen Anstieg bei der zweiten Benebelung war, bleibt vorerst unklar, da die Käferzahl nach der dritten Benebelung trotz weiter reduzierter Ameisenzahl auf 1/10 des Wertes der zweiten Benebelung zurückging.

Unter den Coleopteren waren es vor allem Chrysomeliden, Curculioniden und Anthiciden, die in hohen Individuendichten auftraten und an die Pionierarten gemäßigter Breiten denken lassen. Im vorliegenden Fall handelte es sich aber - wie die vorläufigen Analysen zeigen - nicht um jeweils eine einzelne Pionierart, sondern stets um Komplexe von Arten, die sich äußerlich zum Teil sehr ähnlich sind. Vergleichbare Abundanzschwankungen wie bei den Käfern wurden bislang bei keiner weiteren Gruppe beobachtet.

Starke Effekte einer wiederholten Benebelung waren auch bei den meisten anderen Tiergruppen zu finden. Lediglich die Individuenzahlen der Dipteren blieben durchgängig hoch und deuten auf die hohe Mobilität und damit hohe Kolonisierungsfähigkeit dieser Gruppe hin.

### 4.3 Vergleich mit anderen Kronenbenebelungsversuchen

Bei den Vorbereitungen zur Anwendung der Benebelungsmethode wurde auf Vergleichbarkeit mit anderen Literaturdaten geachtet. Vor allem die Arbeiten von STORK (1991) sind von Interesse, da er ebenfalls auf Borneo (Brunei) benebelt hat.

STORK (1991) konnte von zehn Bäumen insgesamt 23482 Arthropoden sammeln. Dies entspricht 117,4 Tieren pro qm Fangfläche. Dem stehen in unserer Untersuchung 45741 Arthropoden (ohne das Termitennest auf einem Baum) von ebenfalls zehn Bäumen gegenüber, entsprechend 198,9 Tieren pro qm Fangfläche, bzw. 59141 (incl. des Termitennestes), entsprechend 257,1 Tieren pro qm Fangfläche. Dabei ist zu beachten, daß alle von STORK benebelten Bäume weit größer als unsere Probebäume waren und er in einem Überschwemmungswald gearbeitet hat. Aber auch er fand eine konstante Zusammensetzung der Arthropodengemeinschaften, allerdings in einer anderen Rangfolge der Abundanzen der einzelnen Gruppen (s. Tab. 3).

Vor allem die Formiciden waren in seinen Proben in wesentlich geringerer Zahl präsent. Nur von einem Baum fing er über 1000 Tiere, im Mittel waren es hingegen nur 443, gegenüber einem mittleren Wert von 2630 bei den von uns untersuchten Bäumen. Auch prozentual lagen die Formiciden in unseren Proben mit 60% (berechnet ohne das Termitennest) mehr als dreimal so hoch als die von ihm ermittelten 18,2%. Die besonders hohe Zahl der Dipteren, die bei STORKS Benebelungen in Nordsulawesi noch sehr viel ausgeprägter war (STORK & BRENDELL 1990), fand sich in keiner unserer Proben. Diese Ergebnisse sind im Hinblick auf die angenommene strukturierende Rolle, die die Ameisen für die Arthropodengemeinschaften möglicherweise spielen, interessant. Zu bedenken ist allerdings, daß die Zoozönosen in der oberen Kronenschicht und in den Überständern vielleicht generell anders strukturiert sind als in den Bäumen der unteren Strata. Denkbar wäre auch, daß bei den hohen Falldistanzen viele der kleinen Arthropoden nicht in den Fangtrichtern landen. Hinweise auf saisonale Effekte, die diese Unterschiede erklären könnten, lassen sich aus unseren Untersuchungen nicht ablesen.

Bei Kronenbenebelungen im Amazonasregenwald ermittelten ADIS et al. (1984) dagegen ähnlich hohe Prozentwerte für die Formiciden bei den von ihnen benebelten Bäumen. Auffällig ist jedoch, daß von 9 Bäumen nur insgesamt 9639 Arthropoden gefangen wurden und daß die Rangfolge der abundanten Arten jeweils sehr unterschiedlich war. Allerdings verglichen sie drei verschiedene Waldtypen (terra firme-Wald, Schwarz- und Weißwasserüberschwemmungswald, jeweils 3 untersuchte Bäume) miteinander, so daß diese Ergebnisse nur bedingt mit unseren vergleichbar sind.

Auch ein allererster Vergleich bei den Wiederbenebelungen ist möglich. STORK (1991) konnte von einem Baum, den er nach zehn Tagen erneut benebelt hatte,

Tabelle 3. Vergleich der prozentualen Anteile der abundanzmäßig bedeutendsten Arthropodengruppen bei den von STORK (1991) in Brunei durchgeführten Kronenbenebelungen mit den Werten, die diese Gruppen, bei den Benebelungen in Sabah erzielten (n=jeweils zehn Bäume; andere Hymenopteren = Hym. ohne Formiciden). In ( ) ist der jeweilige Rang der Gruppe angegeben.

| | STORK (1991) (28.8-9.9.82) | Diese Arbeit[1] (21.2-20.6.92) |
|---|---|---|
| Arthropoda gesamt | 23482 | 45741 |
| Anteile [%] | | |
| Diptera | 21,50 (1) | 4,72 (4) |
| Formicidae | 18,20 (2) | 60,02 (1) |
| Coleoptera | 16,90 (3) | 4,74 (6) |
| Hemiptera | 11,20 (4) | 5,97 (3) |
| Andere Hymenoptera | 8,80 (5) | 2,61 (7) |

[1] Berechnung der Werte ohne Berücksichtigung der 13400 von einem Baum gesammelten Termiten

nur noch 18% der vorab ermittelten Gesamtindividuenzahl sammeln, während unsere Zahlen, selbst die der dritten Benebelung, wesentlich höher liegen (78,6% bei der 2. und 38,1% bei der 3. Benebelung bezogen auf die Gesamtindividuenzahl der 1. Benebelung). Obwohl es noch zu früh ist, Interpretationen zu wagen, lassen sich STORKs Folgerungen, daß die Dipteren, Formiciden und Acarinen, im Gegensatz zu den Coleopteren und Thysanopteren, sehr schnell rekolonisieren, nur teilweise bestätigen. In unseren Versuchen waren es gerade die Coleopteren (unter ihnen vor allem die Chrysomeliden) und die Dipteren, die die Baumkronen schnell in großer Zahl wiederbesiedelten. Da die Formiciden durch die Benebelung allein nicht aus der Krone zu eliminieren sind und ein Großteil von ihnen in den Nestern überleben kann, ist ihr Auftreten in hohen Abundanzen nach zehn Tagen verständlich und entspricht auch unseren Ergebnissen.
Aus dem vorliegenden Datenmaterial lassen sich natürlich noch keine generellen Schlußfolgerungen ziehen. Insbesondere fehlen weitere Untersuchungen zur Wiederbesiedlungsdynamik freier Baumkronen. Wir erwarten, daß weitere Benebelungen, vor allem nach längeren Zeitspannen, sowie die genauere Auswertung des Tiermaterials aussagekräftigere Ergebnisse erbringen.

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a) Das Stoffdach wird in 30 m Höhe über dem Probenbaum aufgespannt.

b) Während des Benebelungsversuches hält das Dach die aus den höheren Kronenbereichen herabfallenden Arthropoden von den Fangtrichtern ab. Durch genaue Positionierung der Fangtrichter unter dem Dach wird verhindert, daß Tiere von anderen Bäumen in die Probe gelangen.

c) Durch direktes Benebeln in der Baumkrone ist garantiert, daß alle Baumbereiche erfaßt werden.

**andrias, 13:** 29-32, 2 Figs; Karlsruhe, 30. 9. 1994

RICARDO PINTO-DA-ROCHA

# A new species of *Santinezia* from central Amazonia, with systematic comments on the genus (Arachnida, Opiliones, Cranaidae)

**Abstract**

*Santinezia manauara*, a new species from Reserva Ducke, Manaus, Amazonas, Brazil is described. The genus *Santinezia* ROEWER is compared with species of the genera *Nieblia* ROEWER, *Macuchicola* MELLO-LEITÃO and *Carvalholeptes* SOARES, altogether forming a monophyletic group.

**Resumo**

**Uma nova espécie do gênero *Santinezia* da Amazônia central com notas sobre a sistemática do gênero (Arachnida, Opiliones, Cranaidae)**

*Santinezia manauara*, uma nova espécie de opiliões da Reserva Ducke, Manaus, Amazônia é descrita. O gênero *Santinezia* é comparado com espécies dos gêneros *Nieblia* ROEWER, *Macuchicola* MELLO-LEITÃO e *Carvalholeptes* SOARES, com os quais *Santinezia* forma um grupo monofilético.

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## Introduction

The family Cranaidae is composed of approximately 80 genera and 180 species. The species present an Andean-Amazonian distribution and were recorded from Panama/Costa Rica to Bolivia/Chile (ROEWER 1923, MELLO-LEITÃO 1932). The genera *Multumbo*, *Piassagera* and *Pseudotrogulus*, from the Atlantic Forest, were recently transfered from Cranaidae to Gonyleptidae by KURY (1992).

The genus *Santinezia* ROEWER, 1913 (Cranainae) includes 21 large-sized species distributed through Trinidad, Colombia, Venezuela, Guyanas, Brazil, Peru, Ecuador and Bolivia. The new species *Santinezia manauara* is based on material from Reserva Ducke, Manaus, Amazonas in Brazil which I received from Dr. HUBERT HÖFER (SMNK) and ERICA BUCKUP (MCN). The specimens were collected by Dr. J. ADIS and Prof. Dr. L. BECK during their ecological studies on arthropod fauna in central Amazonia in the 1970's and recently by A. D. BRESCOVIT.

## Material and Methods

The material examined is deposited in the following collections: MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo (J.L. LEME); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. MAGALHÃES) and SMNK, Staatliches Museum für Naturkunde, Karlsruhe (H. HÖFER). All measurements are in millimeters.

## Description

### *Santinezia manauara*, new species

(Figures 1, 2)

Type material: Male holotype: Reserva Ducke (02°55'S 59°59'W), Manaus, Amazonas, Brazil, J. ADIS leg., 15.X.-10.XI.1976, (INPA). Paratypes: 1 female, same data (MZSP); 2 males and 1 female, same data (INPA); 1 male, same data (SMNK); 1 male and 1 female, same locality, L. BECK leg. 1972 (SMNK); 1 male, same data (MZSP); 3 males and 3 females, same locality, 20.VIII.1991, A.D. BRESCOVIT leg. (MCN-1090/1092); 1 male and 1 female, same data (MZSP).

Etymology. The specific name comes from the Brazilian Portuguese noun „manauara", which means native from Manaus.

Diagnosis: *S. manauara* differs from the other known species of the genus by the combination of the following characters: femur and tibia IV (fig. 1e) with a curved acute tubercle in the male, absent in female; male chelicerae not swollen; dorsal scute without white or yellowish-white spots.

Description: Male (holotype): Dorsal scute 10.83 long, 10.00 wide, cephalothorax 4.67 long, 6.33 wide. Chelicera: segment II 5.50 long, III 2.67 long.

Dorsal scute (fig. 1a, b): Body outline hexagonal, wider at groove III. Cephalothorax with 2 lateral tubercles on anterior margin and 2 behind the eye mound. Eye mound with 2 long and divergent spines, directed forwards. Area I divided, with 3 tubercles on each side; II with 4 tubercles; III with 2 long and divergent spines directed backwards and 2 tubercles behind the spines. Posterior margin with 2-4 tubercles on each side. Free tergite I with 6 tubercles; II with 1-2 tubercles on each side, 2 large and 2 small medianly; III with 2 large tubercles. Anal operculum with a posterior row of small tubercles.

Venter: Coxae I-III with a median row of tubercles; IV with a long apophysis, perpendicular to body axis. Posterior margin and free sternites with a row of small tubercles. Anal operculum with a row of small tubercles.

Chelicera: Segment I with 5-6 dorsal tubercles; II not swollen, with several tubercles. Chelae swollen.

Pedipalpus (fig. 1c, d): Coxa with 1 ventral tubercle. Trochanter with 2 ventral and 3 dorsal tubercles (1

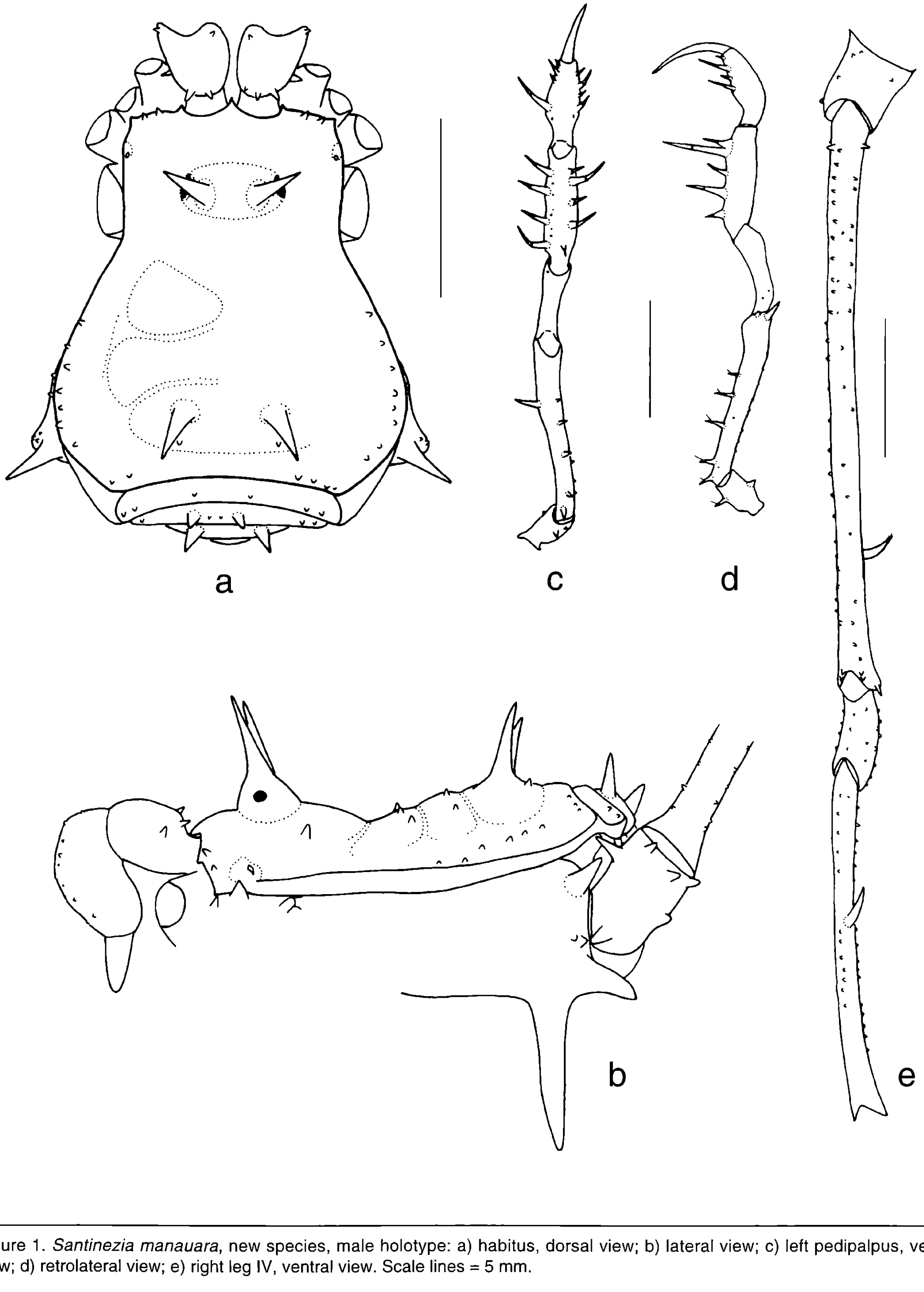

Figure 1. *Santinezia manauara*, new species, male holotype: a) habitus, dorsal view; b) lateral view; c) left pedipalpus, ventral view; d) retrolateral view; e) right leg IV, ventral view. Scale lines = 5 mm.

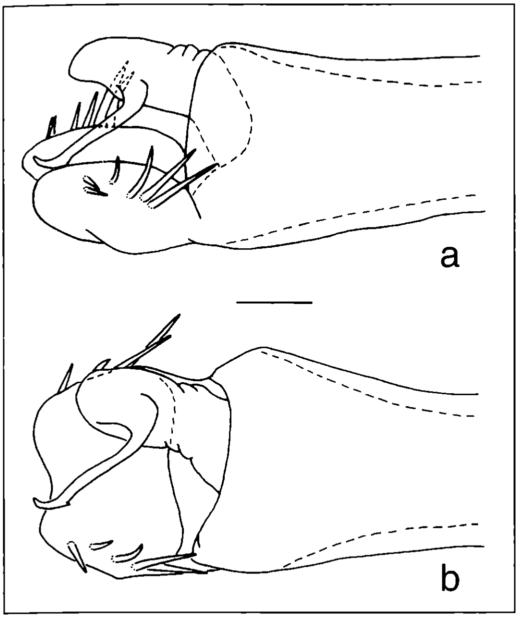

Figure 2. *Santinezia manauara*, new species, male holotype: a) distal part of penis, dorsal view; b) lateral view. Scale line = 0,1 mm.

dorsal larger). Femur straight, with a ventral row of 5 large tubercles, a dorsal row of smaller tubercles, 1 large tubercle prolateral-subapically, a retrolateral row and a dorsal apical acute tubercle (fig. 1d). Patella tuberculate. Tibia (fig. 1c) with 5 ectal (ilili) and 4 mesal setae (liii). Tarsus (fig. 1c) with 4 ectal (iili) and 4 mesal (liii) setae.

Legs (fig. 1e): Coxae I-II with 1 dorso-basal tubercle; IV with a large apical and smaller lateral tubercles. Trochanter I with 3 ventral and 2 retrolateral tubercles; II with 3 ventral, 2 retrolateral and 1 dorsal tubercle; III with 3 ventral, 4 prolateral and 3 retrolateral tubercles; IV with 4 ventral, 3 prolateral, 3 retrolateral and 2 dorsal tubercles. Femor I-IV straight, with several longitudinal rows of tubercles; III-IV with 2 dorso-apical tubercles; IV with a curved and acute prolateral tubercle (fig. 1e). Tibia IV with a curved median ventral tubercle (fig. 1e). Tarsal process long; legs III-IV with 2 parallel claws; scopulae short. Tarsal segmentation: 10(3), 18(3), 11, 12. Appendage measurements are shown in table 1.

Genitalia (fig. 2a, b): Ventral plate hexagonal, concave, clearly distinct from truncus, with 6 lateral setae (the 3 basal longer). Glans: Stylus long and slender, rising at the middle of the glans, with a short seta subapically.

Coloration: Dark brown. Cephalothorax almost black. Eye mound and spines of area III and free tergites II-III yellowish. Chelicera and pedipalpus dark reticulate. Lateral and posterior margins of the dorsal scute and free tergites with black spots.

Female (Paratype, MZSP): Dorsal scute 8.50 long, 7.83 wide; cephalothorax 4.00 long, 5.33 wide. Chelicera: segment II 3.60 long; III 1.84 long.

Dorsal scute narrower than in male; lateral margin with 1-2 tubercles. Free tergites I-III with 2 lateral tubercles; II-III with a pair of long tubercles. Coxa IV without ventral apophysis. Femur IV and patella IV without curved tubercle. Tarsal segmentation: 9(3), 19(3), 10, 11. Appendage measurements are shown in table 1.

Variation (6 males, 3 females): Area I with 3-4 tubercles on females; II with 1-2 tubercles. Posterior margin of the dorsal scute with 2-4 tubercles. Free tergite I with 1-2 tubercles on males, 2-3 on females; II-III with 1-2 lateral tubercles. A single male presents a short ventral apophysis on coxa IV. I believe that this apophysis (secondary sexual character) should be a good character to distinguish the last male instar (very short) from the adult (long).

Distribution: Known only from the type locality in central Amazonia.

Biological notes: Several specimens were collected aggregated in a log on the forest ground in „terra firme" vegetation (J. ADIS, pers. com.).

### Discussion of systematics of the genus *Santinezia*

*Santinezia* ROEWER, 1923 is closely related to *Nieblia* ROEWER, 1925, *Macuchicola* MELLO-LEITÃO, 1940 and *Carvalholeptes* SOARES, 1970. These four genera form a monophyletic group, sharing the following character states: Eye-mound and area III with two long

Table 1. *Santinezia manauara*, new species: appendage measurements of male holotype and female paratype (in parentheses).

| | TR | FE | PT | TI | MT | TA | Total |
|---|---|---|---|---|---|---|---|
| Leg I | 1.00 (1.00) | 10.67 ( 9.17) | 2.5 (2.08) | 6.67 ( 5.00) | 12.17 ( 9.50) | 4.17 ( 3.33) | 38.18 (30.08) |
| II | 1.20 (1.12) | 20.85 (10.33) | 6.67 (2.92) | 16.67 (13.67) | 22.51 (16.67) | 11.33 ( 9.67) | 57.23 (54.38) |
| III | 1.60 (1.40) | 17.00 (13.33) | 3.83 (3.00) | 9.50 ( 7.17) | 16.33 (13.00) | 5.50 ( 5.00) | 53.76 (42.90) |
| IV | 2.40 (1.52) | 21.00 (17.33) | 4.33 (3.17) | 13.83 (10.17) | 22.51 (19.67) | 6.50 ( 5.83) | 70.57 (57.69) |
| Pedipalpus | 1.40 (1.40) | 7.08 ( 6.25) | 3.75 (3.33) | 4.67 ( 4.17) | —— (——) | 3.83 ( 3.33) | 20.73 (18.48) |

spines (the first is synapomorphic for Cranainae plus Stygnicranainae – see KURY in press); coxa IV with a long and ventral apophysis, perpendicular to the antero-posterior body axis (synapomorphic for these genera); pedipalpal femur with a dorso-apical and acute tubercle (seems to be synapomorphic for a group of Cranainae genera); free tergite II-III with two large tubercles. All these genera may be distinguished from *Santinezia* by the internal armature of pedipalpal femur (unarmed in *Santinezia*), and the armature of area IV and free tergite I (both unarmed in *Santinezia*). The original description (ROEWER 1913) of the genus (as *Inezia*, preoccupied) considers area I as armed with two tubercles. Although the armature of area I is usually considered diagnostic at this level, some species of *Santinezia* are unarmed (as in *S. manauara*).

The differences mentioned above are characters which distinguish genera („genus value" according to the ROEWERian system) but, they present sexual and interspecific variations (except internal armature of pedipalpus). Therefore, they are not useful to distinguish these four genera. Another interesting feature is the glans with a membranous region and with rings and stylus rising in the middle or in the subapical region of the glans, instead of the apical region. This occurs in the four Venezuelan species illustrated by GONZÁLEZ-SPONGA (1989, 1991), namely *S. heliae* AVRAM, 1983, *S.circumlineatus* GONZÁLEZ-SPONGA, 1989, *S. duranti* GONZÁLEZ-SPONGA, 1989 and *S. biordi* GONZÁLEZ-SPONGA, 1991; and *S. manauara*. In the related families (Tricommatidae, Gonyleptidae, Cosmetidae and Stygnidae) the membranous region has no rings and the stylus rises apically. KURY (in press) illustrated the genitalia of a Prostygninae, which form, together with Heterocranainae, the sister-group of Cranainae and Stygnicranainae; and the position of the stylus is similar to families related to the Cranaidae. However, at the moment it is impossible to decide if this is a synapomorphy for *Santinezia* or for a group of Cranainae genera, because the information from literature is very poor regarding genitalic features, and the other Cranaidae were not examined. Based on the above mentioned I prefer not to include *Nieblia*, *Macuchicola* and *Carvalholeptes* in the synonymy of *Santinezia* without a careful study of the type-material of these genera.

### Acknowledgments

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ALEXANDRE B. BONALDO & ANTONIO D. BRESCOVIT

# Revision of the Neotropical spider genus *Stethorrhagus* (Araneae, Corinnidae)

**Abstract**

The genus *Stethorrhagus* SIMON, 1896 is characterized and described. Seven previously known species are redescribed: *S. chalybeius* (L. KOCH, 1866) n. comb.; *S. duidae* GERTSCH, 1942; *S. limbatus* SIMON, 1896, the type species; *S. lupulus* SIMON, 1896; *S. nigrinus* (BERLAND, 1913) n. comb.; *S. roraimae* GERTSCH, 1942 and *S. tridentatus* CAPORIACCO, 1955. Seven new species are described: *S. oxossi* and *S. archangelus* from Brazil; *S. latoma* from Venezuela; *S. penai* from Ecuador; *S. planada*, *S. peckorum* and *S. hyula* from Colombia. The male of *S. lupulus*, the female of *S. tridentatus* and the actual female of *S. chalybeius* are described for the first time. *S. abrahami* MELLO-LEITÃO, 1948 is synonymized with *S. limbatus* SIMON. The genus *Parachemmis* is newly transferred from Liocranidae to Corinnidae. *Stethorrhagus hassleri* GERTSCH, 1942 is synonymized with *Stethorrhagus mastigostylus* MELLO-LEITÃO, 1948 and transferred to *Parachemmis*.

**Resumo**

**Revisão do gênero *Stethorrhagus* (Araneae, Corinnidae) da região neotropical**

O gênero *Stethorrhagus* SIMON, 1896 é caracterizado e descrito. Sete espécies conhecidas são redescritas: *S. chalybeius* (L. KOCH, 1866) n. comb.; *S. duidae* GERTSCH, 1942; *S. limbatus* SIMON, 1896, a espécie-tipo; *S. lupulus* SIMON, 1896; *S. nigrinus* (BERLAND, 1913) n. comb.; *S. roraimae* GERTSCH, 1942 e *S. tridentatus* CAPORIACCO, 1955. Sete espécies novas são descritas: *S. oxossi* e *S. archangelus* do Brasil; *S. latoma* da Venezuela; *S. penai* do Ecuador; *S. planada*, *S. peckorum* e *S. hyula* da Colombia. O macho de *S. lupulus*, a fêmea de *S. tridentatus* e a atual fêmea de *S. chalybeius* são descritas pela primeira vez. *S. abrahami* MELLO-LEITÃO, 1948 é sinonimizado com *S. limbatus* SIMON. O gênero *Parachemmis* é transferido de Liocranidae para Corinnidae. *Stethorrhagus hassleri* GERTSCH, 1942 é sinonimizado com *Stethorrhagus mastigostylus* MELLO-LEITÃO, 1948 e transferido para *Parachemmis*.

**Kurzfassung**

**Revision der neotropischen Spinnengattung *Stethorrhagus* (Araneae, Corinnidae)**

Die Gattung *Stethorrhagus* SIMON, 1896 wird charakterisiert und beschrieben. Sieben bereits bekannte Arten werden wiederbeschrieben: *S. chalybeius* (L. KOCH, 1866) n. comb.; *S. duidae* GERTSCH, 1942; *S. limbatus* SIMON, 1896, die Typusart; *S. lupulus* SIMON, 1896; *S. nigrinus* (BERLAND, 1913) n. comb.; *S. roraimae* GERTSCH, 1942 und *S. tridentatus* CAPORIACCO, 1955. Sieben neue Arten werden beschrieben: *S. oxossi* und *S. archangelus* aus Brasilien; *S. latoma* aus Venezuela; *S. penai* aus Ecuador; *S. planada*, *S. peckorum* und *S. hyula* aus Kolumbien. Das Männchen von *S. lupulus*, das Weibchen von *S. tridentatus* und das eigentliche Weibchen von *S. chalybeius* werden erstmals beschrieben. *S. abrahami* MELLO-LEITÃO, 1948 wird synonymisiert mit *S. limbatus* SIMON. Die Gattung *Parachemmis* wird von den Liocranidae zu den Corinnidae transferiert. *Stethorrhagus hassleri* GERTSCH, 1942 wird mit *Stethorrhagus mastigostylus* MELLO-LEITÃO, 1948 synonymisiert und zu *Parachemmis* gestellt.

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## 1. Introduction

The spider genus *Stethorrhagus* was erected by SIMON (1896) for two Amazonian species. Since this time the genus was recognized by the presence of one pair of excavations on anterior margin of the sternum, regarded as a relative of *Megalostrata* KARSCH and *Corinna* C. L. KOCH and listed under Corinninae (Clubionidae or Corinnidae). The genus is exclusively neotropical and includes up to date ten species (SIMON, 1896; FRANGANILLO, 1926, 1930; GERTSCH, 1942; MELLO-LEITÃO, 1948; CAPORIACCO, 1955).

In addition to the sternal excavations, all known species of *Stethorrhagus* have a ventral, apical articulated apophysis on the male palpal tibia. These two characters, however, are not restricted to *Stethorrhagus* and may define a group of genera in Corinninae.

Another representative of this group is *Parachemmis*, described by CHICKERING (1937), who judged it as a relative of *Chemmis* SIMON and *Anachemmis* CHAMBERLIN, both at that time included in Micariinae (Clubionidae). REISKIND (1969) in his reclassification of Micariinae, considered *Parachemmis* a possible Liocraninae (Clubionidae), mainly by the presence of four to six pairs of long ventral spines on the tibiae of the first pair of legs and only simple hairs on abdomen. In our opinion, however, *Parachemmis* is not a Liocranidae, as listed by recent catalogers. Several pairs of ventral spines on anterior tibiae are common among Corinninae and scanning electron micrographs of *Parachemmis hassleri* (GERTSCH) showed feathery setae on abdomen and legs (fig. 3 a-c), a character present in both Corinnidae and Liocranidae. Also, in *Parachemmis* no ventral rows of bristles or modified setae on anterior metatarsi and tarsi do occur, as in some Liocranidae (UBICK & PLATNICK 1991, PLATNICK & DI FRANCO 1992). On the other hand, males of the genus have no median apophysis on the palpal bulb, which was suggested to be a synapomorphic loss for Corinnidae by PENNIMAN (1985). The presence of sternal excavations in both sexes and an articulated apophysis on male palpal tibiae are strong indications that *Parachemmis* is a close relative of *Stethorrhagus*. Thus, *Parachemmis* is newly transferred to Corinninae, Corinnidae.

*Stethorrhagus* is herein characterized by the presence of a bifid embolic apex with the ejaculatory duct opening on the bifurcation in males and in females by a single median copulatory opening and a sclerotized dorsal plate covering the posterior half of the epigynum.

## 2. Material and Methods

The material examined belongs to the following collections: AMNH, American Museum of Natural History, New York (N. I. PLATNICK); BMNH, The Natural History Museum, London (P. D. HILLYARD); CAS, Californian Academy of Sciences, San Francisco (C. E. GRISWOLD); CPDC, Centro de Pesquisas do Cacau -Ceplac, Itabuna (P S. TERRA); CLP, Aracnological collection from Reserva Natural La Planada, La Planada (C. VALDERRAMA A.); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. MAGALHÃES); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E. H. BUCKUP); MCNC, Museo de Ciencias Naturales de Caracas, Caracas (J. E. LATTKE); MCP, Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A. A. LISE); MCZ, Museum of Comparative Zoology, Cambridge, Mass. (H. W. LEVI); MNHN, Museum National d`Histoire Naturelle, Paris (C. ROLLARD); MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (A. TIMOTHEO DA COSTA); MUCV, Museo de Biologia, Universidad Central de Venezuela, Caracas (G. A. PEREIRA); SMNK, Staatliches Museum für Naturkunde, Karlsruhe (H. HÖFER); USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C. (J. CODDINGTON).

All measurements are in millimeters. The epigynes were submerged in clove oil to study internal structures. Micrographs were obtained with scanning electron microscopes in „Laboratorium für Elektronenmikroskopie“ of the university of Karlsruhe, Germany (Cambridge Stereoscan type 73654) and in „Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul“, Brazil (Jeol JSM-5200). Because the micrographs have been reduced for publication, the magnification figures supplied in the legends provide only relative scale information.

## 3. Systematics

### Genus *Stethorrhagus* SIMON

*Stethorrhagus* SIMON, 1896: 421; 1898: 200, figs 198, 199, 202 (type species by subsequent designation, *S. limbatus* SIMON); ROEWER (1954: 604); BONNET (1958: 4167); BRIGNOLI (1983: 557); PLATNICK (1989: 446, 1993: 617).

Diagnosis: *Stethorrhagus* is closely related to *Parachemmis* (see CHICKERING 1937: figs 33, 48 and GERTSCH 1942: fig. 35) through the paired excavations on anterior margin of the sternum and the presence of a ventral, apical articulated apophysis on male palpal tibia. It differs in the bifid embolic apex on the male palp, with the ejaculatory duct opening on the bifurcation (figs 5 c,d, 6 a, 9 a,c, 14 a) and in females by possessing a single central copulatory opening (figs 9 d, 12 d, 18 a) and a sclerotized internal dorsal plate covering the posterior half of the epigynum (figs 9 e, 12 e, 18 b).

Description: Total length (males and females) 5.10 -12.40. Carapace almost oval in dorsal view, widest between coxae II and III; narrowing of cephalic area hardly notable, anterior margin wide and truncated. Generally, cephalic area gradually elevated and not well delimited (fig. 8 a); only in *Stethorrhagus chalybeius* is cephalic area abruptly elevated and well delimited (fig. 1 a). Thoracic groove short, deep. Clypeal height approximately equal to AME diameter. Anterior eye row procurved in frontal view, posterior eye row procurved in dorsal view. Ocular quadrangle longer than wide in dorsal view, front width slightly larger than back width. AME largest, remainders with subequal length; median eyes circular, lateral eyes oval. Interdistances: AME-AME separated by less their diameter; AME-ALE almost contiguous; PME-PME separated by less than twice their diameter; PME-PLE separated at maximum by twice the diameter of PME; ALE-PLE contiguous. Chilum generally entire or bipartite, haired or not; in the female of *S. archangelus* chilum semibipartite. Chelicerae smaller than half the carapace length, slightly longer and more slender in males; generally, slightly geniculate, with a conspicuous lateral boss and a retrolateral proximal field of serrate setae with tubercular insertions (fig. 2 a,c,d). Promargin and retromargin of fang furrow with 3 to 5 teeth (fig. 2 b); in *S. chalybeius* chelicerae geniculate. Endites convergent, promargin slightly concave, retromargin excavated. Labium longer than wide, with marginal, proximal constrictions (fig. 1 d). Sternum slightly longer than wide, with a pair of deep (figs 1 c, 15 a, 18 c) or shallow (figs 10 c, 12 a) lateral anterior excavations; pre-coxal triangles present.

Leg formula 4, 1, 2, 3. Legs moderately long and thin, covered by feathery and simple hairs. Tarsi and metatarsi with sparse scopulae (fig. 4 a,b); metatarsi III and IV with ventral distal clusters of black setae. Leg tarsi with two pectinate claws and dense claw tufts (fig. 3 f); tarsal trichobothria (fig. 4 c-e) in two rows; tarsal organ (fig. 4 c,d,f) with a subapical, circular aperture. Female palpal tarsus clavate, with one pectinate claw; trochanters notched; in *S. chalybeius*, femora I expanded proximally, with a retrolateral field of thin setae with grooved insertions (fig. 3 d,e).

Typical spination: I -femur d1-1-0, p0-0-1, r0, v0; tibia d0, p0, r0, v2-2-2-2-2; metatarsus d0, p0, r0, v2-2-0. II -femur d1-1-0, p1-1-1, r0, v0; tibia d0, p0, r0, v2-2-2-2-2; metatarsus d0, p0, r0, v2-2-0. III -femur d1-1-1, p0-1-1, r-0-1-1, v0; tibia d0, p1-1-0, r1-1-0,

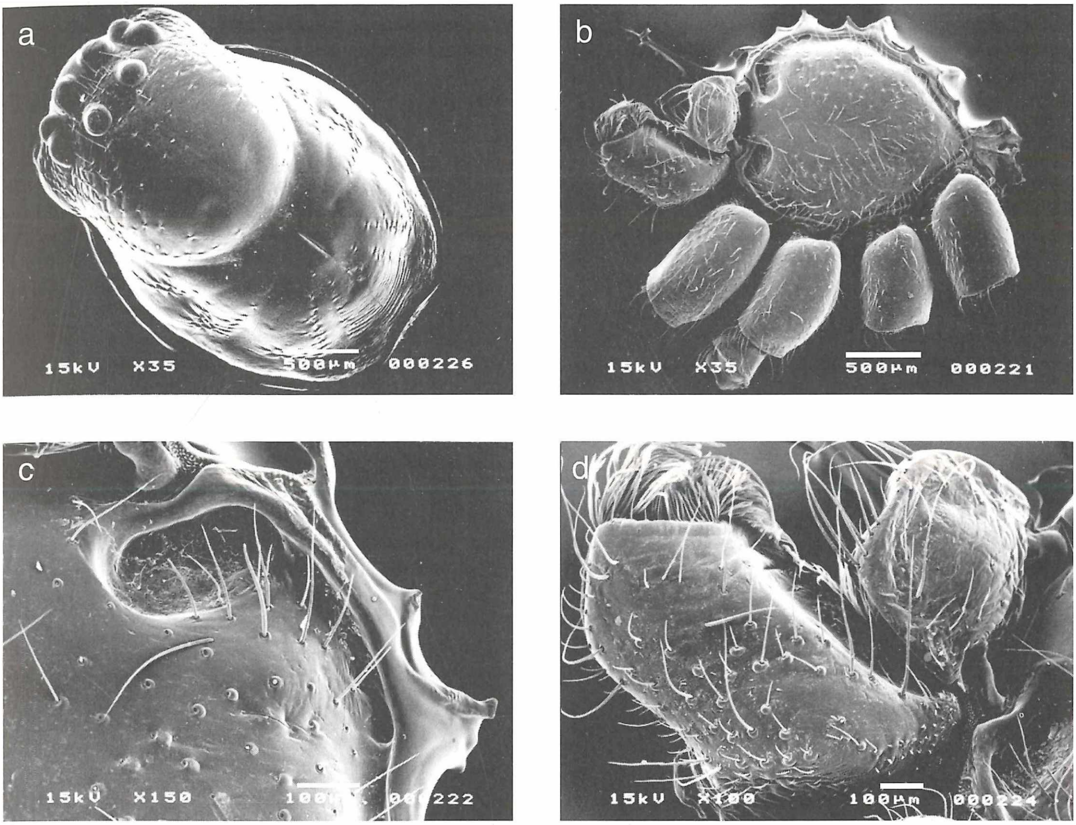

Figure 1. *Stethorrhagus chalybeius* (L. KOCH), male: a) carapace, dorsal; b) sternum, coxae, endite and labium, ventral; c) sternal excavation, ventral; d) endite and labium, ventral.

v2-2-2; metatarsus d0, p1-1-1, r1-1-1, v2-2-1. IV -femur d1-1-1, p0-1-1, r0-0-1, v0; tibia d0, p1-1-0, r1-1-0, v2-2-2; metatarsus d0, p1-1-1, r1-1-1, v2-2-1. Abdomen oval, covered by feathery hairs (fig. 2 e,f), with a dorsal anterior scutum or none. Tracheal tubercle large, sclerotized and without hairs. Colulus a semicircular, long plate, covered by few feathery setae (fig. 6 e). Six spinnerets (fig. 6 f). Anterior lateral spinnerets (fig. 7 c,f) convergent, conical, contiguous at base, two-segmentated, distal segment short, truncate, with two large major ampullate gland spigots on mesal margin and 40-50 small piriform gland spigots. Posterior median spinnerets (fig. 7 b,e) parallel, tubular, contiguous, one-segmentated; apices with few aciniform gland spigots and, at least, two minor ampullate gland spigots; in females, three large cylindrical gland spigots with conic bases and enlarged shafts (fig. 7 e). Posterior lateral spinnerets (fig. 7 a,d) convergent, tubular, separated by, at least, twice their diameter; two-segmentated, distal segment short, truncated, with about 15 aciniform gland spigots; in females, two large cylindrical gland spigots (fig. 7 d). Males without cylindrical gland spigots in both posterior spinnerets (fig. 7 a,b). Anal tubercle not prominent.

Male palp: Apices of femora, patellae and tibiae often with a retrolateral cluster of modified setae (fig. 5 a,b). Tibiae with an entire or bifurcated retrolateral apophysis (fig. 6 b) and often with a dorsal process; tibial ventral distal articulated apophysis always present (figs 6 c, 9 b,c, 10 a,b). Subtegulum visible distally, in the not expanded bulb. Tegulum generally with prolateral or ventral helicoidal duct, often with one or two laminar extentions. Conductor always present, hyaline, arising distally from the tegulum (figs 5 c, 6 a). Embolus normally narrowed and long, arising prolaterally or medianly from the tegulum; embolic apex bifid, with long or short prongs and with the ejaculatory duct opening on the bifurcation (figs 5 d, 10 a, 14 a, 16 a); in *S. duidae* and *S. peckorum*, prongs strongly reduced (figs 19 b, 20 b).

Epigynum: Anterior margin not delimited, except in *S. archangelus* and *S. tridentatus* (figs 12 d, 14 d).

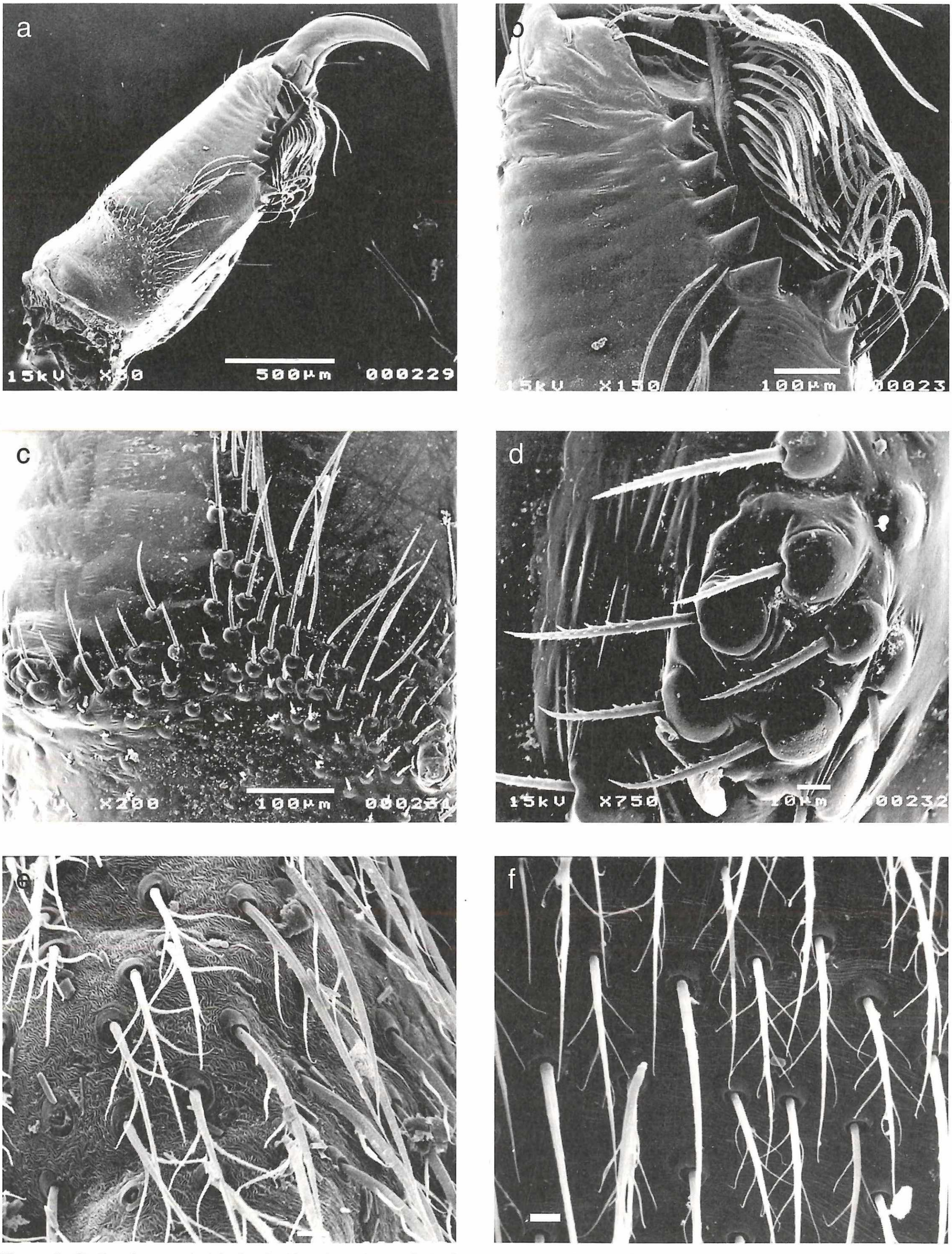

Figure 2. *Stethorrhagus chalybeius* (L. Koch), male: a-d) chelicera, retrolateral; e) abdomen, dorsal; f) *Stethorrhagus oxossi* new species, male: abdomen, dorsal (700 x).

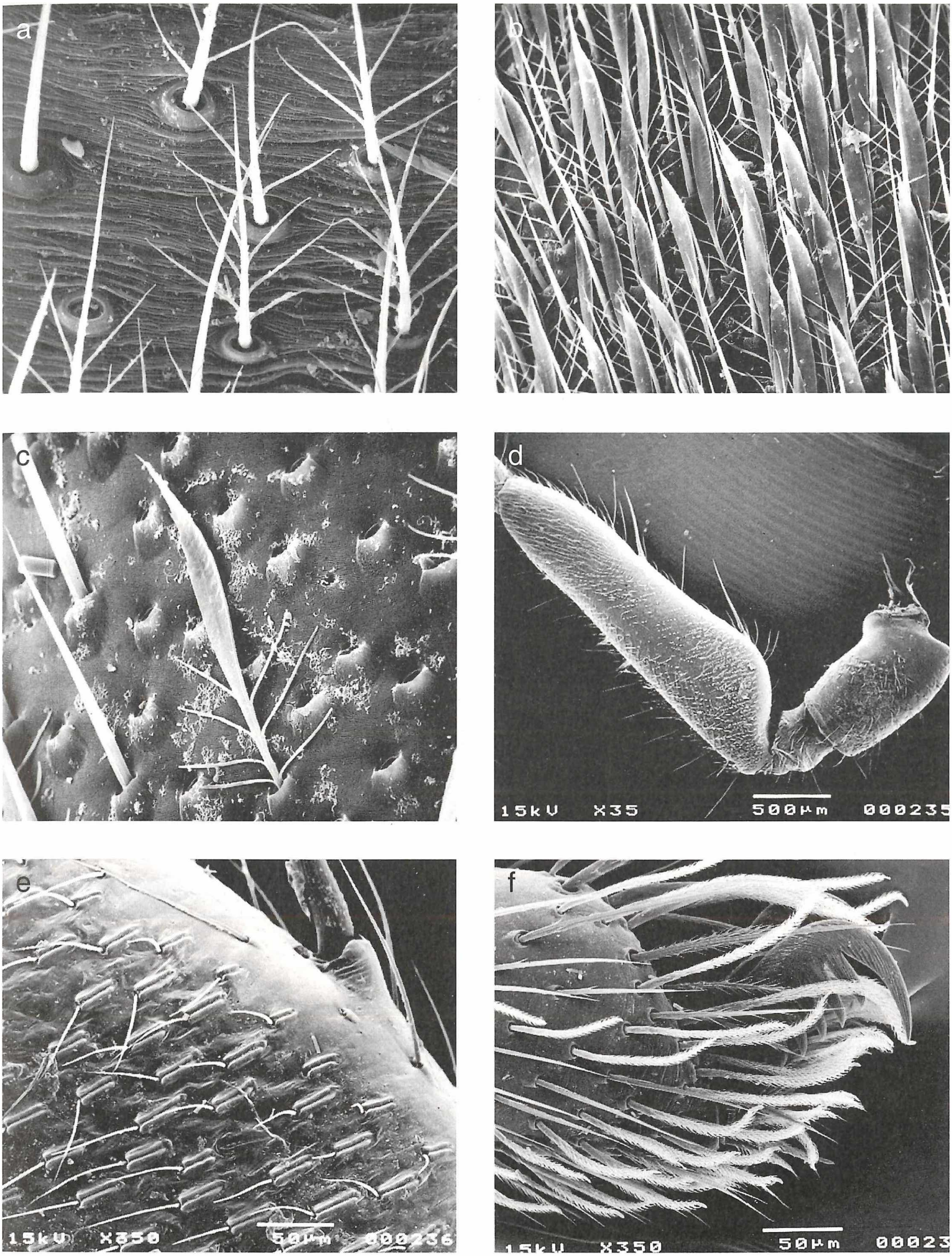

Figure 3. *Parachemmis hassleri* (GERTSCH), male: a) abdomen, dorsal (1000 x) b, c), femur I, lateral (400 x, 800 x); *Stethorrhagus chalybeius* (L. KOCH), male: d, e) femur I, retrolateral; f) apex of tarsus II, lateral.

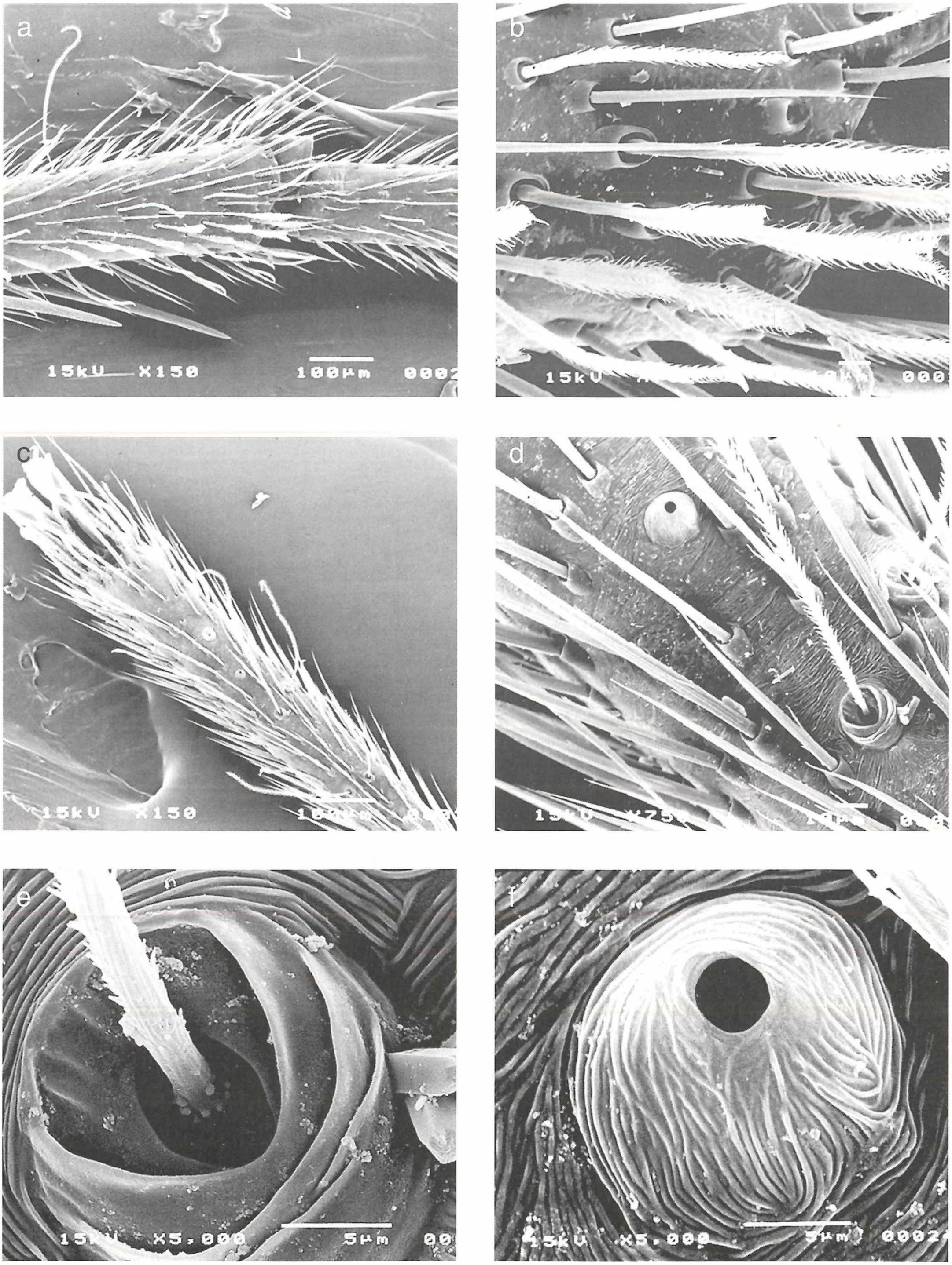

Figure 4. *Stethorrhagus chalybeius* (L. KOCH), male: a, b) leg II, lateral; c-f) tarsus IV, dorsal; e) trichobothrial base; f) tarsal organ.

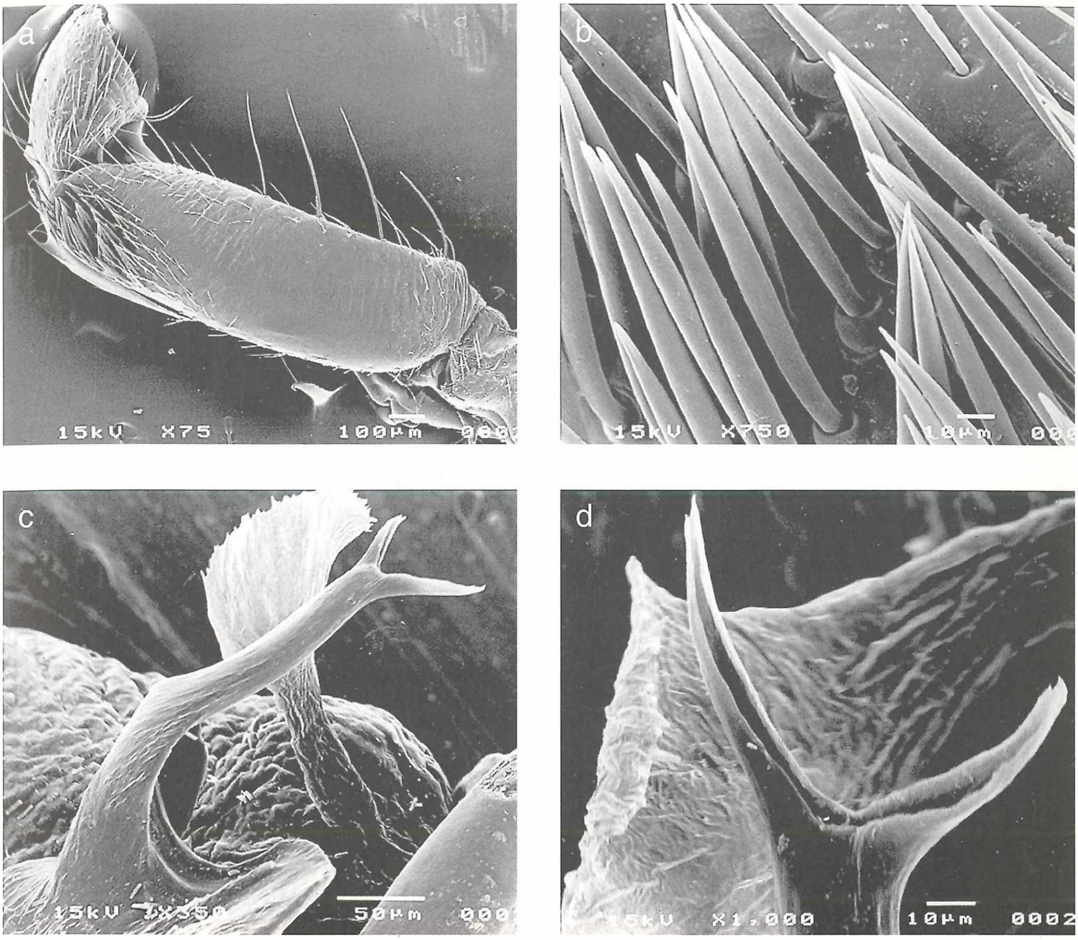

Figure 5. *Stethorrhagus chalybeius* (L. KOCH), male: a, b) palpal femur, retrolateral; c) embolus, prolateral; d) apex of embolus, prolateral.

Unpaired copulatory opening generally small and rounded (figs 11 c, 12 d), except in *S. limbatus*, where it is large and wide (fig. 9 d). Median plate, if present, large (fig. 6 d), except in *S. planada*, where it is small (fig. 18 a). Spermathecae disposed posteriorly in relation to the copulatory opening (figs 9 d, 10 f, 18 a, 23 a), except in *S. chalybeius*, where it is disposed anteriorly (fig.16 d). Copulatory ducts independent (*S. limbatus*, fig. 9 e) or fused anteriorly, connected at basis of a pair of oval or spherical spermathecae (figs 10 g, 19 d). Fertilization ducts connected basally to the spermathecae. Bursae copulatrix apparently always present, not visible in some species due to the presence of a strongly sclerotized dorsal plate, which can bear a median invagination (figs 9 e, 11 d, 14 e, 16 e).
Composition. Fourteen species.

Unrecognizable species: *Stethorrhagus striatus* FRANGANILLO, 1926 and *S. mandibulatus* FRANGANILLO, 1930, both from Cuba (not examined, may be in Cuban Academy of Sciences, Habana) are unrecognizable without examination of the types.
Misplaced species: *Stethorrhagus hassleri* GERTSCH, 1942: 12, fig. 35 (male MCZ, examined) = *Parachemmis hassleri* (GERTSCH, 1942). New combination.
*Stethorrhagus mastigostylus* MELLO-LEITÃO, 1948: 185, fig. 25 (male and female BMNH, examined) = *Parachemmis hassleri* (GERTSCH, 1942). New synonymy.

## *Stethorrhagus limbatus* SIMON

Figures 8, 9

*Stethorrhagus limbatus* SIMON, 1896: 421 (three male and two female syntypes from Tefé and São Paulo de Olivença, Amazonas and Le Para (= Belém), Pará, Brazil, NATHAN, in MNHN

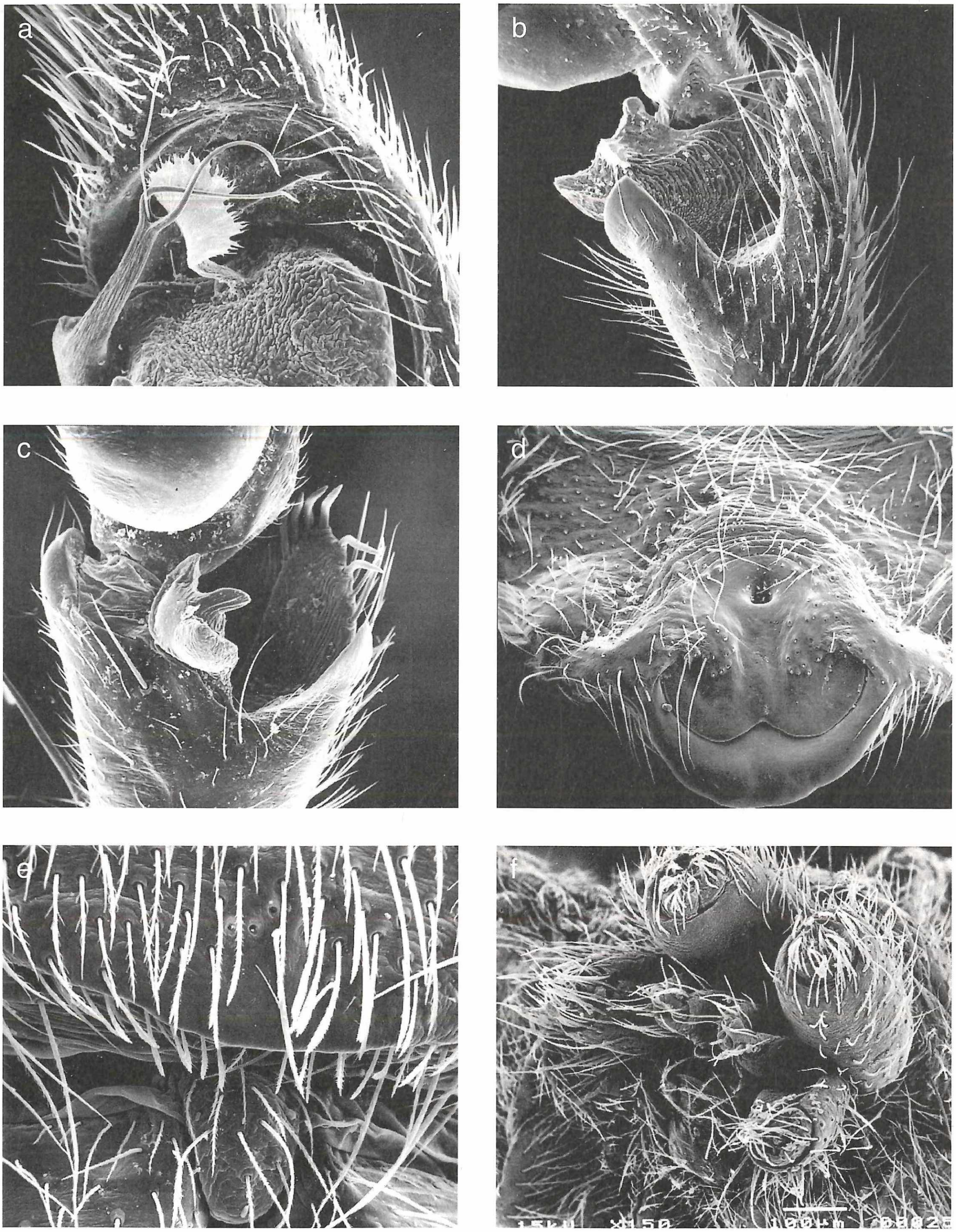

Figure 6. *Stethorrhagus oxossi* new species, male: a) apex of bulb, ventral (160 x); b) palpal tibia, retrolateral (100 x); c) palpal tibia, ventral (110 x); female: d) epigynum, ventral (100 x); e) tracheal tubercle and colulus, ventral (360 x); f) *Stethorrhagus chalybeius* (L. KOCH), male: spinnerets, anterior laterals above.

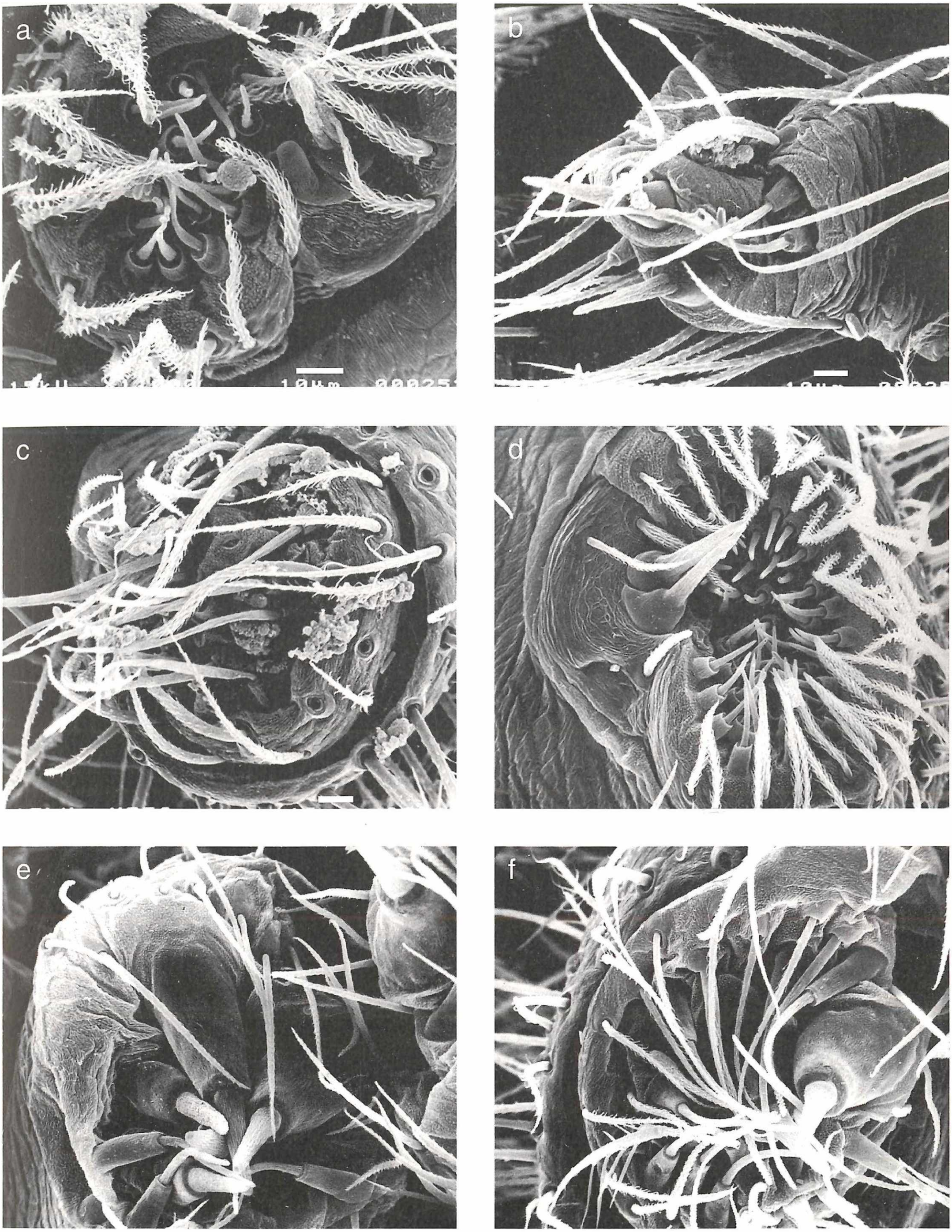

Figure 7. *Stethorrhagus chalybeius* (L. KOCH), male: a) posterior lateral spinnerets; b) posterior median spinnerets; c) anterior lateral spinnerets; *Stethorrhagus oxossi* new species, female: d) posterior lateral spinnerets (800 x); e) posterior median spinnerets (800 x); f) anterior lateral spinnerets (800 x).

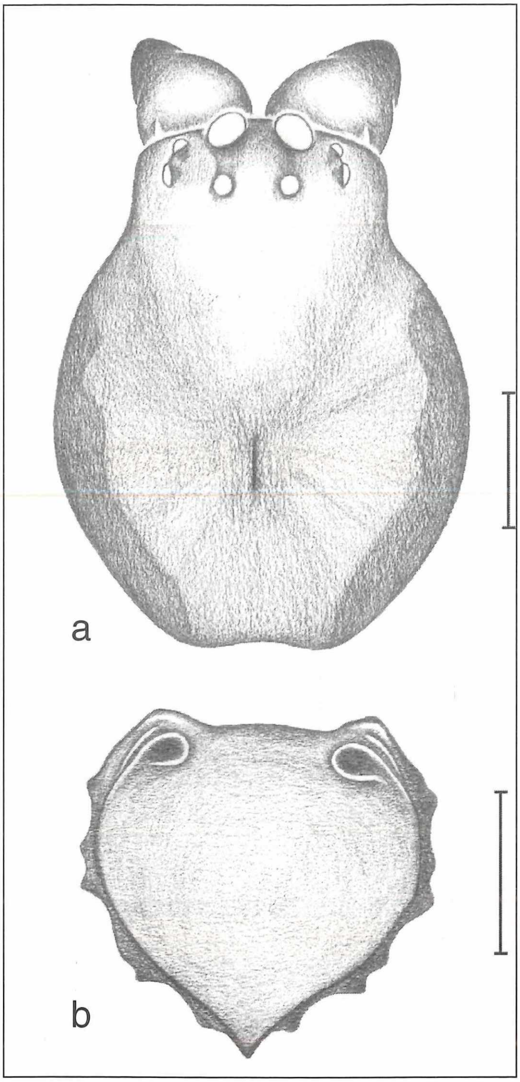

Figure 8. *Stethorrhagus limbatus* Simon, male: a) carapace, dorsal; b) sternum, ventral; scale lines: 1.0 mm.

3616, examined; male lectotype MNHN 3616 and two male and two female paralectotypes MNHN ex 3616, here designated); 1898: 200, figs 198, 199, 202; Roewer (1954: 605); Bonnet (1958: 4167).

*Stethorrhagus abrahami* Mello-Leitão, 1948: 183, fig. 24 (male holotype from Guest, Moraballi River, Essequibo River, 15 miles above Bartica, British Guiana, Aug. 20, 1929, R. W. G. Hingston, in BMNH 1930.4.15.1A, examined); Roewer (1954: 604). New synonymy.

Diagnosis: *Stethorrhagus limbatus* is a distinct species, easily recognized by the entire and pointed retrolateral tibial apophysis, without modified hairs, an uncoiled tegular duct on the male palp (fig. 9 a-c) and the large, wide copulatory opening (fig. 9 d) and the separated copulatory ducts (fig. 9 e) on the female epigynum.

Male (lectotype): Carapace yellow, with two darker lateral stripes on the edges of thoracic region (fig. 8 a); chelicerae, endites and labium lighter reddish brown; sternum, legs and abdomen yellowish.

Total length 8.20. Carapace 3.95 long, 3.00 wide, 1.10 high. Clypeus 0.40. Chilum poorly delimited, bipartite, without hairs. Anterior eye row 1.35 long, posterior eye row 1.47 long. Eye diameters and interdistances: AME 0.37, ALE 0.27, PME 0.22, PLE 0.25; AME-AME 0.17, AME-ALE 0.05, PME-PME 0.35, PME-PLE 0.30, ALE-PLE 0.05. MOQ length 0.70, front width 0,85, back width 0.75. Chelicerae 2.30 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 1.75 long, 1.70 wide, deep sternal excavations, with delimited internal margin (fig. 8 b). Abdomen 4.20 long, 2.00 wide; dorsal scutum long.

Leg measurements: I -femur 4.90 / patella 1.50 / tibia 4.90 / metatarsus 4.80 / tarsus 2.45 / total 18.55 / II -4.70 / 1.40 / 4.60 / 4.80 / 2.40 / 17.90 / III -4.40 / 1.40 / 4.00 / 2.10 / 16.30 / IV -5.20 / 1.40 / 4.70 / 6.20 / 2.40 / 19.90. Leg spination: conforming with the typical pattern.

Palp: retrolateral tibial apophysis not bifid, arising medianly, with pointed tip directed ventrally; dorsal tibial process present, small; articulated apophysis rounded. Tegulum with basal, prolateral, curved duct, laminar extensions lacking; embolus gently curved, moderately enlarged at basis; apical prongs of the embolic tip long, equally wide (fig. 9 a-c).

Female (paralectotype MNHN ex 3616): Coloration as in male.

Total length 9.60. Carapace 3.90 long, 3.10 wide, 1.60 high. Clypeus 0.37 high. Chilum as in male. Anterior eye row 1.35 long, posterior eye row 1.47 long. Eye diameters and interdistances: AME 0.40, ALE 0.22, PME 0.25, PLE 0.25; AME-AME 0.20, AME-ALE 0,07, PME-PME 0,27, PME-PLE 0.32, ALE-PLE 0,05. MOQ length 0.75, front width 0.85, back width 0.75. Chelicerae 2.15 long, with teeth as in male. Sternum 1.75 long, 1.75 wide, excavations as in male. Abdomen 5.70 long, 3.50 wide, without dorsal scutum.

Leg measurements: I -femur 4.70/ patella 1.50/ tibia 4.80/ metatarsus 4.60/ tarsus 2.30/ total 18.00/ II -4.70/ 1.50/ 4.60/ 4.60/ 2.20/ 17.60/ III -4.30/ 1.40/ 4.00/ 4.30/ 2.00/ 16.00/ IV -5.30/ 1.40/ 4.80/ 6.20/ 2.30/ 20.00. Leg spination: IV femur p0-0-1, r0-1-1.

Epigynum: copulatory opening large, wide, recurved; without median plate (fig. 9 d). Internally with two separated copulatory ducts; two spherical spermathecae connected to hook-shaped fertilization ducts; bursa copulatrix present, small, arising ventrally from spermathecae (fig. 9 e).

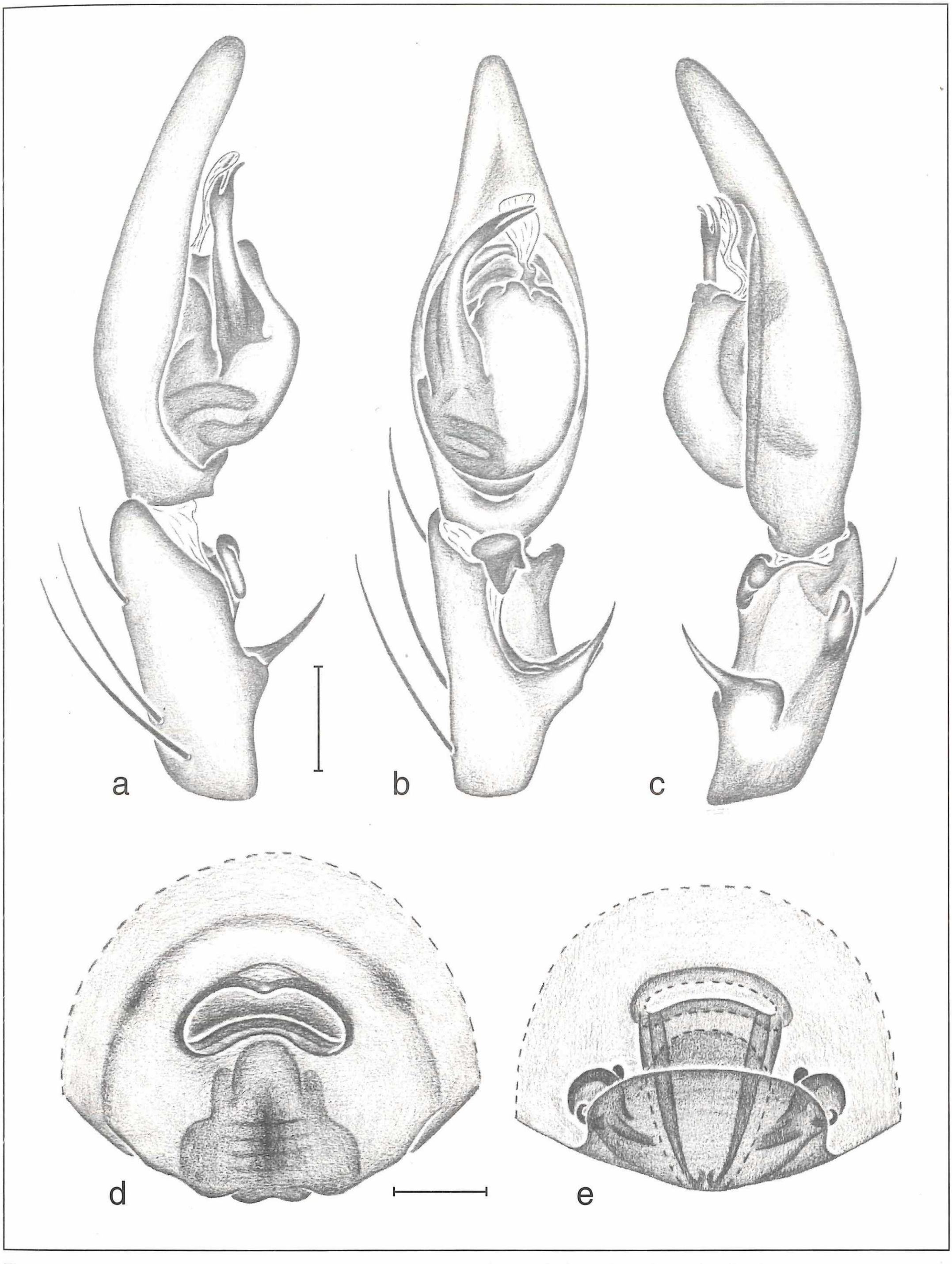

Figure 9. *Stethorrhagus limbatus* SIMON, male: a) palp, prolateral; b) ventral; c) retrolateral; female: d) epigynum, ventral; e) dorsal; scale lines: a-c, 0.5 mm; d, e, 0.25 mm.

Variation: Three males: total length 7.30-9.90; carapace 3.30-4.40; femora I 4.20-5.30; two females: total length 8.20-9.10; carapace 3.70-3.80; femora I 4.60-4.90.

Distribution: Brazilian Amazon and British Guiana.
Material examined: Only the types.

### ***Stethorrhagus lupulus*** **SIMON**
Figure 10

*Stethorrhagus lupulus* SIMON, 1898: 422 (female holotype from São Paulo de Olivença, Amazonas, Brazil, MATHAN, in MNHN 8131, examined); ROEWER (1954: 605); BONNET (1958: 4167).

Diagnosis: *Stethorrhagus lupulus* is closest to *S. oxossi.* Males may be distinguished by palpal tibiae with a rounded dorsal process, an articulated tibial apophysis without retrolateral projection and a prolateral median extension on tegulum (fig. 10 a,b); females by „V"-shaped copulatory opening, with delimited anterior margin and a median plate close to posterior margin of the epigynum (fig. 10 f).

Male (Smithsonian Reserve, Fazenda Esteio, Manaus, Amazonas): Carapace reddish brown, darker on margins; chelicerae reddish brown; endites, labium and sternum orange; abdomen pale yellow, scutum orange, dorsum with posterior black spots.

Total length 6.30. Carapace 2.70 long, 2.10 wide, 0.75 high. Clypeus 0.25. Chilum entire, sclerotized and without hairs. Anterior eye row 0.91 long, posterior eye row 1.01 long. Eye diameters and interdistances: AME 0.26, ALE 0.18, PME 0.18, PLE 0.17; AME-AME 0.10, AME-ALE 0.05, PME-PME 0.17, PME-PLE 0.18, AME-PLE 0.03. MOQ length 0.55, front width 0.56, back width 0.51. Chelicerae 1.25 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 1.30 long, 1.20 wide, shallow sternal excavations, without delimited internal margin (fig. 10 c). Abdomen 3.50 long, 1.25 wide, with dorsal, elongated scutum.

Leg measurements: I -femur 3.05 / patella 1.10 / tibia 2.90 / metatarsus 2.50 / tarsus 1.25 / total 10.80 / II -3.00 / 1.00 / 2.60 / 2.55 / 1.20 / 10.35 / III -2.40 / 0.70 / 2.10 / 2.20 / 1.15 / 8.55 / IV -3.60 / 1.00 / 3.00 / 4.10 / 1.40 / 13.10. Leg spination: I tibiae v1p-2-2-2-2-2-0; II tibiae v2-2-2-2-2-0. Palp: retrolateral tibial apophysis bifurcated at basis, ventral extension laminar distally, with two projections, dorsal extension strong, with a basal process and modified setae on the apex; dorsal process present, large and rounded; articulated apophysis longer than wide, hammer-like in ventral view. Tegulum with basal, prolateral, coiled duct, with two median laminar extensions, one prolateral and one sub-apical; embolus curved, enlarged prolaterally at basis; distal prong longer than proximal prong (fig. 10 a,b).

Female (Reserva Florestal Adolfo Ducke, Manaus, Amazonas): Coloration as in male except abdomen pale brown, dorsum with transversal white stripes and a large black posterior spot.

Total length 6.00. Carapace 2.50 long, 2.00 wide, 0.75 high. Clypeus 0.22 high. Chilum as in male. Anterior eye row 0.82 long, posterior eye row 0.87 long. Eye diameters and interdistances: AME 0.22, ALE 0.16, PME 0.16, PLE 0.15; AME-AME 0.11, AME-ALE 0.03, PME-PME 0.10, PME-PLE 0.14, ALE-PLE 0.05. MOQ length 0.50, front width 0.50, back width 0.47. Chelicerae 1.10 long, dentation as in male. Sternum 1.30 long, 1.15 wide, sternal excavations as in male. Abdomen 3.30 long, 1.60 wide, with reduced, circular dorsal scutum.

Leg measurements: I -femur 2.50 / patella 1.00 / tibia 2.40 / metatarsus 2.10 / tarsus 1.10 / total 9.10 / II -2.50 / 0.85 / 2.25 / 2.10 / 1.10 / 8.80 / III -2.40 / 0.80 / 2.05 / 2.30 / 1.10 / 8.65 / IV -3.10 / 0.85 / 2.50 / 3.50 / 1.30 / 11.25. Leg spination: I femur p0-1-1, v2-2-2-2-2; II femur p0-1-1, tibia v2-1p-2-2-2; III femur p0-1-1, r1-1-1, metatarsus v2-2-1p; III tibia v2-2-0; IV femur p0-1-1, r0-0-1.

Epigynum: copulatory opening „V"-shaped, with delimited anterior margin; median plate large; posterior margin of the epigynum projected posteriorly (fig. 10 f). Internally with long, median copulatory ducts; spermathecae oval, connected distally with long and gently curved fertilization ducts; bursae copulatrix not visible (fig. 10 g).

Variation: Three males: total length 6.30 -6.50; carapace 2. 70 -2.80; femora I 2.90 -3.10. Five females: total length 6.00-6.20; carapace 2.50-2.80; femora I 2.50-2.80. The male from Peru has the basal process of the dorsal extension of the retrolateral tibial apophysis deslocated (fig. 10 d) and the male from Venezuela lacks the basal process (fig. 10 e). The sub-apical median extention on tegulum of the male from Colombia is very reduced.

Distribution: Venezuela, Colombia, Peru and north of Brazil.
Material examined: Venezuela, Upper Yaciba River (igarapé forest), 1 male, 7.XII.1953, W. M. BEEBE (AMNH). Colombia, Meta, Puerto Lleras, Lomalinda (70° 22'W, 3° 18'N, elev. 300), 1 male, S. T. CARROLL (CAS).

Peru, Panguana, confluence of Yuyapichis and Pachitea rivers (9° 37'S 74° 56'W, elev. 260 m.), 1 male, 11.II.1985, M. VERHAAGH (SMNK 1160).

Brazil, Roraima, Ariquemes, Ji-Paraná river, 1 female, 28.X.1986, J. A. RAFAEL (INPA); Amazonas: São Paulo de Olivença, 1 female, MATHAN (MNHN 8131, type); Manaus, Fazenda Esteio (Smithsonian Reserve at km 41), 1 male, 25.III.1986, B. C. KLEIN (INPA); Reserva Florestal Adolfo Ducke, 1 female, 14-22.VIII.1991, A. D. BRESCOVIT (MCN 21428); 1 female, 18-25.II.1992, A. D. BRESCOVIT (MCN 24052); 1 female, 21.X.1991, H. HÖFER (collected with arboreal funnel trap) (SMNK 1161).

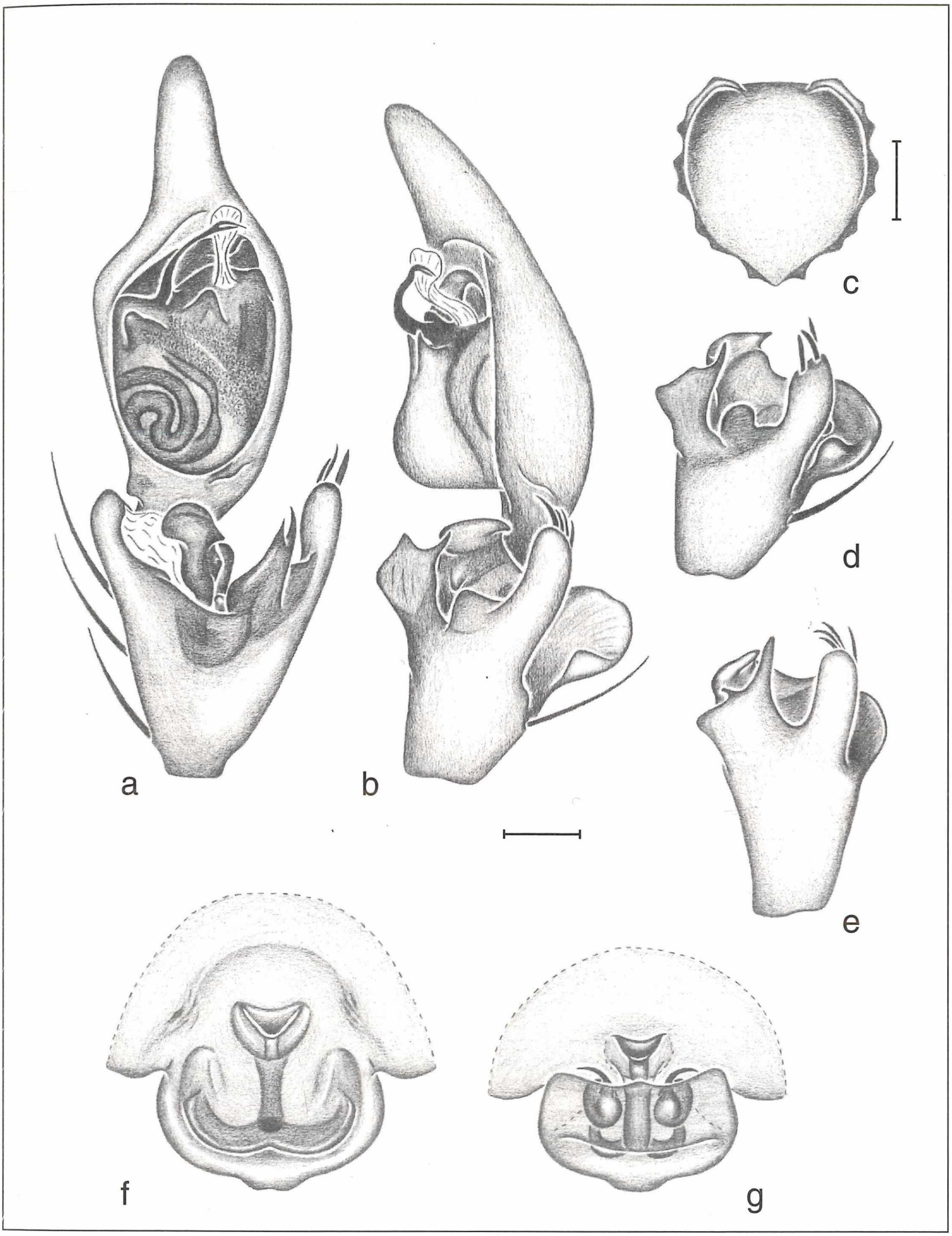

Figure 10. *Stethorrhagus lupulus* SIMON, male: a) palp, ventral; b) retrolateral; c) sternum, ventral (specimen from Amazonas, Brazil); d) palpal tibiae, retrolateral, male from Panguana, Peru; e) same, male from Upper Yaciba River, Venezuela; female from Amazonas, Brazil, epigynum: f) ventral; g) dorsal; scale lines: a, b, d-g, 0.25 mm; c, 0.5 mm.

### ***Stethorrhagus oxossi*, new species**

Figures 2 f, 6 a-e, 7 d-f, 11

Types: Male holotype and female paratype from Itamarajú, Bahia, Brazil, deposited in MCN 24053; paratypes: one male and one female from Fazenda Nossa Senhora da Conceição, Porto Seguro, Bahia, Brazil, deposited in SMNK (1162); one male and one female with same data of the holotype and one male and one female from Fazenda São José, Porto Seguro, Bahia, Brazil, both deposited in MNRJ.
Etymology: From the African language „ioruba", Oxossi is an Afro-Brazilian divinity, protector of the hunters and forests.

Diagnosis: *Stethorrhagus oxossi* is closest to *S. lupulus* but may be distinguished by the absence of the tibial dorsal process, an articulated tibial apophysis with a retrolateral laminar projection and only one tegular laminar projection on the male palp (fig. 11 a,b); in female, copulatory opening „U"-shaped, without delimited anterior margin and median plate distant from posterior margin of the epigynum (fig. 11 c).
Male (holotype): Coloration as in *S. lupulus.*
Total length 6.00. Carapace 2.55 long, 2.20 wide, 0.80 high. Clypeus 0.22. Chilum entire, sclerotized and without hairs. Anterior eye row 0.97 long, posterior eye row 1.03 long. Eye diameters and interdistances: AME 0.26, ALE 0.23, PME 0.19, PLE 0.21; AME-AME 0.11, AME-ALE 0.03, PME-PME 0.16, PME-PLE 0.17, ALE-PLE 0.05. MOQ length 0.52, front width 0.57, back width 0.52. Chelicerae 1.25 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 1.10 long, 1.20 wide, shallow sternal excavations, without delimited internal margins. Abdomen 3.30 long, 1.90 wide, with poorly delimited dorsal scutum.
Leg measurements: I -femur 2.60/ patella 0.85/ tibia 2.30/ metatarsus 2.20/ tarsus 1.10/ total 9.05/ II -2.55/ 0.80/ 2.20/ 2.10/ 1.10/ 8.75/ III -2.40/ 0.80/ 2.00/ 2.20/ 1.10/ 8.50/ IV -3.00/ 0.90/ 2.50/ 3.40/ 1.25/ 11.05. Leg spination: I femur r1-0-1, tibia v2-2-2-2-2-0; II -tibia v2-2-2-2-2-0; III -femur p0-1-1, tibia v2-2-1.
Palp: retrolateral tibial apophysis bifurcated at the basis, ventral extension laminar distally, rounded; dorsal extension strong, with modified setae on the apex; dorsal process absent; articulated apophysis longer than wide, with a retrolateral lamellar projection. Tegulum with basal, ventral, coiled duct, with only one sub-apical laminar extension near the embolic basis; embolus enlarged prolaterally at basis; apical prongs long, equal (fig. 11 a,b).
Female (paratype): Coloration as in male.
Total length 5.75. Carapace 2.80 long, 2.20 wide, 1.10 high. Clypeus 0.25 high. Chilum as in male. Anterior eye row 0.87 long, posterior eye row 0.96 long. Eye diameters and interdistances: AME 0.22, ALE 0.17, PME 0.17, PLE 0.15; AME-AME 0.11, AME-ALE 0.04, PME-PME 0.17, PME-PLE 0.16, ALE-PLE 0.05. MOQ length 0.50, front width 0.52, back width 0.50. Chelicerae 1.20 long, dentation as in male. Sternum 1.30 long, 1.30 wide, excavations as in male. Abdomen 3.00 long, 1.60 wide, without dorsal scutum.
Leg measurements: I -femur 2.55/ patella 1.05/ tibia 2.30/ metatarsus 2.00/ tarsus 1.05/ total 8.95/ II -2.50/ 0.90/ 2.10/ 2.00/ 1.00/ 8.50/ III -2.40/ 0.90/ 2.00/ 2.10/ 1.00/ 8.40/ IV -3.00/ 1.00/ 2.50/ 3.10/ 1.20/ 10.80. Leg spination: I femur p0-1-1, d1-1-1, tibia v2-2-2-2-2-0; II -femur p0-1-1, d1-1-1, tibia v2-2-2-2-2-0; III -femur p0-1-1, tibia v2-2-0. Epigynum: copulatory opening „U"-shaped, with anterior margin not delimited; median plate large; posterior margin of the epigynum projected posteriorly (fig. 11 c); internally with long copulatory duct; spermathecae spherical, connected laterally with short and strongly curved fertilization ducts; bursae copulatrix small, arising ventrally from spermathecae (fig. 11 d).
Variation: ten males: total length 5.70-6.60; carapace 2.55-3.10; femora I 2.60-3.00; ten females: total length 5.75-6.60; carapace 2.30-2.80; femora I 2.20-2.70.

Distribution: Bahia, Brazil.
Material examined: Brazil, Bahia, 1 female (MNRJ); Itamarajú, 2 females (MNRJ); Fazenda Boa Esperança, 3 females (MNRJ 3193); Fazenda Nossa Senhora das Neves, 1 male, 9.X.1987, J. S. Santos (CPDC 4021); Uruçuca, Fazenda Santa Tereza, 3 males (MNRJ 3109); Fazenda Almada, 3 females, 26-27.XI.1977, J. S. Santos (MCN 20251; CPDC 3793; 3779); Gandu, Fazenda Pedra Branca, 2 males, 1 female, 22.X.1979 (MNRJ 2956); Camacan, Fazenda Santa Maria, 1 female (MNRJ 2928); Porto Seguro, Fazenda Nossa Senhora da Conceição, 1 male, 6 females (MNRJ 3044; MCN 24054); Fazenda São José, 6 males, 7 females (MCN 24055; MNRJ 3104; 3203; 3225; 3243).

### ***Stethorrhagus archangelus*, new species**

Figure 12

Types: Male holotype and female paratype from Pico da Neblina, São Gabriel da Cachoeira, Amazonas, Brazil, Nov. 08, 1990, A. A. Lise, deposited in MCP 1210; one male paratype, with same data, deposited in MCN 25461.
Etymology: The specific name is the latin form of archangel, taking pattern from the type locality.

Diagnosis: *Stethorrhagus archangelus* differs from *S. latoma* by the rounded tibial dorsal projection and the short, sculptured tegular projection in the male palp (fig. 12 b, c); females differ from *S. lupulus* and *S. oxossi* by the circular copulatory opening and the large and medianly not invaginated median plate of the epigynum (fig. 12 d).
Male (holotype): Carapace, mouth parts, sternum and legs orange; abdomen gray, with a dark posterior stain.
Total length 9.20. Carapace 4.40 long, 3.50 wide, 1.20 high. Clypeus 0.38. Chilum bipartite, sclerotized and without hairs. Anterior eye row 1.45 long, posterior eye row 1.61 long. Eye diameters and interdistances: AME 0.30, ALE 0.25, PME 0.26, PLE 0.23; AME-AME 0.16, AME-ALE 0.06, PME-PME 0.26, PME-PLE 0.32,

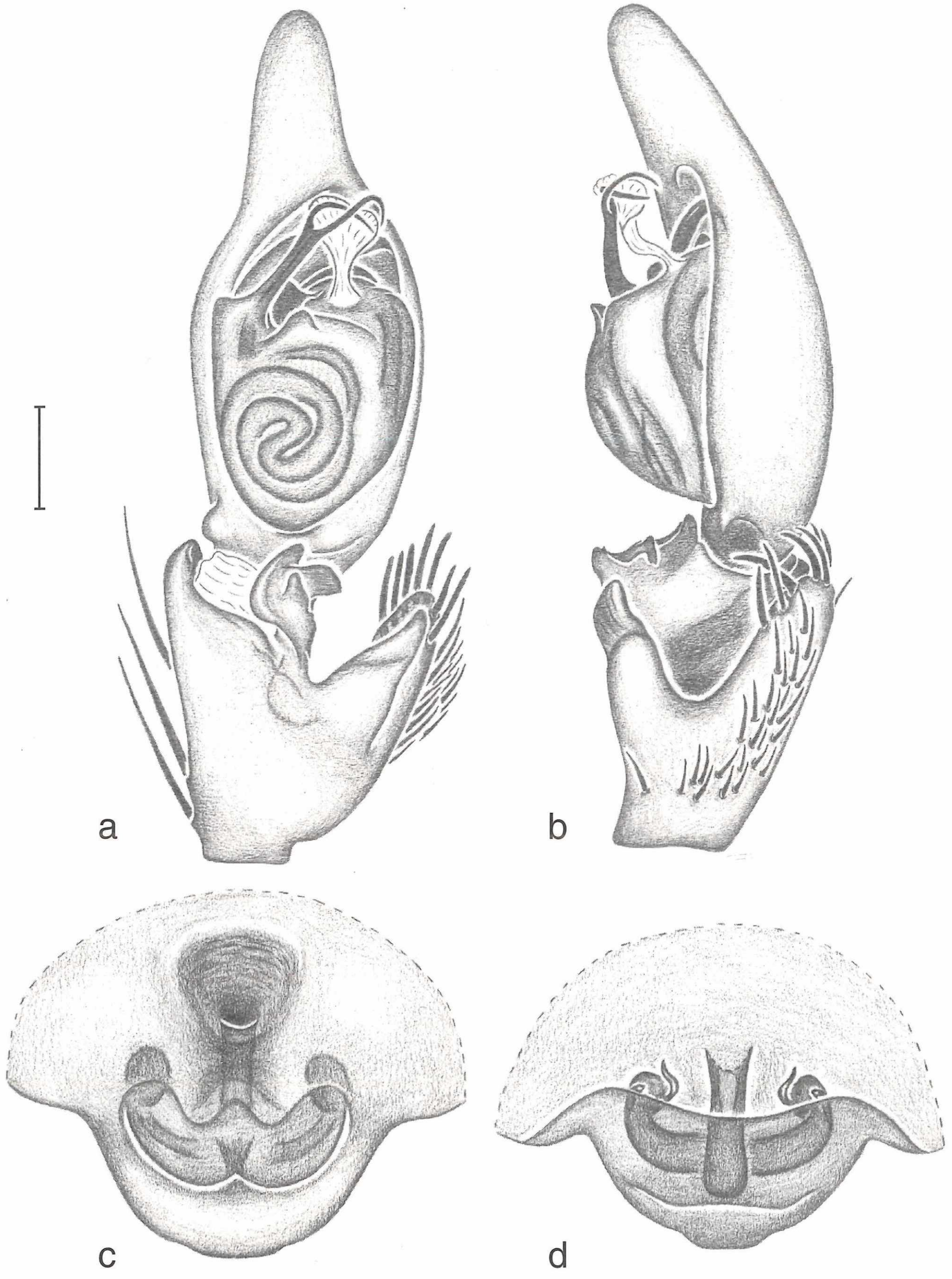

Figure 11. *Stethorrhagus oxossi* new species, male: a) palp, ventral; b) retrolateral; female: c) epigynum, ventral, d) dorsal; scale line: 0.25 mm.

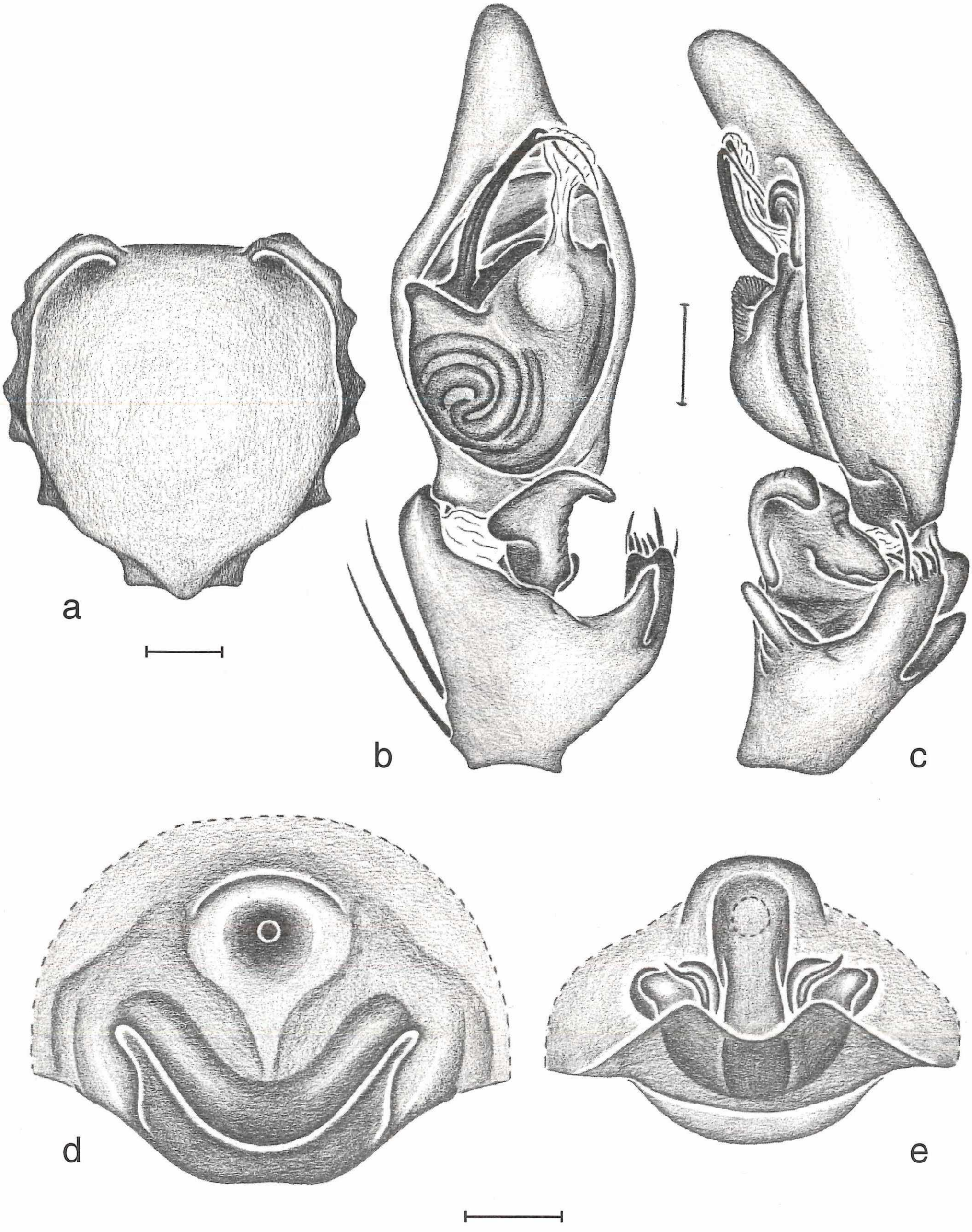

Figure 12. *Stethorrhagus archangelus* new species, male: a) sternum, ventral; b) palp, ventral; c) palp, retrolateral; female: d) epigynum, ventral; e) dorsal; scale lines: a-c, 0.5 mm; d, e, 0.25 mm.

ALE-PLE 0.11. MOQ length 0.75, front width 0.85, back width 0.77. Chelicerae 2.35 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 2.00 long, 2.00 wide, shallow sternal excavations, without delimited internal margin (fig. 12 a). Abdomen 4.90 long, 2.30 wide, without scutum.

Leg measurements: I -femur 4.50/ patella 1.70/ tibia 4.30/ metatarsus 4.10/ tarsus 2.00/ total 16.60/ II -4.40/ 1.60/ 4.25/ 4.00/ 2.00/ 16.25/ III -4.40/ 1.50/ 3.80/ 4.00/ 1.90/ 15.60/ IV -5.40/ 1.65/ 4.50/ 5.90/ 2.00/ 19.45. Leg spination: I tibia v2-2-2-2-2-0; III tibia v2-2-1p.

Palp: retrolateral tibial apophysis bifurcated at the basis, ventral extension finger-shaped, dorsal extension stronger, with obtuse apex covered by modified setae; dorsal process present, rounded; articulated apophysis longer than wide, with an apical, retrolateral projection. Tegulum with prolateral, coiled duct and a short sculptured projection near the embolic basis; embolus arising prolaterally; apical prongs of the embolus long, bent, equally wide and long (fig. 12 b,c).

Female (paratype): Coloration as in male.

Total length 10.00. Carapace 3.90 long, 3.20 wide, 1.20 high. Clypeus 0.22 high. Chilum semibipartite, sclerotized and without hairs. Anterior eye row 1.25 long, posterior eye row 1.41 long. Eye diameters and interdistances: AME 0.30, ALE 0.25, PME 0.19, PLE 0.25; AME-AME 0.16, AME-ALE 0.05, PME-PME 0.27, PME-PLE 0.22, ALE-PLE 0.08. MOQ length 0.62, front width 0.70, back width 0.65. Chelicerae 1.77 long, dentation as in male. Sternum 1.85 long, 1.80 wide, excavations as in male. Abdomen 5.70 long, 3.50 wide, without dorsal scutum.

Leg measurements: I -femur 4.00/ patella 1.50/ tibia 3.70/ metatarsus 3.40/ tarsus 1.70/ total 14.30/ II -4.00/ 1.50/ 3.60/ 3.30/ 1.70/ 14.10/ III -3.80/ 1.50/ 3.30/ 3.55/ 1.60/ 13.75/ IV -4.70/ 1.50/ 4.00/ 5.20/ 1.75/ 17.15. Leg spination: I tibia v2-2-2-2-2-0; II tibia v2-2-2-2-0; III tibia v2-2-1p.

Epigynum: anterior margin of the epigynal area delimited; copulatory opening circular; median plate large and prominent; posterior margin of the epigynum projected posteriorly (fig. 12 d); internally with a large, wide copulatory duct; spermathecae subquadrangular, projected laterally, connected basally with elongated and curved fertilization ducts; bursa copulatrix not visible; dorsal plate with a median, „U"-shaped notch (fig. 12 e).

Variation: Two males: total length 8.50-9.20; carapace 4.00-4.40; femur I 4.20-4.50.

Distribution: Known only from the type locality.
Material examined: Only the types.

### *Stethorrhagus latoma*, new species
Figure 13

Types: Male holotype from La Montana Cable Car Station, Merida, Venezuela, elev. 2442 m, Feb. 23-25, 1968, P. & B. WIGODZINSKY & M. CORMONS, deposited in AMNH; male paratype from a house, between Macuchies and Apartaderos, La Toma, Merida, Venezuela, elev. 3200 m, Oct. 9, 1983, C. SOBREVILA, deposited in USNM.

Etymology: Specific name derived from the locality where the paratype was collected.

Diagnosis: *Stethorrhagus latoma* is easily distinguished by the large tegular projection in the male palp (fig. 13 a).

Male (holotype): Carapace, endites, labium, sternum and legs orange; chelicerae reddish brown; abdomen yellow, with a dark posterior stain.

Total length 11.50. Carapace 5.40 long, 4.10 wide, 2.00 high. Clypeus 0.37. Chilum bipartite, sclerotized and without hairs. Anterior eye row 1.58 long, posterior eye row 1.83 long. Eye diameters and interdistances: AME 0.41, ALE 0.31, PME 0.30, PLE 0.27; AME-AME 0.18, AME-ALE 0.04, PME-PME 0.31, PME-PLE 0.30, ALE-PLE 0.05. MOQ length 0.67, front width 0.93, back width 0.90. Chelicerae 2.25 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 2.20 long, 2.50 wide, shallow sternal excavations, without delimited internal margin (fig. 13 c). Abdomen 6.40 long, 1.50 wide, without scutum.

Leg measurements: I -femur 5.20/ patella 2.30/ tibia 5.30/ metatarsus 4.90/ tarsus 2.30/ total 20.00/ II -5.10/ 2.20/ 4.70/ 4.60/ 2.30/ 18.90/ III -5.00/ 2.10/ 4.00/ 4.30/ 2.10/ 17.50/ IV -6.00/ 2.15/ 5.00/ 6.50/ 2.40/ 22.05. Leg spination: conforming with the typical pattern.

Palp: retrolateral distal end of femora and retrolateral surface of patellae with a cluster of modified setae; retrolateral tibial apophysis bifurcated at the basis, ventral extension pointed, distal half laminar; dorsal extension smaller, with modified setae on the dorsal surface; dorsal process present, small and pointed; articulated apophysis almost as long as wide, with an apical, retrolateral projection. Tegulum with ventral, coiled duct and a conspicuous projection, pointed at tip; embolus arising prolaterally, in ventral view partially covered by the tegular projection; apical prongs of the embolus, subequal, curved (fig. 13 a,b).

Female: Unknown.

Variation: Two males: total length 9.20-11.50; carapace 4.40-5.40; femora I 4.00-5.20.

Distribution: Merida, Venezuela.
Material examined: Only the types.

### *Stethorrhagus tridentatus* CAPORIACCO
Figure 14

*Stethorrhagus tridentatus* CAPORIACCO, 1955: 379, figs 47a,b (male holotype from El Junquito, Distrito Federal, Venezuela, 1948, MARCUZZI, in MUCV 703, examined); BRIGNOLI (1983: 557).

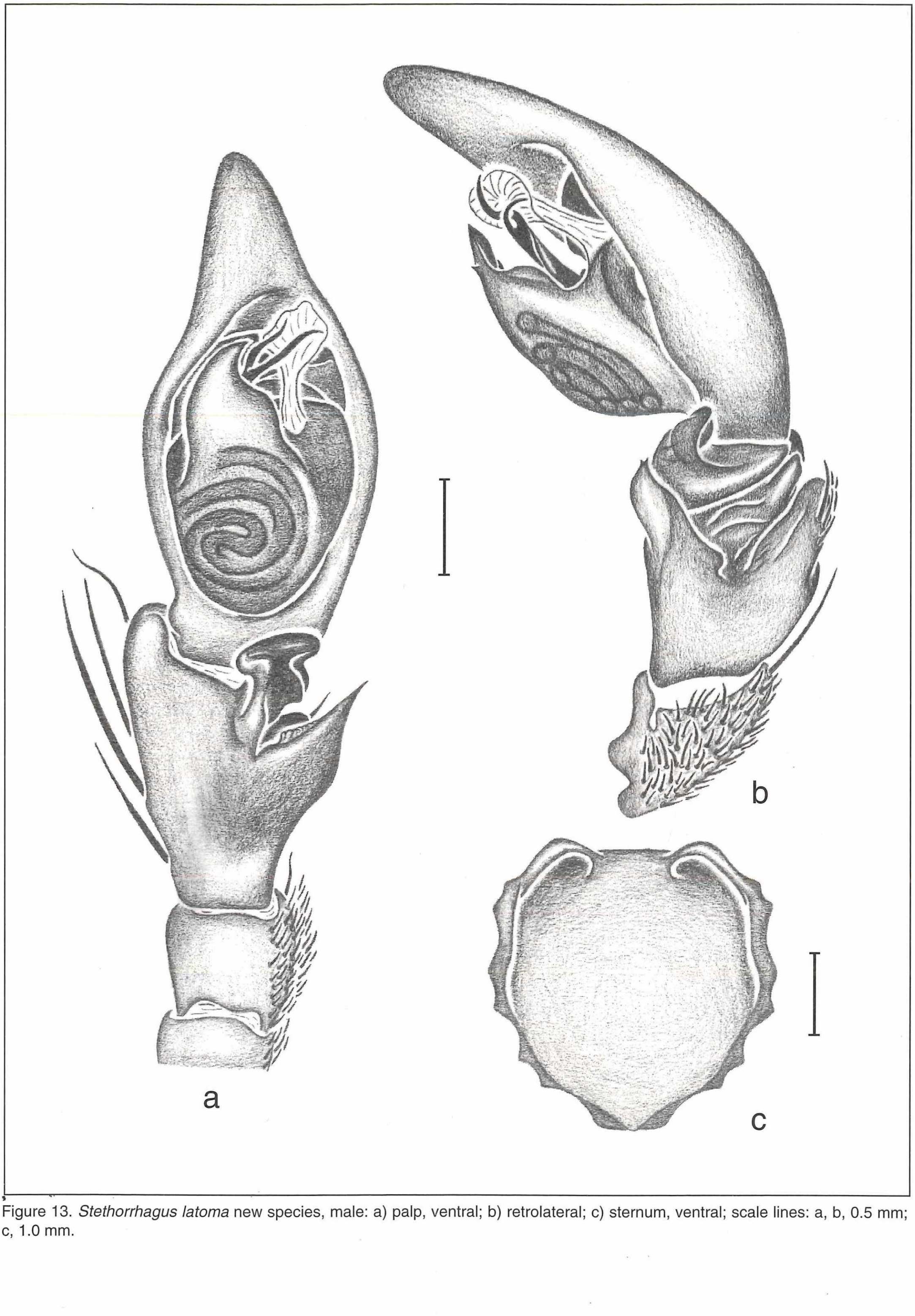

Figure 13. *Stethorrhagus latoma* new species, male: a) palp, ventral; b) retrolateral; c) sternum, ventral; scale lines: a, b, 0.5 mm; c, 1.0 mm.

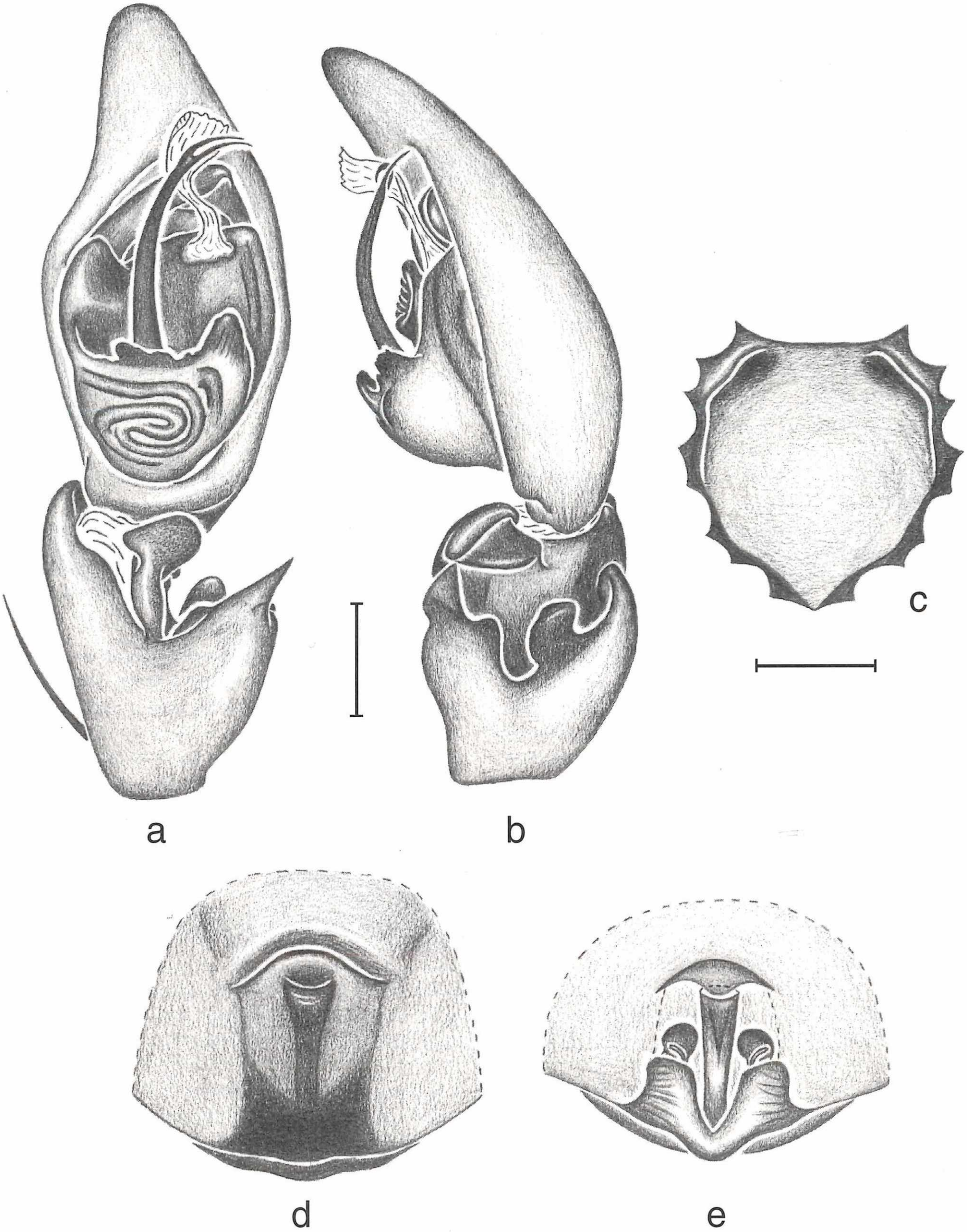

Figure 14. *Stethorrhagus tridentatus* CAPORIACCO, male: a) palp, ventral; b) retrolateral; c) sternum, ventral; female: d) epigynum, ventral; e) dorsal; scale lines: a, b, d, e, 0.5 mm; c, 1.0 mm.

Diagnosis: Males of *Stethorrhagus tridentatus* differ from *S. lupulus* and *S. oxossi* by the embolus arising medianly from the tegulum, which has a large transversal laminar extension (fig. 14 a,b); females differ by the clearly delimited anterior epigynal margin and the absence of a median plate on the epigyne (fig. 14 d).

Male (Vargas, El Limón, Venezuela): Carapace, mouth parts, sternum and legs orange; abdomen brown, dorsum with lighter transversal stripes.

Total length 8.80. Carapace 4.50 long, 3.50 wide, 1.30 high. Clypeus 0.25. Chilum bipartite, with one hair on each part. Anterior eye row 1.37 long, posterior eye row 1.53 long. Eye diameters and interdistances: AME 0.33, ALE 0.25, PME 0.25, PLE 0.26; AME-AME 0.12, AME-ALE 0.06, PME-PME 0.27, PME-PLE 0.26, AME-PLE 0.06. MOQ length 0.77, front width 0.77, back width 0.72. Chelicerae 2.30 long, with 5 promarginal teeth and 3 retromarginal denticles. Sternum 1.85 long, 2.00 wide, shallow sternal excavations, without delimited internal margin (fig. 14 c). Abdomen 4.30 long, 2.20 wide, without scutum.

Leg measurements: I -femur 4.70 / patella 1.90 / tibia 4.60 / metatarsus 4.10 / tarsus 1.90 / total 17.20 II -4.70 / 1.80 / 4.30 / 4.00 / 1.85 / 16.65 / III -4.10 / 1.70 / 3.40 / 3.90 / 1.70 / 14.80 / IV -5.30 / 1.80 / 4.30 / 5.70 / 1.90 / 19.00. Leg spination: conforming with the typical pattern.

Palp: retrolateral tibial apophysis bifurcated; ventral extension large, with the distal third laminar; dorsal extension reduced, with a rounded basal process; dorsal apophysis absent; articulated apophysis hammer-like in ventral view. Tegulum with coiled ventral duct and a median, large transversal laminar extension, covering the basis of the embolus; embolus arising medianly; apical prongs of the embolus equally long (fig. 14 a).

Female (between El Junquito and Carayaca, Venezuela): Coloration as in male, except abdomen pale gray, dorsum with a dark, longitudinal anterior stripe.

Total length 12.40. Carapace 4.50 long, 3.50 wide, 1.20 high. Clypeus 0.22 high. Chilum as in male. Anterior eye row 1.35 long, posterior eye row 1.50 long. Eye diameters and interdistances: AME 0.32, ALE 0.26, PME 0.22, PLE 0.24; AME-AME 0.20, AME-ALE 0.05, PME-PME 0.22, PME-PLE 0.23, ALE-PLE 0.05. MOQ length 0.67, front width 0.77, back width 0.71. Chelicerae 2.07 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 2.15 long, 2.10 wide, excavations as in male. Abdomen 7.20 long, 4.40 wide, without dorsal scutum.

Leg measurements: I -femur 4.10 / patella 1.90 / tibia 3.90 / metatarsus 3.60 / tarsus 1.90 / total 15.40 / II -4.10 / 1.70 / 3.60 / 3.50 / 1.80 / 14.70 / III -3.80 / 1.70 / 3.10 / 3.55 / 1.65 / 13.80 / IV -4.70 / 1.80 / 4.10 / 5.30 / 1.80 / 17.70. Leg spination: I femur p1-1-0; II femur p1-1-0; III tibia v2-2-0.

Epigynum: anterior margin of the epigynum delimited; copulatory opening „U"-shaped; median plate absent; basal half of the epigynal area strongly sclerotized (fig. 14 d). Internally with a large copulatory duct; spermathecae spherical, connected basally with short and curved fertilization ducts; bursae copulatrix not visible; dorsal plate sclerotized, with a median „V"-shaped notch (fig. 14 e).

Variation: Three males: total length 8.50-9.00; carapace 4.30-4.70; femora I 4.50-5.70; two females: total lenght 12.20-12.40; carapace 4.40-4.50; femora I 4.10-4.20.

Distribution: Venezuela.

Material examined: Venezuela, Distrito Federal, El Junquito, 1 male, 1948, MARCUZZI (MUCV 703, type); between El Junquito and Carayaca, 1 male, 1 female, 2.V.1981, A .R. DELGADO & M. A. GONZALES-SPONGA (MCN 24051); Vargas, El Limón, between El Portachuelo and La Hacienda (elev. 1200 m), 1 male, 24.X.1981, A. R. DELGADO (MCNC); Alto de N. León (elev. 2000 m), 1 female, 14.II.1981, A. R. DELGADO & M. A. GONZÁLES (MCNC).

### *Stethorrhagus penai*, new species

Figure 15

Type: Male holotype from north of Ecuador, without specific locality, Sept. 1977, L. E. PEÑA, deposited in AMNH.

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

Diagnosis: Males of *Stethorrhagus penai* differ from *S. lupulus* by having palps with a short retrolateral tibial apophysis and only one tegular projection, directed retrolaterally (fig. 15 b,c).

Male (holotype): Coloration as in *S. latoma.*

Total length 8.00. Carapace 4.00 long, 3.10 wide, 1.50 high. Clypeus 0.37 Chilum entire, sclerotized and without hairs. Anterior eye row 1.15 long, posterior eye row 1.37 long. Eye diameters and interdistances: AME 0.22, ALE 0.22, PME 0.21, PLE 0.22; AME-AME 0.10, AME-ALE 0.05, PME-PME 0.21, PME-PLE 0.25, ALE-PLE 0.05. MOQ length 0.56, front width 0.56, back width 0,63. Chelicerae 2.20 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 2.00 long, 2.00 wide, deep sternal excavations, with well delimited internal margins (fig. 15 a). Abdomen 4.20 long, 2.50 wide, with elongated dorsal scutum.

Leg measurements: I -femur 3.40/ patella 1.55/ tibia 2.90/ metatarsus 2.80/ tarsus 1.80/ total 12.45/ II -3.20/ 1.50/ 2.70/ 2.60/ 1.90/ 11.90/ III -2.90/ 1.30/ 2.30/ 2.70/ 1.50/ 10.70/ IV -3.00/ 1.50/ 3.10/ 4.00/ 1.90/ 13.50. Leg spination: I femur p0-0-1, tibia v1p-2-2-0; II femur p0-0-1, tibia v1r-2-0; III femur p1-1-1, d1-1-0, tibia v2-2-1p; IV femur p0-0-1, d1-1-0, r0.

Palp: retrolateral distal end of femora and retrolateral surface of patellae with a cluster of modified setae; retrolateral tibial apophysis bifurcated, ventral extension sub-quadrangular, dorsal extension smaller, coni-

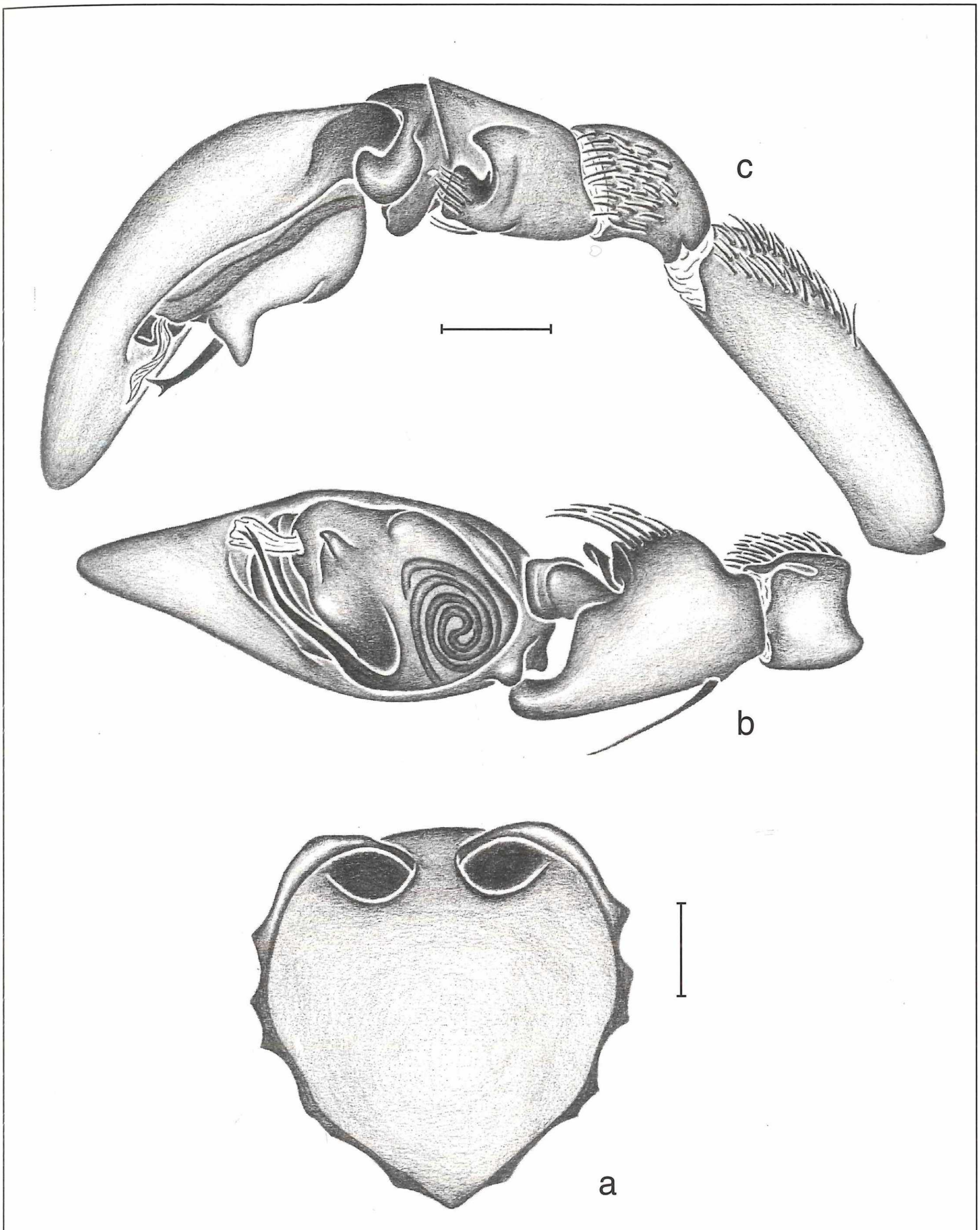

Figure 15. *Stethorrhagus penai* new species, male: a) sternum, ventral; b) palp, ventral; c) retrolateral; scale lines: 0.5 mm.

cal; dorsal process present, large, triangular; articulated apophysis almost as long as wide, apex sub-quadrangular in ventral view. Tegulum with ventral, coiled duct and a projection directed retrolaterally; embolus thin and long, slightly sinuous, arising prolaterally; apical prongs of the embolic tip short (fig. 15 b,c).
Female: Unknown.

Distribution: Known only from the type locality.
Material examined: Only the type.

### *Stethorrhagus chalybeius* (L. KOCH), new comb.

Figures 1, 2 a-e, 3 d-f, 4, 5, 6 f, 7 a-c, 16

*Hypsinotus chalybeius* L. KOCH, 1866: 280 (male and female syntypes from New Granada (probably Colombia), in BMNH 1890.7.I.1241-1242, examined; male lectotype and female paralectotype here designated; female does not belong to *Stethorrhagus*).
*Hypsinotus chalybeus* BERTKAU, 1880: 50 (lapsus).
*Corinna chalybeia* PETRUNKEVITCH, 1911: 465; ROEWER (1954: 596); BONNET (1956: 210).
Note: Because the female paralectotype has no paired sternal excavations, L. KOCH's hypothesis of co-specifity is rejected. The females herein presented were collected together with males in Cauca Valley, Colombia.

Diagnosis: *Stethorrhagus chalybeius* is a distinct species recognized by the presence of modified setae on the ventral extension of the retrolateral tibial apophysis, an articulated apophysis rounded at tip and an elongated prolateral prong on the embolar base on the male palp (fig. 16 a,b); the female epigynum has the anterior margin bilobed and spermathecae disposed anteriorly in relation to the copulatory opening (fig. 16 d,e).
Male (lectotype): Carapace and chelicerae reddish brown; endites, labium and legs dark yellow; sternum orange; abdomen gray.
Total length 7.20. Carapace 3.40 long, 2.70 wide, 1.55 high. Clypeus 0.32. Chilum entire, without hairs, with a basal median notch. Anterior eye row 1.05 long, posterior eye row 1.22 long. Eye diameters and interdistances: AME 0.25, ALE 0.22, PME 0.20, PLE 0.17; AME-AME 0.15, AME-ALE 0.07, PME-PME 0.17, PME-PLE 0.27, ALE-PLE 0.10. MOQ length 0.60, front width 0.60, back width 0.57. Chelicerae 0.77 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 1.80 long, 1.67 wide, deep sternal excavations, with delimited internal margin (fig. 1 b,c). Abdomen 3.70 long, 2.30 wide; dorsal scutum present.
Leg measurements: I -femur 2.95 / patella 1.30 / tibia 2.40 / metatarsus 2.25 / tarsus 1.45 / total 10.35 / II -2.70 / 1.25 / 2.15 / 2.20 / 1.35 / 9.65. III -2.35 / 1.15 / 1.55 / 2.10 / 1.25 / 8.40. IV -3.00 / 1.25 / 2.50 / 3.15 / 1.35 / 11.25. Leg spination: I -tibia v2-2-2. II -tibia v0-1p-1p.
Palp: retrolateral distal end of femora and retrolateral surface of patellae with a cluster of modified setae; retrolateral tibial apophysis bifurcated at basis; ventral extension subtriangular, with a row of strong modified setae on the ventral surface; dorsal extension wide, laminar with a very small, conical basal process; dorsal process absent; articulated apophysis elongated (fig. 16 a-c). Tegulum with a basal, prolateral coiled duct and a median subtriangular laminar extension; embolus relatively short, with an accentuated, pointed prolateral prong (fig. 73 a) and short apical prongs (figs 5 c,d, 16 a,b).
Female (Valle del Cauca): Coloration as in male.
Total length 6.50. Carapace 2.40 long, 1.80 wide, 1.05 high. Clypeus 0.18. Chilum bipartite, without hairs. Anterior eye row 0.81 long, posterior eye row 0.88 long. Eye diameters and interdistances: AME 0.17, ALE 0.13, PME 0.13, PLE 0.15; AME-AME 0.09, AME-ALE 0.06, PME-PME 0.16, PME-PLE 0.14, ALE-PLE 0.06. MOQ length 0.38, front width 0.45, back width 0.41. Chelicerae 1.25 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 1.25 long, 1.20 wide, sternal excavations as in male. Abdomen 4.00 long, 2.60 wide; dorsal scutum present, small, circular.
Leg measurements: I -femur 2.00 / patella 0.80 / tibia 1.70 / metatarsus 1.40 / tarsus 1.00 / total 6.90. II -1.80 / 0.70 / 1.50 / 1.40 / 0.90 / 6.30. III -1.50 / 0.55 / 1.25 / 1.40 / 0.80 / 5.50. IV -2.00 / 0.70 / 1.90 / 2.20 / 1.00 / 7.80. Leg spination: I -tibia v1p-2-2-2-2. II -tibia v2-2-2-2. III -tibia p0-1-0; metatarsus p0-1-1, r0-1-1. IV -tibia v1r-2-2.
Epigynum: anterior margin of the epigynum bilobed; copulatory opening small and rounded; median plate absent; posterior half of epigynal area grooved; spermathecae disposed anteriorly in relation to copulatory opening (fig. 16 d,e). Internally, with short copulatory ducts, spherical spermathecae connected basally with curved fertilization ducts; bursae copulatrix long and narrow, arising basally from spermathecae; dorsal plate sclerotized and grooved (fig. 16 e).
Variation: Five males: total length 5. 10 -6.50; carapace 2.40 -2.80; femora I 2.00 -2.20; two females: total length 6.50 -6.70; carapace 2.40 -2.60; femora I 2.00 -2.05. The male from Cauca valley has an additional tegular projection near the base of the embolus and an obtuse prolateral prong on the embolar base (fig. 5 c).

Distribution: Colombia.
Material examined: Colombia, Cundinamarca, Bogota (Paramo de Montesserate), 1 male, 1968-1969, H. STURM (AMNH); Valle del Cauca: Quindio (1 km S. Calarca), 2 males, 2 females, 8-10.III.1974, S. & J. PECK (MCZ); Cali (El Silencio, elev. 1900 m), 1 male, VII.1973, EBERHARD (MCZ).

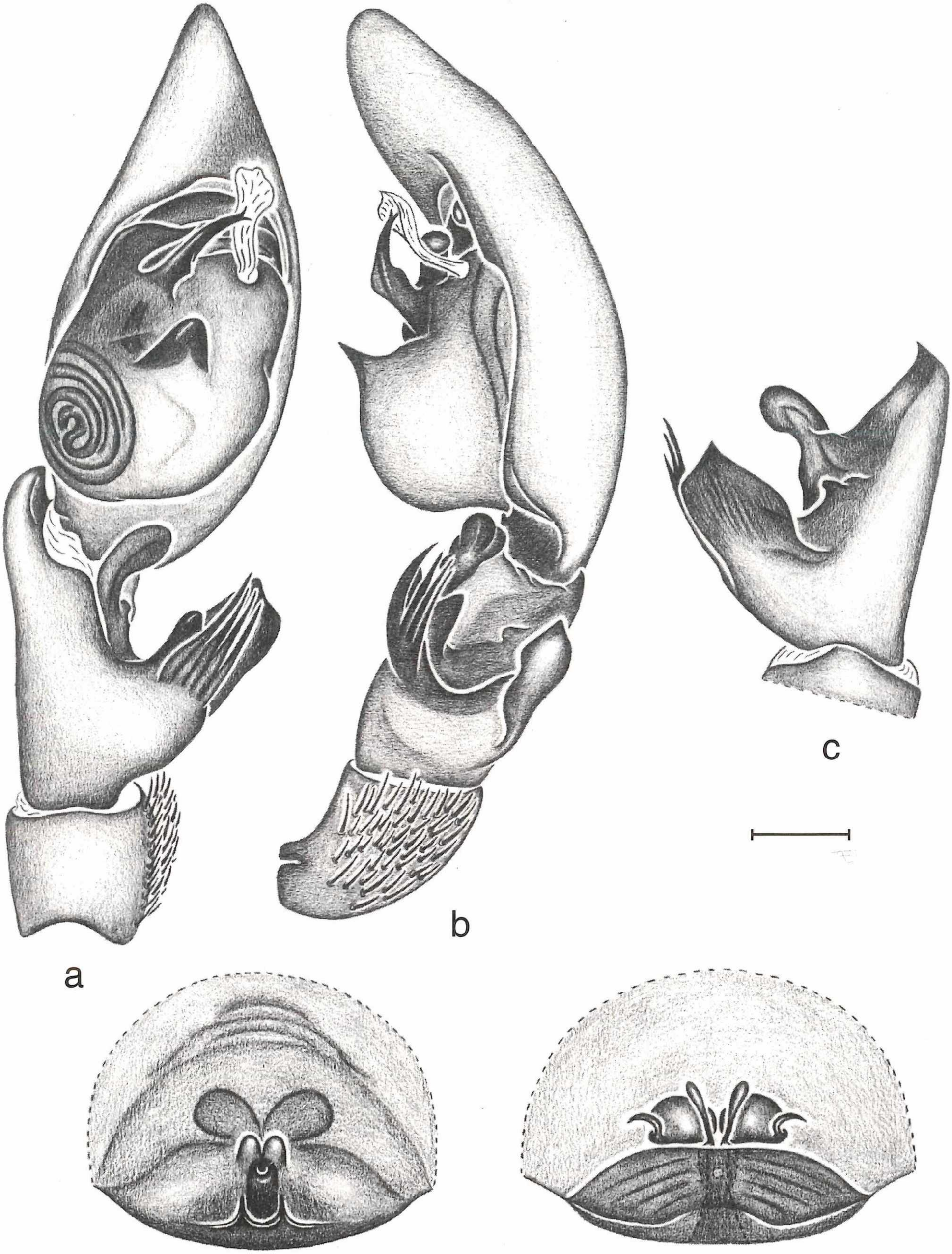

Figure 16. *Stethorrhagus chalybeius* (L. KOCH), male: a) palp, ventral; b) retrolateral; c) palpal tibiae, dorsal; female: d) epigynum, ventral; e) dorsal; scale line: 0.25 mm.

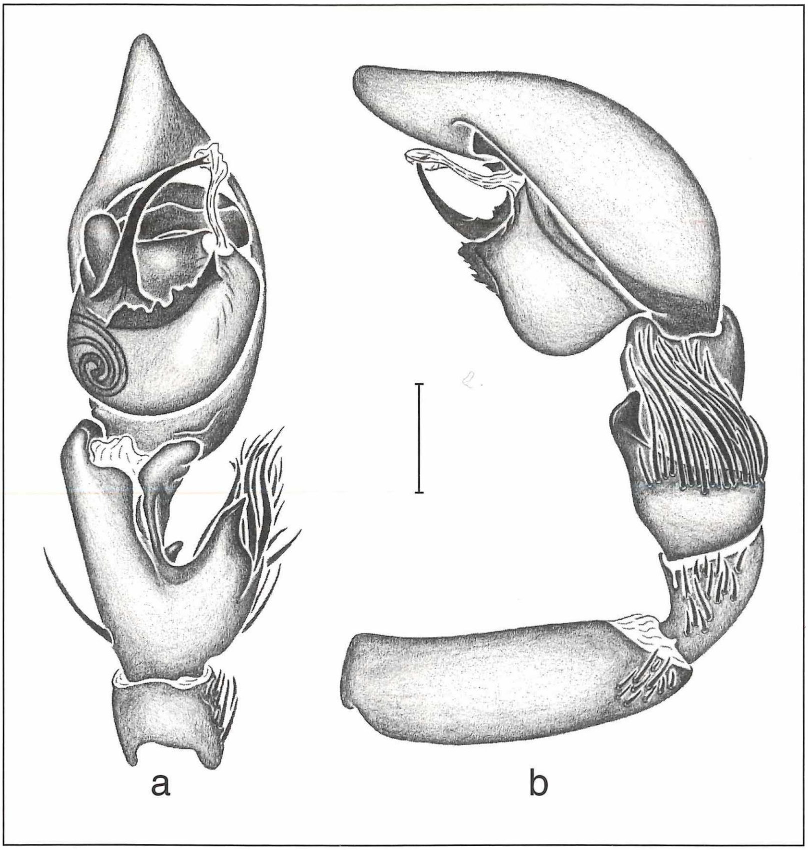

Figure 17. *Stethorrhagus planada* new species, male: a) palp, ventral; b) retrolateral; scale line: 0.5 mm.

### ***Stethorrhagus planada*, new species**

Figures 17, 18

Types: Male holotype and female paratype from Reserva Natural de La Planada, Ricaurte, Nariño, elev. 1850 m, Colombia, Dec. 06, 1991, C. VALDERRAMA A., deposited in MCN 24050; paratypes: one male and one female with same data of the holotype, deposited in CLP; one male paratype from Saladito, Valle, Colombia, Mar., 1976, W. EBERHARD, deposited in MCZ.
Etymology: The specific name is a noun in apposition from the type locality.

Diagnosis: *Stethorrhagus planada* is closest to *S. hyula* but may be distinguished by the transversal median serrated laminar extension on the tegulum and the large and rounded prong on the basis of the embolus of the male palp (fig. 17 a); female epigynum with a small subrectangular median plate and internally with sclerotized dorsal plate, medianly convex and with a straight anterior rim (fig. 18 a,b).
Male (holotype): Carapace and chelicerae dark brown, endites, labium and sternum brown, legs orange, with the distal tip of segments black, dorsum of the abdomen black, with two median white spots, venter yellowish, with a longitudinal, median brown stripe.
Total length 8.60. Carapace 4.40 long, 3.20 wide, 1.85 high. Clypeus 0.43. Chilum bipartite, with one hair on each part. Anterior eye row 1.35 long, posterior eye row 1.53 long. Eye diameters and interdistances: AME 0.33, ALE 0.27, PME 0.27, PLE 0.23; AME-AME 0.17, AME-ALE 0.05, PME-PME 0.30, PME-PLE 0.20, ALE-PLE 0.04. MOQ length 0.63, front width 1.35, back width 1.53. Chelicerae 2.07 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 2.00 long, 1.80 wide, deep sternal excavations, internal margins delimited (fig. 18 c). Abdomen 3.80 long, 2.40 wide, with dorsal scutum.
Leg measurements: I -femur 3.85/ patella 1.60/ tibia 3.40/ metatarsus 3.30/ tarsus 2.10/ total 14.25/ II -3.75/ 1.50/ 3.20/ 3.40/ 1.90/ 13.75/ III -3.40/ 1.40/ 2.70/ 3.10/ 1.60/ 12.20/ IV -4.30/ 1.55/ 3.60/ 4.70/ 1.90/ 16.05. Leg spination: I -femur p0-0-1; tibia 1p-2-2-2-0. II -tibia v2-2-2-0. III -femur r0-0-1.
Palp: retrolateral distal end of femur and retrolateral

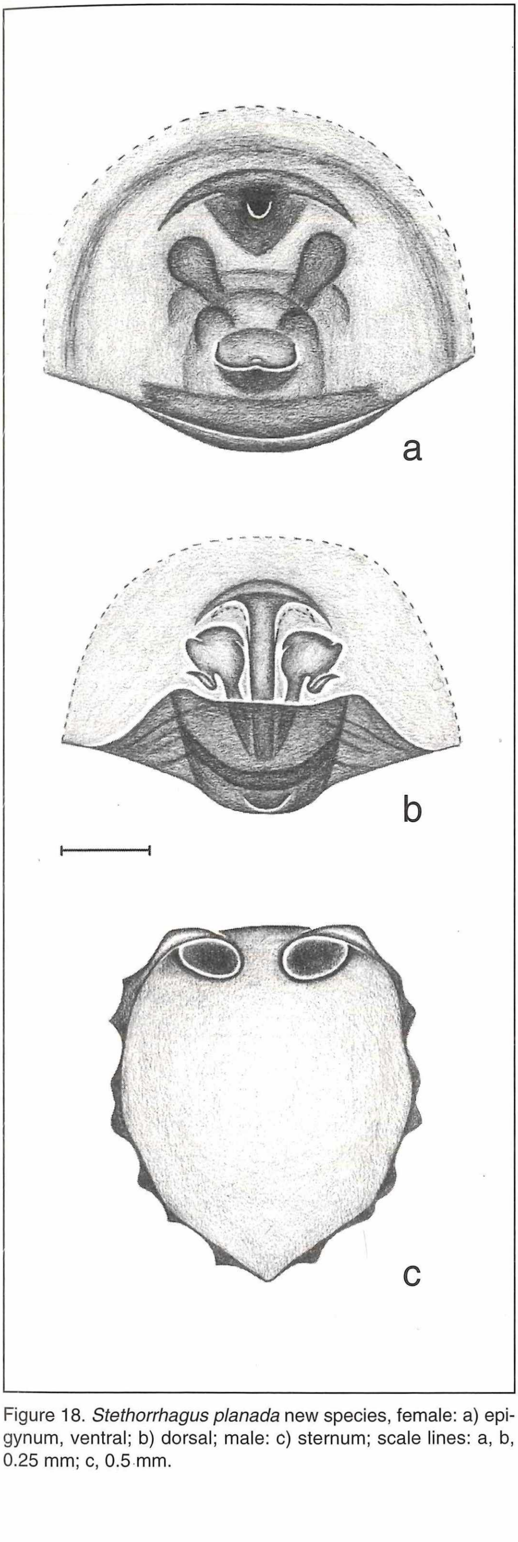

Figure 18. *Stethorrhagus planada* new species, female: a) epigynum, ventral; b) dorsal; male: c) sternum; scale lines: a, b, 0.25 mm; c, 0.5 mm.

surface of patella, with a cluster of modified setae (fig. 17 b); retrolateral tibial apophysis entire, with conical tip and retrolaterally covered by modified setae; dorsal process small; articulated apophysis elongated, rounded at tip; tegulum with prolateral, coiled duct and a long serrated median laminar extension; embolus long and curved with rounded prolateral prong; apical prongs short (fig. 17 a,b).

Female (paratype): Coloration as in male, except carapace reddish brown with a black median dorsal spot and paramedian black spots; sternum orange; abdomen with two additional small dorsal white spots.

Total length 8.20. Carapace 4.20 long, 1.60 wide, 1.60 high. Clypeus 0.35 high. Chilum as in male. Anterior eye row 1.27 long, posterior eye row 1.42 long. Eye diameters and interdistances: AME 0.30, ALE 0.27, PME 0.26, PLE 0.25; AME-AME 0.15, AME-ALE 0.04, PME-PME 0.22, PME-PLE 0.28, ALE-PLE 0.05. MOQ length 0.70, front width 0.71, back width 0.70. Chelicerae 1.90 long, dentation as in male. Sternum 1.90 long, 2.10 wide, excavations as in male. Abdomen 4.20 long, 1.30 wide, without dorsal scutum.

Leg measurements: I -femur 3.70/ patella 1.55/ tibia 3.30/ metatarsus 3.10/ tarsus 1.70/ total 13.35/ II -3.60/ 1.50/ 3.10/ 3.10/ 1.70/ 13.00/ III -3.35/ 1,45/ 2.60/ 3.00/ 1.60/ 12.00/ IV -4.20/ 1.55/ 3.40/ 4.40/ 1.70/ 15.25. Leg spination: I -femur p0-0-1; tibia v2-2-2-2-0. II -femur p0-0-1; tibia v1p-2-2-0. III -femur p0-1-0, r0-0-1.

Epigynum: Copulatory opening „U“-shaped, without delimited anterior margin; median plate small and subrectangular (fig. 18 a); internally with long median copulatory ducts; spermathecae oval, with a small subdistal projection, connected posteriorly by short and sinuous fertilization ducts; bursae copulatrix not visible; sclerotized dorsal plate medianly convex (fig. 18 b).

Variation: Three males: total length 7.60-8.60; carapace 3.60-4.40; femora I 3.10-3.85; two females: total length 8.20-9.50; carapace 4.20-4.30; femora I 3.00-3.70.

Distribution: Colombia.
Material examined: Only the types.

### *Stethorrhagus hyula*, new species
Figure 19

Types: Male holotype and female paratype from Resina (01° 55' N, 75° 42' W), elev. 1600 m, Departamento Huila, Colombia, Jun. 08, 1956, H. STURM (litter, mountain forest), deposited in MCZ.

Etymology: The specific name is an arbitrary combination of letters.

Diagnosis: *Stethorrhagus hyula* is closest to *S. planada*, but may be distinguished by the large tooth-like tegular laminar extension and the triangular basal prong of the embolar base on the male palp (fig. 19 a);

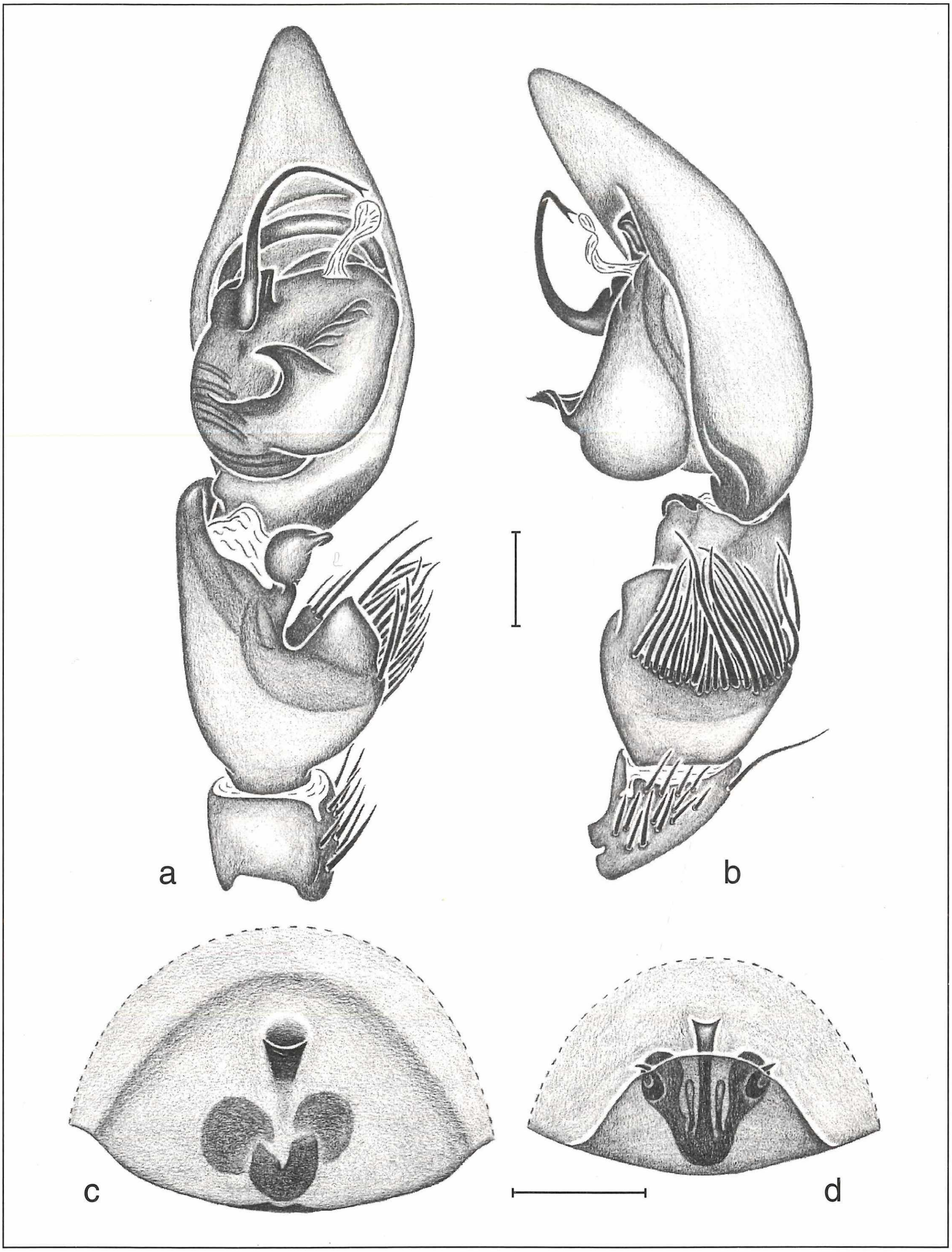

Figure 19. *Stethorrhagus hyula* new species, male: a) palp, ventral; b) retrolateral; female: c) epigynum, ventral; d) dorsal; scale lines: 0.25 mm.

in females by an epigynum without median plate, and with a median luniform sclerotization; internally with a weakly sclerotized dorsal plate (fig. 19 c,d).

Male (holotype): Coloration as in *S. chalybeius*, except dorsum of abdomen with two median white spots.

Total length 5.60. Carapace 2.90 long, 2.20 wide, 1.20 high. Clypeus 0.32. Chilum entire, without hairs, basis notched. Anterior eye row 0.85 long, posterior eye row 0.95 long. Eye diameters and interdistances: AME 0.20, ALE 0.18, PME 0.17, PLE 0.17; AME-AME 0.11, AME-ALE 0.04, PME-PME 0.16, PME-PLE 0.16, ALE-PLE 0.05. MOQ length 0.45, front width 0.47, back width 0.46. Chelicerae 1.27 long, with 3 promarginal teeth and retromarginal 5 denticles. Sternum 1.50 long, 1.30 wide, deep sternal excavations, with delimited internal margins. Abdomen 2.80 long, 1.60 wide; dorsal scutum present, long.

Leg measurements: I -femur 2.30 / patella 1.00 / tibia 2.05 / metatarsus 2.05 / tarsus 1.30 / total 8.70. II - 2.30 / 1.00 / 1.90 / 1.90 / 1.20 / 8.30. III -2.00 / 0.90 / 1.60 / 1.90 / 1.00 / 7.40. IV -2.60 / 0.95 / 2.15 / 2.70 / 1.10 / 9.50. Leg spination: I -tibia v1p-2-2-2-0. II -femur p0-0-1; tibia v1r-2-1p. IV -femur r0-0-1.

Palp: retrolateral surface of patellae with a cluster of modified setae; retrolateral tibial apophysis entire, triangular and retrolaterally covered by modified setae; dorsal process absent; articulated apophysis elongated, projected at tip; tegulum with prolateral coiled duct and a large median tooth-like laminar extension; embolus long and strongly curved with triangular, pointed prolateral prong; apical prongs short (fig. 19 a,b).

Female (paratype): Coloration as in *S. chalybeius*.

Total length 5.20. Carapace 2.20 long, 1.90 wide, 1.00 high. Clypeus 0.20. Chilum as in male. Anterior eye row 0.75 long, posterior eye row 0.90 long. Eye diameters and interdistances: AME 0.18, ALE 0.16, PME 0.16, PLE 0.15; AME-AME 0.06, AME-ALE 0.05, PME-PME 0.11, PME-PLE 0.15, ALE-PLE 0.04. MOQ length 0.40, front width 0.38, back width 0.40. Chelicerae 1.05 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 1.30 long, 1.20 wide, excavations as in male. Abdomen 3.00 long, 1.90 wide; dorsal scutum present, small, circular.

Leg measurements: I -femur 1.80 / patella 0.80 / tibia 1.60 / metatarsus 1.40 / tarsus 0.90 / total 6.50. II -1.75 / 0.70 / 1.50 / 1.40 / 0.85 / 6.20. III -1.50 / 0.55 / 1.20 / 1.40 / 0.75 / 5.40. IV -2.05 / 0.80 / 1.70 / 2.00 / 0.90 / 7.45. Leg spination: I -femur d1-0-0; tibia v2-2-2-2-0. II -femur d1-0-0, p0; tibia 2-2-2-0. III -femur d1-1-0, p0, r0. IV -femur d1-1-0, p0; tibia 1p-2-2.

Epigynum: Copulatory opening „U"-shaped, without delimited anterior margin; median plate absent; medianly with a luniform sclerotization (fig. 19 c); internally with long median copulatory ducts; spermathecae oval, connected posteriorly with short and curved fertilization ducts; bursae copulatrix elongated, arising from the basal third of the copulatory ducts; dorsal plate weakly sclerotized (fig. 19 d).

Distribution: Known only from the type locality.
Material examined: Only the types.

### *Stethorrhagus duidae* GERTSCH

Figures 20, 21 a

*Stethorrhagus duidae* GERTSCH, 1942:12 (male holotype from the summit of Mt. Duida, Amazonas, Venezuela, TATE, deposited in AMNH, examined); ROEWER (1954: 605).

Diagnosis: Males of *Stethorrhagus duidae* differ from *S. peckorum* by the ventral extension of the retrolateral tibial apophysis which is bifid in the distal third and the presence of a finger-like tegular projection (fig. 20 a,b).

Male (holotype): Carapace pale yellow, ocular area darker; mouth parts, sternum and legs pale yellow; abdomen yellowish gray.

Total length 8.90. Carapace 4.20 long, 3.50 wide. Clypeus 0.45. Chilum entire, without hairs. Anterior eye row 1.32 long, posterior eye row 1.45 long. Eye diameters and interdistances: AME 0.30, ALE 0.27, PME 0.22, PLE 0.25; AME-AME 0.22, AME-ALE 0.12, PME-PME 0.27, PME-PLE 0.35, ALE-PLE 0.10. MOQ length 0.70, front width 0.77, back width 0.70. Chelicerae 2.40 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 2.05 long, 1.90 wide, deep sternal excavations, with delimited internal margins (fig. 21 a). Abdomen 4.60 long, 2.60 wide; dorsal scutum present.

Leg measurements: I -femur 5.05 / patella 1.95 / tibia 5.00 / metatarsus 4.45 / tarsus 2.05 / total 18.50. II -5.00 / 1.85 / 4.85 / 4.40 / 1.95 / 18.05. III and IV, missing. Leg spination: I -femur p0-1-1-1; tibia v2-2-2-2-0; II -femur d1-1-1, p0-1-1-1; tibia v2-2-2-2-0; III -tibia v2-2-0.

Palp: retrolateral tibial apophysis bifurcated at basis, ventral extension bifid in the distal third, dorsal extension short and rounded; with a small sculptured process; dorsal process absent; articulated apophysis wider than long in ventral view; tegulum with prolateral, coiled duct, one submedian laminar extension and a finger-like prolateral projection; embolus short and very wide at basis, with a prolateral prong; apical prongs strongly reduced, inconspicuous (fig. 20 a,b).

Female: Unknown.

Distribution: Known only from the type locality.
Material examined: Only the holotype.

### *Stethorrhagus nigrinus* (BERLAND), new combination

Figure 21 b,c

*Corinna nigrina* BERLAND, 1913: 99 (female holotype from El Angel, Carchi, Ecuador, elev. 3000-3200 m, 1903, G. RIVET, in MNHN, examined); ROEWER (1954: 598); BONNET (1956: 1214).

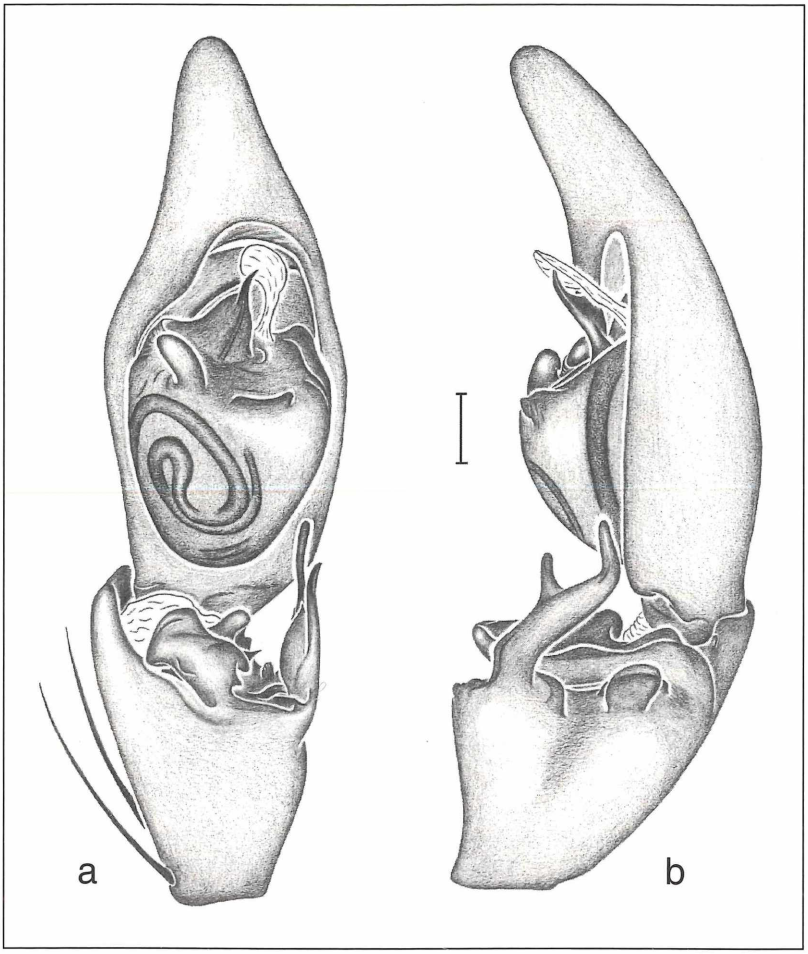

Figure 20. *Stethorrhagus duidae* GERTSCH, male: a) palp, ventral; b) retrolateral; scale line: 0.25 mm.

Diagnosis: Females of *Stethorrhagus nigrinus* differ from *S. roraimae* by the large copulatory opening with sinuous posterior margin and the small spermathecae (fig. 21 b).
Male: Unknown.
Female (holotype). Carapace reddish brown, darker in cephalic region; chelicerae reddish brown; endites, labium, sternum and legs brown; abdomen brownish gray.
Total length 6.90. Carapace 2.60 long, 2.10 wide, 1.10 high. Clypeus 0.22. Chilum bipartite, without hairs. Anterior eye row 0.87 long, posterior eye row 1.00 long. Eye diameters and interdistances: AME 0.18, ALE 0.16, PME 0.16, PLE 0.17; AME-AME 0.10, AME-ALE 0.03, PME-PME 0.14, PME-PLE 0.16, ALE-PLE 0.05. MOQ length 0.45, front width 0.46, back width 0.47. Chelicerae 1.30 long, with 3 promarginal teeth and 5 retromarginal denticles. Sternum 1.40 long, 1.35 wide, deep sternal excavations, with delimited internal margin (fig. 21 c). Abdomen 4.20 long, 3.00 wide; dorsal scutum absent.
Leg measurements: I -femur 2.10 / patella 1.00 / tibia 1.60 / metatarsus 1.50 / tarsus 1.00 / total 7.20. II -2.00 / 0.90 / 1.60 / 1.50 / 1.00 / 7.00. III -1.75 / 0.80 / 1.30 / 1.50 / 0.80 / 6.15. IV -2.20 / 0.80 / 1.90 / 2.25 / 1.05 / 8.20. Leg spination: I -femur p0, r0-0-1; tibia v1p-2-2-2-0. II -femur p0, r0-0-1; tibia v1r-2-2-0. III -femur d1-1-0, p0-1-0, r0; metatarsus p0-1-1, r0-1-1; IV -femur d1-1-0, p0; tibia p0-1-0, r0-1-0, v1r-2-2.
Epigynum: copulatory opening large; median plate absent; long median copulatory ducts and small spermathecae, visible by transparence (fig. 21 b).

Distribution: Known only from the type locality.
Material examined: Only the holotype.

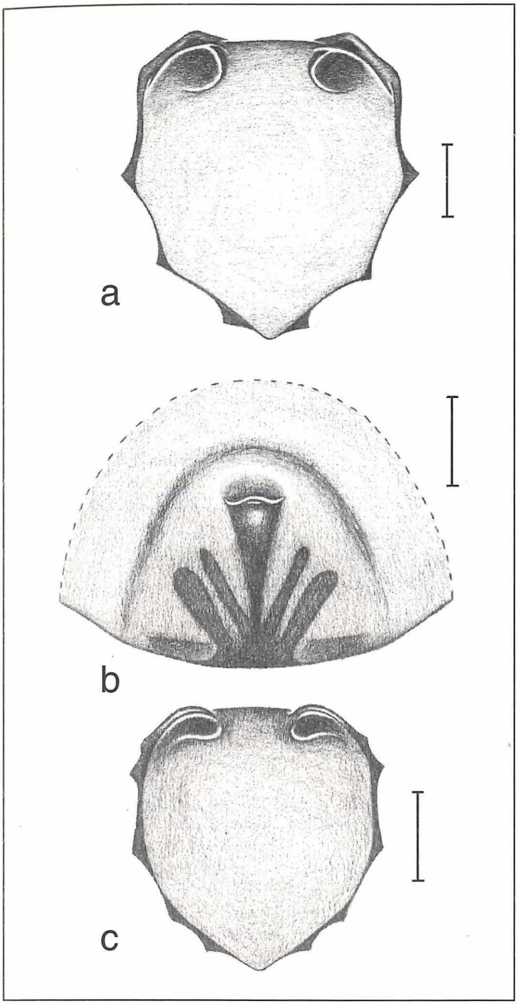

Figure 21. *Stethorrhagus duidae* GERTSCH, male: a) sternum, ventral; *Stethorrhagus nigrinus* (BERLAND), female: b) epigynum, ventral; c) sternum, ventral; scale lines: b, 0.25 mm; a, c, 0,5 mm.

### *Stethorrhagus peckorum,* new species
Figure 22

Types: Male holotype and male paratype from Gran Sabana, 10 km north of Luepa, Bolivar, Venezuela, June 26 -July 11, 1987, S. & J. PECK, deposited in AMNH.
Etymology: The specific name is a patronym in honor of the collectors of the types.

Diagnosis: Males of *Stethorrhagus peckorum* differ from *S. duidae* by the ventral extension of the retrolateral tibial apophysis bifid at basis, the long and large, straight embolus and the absence of a finger-like tegular projection (fig. 22 a, b) on the palpus.

Male (holotype): Coloration as in *S. duidae*, except reddish brown chelicerae; endites, labium and sternum orange.
Total length 7.80. Carapace 3.40 long, 2.60 wide, 1.10 high. Clypeus 0.31. Chilum entire, without hairs, basis notched. Anterior eye row 1.12 long, posterior eye row 1.22 long. Eye diameters and interdistances: AME 0.24, ALE 0.22, PME 0.21, PLE 0.22; AME-AME 0.12, AME-ALE 0.03, PME-PME 0.17, PME-PLE 0.18, ALE-PLE 0.05. MOQ length 0.63, front width 0.71, back width 0.62. Chelicerae 1.82 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 1.50 long, 1.60 wide, shallow sternal excavations, without delimited internal margin. Abdomen 4.20 long, 2.00 wide; dorsal scutum present, long.
Leg measurements: I -femur 3.70 / patella 1.40 / tibia 3.60 / metatarsus 3.55 / tarsus 1.90 / total 14.15. II -3.60 / 1.30 / 3.50 / 3.50 / 1.80 / 13.70. III -3.50 / 1.30 / 3.10 / 3.40 / 1.70 / 13.00. IV -4.40 / 1.30 / 4.00 / 5.00 / 1.80 / 16.50. Leg spination: I -tibia v2-2-2-2-0. II -tibia v2-2-2-2-0. III -tibia v2-2-1r; metatarsus p1-1-0, r1-1-0.
Palp: retrolateral tibial apophysis bifurcated at basis, ventral extension bifid at basis, dorsal extension subquadrangular; dorsal process absent; articulated apophysis longer than wide, subtriangular in ventral view; tegulum with ventral and wide coiled duct, with a small retrolateral apical projection; embolus long and wide, straight, with a long, rounded prolateral prong, covered by the embolus in ventral view; apical prongs strongly reduced, inconspicuous (fig. 22 a,b).
Female: Unknown.
Variation: Two males: total length 7.40 -7.80; carapace 3.40 -3.50; femora I 3.70 -4.10.

Distribution: Known only from the type locality.
Material examined: Only the types.

### *Stethorrhagus roraimae* GERTSCH
Figure 23

*Stethorrhagus roraimae* GERTSCH, 1942: 13, fig. 36 (female holotype from Ireng River in Roraima, Brazil, Aug. 15, 1911, in AMNH, examined); ROEWER (1954: 605).

Diagnosis: Females of *Stethorrhagus roraimae* differ from *S. nigrinus* by the small copulatory opening, with straight posterior margin and the large and spherical spermathecae (fig. 23 a).
Male: Unknown.
Female (holotype): Carapace, endites, labium, sternum and legs pale reddish brown; chelicerae reddish brown; distal third of the labium yellow; abdomen pale yellow.
Total length 9.90. Carapace 4.50 long, 3.30 wide. Clypeus 0.45. Chilum entire, without hairs. Anterior eye row 1.25 long, posterior eye row 1.40 long. Eye dia-

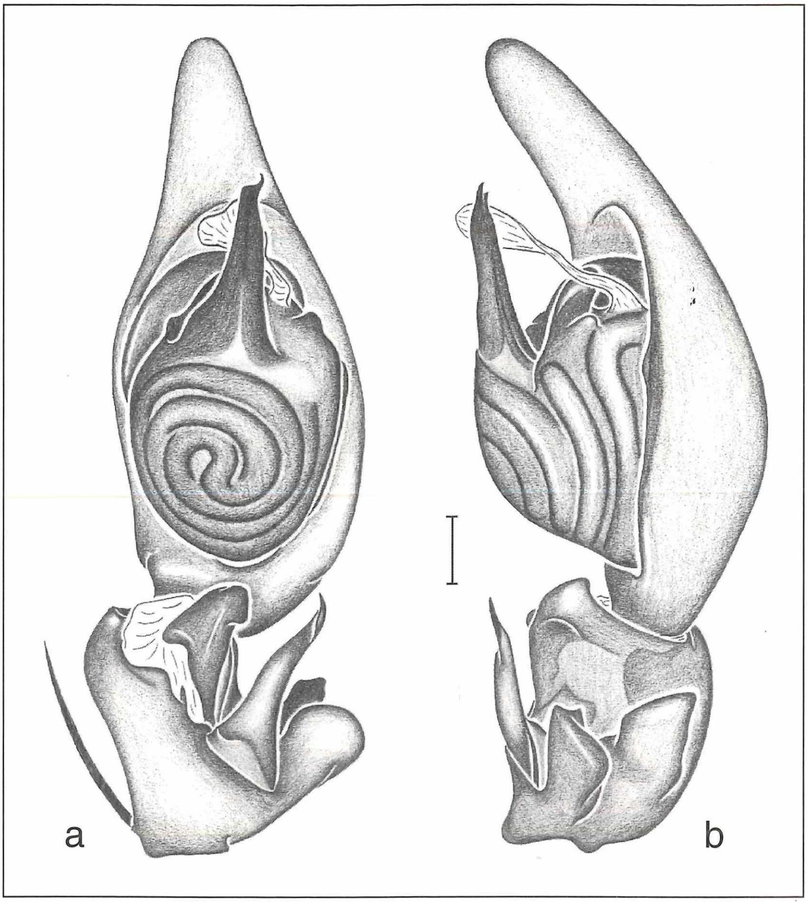

Figure 22. *Stethorrhagus peckorum* new species, male: a) palp, ventral; b) retrolateral; scale line: 0.25 mm.

meters and interdistances: AME 0.32, ALE 0.25, PME 0.20, PLE 0.22; AME-AME 0.22, AME-ALE 0.07, PME-PME 0.32, PME-PLE 0.35, ALE-PLE 0.02. MOQ length 0.62, front width 0.80, back width 0.75. Chelicerae 1.60 long, with 3 promarginal teeth and 4 retromarginal denticles. Sternum 2.00 long, 1.80 wide, deep sternal excavations, with delimited internal margins (fig. 23 b). Abdomen 5.40 long, 3.30 wide; dorsal scutum present.

Leg measurements: I -femur 4.20 / patella 1.60 / tibia 3.90 / metatarsus 3.50 / tarsus 1.90 / total 15.10 / II -4.20 / 1.60 / 3.80 / 3.50 / 1.80 / 14.90 / III -4.10 / 1.40 / 3.40 / 3.40 / 1.60 / 13.90 / IV -5.10 / 1.50 / 4.50 / 5.40 / 1.90 / 18.40. Leg spination: I -femur p0-1-1, tibia v2-2-2-2-0; II -femur 1-1-1, tibia v2-2-2-2-0; III tibia v2-2-0.

Epigynum: copulatory opening small; median plate absent; with long median copulatory ducts and large and spherical spermathecae, visible by transparence (fig. 23 a).

Distribution: Known only from the type locality.
Material examined: Only the holotype.

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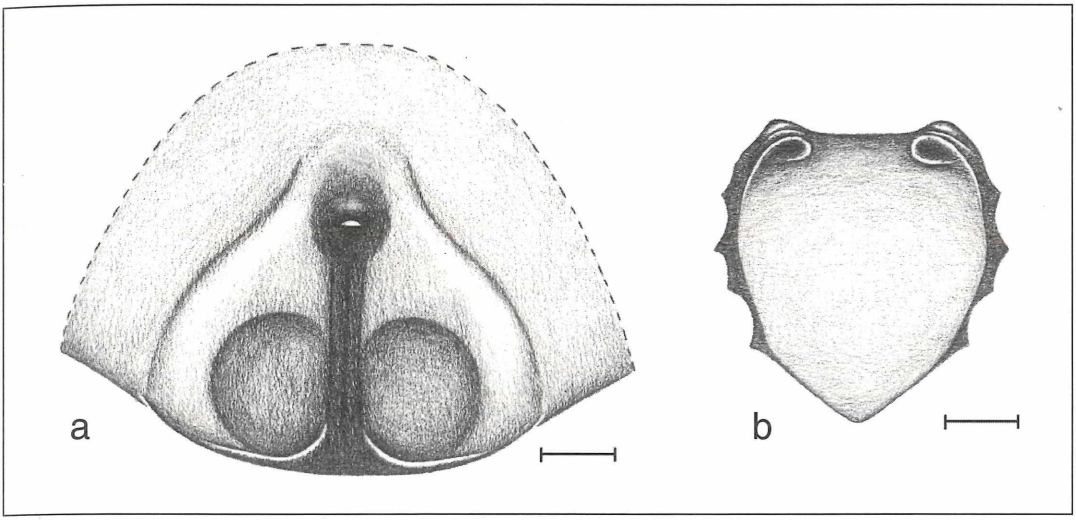

Figure 23. *Stethorrhagus roraimae* GERTSCH, female: a) epigynum, ventral; b) sternum, ventral; scale lines: a, 0.25 mm; b, 0.5 mm.

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## Key to species of *Stethorrhagus*

| | | |
|---|---|---|
| 1. | Males (those of *S. roraimae* and *S. nigrinus* unknown) | .2 |
| | Females (those of *S. duidae*, *S. latoma*, *S. peckorum* and *S. penai* unknown) | .13 |
| 2. | Deep sternal excavations with delimited internal margin | .3 |
| | Shallow sternal excavations without delimited internal margin | .8 |
| 3. | Bifid tibial retrolateral apophysis | .4 |
| | Entire tibial retrolateral apophysis | .6 |
| 4. | Ventral extention of tibial retrolateral apophysis bifid in the distal third (fig. 20 b) | .*duidae* |
| | Ventral extention of tibial retrolateral apophysis entire | .5 |
| 5. | Base of embolus with an elongated prolateral prong; embolus short (fig. 16 a) | .*chalybeius* |
| | Base of embolus without a prolateral prong; embolus long (fig. 15 b) | .*penai* |
| 6. | Tegulum without laminar extentions; embolus with long apical prongs (fig. 9 b) | .*limbatus* |
| | Tegulum with laminar extentions; embolus with short apical prongs (figs 17 a, 19 a) | .7 |
| 7. | Tegular laminar extention transversal, median and serrated;<br>embolus with a rounded prolateral prong (fig. 17 a) | .*planada* |
| | Tegular laminar extention large and tooth-like;<br>embolus with a triangular basal prong (fig. 19 a) | .*hyula* |
| 8. | Tibial retrolateral apophysis with dorsal process (figs 10 b, 13 b) | .9 |
| | Tibial retrolateral apophysis without dorsal process (figs 11 b, 14 b) | .11 |
| 9. | Dorsal process small and pointed; tegular projection large (fig. 13 a,b) | .*latoma* |
| | Dorsal process large and rounded; tegular projection otherwise (figs 10 b, 12 c) | 10 |
| 10. | Ventral extention of the tibial retrolateral apophysis wide and laminar distally;<br>two extentions on the tegulum (fig. 10 a,b) | .*lupulus* |
| | Ventral extention of the tibial retrolateral apophysis finger-shaped;<br>one extention on the tegulum (fig. 12 b,c) | .*archangelus* |
| 11. | Ventral extention of retrolateral tibial apophysis bifid at basis;<br>embolus widened, with reduced apical prongs (fig. 22 a,b) | .*peckorum* |
| | Ventral extention of retrolateral tibial apophysis entire;<br>embolus narrow, with long apical prongs (figs 11 a,b, 14 a,b) | .12 |
| 12. | Dorsal extention of the retrolateral tibial apophysis with a basal process;<br>embolus arising medianly from the tegulum (fig.14 a,b) | .*tridentatus* |
| | Dorsal extention of the retrolateral tibial apophysis without basal process;<br>embolus arising prolaterally from the tegulum (fig. 11 a,b) | .*oxossi* |
| 13. | Deep sternal excavations with delimited internal margin | 14 |
| | Shallow sternal excavation without delimited internal margin | 19 |
| 14. | Copulatory opening large and wide (fig. 9 d) | .*limbatus* |
| | Copulatory opening small and rounded (figs18 a, 23 a) | 15 |
| 15. | Spermathecae disposed anteriorly in relation to copulatory opening (fig. 16 d) | .*chalybeius* |
| | Spermathecae disposed posteriorly in relation to copulatory opening (figs 19 c, 21 b) | .16 |
| 16. | Median plate present, subrectangular (fig. 18 a) | .*planada* |
| | Median plate absent (figs 19 c, 21 b) | 17 |
| 17. | Epigynum with a median luniform sclerotization (fig. 19 c) | .*hyula* |
| | Epigynum without such a sclerotization (figs 21 b, 23 a) | .18 |
| 18. | Small copulatory opening, with straight posterior margin (fig. 23 a) | .*roraimae* |
| | Large copulatory opening, with sinuous posterior margin (fig. 21 b) | .*nigrinus* |
| 19. | Median plate absent;<br>dorsal plate with an accentuated „V“-shaped notch (fig. 14 d,e) | .*tridentatus* |
| | Median plate present; dorsal plate otherwise | .20 |
| 20. | Copulatory opening circular; median plate not invaginated medianly (fig. 12 d) | .*archangelus* |
| | Copulatory opening otherwise; median plate invaginated medianly (figs 10 f, 11 c) | .21 |
| 21. | Copulatory opening „V“-shaped, with a clearly delimited anterior margin (fig. 10 f) | .*lupulus* |
| | Copulatory opening „U“-shaped, without a clearly delimited anterior margin (fig. 11 c) | .*oxossi* |

**andrias, 13:** 65-70, 3 Figs; Karlsruhe, 30. 9. 1994

ANTONIO D. BRESCOVIT & HUBERT HÖFER

# *Amazoromus*, a new genus of the spider family Gnaphosidae (Araneae) from central Amazonia, Brazil

**Abstract**

A new genus, *Amazoromus*, is proposed for four gnaphosid species from a central Amazonian rainforest in Brazil. *Zimiromus cristus* PLATNICK & HÖFER is transfered to the new genus and three new species, *A. kedus*, the type species, *A. becki* and *A. janauari* are described.

**Resumo**

**Um novo gênero de aranhas da família Gnaphosidae (Araneae) da Amazônia central**

O gênero novo, *Amazoromus*, é proposto para quatro espécies de gnafosídeos da Amazônia central, Brasil. *Zimiromus cristus* PLATNICK & HÖFER é transferido para *Amazoromus* e três espécies novas, *A. kedus* (espécie-tipo), *A. becki* e *A. janauari* são descritas.

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## Introduction

The subfamily Echeminae was relimited by PLATNICK & SHADAB (1976a; 1976c; 1979) and is characterized by the combined presence of a strongly procurved posterior eye row, dentate tarsal claws, unadvanced anterior spinnerets and a male palpal structure typically involving a long embolus originating basally on the prolateral side of the tegulum. Three New World echemine genera are known at the moment, *Scopoides* PLATNICK, *Zimiromus* BANKS and *Echemoides* MELLO-LEITÃO and all were revised by PLATNICK & SHADAB (1976b; 1976c; 1979).

During recent examination of gnaphosids collected during ecological projects developed in central Amazonia we found specimens with the characters of the Echeminae. However, these specimens are not congeneric with the New World genera already described, because they possess diagnostically distinct genitalia. Therefore we propose a new genus, *Amazoromus*, and include four species: *Zimiromus cristus* PLATNICK & HÖFER, which is transferred to the new genus and three new species, all from Amazonas, Brazil.

## Material and Methods

The spiders studied are deposited in the following collections: AMNH, American Museum of Natural History, New York (N. I. PLATNICK); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. MAGALHÃES); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E. H. BUCKUP); SMNK, Staatliches Museum für Naturkunde, Karlsruhe (H. HÖFER). The format of descriptions and abbreviations follow PLATNICK & SHADAB (1975). Measurements are in millimeters. The epigynes were cleared in clove oil to study the internal structures, as proposed by LEVI (1965).

## Systematics

### *Amazoromus*, new genus

Type species: *Amazoromus kedus*, new species.

Etymology: The generic name is a contraction of the word Amazonas, region where all known species of the genus occur, and *Zimiromus*, and is masculine in gender.

Diagnosis: *Amazoromus* may be distinguished from all other gnaphosid genera by genitalic characters: male palpi with well developed retrolateral tibial apophyses, bulbus without conductor (figs 1, 2, 3); female epigynum with numerous median transversal striations (fig. 1c, d), spermathecae basal and rounded (fig. 1d). Specimens of *Amazoromus* can be easily separated from the other New World echemine genera by the following characters: from *Echemoides* by lacking the pseudosegmented tarsi on all legs; from *Zimiromus* by lacking a conductor on the male palp and a scape on the female epigynum; from *Scopoides* by having well developed tibial retrolateral apophyses in males and a reduced atrium and globose spermathecae in females.

Description: Total length 2.70-3.56. Carapace oval in dorsal view, widest between coxae II and III, narrowed in front, truncated posteriorly, orange, with black rings around anterior median eyes, with some filiform setae on clypeal margin, shorter setae in ocular area. Cephalic area not elevated. Thoracic groove longitudinal, straight. From above, anterior eye row procurved, posterior row strongly procurved. Anterior median eyes circular, dark, other eyes oval, light, all subequal in size. AME separated by 1/3 their diameter, almost touching ALE; PME separated by half their diameter, from PLE by 1/3 their diameter. MOQ roughly square. Clypeal height slightly smaller than AME diameters. Chelicerae with three promarginal teeth and one retromarginal denticle. Endites short, oblong, with deep median oblique depressions, strong serrulae and weak scopulae. Labium short, subrectangular, anterior margin rounded. Sternum oval, slightly rebordered, subtriangular posteriorly, not projecting between coxae IV. Leg formula 4123. Typical leg spination pattern (only surfaces bearing spines listed): femora I - II d1-1-1, p0-0-1; III - IV d1-1-1, p0-0-1, r0-0-1; tibiae I v0-0-1p, III - IV v1p-2-2, p1-1-1, r1-1-1; metatarsi I  II v2-0-0, III v2-1r-2, p1-1-0, r1-1-0, IV v2-1r-2, p1-0-1, r1-1-1. Tarsi and metatarsi with weak scopulae, more strongly developed in females. Tarsi with two dentate claws and claw tufts. Trochanter notched. Metatarsi without preening comb. Abdomen light gray, with orange anterior scutum in males. Six spinnerets, anteriors long, with three large piriform gland spigots. Palp with well developed tibial retrolateral apophysis, frequently enlarged at base (figs 1b, 2b, 3b); Conductor absent. Embolus long, originating basally on prolateral side of tegulum, usually enlarged at base, coiled at tip (figs 1a, 2a, 3a). Short median apophysis (except in *A. becki*, new species, where it is long). Tegular projection, when present, distal and weakly sclerotized (fig. 3a). Epigynum with anterior hood, numerous transverse striations and a reduced atrium (fig. 1c). Internally with median lobes, short, narrow ducts and basal, globose spermathecae (fig. 1d).

### ***Amazoromus cristus*** **(PLATNICK & HÖFER), new combination**

*Zimiromus cristus* PLATNICK & HÖFER, 1990: 10 (male holotype and female paratype from igapó forest at Rio Tarumã Mirím, Amazonas, Brazil (September 2, 1976: J. ADIS), deposited in INPA, examined.

Diagnosis: *Amazoromus cristus* (see PLATNICK & HÖFER, 1990: 8, figs 19-22) seems closest to *A. kedus*, but may be distinguished by an embolus bifid at its tip and the distally enlarged tibial retrolateral apophysis of the male palp and a short anterior hood and numerous transverse striations of the female epigynum.

Distribution: Known only from the type locality in central Amazonia, Brazil.

### ***Amazoromus kedus*****, new species**

Figure 1

Types: Male holotype and female paratype captured by arboreal funnel traps in Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil (November 1991 - August 1992; H. HÖFER and T. GASNIER), deposited in INPA.
Etymology: The specific name is an arbitrary combination of letters.

Diagnosis: *Amazoromus kedus* seems closest to *A. cristus* (see PLATNICK & HÖFER, 1990: 8, figs 19-22), but may be distinguished by the embolus enlarged at its middle, the distally narrowed retrolateral tibial apophysis of the male palp (fig. 1a,b) and the wide anterior hood and fewer transverse striations of the female epigynum (fig. 1c,d).
Male: Total length 3.20. Carapace 1.40 long, 1.10 wide. Femur II 0.90 long. Eye sizes and interdistances: AME 0.12, ALE 0.10, PME 0.12, PLE 0.10; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.05, PME-PLE 0.05, ALE-PLE 0.04. MOQ length 0.32, front width 0.30, back width 0.27. Embolus strongly enlarged at middle, curved at tip. Median apophysis short (fig. 1a). Retrolateral tibial apophysis very long, with pointed tip (fig. 1b). Leg spination typical for genus.
Female: Total length 3,50. Carapace 1.45 long, 1.05 wide. Femur II 1.00 long. Eye sizes and interdistances: AME 0.14, ALE 0.11, PME 0.10, PLE 0.09; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.06, PME-PLE 0.06, ALE-PLE 0.02. MOQ length 0.28, front width 0.27, back width 0.25. Epigynum with wide hood and few transverse striations (fig. 1c). Spermathecal ducts narrow, spermathecae basal, globose (fig. 1d). Leg spination: femora I - II d0-1-1; tibiae III v0-1p-2, p1-1-0, r1-1-0, IV v1p-2-2, p1-1-0, r1-1-0; metatarsi III v1p-1r-2, r0-1-2; IV v1p-2-2, p0-1-2, r0-1-2.

Other material examined: Brazil, Amazonas, Manaus, Reserva Florestal Adolfo Ducke, arboreal funnel trap, 3 males and 1 female  October 14, 1991 - May 18, 1992 (H. HÖFER and T. GASNIER, MCN 24056; SMNK; AMNH).
Distribution: Known only from the type locality in central Amazonia, Brazil.

### ***Amazoromus becki*****, new species**

Figure 2

Types: Male holotype captured by an arboreal funnel trap in Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil (November 4, 1991; H. HÖFER and T GASNIER), and male paratype from the same locality (October 26, 1992; H. HÖFER and T GASNIER), deposited in INPA and SMNK, respectively.
Etymology: The specific name is a patronym in honor of Prof. Dr. LUDWIG BECK, acarologist and ecologist of Staatliches Museum für Naturkunde in Karlsruhe, for making the ecological project in central Amazonia possible.

Diagnosis: The male of *Amazoromus becki* is easily distinguished from other males by the elongated median apophysis and the short, subtriangular tibial retrolateral apophysis (fig. 2).
Male: Total length 2.70. Carapace 1.30 long, 0.90 wide. Femur II 0.80. Eye sizes and interdistances: AME 0.12, ALE 0.10, PME 0.12, PLE 0.12; AME-AME 0.05, AME-ALE 0.03, PME-PME 0.05, PME-PLE 0.04, ALE-PLE 0.02. MOQ length 0.28, front width 0.27, back width 0.25. Embolus long, coiled at tip; median apophysis strongly developed (fig. 2a); retrolateral tibial apophysis short, subtriangular (fig. 2b). Leg spinati-

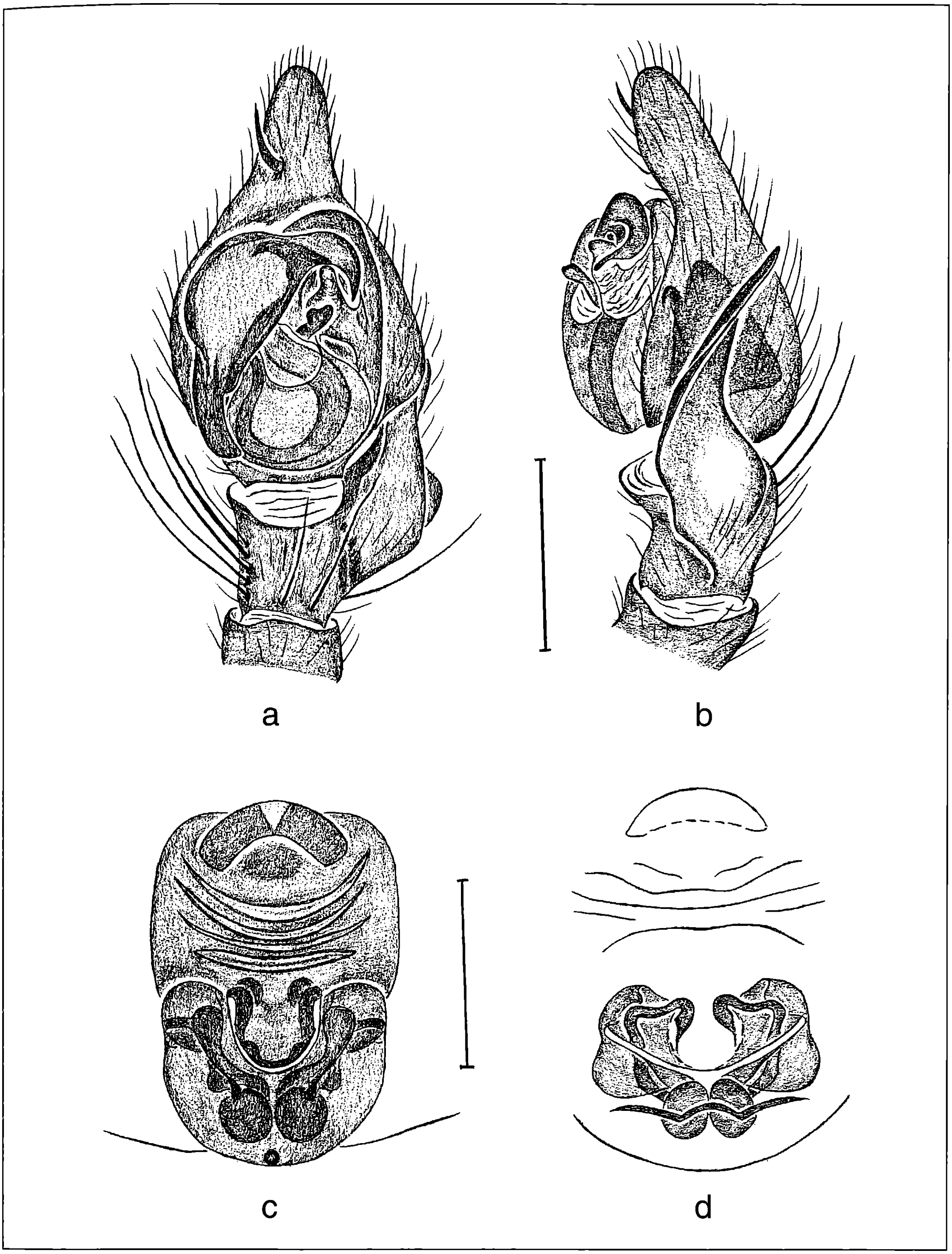

Figure 1. *Amazoromus kedus*, new species: a) Male left palpus, ventral view; b) Same, retrolateral view; c) Epigynum, ventral view; d) Same, dorsal view. Scale lines: 0.25 mm.

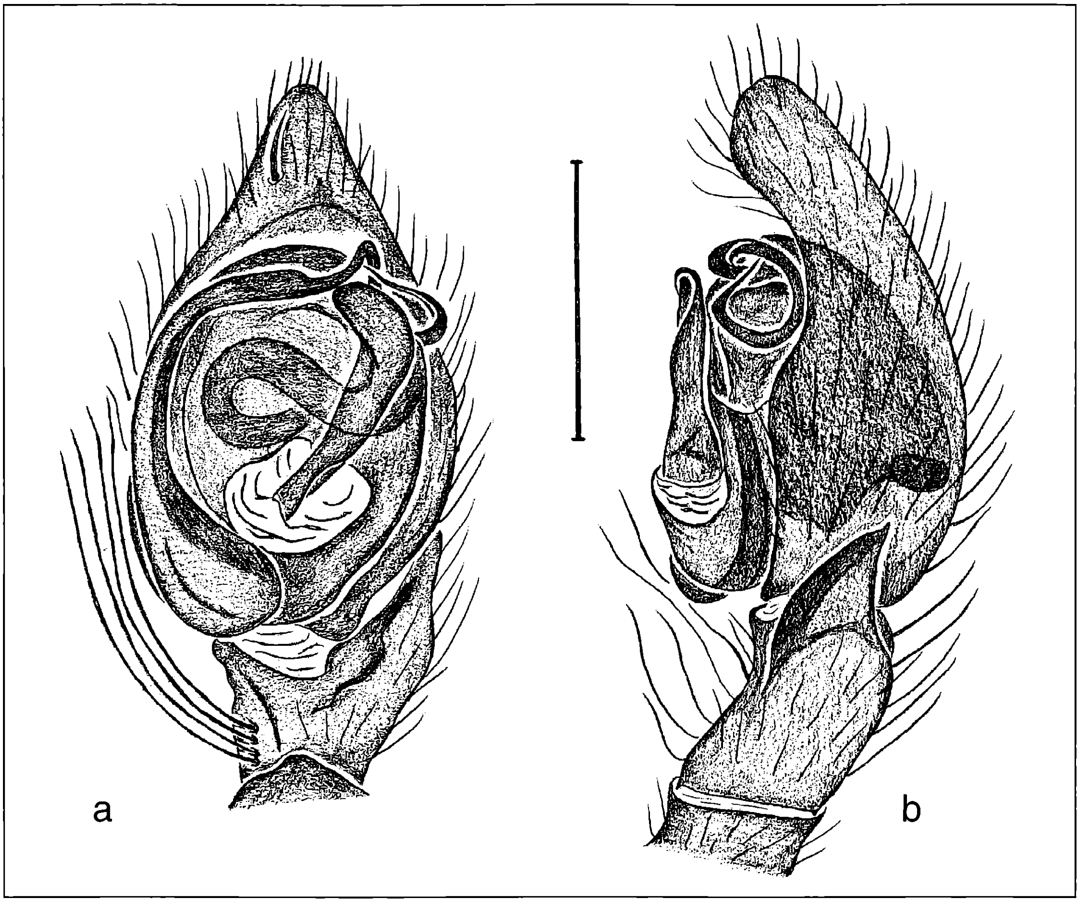

Figure 2. *Amazoromus becki*, new species: a) Male left palpus, ventral view; b) Same, retrolateral view. Scale line: 0.25 mm.

on: femora: I r1-0-0; IV p0-1-1; tibiae: III r1-1-0; IV p0-2-1, r0-1-1; metatarsi: I v1p-0-0, III v1p-2-2, p1-0-1, r1-0-1, IV v1p-2-2, p1-1-1.
Female: Unknown.

Other Material Examined: None.
Distribution: Known only from the type locality in central Amazonia, Brazil.

## *Amazoromus janauari*, new species
Figure 3

Type: Male holotype from a mixed-water inundation forest at Lago Janauari (03 20'S 60 17'W), Manaus, Amazonas, Brazil (October 15, 1987; J. ADIS), deposited in INPA.
Etymology: The specific name refers to the type locality.

Diagnosis: *Amazoromus janauari* is a distinct species easily recognized by the long retrolateral tibial apophysis, with many globose projections on the enlarged base (fig. 3).

Note: The specimen lacks the abdomen.
Male: Carapace 1.70 long, 1.35 wide. Femur II 1.40 long. Eye sizes and interdistances: AME 0.16, ALE 0.12, PME 0.15, PLE 0.12; AME-AME 0.05, AME-ALE 0.03, PME-PME 0.06, PME-PLE 0.06, ALE-PLE 0.02. MOQ length 0.37, front width 0.32, back width 0.35. Tegulum with apical projection, weakly sclerotized. Embolus long, coiled distally; median apophysis short, curved at tip (fig. 3a). Retrolateral tibial apophysis extremely elongated, with dorsal dilation at base, bearing numerous projections (fig. 3b). Leg spination: femora III p0-1-1; tibiae II v1r-1r-1p, III v1p-2-2, p1-1-0, r1-1-0; IV v2-2-2, p1-1-0; metatarsi I v1p-0-0, III r0-0-1, IV v2-0-2, p1-1-1.
Female: Unknown.

Other Material Examined: None.
Distribution: Known only from the type locality in central Amazonia, Brazil.

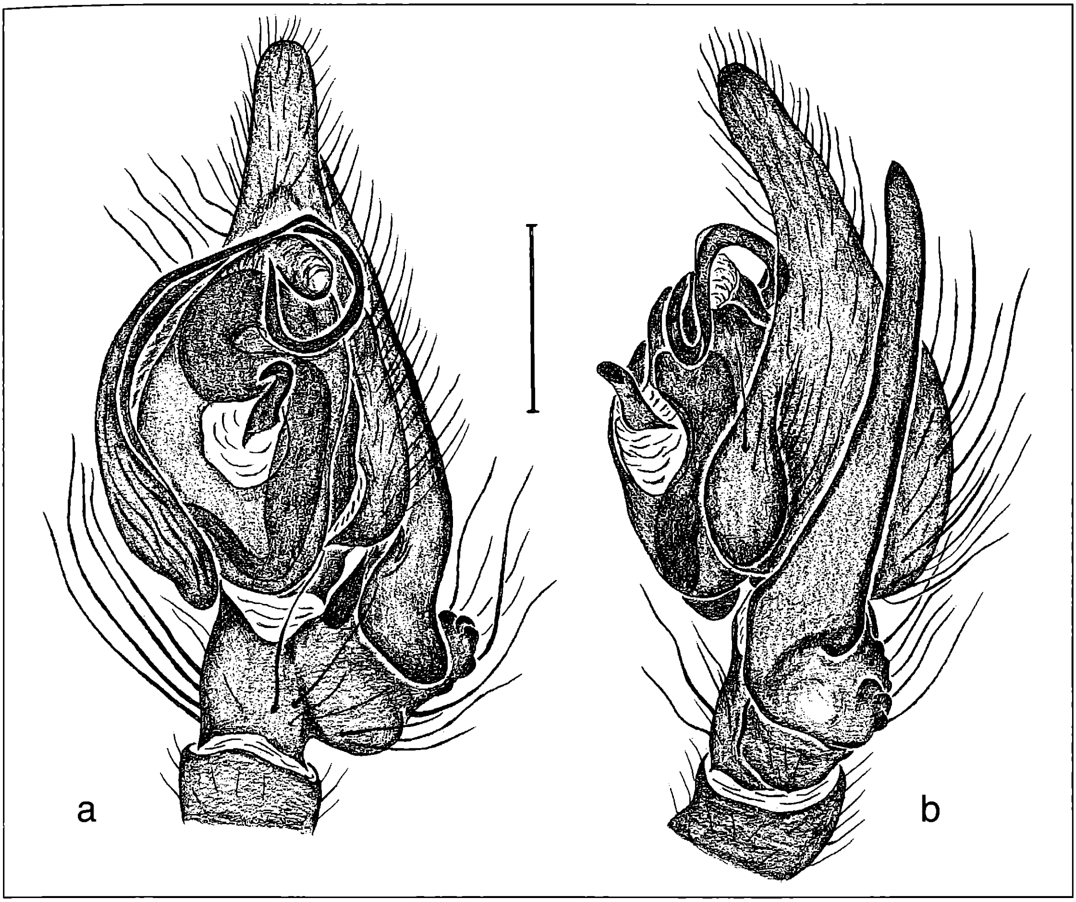

Figure 3. *Amazoromus janauari*, new species: a) Male left palpus, ventral view; b) Same, retrolateral view. Scale line: 0.25 mm.

## Discussion

Our intense collecting in the central Amazon so far did confirm PLATNICK's view of the total allopatry of the echemine genera (PLATNICK & SHADAB 1979, Fig.3). Since his revisions of the three genera and two papers with additional records of *Zimiromus* species (PLATNICK & SHADAB 1979, 1981) we described nine new species of *Zimiromus* from within the supposed range of the genus (PLATNICK & HÖFER 1990, BUCKUP & BRESCOVIT 1993, BRESCOVIT & HÖFER 1994) and one species from northeastern Brazil (BUCKUP & BRESCOVIT 1993), amplifying the genus range. Specimens of *Scopoides* or *Echemoides* were not found within this distribution range. But the new genus *Amazoromus* is totally sympatric with *Zimiromus*. PLATNICK & SHADAB (1979, p.4) in their discussion of the relationships among *Zimiromus*, *Scopoides* and *Echemoides*, used the development of the palpal conductor into a solid sheet surrounding the embolus to relate *Zimiromus* and *Echemoides*. As *Amazoromus* appeared in the center of the distribution range of *Zimiromus*, the two genera could be expected to be sister groups. However, *Amazoromus* seems to be more closely related to *Scopoides*, based on the absence of a conductor on the male palp and the presence of an anterior hood on the female epigynum. On the other hand the possibility of *Zimiromus* becoming paraphyletic by the simple proposal of *Amazoromus* is remote. We do not believe that the scape on the female epigyne of *Zimiromus* species is homologous with the transverse striations of the epigyne of *Amazoromus* species. The presence of a scape on the female epigynum is regarded as a synapomorphic character of *Zimiromus* species.

Within the Manaus region, where we sorted and identified samples from seven forest sites, the *Zimiromus* and *Amazoromus* species seem to have very small distribution areas and are probably restricted to certain habitat types (e.g. inundation forest, terra firme).

*Z. atrifus*, *Z. boistus*, *Z. kleini* and *Z. syenus* have been collected in more than one study site in central Amazonia, but none of the species was found in inundation forests and terra firme forests. On the other hand *Z. beni* was recorded from an inundation forest in the Beni region of Bolivia (Upper Amazon) and from an inundation forest near Manaus (Lower Amazon). Thus for a better understanding of the biogeographic situation and the relationships of the echemine genera we surely need more intense sampling within the large Amazon region.

**Acknowledgments**

The ecological project was financed by the German Science Foundation (DFG, project Prof. Dr. BECK). We thank Prof. Dr. L. BECK for permanent support of our study and for organizing the research period of the first author in Germany. We are grateful to INPA (Instituto Nacional de Pesquisas da Amazônia) and to PD Dr. W. JUNK of the working group „Tropical Ecology“ of the Max-Planck-Institut für Limnologie for including us in the Convênio INPA - Max-Planck and permitting research in Reserva Florestal Adolfo Ducke. We wish to thank PD Dr. J. ADIS for making available spiders collected in the mixed water inundation forest at Lago Janauari. A. B. BONALDO made helpful comments on the manuscript and Dr. N. I. PLATNICK reviewed it.

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ANTONIO D. BRESCOVIT & HUBERT HÖFER

# *Heidrunea*, a new genus of the spider subfamily Rhoicininae (Araneae, Trechaleidae) from central Amazonia, Brazil

**Abstract**

*Heidrunea* is proposed as a new genus of the subfamily Rhoicininae, Trechaleidae. Three new species from central Amazonian inundation forests are described: *H. irmleri* (the type species), *H. arijana* and *H. lobrita*.

**Resumo**

**Um novo gênero da subfamília Rhoicininae (Araneae, Trechaleidae) da Amazônia central**

O gênero novo, *Heidrunea*, é proposto para três espécies novas de Rhoicininae da Amazônia central, Brasil: *H. irmleri* (espécie-tipo), *H. arijana* e *H. lobrita*.

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## Introduction

The subfamily Rhoicininae was recently redefined by SIERWALD (1993), consisting of three genera, *Rhoicinus* SIMON, 1898 and *Barrisca* CHAMBERLIN & IVIE, 1936 from the neotropical region and the genus *Shinobius* YAGINUMA, 1991 from Japan. The subfamily was placed in Trechaleidae by GRISWOLD (1993; see also discussion in CARICO 1993). The genus *Xingusiella* MELLO-LEITÃO, 1940 was included in Rhoicininae by LEHTINEN (1967: 332) and synonymized by SIERWALD (1993) with *Paradossenus* F.O.P.-CAMBRIDGE, 1903, which is formally included in the family Trechaleidae, but not in the subfamily Rhoicininae.

The genus *Rhoicinus* was proposed by SIMON (1898) and actually contains eight species described from Ecuador, Peru, Guiana and the north of Brazil (SIMON 1898; EXLINE 1950, 1960; BRESCOVIT 1993; HÖFER & BRESCOVIT 1994). The second neotropical genus, *Barrisca* was established by CHAMBERLIN & IVIE (1936). In his generic revision, PLATNICK (1979) included two species widespread in South America (Panama, Colombia, Venezuela, Peru). The spider genus *Shinobius* was recently proposed by YAGINUMA (1991) for the Japanese species *S. orientalis* (YAGINUMA, 1967), which was originally described in the African genus *Cispius* SIMON, 1898.

While sorting through extensive material collected during ecological projects in inundation forests near Manaus, we found spiders of the subfamily Rhoicininae, not congeneric with type species of other rhoicinine genera. The new genus *Heidrunea*, is therefore proposed for three new species from central Amazonia.

## Material and Methods

The material examined is deposited in the following collections: INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. MAGALHÃES); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E. H. BUCKUP); SMNK, Staatliches Museum für Naturkunde, Karlsruhe (H. HÖFER). The format of the descriptions follows HÖFER & BRESCOVIT (1994), measurements are in millimeters.

## Systematics

### *Heidrunea*, new genus

Type species: *H. irmleri*, new species.
Etymology: The generic name is a patronym in honour of the second author's wife for the steady support of his field work in Brazil and is feminine in gender.

Diagnosis: *Heidrunea* is recognized as a rhoicinine genus by the following synapomorphies with other rhoicinine genera: male tibial apophysis absent, conductor of the male palp membranous, female epigynum consisting of a median lobe with short epigynal folds and short lateral lobes. *Heidrunea* can be distinguished from *Rhoicinus* and *Barrisca* by the strongly recurved posterior eye row, where the PLE are widely separated from the PME (see fig. 1), the absence of heavy spines on the cymbium of the male palp (figs 2, 3) and the enlarged base of the spermathecae in females (figs 4b,d,f). In characters of the genitalia it resembles *Barrisca* (see PLATNICK 1979: figs 1-6 for comparison), however *Heidrunea* differs by having a hyaline elongated ventral median apophysis on the tegulum and by lacking sinuous ducts in the male palp (figs 2a, 3a, 7b) and by the presence of the prominent posterior lobe separated by distinct epigynal folds from the lateral margins in the female epigyne (figs 4a,c,e, 7c).

Description: Total length (males and females) between 3.30-5.00. Carapace oval, narrowest anteriorly, widest at coxae II, moderately elevated in the cephalic region and invaginated posteriorly, with a black median band behind PME and covered with short plumose

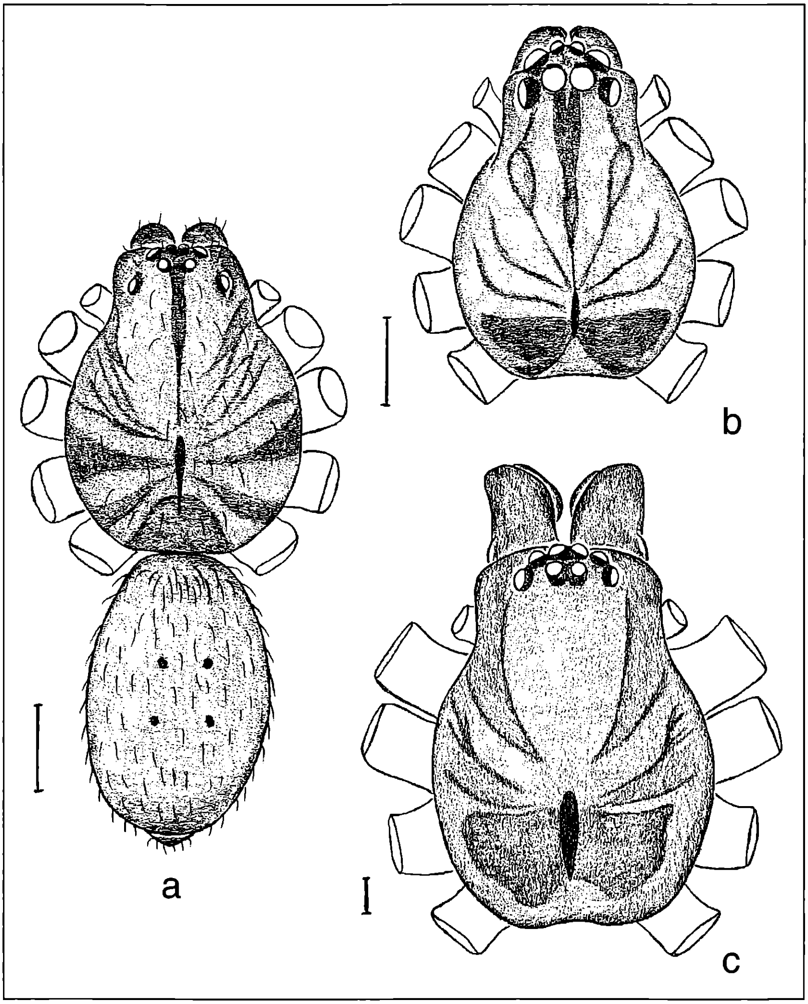

Figure 1. a) *Heidrunea irmleri*, n. sp., body of male, dorsal view; b) *Barrisca nanella* Chamberlin & Ivie, carapace of male, dorsal view; c) *Rhoicinus gaujoni* Simon, carapace of male, dorsal view. Scale lines: 0.25 mm.

setae. Thoracic groove longitudinal, long but not deep (fig. 1a). From above, anterior eye row moderately recurved, posterior eye row strongly recurved; from front, both rows recurved. AME dark, the other eyes surrounded by black pigment. AME separated by 1/3 their diameter, by half their diameter from ALE; PME separated by half their diameter, from PLE by more than their diameter; ALE separated widely from PLE. MOQ with the length equal to the anterior width and almost half the posterior width. Clypeal height equal to the diameter of anterior eyes. Chilum absent. Chelicerae robust, showing median lamina and a distinct lateral boss, with 3-4 promarginal and 3 retromarginal teeth. Fangs of chelicerae short, half the length of chelicerae and enlarged at base. Endites rectangular, not sulcated on the external lateral margin, with anteromedian scopula. Labium longer than wide, with anterior margin truncated, notched at base. Sternum as long as wide, slightly invaginated anteriorly, triangular posteriorly, projecting between coxae IV. Legs thin, with short setae, mainly on ventral side of femur and coxae; and plumose setae on prolateral side of metatarsi (fig. 5a,c). Female palp with conical tarsi and the following spination: femur d1-1-1, v1-1-1-1-1; patella d1-1, p0-1-0; tibia d0-1-0, p2-2; tarsus p1-1-1, r0-1-0; tarsal claws large, bearing about eight teeth. Leg formula 4123. Typical leg spination pattern (only surfaces bearing spines listed): femur I d1-1-1, p0-1-1, r0-0-1; II d1-1-1, p0-1-1, r0-1-1; III d1-1-1, p1-1-1, r0-1-1; IV d1-1-1, p1-1-1, r0-0-1; tibia I v2-2-2-0-2, p0-1-1, r0-1-1; II 2-2-2-0-2, p0-1-0, r0-1-0; III IV v2-2-2, p1-1-0, r1-1-0; metatarsus I - II v2-2-2, p0-1-1, r0-1-1; III - IV v2-2-2, p1-1-1, r1-1-1. Tarsi and metatarsi with scopulae slightly developed. Metatarsi projecting distally over base of the tarsus (fig. 5b). Trichobothria present in one row on tibiae and metatarsi; and two rows on tarsi. Preening combs absent. Tarsi with three claws, superior claws with 10-12 teeth; unpaired claw without teeth (fig. 5d). Trochanters notched. Claw tuft consisting of about six long setae (fig. 5d). Abdomen oval, longer than wide, densely coated by setae, with two pairs of anterior dorsal muscular impressions. Anal tubercle not divided. Six spinnerets (fig. 6a), anterior laterals (ALS) two-segmented, elongated, having two large ampullate gland spigots on mesal margin and more than thirty pyriform gland spigots with elongated shafts (fig. 6b). Posterior medians (PMS) small, one-segmented, with at least one large ampullate gland spigot with a long slender shaft on subdistal margin, few aciniform gland spigots and 3-4 relatively large cylindrical gland spigots with short shafts (fig. 6c). Posterior laterals two-segmented, smaller than anterior laterals, with several aciniform gland spigots (fig. 6d). Cylindrical gland spigots were not observed, if present on PLS, they are covered by the long setae on the margin of the spinnerets. Colulus reduced, with 10-15 setae. Male palpal patellae with a large apical ventral projection (figs 2a, 3a). Tibiae with retrolateral excavation bordered by ventral ledge similar to the one found in *Barrisca* (figs 2b, 3b). Cymbium elongate, narrowed distally, without heavy spines. Palpal bulb with distinct subtegulum. Tegulum projecting behind embolus. Ejaculatory ducts simple, surrounding the ventral face of tegulum. Conductor retrolaterally disposed, heavily sclerotized, flattened and very large. Median apophysis lamelliform, hyaline, elongate, subdistal, in front of the median apophysis. Embolus short, distal-prolateral, enlarged at base and curved at tip (figs 2a, 3a, 7a,b). Epigynum forming a sclerotized plate, divided posteriorly by epigynal folds (ef), with short lateral lobes (ll) and forming a median lobe posteriorly (lp) (figs 4a,c,e, 7c,d). Copulatory openings at confluence of lateral lobes and median posterior lobe. Internally with two median, globose or oval spermathecae, with a terminal receptaculum at base, projecting posteriorly or dorsally. Lateral short curved copulatory ducts attached at base of spermathecae. Fertilization ducts curved, originating from base of spermathecae, close to the origin of copulatory ducts and accompanying them (fig. 4b,d,f).

Composition: Three neotropical species.

### *Heidrunea irmleri*, new species

Figures 2, 4a, b, 5-7

Types: Male holotype from blackwater inundation forest (igapó) at Rio Tarumã Mirím, Amazonas, Brazil, October 20 - November 19, 1971, U. IRMLER, and one female paratype from the same locality, March 9, 1988, H. HÖFER, deposited in SMNK. Other paratypes: one male, with the same data of holotype and one female from the same locality, January 29, 1988, H. HÖFER, both deposited in MCN (24061 and 24062).

Etymology: The specific name is a patronym in honor of the collector of the holotype.

Diagnosis: *Heidrunea irmleri* may be distinguished from *H. lobrita* by the presence of a projection on the apical border of tibiae and the pyriform embolus, curved at tip (figs 2a, 7a) in the male palp; and the rounded border of the median posterior lobe (figs 4a, 7c,d) in the female epigynum.

Male (holotype): Carapace orange, with cephalic area dark. Chelicerae, labium, endites red-brown. Sternum yellow with orange-brown border. Legs orange. Abdomen grayish-brown. Spinnerets yellowish. Total length 3.50. Carapace 1.80 long, 1.40 wide. Clypeus 0.06 high, equal to AME diameter. Anterior eye row 0.38 long and posterior eye row 0.63. Eye sizes and interdistances: AME 0.06, ALE 0.10, PME 0.10, PLE 0.10; AME-AME 0.02, AME-ALE 0.03, PME-PME 0.05, PME-PLE 0.13, ALE-PLE 0.12. MOQ length 0.15, front width 0.15, back width 0.25. Chelicerae 0.75 long with 3 promarginal and retromarginal teeth. Abdomen 1.70 long, 1.15 wide.

Length of legs: I - femur 1.45/ patella 0.65/ tibia 1.10/ metatarsus 1.05/ tarsus 0.70/ total 4.95/ II - 1.40/ 0.60/ 1.00/ 1.10/ 0.65/ 4.75/ III - 1.30/ 0.50/ 1.00/ 1/10/ 0.60/ 4.50/ IV - 1.70/ 0.60/ 1.40/ 1.70/ 0.80/ 6.20. Leg spination: as in the typical spination pattern. Ventral ledge of palpal tibiae narrow, with apical projection (fig. 2). Conductor oval, flattened and lightly invaginated at tip. Median apophysis not curved, narrowed distally. Embolus pyriform, curvate at tip (figs 2, 7a, b).

Female (paratype): Coloration as in male. Total length 4.80. Carapace 2.00 long, 1.50 wide. Clypeus 0.06 high, with the diameter of the AME. Anterior eye row 0.45 and posterior eye row 0.72. Eye sizes and interdistances: AME 0.06, ALE 0.10, PME 0.09, PLE 0.09; AME-AME 0.02, AME-ALE 0.05, PME-PME 0.07, PME-PLE 0.17, ALE-PLE 0.16. MOQ length 0.13, front width 0.13, back width 0.23. Chelicerae 0.82 long with teeth as in male. Abdomen 2.50 long, 1.60 wide.

Length of legs: I - femur 1.70/ patella 0.75/ tibia 1.30/ metatarsus 1.10/ tarsus 0.75/ total 5.60/ II - 1.60/ 0.70/ 1.20/ 1.10/ 0.70/ 5.30/ III - 1.50/ 0.60/ 1.05/ 1.20/ 4.95/ IV - 2.00/ 0.70/ 1.65/ 2.00/ 0,80/ 7.15. Leg spination: I tibia p1-1-0; II femur r0-0-1; III femur r0-0-1; IV femur p0-0-1. Epigynum with rounded posterior median lobe, lightly sulcated anteriorly, with corrugated surface (figs 4a, 7c, d). Spermathecae oval, with terminal receptaculae projecting dorsally, behind spermathecae. Copulatory ducts long. Fertilization ducts leading to the inner part, curved around the copulatory ducts (fig. 4b).

Variation: Three males: total length 3.30-3.50; carapace 1.60-1.80; femur I 1.40-1.45. Five females: total length 4.20-5.00; carapace 1.80-2.20; femur I 1.50-1.90.

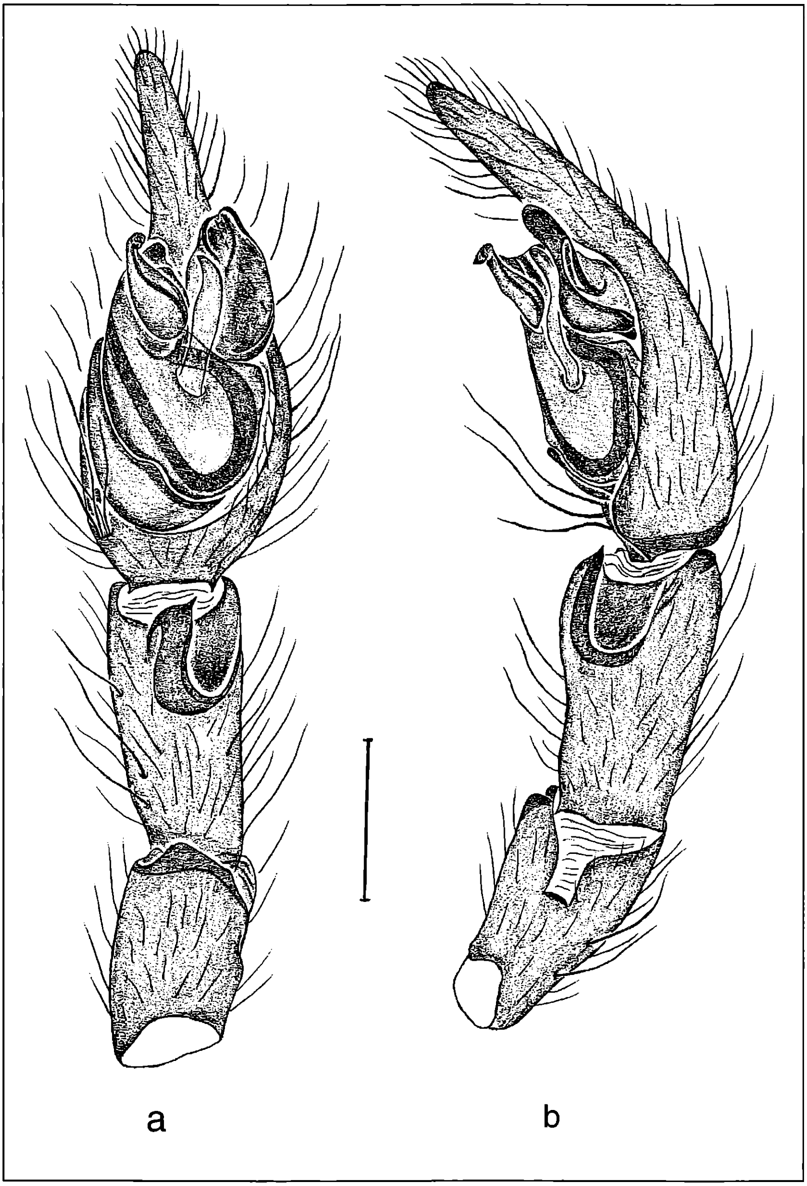

Figure 2. *Heidrunea irmleri*, n. sp., male: a) palp, ventral view; b) retrolateral view. Scale line 0.25 mm.

Distribution: Known only from the type locality in central Amazonia, Brazil.

Additional material examined. Brazil. Amazonas, Rio Tarumã Mirím, 1 male, October 20 - November 19, 1971, U. IRMLER (SMNK); 1 male, November 20, 1987, H. HÖFER, collected in pitfall trap (INPA); 2 females, February 12 - March 11, 1988, in pitfall trap (SMNK); 2 females, March 4, 1988, in pitfall trap (SMNK; INPA); 1 female, March 14, 1988, in ground-photoeclector (SMNK 332); all collected by H. HÖFER.

## ***Heidrunea arijana*, new species**

Figures 3, 4c,d

Types: Male holotype and female paratype from mixed water inundation forest at Lago Janauari, Manaus, Amazonas, Brazil, November 17 - December 21, 1971, U. IRMLER, collected in ground-photoeclector, deposited in SMNK.

Etymology: The specific name is an arbitrary combination of letters.

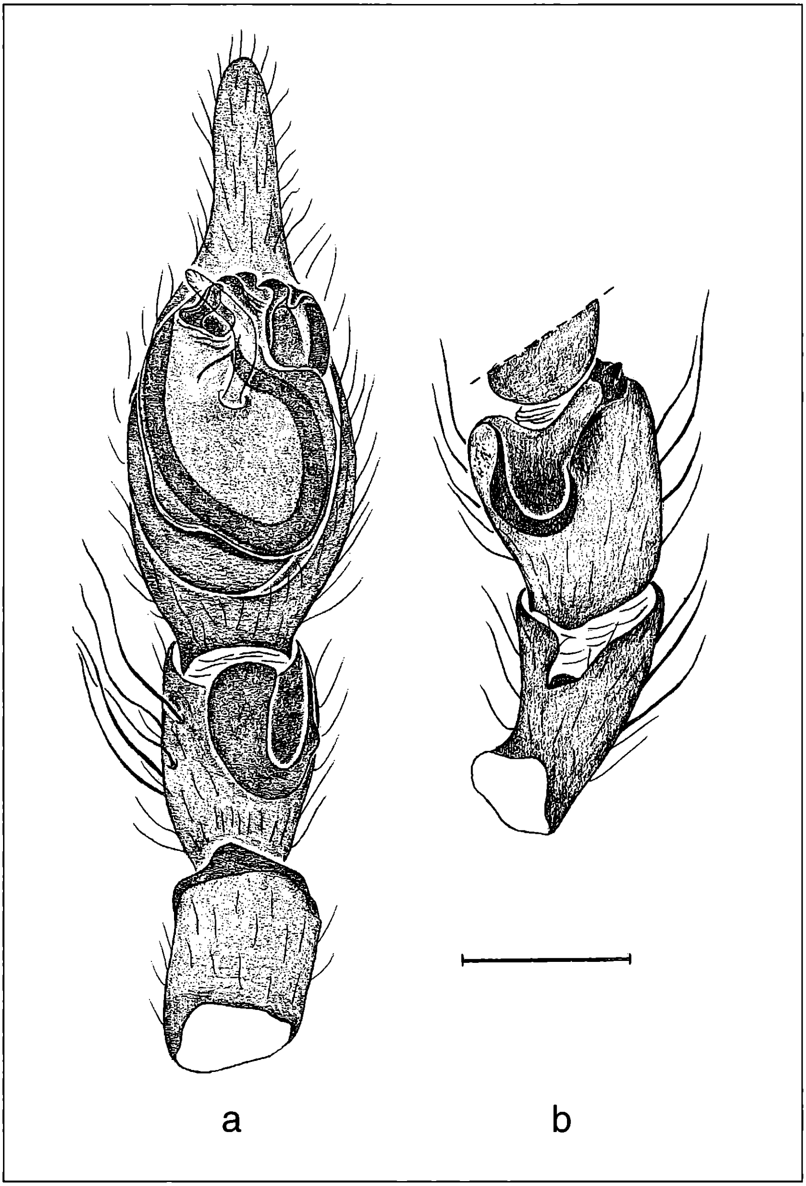

Figure 3. *Heidrunea arijana*, n. sp., male: a) palp, ventral view; b) retrolateral view of tibia and patella. Scale line 0.25 mm.

Diagnosis: *Heidrunea arijana* may be distinguished from *H. irmleri* by the very dilated ventral ledge of palpal tibiae and the reduced, curved embolus (fig. 3) in the male palp. Females resemble *H. lobrita*, but may be distinguished by the rounded and sinuous border of median posterior lobe (fig. 4c) and the voluminous spermathecae (fig. 4d) in the female epigynum.

Male (holotype): Coloration as in *H. irmleri*. Total length 3.70. Carapace 1.90 long, 1.55 wide. Clypeus 0.06 high equal to the diameter of the AME. Anterior eye row 0.47 long and posterior eye row 0.68 long. Eye sizes and interdistances: AME 0.06, ALE 0.10, PME 0.10, PLE 0.11; AME-AME 0.02, AME-ALE 0.06, PME-PME 0.06, PME-PLE 0.15, ALE-PLE 0.11. MOQ length 0.17, front width 0.16, back width 0.26. Chelicerae 0.82 long with 3 promarginal and 4 retromarginal teeth. Abdomen 2.00 long, 1.30 wide.

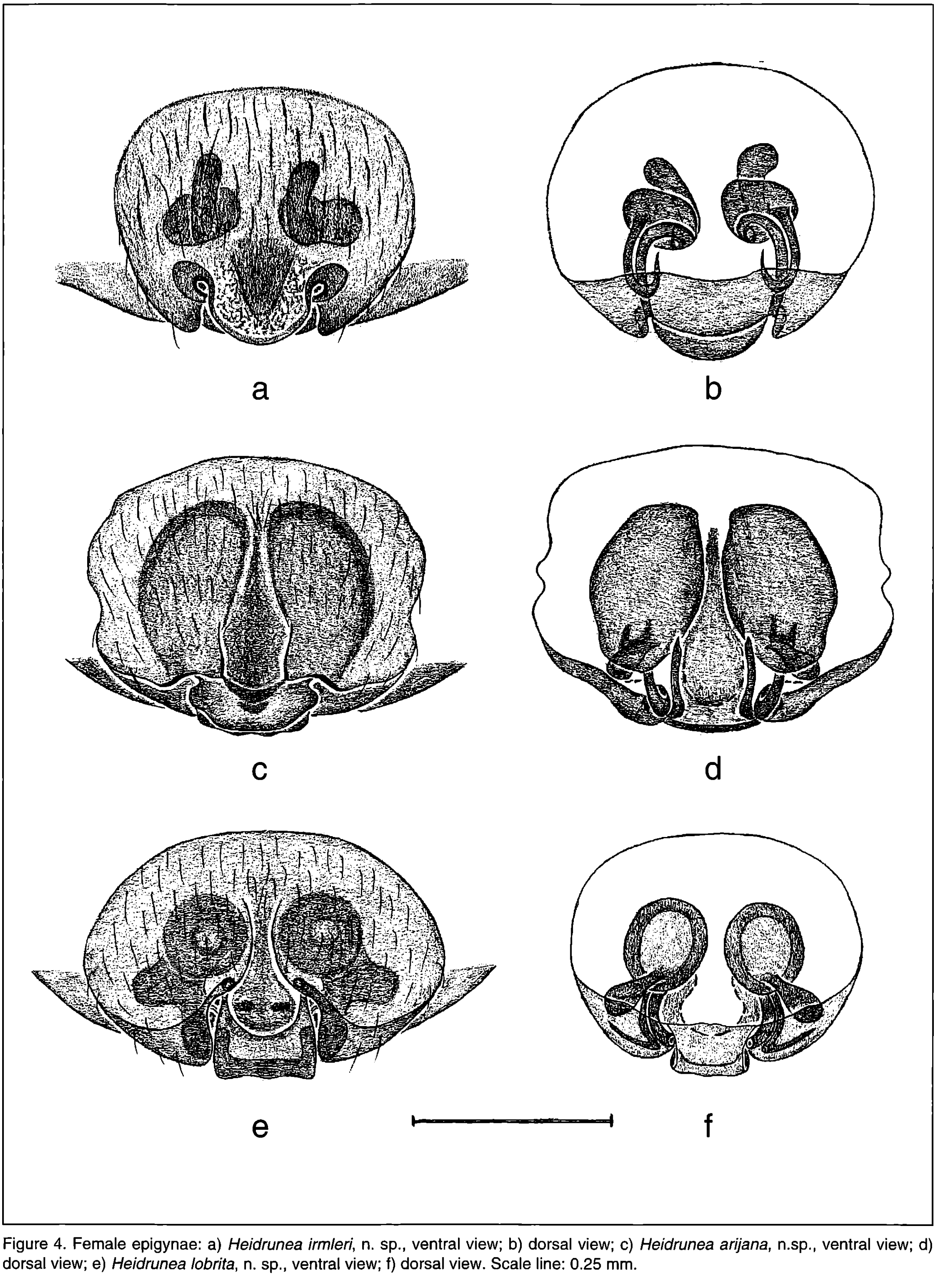

Figure 4. Female epigynae: a) *Heidrunea irmleri*, n. sp., ventral view; b) dorsal view; c) *Heidrunea arijana*, n.sp., ventral view; d) dorsal view; e) *Heidrunea lobrita*, n. sp., ventral view; f) dorsal view. Scale line: 0.25 mm.

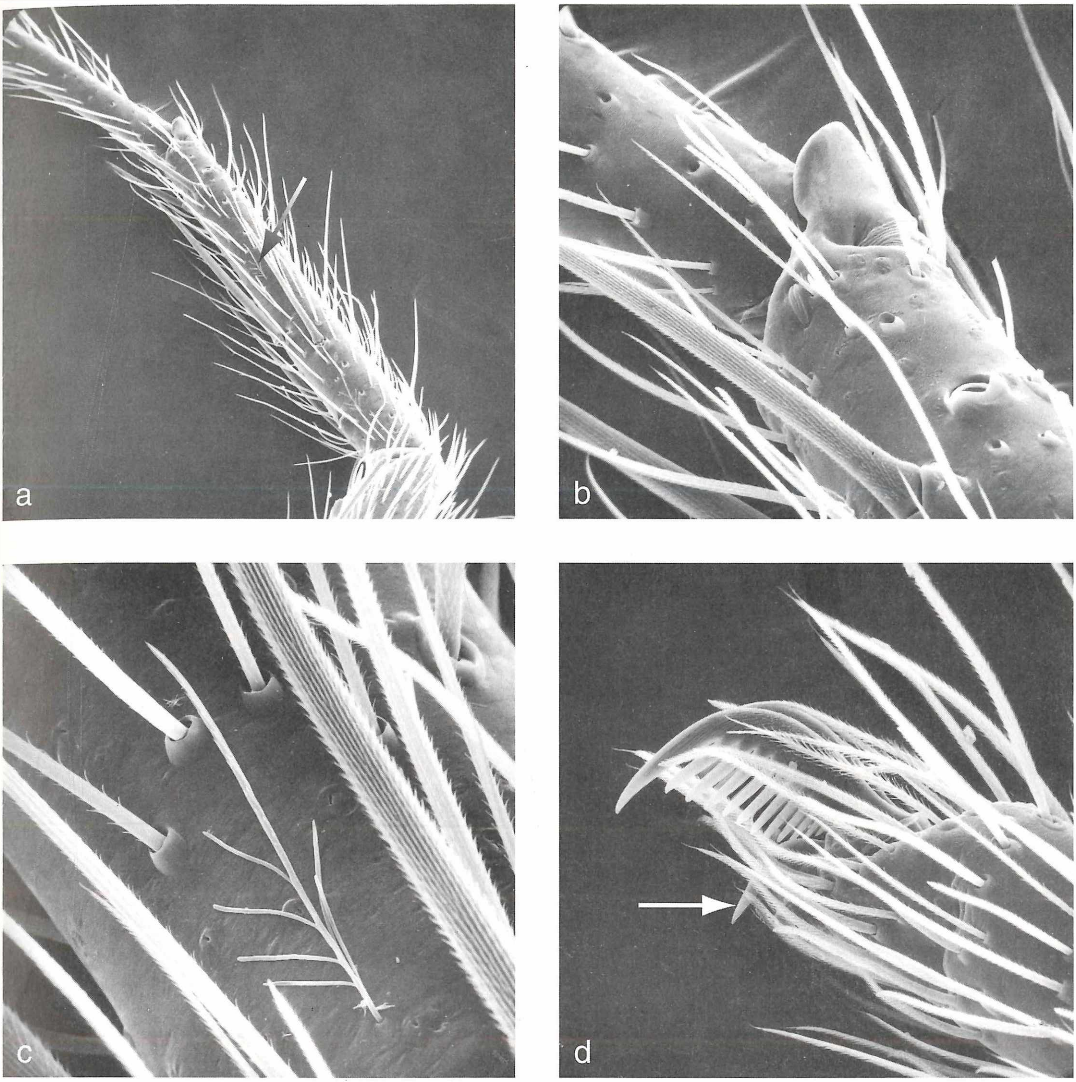

Figure 5. *Heidrunea irmleri*, n. sp., male, leg I: a) metatarsus (arrow indicates plumose setae), 90x; b) distal projection of metatarsus, 450x; c) plumose setae (detail), 900x; d) apex of tarsus I (arrow points to inferior tarsal claw), 450x.

Length of legs: I - femur 1.60/ patella 0.80/ tibia 1.35/ metatarsus 1.30/ tarsus 0.75/ total 5.80/ II - 1.50/ 0.70/ 1.25/ 1.30/ 0.70/ 5.45/ III - 1.50/ 0.60/ 1.00/ 1.20/ 0.55/ 4.85/ IV - 1.70/ 0.60/ 1.50/ 1.80/ 0.70/ 6.30. Leg spination: I femur p1-1-1, r0; tibia p0-1-0; II femur p1-1-1, r0; tibia r1-1-0; III femur p0-1-1-1; IV femur p0-1-1, r0-1-1. Palpal tibiae with dilated ventral ledge, without apical projection (fig. 3). Conductor subquadrangular, with a conical and rounded tip. Median apophysis curved, rounded distally. Embolus short, curved, with a broad base and conical tip (fig. 3a).

Note: Both palps of the holotype are expanded, not permitting illustration of the retrolateral view of the tegulum. Female (paratype): Coloration as in male. Total length 4.70. Carapace 1.80 long, 1.60 wide. Clypeus 0.11 high, 1/3 larger than the diameter of the AME. Anterior eye row 0.51 long, posterior eye row 0.78 long. Eye diameters and interdistances: AME 0.07, ALE 0.10, PME 0.09, PLE 0.11; AME-AME 0.03, AME-ALE 0.08, PME-PME 0.10, PME-PLE 0.20, ALE-PLE 0.13. MOQ length 0.15, front width 0.17, back width 0.26. Chelicerae 0.90 long, with teeth as in male. Abdomen 3.00 long, 2.00 wide.

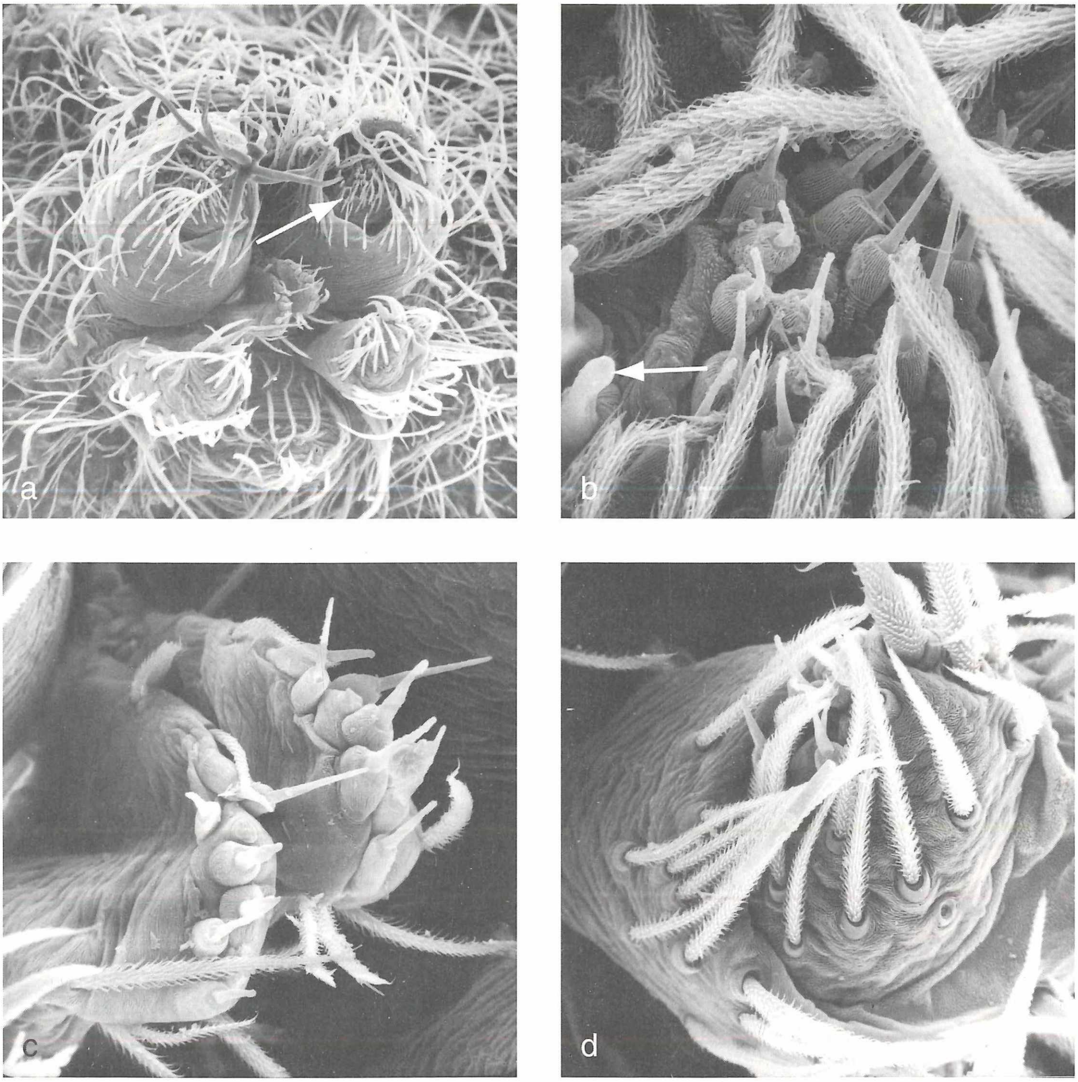

Figure 6. *Heidrunea irmleri*, n. sp., female, spinnerets: a) spinning field (arrows points to major ampullate spigot), 180x; b) left ALS (arrow points to major ampullate spigot), 1800x; c) PMS, 900x; d) left PLS, 900x.

Leg measurements: I - femur 3.40/ patella 0.75/ tibia 1.30/ metatarsus 1.30/ tarsus 0.75/ total 7.50/ II - 3.20/ 0.70/ 1.20/ 1.20/ 0.70/ 7.00/ III - femur 3.00/ the others segments missing/ IV - femur 3.70/ the others segments missing. Leg spination: I tibia p0-1-0, r0-1-0; II tibia p0-1-0, r0-1-0; III and IV missing. Epigynum with rounded and sinuous border of median posterior lobe, notched at base and with laterally projecting lobes. Center of epigynum with a large and deep groove (fig. 4c). Spermathecae oval and voluminous, with terminal receptaculae projecting posteriorly. Copulatory ducts short and coiled. Fertilization ducts elongated and not curved (fig. 4d).

Other material examined: None.
Distribution: Known only from the type locality in central Amazonia, Brazil.

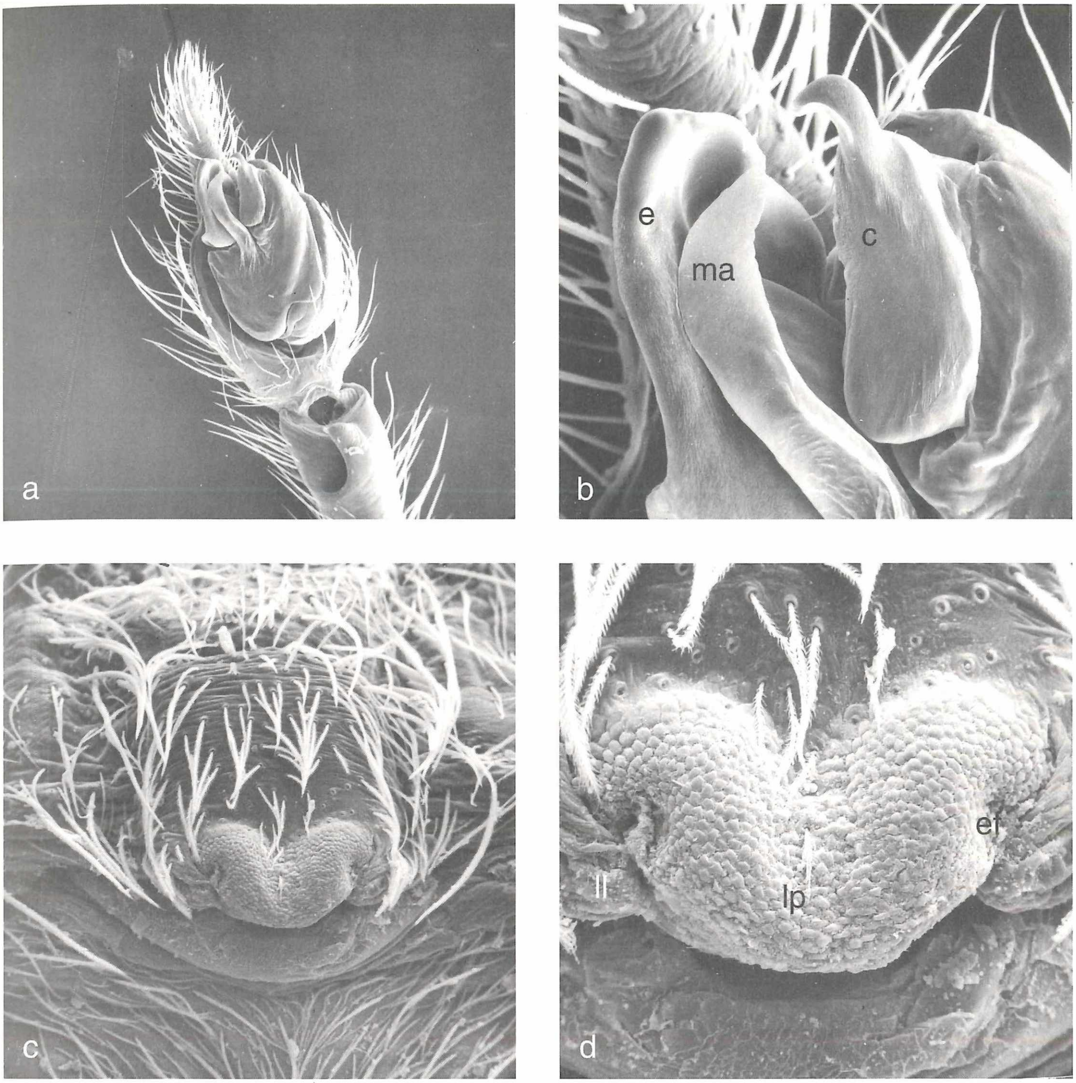

Figure 7. *Heidrunea irmleri*, n. sp., male: a) left palp, ventral view, 90x; b) same, detail of apex (c, conductor; e, embolus; ma, median apophysis), 450x; female: c) epigynum, ventral view, 180x; d) same (major magnification: median posterior lobe, lp; lateral lobes, ll; epigynal folds, ef), 450x.

### ***Heidrunea lobrita*, new species**

Figures 4 e,f

Types: Female holotype from igapó forest at Rio Tarumã Mirím, Amazonas, Brazil, November 25, 1976, J. ADIS, collected by an arboreal funnel trap, deposited in SMNK. Paratype: one female from the same locality of holotype, January 6, 1977, H. HÖFER, collected by an arboreal funnel trap, deposited in MCN (24063).

Etymology: The specific name is an arbitrary combination of letters.

Diagnosis: *Heidrunea lobrita* may be distinguished from females of *H. irmleri* and *H. arijana* by the subquadrangular border of the median posterior lobe (fig. 4e) in the female epigynum.

Male: Unknown.

Female: Coloration as in *H. irmleri*. Total length 4.30. Carapace 1.90 long, 1.50 wide. Clypeus 0.07, equal to the diameter of the AME. Anterior eye row 0.47 long and posterior eye row 0.80 long. Eye sizes and interdistances: AME 0.07, ALE 0.10, PME 0.10, PLE 0.10; AME-AME 0.02, AME-ALE 0.06, PME-PME 0.10, PME-PLE 0.16, ALE-PLE 0.18. MOQ length 0.17, front width 0.17, back width 0.27. Chelicerae 0.95 long with 3 promarginal and 4 retromarginal teeth. Abdomen 2.60 long, 1.80 wide.

Length of legs: I - femur 1.60/ patella 0.70/ tibia 1.20/ metatarsus 1.20/ tarsus 0.70/ total 5.40/ II - 1.55/ 0.65/ 1.10/ 1.10/ 0.65/ 5.05/ III - 1.50/ 0.55/ 1.00/ 1.20/ 0.65/ 4.90/ IV - 1.80/ 0.60/ 1.55/ 1.80/ 0.80/ 6.55. Leg spination: I femur p1-1-1, r0; tibia p1-1-0; II femur p1-1-1, r0; tibia p0-1-1; III femur p0-1-1-1, r0-1-1-1; IV femur p0-1-1, r0-1-1. Epigynum with subquadrangular median posterior lobe. Central groove of epigynum smaller than in *H. arijana* (fig. 4e). Spermathecae globose, with oval terminal receptaculae, projecting posteriorly. Copulatory ducts short. Fertilization ducts curved to the outer part (fig. 4f).

Variation: Four females: total length 3.30-4.30; carapace 1.55-2.00; femur I 1.30-1.60.

Distribution: Known only from the type locality in central Amazonia, Brazil.

Other material examined: Brazil, Amazonas, Rio Tarumã Mirím (igapó forest), 1 female, October 29, 1971, U. Irmler (SMNK); 1 female, December 4 - 28, 1971, U. Irmler (INPA).

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We thank Dr. J. Wunderlich and Dr. J. Adis for making available material and Dr. N. Platnick for loaning spiders of *Barrisca nanella* for comparison. We are grateful to Prof. Dr. L. Beck for organizing and to the German Academic Exchange Service (DAAD) for funding the journey and research period of the first author in Germany. We heartily thank Mr. Zibat of the „Abteilung für Elektronenmikroskopie“ of the university in Karlsruhe for making the scanning electron micrographs. Dr. C. Griswold and Dr. P. Sierwald reviewed the manuscript and made very valuable comments.

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**andrias, 13:** 81-98, 10 Figs, 3 Colour Plates; Karlsruhe, 30. 9. 1994

HUBERT HÖFER, ANTONIO D. BRESCOVIT & THIERRY GASNIER

# The wandering spiders of the genus *Ctenus* (Ctenidae, Araneae) of Reserva Ducke, a rainforest reserve in central Amazonia

**Abstract**

Seven species of wandering spiders belonging to the genus *Ctenus* were collected during an ecological inventory of spiders in a forest reserve in the Brazilian Amazon near Manaus. The males of *Ctenus crulsi* and *Ctenus villasboasi* are described for the first time and the females are redescribed. Males and females of *Ctenus amphora* and *Ctenus minor* are redescribed. *Ctenus planipes* is synonymized with *Ctenus minor*. Three species are described as new species: *Ctenus inaja*, *Ctenus manauara* and *Ctenus tapereba*. Colour patterns of the species are shown by colour photographs and described from living specimens to allow recognition and separation of species in the field. Informations about natural history, ecology and regional distribution of the species are added.

**Resumo**

**As aranhas errantes do gênero *Ctenus* (Ctenidae, Araneae) da Reserva Ducke, uma reserva de floresta tropical húmida na Amazônia central**

Sete espécies de aranhas do gênero *Ctenus* foram coletadas durante um levantamento ecologico de aranhas dentro de uma reserva florestal na Amazônia brasileira perto de Manaus. Os machos de *Ctenus crulsi* e *Ctenus villasboasi* são descritos pela primeira vez e as fêmeas são redescritas. Machos e fêmeas de *Ctenus amphora* e *Ctenus minor* são redescritos. *Ctenus planipes* é sinonimizado com *Ctenus minor*. Três novas espécies são descritas: *Ctenus inaja*, *Ctenus manauara* e *Ctenus tapereba*. Mostram-se padrões de coloração das espécies através de fotografias a cores e descrições de espécimens vivos para possibilitar reconhecimento e separação das espécies no campo. Informações sobre história natural, ecologia e distribuição regional são dadas.

**Kurzfassung**

**Die Laufspinnen der Gattung *Ctenus* (Ctenidae, Araneae) der Reserva Ducke, eines Regenwaldreservats in Zentralamazonien**

Während einer ökologischen Bestandsaufnahme der Spinnen in einem Regenwaldreservat bei Manaus in Zentralamazonien wurden sieben *Ctenus*-Arten gesammelt. Die Männchen von *Ctenus crulsi* und *Ctenus villasboasi* werden erstmals beschrieben und die Weibchen wiederbeschrieben. Männchen und Weibchen von *Ctenus amphora* und *Ctenus minor* werden wiederbeschrieben. *Ctenus planipes* wird synonymisiert mit *Ctenus minor*. Drei Arten werden erstmals beschrieben: *Ctenus inaja*, *Ctenus manauara* und *Ctenus tapereba*. Die Lebendfärbung der Arten wird im Text und durch Farbfotografien wiedergegeben, um die Unterscheidung der Arten im Feld zu ermöglichen. Vorläufige Kenntnisse zur Biologie, Ökologie und Biogeographie der Arten werden zusammengefaßt.

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## 1. Introduction

In 1991 we started an ecological field programm planned to study „Mechanisms maintaining high diversity in spider communities in the tropics" with an inventory of spider species on the ground, on tree trunks and in the canopy of a neotropical rainforest site (Reserva Ducke). Collecting was realized during 15 months by the mean of different trap types (pitfall traps, arboreal funnel traps, ground photoeclectors), by insecticidal canopy fogging and diurnal and nocturnal manual collecting in different strata.

For the purpose of a future study of coexistence of large wandering spiders in the lower strata of the rainforest we observed and collected the members of this guild during more than two years, principally at night with the aid of cap lamps. Altogether we collected fourteen species of Ctenidae and two species of *Ancylometes* (Pisauridae). Two species of the genus *Phoneutria* were frequently observed head down in the lower vegetation, but rarely on the ground. An undescribed species of the genus *Gephyroctenus* was collected on tree trunks, and *Enoploctenus* sp. and *Cupiennius* sp. were very abundant sitting on leaves of low plants. Two species of the genus *Centroctenus*, *C. ocelliventer* and *C.* sp., were observed most often in the lower vegetation and only rarely on the ground. The *Ctenus* species and both species of *Ancylometes* seem to be the real ground living species in Reserva Ducke, although they also appear in lower vegetation and on lower parts of tree trunks.

This paper is supposed to provide enough informations to recognize the *Ctenus* species in the field and thus can serve as a base for ecological studies in the central Amazon region. A future field study will concentrate on the question of how these seven morphologically very similar species co-occur in a given habitat.

Taxonomy and systematics of *Ctenus* are in a poor state, about 150 species have been described in the genus from the neotropics and certainly many of them will not remain as valid species in the genus after a sorrow revision. Unfortunately the type species of the genus, *Ctenus dubius* WALKENAER,1805 is lost and a generic revision, including redefinition and limitation of the genus is far from the range of our present work. We are conscient of problems describing new species in a genus that is not at all resolved. We therefore tried to examine all types of species which have been described for the Amazon area and made a collecting trip to Santarém (Pará), the type locality of several *Ctenus* species. By providing descriptions of the unknown males of two species and redescriptions of males and females described nearly a century ago, resolving a new synonymy and presenting a sorrow description of three new species we hope to contribute to a better understanding of the group. Including informations about habitats and regional distributions we hope to stimulate future taxonomic work.

## 2. Study area and Methods

Collections were made in the northern part of the „Reserva Florestal Adolfo Ducke“ of Instituto Nacional de Pesquisas da Amazônia (INPA), situated 26 km from Manaus at the highway Manaus-Itacoatiara (AM-010; 2°55'S, 59°59'W). Geology and botany of the reserve are described in GENTRY (1990). All collection sites are covered by non-inundated terra firme - forest. The intense study site of about 5 hectars is situated on a small plateau, appr. 1,5 km distant from the reserve station. Collections and observations were made in an area of about 10 hectars around this site and along the dirt road leading to the plateau. Collecting methods are described in HÖFER (1990) - ground photoeclectors and arboreal funnel traps, and in HÖFER et al. (1994) - canopy fogging.

Additional material came from várzea and igapó inundation forests near Manaus (HÖFER 1990) and the following terra firme areas near Manaus: „Reserva de Campina“ of INPA and reserve 1501 (Fazenda Esteio) of the „Projeto Dinâmica Biológica de Fragmentos Florestais“ (PDBFF, INPA/Smithsonian Institution). For comparison we used material collected in a dry forest and a cerrado area near Alter do Chão/Santarém and a terra firme forest near Santarém in Pará. Finally we checked the following collections to amplify the knowledge of distributional ranges of the species: BMNH, The Natural History Museum, London (P HILLYARD); CBF, Colección Boliviana de Fauna, La Paz (R. ALTAMIRANO); IBSP, Instituto Butantan, São Paulo (V. R. VON EICKSTEDT); IMTM, Instituto de Medicina Tropical, Manaus (P. BUHRNHEIM); INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus (C. MAGALHÃES); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E.H. BUCKUP); MCP, Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A.A. LISE); MNB, Museum für Naturkunde, Berlin (M. MORITZ); MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (A. TIMOTHEO DA COSTA); MZS, Museo Zoologico de La Specola, Firenze (S. MASCHERINI); MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo (J. L. LEME); SMNK, Staatliches Museum für Naturkunde, Karlsruhe (H. HÖFER); UA, Universidade do Amazonas, Manaus (N.O. AGUIAR).

Descriptions basically follow PECK (1981). All measurements are in millimeters. Photographs in colour plates were all made by H. HÖFER.

## 3. Descriptions of species

### *Ctenus amphora* MELLO-LEITÃO

Figures 1, 2; colour plate 1a-d

*Ctenus amphora* MELLO-LEITÃO, 1930: 64, figs 22, 23 (holotype from Cuminá River, Pará, Brazil, G. CRULS col., not examined, should be in MNRJ nr. 159, not localized, probably lost); 1936: 6, pr. 1, fig. 6; 1948: 174, figs 16-17 (description of male); ROEWER (1954: 647); BONNET (1956: 1274).

*Ctenus senex*: CAPORIACCO, 1948: 679 (in part, only two females, examined).

Note: The male described by MELLO-LEITÃO (1948) from many localities in Guiana was not examined. These records need a future confirmation.

Diagnosis: *Ctenus amphora* resembles *Ctenus minor* but differs in body size and details of leg spination and details of palpus and epigynum: the modified metatarsus IV with a great number of spinules on the prolateral side (fig. 2), the enlarged basal embolar projection with numerous teeth and the bilobed tip of the embolus on male palps (fig. 1a,b) and the anteriorly strongly invaginated epigynum with medianly originating lateral spurs (fig. 1c,d).

Description: Male (Reserva Florestal Adolfo Ducke, Manaus, Amazonas): Carapace reddish brown, pars thoracica pale brown around the dark brown thoracic groove; black rings around eyes. Legs brown, with ventral faces of coxae and femora lighter. Chelicerae reddish brown. Endites and labium greenish brown, lighter at tips. Sternum reddish brown with white spots at the middle and near lateral borders. Abdomen dark gray, dorsum with two median black spots and darker areas anteriorly and posteriorly. Venter dark gray with two yellowish white transverse longitudinal bands and a whitish central area.

Total length 17.50. Carapace 8.40 long, 6.80 wide. Clypeus 0.38, as wide as the AME diameter. Eye diameters and interdistances: AME 0.38, ALE 0.26, PME 0.56, PLE 0.52; AME-AME 0.22, AME-ALE 0.50, PME-PME 0.33, PME-PLE 0.65, AME-PLE 0.27, Ame-PME 0.12. MOQ length 1.02, front width 1.06, back width 1.40. Chelicerae with 3 promarginal and 5 retromarginal teeth.

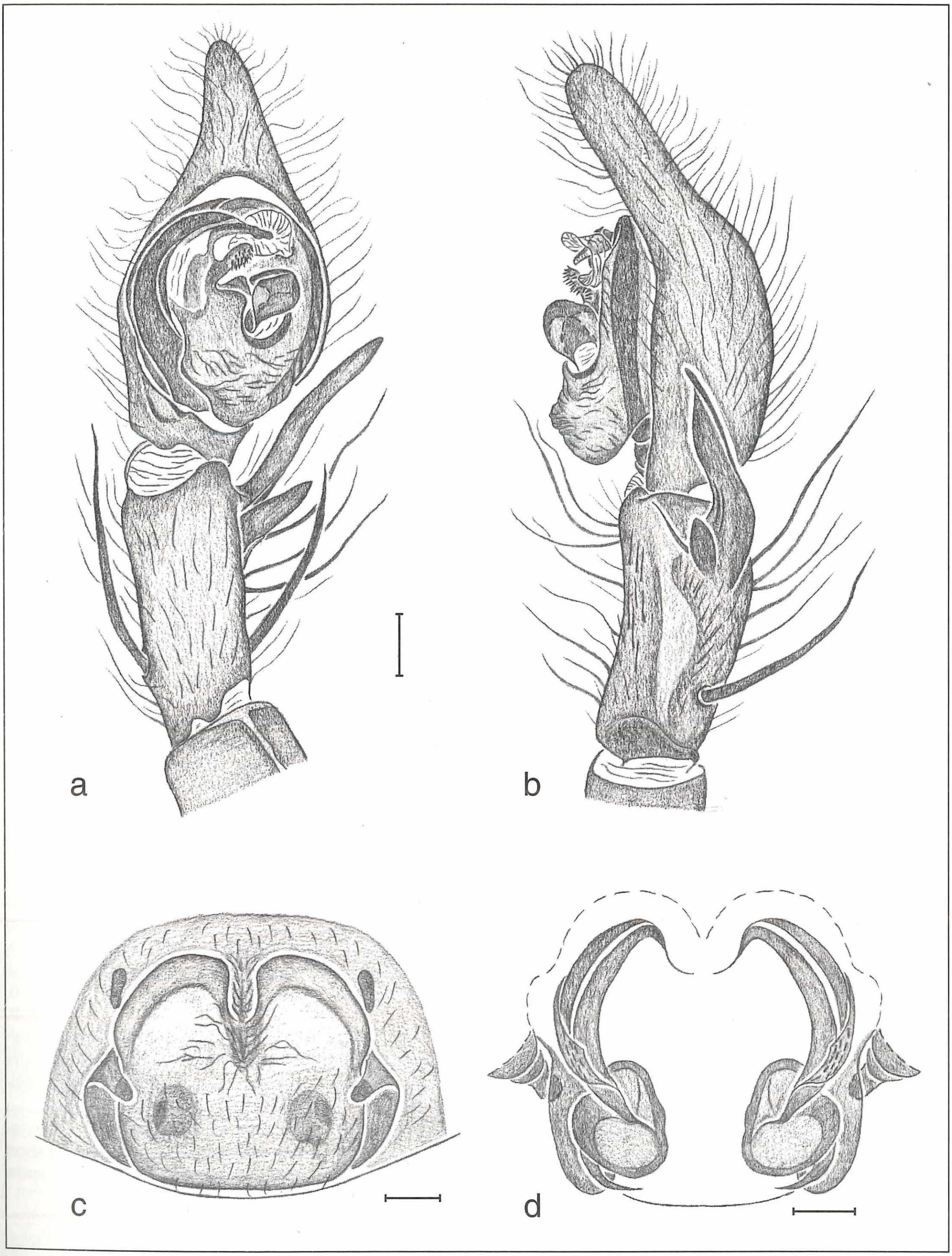

Figure 1. *Ctenus amphora* MELLO-LEITÃO: a) male palp, ventral view; b) retrolateral view; c) female epigyne, ventral view; d) dorsal view; all scale lines 0.25 mm.

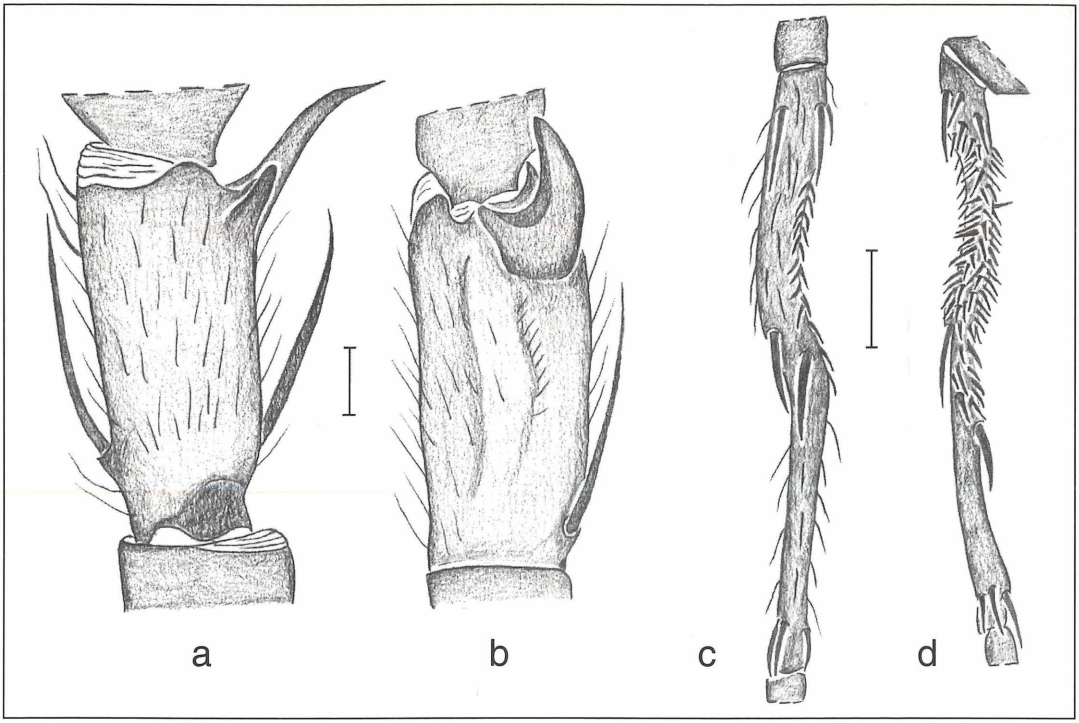

Figure 2. *Ctenus amphora* MELLO-LEITÃO, male: a) variation of palpal tibial apophysis, ventral; b) retrolateral; c) metatarsus IV, dorsal; d) prolateral.

Leg measurements: I -femur 9.80/ patella 4.10/ tibia 10.20/ metatarsus 9.60/ tarsus 3.20/ total 36.90/ II -9.40/ 3.60/ 9.00/ 8.60/ 2.80/ 33.40/ III -8.40/ 3.30/ 7.40/ 7.10/ 2.40/ 28.60/ IV -11.00/ 3.60/ 9.50/ 11.10/ 4.30/ 39.50. Leg spination: tibia I v2-2-2-2-2, p1-1-0, r1-1-0, II v2-2-2-2-2, p1-1-1, r1-1-1, III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-0, p1-1-1, r1-1-1, III -IV v2-2-2, p1-1-2, r1-1-2. Metatarsus IV modified, strongly sinuous at middle, with a large agglomeration of short and thick spinules on the prolateral side (fig. 2c,d). Retrolateral tibial apophysis of palp unequally bifid, ventral branch of which is short and conical and dorsal branch variabel, very long and sinuous (figs 1a, 2a) or moderately short, only slightly sinuous (figs 1b, 2b). Tegulum not projected ventrally, but with many sinuosities. Hyaline conductor enlarged and folded around the tip of the embolus. Median apophysis curved and short. Embolus enlarged at basis, bilobed at tip, with oval and dentate basal embolar projection (fig. 1a,b).

Female (same locality): Coloration basically as in male, except darker·carapace and the dorsally dark gray abdomen, with an orange anterior mark in the form of an inverted amphore.

Total length 18.80. Carapace 9.60 long, 7.60 wide. Clypeus 0.47, slightly wider than the AME diameter. Eye diameters and interdistances: AME 0.45, ALE 0.34, PME 0.62, PLE 0.60; AME-AME 0.30, AME-ALE 0.72, PME-PME 0.38, PME-PLE 0.85, ALE-PLE 0.35, AME-PME 0.12. MOQ length 1.08, front width 1.18, back width 1.55. Chelicerae with 3 promarginal and 5 retromarginal teeth.

Leg measurements: I -femur 7.50/ patella 4.00/ tibia 7.10/ metatarsus 6.30/ tarsus 1.60/ total 26.50/ II -7.40/ 3.70/ 6.40/ 6.00/ 1.70/ 25.20/ III -6.50/ 3.20/ 5.10/ 5.40/ 1.70/ 21.90/ IV -7.60/ 3.30/ 7.20/ 9.20/ 2.70/ 30.00. Leg spination: tibia I v2-2-2-2-2, p0, r0, II v2-2-2-2-2, p0-1-0, r0, III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-0, p0, r0-1-1, III -IV v2-2-2, p1-1-2, r1-1-2. Epigynal plate subquadrangular, invaginated anteriorly between ovoid lobes. Lateral spurs small, originating medianly and directed posteriomesially (fig. 1c). Internally with two large and subtriangular spermathecae, separated by their diameter. Copulatory ducts long, very large and curved. Fertilization ducts short, originating from retrolateral side of spermathecae (fig. 1d).

Variation: Ten males: total length 14.00-18.30; carapace 7.70-9.90; femora I 8.50-10.20; ten females: total length 13.40-18.80; carapace 7.10-9.60; femora I 4.70-7.50.

Description of living specimens: Males: basic colour dark brown to black, often appearing lighter and sometimes spotted through the cover of light hairs. Carapace dark brown, pars cephalica covered by white hairs forming a V-shaped mark narrowing posteriorly, eyes surrounded black, pars thoracica brown, thoracic groove darker (plate 1a). Legs dark brown, dorsally covered by whitish hairs. Retrolateral-dorsal side of curved part of metatarsus IV white. Chelicerae reddish brown. Endites and labium greenish brown, apically lighter. Sternum reddish brown with yellowish white spots at the middle and near borders. Abdomen dark grayish brown to black, dorsum with a distinct amphore-like pattern (plate 1a) or reduced to a narrow longitudinal median white band extending over more than half of the abdomen, ending in two laterally directing tails. Anterior to the tails a pair of white spots. Venter black with one pair of white spots.

Females: Basic colour dark brown to black. Carapace black, with a light median band, widest behind eyes, narrowing constantly until reaching the hind border (plate 1b). Thoracic groove dark. Legs dark brown, with obscure light patches. Tibiae and metatarsi I and II with a subdistal dorsolateral white spot (plate 1c). Chelicerae, endites, labium and sternum reddish brown. Abdomen black, dorsum with a very typical pattern of an inverted amphore (plate 1b,d): starting on anterior border with a narrow median white band which opens to an inverted U or V, from inside of the U continues the narrow white band, enlarges to an oval, than becomes narrow again and ends in a broad rhomb somewhat behind the middle of the abdomen. Abdomen laterally with obscure brown patches. Venter with a black central area, bordered by a V-shaped yellowish white mark converging posteriorly. One median and one lateral pair of larger white spots behind the epigastric furrow.

Variation: Males and females can be less dark, the typical amphore-like pattern of the female may then be reduced, as described for males (compare plate 1b and 1c). The white spots on the front legs may disappear. The median mark on the venter of abdomen can be reduced to rows of white spots.

Distribution: Guiana and north of Brazil.

Material examined: Guiana, 1 female, Aug. 1971, Lyes col. (IBSP 2623); Dora, 1 female and 1 immature female, Apr. 27, 1936, Romiti col. (MZS);

Brazil, Amazonas, São Gabriel da Cachoeira (Maturacá), 1 male, 1 female, Oct. 13, 1990, A. A. Lise col. (MCP 1239); (Morro dos Seis Lagos), 1 male, 1 female, A. A. Lise col. (MCP 1179); Presidente Figueiredo (Usina Hidrelétrica de Balbina), 2 females, Eq. Butantan col. (IBSP); Manaus (campus of INPA), 1 female, 1981, U. Barbosa col. (INPA); 1 male, Mar. 5, 1992, C. Martius col. (INPA); 2 females, Jan. 28, 1992, A. A. Lise & A. B. Bonaldo col. (MCP 1488; 1489); 1 male, Oct. 8, 1990, H. Höfer col. (SMNK 319); (campus of University of Amazonas), 1 female, May 22, 1992, N. O. Aguiar col. (UA); 1 male, Jan. 21, 1994, M. E. Oliveira col. (IMTM); Fazenda Esteio (Smithsonian reserve at km 41), 2 females, R. S. Vieira col. (INPA); 1 male, 1 female, Jan. 18, 1994, T. Gasnier col. (INPA); Reserva de Campina, 2 males, 11 females, Jan. 30, 1994, A. D. Brescovit & T. Gasnier col. (MCN 25266; INPA); Reserva Ducke, 1 female, Feb. 19-24, 1992, A. A. Lise col. (MCP 1686); 1 female, Aug. 25, 1992, M. W. Oliveira & S. Egler col. (IMTM 90); 1 female, Aug. 7, 1990, F. B. Apolinário col. (INPA); 1 female, Jul. 1993, Clemens col. (INPA); 1 male, without date or collector (INPA); 1 male, 1 female, Dec. 1993, T. Gasnier col. (MCN 25264; 25265); 10 males, 3 females, Jan. 18-19, A. D. Brescovit col. (BMNH; MNB; IBSP; MCN 25262; 25263; 25267); 1 female, Sept. 4, 1991 (SMNK 506); 1 female, Mar. 23, 1992 (SMNK 1139); both collected by H. Höfer & T. Gasnier; 2 males, 4 females, Feb. 22-23, 1992 (SMNK 1140); 1 female, Jul. 31, 1991 (SMNK 1141); 3 males, 7 females, Aug. 17-24, 1991 (MCN 21489); 1 male, 1 female, Aug. 6-9, 1992 (MCN 22298); 3 males, Jan. 17-18, 1994 (SMNK 1142), all collected by H. Höfer & A. D. Brescovit; 2 males, Febr. 7, 1994, H. Höfer col. (INPA).

## ***Ctenus villasboasi*** **Mello-Leitão**

Figures 3, 4a; colour plates 1e,f, 2a,b

*Ctenus villasboasi* Mello-Leitão, 1949: 11, fig. 12 (female holotype from confluence of Culuene and Xingu rivers, Mato Grosso, Brazil, J. C. Mello-Carvalho col., deposited in MNRJ 48452, examined.); Roewer (1954: 656); Eickstedt (1983a: 164, figs 3-6).

Diagnosis: *Ctenus villasboasi* is a distinct species easily recognized by the basic coloration and ventral white markings on the coxae I and on apex of the sternum (plate 2a; see also Eickstedt 1983a, fig. 4), the strongly curved embolus without a basal embolar projection (fig. 3a) in the male palp and the strongly developed lateral spurs on the female epigynum (see Eickstedt 1983a, figs 5-6).

Description: Male (Reserva Florestal Adolfo Ducke, Manaus, Amazonas): Carapace uniform reddish brown, with brown thoracic groove. Black rings around eyes. Legs and chelicerae reddish brown. Tibiae I to IV ventrally with broad white marks (as in females: plate 2a). Endites greenish brown and labium darkened, lighter at tip. Sternum reddish brown, distally with a white horizontal band, which continues ventrally on the first coxae (plate 2a; see also Eickstedt 1983a, fig. 4). Abdomen greenish gray, dorsum with two pairs of dark spots. Venter black, with two yellow transverse longitudinal bands and two white marks anterior to genital groove and two spots behind the groove.

Total length 19.60. Carapace 10.60 long, 8.10 wide. Clypeus 0.57, slightly wider than the AME diameter. Eye diameters and interdistances: AME 0.53, ALE 0.27, PME 0.60, PLE 0.58; AME-AME 0.22, AME-ALE 0.55, PME-PME 0.22, PME-PLE 0.55, AME-PLE 0.21, AME-PLE 0.09. MOQ length 1.17, front width 1.22, back width 1.38. Chelicerae with 3 promarginal and 4 retromarginal teeth plus one small denticle.

Leg measurements: I -femur 11.80/ patella 4.40/ tibia 12.50/ metatarsus 11.80/ tarsus 3.00/ total 43.50/ II -11.50/ 5.10/ 11.30/ 11.10/ 2.80/ 41.80/ III -10.00/

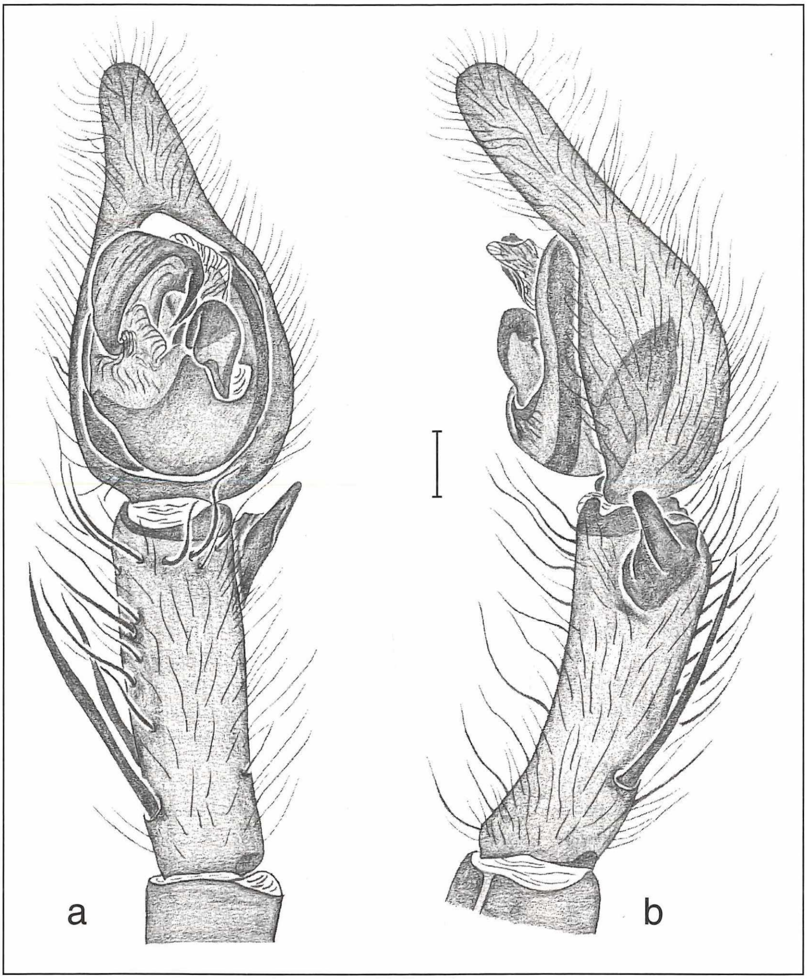

Figure 3. *Ctenus villasboasi* MELLO-LEITÃO: a) male palp, ventral view; b) retrolateral view.

4.00/ 8.20/ 8.70/ 2.50/ 33.40/ IV -12.50/ 4.00/ 11.30/ 9.60/ 2.60/ 40.00. Leg spination: tibia I v2-2-2-2-2, p1-1-1, r1-1-0, II v2-2-2-2-2, p1-1-1, r1-1-1, III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I v2-2-0, p1-0-1, r1-0-1, II v2-2-0, p1-1-1, r1-1-0, III v2-2-2, p1-1-2, r1-1-2, IV v2-2-2, p1-1-1-2, r1-1-1-1-2. Metatarsus IV not modified. Retrolateral tibial apophysis simple, very enlarged at basis, with conical tip (fig. 3). Tegulum not projected and lacking sinuosities on the ventral part. Hyaline conductor large, covering partially the tip of the embolus. Median apophysis curved and distally prolongated. Embolus strongly enlarged at middle, strongly curved distally, with acute tip. Hyaline membrane present at the base of the embolus (fig. 3).

Female: Described and figured by MELLO-LEITÃO (1949) and EICKSTEDT (1983a). Epigynum: epigynal plate subrectangular, with anterior parallel ovoid lobes. Lateral spurs strongly developed, horn-shaped, directed posteriorly (see EICKSTEDT 1983a, figs 5-6). Internally with two voluminous and suboval spermathecae, sulcated subdistally and almost touching. Copulatory ducts short and covered by the apex of the spermathecae. Fertilization ducts long, very enlarged at basis, originating from the base of the spermathecae (fig. 4a).

Variation: Ten males: total length 18.60-23.50; carapace 10.50-12.40; femora I 8.80-12.50. Ten females: total length 18.60-23.50; carapace 10.50-12.40; femora I 8.80-12.50.

Description of living specimens from Reserva Ducke: Females: carapace uniform dark brown to black. Abdomen dorsally with a very characteristic orange-brown or reddish-brown coloration, lightest anterior-laterally. Anterior central area black and a pair of black spots at middle of dorsum (plate 1e,f).

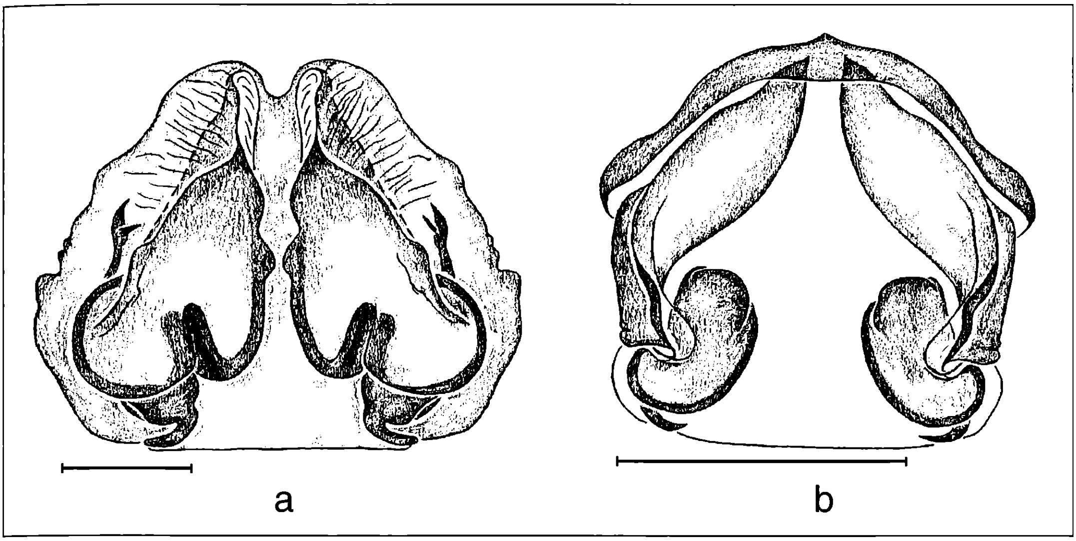

Figure 4. a) *Ctenus villasboasi* Mello-Leitão, female epigyne, dorsal view; b) *Ctenus minor* Pickard-Cambridge, female epigyne, dorsal view.

Males: Basic colour light brown. Carapace covered with yellowish hairs. Abdomen light brown, dorsum with two to three pairs of black spots behind the middle and a central black area before the middle (plate 2b). Both males and females always present the characteristic ventral markings on sternum, coxae I and tibiae I to IV (plate 2a).

Distribution: Ecuador and north of Brazil.
Material examined: Ecuador, Los Tayos, 4 females, Jul. 7-11 Aug. 2-3, 1976, P. Ashmole col. (IBSP 4303-4306);
Brazil, Amazonas, Manaus, Reserva Ducke, 2 males, 2 females, Aug. 14-24, 1991, A. D. Brescovit col. (MCN 21451; 21452; 21490); 1 female, Sept. 22, 1991, H. Höfer col. (SMNK 1143); 2 females, Aug. 6-9, 1992, A. D. Brescovit col. (MCN 22301); 1 female, Mar. 18, 1992, H. Höfer col. (SMNK 1144); 1 female, Jul. 19, 1991, H. Höfer col. (SMNK 416); 1 female, Sept. 1991, H. Höfer col. (SMNK 415); 3 males, 4 females, Jul. 23-Dec. 6, 1993, T. Gasnier & H. Höfer col. (MCN 25269; SMNK 1145; INPA; BMNH); 2 males, 5 females, Jan. 18-19, 1994, A. D. Brescovit & H. Höfer col. (MCN 25270; SMNK 1146; INPA); (igarapé Acará), 1 female, 1992, T. Gasnier col. (with eggsac) (INPA); road AM 10, km 32, 1 female, Feb. 21, 1991, M. Gordo col. (IMTM 59); Reserva de Campina, 1 male, Jan. 30, 1994, A. D. Brescovit col. (MCN 25268); Fazenda Esteio (Smithsonian Reserve at km 41), 2 females, Jan. 12, 1994, A. D. Brescovit col. (MCN 25271; 25272); Coari, Urucú River, 1 female, May 12, 1991, M. E. Oliveira col. (UA); Pará, Belém, 1 female, P. Vanzolini col. (MZSP 5658).

### ***Ctenus crulsi* Mello-Leitão**

Figure 5; colour plates 2c-e

*Ctenus crulsi* Mello-Leitão, 1930: 63, figs 20-21 (female holotype from Cuminá River, Pará, Brazil, G. Cruls col., deposited in MNRJ 166, examined); 1936: 7, pr. 1, fig. 5; Roewer (1954: 649); Bonnet (1956: 1278).

Diagnosis: Males of *Ctenus crulsi* strongly resemble those of *Ctenus manauara*, but may be distinguished by the size and details of the genitalia: the acute embolus and the bifid retrolateral tibial apophysis (fig. 5a,b) of the male palp. Females differ from other species by details of coloration and genitalia: the anteriorly bipartite apex of ovoid lobes and the subbasally originating lateral spurs (fig. 5c) on the epigynum.
Description: Male (Reserva Florestal Adolfo Ducke, Manaus, Amazonas): Carapace light brown with obscure lateral stripes; black rings around eyes. Legs brown, with ventral faces lighter and distal articles greenish gray. Chelicerae brown. Endites, labium and sternum orange. Abdomen light brown, dorsum with four median black spots and black anterio-lateral borders. Venter with a subtriangular light brown central area.
Total length 15.30. Carapace 8.20 long, 6.30 wide. Clypeus 0.45, as wide as the AME diameter. Eye diameters and interdistances: AME 0.45, ALE 0.23, PME 0.50, PLE 0.47; AME-AME 0.16, AME-ALE 0.52, PME-PME 0.26, PME-PLE 0.47, AME-PLE 0.18, AME-PLE 0.12. MOQ length 0.92, front width 1.00, back width 1.20. Chelicerae with 3 promarginal and 4 retromarginal teeth plus three small denticles.

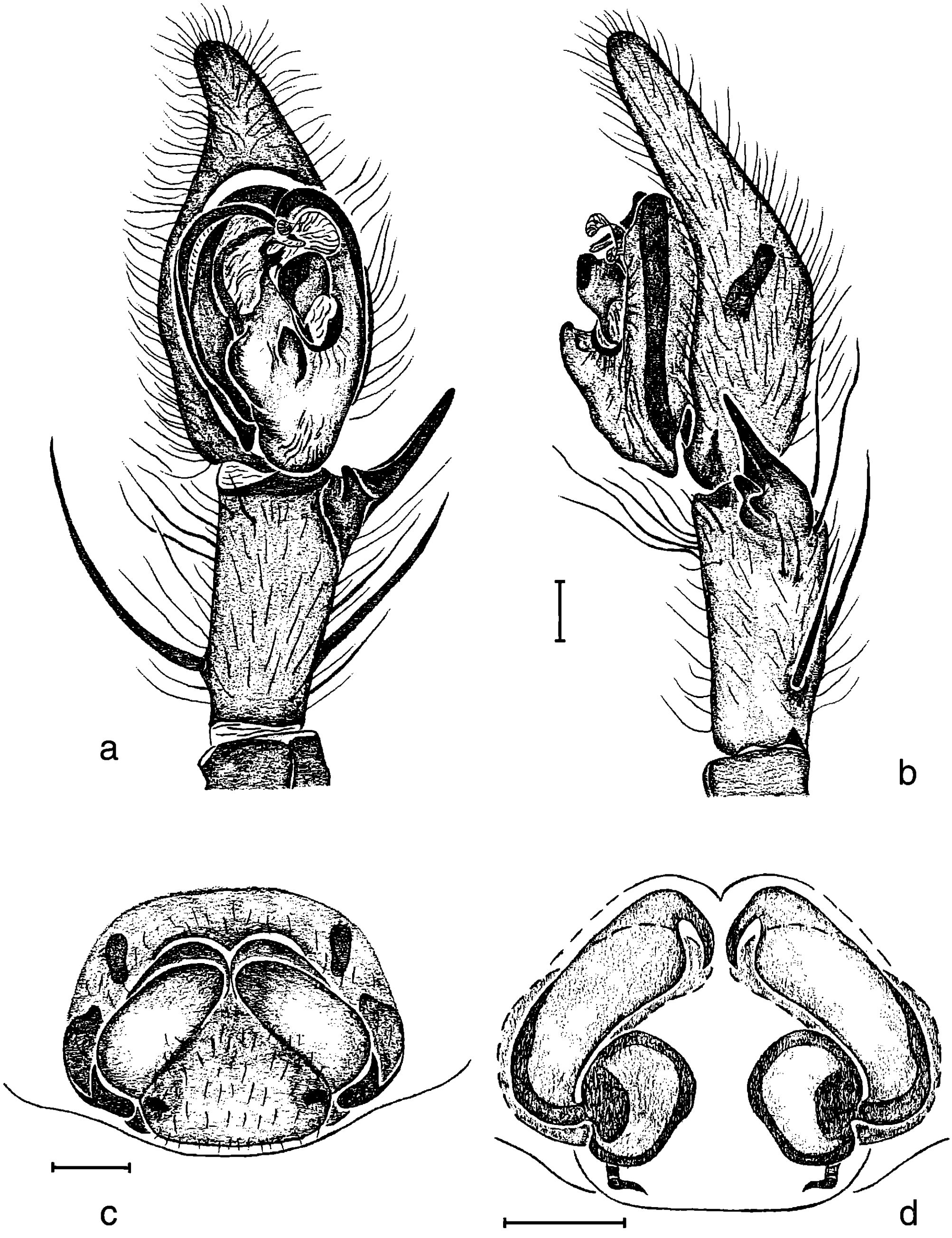

Figure 5. *Ctenus crulsi* MELLO-LEITÃO: a) male palp, ventral view; b) retrolateral view; c) female epigyne, ventral view; d) dorsal view.

Leg measurements: I -femur 9.60/ patella 3.40/ tibia 9.70/ metatarsus 10.00/ tarsus 3.10/ total 35.80/ II -9.20/ 3.20/ 8.90/ 9.60/ 2.70/ 33.60/ III -8.20/ 3.00/ 7.00/ 8.20/ 2.10/ 28.50/ IV -10.00/ 3.20/ 8.50/ 13.30/ 3.00/ 38.00. Leg spination: tibia I v2-2-2-2-2, p1-1-0, r1-1-0, II v2-2-2-2-2, p1-0-1, r1-1-1, III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I v2-2-0, p1-1-1, r1-1-1, II v2-2-0, p1-0-1, r1-1-1, III v2-2-2, p1-1-2, r1-1-2. Metatarsus IV not modified. Palpal tibiae with a bifid retrolateral apophysis, ventral branch short and with rounded tip, dorsal branch elongated and acute, with apex very distant from cymbium (fig. 5a,b). Tegulum directed basally and ventrally, with a distinct distal projection (fig. 5a,b). Hyaline conductor large, partially covering the tip of the embolus. Median apophysis short and rounded. Embolus enlarged basally, forming a mesial groove, narrowed and conical at tip, with a laminar, subrectangular basal embolar projection, dentate at tip (fig. 5a).

Female (same locality): Carapace darker than in male, with a yellow median band; thoracic groove brown. Legs reddish brown with dispersed greenish gray bands. Chelicerae reddish-brown. Endites and labium orange, white at tips. Abdomen brown, dorsum with a folium-like yellow band. Venter with two white transverse longitudinal bands and a dark brown, almost black central area.

Total length 14.40. Carapace 7.00 long, 5.70 wide. Clypeus 0.37, about two-thirds the diameter of the AME. Eye diameters and interdistances: AME 0.45, ALE 0.26, PME 0.52, PLE 0.50; AME-AME 0.22, AME-ALE 0.47, PME-PME 0.28, PME-PLE 0.62, ALE-PLE 0.25, AME-PLE 0.16. MOQ length 1.00, front width 1.02, back width 1.21. Chelicerae with 3 promarginal and 5 retromarginal teeth.

Leg measurements: I -femur 6.00/ patella 3.00/ tibia 5.70/ metatarsus 5.20/ tarsus 1.70/ total 21.60/ II -5.80/ 2.70/ 5.00/ 4.80/ 1.50/ 19.80/ III -5.10/ 2.10/ 3.70/ 4.70/ 1.50/ 17 10/ IV -6.40/ 2.50/ 5.40/ 8.20/ 1.90/ 24.40. Leg spination: tibia I v2-2-2-2-2, p0, r0, II v2-2-2-2-2, p0-1-0, r0, III v2-2-2, p1-1-0, r1-1-0, IV v2-2-2, p1-1-1, r1-1-1; metatarsus I -II v2-2-2, p0, r0, III v2-2-2, p1-1-2, r1-1-2, IV v2-2-2, p1-1-2, r1-1-1-2. Epigynal plate with marked, oblique ovoid lobes, bipartite anteriorly. Lateral spurs originating subbasally, elongated, rounded at tip, directed mesially and sulcated posteriorly (fig. 5c). Internally with two circular spermathecae, separated by half their diameter. Copulatory ducts long and wide, narrowed and curved distally. Fertilization ducts narrow and long, originating from basis of spermathecae (fig. 5d).

Variation: Ten males: total length 13.60-17.50; carapace 7.60-8.90; femora I 8.70-9.80; ten females: total length 13.20-18.60; carapace 6.20-7.70; femora I 5.20-6.40. The bipartite part on the apex of the ovoid lobes on the female epigyne is quite variable, the anterior rim sometimes totally covering the posterior rim.

Description of living specimens from Reserva Ducke: Males and females: Basic colour brown. Carapace dark brown, light brown hairs behind the eyes and forming a longitudinal straight median line, broader around the dark thoracic groove, not reaching hind border of carapace (plate 2 c-e). Fine light lines diverging from the median line to the lateral borders. Coloration often less conspicuous. Legs dark brown, in females femora dorsally with light brown patches (plate 2c,d), in males tibiae lighter than femora (plate 2e). Chelicerae dark brown. Abdomen light brown, laterally with obscure light patches, dorsum with a light folium-like pattern consisting of a string of triangles reaching the spinnerets and bordered by black coloration (plate 2c,e). Some females present only a narrow white line instead of the folium, sometimes starting on the carapace behind the eyes and continuing until the spinnerets. Some females present the combination of the two color variations (plate 2d).

Distribution: States of Amazonas, Pará and Rondônia, Brazil.

Material examined: Brazil, Amazonas, Tefé (Solimões River), 1 female, Nov. 1952, HOGGE & JOÃO col. (IBSP 850); Coari, (Urucú river), 3 females, 1992, M. E. OLIVEIRA col. (UA); 1 male, M. E. OLIVEIRA col., May 11-18, 1991 (UA); Presidente Figueiredo (Usina Hidrelétrica de Balbina), 3 females, Eq. Butantan col. (IBSP); 1 female, Jun. 14, 1990, J. VIDAL col. (MCN 19848); 1 male, Apr. 18, 1984 (UA); 1 female, Jul. 1972, W. BÜCHERL col. (IBSP 2758); Manaus, Fazenda Esteio (Smithsonian reserve at Km 23), 2 females, Febr. 4, 1986, Mar. 25, 1987, B. C. KLEIN col. (INPA); (Smithsonian reserve at Km 41), 4 females, R. S. VIEIRA col. (INPA); 1 male, 7 females, Jan. 12-13, 1994, T. GASNIER & A. D. BRESCOVIT col. (SMNK 1147; INPA; MCN 25273); Tarumã Mirím river (Igapó), 2 females, Febr. 25-September 11, 1987, H. HÖFER col. (SMNK 317; 318); Reserva de Campina, 2 males, 1 female, Jan. 1, 1994, A. D. BRESCOVIT col. (MCN 25274; 25275); (Campus INPA), 1 female, Febr. 1985, M. YAMAKOSHI col. (IBSP 3813); Reserva Ducke, 1 male, Jan. 26, 1985, M. YAMAKOSHI col. (IBSP 3818); 1 female, Dec. 1992, M. MARTINS col. (IMTM); 6 females. Aug. 6-9, 1992, A. D. BRESCOVIT col. (MCN 22296); 1 male, 2 females, Jul. 31-Aug. 2, 1991, H. HÖFER col. (SMNK 410, 935, 936); 1 female, Jul. 30, 1971, J. BECKER col. (MCN 25277); 2 females, Aug.-Sep. 1993, E. WOLLSCHEID & I. CURDT col. (INPA); 3 males, 10 females, May-Dec. 1993, T. GASNIER & B. GUTZMANN col. (INPA; MCP); 3 males, 7 females, Jan. 18-19, 1994, A.D. BRESCOVIT col. (BMNH; MNB; MCN 25276); 1 female, Oct. 4, 1990 (SMNK 1148); 2 females, Aug. 7-24, 1991 (MCN 21491); 2 females, Febr. 22-23, 1992 (INPA); 1 male, 2 females, Mar. 17-26, 1992 (SMNK 1149); 2 males, 1 female, Aug. 6-9, 1992 (MCN 22299; 22300; 22285), all collected by H. HÖFER & A. D. BRESCOVIT; Pará, Cuminá River, 1 female, G. CRULS col. (MNRJ 166, holotype); Carajás (Serra Norte), 1 female, Nov. 1984, R. J. R. MORAES col. (IBSP 4177); Belém, 1 female, Aug. 8, 1962, K. LENKO col. (MZSP 11945); 1 male, Aug. 1966, P. VANZOLINI col. (MZSP 5659); Gurupi River, 2 females, 1963, B. MALKIN col. (MZSP 3389; 3350); Trombetas River (Jacaré Island), 1 female, Sept. 29-Oct. 13, 1965, Eq. CDZ col. (MZSP 5690); Biological Reserve of Trombetas river, 2 females (both with egg-sac), Aug. 29, 1979, J. GRAZIA col. (MCP); Tucuruí (Usina Hidrelétrica de Tucuruí), 2 males, 2 females, Jul.-Aug.

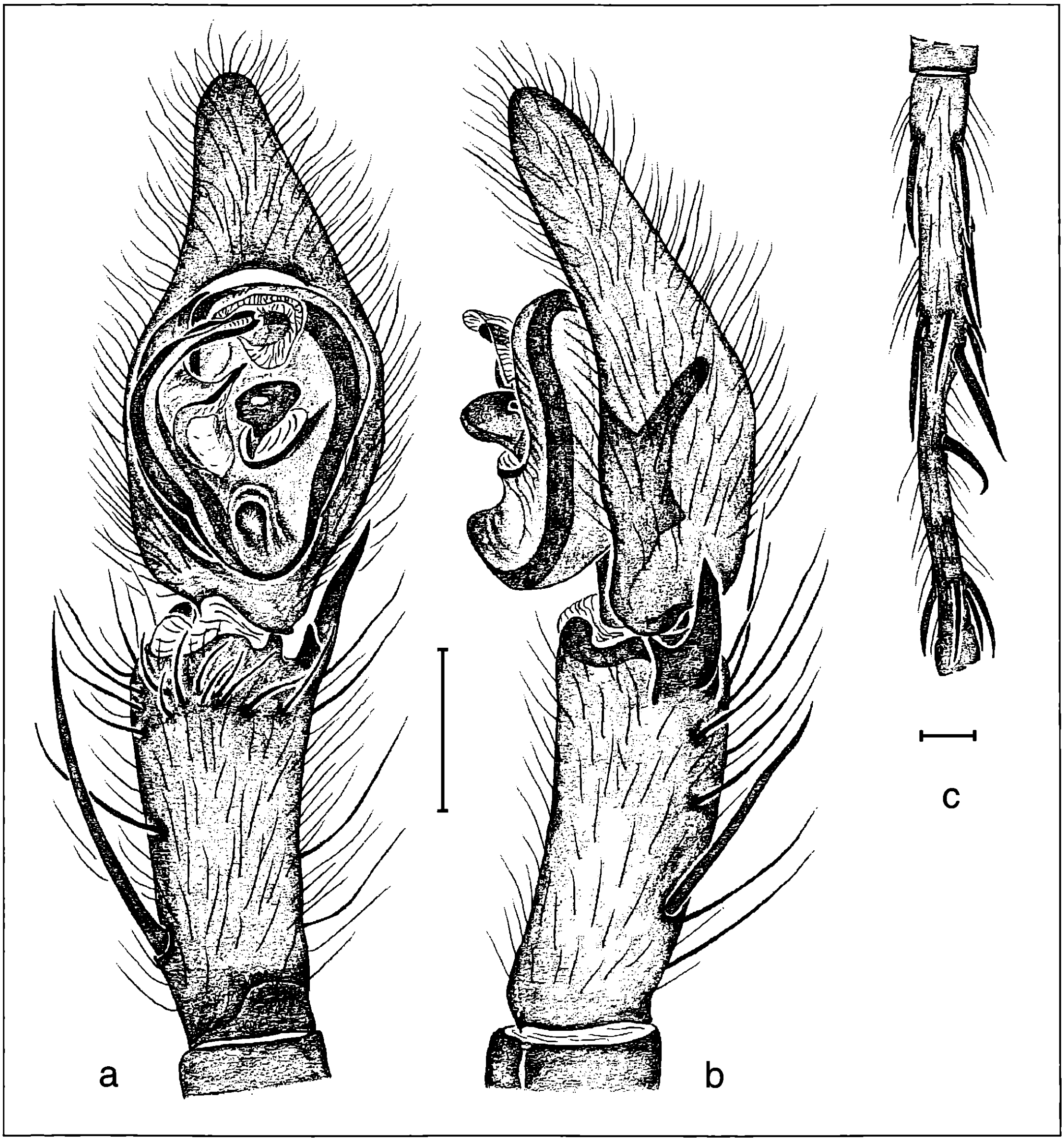

Figure 6. *Ctenus minor* PICKARD-CAMBRIDGE: a) male palp, ventral view; b) retrolateral view; c) male metatarsus IV, dorsal.

1984, Eq. Butantan col. (IBSP 5418; 5419; 5348; 5349); Rondônia, near Porto Velho (Usina Hidrelétrica de Samuel), 2 females, Eq. Butantan col. (IBSP).

### *Ctenus minor* PICKARD-CAMBRIDGE
Figures 4b, 6

*Ctenus minor* PICKARD-CAMBRIDGE, 1897: 83, pr. 3, fig. 4c (female holotype from Santarém, Pará, Brazil, 1896, F. O. PICKARD-CAMBRIDGE col., deposited in BMNH 1896.12.13.100, not examined); ROEWER (1954: 652); BONNET (1956: 1285); EICKSTEDT (1983b: 176, figs 3, 7-8); PLATNICK (1989: 501).
*Ctenus planipes* PICKARD-CAMBRIDGE, 1897: 84, pr. 3, fig. 6b (male holotype from Santarém, Pará, Brazil, 1896, F. O. PICKARD-CAMBRIDGE col., deposited in BMNH 1896.12.13.101, examined); ROEWER (1954: 654); BONNET (1956:1287). New synonymy.

Diagnosis: *Ctenus minor* resembles *Ctenus amphora* but differs in size and details of the genitalia: the conic apex of the basal embolar projection (fig. 6a) and the projected tegulum (fig. 6b) of the male palp, the epigynal plate is not invaginated anteriorly and the lateral spurs originate subdistally (see EICKSTEDT 1983b, fig. 8).

Description: Male (Alter do Chão, Santarém, Pará): Carapace yellow, with gray paramedian longitudinal bands, darker posteriorly; black rings around eyes; a cluster of fine white setae behind the posterior eye row and next to thoracic groove. Legs orange, greenish gray distally on femora, patellae and tibiae; white scopulate setae prolaterally on legs I and II. Chelicerae orange. Endites and labium orange, yellow at tips. Abdomen greenish gray, dorsum with black anterior border and a yellow anterior dorsal spot. Venter light brown and black around the spinnerets.

Total length 10.50. Carapace 5.40 long, 4.50 wide. Clypeus 0.27, about one third smaller than the diameter of AME. Eye diameters and interdistances: AME 0.34, ALE 0.23, PME 0.37, PLE 0.37; AME-AME 0.12, AME-ALE 0.35, PME-PME 0.25, PME-PLE 0.35, AME-PLE 0.15, AME-PME 0.08. MOQ length 0.58, front width 0.75, back width 0.87 Chelicerae with 3 promarginal and 4 retromarginal teeth and three small denticles.

Leg measurements: I -femur 5.80/ patella 2.30/ tibia 5.80/ metatarsus 5.50/ tarsus 2.30/ total 21.70/ II -5.60/ 2.30/ 5.50/ 5.40/ 2.10/ 20.90/ III -5.30/ 2.00/ 4.70/ 4.10/ 1.60/ 17.70/ IV -6.60/ 2.10/ 6.00/ 7.00/ 2.70/ 24.40. Leg spination: tibia I -II v2-2-2-2-2, p1-1-0, r1-1-0, III v2-2-2, p1-1-0, r1-1-0; metatarsus I v2-2-2, p0-1-1, r1-1-0, II v2-2-2, p1-1-0, r1-1-0, III v2-2-2, p1-1-2, r1-1-1-2, IV v2-2-2, p1-1-2, r1-1-2-2-2-1-1. Metatarsus IV modified, sinuous in the distal half, with a single heavy spine on prolateral side, which is curved at tip and other heavy spines (fig. 6c). Palpal tibia with a bifid retrolateral apophysis, ventral branch short and conical, dorsal branch slightly elongated, straight, triangular at tip (fig. 6b). Tegulum projected ventrally, with rounded apex (figs 6 a, b). Hyaline conductor large, enwrapping the tip of the embolus only apically. Median apophysis curved and short. Embolus narrow, sulcated and invaginated at tip, with a conical basal embolar projection (fig. 6a).

Female: Described and illustrated by PICKARD-CAMBRIDGE (1897) and EICKSTEDT (1983b). Coloration basically as in male, but lacking the white setae behind the posterior eye row and the abdomen light gray to dark gray, presenting a posterior black spot. Epigynum: epigynal plate subquadrangular, with an anterior subtriangular projection between ovoid lobes. Small elongated subdistal lateral spurs, directed posteriomesially (see EICKSTEDT 1983b, fig. 8). Internally with two ovoid, apically projected spermathecae, separated by more than their diameter. Copulatory ducts long, very enlarged anteriorly. Fertilization ducts short, conical, originating from basis of spermathecae (fig. 4b).

Variation: Ten males: total length 9.00-10.50; carapace 5.00-5.50; femora I 5.20-6.00; retromarginal teeth 4-5; Ten females: total length 9.00-14.30; carapace 4.00-5.50; femora I 3.20-3.30, retromarginal teeth 4-5.

Distribution. North of Brazil.

Material examined: Brazil, Amazonas, São Gabriel da Cachoeira (Morro dos Seis Lagos), 1 female, Sept. 28-Oct. 3, 1990, A. A. LISE col. (MCP 1181); Presidente Figueiredo (Usina Hidrelétrica de Balbina), 1 female, 1 immature, Eq. Butantan col. (IBSP); Manaus, Reserva de Campina, 1 female, Dec. 3, 1975, L. P. ALBUQUERQUE col. (INPA); 26 males, 31 females, Jan. 30, 1994, A. D. BRESCOVIT & T GASNIER col. (SMNK 1150; MCN 25261; INPA); Reserva Ducke, 2 males, 1 female, Apr. 3, 1990, J. VIDAL col. (MCN 19886, 19888); Pará, Santarém (near airport), 5 males, 21 females, Jan. 28, 1994, A. D. BRESCOVIT & H. HÖFER col. (SMNK 1151; MCN 25259); Ponta de Pedra, 1 male, 1 female, Jan. 25, 1994, H. HÖFER col. (MCN 25258); Alter do Chão, 75 males, 65 females, Jan. 26-28, 1994, A. D. BRESCOVIT & H. HÖFER col. (SMNK 1152; INPA; BMNH; MNB; IBSP; MCP; MCN 25256, 25257, 25260).

### *Ctenus manauara* new species

Figures 7, 8a,b; colour plate 3a,b

Types: Male holotype from Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil, January 19, 1994, A. D. BRESCOVIT col., deposited in MCN 25250. Paratypes: one male, SMNK 959, from same locality and collector, January 1, 1994; one female, SMNK 1010, from same locality, August 7, 1992, H. HÖFER col.; one female, MCN 25254, from Fazenda Esteio (Smithsonian reserve at km 41), Manaus, Amazonas, Brazil, January 12, 1994, A. D. BRESCOVIT col.; one male and one female, INPA, from Reserva de Campina, Manaus, Amazonas, Brazil, January 30, 1994, A. D. BRESCOVIT col.

Etymology: The specific name originates from the Brazilian Portuguese and means „who lives in Manaus"

Diagnosis: Males of *Ctenus manauara* resemble males of *Ctenus crulsi*, but may be distinguished by the smaller body size and the curved and lobed tip of the embolus and the simple retrolateral tibial apophysis (fig. 7) of the palp. Females resemble *Ctenus amphora* but are easily distinguished by the smaller body size and the presence of a distinct plate behind the ovoid lobes and subdistally originating lateral spurs on the epigyne (fig. 8a).

Description: Male (holotype): Carapace yellow, with gray paramedian longitudinal bands; black rings around eyes. Legs orange, greenish gray distally on the femora, patellae and tibiae and yellow on the venter of femora and coxae. Chelicerae reddish brown. Endites and labium yellow, white at tips. Sternum yellow, bordered with brown. Abdomen grayish brown, dorsum with black anterior border, lighter centrally, with four median spots. Venter light gray. Anterior spinnerets laterally black.

Total length 10.00. Carapace 5.50 long, 4.00 wide. Clypeus 0.26, slightly smaller than the diameter of AME. Eye diameters and interdistances: AME 0.32, ALE 0.17, PME 0.40, PLE 0.41; AME-AME 0.13, AME-ALE 0.33, PME-PME 0.18, PME-PLE 0.45,

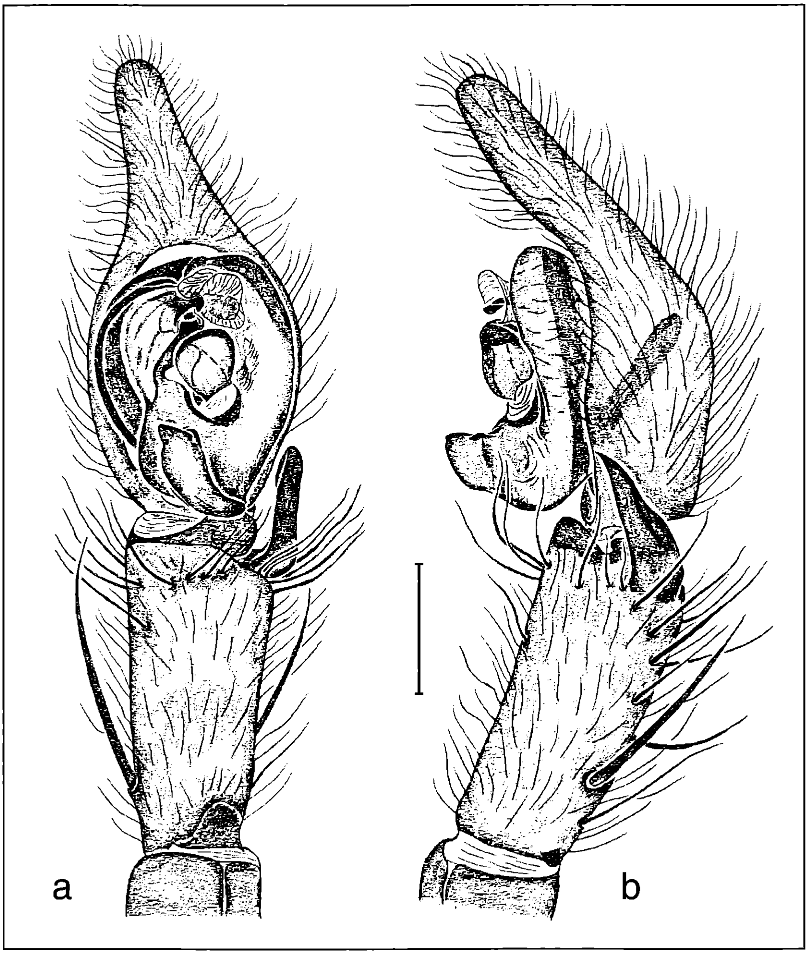

Figure 7. *Ctenus manauara* new species: a) male palp, ventral view; b) retrolateral view.

AME-PLE 0.17, AME-PME 0.12. MOQ length 0.78, front width 0.72, back width 0.95. Chelicerae with 3 promarginal and 5 retromarginal teeth.

Leg measurements: I -femur 7.10/ patella 2.60/ tibia 7.50/ metatarsus 7.30/ tarsus 2.30/ total 26.80/ II -6.70/ 2.60/ 6.60/ 6.80/ 2.10/ 24.80/ III -5.80/ 2.00/ 5.10/ 6.10/ 1.80/ 20.80/ IV -7.20/ 2.10/ 6.80/ 10.00/ 2.70/ 28.80.

Leg spination: tibia I v2-2-2-2-2, p1-0-1, r1-1-0; II v2-2-2-2-2, p1-1-0, r1-1-0; III v2-2-2, p1-1-0, r1-1-1; IV v2-2-2, p1-1-0, r1-1-1; metatarsus I v2-2-0, p1-1-0, r1-1-1; II v2-2-2, p1-1-1, r1-1-1; III v2-2-2, p.1-1-2, r1-1-2; IV v2-2-2, p1-1-1-2, r1-1-2. Metatarsus IV not modified. Palpal tibia with a long, simple retrolateral apophysis, inclined, narrowing to the apex, with acute tip. Tegulum strongly projected ventrally, with a distinct distal projection (fig. 7a,b). Hyaline conductor large, partially covering the tip of the embolus. Median apophysis short and rounded. Embolus large, narrowed distally, with curved and lobed tip, and a subrectangular, basal embolar projection, not dentate (fig. 7a).

Female (paratype MCN 25244): Coloration basically as in male, except darker legs, banded with greenish gray. Labium orange. Abdomen without dorsal median black spots.

Total length 10.80. Carapace 5.00 long, 3.80 wide. Clypeus 0.25, slightly smaller than the diameter of OMA. Eye diameters and interdistances: AME 0.30, ALE 0.20, PME 0.38, PLE 0.37; AME-AME 0.12, AME-ALE 0.36, PME-PME 0.22, PME-PLE 0.43, ALE-PLE 0.17, AME-PME 0.12. MOQ length 0.75, front width 0.75, back width 0.95. Chelicerae with 3 promarginal and 5 retromarginal teeth.

Leg measurements: I -femur 4.20/ patella 2.00/ tibia 4.10/ metatarsus 3.80/ tarsus 1.30/ total 15.40/ II -4.10/ 1.90/ 3.60/ 3.60/ 1.20/ 14.40/ III -3.60/ 1.70/ 3.00/ 3.45/ 1.10/ 12.85/ IV -4.70/ 1.80/ 4.20/ 6.30/

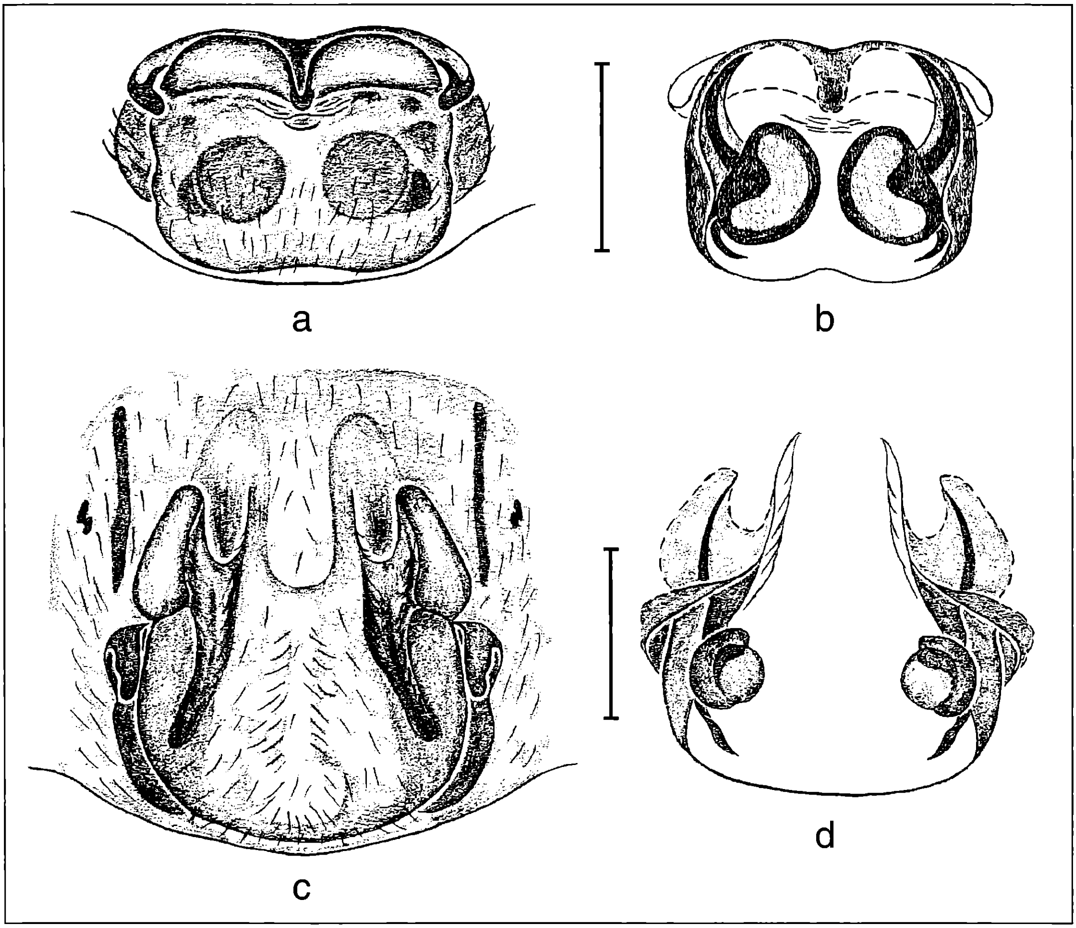

Figure 8. *Ctenus manauara* new species: a) female epigyne, ventral view; b) dorsal view; *Ctenus tapereba*, new species: c) female epigyne, ventral view; d) dorsal view.

1.90/ 18.90. Leg spination: tibia I v2-2-2-2-2, p0, r0; II v2-2-2-2-2, p0, r0; III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-0, p0-0-1, r0-0-1; III v2-2-2, p1-1-2, r1-1-2; IV v2-1-2-2, p1-1-1-2, r1-1-1-2. Epigynum rectangular, showing the spermathecae by transparency, consisting of anterior ovoid lobes and a distinct plate behind the lobes. Lateral spurs short, rounded at tip, originating at the front border of the plate, directed mesially (fig. 8a). Internally with two oval spermathecae, separated by less than half their diameter. Copulatory ducts short, narrowed distally. Fertilization ducts relatively long and curved, originating from retrolateral side of spermathecae (fig. 8 b).

Variation: Ten males: total length 8.60-11.40; carapace 4.60-6.20; femora I 6.10-7.80. Ten females: total length 7.50-11.10; carapace 3.80-5.10; femora I 3.40-4.30.

Description of living specimens: Female: basic colour dark brown, carapace with a median light band, widest around thoracic groove and sublateral light bands. Legs brown with light brown bands. Abdomen dark brown with a median folium-like band and laterally with obscure light spots (plate 3a,b).

Distribution. Known only from the region of Manaus, central Amazonia.

Material examined: Brazil, Amazonas, Manaus, Fazenda Esteio, (Smithsonian reserve at km 23), 1 female, Feb. 19, 1986, B. C. KLEIN col. (INPA); 1 male, Oct. 30, 1985, B. C. KLEIN col. (INPA); 1 female, Mar. 11, 1986, B. C. KLEIN col. (INPA); 1 female, May 22, 1990, B. C. KLEIN col. (MCN 19849); Smithsonian reserve at km 41, 10 males, 5 females, Jan. 12, 1994, T. GASNIER, A. D. BRESCOVIT & H. HÖFER col. (MCN 25255, 25253; SMNK; INPA); 6 females, R. S. VIEIRA col. (INPA); Reserva Ducke, 1 female, Sept. 04, 1991, H. HÖFER & T GASNIER col. (SMNK 1153); 1 male, Jan. 17, 1991, H. HÖFER col. (SMNK); 1 male, Feb. 17, 1994, H. HÖFER col. (INPA); 3 males, Jan. 18, 1994, A. D. BRESCOVIT & H. HÖFER col. (MCN 25251); 1 female, Feb. 22, 1992, A. D.

Brescovit col. (SMNK 964); 1 female, Aug. 31, 1991, H. Höfer col. (SMNK 413); 1 male, Aug. 07, 1992, M. E. De Oliveira col. (SMNK 1009)

### *Ctenus tapereba* new species

Figure 8c,d; colour plate 3c,d

Types: Female holotype from Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil, Jan. 18, 1994, A. D. Brescovit col., deposited in MCN 25245. Paratypes: two females (SMNK 1155 and INPA), from same locality of holotype, Jan. 17-18, 1994, H. Höfer col.

Etymology: The specific name comes from the Indian dialect Tupi-Guarani, where it is a name for a big Amazon tree with delicious fruits.

Diagnosis: The females of *Ctenus tapereba* differ from other species by the presence of deep lateral grooves and vertical anterior lobes on the epigynal plate (fig. 8c).

Description: Female (holotype): Carapace orange, with short transverse striations. Thoracic groove brown. Clypeus reddish brown, black rings around eyes. Legs orange, femora dark orange, dorsally with white setae at basis of spines, ventral faces yellow; white scopulae on tibiae, metatarsi and tarsi. Chelicerae reddish brown. Endites and labium orange, medianly with black spots and white at tips. Sternum orange. Abdomen black, dorsum with a folium-like yellow longitudinal band, venter with a dark gray central area.

Total length 19.00. Carapace 9.60 long, 7.00 wide. Clypeus 0.62, one third wider than the diameter of AME. Eye diameters and interdistances: AME 0.45, ALE 0.37, PME 0.62, PLE 0.57; AME-AME 0.25, AME-ALE 0.57, PME-PME 0.25, PME-PLE 0.45, ALE-PLE 0.17, AME-PME 0.20, MOQ length 1.40, front width 1.25, back width 1.57 Chelicerae with 3 promarginal and 4 retromarginal teeth plus one small denticle.

Leg measurements: I -femur 9.80/ patella 4.20/ tibia 10.10/ metatarsus 7.70/ tarsus 2.60/ total 34.40; II -9.00/ 4.00/ 8.30/ 7.60/ 2.50/ 31.40/ III -7.70/ 3.30/ 7 10/ 7.40/ 2.40/ 27.90/ IV -10.00/ 3.70/ 9.40/ 11.80/ 2.80/ 37.70. Leg spination: tibia I -II v2-2-2-2-2, p0, r0; III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-0, p0-0-1, r0-0-1, III -IV v2-2-2, p1-1-2, r1-1-2. Epigynal plate subquadrangular, with rim of copulatory openings curved, marked lateral grooves and vertical anterior ovoid lobes. Large, medianly originating lateral spurs, rounded at tip and directed posteriorly (fig. 8c). Internally with two spherical spermathecae, with small lateral lobes, separated by twice their diameter. Copulatory ducts short, enlarged distally. Fertilization ducts laminar and sinuous, originating from basis of spermathecae (fig. 8d).

Variation: Ten females: total length 15.00-20.00; carapace 7.40-10.00; femora I 7.20-10.60.

Description of living specimens from Reserva Ducke: Females: Basic colour brown. Carapace dark brown, light brown hairs behind the eyes and forming a longitudinal straight median line, broader around the dark thoracic groove, not reaching hind border of carapace (plate 3c,d). Fine light lines diverging from the median line to the lateral borders. Legs dark brown, femora dorsally with light brown patches. Chelicerae dark brown. Abdomen dark brown to black, laterally with obscure light patches, dorsally with a light brown to yellow median band, consisting of a row of triangles (plate 3d). The first two anterior triangles can be reduced to a median narrow line bordered by a pair of spots, the median band ends in small subtriangular spots posteriorly (plate 3c). Venter with a light to dark gray central area.

Distribution: North of Brazil.

Material examined: Brazil, Amapá, Serra do Navio, 1 female, May 7-15, 1992, G. Skuk col. (SMNK 1156); Amazonas, Presidente Figueiredo (Usina Hidrelétrica de Balbina), 2 females, Eq. Butantan col. (IBSP); Manaus, 1 female, Bicego col. (MZSP 10729); Fazenda Esteio (Smithsonian reserve at Km 41), 2 females, Jan. 13, 1994, T. Gasnier col. (MCN 25246; 25247); 1 female, Febr. 1994, T. Gasnier & H. Höfer col. (INPA); Reserva Ducke, 1 female, without date or collector (INPA); 1 female, Oct. 4, 1990, H. Höfer col. (SMNK 320); 1 female, May 16, 1994, H. Höfer col. (INPA); Coari (Urucú River), 1 female, Febr. 9, 1992, M. E. De Oliveira col. (UA); Pará, Anarindena (BR 316, km 6, Seminário São Pio X), 1 female, Mar. 31, 1971, R. F. Da Silva col. (IBSP 2953).

### *Ctenus inaja* new species

Figures 9, 10; plate 3e,f

Types: Male holotype from Reserva Florestal Adolfo Ducke, Manaus, Amazonas, Brazil, Dec. 6, 1993, H. Höfer col., deposited in MCN 25248. Paratypes: one male (SMNK 1157), from same date and locality; one male, Conjunto Petro, Manaus, Jan. 10, 1994, H. Höfer col. (INPA); one male, from Reserva de Campina, Oct. 1976, L. P. Albuquerque col. (INPA); one female (SMNK 1158), from same locality, Jan. 30, 1994, A. D. Brescovit col.; one female, Jamari River, Porto Velho, Rondônia, Brazil, Dec. 26, 1988, Op. Jamari col. (MCN 18584); one male (SMNK 349), Panguana, Río Yuyapichis, Amazonas, Peru, Apr. 2, 1985, M. Verhaagh col.

Etymology: The specific name comes from the indian dialect tupi-guarani, where it is a name for a big Amazon palm with edible fruits.

Diagnosis: *Ctenus inaja* is a distinct species easily recognized by the blunt spines set in large sockets on metatarsus IV (fig. 10c,d), the ventral dilatation on the femora IV in males (fig. 10e) and the strongly developed median apophysis of the male palp (fig. 9a,b); in females by a suboval epigynal plate, with an anterior laminar projection and basal lateral spurs (fig. 10).

Description: Male (holotype): Carapace orange, with brown paramedian longitudinal bands; thoracic groove brown; black rings around eyes. Legs orange with dark brown dispersed bands, except on tarsi. Chelicerae reddish brown. Endites orange, white at tips. Labium orange, yellow at tip. Sternum yellow, orange at border. Abdomen greenish gray to black, dorsum

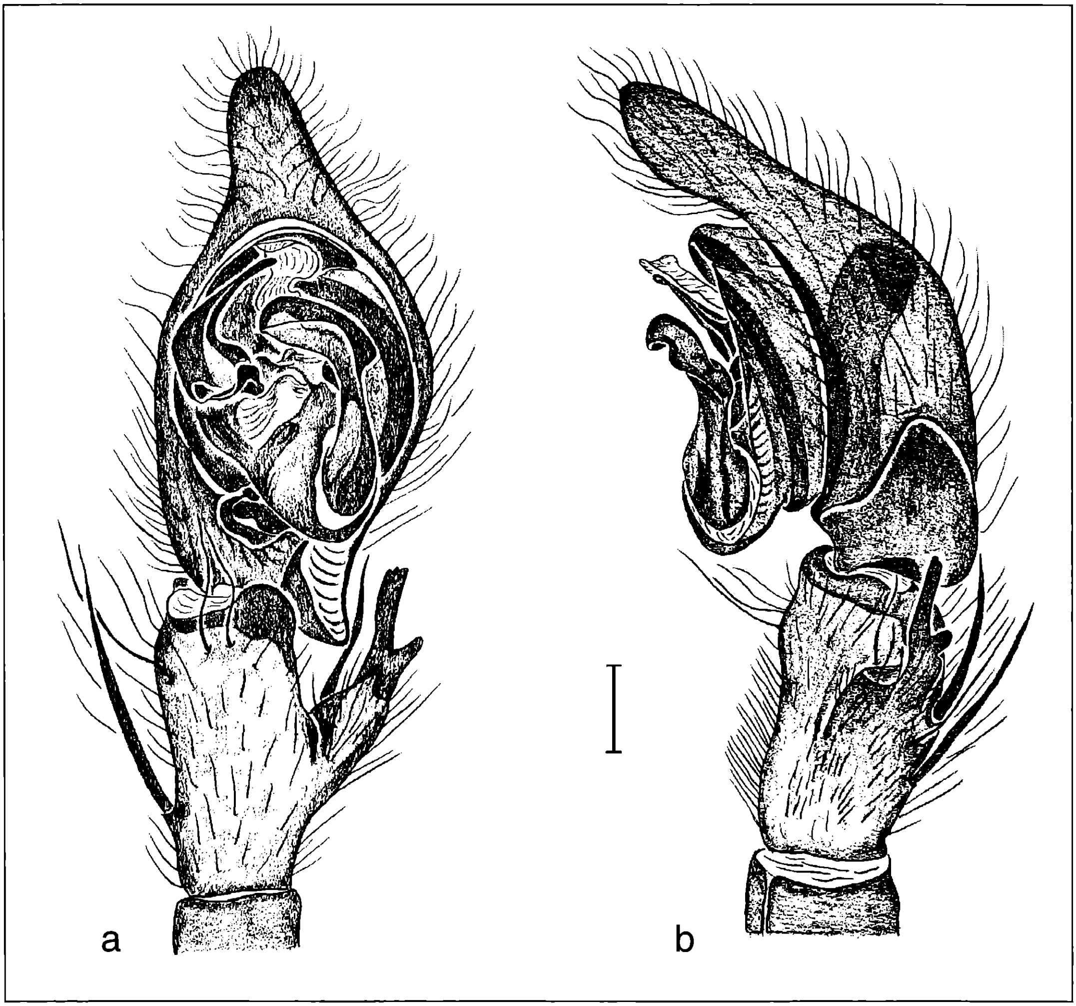

Figure 9. *Ctenus inaja* new species, male palp: a) ventral view; b) retrolateral view.

with an orange longitudinal band of subtriangular spots and short lateral bands. Venter with a light to dark gray central area.

Total length 16.00. Carapace 9.00 long, 6.90 wide. Clypeus 0.37, about two-thirds the diameter of the AME. Eye diameters and interdistances: AME 0.57, ALE 0.37, PME 0.57, PLE 0.52; AME-AME 0.17, AME-ALE 0.42, PME-PME 0.20, PME-PLE 0.45, AME-PLE 0.20, AME-PME 0.17; MOQ length 1.35, front width 1.17, back width 1.40. Chelicerae with 3 promarginal and 4 retromarginal teeth plus one small denticle.

Leg measurements: I -femur 9.60/ patella 3.80/ tibia 9.10/ metatarsus 8.60/ tarsus 3.50/ total 34.60/ II -8.70/ 3.70/ 8.00/ 8.00/ 3.20/ 31.60/ III -7.30/ 3.40/ 6.60/ 7.00/ 2.40/ 26.70/ IV -9.70/ 3.70/ 8.70/ 11.80/ 3.00/ 36.90. Leg spination: tibia I -II v2-2-2-2-2, p1-1-0, r1-1-0; III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-0, p1-1-1, r1-1-1; III -IV v2-2-2, p1-1-2, r1-1-2. Femora III and IV ventrally with a conspicuous agglomeration of spinules, femora IV modified, presenting a rounded basal dilatation (fig. 10e). Metatarsus III pro- and retrolaterally with blunt spines set in large sockets (fig. 10c,d). Palpal tibia with a voluminous retrolateral apophysis, strongly enlarged at basis, distally narrowed, bifid. Ventral branch longer and straight, with sinuous apex, dorsal branch short and rounded (figs 9a,b). Cymbium with a pronounced retrolateral basal keel (fig. 9 b). Tegulum projected towards the basis of the median apophysis (fig. 9b).

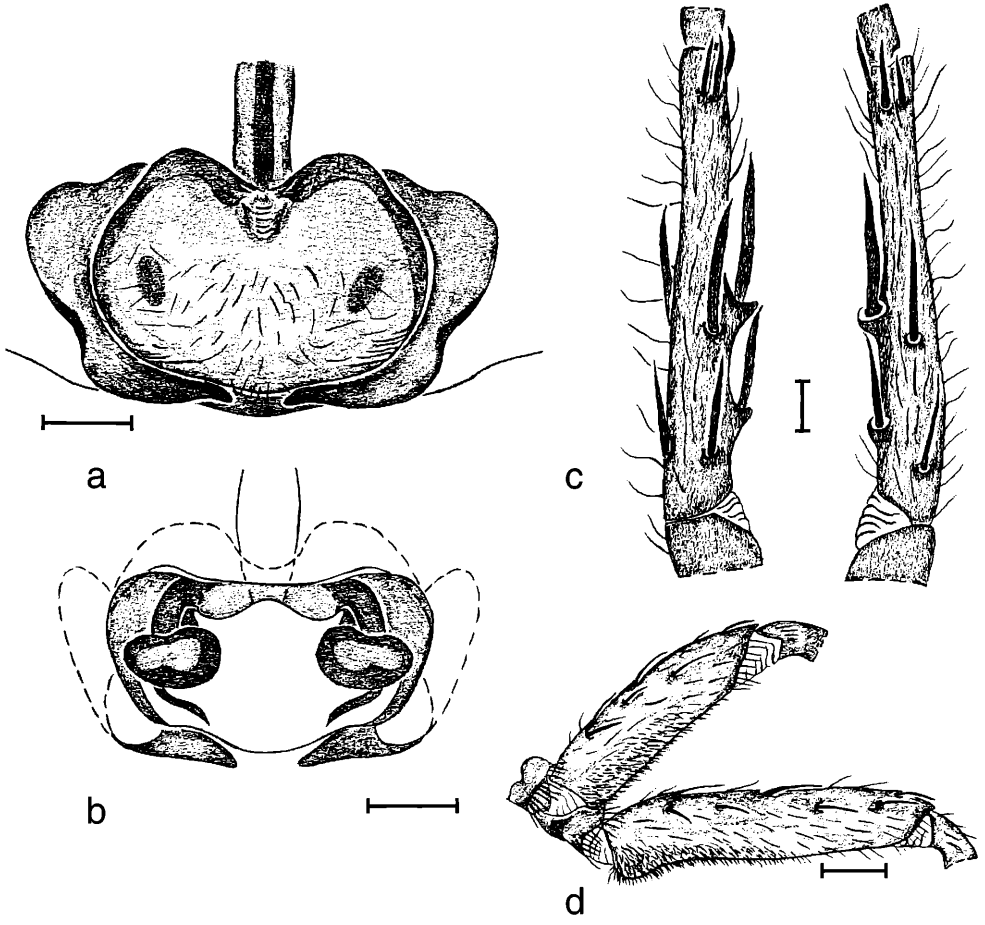

Figure 10. *Ctenus inaja* new species: a) female epigyne, ventral view; b) dorsal view; c) male metatarsus III, retrolateral; d) prolateral; e) femur III.

Hyaline conductor elongated, not very large, covering the tip of the embolus. Median apophysis strongly developed, elongated, basally enlarged, curved at middle, apex canoe-shaped. Embolus short, enlarged at basis and narrowed at tip, basal embolar projection small (fig. 9a).

Female (MCN 18584): Coloration basically as in male, except red brown carapace and black thoracic groove. Sternum uniformly orange. Labium reddish brown. Abdomen with an orange irregular band.

Total length 20.90. Carapace 10.00 long, 6.80 wide. Clypeus 0.35, about two-thirds the diameter of the AME. Eye diameters and interdistances: AME 0,52, ALE 0.40, PME 0.52, PLE 0.55; AME-AME 0.35, AME-ALE 0.55, PME-PME 0.37, PME-PLE 0.70, ALE-PLE 0.30, AME-PME 0.20. MOQ length 1.30, front width 1.37, back width 1.42. Chelicerae with 3 promarginal and 4-5 retromarginal teeth.

Leg measurements: I -femur 8.30/ patella 4.20/ tibia 8.00/ metatarsus 6.70/ tarsus 2.80/ total 30.00/ II -7.80/ 4.00/ 7.00/ 6.20/ 2.40/ 27.40/ III -6.80/ 3.60/ 5.80/ 6.30/ 1.80/ 24.30/ IV -8.00/ 3.80/ 7.90/ 10.00/ 2.80/ 32.50. Leg spination: tibia I -II v2-2-2-2-2, p0-1-0, r0; III -IV v2-2-2, p1-1-0, r1-1-0; metatarsus I -II v2-2-2, p0, r0; III v2-2-2, p1-1-2, r1-1-2; IV v2-2-2, p1-1-1-2, r1-1-1-2. Epigynal plate suboval, sulcated anteriorly, with a median anterior laminar projection. Lateral spurs conical, originating basally from lateral

Plate 1. a) *Ctenus amphora* MELLO-LEITÃO, male; b-d) *Ctenus amphora* MELLO-LEITÃO, females; e-f) *Ctenus villasboasi* MELLO-LEITÃO, females.

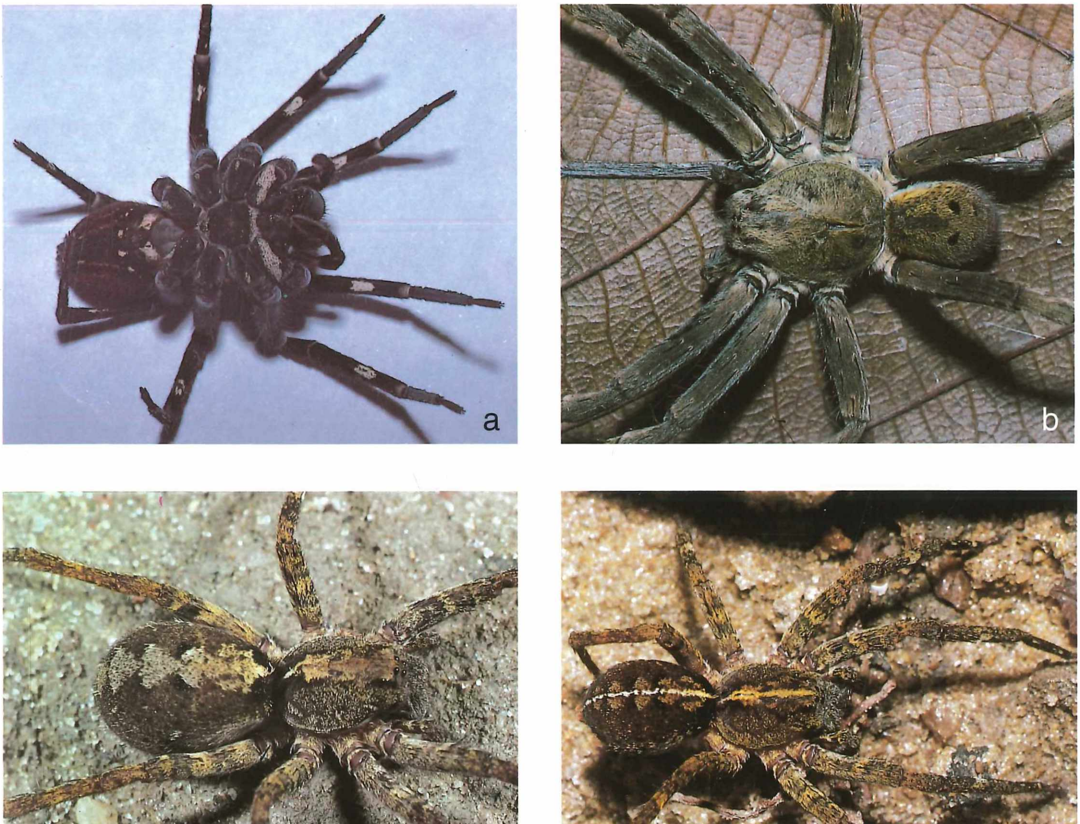

Plate 2. *Ctenus villasboasi* MELLO-LEITÃO: a) venter of female; b) male; *Ctenus crulsi* MELLO-LEITÃO: c) female with typical abdominal pattern; d) female with a combination of both colour variations; e) male; *Centroctenus* sp.: f) female.

Plate 3. a-b) *Ctenus manauara* new species, females; c-d) *Ctenus tapereba*, new species, females; e-f) *Ctenus inaja* new species, males.

plates (fig. 10a). Internally with two oval spermathecae, separated by their diameter. Copulatory ducts short, wide and medianly curved. Fertilization ducts relatively long and narrow, originating from basis of spermathecae (fig. 10b).

Variation: Ten males: total length 17.40-20.90; carapace 9.00-11.60; femora I 8.00-8.30; ten females: total length 14.00-17.60; carapace 7.60-9.20; femora I 8.00-10.00.

Distribution: North of Bolivia and Peru, north and central-east of Brazil.

Material examined: Peru, Amazonas, Panguana, Yuyapichis River, 1 male, Sept. 7, 1977, MEEDE col. (IBSP 2922); 1 female, Aug. 8, 1977, MEEDE col. (IBSP);

Brazil, Acre, Iquiri River, 1 male, Exp. Depto Zool. col. (MZSP 11955); Amazonas, Presidente Figueiredo (Usina Hidrelétrica de Balbina), 1 female, Eq. Butantan col. (IBSP); Manaus, 1 male, F. D. A. NEO col. (IBSP 4144); 1 female, 1899, BICEGO col. (MZSP 8956); ramal água preta, road AM 10, km 32, 1 female, Febr. 21, 1991, M. E. OLIVEIRA col. (IMTM 60); Manaus, conjunto Petro, 1 male, 1993, H. HÖFER col. (CBF); Ilha da Marchantaria, várzea forest, 1 female, Nov. 17, 1981, J. ADIS col. (SMNK 958); Manaus, campus of INPA, 1 male, Aug. 01, 1992, A. D. BRESCOVIT col. (MCN 22244); Reserva Ducke, 1 male, Aug. 14-23, 1991, A. D. BRESCOVIT col. (MCN 21453); Reserva Ducke, 1 male, Sept. 21, 1992, H. HÖFER & T. GASNIER col., in arboreal funnel trap (SMNK); Fazenda Esteio (Smithsonian reserve at km 60), 1 male, Jan. 07, 1986, B. C. KLEIN col. (INPA); 1 male, Mar. 11, 1987, B. C. KLEIN col. (INPA); Coari, Urucú river, 1 male, Mar. 9-10, 1994, P. BUHRNHEIM et al. col. (UA); Pará, Óbidos, 1 female, May 3, 1967, Exp. Depto Zool. col. (MZSP 6332); Tucuruí, Inajá (Vila Braba), 1 female, Jul. 9, 1980, B. MASCARENHAS col. (IBSP 3281); Santarém, Ilha de Urucurituba (Várzea), 1 male, Jan. 24, 1994, A. D. BRESCOVIT & H. HÖFER col. (SMNK 1159); Rondônia, Porto Velho, 1 female, Dec. 1982, I. STRAINER col. (IBSP 3603); near Porto Velho (Usina Hidrelétrica de Samuel), 2 males, 2 females, Eq. Butantan col. (IBSP); Jamari River, 1 male, 1 female, Jan. 19-20, 1989, Eq. Op. Jamari col. (MCN 18720; 18551); Mato Grosso: Alta Floresta, 1 male, Jan. 1978, L. LINHARES col. (IBSP 2895); Bahia: Uruçuca, 1 female, Oct. 1-14, 1967, Exp. Depto Zool. col. (MZSP 10761); Bolivia. Beni: Estación Biológica del Beni, 2 females, Jul. 21-25, 1993, H. HÖFER col. (CBF).

## 4. Natural history and ecology of the species

All *Ctenus* spiders of Reserva Ducke are nocturnal, sedentary, ground living spiders. During the day these spiders hide under dead leaves in litter or in small crevices on the ground. Accumulations of litter in bases of stemless palms and thick root layers at the base of trees seem to be very attractive hiding places. Only few spiders were seen active during the day. Most of the observed spiders came out of the retreat only two or three hours after sunset (e. g. 21:00) and stayed within a small distance from the retreat. The spiders are sit-and-wait predators and most of them keep a long time motionless sitting on the ground or on lower plants. Males were more often observed moving around, sometimes climbing on low plants.

*Ctenus amphora* and *C. crulsi* specimens have been observed eating cockroaches, crickets, mothes, termites (*Syntermes*), whip-scorpions and other *Ctenus* spiders in the field.

Adults of *Ctenus amphora* and *Ctenus crulsi* have been observed and collected throughout the year. No seasonality has been detected yet. Females of *Ctenus amphora* and *Ctenus crulsi* carry their egg sacs attached to the chelicerae (plate 1d). In captivity pregnant females were observed to be very aggressive against conspecific males and preyed upon them. After constructing an egg sac they hided day and night under leaves and did not accept prey. Even in periods when we observed females in captivity with egg sacs we rarely encountered egg sac-carrying females in the field. They probably keep hiding during hatching. The hatched spiderlings stayed aggregated close to the female for about one week before they dispersed. Females can store sperm and construct a second fertile egg sac without new copulation (2 observations). When disturbed, males of *Ctenus amphora* and *Ctenus crulsi* spread out dense tufts of long hairs on the front legs (tibiae and metatarsi) and eventually raise the first pair of legs in defence. Especially males, but also females make large jumps of several centimeters to escape predators. However they seldom escape when swarm raiding army ants (*Eciton burchelli*) hunt through their habitat (see VIEIRA & HÖFER 1994).

*Ctenus manauara* is a distinctly smaller species than the other species from Reserva Ducke, and seems to be more actively wandering around. Females also carry their egg sac attached to the chelicerae (plate 3b). Three females kept in captivity started soon eating their eggs. One female was observed eating a conspecific male.

*Ctenus villasboasi* was the most abundant of the three larger species in Reserva Ducke. Females are easily recognized in field by the bright orange-brown or reddish-orange colour of the abdomen, whereas males are more inconspicuous light brown (see colour plates). Both females and males present a striking white pattern on the venter (plate 2a), but we never observed them showing the venter in defense. Although all females and most of the males were observed on the ground in the field, in captivity specimens of both sexes rested most of the time hanging on the cage walls. Two females in captivity constructed large (diameter 2 cm), flattened egg sacs, attached them with a few silken lines to the underside of the cover of the cage and sat over them guarding. One egg sac collected from a female in the field was parasited by mantispids.

The large species *Ctenus tapereba* was rarely observed by us in Reserva Ducke. Two females rested only few centimeters from small entrances of deep cavities in the ground and retreated very quickly when the observer approached.

*Ctenus inaja* was also rarely observed in Reserva Ducke. Three males appeared in buildings, one in Reserva Ducke, two in Manaus. One male was caught in an arboreal funnel trap in Reserva Ducke (appr. 2 m above the ground). Males from a whitewater inundation forest near Santarém were observed in the field and in captivity resting head down on trunks or other vertical structures (plate 3f).

*Ctenus minor* was never observed or collected by ourselves in Reserva Ducke. As we encountered this species in very high numbers in campina and campinarana sites near Manaus and in dry forest and cerrado sites near Santarém (Pará) we consider it to prefer these drier habitats and suppose that the specimens from Reserva Ducke were collected in one of the campinarana patches within the humid rainforest.

The *Centroctenus* species mentioned in the introduction are very similar to *Ctenus* species. One species (plate 2f) was quite abundant in Reserva Ducke, mostly observed on lower vegetation or on vertical structures like trunks and stems, but also on the ground.

In 1993 we started intensive nocturnal sampling and observing trips in Reserva Ducke and the Smithsonian reserve 1501 to study density and activity patterns of all *Ctenus* species. Preliminary analyses show that the relative number of adults of the different species might be inversely proportional to the body size. *C. manauara*, the smallest species was most abundant and *C. villasboasi*, the largest species the less abundant, *C. amphora* and *C. crulsi* were intermediate. For all species we calculated a sex ratio of 3:1 (females - males) from our samples. *Ctenus* spiders become active at night, highest predation activity has been observed between 21:30 and 02:00 in the morning. Most of the specimens observed during this time were successfully capturing prey and then proceeded to other activities (eating, cleaning, mating). High numbers of small specimens (adults of *C. manauara* and juveniles of the other species) have been counted repeatedly in nights (or hours) when the number of large specimens was low. It seems possible to us that the smaller species and the juveniles of the larger species avoid intraguild predation by this way. Abundances of *Ctenus* species seem to be most affected by litter quantity (depth) and probably very much by arthropod-hunting army ants (VIEIRA & HÖFER 1994). Vegetation structure and ground relief seem to be less important factors (GASNIER unpubl.).

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HUBERT HÖFER & ANTONIO D. BRESCOVIT

# Ergebnisse der Bolivien-Expedition des Staatlichen Museums für Naturkunde Karlsruhe: Spinnen (Araneae)

**Kurzfassung**

Während einer Bolivienexpedition, organisiert vom Staatlichen Museum für Naturkunde in Karlsruhe über ein Kooperationsabkommen mit der „Colección Boliviana de Fauna" in La Paz, wurden von den Autoren die echten Spinnen (Araneae) gesammelt und im Anschluß an die Reise sortiert und identifiziert. Die Ergebnisse werden in Form eines Reiseberichts mit Artenlisten dargestellt. Faunistische Bestandsaufnahmen wurden an neun Standorten auf unterschiedlichen Höhenstufen durchgeführt, imTiefland des Beni (100 m), in der Yungas-Region (400 m - Sapecho, 1200-1500 m - Coroico), im Valle de Zongo (2000 - 4500 m) und auf dem Planalto bei La Paz. Die aufgelisteten Spinnen sind in den Sammlungen in La Paz (CBF), Porto Alegre (MCN) und Karlsruhe (SMNK) hinterlegt.

**Resumen**

**Resultados de la expedición del Staatliches Museum für Naturkunde Karlsruhe a Bolivia: Arañas (Araneae)**

Durante una expedición científica a Bolivia, dentro el convenio entre el „Staatliches Museum für Naturkunde", Karlsruhe y la „Colección Boliviana de Fauna", La Paz, se han realizadas colecciones en diferentes partes de la fauna. Los siguientes grupos de animales fueron colectados por los ocho participantes: mamíferos (principalmente murciélagos y roedores), anfíbios y reptiles por los estudiantes bolivianos NURIA BERNAL y ESTER PÉREZ (CBF); lepidópteros por Dr. HELMUTH ROGG (CBF); hormigas por Dipl. Biol. KRZYSZTOF ROŚCISZEWSKI (SMNK); heterópteros por Prof. Dr. HANS-DIETER ENGELMANN (SMNK), ácaros por Prof. Dr. LUDWIG BECK (SMNK); y arañas por los autores (SMNK/MCN). Fueron exploradas nueve localidades desde una altura de 100 m en la cuenca del río Beni, subiendo por la zona de las Yungas (Sapecho, 400 m; Coroico, 1200-1500 m) hasta una altura de 4500 m en el altiplano de La Paz. Depués una descripción de cada localidad las correspondientes arañas colectadas estan alistadas. El material fue depositado en las colecciones aracnológicos de La Paz (CBF), Porto Alegre (MCN) y Karlsruhe (SMNK).

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## Einleitung

Im Juli 1993 hatten wir die Gelegenheit, im Rahmen eines bestehenden Übereinkommens zwischen dem Staatlichen Museum für Naturkunde in Karlsruhe und der Colección Boliviana de Fauna in La Paz an einer Sammelreise nach Bolivien unter der Leitung von Prof. Dr. LUDWIG BECK teilzunehmen. Hauptziel dieser Expedition war zunächst eine faunistische Besammlung unterschiedlicher Regionen in Bolivien zum Zweck der Erweiterung der immer noch spärlichen Kenntnis der Fauna Boliviens. Die Auswahl der zu sammelnden Tiergruppen ergab sich dabei zwangsläufig durch die an der Exkursion teilnehmenden Wissenschaftler, bzw. die Interessen der durch sie vertretenen Museen. So wurden speziell für das Museum in La Paz Fledermäuse und Kleinsäuger, Amphibien und Reptilien von zwei bolivianischen Studentinnen NURIA BERNAL und ESTER PÉREZ gesammelt, Schmetterlinge von Dr. HELMUTH ROGG (La Paz), Ameisen von Dipl. Biol. KRZYSZTOF ROŚCISZEWSKI (Karlsruhe), Wanzen von Prof. Dr. HANS-DIETER ENGELMANN (Karlsruhe/Görlitz), Milben von Prof. Dr. LUDWIG BECK (Karlsruhe) und die Webspinnen von den Autoren des vorliegenden Artikels (Karlsruhe/Porto Alegre). Alle Aufsammlungen wurden teilweise bereits während, vorwiegend aber im Anschluß an die Sammelreise sortiert und protokolliert und die Tiere so weit wie möglich identifiziert. Das gesamte Material wurde in die wissenschaftlichen Sammlungen in La Paz (Colección Boliviana de Fauna - CBF), Porto Alegre (Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul - MCN) und Karlsruhe (Staatliches Museum für Naturkunde - SMNK) eingegliedert. Da lediglich an den beiden letztgenannten Museen umfangreiche, wissenschaftliche Spinnensammlungen vorhanden sind und dort auch aktuell mit diesen Sammlungen gearbeitet wird, wurde bei den Spinnen so verfahren, daß ein Großteil des Materials, das für eine weitere taxonomisch-systematische Bearbeitung von Interesse ist, entweder direkt interessierten Spezialisten zugesandt wurde oder zunächst bei den Bearbeitern an deren Museen verbleibt. In der sich noch im Aufbau befindlichen Sammlung in La Paz wurden zunächst die bereits bis zur Art identifizierten Exemplare hinterlegt, außerdem eine repräsentative Sammlung häufig gesammelter Tiere auf Familien- oder Gattungsniveau. Diese Sammlung kann und soll zunächst vorwiegend didaktischen Anforderungen genügen und gleichzeitig einen Überblick über die Diversität der bolivianischen Spinnenfauna ermöglichen.

Allerdings ging und geht das Interesse aller Teilnehmer weit über das Ziel einer faunistischen Bestandsaufnahme hinaus, zumal die meisten von ihnen auch ökologisch arbeiten. Nach unserem Selbstverständnis endet moderne Museumsarbeit keineswegs bei faunistischen Aufsammlungen und deren taxonomischer Bearbeitung (vgl. BECK 1991). Vielmehr sehen wir Bestimmungs- und Sammlungsarbeit als notwendige Grundlage für tropenökologische Untersuchungen. So zeigt bereits der Reiseverlauf und die Verteilung der besammelten Gebiete (entlang von Höhentransekten) unser ökologisches Interesse, welches dann im Tiefland des Rio Beni im Vordergrund stand und die Methodik und Intensität der Sammlungen dort bestimmt hat.

Der vorliegende Artikel und die ihm zugrunde liegenden Aufsammlungen sind ein Ergebnis der Kooperation eines Ökologen und eines Taxonomen. Er stellt die gemeinsam erarbeitete Basisauswertung dar, aufgrund derer beide Wissenschaftler zukünftige taxonomische (Beschreibungen neuer Arten, Revisionen) und ökologische Arbeiten (Abschätzung von Artenzahlen, Inselökologie) durchführen werden.

## Material und Methoden

Die Reihenfolge der unten aufgeführten Sammelstandorte entspricht nicht völlig dem Reiseverlauf. Vielmehr sind sie nach einem imaginären Höhenstufen-Transekt geordnet.

Im Beni-Tiefland haben beide Arachnologen jeweils tagsüber und nachts mit den folgenden, von CODDINGTON ET AL. (1991) vorgeschlagenen Methoden in drei Waldinseln Spinnen gesammelt:

1 Stunde mittels „looking down", d.h. einer im wesentlichen auf den Knien durchgeführten intensiven Suche auf dem Boden (in Laubstreu),

1 Stunde „looking up", d.h. einem intensiven Absuchen der über kniehohen Vegetation (Taf. 3c),

20 mal ausgiebiges Klopfen der Vegetation über einem 60x60 cm großen, weißen Baumwolltuch (Klopfschirm) und dem anschließenden Aufsammeln der heruntergefallenen Spinnen,

in jeder Waldinsel wurde Laubstreu aus einer 2 m$^2$ großen Fläche in Plastiktüten gesammelt und am folgenden Tag per Handauslese nach Spinnen durchsucht.

An allen anderen Standorten wurden Spinnen durch Handfang in allen zugänglichen Straten und Klopfen der Vegetation gesammelt.

Die Artenlisten sind alphabetisch nach Familie und Gattung geordnet. Die Nomenklatur folgt dem Katalog von PLATNICK (1993). Innerhalb einer Aufsammlung wurden alle adulten und nahezu alle juvenilen Individuen als Morphospezies identifiziert, d.h. als morphologisch differenzierbare Arten, die aber in vielen Fällen nicht mit einem Artnamen versehen werden konnten, entweder weil nur Jungtiere vorlagen, weil die existierenden Beschreibungen unzureichend sind, oder weil die Art noch unbeschrieben ist. Lediglich in Fällen, in denen wir dies durch Kenntnis aller beschriebenen Arten sicher wissen, haben wir die Art als „sp. n." gekennzeichnet. Außer in den Artenlisten der Waldinseln geben wir für jede Art die Anzahl der gefangenen Individuen, getrennt nach Juvenilen und Adulten an, um eine Vorstellung von Intensität und Umfang des Gesamtfangs und dem Anteil einzelner Arten zu vermitteln.

## Ergebnisse

Im Beni-Tiefland war unser Hauptstandort die Estación Biológica del Beni - El Porvenir (EBB, Taf. 1a) im Biosphärenreservat Beni. Dieser auf ca. 100 m ü.NN gelegene Park besteht aus Überschwemmungssavannen, in denen Waldinseln verschiedenster Größen und Stadien liegen und aus dem sogenannten Hochwald (bosque alto), einem tropischen Tieflandregenwald, der innerhalb des Reservats etwa die Hälfte (60.000 ha) der Fläche bedeckt (HANAGARTH 1993). In den zur Untersuchungszeit trockenen Savannen haben wir nur recht sporadisch faunistisch gesammelt (Tab. 2, 3). Wesentlich intensiver und unter ökologischen Gesichtspunkten haben wir drei verschieden große Waldinseln untersucht. Uns interessierte vor allem, inwieweit die Artenzahl in solchen Inseln von der Inselgröße abhängt, und ob sie ein Ökoton, d.h. ein Übergangsbiotop zwischen Savanne und Wald darstellen oder eine verarmte Waldfauna beherbergen. Wir haben dazu drei Waldinseln in relativer Nähe zur Station ausgewählt, die kleinste mit einer Fläche von ca. 20 x 30 m (ca. 0,06 ha, Taf. 1b), die zweite mit ca. 1,5 ha (Taf. 1c, 3b) und eine große Waldinsel mit über 10 ha Fläche.

Als Referenz für die Beurteilung der Inselsituation können wir mit derselben Methodik durchgeführte Aufsammlungen der amerikanischen Kollegen (CODDINGTON ET AL. 1991) im Hochwald bei El Trapiche (ca. 3 Fußstunden von der Station entfernt) heranziehen. Dort haben wir auch selbst faunistisch gesammelt.

Da die ökologischen Ergebnisse nach umfangreicheren Auswertungen an anderer Stelle publiziert werden sollen, präsentieren wir hier lediglich Artenlisten, getrennt nach Savanne, Waldinseln und Hochwald und einige wenige ökologische Parameter wie Gesamtartenzahlen und Artidentitäten der Habitate.

Während der systematischen Aufsammlungen in den drei Waldinseln vom 21.7. – 24.7.93 haben wir insgesamt 1303 Individuen gesammelt, weitere 270 Individuen durch zusätzliche Handfänge. Aus diesem Material konnten wir 190 Morphospezies aus 37 Familien separieren (Tab. 1, 4). Die tatsächliche Zahl der Arten in dieser Aufsammlung liegt sicher höher, da in Zweifelsfällen juvenile Tiere unter einer Morphospezies der gleichen Gattung eingeordnet wurden. Dies gilt vor allem für schlecht bearbeitete Familien, wie Heteropodidae, Lycosidae und Salticidae.

In der nur 20 x 30 m großen Waldinsel I haben wir während unserer sechsstündigen Arbeit nahezu jeden Quadratmeter begangen und besammelt. Wir rechnen deshalb damit, die dortige Spinnenfauna weitgehend erfaßt zu haben. 110 Morphospezies konnten wir aus den 502 gesammelten Spinnen separieren. Obwohl die anderen zwei Inseln zumindest in ihrer Größe und Vegetationsstruktur deutlich verschieden sind, liegen deren Individuen- und Artenzahlen doch sehr nahe bei diesen Zahlen (Tab. 1). Auch die Artidentitäten in den Fängen sind recht hoch: die Aufsammlung in der kleinsten Waldinsel hat mindestens 33 Arten mit der Insel III und 37 Arten mit der sehr viel größeren Insel IV gemeinsam. Die Aufsammlungen in den beiden größeren Waldinseln weisen mindestens 40 gemeinsame Arten auf.

Am 25.7 machten wir uns frühmorgens zu Fuß auf, um, von 2 Ochsenkarren begleitet (Taf. 3a), den Hochwald bei El Trapiche, etwa 2-3 Marschstunden von El Porvenir entfernt, zu erreichen und dort 3 Tage und Nächte zu verbringen. Während dieser Zeit sammelten wir per Hand und nahmen Klopfproben aus der Vegetation. Obwohl wir weniger intensiv sammelten als in den Waldinseln, konnten wir aus den 372 Individuen 133 Morphospezies separieren (Tab. 5). Im Vergleich dieser Aufsammlung mit den Aufsammlungen in den drei Waldinseln konnte die Artidentität nicht in allen Fällen ermittelt werden. 10 identifizierte Arten sind identisch und 32 der 81 Gattungen traten auch in den Waldinseln auf. 36 Arten wurden zweifelsfrei in den Waldinseln nicht gefangen, dort wiederum wurden 90 Arten gefangen, die in der Aufsammlung des Hochwaldes nicht auftraten. Die Waldinseln scheinen damit durchaus eine spezifische Fauna zu beherbergen, auf teilweise sehr kleiner Fläche weisen sie einen ähnlichen Artenreichtum an Spinnen auf wie der Hochwald, eventuell bedingt durch eine „Mischbesiedlung" der Inselhabitate von den angrenzenden Savannen, von den benachbarten Waldinseln und dem Hochwald. Die bei vielen Spinnenarten mögliche Verbreitung der Jungspinnen am Fadenfloß läßt eine solche Besiedlung möglich erscheinen. Die kleinste der Waldinseln ist am wenigsten hochwaldähnlich, und scheint sowohl von der Vegetation, als auch von der Spinnenfauna ein Ökoton, d.h. ein Mischhabitat zu sein. So dringen zum einen die Savannengräser einige Meter in die Waldinsel ein, zum anderen sind viele lichte Stellen vorhanden, an denen der Boden von stacheligen Bromelien bedeckt ist. In diesen schwer zugänglichen Blattrosetten leben beispielsweise zwei (oder drei) Arten der Springspinnengattung *Psecas* (Taf. 2a) und Radnetzspinnen der Gattungen *Leucauge* (Tetragnathidae) und *Philoponella* (Uloboridae) spannen dazwischen ihre Netze auf. Netzbauende Lycosiden (Wolfsspinnen) der Gattung *Porrimosa* mit ihren großen Trichternetzen (Taf. 2b) konnten wir in großer Zahl sowohl in der Savanne als auch in den Waldinseln, seltener auch im Hochwald beobachten. Auch die hohe Zahl an Lycosidenarten in den Waldinseln weist auf eine Verbindung mit offeneren Habitaten hin, da in neotropischen Regenwäldern Lycosiden eher selten, dagegen Car Cteniden sehr abundant und artenreich auftreten (HÖFER et al. 1994). Allerdings fanden wir auch *Ctenus taeniatus* (Ctenidae, Taf. 2c) in Waldinseln und in der Savanne.

Sowohl in den Aufsammlungen in Waldinseln, als auch in den Aufsammlungen im Hochwald beträgt das Verhältnis Netzspinnenarten zu Jagdspinnenarten 0,8. Theridiidae, Araneidae und Salticidae sind in allen Waldhabitaten die artenreichsten Familien. Aus den beiden ersten konnten wir nahezu alle Individuen in Morphospezies separieren, für die Springspinnen war das aufgrund der großen Artenzahl in Südamerika und der unzureichenden Bearbeitung nicht möglich. Die hier ermittelte Zahl der Morphospezies in dieser Familie ist als untere Grenze der tatsächlichen Artenzahl zu sehen.

Als biologische Besonderheiten seien hier noch zwei Arten erwähnt. Zum einen konnten wir mehrere Exemplare von *Aphantochilus rogersi* (Aphantochilidae, Taf. 2d) fangen, Spinnen, die ihre verblüffende Ähnlichkeit mit Ameisen des Tribus Cephalotini dazu benützen, diese zu erbeuten, was man als aggressive Mimikry bezeichnet. Zum anderen fanden wir im Hochwald bei El Trapiche ein ca. drei Kubikmeter umfassendes Gemeinschaftsnetz mit sicherlich über 50 Spinnen der sozialen Spinnenart *Philoponella republicana* (Uloboridae).

Auf dem Hin- und Rückweg in das Hauptuntersuchungsgebiet im Beni-Tiefland machten wir in einer Station des Deutschen Entwicklungsdienstes (DED) in Sapecho halt. Die Station liegt auf ca. 400 m ü.NN und ist umgeben von den ersten Ausläufern der Bergwälder der Yungas am Ostabhang der bolivianischen Anden. Neben sporadischen Handfängen auf kurzen Ausflügen in die Umgebung hatten wir Gelegenheit in einer Daueruntersuchungsfläche des DED in einem Hochwald zu sammeln (Tab. 6), allerdings lediglich an einem sehr regnerischen und kühlen Tag.

Tabelle 1. Individuen- und Artenzahlen aus den systematischen Aufsammlungen in drei Waldinseln im Beni-Tiefland.

| | Größe [ha] | Ind. gesamt | Adulte | Morphospezies |
|---|---|---|---|---|
| Insel I | 0,06 | 502 | 114 | 110 |
| Insel III | 1,5 | 416 | 103 | 92 |
| Insel IV | > 10 | 385 | 119 | 101 |
| Gesamt | | 1303 | 336 | 190 |

Auf dem Rückweg nach La Paz machten wir zwei Tage Station in Coroico, einem touristisch erschlossenen Dorf am Andenabhang auf ca. 1600 m ü. NN. Von dort aus führten uns zwei Tagesausflüge in das Huarinilla-Tal, wo wir zwischen 1200 und 1500 m Höhe im Flußbett, entlang des Flußes und entlang von Wegen, die zu kleineren Rodungsflächen mit Citrus- und Kaffeekulturen führen, gesammelt haben (Tab. 7).
Auf der allerersten Exkursion unserer Reise, konnten wir, trotz teilweise sehr deutlicher Symptome der Höhenkrankeit, einige Stunden im Nebelwald von Cotapata (3500 m ü. NN), der über einen Paß (Cumbre) in rund 4600 m Höhe erreicht wird, sammeln (Tab. 8).
Nach unserer Rückkehr aus dem Tiefland nutzten wir die Gelegenheit, auf einer 2-tägigen Exkursion unter der Führung von Dr. WERNER HANAGARTH eine Höhenabfolge innerhalb des verkehrstechnisch leicht zugänglichen Zongo-Tales nord-östlich von La Paz zu besammeln.
Am ersten Nachmittag und in der Nacht sammelten wir unterhalb des Ortes Sainani, auf ca. 2000 m Höhe, vorwiegend in Ruderalvegetation, in Steinhalden und am Rand des an den äußerst steilen Hängen wachsenden Waldes (Tab. 9). Auffällig war die große Artenzahl an Anyphaeniden, die wir in der Vegetation und am Boden unter Steinen sammeln konnten, sowie eine große *Ctenus*-Art (Taf. 2e) und eine große Pholcidae (Zitterspinne), die beide nachts in den Steinhalden und Felsböschungen häufig zu finden waren. Eine außerordentliche faunistische Rarität stellt der Fund einer noch unbeschriebenen *Naevius* - Art (Desidae) dar. Von dieser in Australien und Neuseeland artenreichen Familie sind aus Südamerika bisher erst 2 Arten beschrieben, *Desis galapagoensis* von den Galapagos-Inseln und *Naevius varius* aus Peru.
Am nächsten Tag sammelten wir zunächst auf ca. 3200 m Höhe, in einer Übergangszone von ceja de montaña (immergrüne Strauchvegetation, Taf. 4c) zu puna húmeda, der für große Höhen typischen Gras-Vegetation (Tab. 10). Die meisten Netzspinnen der Artenliste stammen aus der höheren Vegetation, die meisten Jagdspinnen (Anyphaenidae, Amaurobiidae, Corinnidae und Gnaphosidae) wurden unter im Gras liegenden Steinen gesammelt (Taf. 2f). Diese geschützten Mikrohabitate inmitten des Puna-Grases waren dann an den letzten zwei Sammelstandorten, an der laguna Viscachani auf 3660 m (Taf. 4b) und an der Straßenkreuzung Chacaltaya/Valle de Zongo auf 4500 m (Taf. 4a), die einzigen Stellen, an denen wir Spinnen, allerdings in großer Häufigkeit und Stetigkeit, sammeln konnten (Tab. 11, 12).
Unsere letzte Exkursion führte uns an den Titicacasee, wo wir an zwei Stellen sammelten. Direkt am Ufersaum des Sees bei Huatajata fanden wir wieder große Mengen an Jagdspinnen unter Steinen, und winzige Netzspinnen (Linyphiidae) im trockenliegenden Seegras (Tab. 13). An einer weiter vom Ufer entfernten und höherliegenen Stelle vor San Pablo de Tiquina sammelten wir zwischen und unter größeren Steinblöcken (Tab. 14). Die an diesen beiden Standorten gemachten Funde der Gnaphosiden-Arten *Apopyllus silvestrii* und *Apodrassodes araucanius* erweitern die Verbreitungsgebiete dieser Arten (BRESCOVIT & LISE 1993).

## Schlußbemerkung und Danksagung

Selbstverständlich können vierwöchige Sammelexkursionen nur einen kleinen Beitrag zur Erfassung einer so artenreichen Fauna leisten, wie sie in Bolivien zu erwarten ist, einem Land das über eine ungeheure Vielfalt an verschiedensten Lebensräumen verfügt, von Tieflandregenwäldern und Überschwemmungssavannen über Bergregenwälder bis zu andinen Hochebenen und Trockentälern. Umfassendere Bestandsaufnahmen müssen über viele Jahre hinweg, an sehr viel mehr Orten und natürlich überwiegend von einheimischen Wissenschaftlern realisiert werden. Dafür soll und wird die mit GTZ-Unterstützung aufgebaute Colección Boliviana de Fauna in La Paz die Voraussetzungen bieten. Wir hoffen, daß wir mit unseren Aufsammlungen und mit der Hinterlegung einer Sammlung am dortigen Museum zukünftige Untersuchungen der Spinnenfauna anregen und erleichtern.

Wir danken Dr. WERNER HANAGARTH und Dr. HELMUTH ROGG für die erstklassige Organisation und Betreuung in Bolivien und der VON KETTNER-Stiftung Karlsruhe für die finanzielle Unterstützung der Reise. Besonderer Dank gilt unseren Kollegen ALEXANDRE BONALDO, ERICA BUCKUP und MARIA APARECIDA MARQUES (alle Porto Alegre) für ihre Beteiligung an der Identifizierung des Spinnenmaterials.

Tabelle 2. Estación Biológica del Beni, Beni, Handfänge um die Station El Porvenir herum - 20.7.- 28.7.93 (Tag/Nacht).

| Familie | Gattung/Art | ♂♂ | ♀♀ | juv. |
|---|---|---|---|---|
| Aphantochilidae | *Aphantochilus rogersi* O.P.Cambridge | | 1 | 1 |
| Araneidae | *Alpaida truncata* (Keyserling) | | | 1 |
| Corinnidae | *Castianeira* sp. | 1 | | |
| Gnaphosidae | *Cesonia* sp. | | | 2 |
| Palpimanidae | *Otiothops* sp. | 1 | | 1 |
| Pisauridae | *Ancylometes* sp. | | | 2 |
| Salticidae | *Euophrys* sp.1 | | 1 | |
| | *Euophrys* sp.2 | | 1 | |
| | *Marpissae* sp. | | | 1 |
| | *Myrmarachne* sp. | 1 | 1 | |
| | *Sarinda* sp.1 | 1 | | |
| | *Sarinda* sp.2 | 1 | 1 | 7 |
| | *Synemosyna* sp. | | | 1 |
| | *Tullgrenella* sp. | 1 | 2 | |
| | unidentatae sp.1 | 1 | | |
| | unidentatae sp.2 | 1 | | |
| | unidentatae sp.3 | 1 | | |
| Selenopidae | *Selenops* sp. | 3 | 7 | |
| Thomisidae | Thomisinae sp. | 1 | | |
| 9 Familien | 19 Morphospezies | 13 | 14 | 16 |

Tabelle 3. Estación Biológica del Beni, Beni, Handfänge in der Savanne - 20.7.- 28.7.93 (Nacht).

| Familie | Gattung/Art | ♂♂ | ♀♀ | juv. |
|---|---|---|---|---|
| Araneidae | *Alpaida veniliae* | | | 1 |
| | *Eustala* sp. (gr.*fuscovittata)* | | 3 | 8 |
| | *Metazygia atalaya* Levi (in press) | | 11 | |
| | *Metazygia chenevo* Levi (in press) | | 1 | |
| | *Metazygia gregalis* (F.O.P.Cambridge) | 1 | 3 | 12 |
| | *Parawixia* sp. | 1 | | |
| Ctenidae | *Ctenus taeniatus* Keyserling | 2 | | |
| Lycosidae | sp. | | 1 | |
| | *Porrimosa* sp. | | | zahlreich |
| Salticidae | unidentatae sp. | 1 | | |
| Tetragnathidae | *Tetragnatha* sp. | 1 | 1 | 1 |
| Trechaleidae | cf. *Paradossenus* sp. | 1 | | 1 |
| 6 Familien | 11 Morphospezies | 6 | 20 | 25 |

Tabelle 4. Estación Biológica del Beni, Beni, systematische Aufsammlungen in drei Waldinseln in der Savanne, ca. eine halbe Marschstunde von El Porvenir.

| Familie | Gattung/Art |
|---|---|
| Amaurobiidae | gen.? sp. |
| Anyphaenidae | gen.n. sp. |
| | *Hibana discolor* (Mello-Leitão) |
| | *Teudis* sp. |
| | *Wulfila* sp. |
| Aphantochilidae | *Aphantochilus rogersi* O.P.Cambridge |
| | *Majellula* sp. |
| Araneidae | *Acacesia* sp. |
| | *Alpaida* sp.1 |
| | *Alpaida* sp.2 |
| | *Alpaida tabula* (Simon) |
| | *Alpaida truncata* (Keyserling) |
| | *Araneus* sp. |
| | *Araneus bogotensis* (Keyserling) |
| | *Araneus guttatus* (Keyserling) |
| | *Argiope* sp. |
| | *Cyclosa* sp. |
| | cf. *Enacrosoma* sp. |
| | *Eustala* sp.1 |
| | *Eustala* sp.2 |
| | *Gasteracantha cancriformis* (Linnaeus) |
| | *Hypognatha* sp. |
| | *Mangora* sp. |
| | *Kaira* sp. |
| | *Metazygia gregalis* (F.O.P.Cambridge) |
| | *Metazygia erratica* Levi (in press) |
| | *Metazygia ducke* Levi (in press) |
| | *Metazygia ituari* Levi (in press) |
| | *Metazygia lopez* Levi (in press) |
| | *Metazygia peckorum* Levi (in press) |
| | *Micrathena peregrinatora* (Holmberg) |
| | *Micrathena* sp.1 |
| | *Micrathena* sp.2 |
| | *Micrathena* sp.3 |
| | *Parawixia audax* (Blackwall) |
| | *Parawixia kochi* (Taczanowski) |
| | *Verrucosa* sp.1 |
| | *Verrucosa* sp.2 |
| | *Wagneriana* sp. |
| *Clubionidae* | *Elaver* sp.1 |
| | *Elaver* sp.2 |
| *Corinnidae* | *Apochinomma* sp. |
| | *Castianeira* sp.1 |
| | *Castianeira* sp.2 |
| | *Castianeira* sp.3 |
| | *Castianeira* sp.4 |
| | *Castianeira* sp.5 |
| | *Corinna* sp. |
| | *Myrmecotypus* sp. |
| | *Parachemmis* sp. |
| | *Trachelopachys* sp. |
| Ctenidae | *Ctenus* sp. |

| Familie | Gattung/Art |
|---|---|
| | *Ctenus maculisternis* STRAND |
| | *Ctenus taeniatus* KEYSERLING |
| | gen.? sp. |
| | *Phoneutria* sp. |
| Dictynidae | *Thallumetus* sp. |
| Dipluridae | *Diplura* sp. |
| | *Ischnothele* sp. |
| Gnaphosidae | *Cesonia* sp. |
| | *Eilica* sp. |
| | cf.*Zimiromus* sp. |
| Hahniidae | sp. |
| Hersiliidae | *Tama* sp. |
| Heteropodidae | gen.*?* sp. |
| | *Olios* sp. |
| | *Polybetes* sp. |
| | *Sparianthinae* sp.1 |
| | *Sparianthinae* sp.2 |
| Linyphiidae | *Meioneta* sp. |
| | sp.1 |
| | sp.2 |
| | sp.3 |
| Liocranidae | *Orthobula* sp. |
| Lycosidae | *Lycosa* sp. |
| | *Porrimosa* sp. |
| | sp.1 |
| | sp.2 |
| | sp.3 |
| | sp.4 |
| | sp.5 |
| | sp.6 |
| | sp.7 |
| Mimetidae | *Ero* sp. |
| | *Gelanor* sp. |
| Miturgidae | *Eutichurus* sp. |
| | *Teminius* sp. |
| Mysmenidae | *Mysmenopsis* sp. |
| Oonopidae | *Gamasomorphinae* sp. |
| | sp.1 |
| | sp.2 |
| Oxyopidae | gen.? sp.1 |
| | *Oxyopes* sp. |
| | *Schaenioscelis* sp. |
| | *Tapinillus* sp. |
| Palpimanidae | *Otiothops* sp. |
| Philodromidae | *Cleocnemis* sp. |
| | gen.*?* sp. |
| Pholcidae | cf.*Physocyclus* sp. |
| | gen.*?* sp. |
| Pisauridae | *Ancylometes* sp. |
| | *Architis* sp. |
| | *Staberius* sp. |
| | *Thaumasia* sp. |
| Salticidae | *Bellota* sp. |
| | *Chira* sp.1 |
| | *Chira* sp.2 |
| | *Euophrys* sp. |
| | fisidentatae sp.1 |
| | fisidentatae sp.2 |
| | fisidentatae sp.3 |
| | formiciform sp.1 |
| | formiciform sp.2 |
| | *Lyssomanes* sp. |
| | *Menemerus* sp. |
| | *Myrmarachne* sp. |
| | *Noegus* sp. |
| | *Phiale gratiosa* C.L.KOCH |
| | *Phiale tristis* MELLO-LEITÃO |
| | pluridentatae div. sp. |
| | *Psecas* cf.*chapoda* (PECKHAM) |
| | *Psecas* sp. |
| | *Rudra* sp.n. |
| | *Sarinda camba* GALIANO |
| | *Sarinda nigra* PECKHAM |
| | *Scoturius* sp. |
| | sp. (prox.*Wedoquella/Nycerella)* |
| | *Synemosyna* sp. |
| | *Thiodina* sp. |
| | unidentatae div. sp. |
| Scytodidae | *Scytodes* sp. |
| Selenopidae | *Selenops* sp. |
| Senoculidae | *Senoculus* sp. |
| Tetragnathidae | *Leucauge* sp. |
| | *Leucauge argyra* (WALCKENAER) |
| | *Nephila clavipes* (LINNAEUS) |
| | *Tetragnatha* sp. |
| Theridiidae | *Achaearanea* sp.a |
| | *Achaearanea* sp.b |
| | *Achaearanea* sp.c |
| | *Achaearanea* sp.e |
| | *Achaearanea* sp.f |
| | *Achaearanea* sp.j |
| | *Achaearanea* sp.n.1 |
| | *Achaearanea* sp.n.2 |
| | *Anelosimus studiosus* (HENTZ) |
| | *Argyrodes americanus* (TACZANOWSKI) |
| | *Argyrodes attenuatus* (O.P.CAMBRIDGE) |
| | *Argyrodes* sp. |
| | *Chrysso sulcata* (KEYSERLING) |
| | *Dipoena kuyuwini* LEVI |
| | *Dipoena* sp.1 |
| | *Dipoena* sp.2 |
| | *Enoplognatha* sp. |
| | *Episinus cognatus* O.P.CAMBRIDGE |
| | *Euryopis taczanowskii KEYSERLING* |
| | sp.a |
| | sp.b |
| | sp.c |
| | sp.d |
| | sp.e |
| | sp.f |

| Familie | Gattung/Art |
|---|---|
| | sp.g |
| | sp.h |
| | *Steatoda* sp. |
| | *Styposis selis* Levi |
| | *Tekellina bela* Marques & Buckup |
| | *Theridion* sp. |
| | *Thwaitesia* sp. |
| | *Thymoites* sp. |
| | *Tidarren haemorrhoidale* (Bertkau) |
| Theridiosomatidae | *Ogulnius obtectus* O.P.Cambridge |
| | *Naatlo* sp. |
| | sp.1 |
| | sp.2 |
| Thomisidae | *Acentroscelus* sp. |
| | Misumeninae sp. |
| | aff. *Misumenops* sp.1 |
| | aff. *Misumenops* sp.2 |
| | *Strophius* sp. |
| | *Synaema* sp. |
| | *Synstrophius* sp. |
| | *Tmarus* sp. |
| | *Tobias* sp. |
| Theraphosidae | gen.? sp. |
| Trechaleidae | *Dossenus* sp. |
| | *Trechalea boliviensis* Carico |
| Uloboridae | *Philoponella vittata* (Simon) |
| | *Uloborus trilineatus* Keyserling |
| | *Uloborus* sp. |
| 37 Familien | 189 Morphospezies |

Tabelle 5. Estación Biológica del Beni, Beni, Handsammlungen im Hochwald bei El Trapiche.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Anyphaenidae | | | | |
| gen.? sp. | 1 | | | 1 |
| gen.n.1 sp. | | | 7 | 7 |
| *Patrera* sp. | | | 1 | 1 |
| *Temnida* sp. | | 1 | | 1 |
| *Teudis* sp. | | | 1 | 1 |
| Aphantochilidae | | | | |
| *Aphantochilus rogersi* (O.P.Cambridge) | 1 | | | 1 |
| *Majellula* sp. | | | 1 | |
| Araneidae | | | | |
| *Acacesia* sp. | | | 3 | 3 |
| *Alpaida* sp.1 | | 1 | 1 | 2 |
| *Alpaida* sp.2 | | | 1 | 1 |
| *Alpaida truncata* (Keyserling) | 1 | | | 1 |
| *Araneus* sp. | | | 5 | 5 |
| *Argiope argentata* (Fabricius) | 1 | | | 1 |
| *Cyclosa* sp. | | 2 | | 2 |
| *Eriophora fuliginea* (C.L.Koch) | | 1 | | 1 |
| *Eustala* sp. | | | 6 | 6 |
| gen.? sp.1 | | | 1 | 1 |
| gen.? sp.2 | | | 1 | 1 |
| gen.n. sp. | 1 | | | 1 |
| *Micrathena excavata* (C.L.Koch) | | 1 | 1 | 2 |
| *Parawixia hypocrita* (O.P.Cambridge) | | 1 | | 1 |
| *Parawixia kochi* (Taczanowski) | 1 | 1 | 6 | 8 |
| *Testudinaria* sp. | | | 1 | 1 |
| *Verrucosa* sp. | 1 | | | 1 |
| *Wagneriana jelskii* (Taczanowski) | 1 | 1 | | 2 |
| Clubionidae | | | | |
| *Elaver* sp. | | | 2 | 2 |
| Corinnidae | | | | |
| *Apochinomma* sp. | | | 1 | 1 |
| *Castianeira* sp. | 1 | | | 1 |
| *Corinna* sp. | 1 | 1 | 5 | 7 |
| *Myrmecium* sp. | 1 | 1 | 9 | 11 |
| Ctenidae | | | | |
| *Ctenus maculisternis* Strand | | 1 | 2 | 3 |
| *Ctenus* sp. B1 | | 1 | | 1 |
| gen.? sp. | 1 | | | 1 |
| *Phoneutria boliviensis* (F.O.P.Cambridge) | 1 | | | 1 |
| Deinopidae | | | | |
| *Deinopis* sp. | | | 1 | 1 |
| Dictynidae sp. | | | 1 | 1 |

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Dipluridae | | | | |
| *Ischnothele* sp. | | 1 | 5 | 6 |
| Gnaphosidae gen.? | | | 6 | 6 |
| Hahniidae sp. | | 1 | | 1 |
| Heteropodidae | | | | |
| *Polybetes* sp. | | 1 | 1 | 2 |
| sp. | | | 6 | 6 |
| Idiopidae | | | | |
| *Idiops* sp. | | | 1 | 1 |
| Linyphiidae | | | | |
| sp.1 | | | 2 | 2 |
| sp.2 | | 1 | | 1 |
| Liocranidae | | | | |
| sp. | | 1 | | 1 |
| Lycosidae | | | | |
| *Porrimosa* sp. | | 1 | | 1 |
| sp. | | 1 | 1 | 2 |
| sp. | | 1 | | 1 |
| Mimetidae | | | | |
| *Arocha* sp. | 1 | | | 1 |
| *Gelanor* sp. | 1 | 2 | 1 | 4 |
| Miturgidae | | | | |
| *Eutichurus* sp. | | | 1 | 1 |
| Mysmenidae | | | | |
| *Mysmenopsis* sp. | 6 | 15 | 14 | 35 |
| Oonopidae | | | | |
| sp. | | 1 | | 1 |
| Oxyopidae | | | | |
| *Hamataliwa* sp. | 1 | 1 | 1 | 3 |
| *Oxyopes* sp. | | | 12 | 12 |
| *Schaenioscelis* sp. | | | 4 | 4 |
| Philodromidae | | | | |
| *Berlandiella* sp. | | | 8 | 8 |
| *Pholcidae* sp.1 | | 1 | | 1 |
| sp.2 | 1 | | | 1 |
| sp.3 | | 1 | | 1 |
| Pisauridae | | | | |
| *Architis* sp. | | | 6 | 6 |
| sp. | | | 3 | 3 |
| Salticidae | | | | |
| *Breda* sp. | 1 | | | 1 |
| *Chirothecia* sp. | 1 | 2 | | 3 |
| *Euophrys* sp. | 1 | | | 1 |
| fisidentatae sp. | | 1 | | 1 |
| *Fluda* sp. | 1 | 3 | | 4 |
| grupo Marpissae sp.1 | 2 | 3 | 2 | 7 |
| grupo Marpissae sp.2 | 1 | | | 1 |
| grupo Marpissae sp.3 | | 1 | | 1 |
| *Lyssomanes* sp.1 | 1 | | | 1 |
| *Lyssomanes* sp.2 | | | 9 | 9 |
| *Mago* sp. | 2 | 2 | | 4 |
| *Myrmarachne* sp. | 2 | 1 | 1 | 4 |
| *Neonella* sp. | | 1 | 10 | 11 |
| *Phiale crocea* C.L.Koch | 1 | | | 1 |
| pluridentatae sp. | 2 | | | 2 |
| *Sarinda* sp. | 1 | 1 | | 2 |
| *Synemosyna* sp.1 | 1 | 1 | | 2 |
| *Synemosyna* sp.2 | | 1 | | 1 |
| unidentatae sp.1 | 1 | | | 1 |
| unidentatae sp.2 | 1 | | | 1 |
| unidentatae sp.3 | 1 | | | 1 |
| unidentatae sp.4 | 1 | 2 | | 3 |
| unidentatae sp.5 | 3 | 3 | | 6 |
| unidentatae sp.6 | 1 | 1 | | 2 |
| unidentatae sp.7 | | 1 | | 1 |
| Tetragnathidae | | | | |
| *Glenognatha* sp. | | 1 | | 1 |
| *Leucauge* sp. | | 1 | | 1 |
| *Tetragnatha* sp. | 3 | 2 | 1 | 6 |
| Theridiidae | | | | |
| *Achaearanea* sp.1 | | 1 | 1 | |
| *Achaearanea* sp.2 | | | 1 | 1 |
| *Achaearanea* sp.3 | | 1 | | 1 |
| *Achaearanea trapezoidalis* (Taczanowski) | 1 | | | 1 |
| *Argyrodes attenuatus* (O.P.Cambridge) | 1 | | 1 | 2 |
| *Argyrodes metaltissimus* (Soares & Camargo) | 1 | 2 | | 3 |
| *Argyrodes* sp.1 | | 1 | | 1 |
| *Argyrodes* sp.2 | | | 1 | 1 |
| *Cerocida ducke* Marques & Buckup | 4 | 5 | | 9 |
| *Dipoena alta* Keyserling | | 1 | | 1 |
| *Dipoena atlantica ?* | 1 | 1 | | 2 |
| *Dipoena* sp.1 | | 2 | 2 | 4 |
| *Dipoena* sp.2 | | 1 | | 1 |
| *Enoplognatha* sp. | | 6 | | 6 |
| *Episinus cognatus* O.P.Cambridge | 1 | | | 1 |
| *Episinus erythrophtalmus* (Simon) | 4 | 7 | 3 | 14 |
| *Episinus* sp.1 | | 2 | | 2 |
| gen.? sp. | | 2 | | 2 |
| *Helvibis germaini* Simon | 5 | 2 | | 7 |
| *Spintharus flavidus* Hentz | | 2 | | 2 |
| *Tekelina bela* Marques & Buckup | 1 | | | 1 |
| *Theridion crispulum* Simon | | 1 | | 1 |
| *Theridion petrum* Levi | 1 | 3 | | 4 |
| *Theridion* sp.1 | 1 | 1 | | 2 |
| *Theridion* sp.2 | | 1 | | 1 |
| *Theridion* sp.3 | | | 1 | 1 |
| *Theridion* sp.4 | | | 1 | 1 |
| *Theridion* sp.5 | | | 2 | 2 |
| *Tidarren haemorrhoidale* (Bertkau) | | 1 | | 1 |
| Thomisidae | | | | |
| *Acentroscelus* sp.n. | | 1 | | 1 |
| *Epicadus* sp. | 2 | | | 2 |

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| gen. aff. *Titidius* sp. | 1 | | 1 | 2 |
| *Onoculus echinatus* (Taczanowski) | 1 | | | 1 |
| *Stephanopoides* sp.1 | 1 | | 2 | 3 |
| *Stephanopoides* sp.2 | | | 1 | 1 |
| Thomisinae sp. | | 1 | | 1 |
| *Titidius quinquenotatus* Mello-Leitão | | 1 | | 1 |
| *Tmarus* sp. | | | 19 | 19 |
| *Tobias* sp.1 | | | 1 | 1 |
| *Tobias* sp.2 | 1 | | | 1 |
| Uloboridae | | | | |
| *Miagrammopes* sp. | | | 2 | 2 |
| *Philoponella republicana* (Simon) | 6 | 25 | | 31 |
| *Philoponella* sp. | 1 | | | 1 |
| 29 Familien | | | | |
| 133 Morphospezies | 82 | 97 | 193 | 372 |

Tabelle 6. Sapecho, La Paz, 400 m ü. NN, Handaufsammlungen: 18.7.93, 30.07.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Anyphaenidae | | | | |
| Anyphaeninae sp. | | | 3 | 3 |
| Araneidae | | | | |
| *Alpaida* aff. *truncata* | | | 2 | 2 |
| *Alpaida* sp. 2 | | | 2 | 2 |
| *Argiope* sp. | 2 | 2 | | 4 |
| *Chaetacis* sp. | | | 1 | 1 |
| *Cyclosa* sp. | | 3 | 1 | 4 |
| *Eustala* sp. | | 1 | 4 | 5 |
| *Mangora* sp. | | | 1 | 1 |
| *Metazygia* aff. *laticeps* | | 1 | 1 | 2 |
| *Micrathena* sp. | | | 1 | 1 |
| *Parawixia* sp. | | | 1 | 1 |
| *Wagneriana* sp. | | | 1 | 1 |
| Clubionidae | | | | |
| *Elaver* sp. | | | 1 | 1 |
| *Cheiracanthium inclusum* (Hentz) | | | 1 | 1 |
| Corinnidae | | | | |
| *Apochinomma* sp. | | | 1 | 1 |
| *Corinna* sp.1 | | 1 | | 1 |
| *Corinna* sp.2 | | 1 | | 1 |
| *Myrmecium* sp. | | 1 | | 1 |
| *Parachemmis* sp. | | | 1 | 1 |
| Ctenidae | | | | |
| *Ctenus* sp. | | 1 | 2 | 3 |
| Dipluridae | | | | |
| *Ischnothele* sp. | | 1 | | 1 |
| Heteropodidae | | | | |
| *Polybetes* sp. | 1 | | 1 | 2 |
| gen. 1 sp. | | | 3 | 3 |
| gen. 2 sp. | | | 2 | 2 |
| Linyphiidae | | | | |
| *Dubiaranea* sp. | 2 | | 1 | 3 |
| *Exechopsis* sp. | 1 | | | 1 |
| Liocranidae | | | | |
| gen.? sp. | | | 3 | 3 |
| Lycosidae | | | | |
| sp. | | 1 | 1 | 2 |
| Mimetidae | | | | |
| *Ero* sp. | 1 | | | 1 |
| Oonopidae | | | | |
| Gamasomorphinae sp. | | 1 | | 1 |
| Oxyopidae | | | | |
| gen.*?* sp. | | | 1 | 1 |
| *Hamataliwa* sp. | | | 1 | 1 |
| *Peucetia* sp. | 1 | 1 | | 2 |
| Pholcidae | | | | |
| sp.1 | 1 | | | 1 |
| sp.2 | 1 | | 3 | 4 |
| *Physocyclus* sp. | 4 | 1 | 6 | 11 |
| Pisauridae | | | | |
| sp. | | | 5 | 5 |
| Salticidae | | | | |
| *Chira* sp. | 1 | | 4 | 5 |
| *Sarinda camba* Galiano | 1 | | | 1 |
| *Tullgrenella* sp. | 1 | | 1 | 2 |
| unidentatae sp. | 1 | | 1 | 2 |
| fisidentatae sp. | | 1 | | 1 |
| pluridentatae sp. | 1 | | 2 | 3 |
| Tetragnathidae | | | | |
| *Chrysometa guttata* (Keyserling) | 1 | | | 1 |
| *Leucauge* sp. | | | 1 | 1 |
| Theridiidae | | | | |
| *Achaearanea* sp. | | | 4 | 4 |
| *Steatoda diamantina* Levi | 1 | 1 | | 2 |
| *Theridion* sp.1 | | 1 | | 1 |
| *Theridion* sp.2 | | 1 | | 1 |
| Theridiosomatidae | | | | |
| *Naatlo splendida* (Taczanowski) | 1 | 3 | | 4 |
| Thomisidae | | | | |
| *Thomisinae* sp. | | | 1 | 1 |
| Uloboridae | | | | |
| *Uloborus* sp. | 1 | 1 | 4 | 6 |
| 21 Familien | | | | |
| 52 Morphospezies | 23 | 23 | 70 | 116 |

Tabelle 7. Tal des Rio Huarinilla, nahe Coroico, La Paz, 1200 - 1500 m ü. NN, Handaufsammlungen: 1.08.- 2.08.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Anyphaenidae | | | | |
| gen.n.1 sp. | | 1 | 10 | 11 |
| *Tafana* sp. | | | 1 | 1 |
| gen.n.2 sp. | | | 1 | 1 |
| *Wulfila modesta* CHICKERING | 1 | | | 1 |
| Aphantochilidae | | | | |
| *Majellula* sp. | | 4 | | 4 |
| Araneidae | | | | |
| *Acacesia* sp. | | | 7 | 7 |
| *Alpaida bicornuta* (TACZANOWSKI) | | | 3 | 3 |
| *Alpaida* sp. | 1 | | | 1 |
| *Alpaida* sp.? | | | 2 | 2 |
| *Araneus* sp. | | | 1 | 1 |
| *Eustala* sp.1 | 1 | | 10 | 11 |
| *Eustala* sp.2 | 1 | | 5 | 6 |
| *Hypognatha* sp. | | | 2 | 2 |
| *Mangora* sp. | 1 | | 1 | 2 |
| *Metazygia yobena* LEVI (in press) | | 1 | | 1 |
| *Micrathena* aff. *agriliformis* | 1 | | 4 | 5 |
| *Ocrepeira* sp. | | | 1 | 1 |
| *Parawixia* sp. | | | 5 | 5 |
| Araneidae | | | | |
| *Wagneriana* sp. | | | 6 | 6 |
| Clubionidae | | | | |
| *Elaver* sp. | | | 2 | 2 |
| Corinnidae | | | | |
| *Apochinomma* sp. | 1 | | | 1 |
| *Castianeira* sp. | 1 | | | 1 |
| *Corinna* sp.1 | 1 | | 2 | 3 |
| *Corinna* sp.2 | | | 6 | 6 |
| *Myrmecium* sp.1 | 1 | | 2 | 3 |
| *Myrmecium* sp.2 | | 1 | | 1 |
| *Myrmecotypus* sp. | | | 1 | 1 |
| *Trachelas* sp. | 1 | 1 | 1 | 3 |
| Ctenidae | | | | |
| *Ctenus* sp. | | | 3 | 3 |
| Deinopidae | | | | |
| *Deinopis* sp. | | | 1 | 1 |
| Dictynidae | | | | |
| *Dictyna* sp. | | 1 | | 1 |
| Heteropodidae | | | | |
| *Polybetes* sp. | | 1 | | 1 |
| Linyphiidae | | | | |
| *Dubiaranea* sp. | | 3 | 1 | 4 |
| *Meioneta* sp. | 1 | 2 | | 3 |
| Lycosidae | | | | |
| *Porrimosa* sp. | | 1 | | 1 |
| sp.1 | | | 1 | 1 |
| sp.2 | | 1 | | 1 |
| Mimetidae | | | | |
| *Arocha* sp. | 3 | | | 3 |
| *Ero* sp. | 1 | 1 | 1 | 3 |
| *Gelanor* sp. | | 2 | | 2 |
| Miturgidae | | | | |
| *Eutichurus* sp. | | | 1 | 1 |
| Oxyopidae | | | | |
| *Hamataliwa* sp. | | | 2 | 2 |
| Philodromidae | | | | |
| *Berlandiella* sp. | | | 7 | 7 |
| Pholcidae | | | | |
| *Blechroscelis* sp. | | 1 | | 1 |
| sp.1 | 1 | 1 | | 2 |
| sp.2 | 1 | 4 | | 5 |
| Pisauridae | | | | |
| sp. | 1 | | 4 | 5 |
| Salticidae | | | | |
| aff. *Euophrys* sp. | | 1 | | 1 |
| *Bellota* sp.1 | 8 | 1 | 4 | 13 |
| *Bellota* sp.2 | 2 | | | 2 |
| *Breda* sp.1 | 3 | | | 3 |
| *Breda* sp.2 | 1 | 1 | | 2 |
| *Chira* sp.1 | | 1 | | 1 |
| *Chira* sp.2 | | 1 | | 1 |
| *Chira spinosa* (MELLO-LEITÃO) | 1 | | | 1 |
| *Coryphasia* sp.1 | 8 | 1 | 4 | 13 |
| *Eustiromastix moraballi* MELLO-LEITÃO | 1 | | | 1 |
| fisidentatae sp.1 | | | 1 | 1 |
| fisidentatae sp.2 | | 1 | | 1 |
| *Fluda* sp. | 1 | | | 1 |
| *Hisukatus* sp. | 2 | | | 2 |
| *Mago steindacheri* (TACZANOWSKI) | 9 | 6 | | 15 |
| *Sarinda camba* GALIANO | 2 | | | 2 |
| *Sarinda nigra* PECKHAM | 3 | | | 3 |
| *Sarinda* sp. | | | 4 | 4 |
| *Scopocira* sp. | 2 | | 1 | 3 |
| *Siloca* sp. | 1 | | | 1 |
| *Synemosyna* sp.1 | 1 | | | 1 |
| *Synemosyna* sp.2 | | 1 | 1 | 2 |
| *Thiodina* sp. | 1 | | | 1 |
| *Tullgrenella* sp.1 | | 1 | | 1 |
| *Tullgrenella* sp.2 | 1 | | 1 | 2 |
| unidentatae sp.1 | | 1 | 4 | 5 |
| unidentatae sp.2 | | 1 | | 1 |
| unidentatae sp.3 | | 1 | | 1 |
| unidentatae sp.4 | 1 | | | 1 |
| unidentatae sp.5 | 1 | | | 1 |
| unidentatae sp.6 | 1 | | | 1 |
| Scytodidae | | | | |
| *Scytodes* sp. | | | 1 | 1 |
| Senoculidae | | | | |
| *Senoculus* sp. | | | 7 | 7 |

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Tetragnathidae | | | | |
| *Leucauge* sp. | | 2 | | 2 |
| *Tetragnatha* sp. | 2 | | 4 | 6 |
| Theridiidae | | | | |
| *Achaearanea migrans* (KEYSERLING) | | 1 | | 1 |
| *Achaearanea uviana* LEVI | 1 | | | 1 |
| *Argyrodes* sp. | | 1 | | 1 |
| *Steatoda chinchipe* LEVI | | 3 | | 3 |
| *Thymoites* sp. | | 1 | | 1 |
| *Tidarren* cf. *haemorrhoidale* (BERTKAU) | | 3 | | 3 |
| Theridiosomatidae | | | | |
| *Ogulnius* sp. | 1 | 4 | 1 | 6 |
| Thomisidae | | | | |
| *Acentroscelus* aff. *guyanensis* | | 1 | | 1 |
| aff. *Titidius* sp. | 4 | 1 | 2 | 7 |
| *Epicadus* sp. | | | 1 | 1 |
| *Misumenops* sp. | | | 3 | 3 |
| *Stephanopoides* sp. | | | 6 | 6 |
| *Strophius fidelis* | | 1 | 1 | 2 |
| *Strophius* sp. | | | 1 | 1 |
| *Synaema* sp.1 | 2 | | | 2 |
| *Synaema* sp.2 | 1 | | 3 | 4 |
| *Tmarus* sp. | | 1 | 2 | 3 |
| *Tobias* sp. | | | 1 | 1 |
| Trechaleidae | | | | |
| *Trechalea* sp. | 5 | 7 | 10 | 22 |
| Uloboridae | | | | |
| *Miagrammopes* sp. | 2 | | 1 | 3 |
| *Uloborus* sp. | 2 | | 2 | 4 |
| 26 Familien | | | | |
| 105 Morphospezies | 89 | 70 | 160 | 319 |

Tabelle 8. Cotapata, an der Straße La Paz - Coroico, 3500 m ü. NN, Handfänge: 16.7.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Agelenidae ? | | | | |
| sp. | | 1 | | 1 |
| Anyphaenidae | | | | |
| gen.n.1 sp. | | 1 | | 1 |
| *Josa* sp. | 3 | 2 | 3 | 8 |
| Amaurobiidae | | | | |
| sp. | | | 1 | 1 |
| Araneidae | | | | |
| *Araneus* sp. | | | 3 | 3 |
| Corinnidae | | | | |
| *Trachelopachys* sp. | | 1 | | 1 |
| Linyphiidae | | | | |
| *Meioneta* sp. | | 2 | | 2 |
| *Dubiaranea* sp. | | 2 | 1 | 3 |
| Salticidae | | | | |
| *Tullgrenella* sp. | | 1 | | 1 |
| unidentatae sp. | 1 | 1 | | 2 |
| Segestriidae | | | | |
| sp. | | 2 | | 2 |
| Theridiidae | | | | |
| *Enoplognatha* sp. | | 1 | 3 | 4 |
| 9 Familien | | | | |
| 12 Morphospezies | 4 | 14 | 11 | 29 |

Tabelle 9. Valle de Zongo, Sainani, 2000 m ü. NN, Handfänge: 4.8. - 5.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Amaurobiidae | | | | |
| gen.? sp. | 1 | 1 | | |
| Anyphaenidae | | | | |
| gen.n.2 sp. | 1 | | 1 | 2 |
| gen.n.3 sp.1 | 1 | | | 1 |
| gen.n.3 sp.2 | 1 | | | 1 |
| *Josa* sp. | | 1 | 1 | 2 |
| *Tafana* sp. | | 2 | 2 | 4 |
| *Teudis* sp. | | | 1 | 1 |
| Araneidae | | | | |
| *Acacesia* sp. | | 1 | 4 | 5 |
| *Araneus bogotensis* (Keyserling) | | 1 | 1 | 2 |
| *Cyclosa* sp. | 1 | 4 | 1 | 6 |
| *Eustala* sp. | 1 | 2 | 2 | 5 |
| *Metazygia* sp. | | | 2 | 2 |
| *Micrathena* sp. | | 1 | 2 | 3 |
| *Parawixia* sp. | | | 3 | 3 |
| Corinnidae | | | | |
| *Castianeira* sp. | | | 1 | 1 |
| *Corinna* sp. | | 2 | | 2 |
| Ctenidae | | | | |
| *Ctenus* sp. | | 4 | 1 | 5 |
| Hahniidae | | | | |
| sp. | | 1 | | 1 |
| Linyphiidae | | | | |
| *Dubiaranea* sp.1 | | 1 | 6 | 7 |
| *Dubiaranea* sp.2 | | 1 | | 1 |
| *Dubiaranea* sp.3 | | 1 | | 1 |
| gen.1 sp.1 | 14 | 11 | | 25 |
| gen.2 sp.1 | 3 | 2 | | 5 |
| gen.2 sp.2 | | 2 | | 2 |
| *Laminacauda* sp. | 2 | 4 | | 6 |
| Lycosidae | | | | |
| sp. | | | 1 | 1 |
| Miturgidae | | | | |
| *Eutichurus* sp. | 1 | 1 | | 2 |
| Oonopidae | | | | |
| *Gamasomorphinae* sp. | | 3 | | 3 |
| Oxyopidae | | | | |
| sp. | | 1 | 1 | 2 |
| Pholcidae | | | | |
| sp. | | 3 | | 3 |
| Salticidae | | | | |
| *Bellota* sp.1 | 2 | 1 | 1 | 4 |
| *Bellota* sp.2 | 5 | 3 | 6 | 14 |
| *Phiale crocea* C.L.Koch | 1 | | | 1 |
| *Sarinda* sp. | | 1 | 1 | 2 |
| unidentatae sp.1 | 5 | 7 | 3 | 15 |
| unidentatae sp.2 | 1 | | | 1 |
| Scytodidae | | | | |
| *Scytodes* sp. | 1 | | | 1 |
| Tetragnathidae | | | | |
| *Chrysometa* sp.1 | 1 | | 1 | 2 |
| *Chrysometa* sp.2 | | 1 | | 1 |
| *Chrysometa* sp.3 | | 1 | | 1 |
| *Chrysometa* sp.4 | | 1 | | 1 |
| *Leucauge* sp. | 1 | 3 | 3 | 7 |
| *Tetragnatha* sp. | 1 | 3 | 6 | 10 |
| Theridiidae | | | | |
| *Achaearanea* sp. | | 2 | 1 | 3 |
| *Anelosimus studiosus* (Hentz) | | 1 | | 1 |
| *Thymoites* sp. | 1 | 1 | | 2 |
| Theridiosomatidae | | | | |
| *Ogulnius obtectus* O.P.Cambridge | 1 | 1 | 2 | 4 |
| Thomisidae | | | | |
| *Thomisinae* sp. | | 1 | | 1 |
| Uloboridae | | | | |
| *Philoponella* sp. | | | 2 | 2 |
| *Uloborus* sp. | | 2 | | 2 |
| 20 Familien | | | | |
| 50 Morphospezies | 44 | 80 | 56 | 180 |

Tabelle 10. Valle de Zongo, ceja/puna húmeda, 3200 m ü. NN: Handfänge 5.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Amaurobiidae | | | | |
| gen.? sp. | | 2 | | 2 |
| Anyphaenidae | | | | |
| *Gayenna* sp. | | 5 | | 5 |
| gen.n.3 sp.1 | 3 | 3 | 14 | 20 |
| gen.n.3 sp.2 | | 1 | | 1 |
| *Josa* sp. | | | 3 | 3 |
| *Tomopisthes* sp. | | 3 | | 3 |
| Araneidae | | | | |
| *Araneus* aff. *carchi* | 1 | 2 | 9 | 12 |
| *Araneus bogotensis* (Keyserling) | | 2 | 3 | 5 |
| *Eustala* sp. | | | 5 | 5 |
| Corinnidae | | | | |
| *Cetonana* sp. | | 1 | | 1 |
| *Trachelopachys* sp. | | | 1 | 1 |
| Desidae | | | | |
| *Naevius* sp.n. | 1 | 2 | 1 | 4 |
| Gnaphosidae | | | | |
| *Apopyllus silvestrii* (Simon) | | 1 | 2 | 3 |
| Linyphiidae | | | | |
| *Dubiaranea* sp.1 | 7 | 6 | 22 | 35 |
| *Dubiaranea* sp.2 | 7 | 8 | | 15 |
| *Dubiaranea* sp.3 | 3 | 1 | | 4 |
| gen.? sp. | 1 | | | 1 |
| *Gymnocymbium* sp. | 6 | 10 | 6 | 22 |
| Pisauridae | | | | |
| sp. | | | 1 | 1 |
| Salticidae | | | | |
| *Euophrys* sp. | 1 | | | 1 |
| Salticidae | | | | |
| unidentatae sp. | | 1 | 6 | 7 |
| Segestriidae | | | | |
| sp. | 1 | 1 | 1 | 3 |
| Tetragnathidae | | | | |
| *Chrysometa* sp.1 | 5 | 11 | 8 | 24 |
| *Chrysometa* sp.2 | 1 | | | 1 |
| *Tetragnatha* sp. | 4 | 5 | 4 | 13 |
| Thomisidae | | | | |
| *Sidymella* aff. *obscura* | 1 | | 1 | 2 |
| Thomisinae sp.1 | | | 3 | 3 |
| Thomisinae sp.2 | | | 1 | 1 |
| 12 Familien | | | | |
| 28 Morphospezies | 42 | 65 | 91 | 198 |

Tabelle 11. Valle de Zongo, Laguna Viscachani, 3660 m ü. NN, Handfänge: 5.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Amaurobiidae | | | | |
| gen.? sp. | | 1 | | 1 |
| gen.? | | 4 | | 4 |
| *Metaltella* sp. | | 6 | | 6 |
| *Gayenna* sp. | | 3 | | 3 |
| *Josa* sp. | | 1 | | 1 |
| *Tomopisthes* sp. | | 2 | | 2 |
| Corinnidae | | | | |
| *Cetonana* sp. | | 1 | | 1 |
| *Trachelopachys* sp. | | | 1 | 1 |
| Gnaphosidae | | | | |
| *Apopyllus silvestrii* (Simon) | | | 5 | 5 |
| gen.? sp. | | | 1 | 1 |
| Linyphidae | | | | |
| *Gymnocymbium* sp. | | 1 | | 1 |
| Lycosidae | | | | |
| sp. | | 9 | 1 | 10 |
| Pholcidae | | | | |
| sp.2 | 1 | | 1 | 2 |
| Salticidae | | | | |
| *Tullgrenella* sp. | 1 | 2 | 1 | 4 |
| Segestriidae | | | | |
| sp. | | 11 | 4 | 15 |
| Theraphosidae | | | | |
| gen.? sp. | | 1 | 1 | 2 |
| Theridiidae | | | | |
| *Enoplognatha* sp. | | 6 | 6 | 12 |
| 11 Familien | | | | |
| 17 Morphospezies | 2 | 48 | 21 | 71 |

Tabelle 12. Valle de Zongo, Chacaltaya, 4500 m ü. NN, Handfänge: 5.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Anyphaenidae | | | | |
| *Gayenna* sp. | | 31 | 3 | 34 |
| Corinnidae | | | | |
| *Cetonana* sp. | | 2 | 1 | 3 |
| Linyphiidae | | | | |
| sp. | | 1 | | 1 |
| Lycosidae | | | | |
| *Lycosa* sp. | | 5 | 8 | 13 |
| Lycosidae | | | | |
| sp.*2* | | 2 | | 2 |
| Salticidae | | | | |
| unidentatae sp. | | 1 | | 1 |
| Theridiidae | | | | |
| *Enoplognatha tecta* (KEYSERLING) | | 1 | 2 | 3 |
| Theridiidae | | | | |
| *Steatoda ancorata* (HOLMBERG) | | 2 | 8 | 10 |
| 6 Familien | | | | |
| 8 Morphospezies | 0 | 45 | 22 | 67 |

Tabelle 13. Huatajata, Lago Titicaca, La Paz, 3600 m ü. NN, Handfänge: 8.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Anyphaenidae | | | | |
| *Gayenna* sp.1 | 1 | 44 | 5 | 50 |
| *Gayenna* sp.2 | | 1 | | 1 |
| Araneidae | | | | |
| *Metepeira* sp. | | | 2 | 2 |
| Gnaphosidae | | | | |
| *Apopyllus silvestrii* (SIMON) | 5 | 3 | 1 | 9 |
| Linyphiidae | | | | |
| *Gymnocymbium* sp. | 2 | 11 | 1 | 14 |
| *Laminacauda* sp. | 2 | 2 | | 4 |
| *Meioneta* sp. | | 4 | | 4 |
| Lycosidae | | | | |
| *Lycosa* sp.1 | | 2 | | 2 |
| *Lycosa* sp.2 | 5 | 3 | 2 | 10 |
| *Lycosa* sp.3 | | 5 | | 5 |
| Salticidae | | | | |
| *Tullgrenella* sp. | 1 | 1 | | 2 |
| 6 Familien | | | | |
| 11 Morphospezies | 16 | 76 | 11 | 103 |

Tabelle 14. San Pablo de Tiquina, Lago Titicaca, La Paz, 3600 m ü. NN, Handfänge: 8.8.93.

| Familie | ♂♂ | ♀♀ | juv. | Gesamt |
|---|---|---|---|---|
| Araneidae | | | | |
| *Metepeira* sp. | | 2 | 8 | 10 |
| Corinnidae | | | | |
| *Trachelopachys bicolor* CHAMBERLIN | 2 | 4 | | 6 |
| Gnaphosidae | | | | |
| *Apodrassodes araucanius* (CHAMBERLIN) | | 3 | | 3 |
| Lycosidae | | | | |
| *Lycosa* sp. | | 1 | 1 | 2 |
| Philodromidae | | | | |
| *Cleocnemis* sp. | | | 1 | 1 |
| *Paracleocnemis* sp. | 1 | | | 1 |
| 5 Familien | | | | |
| 6 Morphospezies | 3 | 10 | 10 | 23 |

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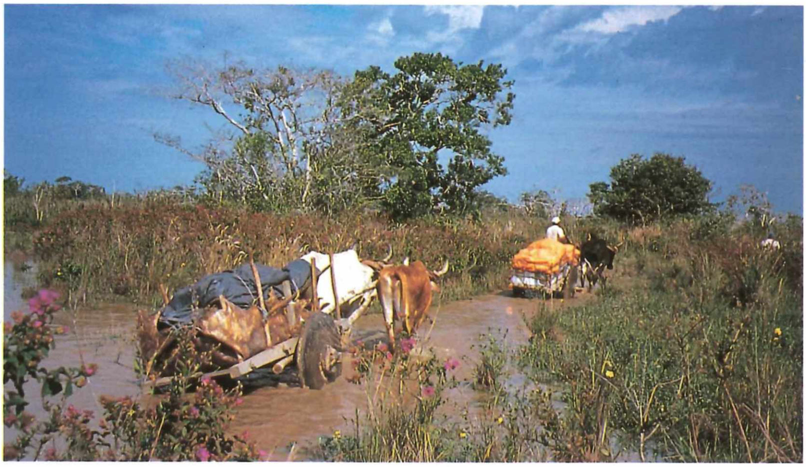

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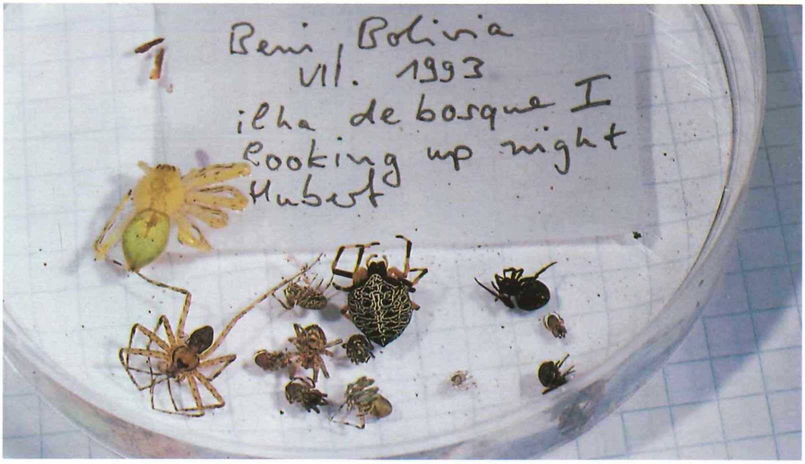

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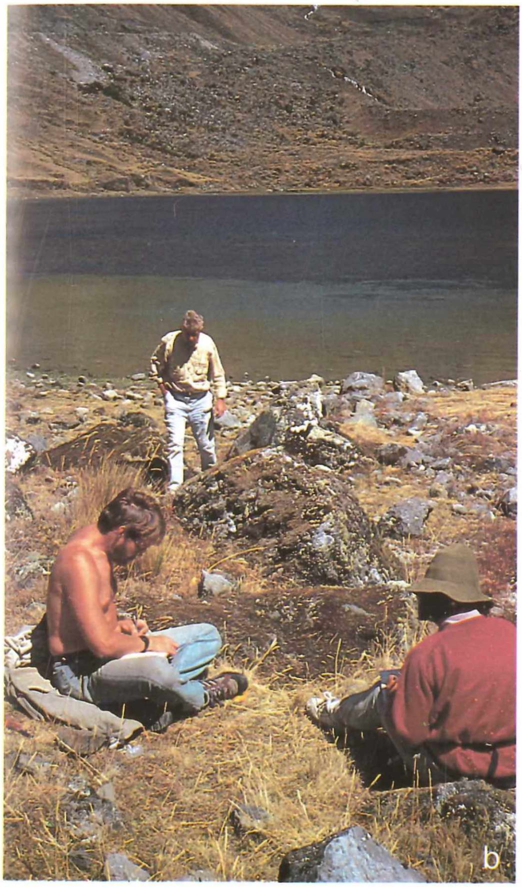

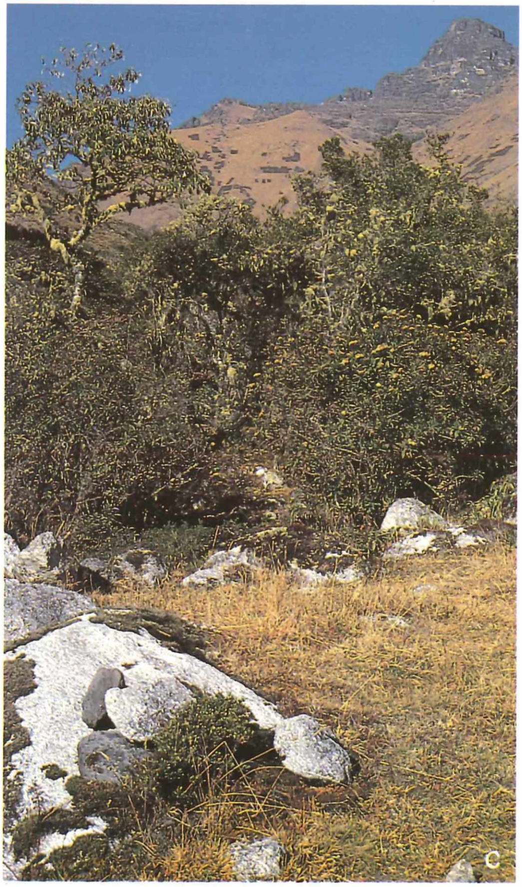

**andrias, 13:** 113-136, 19 Figs; Karlsruhe, 30. 9. 1994

GERHARD BRETFELD & ULRICH GAUER

# Diagnostic description of the males of new *Sphaeridia* species (Insecta, Collembola) from South America

**Abstract**

This description of new *Sphaeridia* species is part of an ecological study of the Collembola of the Amazon inundation forests. The species are described after the male characters. Collections from Colombia and Paraguay supplement those from Brazil. We have added 18 new species to the 14 known in South America, and suggest dividing all the species described into several species groups. The ecology of the new species is briefly characterized. A key considers all species from South America.

**Kurzfassung**

**Diagnostische Beschreibung von Männchen neuer *Sphaeridia*-Arten (Insecta, Collembola) aus Südamerika**

Als erster Schritt zu einer Darstellung der Ökologie der Collembolen der Überschwemmungswälder des Amazonas werden die Arten der Gattung *Sphaeridia* nach den Merkmalen der Männchen beschrieben. Material aus Kolumbien und Paraguay ergänzt die Sammlungen aus Brasilien. Zu den 14 aus Südamerika bekannten Arten kommen 18 neue hinzu. Wir schlagen vor, alle beschriebenen Arten in mehrere Artengruppen aufzuteilen. Die Ökologie der neuen Arten wird kurz charakterisiert. Für alle südamerikanischen Arten ist eine Bestimmungstabelle aufgestellt worden.

**Resumo**

**Descrição diagnostica de machos de espécies novais do gênero *Sphaeridia* (Insecta, Collembola) da América do Sul**

Como primeiro passo para um entendimento da ecologia de colêmbolos em florestas inundáveis da Amazônia, as espécies do gênero *Sphaeridia* são descritas com as características dos machos. O material do Brasil é complementado por material da Colômbia e do Paraguai. Às 14 espécies conhecidas da América do Sul juntam-se 18 novas espécies. Propomos distribuir todos as espécies descritas em alguns grupos de espécies. A ecologia das novas espécies é caracterizada de forma breve. Para todas as espécies da América do Sul é feita uma chave de identificação.

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**Contents**

## 1. Introduction

The soil is an integral and highly diagnostic stratum of terrestrial ecosystems. It is generally rich in arthropods and can be easily studied. In tropical regions knowledge of the soil and its fauna is increasingly important because the destruction of the forests and the ensuing destruction of the soils wipes out numerous species which are both functional components of the ecosystem and the basis for an understanding of its evolution.

Among the arthropods of tropical soils the Collembola are frequent but little known. In large parts of South America, the Collembola are completely unknown; they were mostly found on small scale excursions or as additional catch during ecological studies, and often remained unexamined due to their large numbers and taxonomical problems.

A current ecological study of the Collembola of the inundation forests of central Amazonia by the junior author requires an examination of the taxonomy of some genera of this group.

This paper deals with the genus *Sphaeridia* LINNANIEMI, 1912. We have added 18 new species from Brazil, Colombia, and Paraguay to the 14 known in South America; thus, the number of *Sphaeridia* species of South America increases to 32. We have, for practical purposes, these and the 23 species described from other regions of the world, subdivided into several species groups.

## 2. Material and Methods

The specimens studied belong to four collections:

1. Coll. K. BÖTTGER, Kiel, Germany: Paraguay, one sample taken near Concepción, 1985.
2. Coll. U. GAUER, Karlsruhe, Germany: Brazil, samples from the inundation forests várzea and igapó near Manaus, 1989-1991.
3. Coll. U. IRMLER, Kiel, Germany: Brazil, same locality and biotopes as in coll. GAUER, 1971.
4. Coll. H. STURM, Hildesheim, Germany: Colombia, samples from the Andean páramo regions near Bogotá, 1985, 1986, and 1989.

Types of the following species were also studied (they will be redescribed in a later paper): *Sphaeridia denisi* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, *Sph. schalleri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, *Sph. winteri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, Sph. spec. MASSOUD & DELAMARE DEBOUTTEVILLE, 1964.

In this paper we offer a preliminary description of the males of the new species. We fully describe the ventral tube and tibiotarsus III because these parts show singular species specific characters (MURPHY 1966); these structures may be used during sperm transfer (BLANCQUAERT & MERTENS 1977), but because of their minute dimensions their exact role is unknown and is likely to remain so.

We add some features of the head, antennal segment II and III, and furca to distinguish the males when the ventral tube and tibiotarsus III are similar, and to facilitate the later placement of the females. We did not study the antennae in detail as there were mostly proportional differences between the species.

The following measurements are taken: total length, measured from alcohol specimens, from the antennal base to the posterior tip of the small abdomen; head length from the head apex to the lower edge of the sclerotic margin of the clypeus; antennal segments II and III measured ventrally; dens measured anteriorly, mucro posteriorly. After „Marc André I" as intermedium, „Hoyer's mixture" was the preparation fluid (BRETFELD 1991). The figures of the ventral tube mainly show the posterior side as most of its structures lie on this side. On tibiotarsus III the setae Ia, Ii, Ip, IIIp, Va, Vai, Vp and all secondary ones are missing; in position 2ae and 2pe small papillae without setae are present. The chaetotaxic nomenclature is that of the previous papers of the senior author (BRETFELD 1990, 1992a, 1992b), but counting the setae of dens starts distally with E1, P1, J1 instead of E0, P0, J0; the chaetotaxic nomenclature of the tibiotarsus combines that of the senior author with that of NAYROLLES (1988).

The types have been deposited at the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); the Museo de História Natural, Universidad Nacional de Colômbia, Bogotá, Colômbia (MNCB); the Muséum National d' Histoire Naturelle, Paris/Brunoy, France (MNHN); the Senckenberg Museum, Frankurt/Main, Germany (SMF); and in the authors' collections; the collection GAUER is deposited at the Staatliches Museum für Naturkunde Karlsruhe (SMNK).

**Acknowledgements**
We gratefully acknowledge the opportunity to study the collections of K. BÖTTGER, U. IRMLER, and H. STURM. The junior author expresses his gratitude to the Working Group Tropical Ecology of the Max-Planck-Institut for Limnology, Plön, Germany, and the Instituto Nacional de Pesquisas da Amazônia, INPA, Manaus, Brazil, for supporting his stay in Manaus. Our thanks are also due to J.-M. BETSCH for lending types of *Sphaeridia* species. We thank P. F. BELLINGER, Northridge, J.-M. BETSCH, Brunoy, W. N. ELLIS, Amsterdam, and H. STURM, Hildesheim, for their valuable comments on our manuscript. We thank also Mrs. D. OLIMART, who made the ink drawings of the figures (except Fig. 1, which is drawn by the junior author), and D. O'BRIEN, who corrected our English.

## 3. History

The view that only the Palaearctic or Holarctic *Sphaeridia pumilis* (KRAUSBAUER) occurs in South America (summary in MARI MUTT & BELLINGER 1990) was refuted by MASSOUD & DELAMARE DEBOUTTEVILLE, who in 1964 noted the special setae of the male tibiotarsus III and described three new species (*denisi, schalleri, winteri*) and an unnamed male (spec.) from the Peruvian Amazon lowland and the Andean Amazon region. In the same year, 1964, DELAMARE DEBOUTTEVILLE & MASSOUD added *Sph. gladiolifer* and an uncertain *Sph. pumilis* from Surinam. In 1966, MURPHY introduced the study of the male ventral tube structures. Then, in 1984, ARLÉ described another six new species from Southern Brazil (*betschi, cardosi, carioca, fluminensis, heloisae, paroara*), he mentioned *Sph. biniserrata* (SALMON) from Minas Gerais and Rio de Janeiro, and noted specimens looking like *Sph. pumilis* (KRAUSBAUER). The last species described from South America was *Sph. aserrata* by MARI MUTT 1987

The problematic group remains „*Sphaeridia pumilis* (KRAUSBAUER)", the males of which have only 1+1 small vesicles on the posterior ventral tube (this is also the only special structure of the female ventral tube of

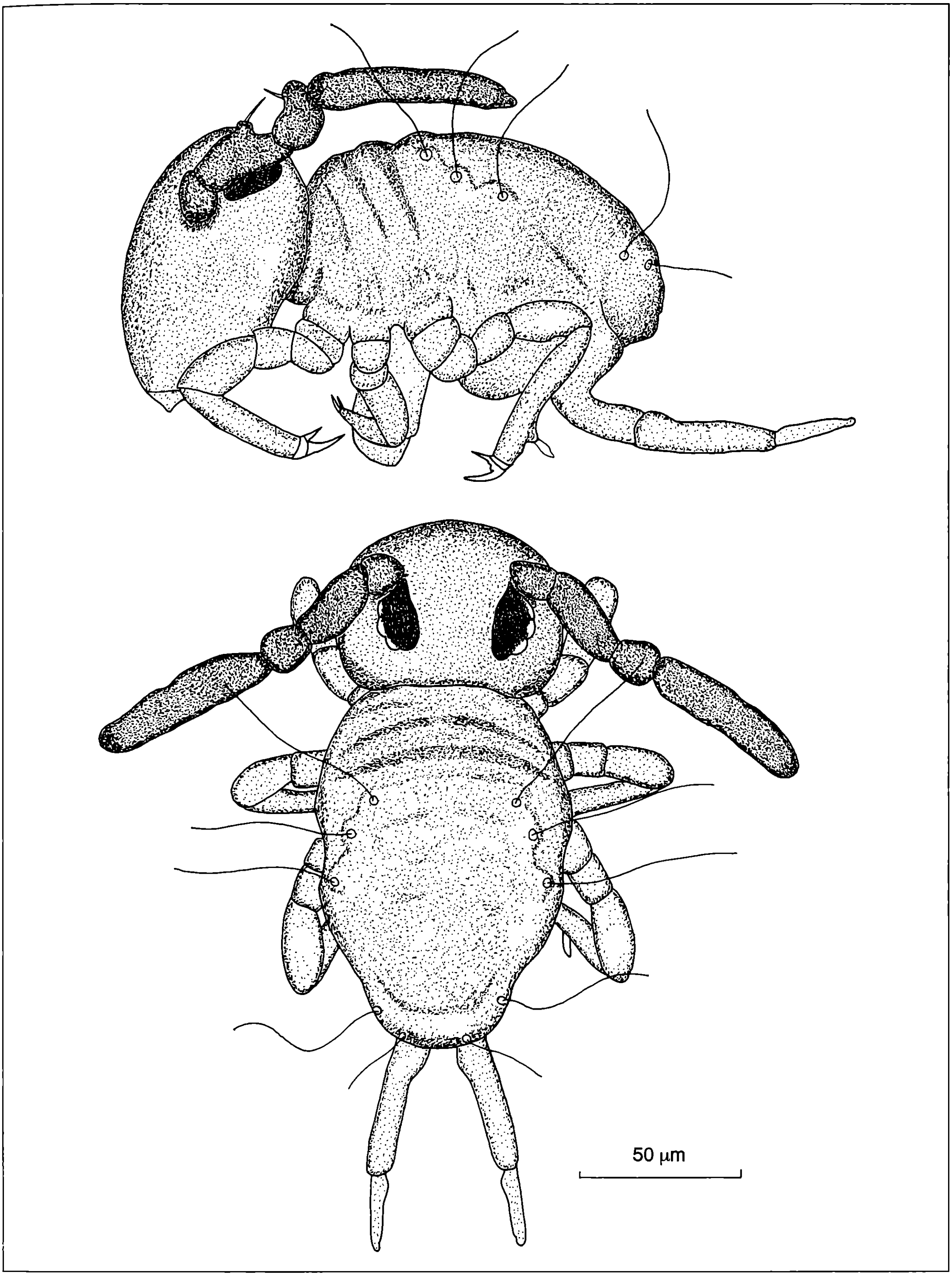


Figure 1. *Sphaeridia squamifera* n. sp.: male: habitus

all known *Sphaeridia* species) and an outer, long seta (IIpe) besides other normal ones on the tibiotarsus III (these characters apply to specimens from Western Europe, see Dunger & Bretfeld 1989). This „species“ has been found in large parts of South America (Mari Mutt & Bellinger 1990). Our material also contains such specimens, but characters other than those of ventral tube and tibiotarsus III allow us to distinguish several new species.

## 4. Description of the new species

### 4.1 The species from Brazil

### *Sphaeridia cerastes* nov. spec.

Type locality: Brazil, Amazonas, Manaus.
Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 3. X. 1989 leg. Gauer (no. 3.1.2. II F), at INPA. – Paratypes: 1 male (slide) from the holotype sample, in coll. Bretfeld; 1 male (slide), same locality, 29. VIII. 1989 leg. Gauer (no. 3.1.2.), in coll. Gauer; 5 males (slides), same locality, 10. – 24. IX. 1971 leg. Irmler, 1 and 2 m above water level: 1 (3 slides) at SMF (Ap 2419), 1 at MNHN, 2 at INPA (these 4 have coll. Bretfeld no. 26/90), 1 in coll. Bretfeld (no. 25/90).
Further material: 1 male (slide), Brazil, Amazonas, Manaus, Ilha de Marchantaria, soil from Várzea forest, 17 I. 1991 leg. Gauer (no. 1.2.1. K 10), at INPA.

Total male 0.2 mm, dark blue (sometimes only laterally). Ventral tube (Fig. 2 a, b, c) posteriorly with 1+1 round vesicles and a slightly knobbed, median process; anteriorly with 1+1 lateral processes bifurcated at their tips; 1+1 setae. Tibiotarsus III with normal setae, only IIpe slightly longer and stronger than others. Head frons setae a+d 2, 3, 4 and b+c 2 with thickened basal half (Fig. 2 d). Dens as in Fig. 4 c, but seta E1 long; tip of mucro a shrunk cap (Fig. 2 e); dens  mucro = 2.6.
The name of this new species is derived from Greek kerastes = horned, relating to its ventral tube processes.
*Sphaeridia cerastes* clearly differs from other species by its ventral tube structures.

### *Sphaeridia clara* nov. spec.

Type locality: Brazil, Amazonas, Manaus.
Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 31. X. 1990 leg. Gauer (no. 1.1.3./2), at INPA. – Paratypes: 7 males, same locality, leg. Gauer: 1 (slide), 21. IX. 1989 (no. 3.1.2.), at SMF (Ap 2420); 1 (slide), same sample, at MNHN; 1 (slide), 29. VIII. 1989 (no. 3.1.2.), in coll. Gauer; 4 (alc.), 3. X. 1989 (no. 3.1.2. II F), at INPA.
Further material: 9 males (slides), same locality as the types, 10. – 24. IX. 1971 leg. Irmler, 2 m above water level, coll. Bretfeld 26/90: 5 in coll. Bretfeld, 4 at INPA.

Total male 0.18 mm, pale. Ventral tube posteriorly with 1+1 small vesicles (as in *Sphaeridia pumilis*); 1+1 setae. Tibiotarsus III seta IIpe of normal shape, IIIpi and IVpi slender, with few teeth (Fig. 3 a). Head large (100 µm, n = 10); frons setae a+d 1, 2, b+c 1, 2 stronger than others, setae of rows a, b and c, d clearly separated and setae b+c 1 – 3 not so far dorsally shifted as in *Sphaeridia pilleata*. (Fig. 3 b). Antennae long with segment II  III = 2.0 (n = 16). Dens as in Fig. 4 c, but basal papilla small; mucro with about 15 inner teeth, tip a separated, shrunk cap (Fig. 3 c); dens  mucro = 2.5.
The name of this new species is derived from Latin clarus = clear, relating to its weak pigmentation.
*Sph. clara* resembles *Sphaeridia pilleata* n. sp., but differs by its larger body size and its characters of head, antenna, and mucro.

### *Sphaeridia coronata* nov. spec.

Type locality: Brazil, Amazonas, Manaus.
Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 29. VIII. 1989 leg. Gauer (no. 3.1.2.), at INPA. – Paratypes: 12 males from the holotype sample: 6 (alc.) at INPA, 1 (no. 1, slide) at MNHN, 1 (no. 2, slide) at SMF (Ap 2426), 1 (no. 3, 3 slides) in coll. Bretfeld, 3 (no. 4, 5, 6; 8 slides) in coll. Gauer.

Total male 0.14 – 0.18 mm, great abdomen with dark blue horizontal band. Ventral tube (Fig. 4 a) posteriorly with 1+1 small vesicles connected by a membrane, anteriorly of which a larger semicircular membrane and 1+1 small points; 1+1 setae. Tibiotarsus III (Fig. 4 b) seta IIpe slightly stronger than others, IIIpi and IVpi strong, toothed; also IIIi a strong seta. Dens (Fig. 4 c) with large basal papilla, distal setae J proximally thickened, seta E1 with normal shape, length of seta P1 > P2 > P3 ; mucro with few inner teeth, tip a round tooth (Fig. 4 d); dens  mucro = 2.2.
The name of this new species is derived from Latin coronare = to wreathe, relating to its pigmentation.
*Sphaeridia coronata* differs from other species by the membrane connecting its 1+1 ventral tube vesicles.

### *Sphaeridia fibulifera* nov. spec.

Type locality: Brazil, Amazonas, Manaus.
Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 3. X. 1989 leg. Gauer (no. 3.1.2. II P), at INPA. – Paratypes: 1 male (4 slides) from the holotype sample in coll. Gauer; 1 male (slide), same locality, 31. X. 1990 leg. Gauer (no. 1.1.3./2), at MNHN; 4 males, same locality, 31. X. 1990 leg. Gauer (no. 1.1.3./5): 1 (slide) at SMF (Ap 2421), 3 (alc.) at INPA.
Further material: 11 males, same locality as the types, 10. – 24. IX. 1971 leg. Irmler, 1 and 2 m above water level: 4 (slides) in coll. Bretfeld (no. 25/90, 26/90), 7 (alc.) at INPA; 2 males (slides), Brazil, Amazonas, inundation forest of mixed white and black waters at Lago Janauarí near Manaus, 6. – 21. IX. 1971 leg. Irmler, 1 m above water level, in coll. Bretfeld (no. 31/90).

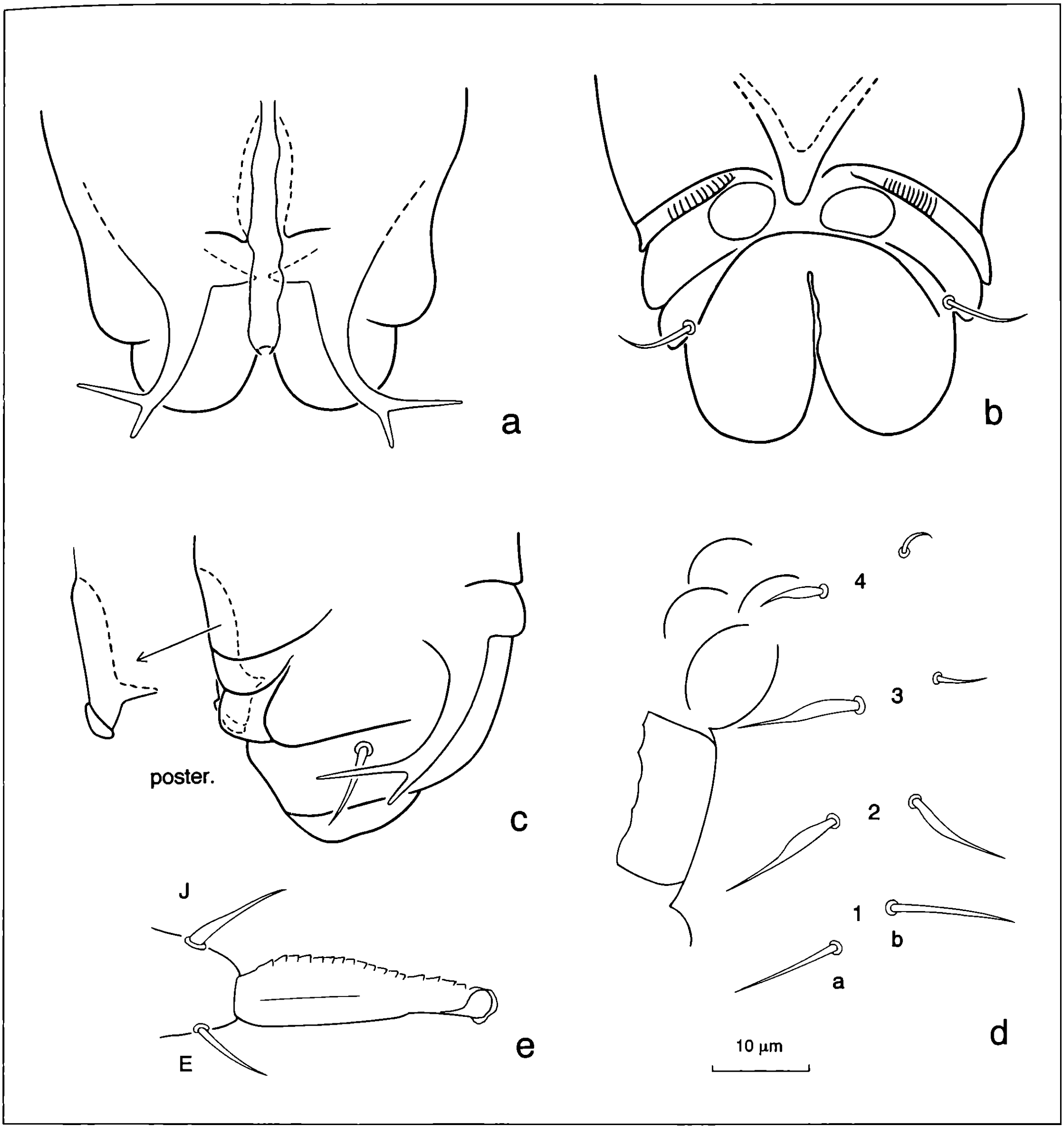


Figure 2. *Sphaeridia cerastes* n. sp.: male: a) ventral tube from anterior; b) from posterior; c) from the right; d) right setae of head frons; e) tip of dens and mucro

Total male 0.2 mm, lateral great abdomen dark. Ventral tube (Fig. 5 a, b) posterolaterally with 1+1 long, waved processes; laterally with 1+1 thick knobs like an abutment of the lateral processes; anteriorly with 1+1 vesicles; 1+1 setae. Tibiotarsus III (Fig. 5 c, d) seta IIpe slightly stronger than others, IIIpi and IVpi strong, toothed. Head setae near the antennae longer and stronger than in most other species. Dens as in Fig. 4 c, but basal papilla small; mucro with many inner teeth and distal half slender, tip a shrunk cap (Fig. 5 e); dens mucro = 2.2.

The name of this new species is derived from Latin fibula = clasp, and ferre = to wear, relating to the shape of its ventral tube processes.

*Sphaeridia fibulifera* clearly differs from other species by its ventral tube structures.

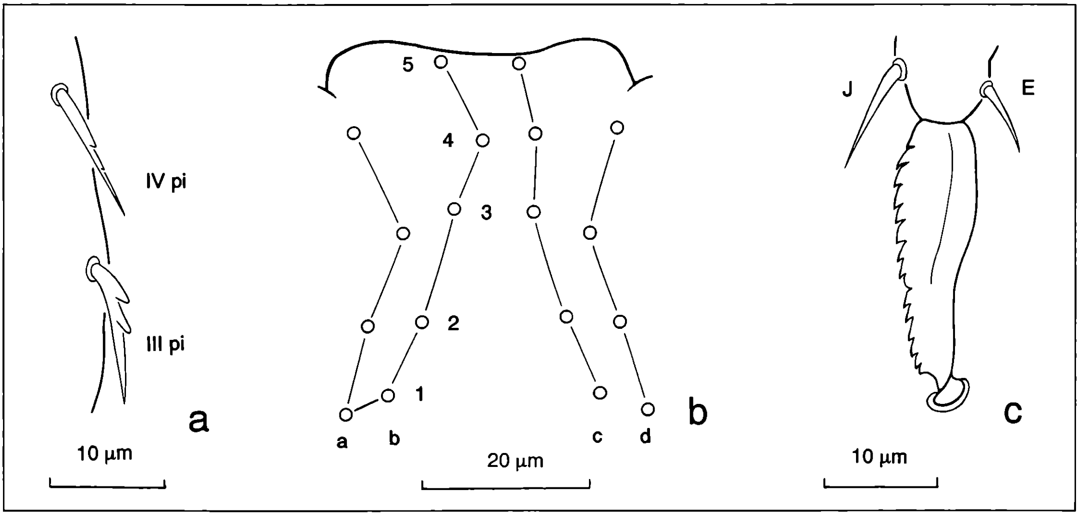


Figure 3. *Sphaeridia clara* n. sp.: male: a) tibiotarsal setae; b) head frons; c) tip of dens and mucro

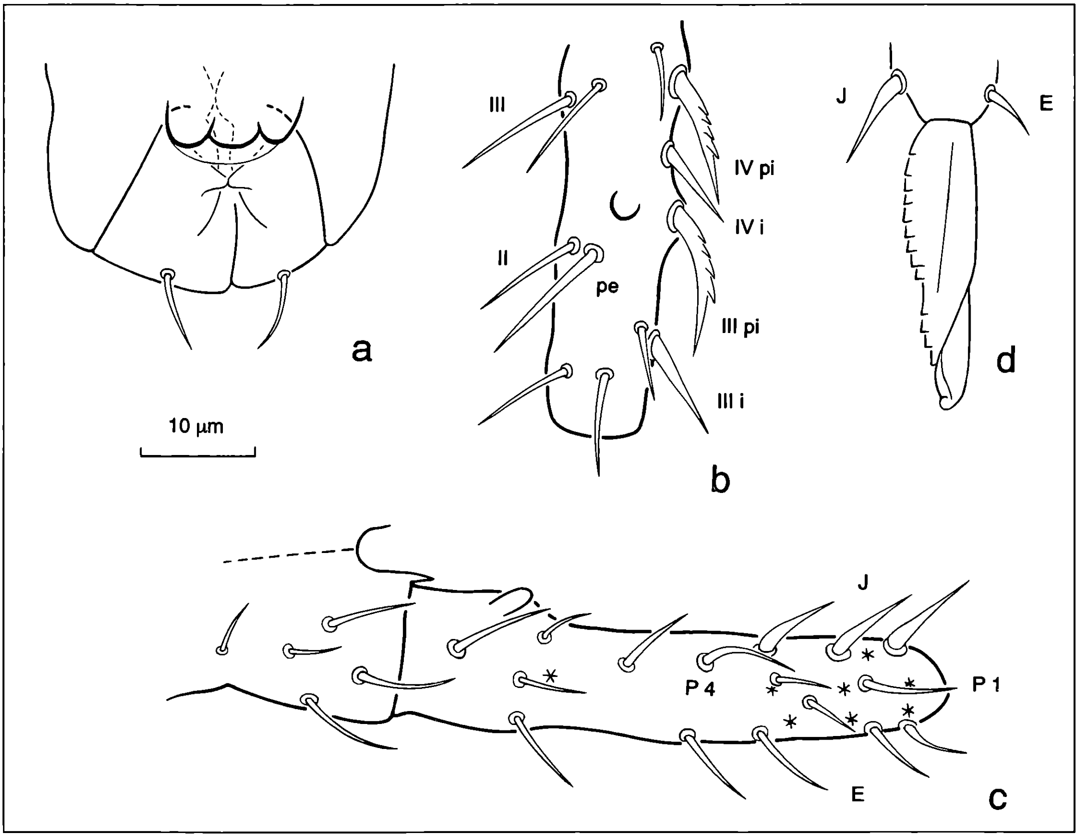


Figure 4. *Sphaeridia coronata* n. sp.: male: a) ventral tube from posterior; b) modified setae of tibiotarsus III; c) left half of furca from posterior; d) tip of dens and mucro

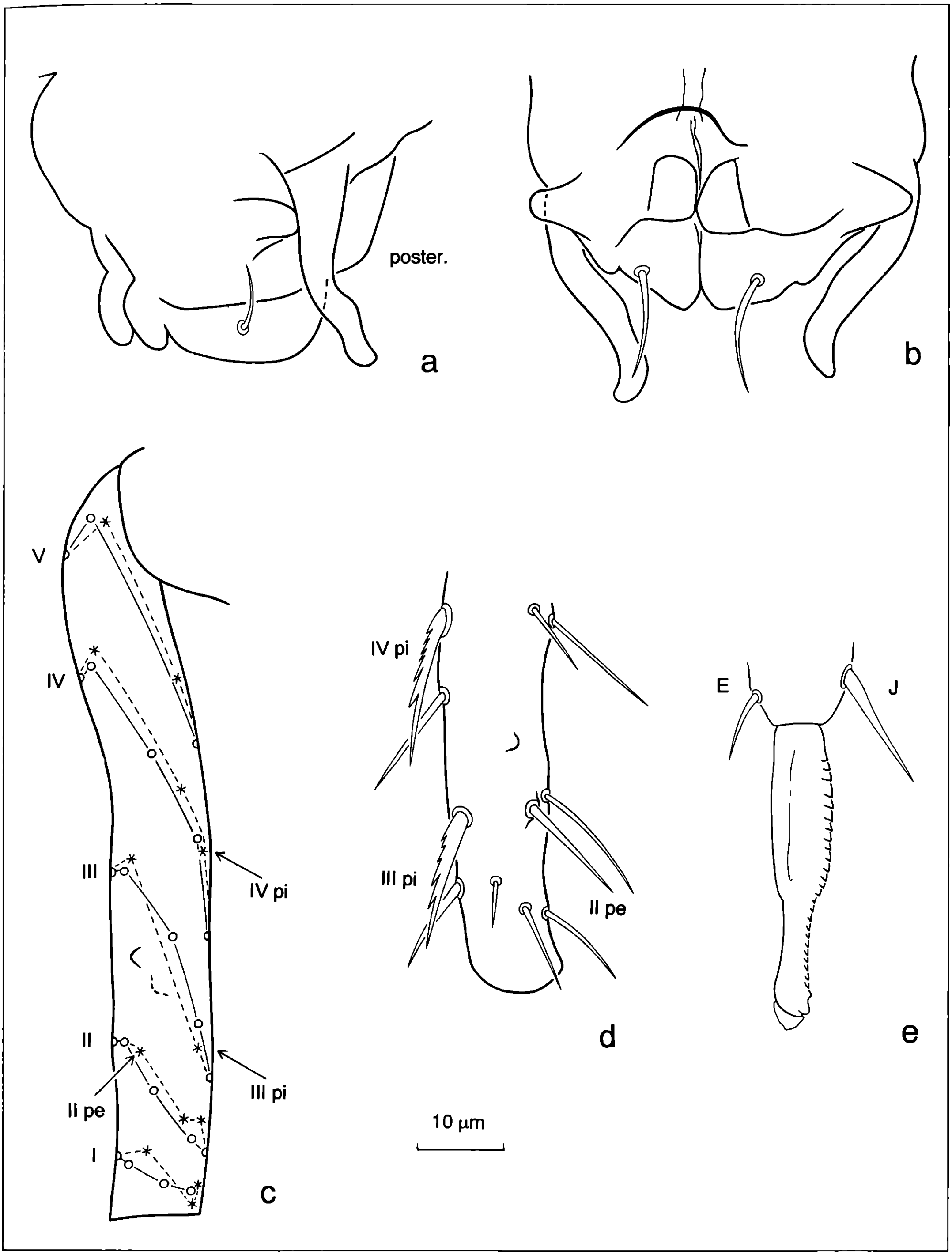


Figure 5. *Sphaeridia fibulifera* n. sp.: male: a) ventral tube from the left; b) from anterior; c) chaetotaxy of tibiotarsus III; d) modified setae of tibiotarsus III; e) tip of dens and mucro

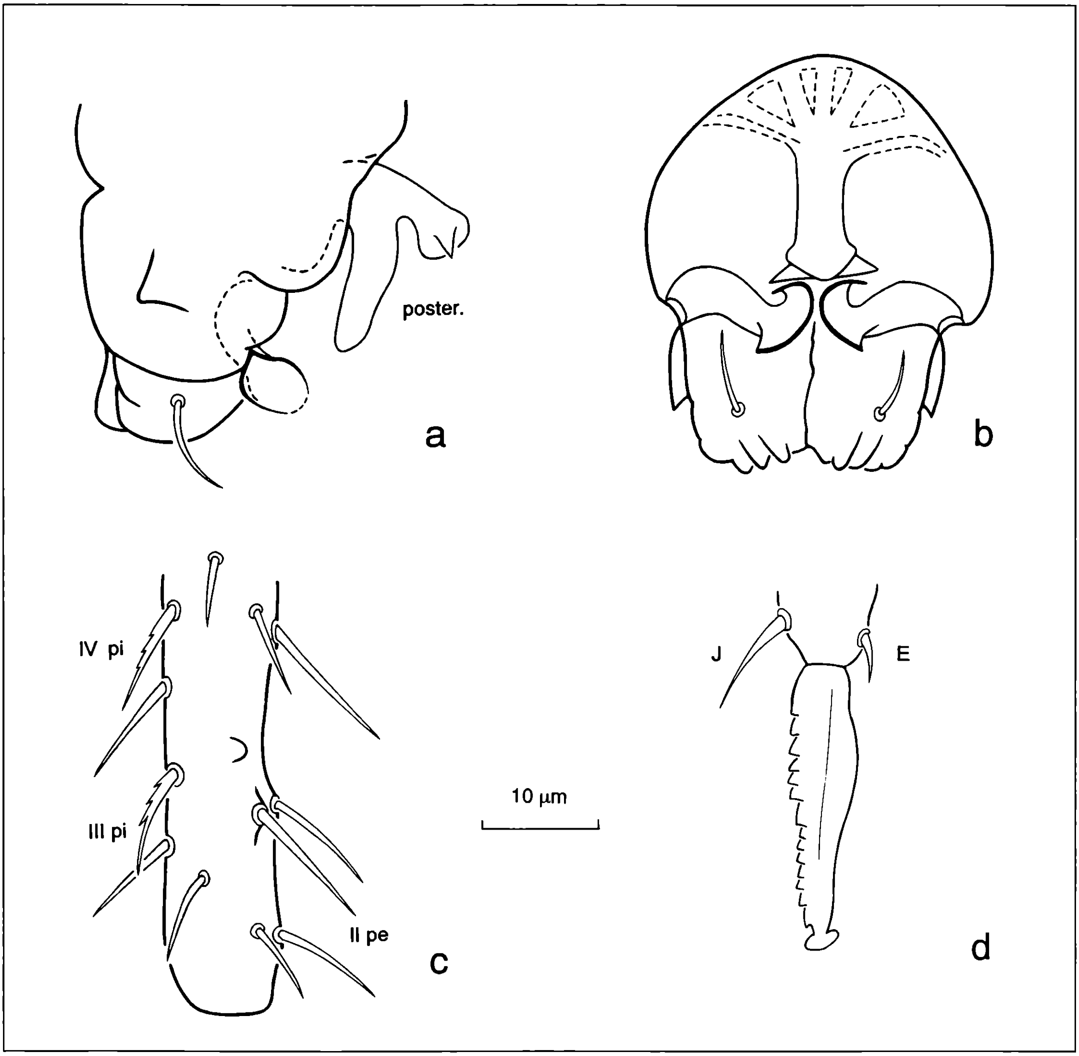


Figure 6. *Sphaeridia franklinae* n. sp.: male: a) ventral tube from the left; b) from posterior; c) modified setae of tibiotarsus III; d) tip of dens and mucro

## ***Sphaeridia franklinae* nov. spec.**

Type locality: Brazil, Amazonas, Manaus.

Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 31. X. 1990 leg. GAUER (no. 1.1.3./5), at INPA. – Paratypes: 4 males (3 alc., 1 slide) from the holotype sample, at INPA; 4 males (alc.), same locality, 31. X. 1990 leg. GAUER (no. 1.1.3./2) in coll. GAUER; 1 male (slide), same locality, 10. X. 1990 leg. GAUER (no. 1.1.3./1), at MNHN; 1 male (slide), same locality, 15. XII. 1989 leg. GAUER (no. 1.1.1. K 22), at SMF (Ap 2422).

Further material: 2 males (slides), same locality as the types, 10. – 24. IX. 1971 leg. IRMLER, 1 m above water level, in coll. BRETFELD (no. 25/90); 19 males (slides), same data, 2 m above water level: 10 at INPA and 9 in coll. BRETFELD (no. 26/90); 1 male (slide), Brazil, Amazonas, inundation forest of mixed white and black waters at Lago Janauarí near Manaus, 17 XI. – 2. XII. 1971 leg. IRMLER, 5 m above water level, coll. BRETFELD 37/90, at INPA.

Total male 0.16 mm, light blue or brownish. Ventral tube (Fig. 6 a, b) posteriorly with a thick median process, having a broadened tip with 1+1 lateral teeth, a strong fanlike root, and an anterior branch; posterolaterally with 1+1 curved processes, each with an earlike medial border; laterally with 1+1 small teeth; 1+1 se-

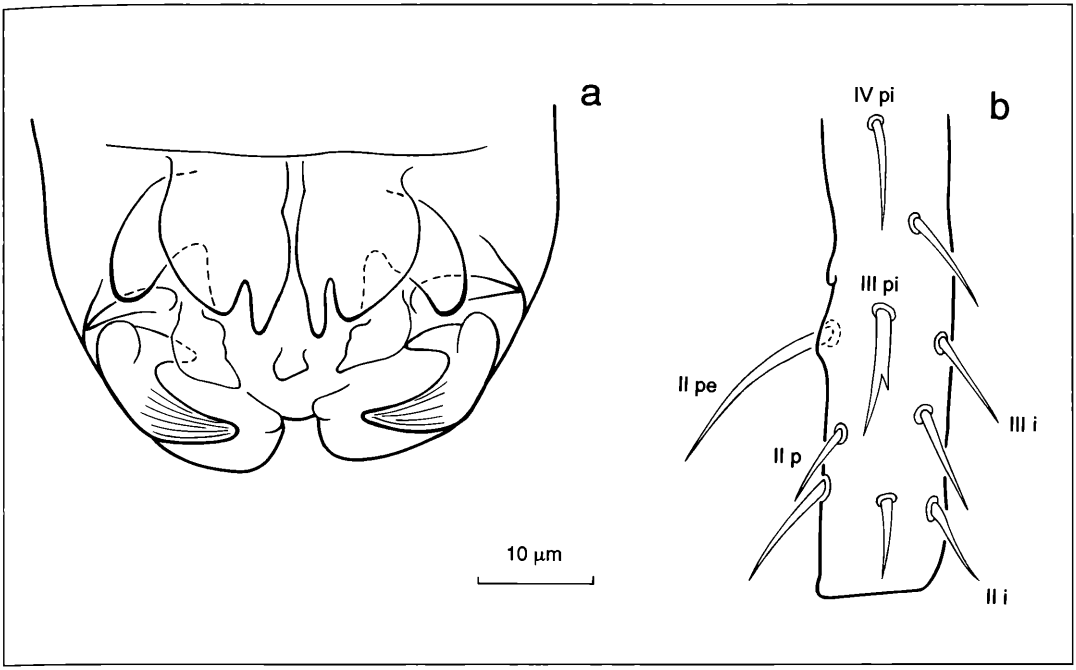


Figure 7. *Sphaeridia irmleri* n. sp.: male: a) ventral tube from posterior; b) modified setae of tibiotarsus III

tae. Tibiotarsus III (Fig. 6 c) seta IIpe slightly longer than others, IIIpi and IVpi with small teeth, not always observable at low magnification. Dens as in Fig. 4 c, but basal papilla small; mucro with few inner teeth, tip a shrunk cap (Fig. 6 d); dens mucro = 2.2.

This new species is gratefully dedicated to Dr. ELIZABETH FRANKLIN, head of the Laboratory of Entomology (casa 20), INPA, Manaus, Brazil.

The ventral tube of *Sphaeridia franklinae* resembles that of *Sph. cardosi* ARLÉ, 1984, but differs by a long branch (instead of short) of the posterior, median process directed towards anterior, and 1+1 lateral processes (instead of 2+2). *Sph. franklinae* also differs from that species by its toothed tibiotarsal setae (instead of smooth).

### ***Sphaeridia irmleri*** **nov. spec.**

Type locality: Brazil, Amazonas, Manaus.

Type material: Holotype: Male (slide), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 10. – 24. IX. 1971 leg. IRMLER, 1 m above water level, coll. BRETFELD 25/90/5, at INPA. – No further specimen known.

Total male 0.18 mm, deep black. Ventral tube (Fig. 7 a) with several complicated but symmetrical structures: posteriorly with 1+1 cuticular blades with 3 lobes each, of these blades one median and 1+1 lateral cuticular processes reach into the ventral tube towards anterior (not figured); anteriorly with 1+1 strong borders with laterally 1+1 large doubled teeth; without setae. Tibiotarsus III (Fig. 7 b) seta IIpe long, IIIpi strong with one tooth, IVpi of normal shape without teeth. Head setae obscured by the pigment. Furca not clearly observed due to preparation, but dens without basal papilla, seta E1 thick, mucro with about 20 inner teeth, tip a shrunk cap.

This new species is gratefully dedicated to its collector, the senior author's colleague, Dr. ULRICH IRMLER, Kiel, Germany.

*Sphaeridia irmleri* clearly differs from other species by its ventral tube structures.

### ***Sphaeridia martii*** **nov. spec.**

Type locality: Brazil, Amazonas, Manaus.

Type material: Holotype: Male (slide), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 10. – 24. IX. 1971 leg. IRMLER, 2 m above water level, coll. BRETFELD 26/90/36, at INPA. – Paratype: 1 male (3 slides) from the holotype sample, coll. BRETFELD 26/90/7, at SMF (Ap 2423).

Total male 0.16 mm, light grey. Ventral tube posteriorly with 1+1 small vesicles; 1+1 setae. Tibiotarsus III (Fig. 8 a) seta IIpe of normal shape, IIIpi and IVpi with teeth. Head frons (compare Fig. 3 b) without setae a4, d4; the setae near the antennae longer than in most other species. Antennal segment II with two additional spines (Fig. 8 b); ant. II much longer than

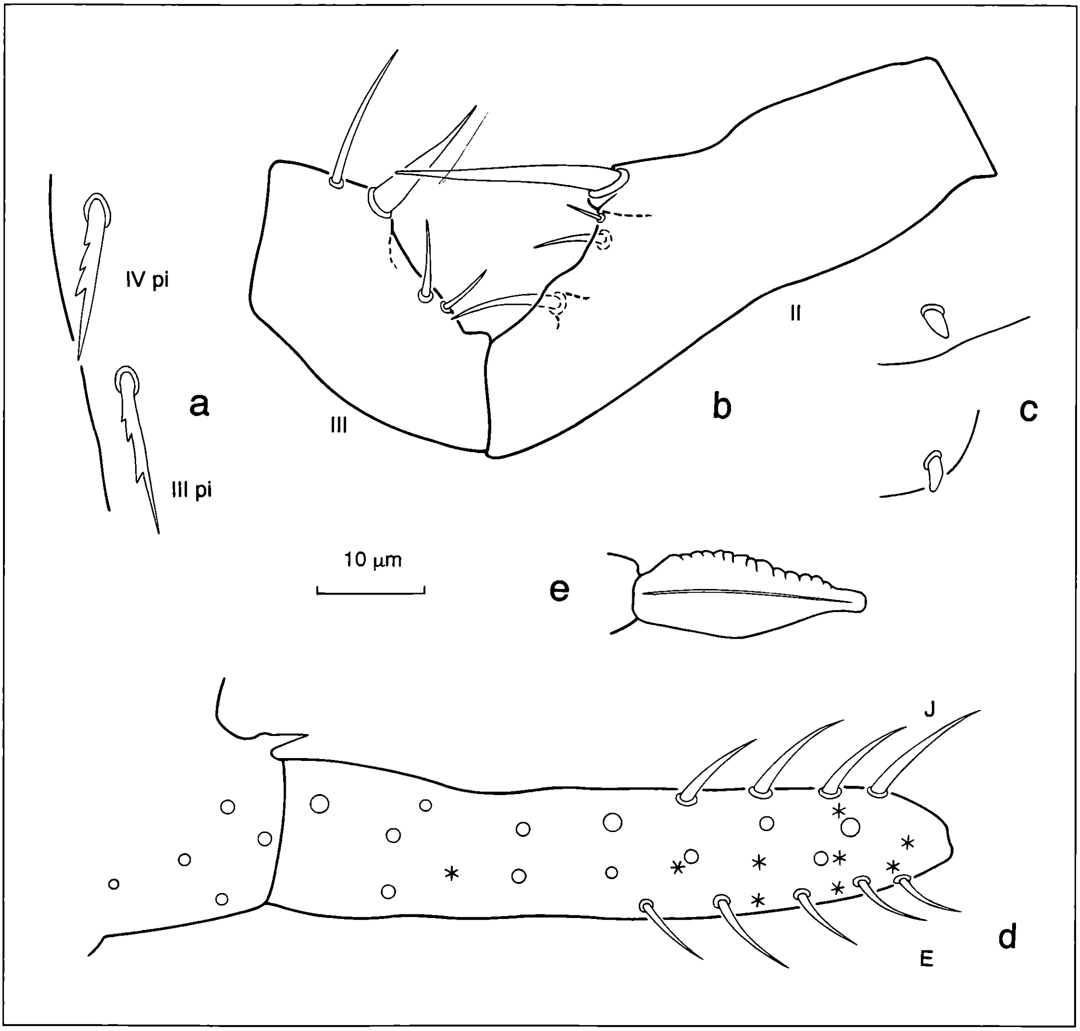


Figure 8. *Sphaeridia martii* n. sp.: male: a) modified setae of tibiotarsus III; b) antennal segments II and III; c) spine of femur III; d) left half of furca from posterior; e) mucro

ant. III (3  1); ant. IV as long as the head (130 µm). Femur III posterior side (Fig. 8 c) with a short, blunt spine instead of a small seta as in other species. Dens distal part with more setae than in most other species (the setae varied, J 2 – 5, P 7 – 9, E 4 – 5, Fig. 8 d), without basal papilla, seta E1 of normal shape, inner setae strong; mucro with irregular, inner teeth, tip a long tooth (Fig. 8 e); dens  mucro = 3.2.

We gratefully dedicate this new species to Dr. Christopher Martius, Manaus, Brazil, who as a friend supported the junior author during his two-year stay in Manaus.

*Sphaeridia martii* resembles *Sphaeridia robusta* n. sp. by its setae of head frons, but differs from this and other species by its characters of antenna, femur, and dens.

## ***Sphaeridia pilleata* nov. spec.**

Type locality: Brazil, Amazonas, Manaus.
Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 3. X. 1989 leg. Gauer (no. 3.1.2. II F), at INPA. – Paratypes: 1 male (slide), same locality as the holotype, 31. X. 1990 leg. Gauer (no 1.1.3./2), at SMF (Ap 2424); 1 male (slide), same locality, 10. X. 1990 leg. Gauer (no. 1.1.3./1), at MNHN; 1 male (slide), same locality, 31. X. 1990 leg. Gauer (no. 1.1.3./5), in coll. Gauer; 3

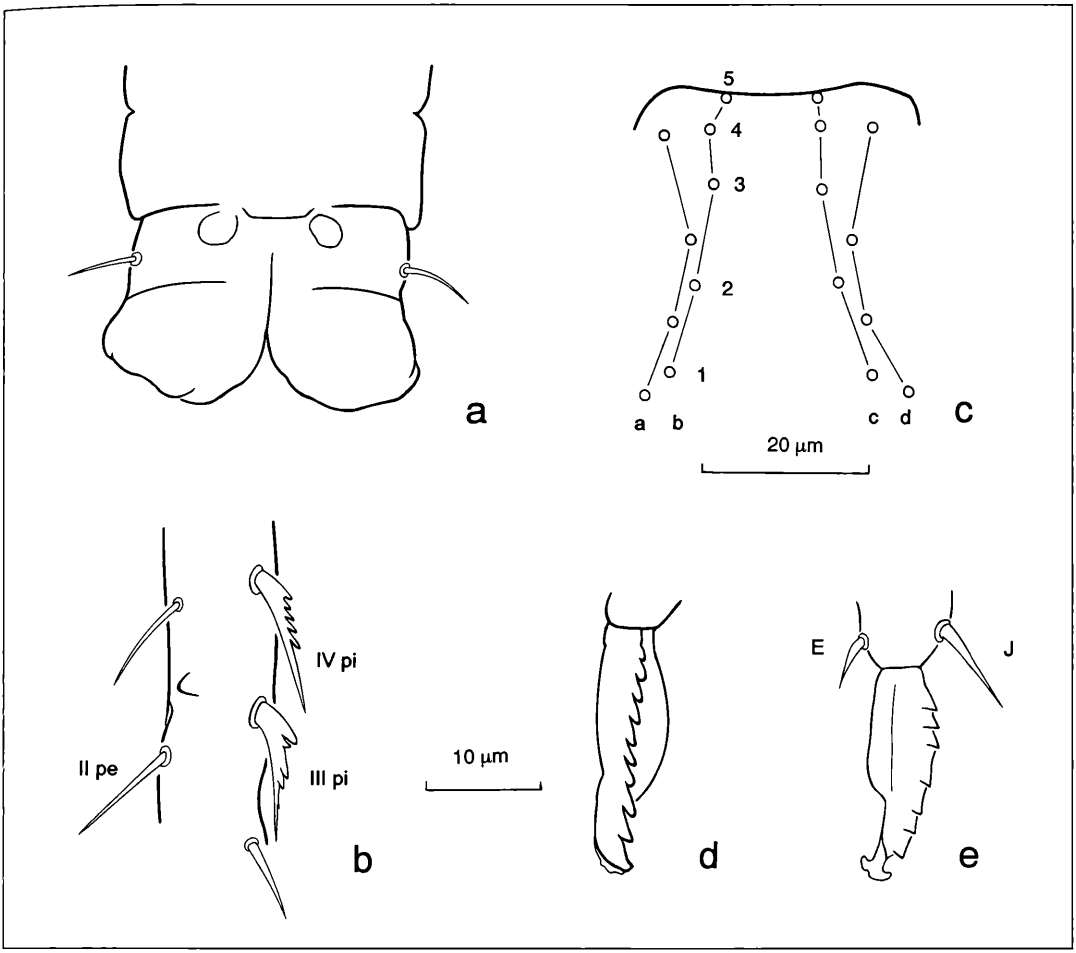


Figure 9. *Sphaeridia pilleata* n. sp.: male: a) ventral tube from posterior; b) modified setae of tibiotarsus III; c) setae of head frons; d) mucro from the inner side; e) tip of dens and mucro.

males (2 alc., 1 slide), same locality, 15. XII. 1989 and 31. X. 1990 leg. GAUER (no. 1.1.1. K 10 and 1.1.3./5, resp.), at INPA.

Total male 0.12 – 0.16 mm, great abdomen often with a blue dorsal cap (like *Sphaeridia carioca* ARLÉ) but also completely blue, only with a blue lateral band, or brownish, grey, or nearly white. Ventral tube (Fig. 9 a) posteriorly with 1+1 small vesicles. Tibiotarsus III (Fig. 9 b) seta IIpe of normal shape, IIIpi and IVpi strong, toothed. Head small (80 µm, n = 10); setae near the antennae longer than in most other species; frons (Fig. 9 c) with setae of rows a, b and c, d close together and setae b+c 1 – 3 shifted dorsally. Antennae short with segment II  III = 1.4 (n = 7). Dens as in Fig. 4 c, but basal papilla small; mucro with about 10 inner teeth, tip a separated, shrunk cap (Fig. 9 d, e); dens  mucro = 2.4.

The name of this new species is derived from Latin pilleatus = wearing a cap, relating to its pigmentation. *Sphaeridia pilleata* differs from *Sphaeridia carioca*, by its simple ventral tube (instead of complicated). It resembles *Sphaeridia clara* n. sp., but differs by its small body size and its characters of head, antenna, and mucro.

### ***Sphaeridia robusta*** **nov. spec.**

Type locality: Brazil, Amazonas, Manaus.

Type material: Holotype: Male (3 slides), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 10. – 24. IX. 1971 leg. IRMLER, 2 m above water level, coll. BRETFELD 26/90/3, at INPA. – No further specimen known.

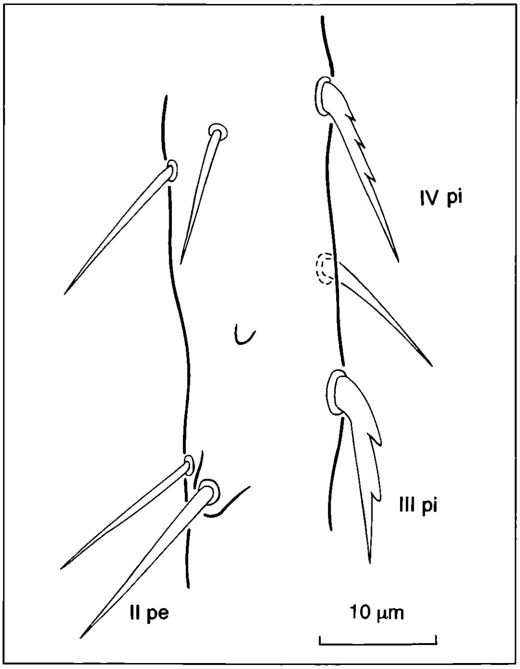
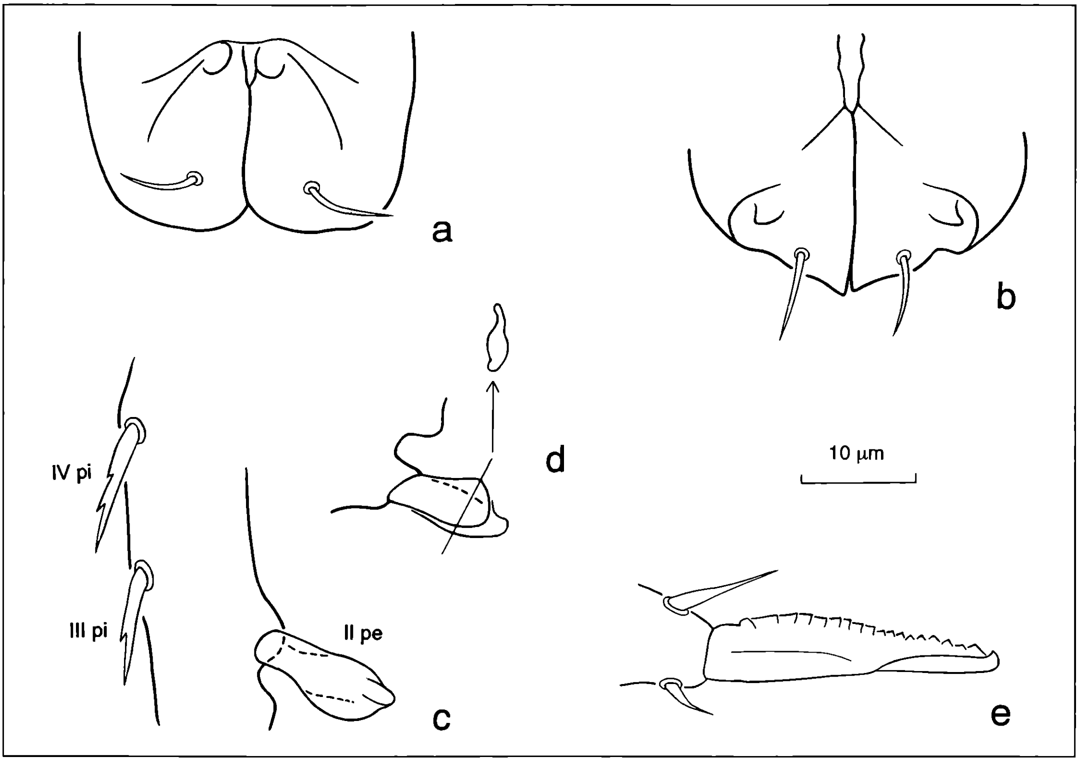


Figure 10. *Sphaeridia robusta* n. sp.: male: modified setae of tibiotarsus III.

Figure 11. *Sphaeridia squamifera* n. sp.: male: a) ventral tube from posterior; b) from anterior; c) modified setae of tibiotarsus III; d) other view of seta II pe of tibiotarsus III; e) tip of dens and mucro.



Total male 0.22 mm, dark blue. Ventral tube posteriorly with 1+1 small vesicles; 1+1 setae. Tibiotarsus III (Fig. 10) seta IIpe strong, IIIpi strong with few large teeth, IVpi thin with small teeth. Head frons (compare Fig. 3 b) without setae a4, d4; all setae longer and stronger than in other species, the setae near the antennae longer than others. Dens as in Fig. 4 c, but basal papilla small and round; mucro with few inner teeth, tip a separated, shrunk cap; dens mucro = 2.7.

The name of this new species is derived from Latin robustus = robust, relating to its large body parts.

*Sphaeridia robusta* resembles *Sphaeridia martii* n. sp. by its setae of head frons, but differs by its tibiotarsal setae and because the other special characters of *Sph. martii* are missing. It differs from other species by its large body size and equivalent larger body parts.

### *Sphaeridia squamifera* nov. spec.

Type locality: Brazil, Amazonas, Manaus.

Type material: Holotype: Male (alcohol), Brazil, Amazonas, Igapó of Rio Tarumã Mirím near Manaus, 3. X. 1989 leg. Gauer (no. 3.1.2. II F), at INPA. – Paratypes: 2 males (alc.) from the holotype sample, at INPA; 4 males (slides), same locality, 10. – 24. IX. 1971 leg. Irmler, 1 and 2 m above water level: 1 at SMF (Ap 2425), 2 at INPA (these 3 have coll. Bretfeld no. 26/90), 1 at MNHN (coll. Bretfeld no. 25/90).

Further material: 1 male (slide), Brazil, Amazonas, Manaus, Ilha de Marchantaria, soil of várzea forest, 1. XI. 1990 leg. Gauer (no. 1.2.3.), in coll. Bretfeld; 1 male (slide), same locality, 17 I. 1991 leg. Gauer (no. 1.2.1. K 22), in coll. Gauer.

Total male 0.16 mm, grey-blue. Ventral tube (Fig. 11 a, b) posteriorly with 1+1 small vesicles, anteriorly with 1+1 small points; 1+1 setae. Tibiotarsus III (Fig. 11 c, d) seta IIpe a large, thick and blunt blade observable at low magnification, IIIpi and IVpi strong with few strong teeth. Dens as in Fig. 4 c, but basal papilla varied (without or with a large one); tip of mucro a round tooth (Fig. 11 e); dens mucro = 2.1.

The name of this new species is derived from Latin squama = scale, and ferre = to wear, relating to its tibiotarsal blade.

The tibiotarsal blade of *Sph. squamifera* resembles those of *Sph. denisi* Massoud & Delamare Deboutteville, 1964, *Sph.* spec. Massoud & Delamare Deboutteville, 1964, and *Sph. heloisae* Arlé, 1984, but their fine structures differ: in *denisi* long, asymmetrical, in spec. short, with two different tips, in *heloisae* long, bent and tip cut. The simple ventral tube of *Sph. squamifera* differs from that of *Sph. heloisae*, which has a posterior, median process (the ventral tubes of *Sph. denisi* and *Sph.* spec. are also simple).

## 4.2 The species from Paraguay

### *Sphaeridia boettgeri* nov. spec.

Type locality: Paraguay, Concepción, Estancia Ybú.

Type material: Holotype: Male (no. 2, slide), Paraguay, 4.5 km SE Concepción, Estancia Ybú, mixed sample of Berlese extraction and sweeping the vegetation, X/1985 leg. Böttger, coll. Bretfeld 1085-59, at SMF (Ap 2427). – Paratypes: 1 male (no. 1, slide) from the holotype sample, at MNHN; 7 males (3 alcohol, 4 slides) from the same sample in coll. Bretfeld.

Further material: 2 males (slides), Brazil, Amazonas, Manaus, Ilha de Marchantaria, soil of várzea forest, 1. XI. 1990 leg. Gauer (no. 1.2.3.), no. 1 at INPA, no. 2 in coll. Gauer.

Total male 0.2 mm, dark blue. Ventral tube (Fig. 12 a, b, c, d) posteriorly with a straight, knobbed median process; posterolaterally with 1+1 striated blades; anteriorly with 1+1 mandible-like processes, laterally pointed, medially strongly cuticularized; 1+1 setae. Tibiotarsus III without special setae. Head frons setae a+d 2, 3 and b+c 2 slightly stronger than others. Dens with basal papilla small, up to 5 setae missing (Fig. 12 e, compare Fig. 4 c), seta E1 thick (Fig. 12 f); mucro slender, tip a round tooth (Fig. 12 f); dens mucro = 1.8.

We gratefully dedicate this new species to its collector, the senior author's former fellow-student and present colleague, Prof. Dr. Klaus Böttger, Kiel, Germany.

*Sphaeridia boettgeri* clearly differs from other species by its ventral tube structures.

## 4.3 The species from Colombia

### *Sphaeridia catapulta* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Chingaza.

Type material: Holotype: Male (4 slides), Colombia, Páramo de Chingaza, 20 km W Bogotá, 4° 40' N, 73° 47' W, epiphytes (mosses and ferns) in a mountain forest remainder at 3250 m near Laguna de Chingaza, 22. VIII. 1985 leg. Sturm (sample 85/132), coll. Bretfeld 16/89, at SMF (Ap 2428). – Paratypes: 2 males (slides), from the holotype sample, coll. Bretfeld 63/92: no. 1 in coll. Bretfeld, no. 2 at MNHN.

Total male 0.25 mm, light blue. Ventral tube complicated: in lateral view the inner, posterior part occupied by a large, semicircular muscle; in posterior view (Fig. 13 a, only the main structures are figured) behind a strong wall with a median, broad, bifurcated process (which has 3 processes directed towards anterior = a in Fig. 13 a) and with 1+1 thinner ones; more laterally with 2+2 processes (= p in Fig. 13 a, which have a process each directed towards posterior), and 1+1 vesicles (= b in Fig. 13 a); 1+1 setae. Tibiotarsus III seta IIpe large, IIIpi and IVpi with small teeth. Head setae near the antennae longer than in most other species. Dens as in Fig. 4 c, but basal papilla small, seta E1 thick; tip of mucro a shrunk cap (Fig. 13 b); dens mucro = 2.1.

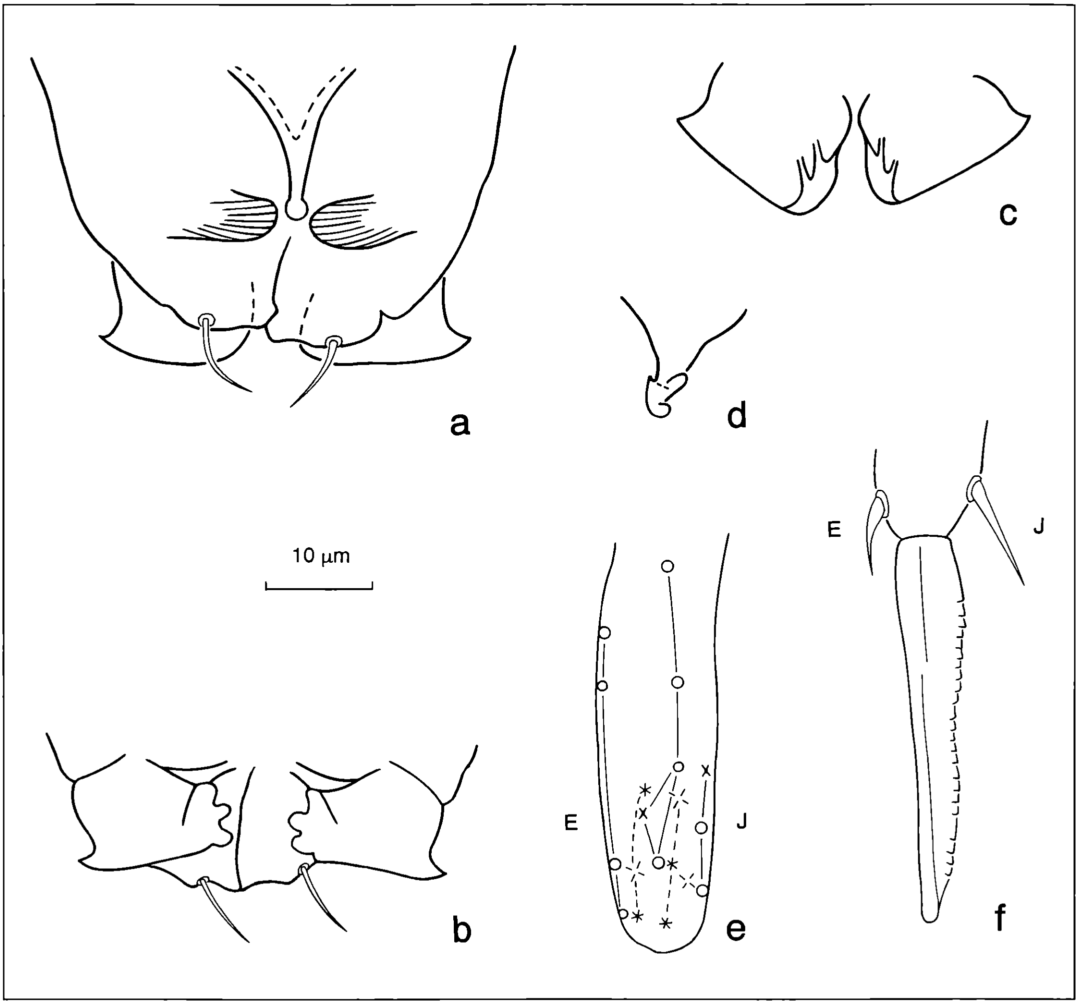


Figure 12. *Sphaeridia boettgeri* n. sp.: male: a) ventral tube from posterior; b) from anterior; c) other view of mandible-like processus; d) other view of posterior median processus; e) left dens from posterior; f) tip of dens and mucro.

The name of this new species is derived from Latin catapulta = catapult, relating to the posterior process of its ventral tube.

*Sphaeridia catapulta* clearly differs from other species by its ventral tube structures.

### *Sphaeridia chisacae* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Chisacá.

Type material: Holotype: Male (no. 2, 4 slides), Colombia, Páramo de Chisacá, about 40 km SSW Bogotá, 4° 17' N, 74° 12' W, low vegetation on soil surface (mosses, herbs) of grassland (pajonal) near Laguna Negra at 3720 m, 18. IX. 1986 leg. STURM (sample 86/97), coll. BRETFELD 22/89, at SMF (Ap 2429). – No further specimen known.

Total male 0.2 mm, blue, laterally darker. Ventral tube (Fig. 14 a, b) posteriorly with two median and 1+1 middle processes; laterally with 1+1 short, blunt processes; anterolaterally with 1+1 pointed teeth; 1+1 setae. Tibiotarsus III seta IIpe long (see *Sph. lobata*, Fig. 15 b), the other setae normal, without teeth. Dens as in Fig. 4 c, but basal papilla small, without seta P2; mucro with many small, inner teeth, tip a shrunk cap (Fig. 14 c); dens mucro = 2.5.

This new species is named after its type locality, the Páramo de Chisacá.

*Sphaeridia chisacae* resembles *Sphaeridia lobata* n. sp. by its tibiotarsus III seta IIpe, but clearly differs from this and other species by its ventral tube structures

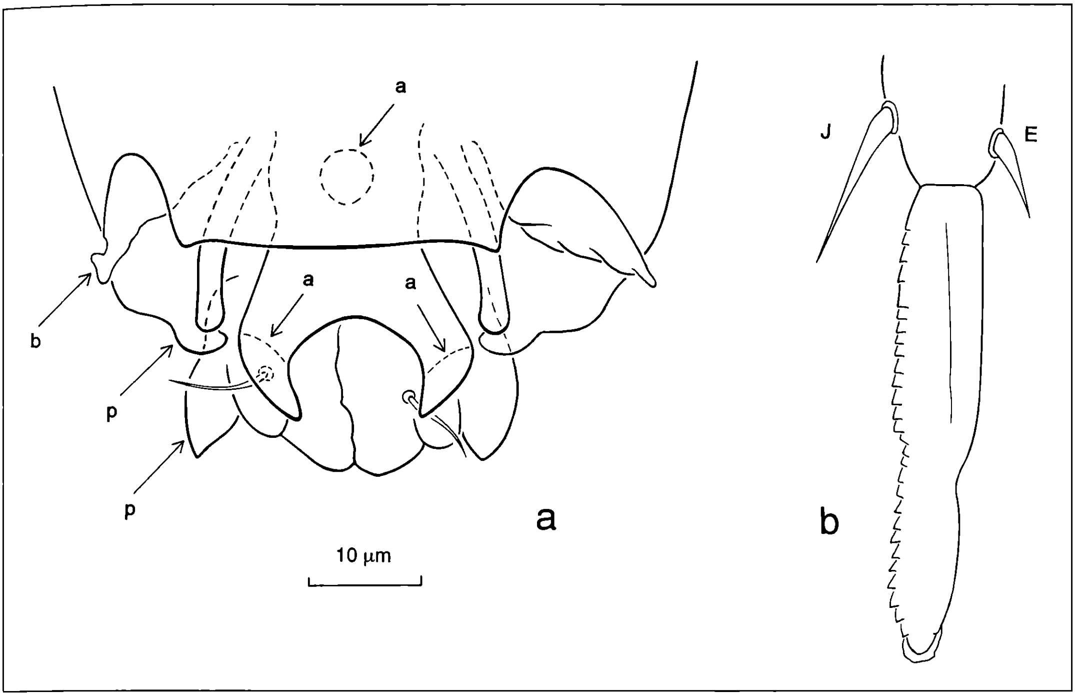


Figure 13. *Sphaeridia catapulta* n. sp.: male: a) ventral tube from posterior, see text; b) tip of dens and mucro.

## *Sphaeridia lobata* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Chingaza.
Type material: Holotype: Male (no. 1, 2 slides), Colombia, Páramo de Chingaza, 20 km W Bogotá near Chuza, 4° 40' N, 73° 47' W, epiphytes (mosses and ferns) in a mountain forest remainder at 3000 m, 21. IX. 1989 leg. STURM (sample 89/94), coll. BRETFELD 13/90, at SMF (Ap 2430). – Paratypes: 1 male (no. 2, slide) from the holotype sample, in coll. BRETFELD; 3 males, same locality and biotope as the holotype but at 3250 m, 22. VIII. 1985 leg. STURM (samples 85/37, 85/132), coll. BRETFELD 58/92, 63/92: 1 (slide) at MNCB, 1 (slide) at MNHN, 1 (alc.) in coll. BRETFELD; 1 male (3 slides), same locality and biotope but at 3550 m, 14. IX. 1985 leg. STURM (sample 85/178), in coll. BRETFELD (no. 64/92).

Total male 0.2 mm, dark blue. Ventral tube (Fig. 15 a) posteriorly with a median process; laterally with 2+2 main lobes; 1+1 setae. Tibiotarsus III (Fig. 15 c) seta IIpe long, IIIpi and IVpi short and strong. Dens as in Fig. 4 c, but basal papilla small, seta E1 thick; mucro with irregular, inner teeth, tip a long tooth (Fig. 15 b); dens mucro = 2.1.

The name of this new species is derived from New Latin lobatus = lobe-like, relating to the lateral processes of its ventral tube.

*Sphaeridia lobata* resembles *Sph. chisacae* n. sp. by its tibiotarsus III seta IIpe, but clearly differs from this and other species by its ventral tube structures.

## *Sphaeridia mandibulata* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Monserrate.
Type material: Holotype: Male (4 slides), Colombia, Páramo de Monserrate 7 km NE Bogotá, 4° 15' N, 74° 1' W, litter of mountain forest remainder at 3230 m, 10. IX. 1986 leg. STURM (sample 86/116), coll. BRETFELD 24/89a3, at SMF (Ap 2431).
Further material: 4 males (1 alc., 3 slides), Colombia, Páramo de Chingaza, 20 km W Bogotá, 4 40' N, 73 47' W, epiphytes (mosses and ferns) in a mountain forest remainder at 3250 m near Laguna de Chingaza, 22. VIII. 1985 leg. STURM (sample 85/37, 85/132), in coll. BRETFELD (no. 58/92, 63/92).

Total male 0.2 mm, with violet median and horizontal bands, the latter reaching from the posterior tip of small abdomen to the head behind the eyes, antennae and legs blue, furca pale. Ventral tube (Fig. 16 a) posteriorly with a thin, protruding membrane in form of a hand-glass; more anteriorly with one short, median and 1+1 slender, lateral processes; laterally with 1+1 blunt, tridentate processes; anteriorly with several symmetrical cuticular lobes (simplified in Fig. 16 b); 1+1 setae. Tibiotarsus III (Fig. 16 c) seta IIpe long, IIIpi and IVpi strong with one tooth each, setae IIpi and IIIi also strong. Head setae of frons and apex strong and basal third thickened. Dens as in Fig. 4 c, but basal papilla small, seta E1 thick, J1 thicker than usual, P3 thinner (Fig. 16 d); tip of mucro a small cap (Fig. 16 e); dens mucro = 2.4.

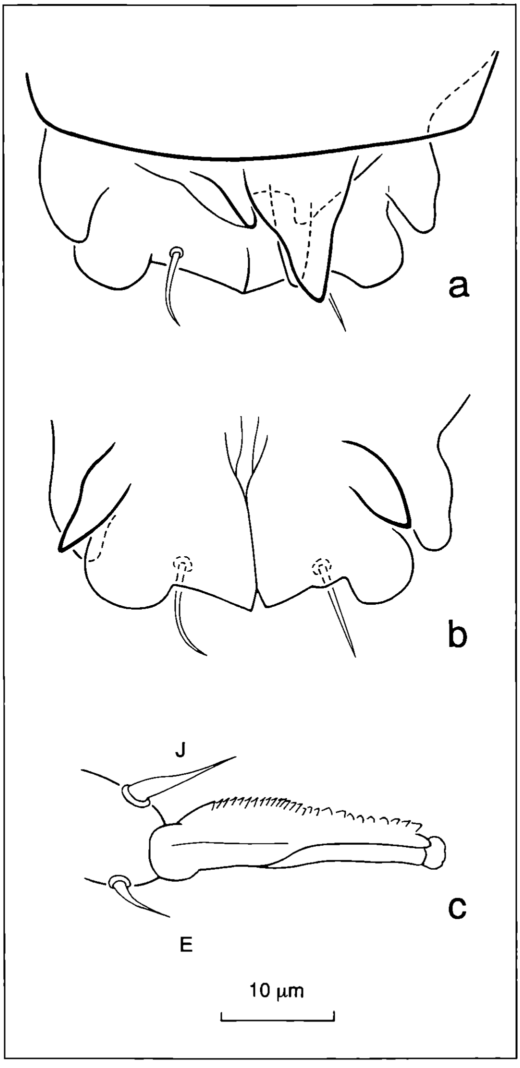


Figure 14. *Sphaeridia chisacae* n. sp.: male: a) ventral tube from posterior; b) from anterior; c) tip of dens and mucro.

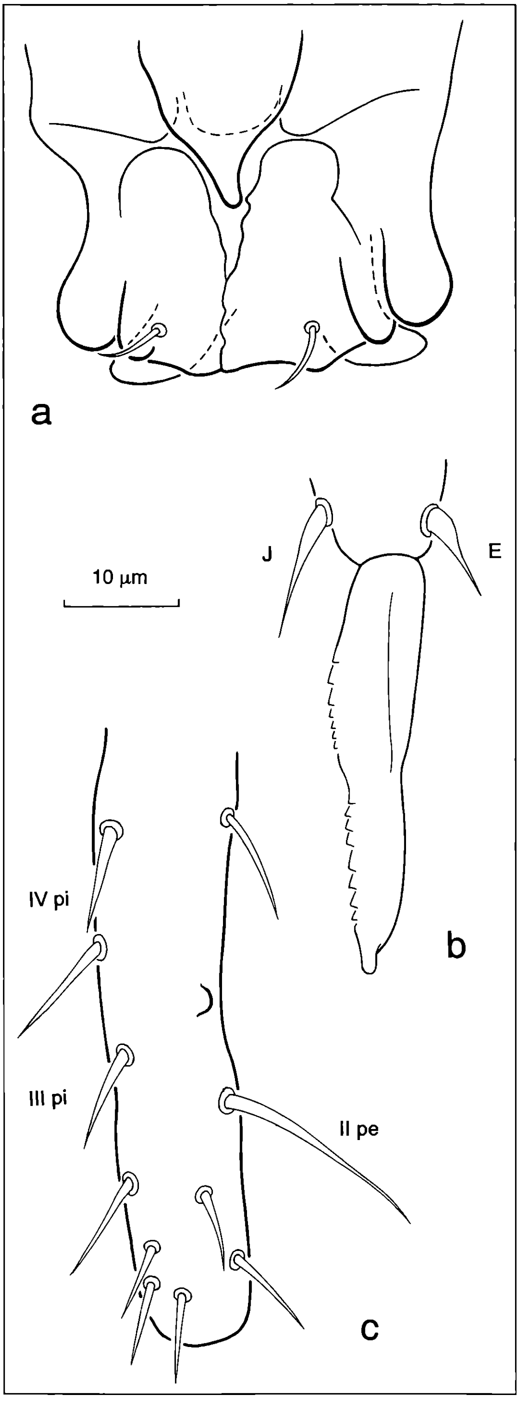


Figure 15. *Sphaeridia lobata* n. sp.: male: a) ventral tube from posterior; b) tip of dens and mucro; c) modified setae of tibiotarsus III.

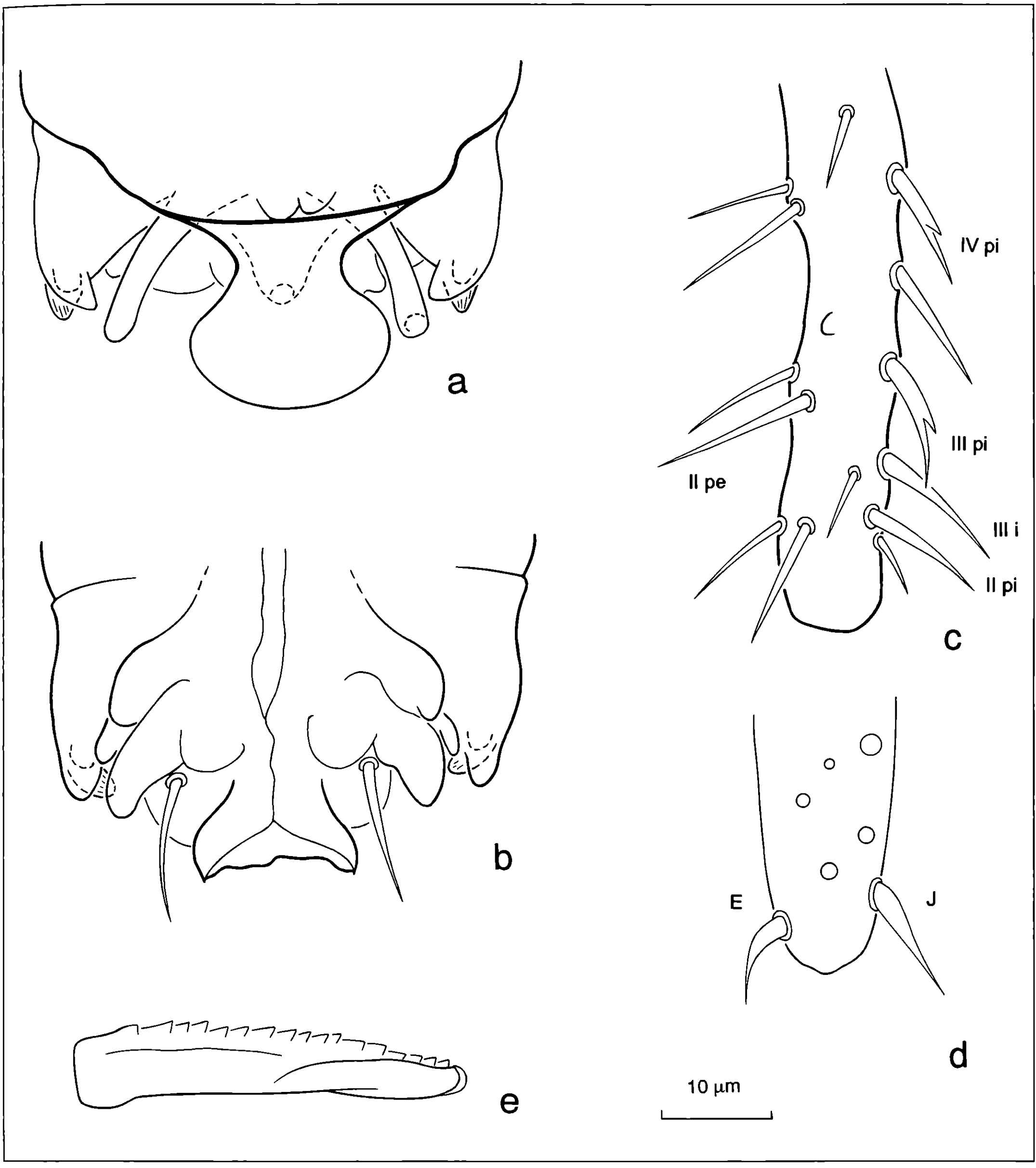


Figure 16. *Sphaeridia mandibulata* n. sp.: male: a) ventral tube from posterior; b) from anterior; c) modified seta of tibiotarsus III; d) tip of dens; e) mucro.

The name of this new species is derived from Late Latin mandibula = mandible, jaw, relating to the mandible-like processes of its ventral tube.

*Sphaeridia mandibulata* clearly differs from other species by its ventral tube structures.

### ***Sphaeridia neopumilis* nov. spec.**

Type locality: Colombia, Bogotá, La Calera.

Type material: Holotype: Male (no. 2, 3 slides), Colombia, La Calera (region of the Páramo de Monserrate), 7 km NE Bogotá, raw humus of a mountain forest remainder at 3080 m, 25. VIII. 1985 leg. STURM (sample 85/17), coll. BRETFELD

11/89, at SMF (Ap 2432). – Paratypes: 3 males (slides) from the holotype sample: no. 1 in coll. BRETFELD, no. 3 at MNCB, no. 4 at MNHN.

Total male 0.2 mm, dark blue, but paler between the eyes and on dorsal great abdomen, ventral side palest. Ventral tube with 1+1 small vesicles as in *Sphaeridia pumilis*. Tibiotarsus III seta IIpe long and thin, IIIpi and IVpi strong without teeth. Head apex with thin setae. Dens as in Fig. 4 c, but basal papilla small and pointed, seta E1 thick; mucro with small inner teeth, tip a broad, shrunk cap (Fig. 17); dens mucro = 2.3 – 3.1 (length of mucro varied).

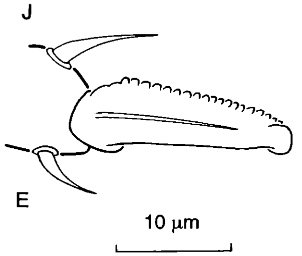


Figure 17 *Sphaeridia neopumilis* n. sp.: male: tip of dens and mucro.

The name of this new species relates to its resemblance to *Sph. pumilis*.
*Sphaeridia neopumilis* resembles *Sphaeridia pumilis* (KRAUSBAUER), but differs by its thin tibiotarsal III seta IIpe (instead of strong) and its short mucro (instead of long, DUNGER & BRETFELD 1989).

### *Sphaeridia spira* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Monserrate.
Type material: Holotype: Male (no. 1, 4 slides), Colombia, Páramo de Monserrate 7 km NE Bogotá, 4° 15' N, 74° 1' W, litter of a mountain forest remainder at 3230 m, 10. IX. 1986 leg. STURM (sample 86/116), coll. BRETFELD 24/89a1, at SMF (Ap 2434). – Paratypes: 1 male (no. 2, slide) from the holotype sample, at MNCB; 3 males, same locality but wet mosses on soil surface at 3300 m, 14. X. 1985 leg. STURM (sample 85/180), coll. BRETFELD 65/92: 2 (alc. and slide) in coll. BRETFELD, 1 (no. 1, slide) at MNHN.
Further material: 1 male (4 slides), Colombia, Páramo de Chisacá about 40 km SSW Bogotá, 4° 17' N, 74° 12' W, low vegetation on soil surface (mosses and herbs) of grassland (pajonal) near Laguna Negra at 3720 m, 18. IX. 1986 leg. STURM (sample 86/97), in coll. BRETFELD (no. 22/89).

Total male 0.18 mm, pale with some violet pigment as a horizontal band or as lateral spots; in sample 85/180 eye-patches slightly pigmented, i. e. the single omma-

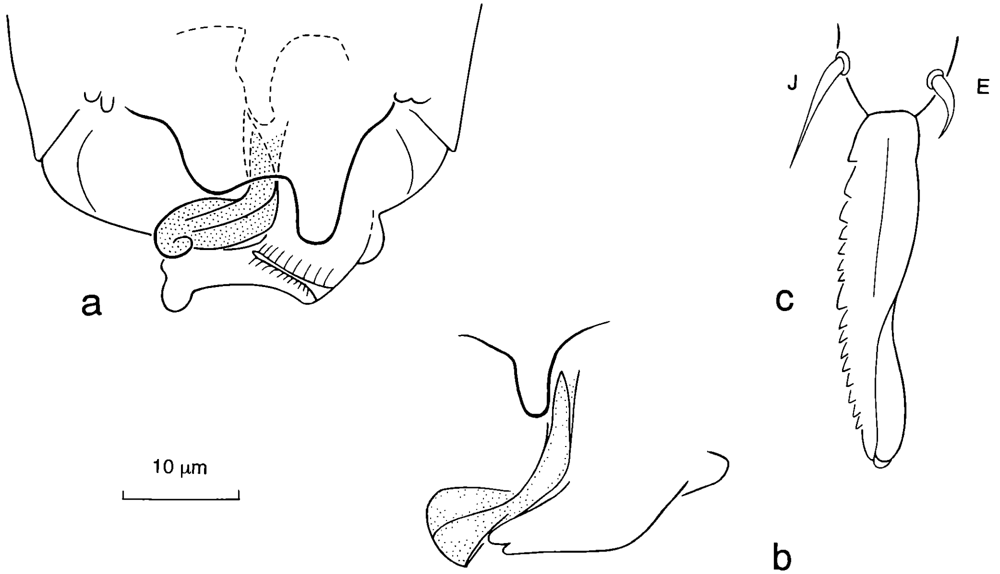


Figure 18. *Sphaeridia spira* n. sp.: male: a) ventral tube from posterior; b) ventral tube, other view of the two asymmetrical lobes, posterior membrane omitted; c) tip of dens and mucro.

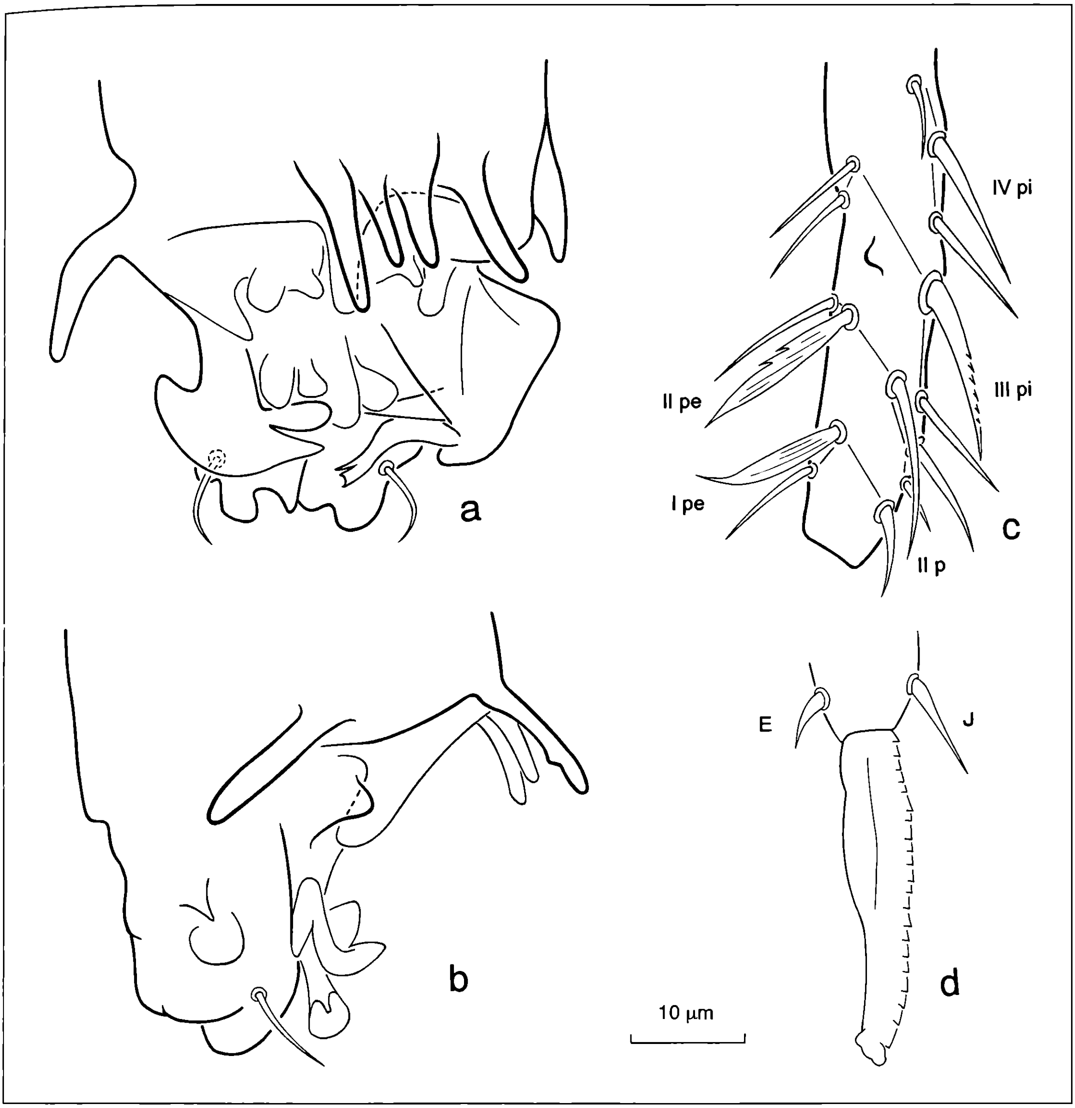


Figure 19. *Sphaeridia sturmi* n. sp.: male: a) ventral tube from posterior; b) from the left; c) modified seta of tibiotarsus III; d) tip of dens and mucro.

tidia observable. Ventral tube with asymmetrical structures (Fig. 18 a, b): posteriorly with an asymmetrical membrane, anteriorly of which a small median process; medially with a twisted lobe bent to the left with a basal spine directed towards posterior; anteriorly with a second asymmetrical lobe bent from the right to the left; without setae. Tibiotarsus III (see *Sph. sturmi*, Fig. 19 c) with other setae modified than in most other species: setae Ipe and IIpe long, daggerlike blades, IIp long, IIIpi strong and toothed, IVpi strong. Head setae strong. Dens as in Fig. 4 c, but without basal papilla, seta E1 thick, P3 a microchaeta; tip of mucro a small cap (Fig. 18 c); dens mucro = 2.2.

The name of this new species is derived from Latin spira = whorl, relating to the twisted process of its ventral tube.

*Sphaeridia spira* resembles *Sph. sturmi* n. sp. in that both have asymmetrical ventral tube structures and the same modification of the tibiotarsal setae. It differs from that species by the fine structures of its ventral tube.

### *Sphaeridia sturmi* nov. spec.

Type locality: Colombia, Bogotá, Páramo de Monserrate.
Type material: Holotype: Male (no. 2, 4 slides), Colombia, Páramo de Monserrate 7 km NE Bogotá, 4° 15' N, 74° 1' W, litter of a mountain forest remainder at 3230 m, 10. IX. 1986 leg. STURM (sample 86/116), coll. BRETFELD 24/89a2, at SMF (Ap 2433). – Paratypes: 3 males (slides) from the holotype sample: no. 1 in coll. BRETFELD, no. 3 at MNHN, no. 4 at MNCB.
Further material: 2 males (slides), Colombia, Páramo de Chisacá about 40 km SSW Bogotá, 4° 17' N, 74° 12' W, mountain forest remainder near Laguna Negra at 3720 m, 17. IX. 1986 leg. STURM by beating branches (sample 86/57), in coll. BRETFELD (no. 18/89).

Total male about 0.2 mm, horizontal band and ventral side blue. Ventral tube with complicated, asymmetrical structures (Fig. 19 a, b): posteriorly with 3 – 5 fingerlike processes, anteriorly of which a median process; medially with 1+1 processes ending in asymmetrical medial tips: the right ending in a band, the left in a lobe; laterally with 1+1 thin processes of different length. Tibiotarsus III (Fig. 19 c) with other setae modified than in most other species: setae Ipe and IIpe long, daggerlike blades, IIp long, IIIpi strong and toothed, IVpi strong. Dens as in Fig. 4 c, but without basal papilla, seta E1 thick; tip of mucro a shrunk cap (Fig. 19 d); dens   mucro = 2.2.

We gratefully dedicate this new species to its collector, Prof. Dr. HELMUT STURM, University of Hildesheim, Germany, whose expeditions to Colombia contributed so much to our knowledge of the Arthropoda of the Andean páramo regions.

*Sphaeridia sturmi* resembles *Sphaeridia spira* n. sp. in that both have asymmetrical ventral tube processes and the same modification of the tibiotarsal setae. It differs from that species by the fine structure of its ventral tube processes.

The pattern of the modified tibiotarsal setae of *Sphaeridia spira* and *Sph. sturmi* resembles that of *Sph. schalleri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, *winteri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, and *betschi* ARLÉ, 1984, because there are other setae modified than in the other species.

The ventral tube of *Sph. betschi* is simple (ARLÉ 1984), whereas the tubes of *Sph. schalleri* and *winteri* (after the re-examination of the types) have complicated but symmetrical structures with a posterior median process.

Thus *Sph. spira* and *sturmi* remain isolated within the known species, and *Sph. schalleri* and *winteri* seem to occupy an intermediate position between *Sph. spira* and *sturmi* and the other species. Whether the ventral tube of *Sph. betschi* is really simple should be shown by the types or by new collections.

## 5. Systematic comparison

For practical purposes the genus *Sphaeridia* is divided into several species groups by the structure of the male ventral tube.

### ***pumilis*-group**

These species have a male ventral tube with 1+1 posterior, small vesicles. The group is named after *Sphaeridia pumilis* (KRAUSBAUER, 1898). The following species belong to this group (a short characterization of the tibiotarsus III structures is added: seta IIpe-setae IIIpi, IVpi): *Sphaeridia pumilis* (KRAUSBAUER, 1898) (strong and long-normal); *proxima* (MURPHY, 1960) (long-toothed); *denisi* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964 (asymmetrical lobe, proximal part short and round, distal part long and pointed-toothed); spec. MASSOUD & DELAMARE DEBOUTTEVILLE, 1964 (asymmetrical lobe on a large papilla, proximal part of lobe short and round, distal part short and pointed [new observations after re-examination of the type which will be described in detail in a later publication]-toothed); *spinifrons* MURPHY, 1966 (long-one toothed); *zaheri* YOSII, 1966 (long and straight-normal); *asiatica* RUSEK, 1971 (symmetrical fork-normal); *aserrata* MARI MUTT, 1987 (asymmetrical fork-normal); *clara* n. sp. (normal-toothed); *coronata* n. sp. (stronger-toothed); *martii* n. sp. (normal-toothed); *neopumilis* n. sp. (long and thin-strong without teeth); *pilleata* n. sp. (normal-strong, toothed); *robusta* n. sp. (strong-toothed); *squamifera* n. sp. (large blade-toothed).

*Sph. betschi* ARLÉ, 1984, may be provisionally added to this group (see for a discussion of its characters above).

### ***brevipila*-group**

These species have a male ventral tube with a posterior, median process. The group is named after *Sphaeridia brevipila* (MURPHY, 1960). The following species belong to this group (tibiotarsus III structure is added as above): *Sphaeridia brevipila* (MURPHY, 1960) (normal); *cornuta* MURPHY, 1966 (normal); *fernandoi* MURPHY, 1966 (normal-toothed); *massoudi* MURPHY, 1966 (normal); *obtusa* MURPHY, 1966 (normal); *pippetti* MURPHY, 1966 (normal-toothed); *serrata* (FOLSOM & MILLS, 1938), sensu CHRISTIANSEN & BELLINGER, 1980 (normal); *cardosi* ARLÉ, 1984 (normal); *carioca* ARLÉ, 1984 (normal-toothed); *fluminensis* ARLÉ, 1984 (one curved seta); *heloisae* ARLÉ, 1984 (long, tip cut-one toothed); *paroara* ARLÉ, 1984 (long, thick, blunt-toothed); *furcata* DUNGER & BRETFELD, 1989 (long, knob-normal); *leutrensis* DUNGER & BRETFELD, 1989 (long, knob-normal); *boettgeri* n. sp. (normal); *catapulta* n. sp. (long-toothed); *cerastes* n. sp. (normal); *chisacae* n. sp. (long-normal); *franklinae* n. sp. (longer-small teeth); *lobata* n. sp. (long-short, strong); *mandibulata* n. sp. (long-toothed).

*Sphaeridia schalleri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, and *winteri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964, may be provisionally added to this group, but both species have other modifications of the tibiotarsus III setae (see p. 132 for a discussion of their characters).

**_irmleri_-group**

These species have a male ventral tube with posterior and lateral, complicated, symmetrical structures. The group is named after *Sphaeridia irmleri* n. sp. Also *Sphaeridia fibulifera* n. sp. belongs to this group.

**_spira_-group**

These species have a male ventral tube with complicated asymmetrical structures and other tibiotarsal setae modified than the other species. The group is named after *Sphaeridia spira* n. sp. Also *Sphaeridia sturmi* n. sp. belongs to this group.

**Male incompletely known**

We are not able to classify the following species into groups because the male ventral tube is unknown and the types were not yet available (tibiotarsus III structure is added as above): *Sphaeridia minima* (SCHÖTT, 1893) (unknown); *biniserrata* (SALMON, 1951) (asymmetrical fork-normal); *pumilis* (KRAUSBAUER, 1898) sensu DELAMARE DEBOUTTEVILLE & MASSOUD, 1964 (unknown); *salmoni* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964 (long, waved-normal); *spinifer* (GAMA, 1964) (unknown); *murphyi* YOSII, 1966 (long, thick, pointed-toothed); *pumilis* (KRAUSBAUER, 1898) sensu ARLÉ, 1984 (unknown).

**Male not known**

We are also not able to classify the following species because they were described only after females: *Sphaeridia sphaera* (SALMON, 1946), MASSOUD & DELAMARE DEBOUTTEVILLE, 1964; *tunicata* (YOSII, 1954); *gladiolifer* DELAMARE DEBOUTTEVILLE & MASSOUD, 1964; *posterospina* MURPHY, 1966; spec. YOSII, 1966; *indica* PRABHOO, 1971.

## 6. Ecology

*Sph. boettgeri* from Paraguay was found in a mixed sample, therefore its ecology is unknown; we note, however, that this species was also found in Brazil near Manaus.

The new species from Brazil were collected in the inundation forests of central Amazonia near Manaus. We mention briefly (see IRMLER 1975, ADIS 1984, JUNK 1984) that the water of the Rio Solimões – Rio Amazonas, which is loaded with nutrient-rich minerals (whitewater), deposits a fertile soil and covers and condenses the litter layer with clay (várzea-region, Ilha de Marchantaria studied here). On the other hand, the water of the Rio Negro and its tributaries, which is very poor in minerals (blackwater), deposits a soil poor in nutrients with a loose litter layer of some cm thickness (igapó-region, forests at Rio Tarumã Mirím studied here). The region of Lago Janauarí is inundated by the mixed water of both river systems.

We cannot give detailed ecological data because of the still low number of samples studied definitively, and refer to the paper which the junior author is preparing.

The new *Sphaeridia* species from Colombia occur in small numbers in all the strata studied in the Andean páramo region: in raw humus, litter, mosses and herbs on soil, on tree branches, and in epiphytes (mosses and ferns).

The species are distributed in the biotopes as follows: raw humus at 3080 m, *Sph. neopumilis*; litter at 3230 m, *Sph. mandibulata, sturmi, spira*; mosses and herbs on soil at 3300 m and 3720 m, *Sph. spira, chisacae*; tree branches at 3720 m, *Sph. sturmi*; epiphytes at 3000 m, 3250 m, and 3550 m, *Sph. mandibulata, lobata, catapulta* (accompanied by *Sturmius epiphytus* BRETFELD, in press).

*Sph. neopumilis, chisacae,* and *catapulta* were collected only in one stratum or at one altitude, *Sph. lobata* only in epiphytes but at all altitudes, *Sph. sturmi* in litter and on branches, *Sph. spira* in litter and soil mosses, i. e. always near the soil surface, and *Sph. mandibulata* in litter and epiphytes at one altitude.

The data show that altitude does not restrict occurrence; most species, however, were found in the strata with a large inner surface (litter, mosses on soil or as epiphytes).

## 7. Key of Sphaeridia males of South America

(Abbreviations: Ant. II or III = antennal segment II or III, post. = posterior, proc. = process or processes; Tita III = tibiotarsus III; VT = ventral tube)

Four species are not included in this key because the males were not at all or not completely described:

- *Sph. biniserrata* Salmon, 1951, sensu Arlé, 1984 (Tita III seta IIpe asymmetrically furcated, both parts pointed, the proximal one shorter than the distal, Tita III without toothed setae, VT unknown)
- *Sph. pumilis* (Krausbauer, 1898) sensu Delamare Deboutteville & Massoud, 1964 (no significant male characters described)
- *Sph. gladiolifer* Delamare Deboutteville & Massoud, 1964 (described only after females)
- *Sph. pumilis* (Krausbauer, 1898) sensu Arlé, 1984 (no significant male characters described)

| | | |
|---|---|---|
| 1. | VT with asymmetrical structures; Tita III setae Ipe, IIpe long, daggerlike blades: *spira*-group | 2 |
| – | VT with symmetrical structures; Tita III with normal setae or other setal modifications: | 3 |
| 2. | VT with 3 – 5 fingerlike post. proc. | *sturmi* n. sp. |
| – | VT with an asymmetrical post. membrane and two distal lobes bent from the right to the left | *spira* n. sp. |
| 3. | VT with 1+1 small post. vesicles: *pumilis*-group | 4 |
| – | VT with more or less complicated structures | 14 |
| 4. | VT with two post. membranes; Tita III seta IIpe stronger than normal setae, IIIpi and IVpi strong, toothed | *coronata* n. sp. |
| – | VT with only the 1+1 post. vesicles | 5 |
| 5. | Tita III seta IIpe of normal setal shape | 6 |
| – | This seta of other shape | 10 |
| 6. | Setae of Tita III without teeth, seta IIpe long and thin; head apex with thin setae | *neopumilis* n. sp. |
| – | Tita setae IIIpi, IVpi strong and toothed | 7 |
| 7. | Head with setae a4, d4 | 8 |
| – | Head without setae a4, d4 | 9 |
| 8. | Head frons rows a, b and c, d close together; length of Ant. II  III = 1.4; mucro with 10 inner teeth | *pilleata* n. sp. |
| – | Head frons rows a, b, c, d clearly separated; length of Ant. II  III = 2.0; mucro with 15 inner teeth | *clara* n. sp. |
| 9. | Ant. II with two additional spines, length of Ant. II  III = 3.0; femur III with a short blunt post. spine | *martii* n. sp. |
| – | Without these characters; total length up to 0.22 mm; Tita III seta IIIpi strong with few large teeth, IVpi thin with small teeth | *robusta* n. sp. |
| 10. | (5.) Tita III seta IIpe an asymmetrical fork, proximal part short (and blunt?), distal part longer and pointed | *aserrata* Mari Mutt, 1987 |
| – | Seta IIpe a large blade | 11 |
| 11. | Tita III seta IIpe sickle-shaped, IIIpi and IVpi toothed, Ipe and IIp (?) longer than others | *betschi* Arlé, 1984 |
| – | Tita III seta IIpe of other shape, IIIpi and IVpi toothed, other setae of Tita III normal | 12 |
| 12. | Tita III seta IIpe a thick and blunt blade, IIIpi and IVpi strong with few teeth | *squamifera* n. sp. |
| – | Tita III seta IIpe an asymmetrical lobe, proximal part round, distal part pointed | 13 |
| 13. | Tita III seta IIpe with long distal tip | *denisi* Massoud & Delamare Deboutteville, 1964 |
| – | Tita III seta IIpe with short distal tip | spec. Massoud & Delamare Deboutteville, 1964 |
| 14. | (3.) VT with a median post. proc.: *brevipila*-group | 15 |
| – | VT without such a proc.: *irmleri*-group | 24 |
| 15. | Tita III seta IIpe of normal setal shape | 16 |
| – | This seta long and thin, or of other special shape | 21 |

16. Tita III with toothed setae 17
– Tita III setae without teeth 20

17 VT with 1+1 or 2+2 lateral and anterior proc. 18
– VT with more lateral proc. 19

18. VT post. proc. with 1+1 furcated lateral parts; Tita III with one toothed seta *carioca* ARLÉ, 1984
– VT post. proc. with 1+1 apical teeth, strong fanlike root, and a large anterior branch, VT also with 1+1 curved post.-lateral proc. with an earlike medial border each; Tita III setae IIIpi and IVpi with small teeth *franklinae* n. sp.

19. VT post. proc. in front of a strong wall, broad furcated, VT also with 1+1 thin post.-lateral proc. and 2+2 lateral lobes; Tita III setae IIIpi and IVpi with small teeth *catapulta* n. sp.
– VT post. proc. in front of a thin membrane in form of a handglass, VT also with 1+1 thin post.-lateral proc., 1+1 tridentate lateral proc., and several symmetrical anterior lobes; Tita III setae IIIpi and IVpi strong with one tooth each *mandibulata* n. sp.

20. (16.) In lateral view, VT post. proc. in form of a semicircle, VT also with 2+2 bidentate lateral proc.; Tita III with a curved seta *fluminensis* ARLÉ, 1984
– VT post. proc. with a short anterior branch, VT also with 2+2 lateral lobes *cardosi* ARLÉ, 1984
– VT post. proc. simple, VT also with 2+2 or 3+3 lateral lobes; Tita III seta IIpe long, IIIpi and IVpi short and strong *lobata* n. sp.
– VT with two median post. proc. and 3+3 other proc. (post., lateral, anterior) *chisacae* n. sp.
– VT post. proc. with a knobbed tip, VT also with 1+1 striated post. blades and 1+1 mandible-like anterior proc. *boettgeri* n. sp.
– VT post. proc. only slightly knobbed, VT also with 1+1 large post. vesicles and 1+1 long, furcated anterior proc. *cerastes* n. sp.

21. (15.) Tita III with toothed setae 22
– Tita III setae without teeth 23

22. Tita III seta IIpe a long, thick spine, IIIpi and IVpi with only one tooth each; VT post. proc. thick with 1+1 vaulted lateral blades *paroara* ARLÉ, 1984
Tita III seta IIpe long, leaflike, distal part long and narrow, tip cut, one seta toothed (IVpi?); VT post. proc. with a narrowing in basal third, tip blunt, VT also with 1+1 lateral proc. with a long, curved, acuminated tip each; dens seta E1 a thick spine *heloisae* ARLÉ, 1984

23. Tita III seta IIpe long and thin, IIIpi a long, thick spine, IIp thicker than normal setae *winteri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964
– Tita III setae Ipe, IIpe, IIp thick with a long acuminated tip each *schalleri* MASSOUD & DELAMARE DEBOUTTEVILLE, 1964

24. (14.) VT with 1+1 post. blades with three lobes each and 1+1 strong anterior lobes with large, doubled teeth; Tita III seta IIpe long, IIIpi strong with one tooth, IVpi normal, without teeth *irmleri* n. sp.
– VT with 1+1 post.-lateral, long, waved proc., 1+1 lateral, thick knobs, and 1+1 anterior vesicles; Tita III seta IIpe stronger than normal setae, IIIpi and IVpi strong, toothed *fibulifera* n. sp.

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CHRISTOPHER MARTIUS

# Termite nests as structural elements of the Amazon floodplain forest

### Abstract

In periodically flooded várzea forests of the Amazon River the most dominant termite constructions were arboreal nests of 5 wood-feeding *Nasutitermes* spp. with densities of 37-68 nests per hectare and nests of the geophagous *Anoplotermes* sp. A (Apicotermitinae) with 3-333 nests per hectare. A bark-feeding species, *Anoplotermes* sp. C, which covers tree trunks with soil coatings, showed densities of up to 389 „covered trees" per hectare.

Of all *Nasutitermes* nests in one of the investigated plots, 73% were „living" nests inhabited by termites (2/3 „juvenile" and „adult", 1/3 „senile" nests), and 27% were abandoned („dead") nests. The decaying nests or nest parts („dead" and „senile" nests together; 51%) represent a spatial resource which can be used by secondary colonizers. *Nasutitermes corniger* nests accounted for 69-86% of the *Nasutitermes* nests and for 31-70% of the total nest volume. The surface of the chambers in all dead nests on trees of *N. corniger* was calculated to 197-408 m$^2$ ha$^{-1}$ (up to 1/25 ha per ha of forest; 0.43 ± 0.06 m$^2$ per liter of nest volume). One ant species, *Dolichoderus bispinosus*, occupied 62% of the living and 69% of the dead nests of *N. corniger*.

The nests of *Anoplotermes* sp. A are built in the soil during the dry season. At the beginning of the flood season, the termites erect voluminous epigeic nest extensions which reach beyond the future flood level and where the colonies survive the flood. Colonies of *Coptotermes, Rhinotermes,* and *Anoplotermes* sp. D, and other arthropods as well, use these constructions for survival of the flood, too. The submerged parts of the *Anoplotermes* sp. A nests are colonized by Oligochaeta which accelerate the decomposition of the flooded nest parts. This results in an almost complete turnover of the nest constructions every year, and almost no dead nests are left for potential invaders.

*Anoplotermes* sp. C builds 0.5-0.8 cm thick soil coatings which cover the tree trunks. The species affected 23% of all trees >3 cm Ø and extended the soil coatings up to a height of 12-14 m on the trunks. These „covered feeding places" probably allow the survival of these bark-feeding termites and other soil arthropods during the flood.

### Kurzfassung

### Termitennester als strukturelle Elemente im amazonischen Überschwemmungswald

In periodisch überschwemmten Várzea-Wäldern des Amazonas waren die Baumnester von 5 holzverzehrenden *Nasutitermes*-Arten mit Dichten von 37-68 Nestern pro Hektar und die Nester der geophagen Art *Anoplotermes* sp. A (Apicotermitinae) mit 3-333 Nester pro Hektar die häufigsten Termitenbauten. Eine rindenfressende Art, *Anoplotermes* sp. C, die die Baumstämme mit Schichten aus Erdmaterial überzieht, wies Dichten von bis zu 389 „überdeckten Stämmen" pro Hektar auf.

Von allen *Nasutitermes*-Nestern auf einer der Untersuchungsflächen waren 73% „lebende" Nester (von Termiten bewohnt; 2/3 „juvenile" und „adulte", 1/3 „senile" Nester), und 27% waren verlassene („tote") Nester. Die verfallenden Nester oder Nestteile („tote" und „senile" Nester zusammen; 51%) stellen eine Raumnische dar, die von sekundären Besiedlern genutzt werden kann. Der Anteil der Nester von *Nasutitermes corniger* betrug 69-86% aller *Nasutitermes*-Nester und 31-70% des Gesamt-Nestvolumens. Die innere Oberfläche der Nestkammern in allen toten Nestern von *N. corniger* auf Bäumen wurde auf 197-408 m$^2$ ha$^{-1}$ berechnet (= bis zu 1/25 ha pro Hektar Wald; 0.43 ± 0.06 m$^2$ pro Liter Nestvolumen). Eine Ameisenart, *Dolichoderus bispinosus*, besetzte 62% der lebenden und 69% der toten Nester von *N. corniger*.

Die Nester von *Anoplotermes* sp. A werden während der Trockenzeit im Boden errichtet. Zu Beginn der Überschwemmungsperiode bauen die Termiten voluminöse Anbauten, die über den kommenden Hochwasserspiegel herausragen, und wo die Termiten die Überschwemmung überdauern. Kolonien von *Coptotermes, Rhinotermes,* und *Anoplotermes* sp. D sowie andere Arthropoden überdauern ebenfalls die Flut in diesen Bauten. Die gefluteten Teile der Nester von *Anoplotermes* sp. A werden von Oligochaeten besiedelt, die den Abbau dieser Nestteile beschleunigen. Das Resultat ist ein fast vollständiger Umsatz aller Nestkonstruktionen in jedem Jahr, so daß für potentielle sekundäre Besiedler kaum tote Nester übrigbleiben.

*Anoplotermes* sp. C überzieht die Stämme der lebenden Bäume mit 0.5-0.8 cm dicken Schichten aus Bodenmaterial. Diese fanden sich auf 23% aller Bäume >3 cm Ø und reichten bis zu einer Höhe von 12-14 m auf den Stämmen. Diese „überdachten Fraßplätze" erlauben vermutlich das Überleben dieser rindenfressenden Termiten und anderer Bodenarthropoden während der Überschwemmungsperiode.

### Resumo

### Ninhos de térmitas como elementos estruturais em florestas inundadas da Amazônia

As construções de térmitas mais dominantes em florestas de várzea periódicamente inundadas do río Amazonas foram ninhos arbóreos de 5 espécies xilófagas de *Nasutitermes* spp. com densidades de 37-68 ninhos por hectare, e ninhos da espécie geófaga *Anoplotermes* sp. A (Apicotermitinae) com 3-333 ninhos pro hectare. *Anoplotermes* sp. C, uma espécie que se alimenta de casca e cobre os troncos das árvores com coberturas de material de solo, ocorreu em densidades de até 389 „árvores cobertas" pro hectare.

De todos os ninhos de *Nasutitermes* numa das áreas em investigação, 73% foram ninhos „vivos" inabitados por cupins (2/3 dos ninhos „juvenis" e „adultos", 1/3 „senis"), e 27% foram ninhos abandonados („mortos"). Os ninhos ou partes de ninhos em decadência (ninhos „mortos" e „senis" juntos; 51%) representam um espaço que pode ser usado por colonizadores secundários. Ninhos de *Nasutitermes corniger* representaram 69-86% dos ninhos de *Nasutitermes* e 31-70% do volume total dos ninhos. A área calculada da superfície de todas as câmaras em todos os ninhos mortos de *N. corniger* foi de 197-408 m$^2$ ha$^{-1}$ (até 1/25 ha por hectare de floresta; 0.43 ±

0.06 m$^2$ por cada litro de volume de ninho). Uma espécie de formiga, *Dolichoderus bispinosus*, ocupou 62% dos ninhos vivos e 69% dos ninhos mortos de *N. corniger*.

Os ninhos de *Anoplotermes* sp. A são construídos no solo durante a estação seca. No início da enchente, estes cupins constroem extensões epígeas dos seus ninhos que são mais altos que o futuro nível da enchente, e onde as colônias sobrevivem a inundação. Colônias de *Coptotermes, Rhinotermes,* e *Anoplotermes* sp. D além de outros artrópodos usam estas construções para sobreviver a enchente. As partes submersas dos ninhos de *Anoplotermes* sp. A são colonizadas por Oligochaeta que aceleram a decomposição das partes inundadas dos ninhos. Isto resulta numa reciclagem quase total de todos os ninhos em cada ano, e quase não sobram ninhos mortos desta espécies para possíveis invasores.

Os cupins de *Anoplotermes* sp. C constroem camadas de solo sobre troncos de árvores, de uma grossura de 0.5-0.8 cm. Estas construções afetaram 23% de todas as árvores >3 cm Ø e extenderam até uma altura de 12-14 m nos troncos. Estes „lugares de forageio cobertos“ provávelmente permitem a sobrevivência desta espécie e de outros artrópodos de solo durante a inundação.

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## 1. Introduction

Termites are important decomposers in tropical ecosystems. Their social life requires the construction of nests which provide isolation from climatic factors and from predators. This building behaviour puts termites among the few animals which accomplish work in the physical sense of the word (BRAFIELD & LLEWELLYN 1982). Termitaria, made from degraded organic matter, feces, and saliva, are generally solid structures, which often persist for a long time even after the death of the colony. These structures are important and frequently determining characteristics of many landscapes, particularly of savannas („Termitensavannen“: TROLL 1936; also LEE & WOOD 1971, GRASSÉ 1984, 1986, SATTAUR 1991). WOOD & SANDS (1978) recognized several aspects of the „role“ of termites in ecosystems:

- physical and chemical change of soil characteristics, particularly the disturbance of soil profiles and re-allocation of organic matter;
- modification of the vegetation: either damage (due to feeding on plant seedlings, roots, leaves or due to ring barking), or benefits (from changed soil structure or enhanced fertility);
- the building of more or less persistent constructions which often considerably modify and structure the environment, and to which other fauna can adapt. In the German literature these structures are referred to as „Biochorion“, which is translated as „minor habitat“ (SCHAEFER & TISCHLER 1983).

The first two aspects are matter of many studies (to mention only a few: LEE & WOOD 1971, WIELEMAKER 1984; SPAIN et al. 1985, CÉSAR et al. 1986, LAL 1987, LOBRY DE BRUYN & CONACHER 1990). Regarding the third aspect, there exists much information about the fauna associated with termites (termitophiles: KISTNER 1969, 1990, WILSON 1971, FONTES 1977, 1978, JACOBSON & PASTEELS 1992, COSTA-LEONARDO & SOARES 1993) and their nests (termitariophiles: BERG 1900).

ARAUJO (1970), for example, provided extensive lists of mostly non-obligatory associations between termites and non-termite fauna in the neotropics. The amazing behavioural adaptations shown by some termitariophilous bees have been described in detail by KERR et al. (1967) and CAMARGO (1970, 1984). REDFORD (1984) identified *Cornitermes cumulans* as a „keystone species“ in Brazilian savannas („cerrado“), because it is the dominant mound builder whose constructions are an important structural element used by many other arthropods. BANDEIRA (1983) found, on average, 320-1180 non-termite cohabitants per dm$^3$ nest volume in *Cornitermes ovatus* and *Nasutitermes minimus* in eastern Amazonia, mostly Acari (92.2-92.7%), Collembola (1.8-4.2%), and ants (0.2-4.8%). APOLINÁRIO (1993) identified various groups of Plathelmintes, Mollusca, Annelida, Arthropoda, and Vertebrata associated with termite nests in terra firme rain forest. And MARTIUS et al. (1994) recorded the fauna associated with abandoned termite nests in floodplain forests.

Peculiar earth mounds (murundus) in southern Brazilian savannas are sometimes the result of termite activity (OLIVEIRA 1992); although in other cases these landscape patterns seem to be produced by erosion processes (FURLEY 1986, HARIDASAN 1990). In closed forests, termite constructions are not so conspicuous as in savannas, but their high density (BANDEIRA 1978, 1979, 1983, 1989, MARTIUS in press) suggests that they are also important features here. The present paper is an attempt to establish an inventory of structures and spaces offered by termite nests in floodplain forests (várzea = white water floodplains; SIOLI 1956, PRANCE 1980). In this ecosystem, characterized by periodic floodings (JUNK 1984, 1989, JUNK et al. 1989), and which covers about 150.000 km$^2$ of Amazonia (SIPPEL et al. 1992), the termite density is high (MARTIUS 1989, in press), and their population structure is simple and relatively easy to study.

In the following, the terms „nest“, „mound“ or „termitarium“ are used as synonyms for the constructions of the termites, whereas „colony“ refers to the socially organized group of termites living in one or several of such nests. (Some colonies extend over various nests; cf. MARTIUS 1989; this is neglected here). Nests in the várzea are either arboreal (on trees, being connected to the ground only by galleries) or „intermediate“ between arboreal and soil nests (a term introduced by

Apolinário (1993), which refers to nests attached to trees but still in broad contact with the ground, and normally made of soil). Nests can also be completely confined to dead wood. „Galleries“ are the covered runways built by termites to cover the trails which lead to their feeding places.

A termite colony („living“ nest) passes through various life stages (Noirot 1969):

1. the juvenile phase, with a high percentage of larvae in the colony, when the nest grows according to the size requirements of the colony;
2. the adult phase, marked by the formation of sexual reproductives (alates) and the nuptial flight(s), which represent a severe loss of living biomass to the colony (Wood & Sands 1978);
3. the senile phase, with reduced or declining individual numbers. Abandoned peripheral nest chambers become subject to erosion; nest walls break down and the open chambers represent a spatial niche which is soon invaded by animals of other taxa.

A natural population comprises colonies in all these phases plus the „dead“ nests which have been abandoned by their colonies, generally due to the death of the termites. Dead nests are completely, and senile nests at least partially accessible for secondary invaders.

## 2. Material and Methods

### Locality

The study was carried out on 3 sites on Ilha de Marchantaria, an island in the River Amazon („Solimões“; i.e. the Amazon above its confluence with Rio Negro), near Manaus, Brazil (see Worbes 1986, and Martius 1989, for a site description). Site P (an area of 1.465 ha) was a forest stand in the early secondary stage („lightwood association“; Worbes et al. 1992) which had been deforested 20 years ago. The second site (Z = 0,601 ha), about 80 years old, corresponds to the late secondary stage of Worbes et al. (1992). Site C, similar and near to site Z, was established to study a population of *Anoplotermes* sp. A.

Only the higher areas of the floodplains, which are flooded for shorter periods, are covered by forest. Many of the more accessible sites are frequently logged for wood, and secondary forest evolves which seems to be able to support higher termite densities than the later successional stages (Martius 1989 and unpubl.).

### Material

The *Nasutitermes* spp. were determined by Dr. S. Bacchus, then Natural History Museum, London (U.K.), and Dr. Luis R. Fontes, then Universidade de São Paulo, São Paulo (Brazil). The species belonging to the subfamily of Apicotermitinae were grouped into morphospecies and placed into the genus *Anoplotermes*; however, they do not agree with any description given by Fontes (1985, 1986) for the 5 existing genera of Apicotermitinae. *Anoplotermes* sp. A is a new species and probably a new genus (Fontes in litt. 1992).

The ant *Dolichoderus bispinosus* (Olivier, 1791) (formerly *Monacis bispinosa*, cf. Martius 1989) was determined by comparison with specimens from the Entomological Collection of the INPA, Manaus.

Oligochaeta found in termite nests were identified by Dr. G. Righi, Universidade de São Paulo.

### Methods

The termite nests in the plots were marked and mapped; maximum height and circumference were measured in *Nasutitermes* nests, and maximum height and diameter in nests of *Anoplotermes* sp. A. In *Anoplotermes* sp. C, maximum height of the constructions on the tree stems was recorded only. Termites were sampled from nests or connected galleries. Nests with termites were considered as „living“ independently of how many individuals were found. Nests without termites were recorded as „abandoned“ (they are free of termites, but can be inhabited by „secondary“ colonizers, mostly arthropods). Ant colonies associated with termite nests were recorded without regarding their colony size.

For Nasutitermitinae, the nest volume $V_{Nest}$ was calculated on the basis of a simplified geometrical model of the nest shape (a cylinder combined with two half spheres), using nest height $H_N$ and maximum circumference $U_N$ as follows:

$V_{Nest} = \pi r^2(H_N-2r)+4/3\pi(U_N/2\pi)^3$ with $r = U_N/2\pi$

I neglected the generally small volume of the tree trunk around which the nest was built.

The external surface of the *Nasutitermes* nests was calculated according to:

$O_{Nest} = U_N(H_N+U_N/\pi)$

The volume of *Anoplotermes* sp. A nests was calculated from their height $H_N$ and maximum diameter $D_N$ (= distance from nest surface to tree surface) using as basic shape a half cylinder (in which $D_N = r_{Cylinder}$), according to:

$V_{Nest} = \pi D_N^2 H_N/2$

and the nest surface was calculated from:

$O_{Nest} = \pi D_N(D_N+H_N)$

The real area of the inner surface of the chambers in a termite nest is difficult to assess. The „idealized internal surface“ of *Nasutitermes* nests was determined from transverse and radial slices which were cautiously cut from a nest of *N. corniger*. On the surfaces exposed by the cut, areas of 4 x 4 cm were chosen at random, from which all nest walls which crossed the cutting plane were copied to a transparent sheet. The length of the lines on the sheet was then determined with the help of a map measurer (a device used in determining distances on maps). Each single area (n = 8) was measured 5 times, and the average calculated. This procedure gave a value of the total length of all nest walls crossing the cut. If the cutting plane is seen as one side of a block, 4 x 4 cm large and wide, and 0.5 cm deep (= 8 $cm^3$), the total internal surface of this block can be calculated by multiplying the average extension of the nest walls in the block by 0.5, and then by 2 (each wall has two sides). The total internal surface of one liter nest volume is then calculated by multiplying the block surface by 125. Due to the breaking of nest parts during cutting, this method probably underestimates the inner surface (at an estimated rate of 10%) of the nests of *N. corniger*. The nests of *N. macrocephalus* and *N. surinamensis* were not measured, but the individuals of these species are larger and produce wider nest chambers, and probably therefore the internal area of the nests of these species is smaller.

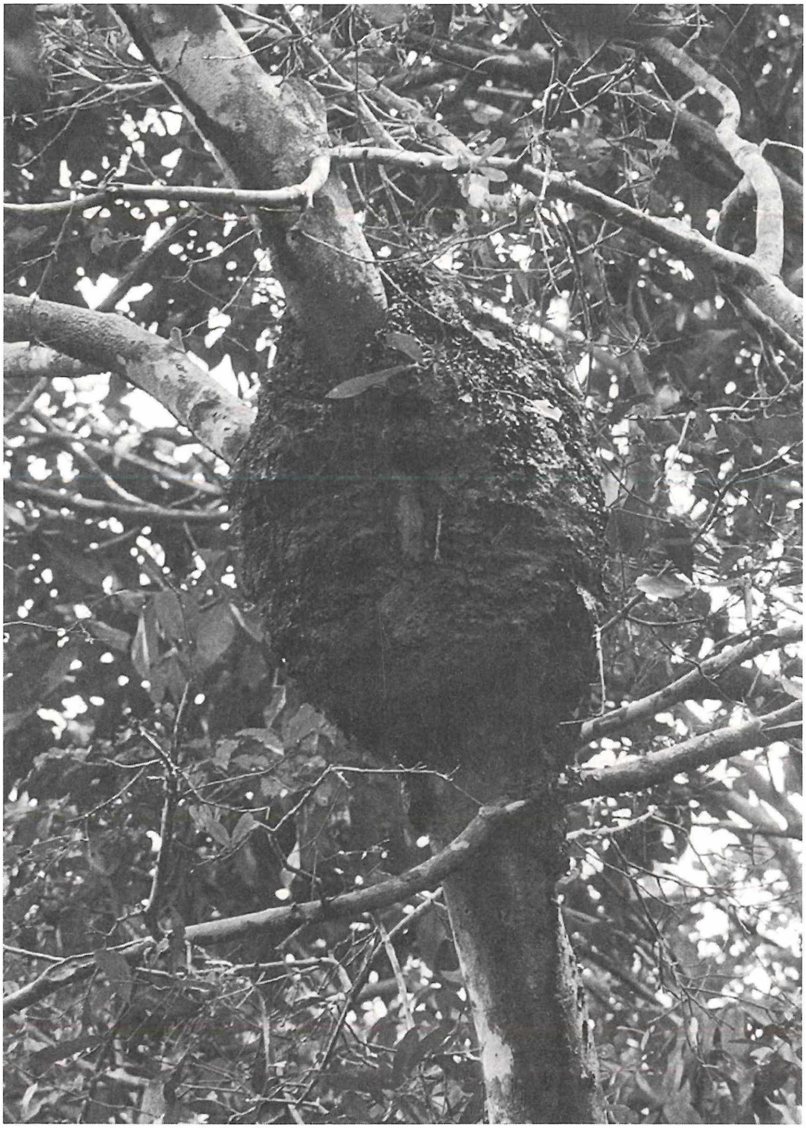

Figure 1. View of a nest of *Nasutitermes surinamensis* on the tree species *Crataeva benthamii* in várzea forest, Ilha de Marchantaria. Nest height approx. 0.9 m, nest above ground approx. 6.5 m. Note the eroding nest parts on the upper right side of the nest.

The *Nasutitermes* nests on site P were surveyed in monthly intervals between 17.6.1985 and 8.4.1986 (due to technical reasons, the annual cycle could not be completed); the number of living and dead nests (on trees and on the ground), and the dates of the death of old nests and advent of new nests, as well, were recorded.

Tree trunks (>3 cm diameter) and the occurrence of used and abandoned *Nasutitermes* galleries on the trunks were counted within an area of 900 m$^2$ (12 plots of 5 x 15 m; Tab. 5) on site P (>1 gallery of the same termite species per tree was counted as one case). The idealized trunk surface from the ground to a height of 10 m was calculated from these data using the dbh (diameter at breast height) of the trees.

## 3. Results and Discussion

Thirteen termite species were found in the várzea (Martius 1989) (tab. 1). From a structural viewpoint, the most abundant species among them divide into 3 groups according to their nest types: 5 wood-feeding *Nasutitermes* species with arboreal nests, the geophagous *Anoplotermes* sp. A living in intermediate nests, and the bark-feeding *Anoplotermes* sp. C with intermediate constructions, too.

Among the less frequent species, *Termes medioculatus* and *Microcerotermes* build arboreal nests from

Table 1. Termites species, nest types and feeding biology in várzea floodplain forest (Ilha de Marchantaria and * Ilha do Careiro).

| | |
|---|---|
| Wood feeders | |
| Tree nest builders | *Nasutitermes corniger* |
| | *Nasutitermes tatarendae* |
| | *Nasutitermes macrocephalus* |
| | *Nasutitermes surinamensis* |
| | *Nasutitermes ephratae* |
| | *Microcerotermes* sp.* |
| Nests in dead wood | *Rhinotermes marginalis* |
| | *Rhinotermes* sp. 1 |
| | *Coptotermes* sp. 1 |
| Soil feeders | |
| Intermediate nests (epigeic/arboreal) | *Anoplotermes* sp. A |
| | *Anoplotermes* sp. C |
| Arboreal nests | *Termes medioculatus* |
| Inquilines (in nests of other species) | *Anoplotermes* sp. D |

earth and carton laterally on tree trunks. *Coptotermes* and *Rhinotermes* species generally establish their nests within decaying moist wood. Considerable numbers of Kalotermitidae colonies must exist in the várzea (REBELLO & MARTIUS in press), but their habits are very cryptic and they were never recorded in termite nest assessments (MARTIUS 1989, CONSTANTINO 1992).

### 3.1 Nest types

#### Arboreal *Nasutitermes* nests

These more or less rounded nests, made from carton material (= digested cellulosic material), are attached to trees in varying heights (2-15 m) (fig. 1-2). Although the nests of the 5 *Nasutitermes* species are all very similar in their general features, they differ in characteristical, species-specific manners which allow to distinguish the species in the field, even after the death of the colony (MARTIUS 1989, cf. also THORNE 1980).

#### Intermediate nests

*Anoplotermes* sp. A termitaria are long soil „columns“ attached to the sides of tree trunks, from the ground up to a height of 4.8 meters on average (MARTIUS 1990, and unpubl. data) (fig. 3-5). The nests of *Anoplotermes* sp. C are thin soil coatings which extend irregularly over the tree trunks up to a maximum height of 14 m (fig. 6). Some of the tree trunks in their lower parts are completely covered by these crusts which are not thicker than 0.5-0.8 cm.

Table 2. Average nest volume and surface for 5 *Nasutitermes* species of the várzea floodplain (average ± standard deviation).

| Species | | Nest volume [liter/nest] | Nest surface [dm$^2$/nest] |
|---|---|---|---|
| *N. corniger* | 92 | 35.36 ± 41.40 | 48.7 ± 37.1 |
| *N. ephratae* | 6 | 118.59 ± 89.97 | 127.2 ± 74.7 |
| *N. macrocephalus* | 6 | 350.80 ± 121.52 | 257.3 ± 69.4 |
| *N. surinamensis* | 5 | 405.41 ± 323.92 | 279.4 ± 191.3 |
| *N. tatarendae* | 21 | 46.34 ± 67.85 | 61.0 ± 60.3 |

### 3.2 Termitarium inventories

### 3.2.1 Arboreal *Nasutitermes* nests and galleries

#### Nests

The largest nests were those of *Nasutitermes surinamensis* and *N. macrocephalus* (tab. 2); their volume was, on average, 6-11 times higher than in *N. corniger* and *N. tatarendae*, and their external surface about 4-6 times. However, due to the different size of young and old nests the intraspecific nest size variation was high.

Table 3 shows the number, total volume and total surface of the *Nasutitermes* nests on the two várzea plots. The nest density (n/ha) on site P was about 2 times higher than on site Z, the total nest volume was 2.7 times, and the total nest surface 2.4 times higher. For all nests, total volume amounted to 2.0-5.3 m$^3$ ha$^{-1}$, and total surface to 2.2-5.3 m$^2$ ha$^{-1}$, respectively, for site Z and P.

*Nasutitermes corniger* had the highest nest density and volume of all species. It accounted for 69.1% of the nest number and for 31.4% of the total nest volume on plot P, and for 86.3% of the nests and 69.5% of the nest volume on plot Z. Approximately 3/4 of all *N. corniger* nests on trees on site P were „living“ nests (juvenile, adult, and senile), and 1/4 were „dead“ (fig. 7). Dead and senile nests together amounted to half of the nest number. Figure 7 shows the composition of the nests as a snap shot, but table 4 shows that the proportion of living and dead nests remained almost stable in the course of a year.

The idealized inner surface of nests of *N. corniger* was determined to 0.43±0.06 m$^2$ per l of nest volume (fig. 2), which for all living *N. corniger* nests on site P (cf. tab. 3) gave a total internal surface area of 716 m$^2$ ha$^{-1}$ (1/14 ha per hectare of forest). The internal surface area of all dead nests amounted to 265 m$^2$ ha$^{-1}$ I estimate that dead parts of senile nests accounted for approximately 20% of the total nest volume. Corrected by this figure, the internal surface area in inhabited and abandoned nests of this site amounted to 573 and 408 m$^2$ ha$^{-1}$, respectively (1/17 and 1/25 ha per ha forest). On site Z a calculated internal surface of 384 and 197 m$^2$ ha$^{-1}$ was available in living and dead *N. corniger* nests (using the same assumption for senile nests).

Figure 2. A tangential view of the internal structure of *Nasutitermes corniger* nest. Same size as in Figure 4.

Nests of senile colonies often fall from the tree when the attachment of the nest loosens. A few nests are knocked down by falling trees or branches. About half (8 of 15) of the dead nests on the ground registered in 1986 (tab. 4) were living nests which fell to the ground while the colony was dying. The other half (7 of 15) were nests which had died on the tree and fallen later.

Roughly 80% of the dead nests remained longer than 7 months on the tree (n=18), 17% longer than 10 months (fig. 8a). Dead nests on the ground vanished faster (fig. 8b). There, the higher humidity (particularly after the flood) and increased abundance of decomposers on the ground are likely to accelerate the decay of the nests. Nests on the ground are not protected from flooding and can only temporarily be used by secondary colonizers.

The total number and volume of dead nests on the ground is given in table 3. Their external surface was broken and therefore not assessed. Their internal surface area amounted to 88-231 $m^2$ $ha^{-1}$ (using the average size of 35.36 l per nest from table 2; they were mostly nests of *N. corniger*).

It is mainly the internal surface of the dead and eroding nests which is interesting in the context of this paper. The numbers seem relatively high; however, the calculated surface of only the lower parts of the tree trunks (between 0 and 10 m from the ground) amounted to 12 650 $m^2$ $ha^{-1}$ in plot P. In comparison to this value, the deserted *Nasutitermes* nests certainly represent only a very small area to be occupied by secondary fauna. (The trunk surface is a roughly calculated value, not the real surface which includes spaces in fissures of the bark, hollow branches etc.; in addition the surface of the branches, twigs, and leaves in the crown has been neglected.) However, tree trunks and termite nests are only in part comparable, as termite nest matter is more soil-like, more malleable and as such represents a substrate probably preferred by many (soil) arthropods. In fact, dead termite nests are poorly inhabited by other fauna, except for ants (cf. 3.3.2) and for the periods when the ground is flooded (MARTIUS et al. 1994).

#### Galleries

Total gallery lengths of 45-150 m were recorded for 5 nests of *Nasutitermes macrocephalus*. Termites abandon galleries when new feeding places are found, and when nests die. The gallery walls break up, and other arthropods, e.g. small ants and springtails, invade them. Sometimes, other termite colonies of the same or different species „reactivate“ such unoccupied runways. I found that abandoned galleries remained for several years on the tree trunks. They persisted even flooding and were only destroyed by mechanical impact (falling branches, climbing animals). A count of used and deserted galleries on trunks (tab. 5) shows that, on average, 19.3% of all trunks (emergent and understorey trees) had at least one abandoned gallery (333 galleries per ha). On the assumption of an average tree height of 20 m and only one gallery running linearly from the base to the top of the tree I calculated a total gallery length of 5.7 km per hectare. This does not take into account the galleries within the litter layer, but their contribution to space for secondary colonizers in the litter is certainly insignificant.

### 3.2.2 Intermediate nests I: *Anoplotermes* sp. A

#### Living nests

*Anoplotermes* sp. A seems to be particularly adapted to the periodical floodings (MARTIUS in press). The colony starts with a soil nest, which later is transformed into an epigeic nest extending in height beyond the water level of the coming flood, which allows the survival of the colony (fig. 3). Contrary to the nests of *Nasutitermes*, the nests of this species consist of thick layers of soil containing only small tunnels or nest chambers (fig. 4). The internal surface area was not determined.

The density of this species varied between 3 (site Z) and 219 (site P) nests per ha, due to differences in

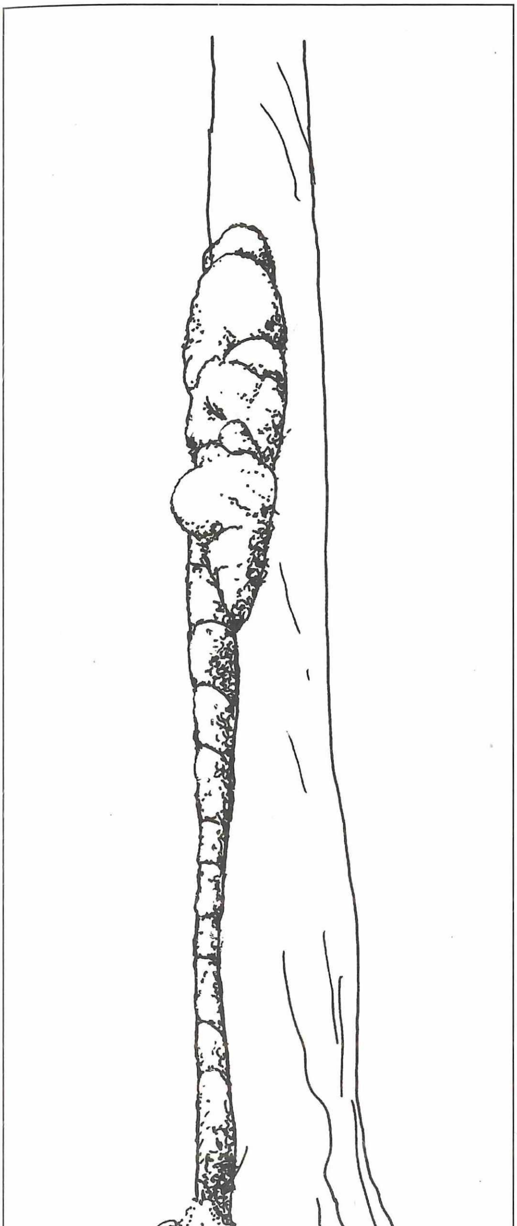

Figure 3. Epigeic nest parts of *Anoplotermes* sp. A in várzea forest, Ilha de Marchantaria. Nest height approx. 4 m from ground to top Note the heap of old nest matter at the foot of the tree. Drawn from a photograph by the author.

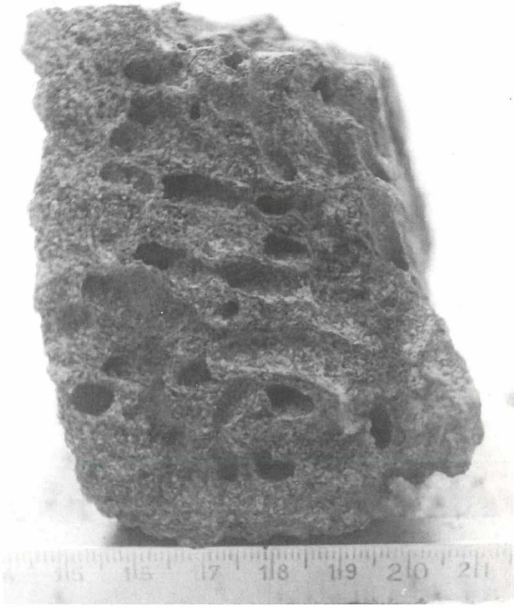

Figure 4: Radial view of the internal structure of a nest of *Anoplotermes* sp. A. Compare the thickness of the walls with Figure 2. The right side is the one which was attached to the tree.

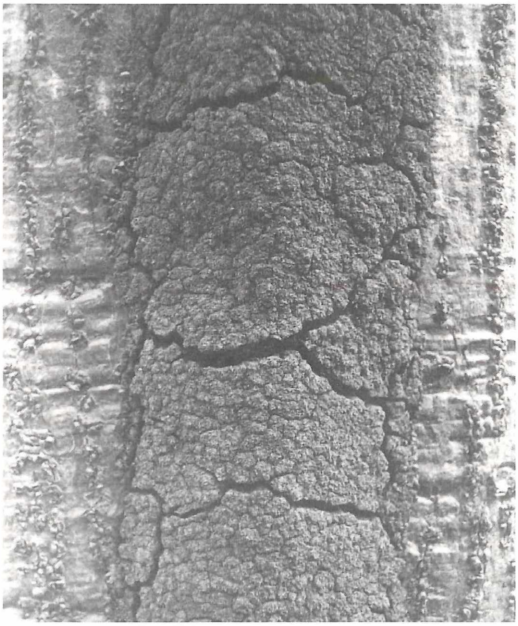

Figure 5. External view of a nest of *Anoplotermes* sp. A on the tree *Pseudobombax munguba*. Note the cracks which appear after the nest dries.

flood duration and soil particle size at the different sites, and the total volume of the nests varied accordingly between 0.3 and 16.4 $m^3$ $ha^{-1}$ (tab. 6).

**Dead nests**

Due to the peculiar life cycle and the activity of earthworms which invade the drowned nest parts (cf. 3.3.2), almost no dead nests of *Anoplotermes* sp. A remained for longer than one year on the plot. If nests died naturally, they soon fell from the tree. The only remnants were the „heaps“ (fig. 3) of accumulated old nest material found at the base of the trees. Their size varied according to how many cycles (years) had been fulfilled by the colony at the site. As these heaps were very persistent through time, their number in a given area was 4-6 times higher than the number of the active nests (tab. 6). This means that 0.7-50.9% of the trees are provided with a heap (tab. 5, 6). The chemical and physical soil parameters of the heap material are likely to influence tree growth (MARTIUS 1990).

### 3.2.3 Intermediate nests II: *Anoplotermes* sp. C

*Anoplotermes* sp. C covers the tree trunks with a thin soil layer, probably in order to graze on the bark or on the lichens and mosses growing on the tree trunks (similar „covered feeding places“ have been found in other termite species in India and Java: BECKER 1972, GRASSÉ 1984: 487). As neither alates nor larvae or eggs have ever been found in these constructions I think that the proper nest must be in the soil. Probably the colony uses these constructions for flood survival as in *Anoplotermes* sp. A.

As much as 23% of all trees >3 cm Ø were covered by these soil sheaths (tab. 5). Soily nest matter rich in or-

Figure 6. View of the „covered feeding places“ of *Anoplotermes* sp. C, várzea forest, Ilha de Marchantaria.

Table 3. Volume and external surface of nests of *Nasutitermes* spp. in the várzea forest, Ilha de Marchantaria.

| | Site P = 1.465 ha | | | Site Z = 0.601 ha | | |
|---|---|---|---|---|---|---|
| Species | n/ ha | Nest volume [liter/ha] | External nest surface [$dm^2$/ha] | n/ ha | Nest volume [liter/ha] | External nest surface [$dm^2$/ha] |
| Living nests | | | | | | |
| *N. corniger* | 47.1 | 1665.5 | 2293.8 | 31.6 | 1117.4 | 1538.9 |
| *N. ephratae* | 2.7 | 320.2 | 343.4 | 0 | 0 | 0 |
| *N. macrocephalus* | 4.1 | 1438.3 | 1054.7 | 0 | 0 | 0 |
| *N. surinamensis* | 3.4 | 1378.4 | 950.0 | 1.7 | 689.2 | 475.0 |
| *N. tatarendae* | 10.9 | 505.1 | 664.7 | 3.3 | 152.9 | 201.2 |
| Total | 68.2 | 5307.4 | 5306.5 | 36.6 | 1959.5 | 2215.1 |
| Dead nests | | | | | | |
| On trees | 16.4 | 579.9 | n.d. | 6.6 | 233.4 | n.d. |
| On the ground | 14.3 | 505.6 | n.d. | 5.8[1] | 205.1 | n.d. |
| Total | 30.7 | 1085.5 | | 12.4 | 438.5 | |

([1] calculated form the proportion of dead nests on ground to dead nests on trees on site P.

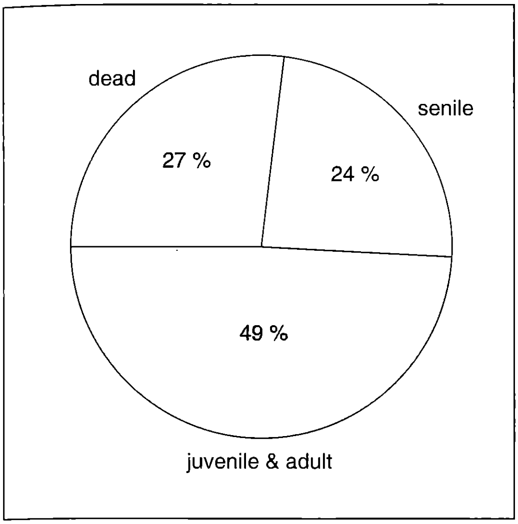

Figure 7 Proportion of juvenile, adult, senile and dead nests on trees in a population of *Nasutitermes corniger* on Ilha de Marchantaria (site P).

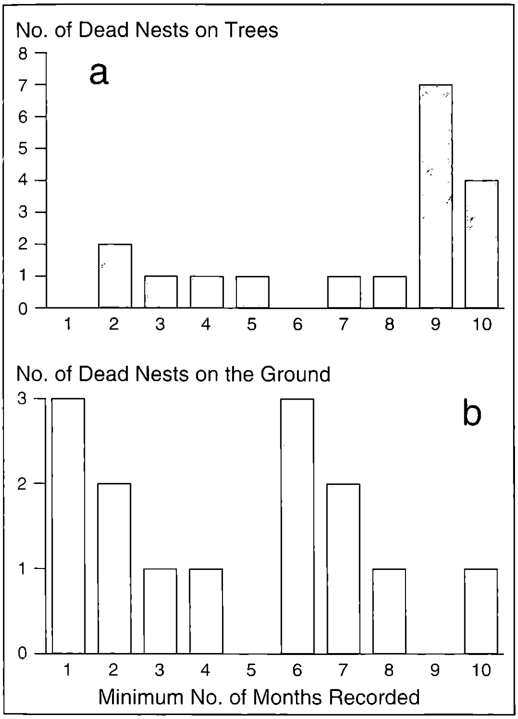

Figure 8. Persistence of dead nests in a population of *Nasutitermes corniger* in a várzea forest (site P, Ilha de Marchantaria). a) Number of dead nests on trees observed for 1 to 10 months during the nest population survey. b) Number of dead nests on the ground observed for 1 to 10 months.

Table 4. Survey of *Nasutitermes* nests on part of site P, Ilha de Marchantaria; month 1 = 17.6.1985, month 10 = 8.4.1986.

| Month | Living nests | Dead nests | |
|---|---|---|---|
| | | on trees | on ground |
| *Nasutitermes* (5 species) | | | |
| 1 | 71 | 17 | n.d. |
| 10 | 72 | 19 | 15 |
| *N. corniger* | | | |
| 1 | 40 | 15 | n.d. |
| 10 | 42 | 15 | 10 |

ganic compounds which erodes from these constructions will concentrate near the tree base, with possible consequences for tree growth, very much like in *Anoplotermes* sp. A, however to a much lesser extent.

### 3.3 Non-termite organisms associated with termite nests

External and internal surfaces of living nests of all termite species are colonized by microorganisms, for example methanotrophic (HEYER 1990, ROULAND et al. 1992), and probably nitrogen-fixing as well as decomposing bacteria (HEYER & BERGER unpubl.).

#### 3.3.1 Fauna in termite-inhabited nests

Unfortunately, termitophiles have never been studied in the várzea. Some termitariophiles which use the spaces offered in *Nasutitermes* nests in this ecosystem during the flood are listed in MARTIUS et al. (1994). Additional qualitative information follows here.

Termites are generally not active during the day on their nest surface, and all kinds of other arthropods can run freely around. Spider webs are often found on termite-inhabited nests. Some termitariophilous meliponid bees (CAMARGO 1970, 1984) are observed in the várzea. Local farmers know that parrots frequently construct their nests within *Nasutitermes* termitaria. Use of termite nests by breeding birds is also known from other parts of Amazonia (KOEPCKE 1972).

In the flood-safe parts of inhabited, vigorous nests of *Anoplotermes* sp. A other termite species (*Coptotermes, Rhinotermes, Anoplotermes* sp. D) could sometimes be found. The latter species was exclusively recorded here and seems to be an „inquiline" species which never builds a nest of its own. *Coptotermes* and *Rhinotermes* are colonizers of dead wood, and when this is flooded some colonies manage to invade nearby nests of *Anoplotermes* sp. A. Consequently, the nests of *Anoplotermes* sp. A can be seen as a key structure which positively influences the survival of other termite species in the várzea.

### 3.3.2 Fauna in senile and dead nests

#### *Nasutitermes*-nests

The composition of the colonizer fauna of eroding nest areas and totally dead nests of *Nasutitermes* species is probably identical. Major differences depend on the season (Martius et al. 1994). During the dry season, particularly ants use abandoned parts of termite nests to settle their own colonies, but abandoned termite nests are also frequently recolonized by other colonies of the same or different species.

*Dolichoderus bispinosus* (Olivier, 1791), a widely distributed neotropical ant of the subfamily Dolichoderinae, has a close affinity to *N. corniger* nests (tab. 7). Of the studied set of nests, 70.9% were inhabited by termites, and 63.6% by ants. Ants were found in 61.5% of all nests inhabited by termites, and 68.8% of the „dead" nests were occupied by ants. The ants stayed permanently in the termite nests over the course of the

Table 5. An assessment of *Nasutitermes* galleries and constructions („covered feeding places") of *Anoplotermes* sp. C in várzea forest; site P, Ilha de Marchantaria; gall. = galleries, aband. gall. = abandoned galleries, constr. = constructions.

| | | | *Nasutitermes* spp. | | | *Anoplotermes* sp.C | |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Subplot Nº | N trees >3cm Ø | Used gall. | % of gall. (3) per trees(2) | Aband. gall. | % of aband. gall.(5) per trees (2) | N constr. per subplot | % of constr. (7) per trees (2) |
| 1 | 11 | 4 | 36 | 6 | 54 | 3 | 27 |
| 2 | 11 | 2 | 18 | 0 | 0 | 3 | 27 |
| 3 | 7 | 3 | 43 | 0 | 0 | 1 | 14 |
| 4 | 17 | 2 | 12 | 3 | 18 | 4 | 24 |
| 5 | 25 | 6 | 24 | 2 | 8 | 4 | 16 |
| 6 | 21 | 1 | 5 | 5 | 24 | 0 | 0 |
| 7 | 16 | 2 | 13 | 6 | 38 | 0 | 0 |
| 8 | 9 | 0 | 0 | 1 | 11 | 3 | 33 |
| 9 | 5 | 2 | 40 | 0 | 0 | 0 | 0 |
| 10 | 10 | 4 | 40 | 3 | 30 | 4 | 40 |
| 11 | 11 | 1 | 9 | 3 | 27 | 7 | 64 |
| 12 | 12 | 2 | 17 | 1 | 8 | 6 | 50 |
| sum | 155 | 29 | 19 | 30 | 19 | 35 | 23 |
| $ha^{-1}$ | 1722.2 | 322.2 | | 333.3 | | 388.9 | |

Table 6. Density, volume, and weight of nests and heaps of *Anoplotermes* sp. A, várzea forest, Ilha de Marchantaria. Total nest weight calculated from nest volume and physical density of nest/heap matter (0.6 g $cm^3$; Martius 1990). Plot C was investigated before flood, Plot P and Z during the flood, therefore heap numbers in sites Pand Z were calculated from nest-to-heap-ratio in site C.

| Plot | Area studied [$m^2$] | Density of nests or heaps [$ha^{-1}$] | Total nest volume [$m^3$/ha] | Total nest weight [t/ha] |
|---|---|---|---|---|
| Nests | | | | |
| C before flood | 6000 | 30-50 | 2.3-3.8 | 1.4-2.3 |
| P | 1050 | 219 | 16.4 | 9.8 |
| Z | 6013 | 3 | 0.3 | 0.2 |
| Heaps | | | | |
| C before flood | 6000 | 200 | 26.7-35.6 | 16.0-21.4 |
| P | | 876-1445 | | |
| Z | | 12-20 | | |

Table 7 Ants and termites: *Dolichoderus bispinosus* in nests of *Nasutitermes corniger*, site P, Ilha de Marchantaria

| | Number of nests on subplot | Number of nests [%] |
|---|---|---|
| Total | 55 | 100.00 |
| Only inhabited by *N. corniger* | 15 | 27.27 |
| Only inhabited by *D. bispinosus* | 11 | 20.20 |
| Termites and ants in one nest | 24 | 43.64 |
| Nest without ants or termites | 5 | 9.09 |
| Total nests with termites | 39 | 70.91 |
| Total nests with ants | 35 | 63.64 |

year. In nest parts hold by the ants no termites were found; often both colonies were separated only by a thin nest wall. The ants preyed heavily on the much smaller termites when the isolating walls were destroyed experimentally. However, if fights were carried out in the open, the ants clearly avoided encounters with nasute soldiers, probably in consequence of their chemical defense (EISNER et al. 1976, MILL 1982a, b). It is also likely that *N. corniger* soldiers are in advantage in the narrow nest chambers, which could explain why termites and ants could coexist over more than a year in some cases. Although *D. bispinosus* seems to colonize termite nests mainly for reasons of space, the ants were the observed mortality factor in 5 of 9 nests of *N. corniger* during the observation period.

On the other hand the termite colonies probably take advantage from the reaction of the ants to disturbances: Knocking on the trunk of the nesting tree provokes the ants to emerge immediately from the nest, rushing all over it and up and down the tree. The nest surface is virtually transformed into a whirling mass of ants which exhale a strong smell (alarm pheromone?) and bite every living being in their way. Many ants fall to the ground. All these reactions practically impede any approximation to the nest.

*D. bispinous* has also been reported as a colonizer of living and dead termite nests in Panama (WHEELER 1936). Termite nests are also important for nesting ants in other parts of Amazonia (cf. BANDEIRA 1978 MILL 1984, M. VERHAAGH, Karlsruhe, pers. comm.), and in other ecosystems (savanna: REDFORD 1984, OKWAKOL 1991). *D. bispinosus*, however, is not exclusively termitariophilous, as it can also be found in hollow dead trees, in accumulations of litter trapped in the canopy and similar places.

### *Anoplotermes* sp. A nests

Nest parts which emerge from the water often show holes made by termite-preying birds (particularly in older nests). Arthropods like myriapods, spiders, ants (*Crematogaster* sp. and others) and even small vertebrates (frogs, lizards) can often be found in abandoned parts of decaying nests. They sometimes dig their way into the nest like into soil, although the very hard nest walls normally impede this.

Various Oligochaeta were found in submerged nest parts of *Anoplotermes* sp. A (juveniles of *Drilocrius* sp., family Almidae, and juveniles and adults of *Glossodrilus* sp., Fam. Glossoscolecidae). They seem to be the only responsibles for transforming all the nest matter, which is very hard, into heap material. During the rising of the flood, these heaps are the last islands of soil emerging above the water level, and many arthropods can then be found here, an easy prey for birds which are attracted to these places.

### *Anoplotermes* sp. C nests

Many small arthropods are found in abandoned parts of the constructions of this species. These soil layers on trees are likely to extend the activity radius of the more mobile elements of the soil fauna onto the trunks and may play an important role in the survival of these animals during the flood. However, this relationship has never been investigated (e.g. IRMLER 1979, ADIS 1992).

### 3.3.3 Termite-plant interactions

It is not the purpose of this paper to discuss the termite-plant interactions in the várzea, but some ideas should be mentioned. Future research should be directed to this important area. One major accomplishment of the *Anoplotermes* species is the concentration of organic-rich soil in „heaps“ near the base of the trees. The activity of the nest-burrowing annelids results in one of the highest turnover rates of termite nest material found in the world (MARTIUS 1990). Almost 1/10 of the nutrient rich upper soil of the várzea is concentrated in the heaps. The possible consequences for tree growth are still to be analyzed.

Trees might possibly be destroyed by bark-feeding *Anoplotermes* sp. C, but I could not observe any damage beyond superficial bark scraping. On the other hand, the trees might be protected from attack by bark-beetles and other wood-attacking organisms by the soil cover which these termites build around the trunks, but this also remains to be studied.

It should be mentioned that the outer surface of living *Nasutitermes* nests is often colonized by mosses, algae, lichens, and sometimes small ferns, in the same manner as tree trunks.

## 4. Conclusion

Living *Nasutitermes*-nests contain an astonishing large volume and internal surface area. This huge space is fiercely defended by the termites. Only those animals can have access to the nest which are able to overcome the defense and recognition barriers of the termites. These animals must either eliminate the termites in a war-like encounter like ants do, or they have to use some „tricks" to „smuggle" themselves into the termite colony. These tricks are the amazing adaptations of the termitophiles and some termitariophiles (e.g. the meliponine bees). An aggressive strategy generally ends with the retreat or death of the termites and allows the appropriation of whole nests or at least parts of them by a large number of secondary users, whereas the infiltration tactics allow only a small number of termitophiles to survive in a termite colony. Termitophile biomass has been assessed to be <1% of that of the termites (BANDEIRA 1983). With an average termite colony of 111 000 individuals (BANDEIRA & TORRES 1985) and an average termite biomass of 1 mg per individual (MARTIUS in press) this makes ideally 111 g of termites per nest and about 1 g of termitophiles per nest, or 35-70 g $ha^{-1}$ of termitophiles (tab. 3), which is 0.03-0.07% of the soil arthropod mass (10.5 $g \cdot m^{-2}$ without termites; ADIS & RIBEIRO 1989). In spite of their insignificant biomass, termitophiles are important elements of the genetic information of the ecosystem, and attention should be directed to the study of termitophiles in Amazonia, with particular focus on the differences between várzea and terra firme forest.

Dead *Nasutitermes* nests together with senile parts of inhabited nests have a minor total volume than the living nests, however, they are the only structures which are totally accessible to secondary colonizers. The occupation of dead nests is particularly high when ants are present (cf. 3.3.2) or during the flood when soil fauna migrates onto trees with termite nests (cf. MARTIUS et al. 1994).

Inhabited nests of *Anoplotermes* sp. A are temporary resources which provide flood-survival not only for the constructing species itself but also for other termite species. The constructions of *Anoplotermes* sp. C are likely to have a similar function for the builders themselves and for the soil fauna as well.

The study presented here was carried out in secondary floodplain forests which seem to have higher termite densities than older stands. The question remains open whether the lack of termite nests in late successional stages is compensated for in other ways. We observed also partially deforested várzea areas with much higher termite nest densities (mainly *Nasutitermes corniger* and *N. ephratae*; MARTIUS & HURTADO unpubl.), where, due to the reduced number of trees, abandoned nests might be much more important for the survival of other fauna.

In non-flooded terra firme forest there is no need for flood survival (unless in water-logged depressions). The termite community in terra firme forest is generally much more diversified in terms of species and nest types. We recently started to sample fauna from conspicuous termite nests in rain forest (MARTIUS & HANNE in press).

The present study on purpose concentrated on a look at the ecosystem structure in the Amazon floodplains in order to show that termites, although they are not as conspicuous as in other ecosystems, generally occur in high densities and are significantly structuring this ecosystem. There is good reason to believe that termites and their nests are important key elements of várzea forests, which affect and determine the performance and diversity of other organisms including animals and plants.

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KLAUS RIEDE & KLAUS DUFFNER

# Systematik und Biogeographie nordwestamazonischer Orthopteren

**Kurzfassung**

Der gegenwärtige Kenntnisstand der Orthopterenfauna Nordwestamazoniens wird beschrieben: Langfühlerschrecken (Ensifera: Gryllidae und Tettigoniidae) wurden bisher nicht systematisch gesammelt, während Kurzfühlerschrecken (Caelifera) vergleichsweise gut erfaßt sind. Systematische, ökologische und biogeographische Untersuchungen der einzelnen Unterfamilien werden zusammengefaßt, laufende Forschungsprojekte skizziert und offene Probleme aufgezeigt. Erstmals werden „Chromotypen" der an den Ostabhängen der ecuadorianischen Anden vorkommenden flügellosen Gattungen *Galidacris* und *Psiloscirtus* beschrieben. Es wird diskutiert, daß die Bergregenwälder der Andenostabhänge gegenwärtige Refugien für eine artenreiche Fauna waldbewohnender Feldheuschrecken darstellen, innerhalb derer Speziationsprozesse zu beobachten sind.

**Abstract**

**Systematics and biogeography of Orthoptera from northwestern Amazonia**

The present state of knowledge of the Orthoptera from Northwestern Amazonia is outlined: long-horned grasshoppers (Ensifera: Gryllidae and Tettigoniidae) have not been collected systematically, while short-horned grasshoppers (Caelifera) have been sampled reasonably well. Systematics as well as ecological and biogeographical data for the different subfamilies of short-horned grasshoppers are reviewed, current research projects sketched, and open problems for future research are outlined. „Chromotypes" of the wingless genera *Galidacris* and *Psiloscirtus* from the eastern slopes of Amazonian Ecuador are described and their systematic status discussed. It is hypothesized that mountain forests at the eastern Andean slopes are „present-day refuges" for a species-rich fauna of forest grasshoppers undergoing actual speciation.

**Resumen**

**Sistemática y biogeografía de los ortópteros del Noroeste amazónico**

Se delinea el estado actual del conocimiento de los ortópteros del Noroeste amazónico: los saltamontes de antenas largas (Ensifera, Gryllidae y Tettigoniidae) no han sido coleccionados sistemáticamente, mientras que las muestras de saltamontes de antenas cortas (Caelifera) son suficientemente representativas. Se revisan tanto las informaciones sistemáticas como las ecológicas y biogeográficas para las diferentes subfamilias de Caelifera, además se presentan proyectos actuales de investigación y se plantean los problemas que permanecen abiertos para próximas investigaciones. Se describen los „cromotipos" de los géneros carentes de alas *Galidacris* y *Psiloscirtus* de las vertientes orientales de la Amazonía ecuatoriana y se discute su estado sistemático. Se postula la hipótesis que las selvas de montaña de las vertientes orientales andinas son „refugios actuales" para una fauna de saltamontes selváticos, rica en especies, y que se halla en un proceso actual de especiación.

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**Inhalt**

Mit Unterstützung der Deutschen Forschungsgemeinschaft im Rahmen des Schwerpunktprogramms „Mechanismen der Aufrechterhaltung tropischer Diversität".

## 1. Einleitung

Wie viele andere Insektengruppen entfalten auch die Orthopteren (Geradflügler, „Grillen und Heuschrecken") ihren größten Artenreichtum in den Tropen. Einige Familien kommen in den Außertropen gar nicht vor, und viele Lebensformtypen (sensu UVAROV 1977) zeigen hochspezialisierte Anpassungen an das Leben in tropischen Regenwäldern. In der Neotropis und insbesondere in Nordwestamazonien sind die tagaktiven Kurzfühlerschrecken (Caelifera) arten- und individuenreich vertreten. Zahlreiche große und auffällig bunt gefärbte Arten lenken die Aufmerksamkeit auch des ungeübten Betrachters auf sich, so daß sie bei einem Dschungelspaziergang neben den Schmetterlingen mit zu den auffälligsten Insekten gehören. Im Gegensatz zu letzteren sind sie jedoch keine attraktiven Sammelobjekte und unsere Kenntnis der Arten ist entsprechend lückenhaft. Zudem bewohnt eine große Anzahl dieser Tiere die schwer zugängliche Kronenregion der Urwaldbäume. Auch die artenreich vertretenen Langfühlerschrecken (Ensifera), also Grillen (Gryllidae) und Laubheuschrecken (Tettigoniidae), sind aufgrund ihrer nächtlichen Lebensweise nur schwer zu entdecken. Ihre Lautäußerungen hingegen sind ein Hauptbestandteil des nächtlichen Dschungelkonzerts. Wie alle eng an ihren tropischen Lebensraum angepaßten Organismen sind auch die zahlreichen, vielfach noch unbekannten Orthopterenarten durch die fortschreitende Vernichtung des Tropenwaldes stark gefährdet (RIEDE 1994).

Im folgenden sollen Kenntnisstand und diagnostische Merkmale der wichtigsten Unterordnungen nordwestamazonischer Orthopteren zusammengefaßt werden. Der Artikel folgt der systematischen Gliederung unter besonderer Berücksichtigung der Acridoidea. Am Beispiel ausgewählter Feldheuschrecken (Acrididae) sollen außerdem aktuelle Forschungsergebnisse zur Biogeographie sogenannter „Chromotypen", also farblicher Varianten einer bzw. nahe verwandter Arten dargestellt werden.

## 2. Kenntnisstand und Systematik

Die Ergebnisse der Forschungsreisen von GIGLIO-TOS (1898) und HEBARD (1923) sind immer noch die einzigen zusammenfassenden Darstellungen der Orthopterenfauna Nordwestamazoniens.

In einem programmatischen Artikel faßte DESCAMPS (1970) den beklagenswerten Kenntnisstand tropischer Caelifera zusammen. Seither wurde durch Aufsammlungen der Baumkronenfauna sowie systematische Bearbeitung durch AMÉDÉGNATO & DESCAMPS (1980a) unsere Kenntnis insbesondere der Acridenfauna Perus und Kolumbiens wesentlich erweitert. In Ecuador haben MORRIS et al. (1989) Untersuchungen an Tettigoniiden und RIEDE (1987) an Acrididen durchgeführt. Schwerpunkt dieser Untersuchungen waren zwar bioakustische und verhaltensökologische Fragestellungen, dennoch konnte eine erhebliche Anzahl bislang unbekannter Arten gesammelt werden, die im Muséum d'Histoire Naturelle de Paris (MHNP) hinterlegt sind (cf. Abb. 5). Systematische Aufsammlungen im ecuadorianischen „Oriente" werden derzeit von AMÉDEGNATO und POULAIN (MHNP) sowie von DUFFNER 1993/94 (siehe unten) durchgeführt.

Die Charakteristika der wichtigsten Orthopteren-Familien sowie eine Diskussion der Großsystematik der „Orthopteroidea" findet man bei KEVAN (1982). Diese Großeinteilung ist für die meisten Gruppen noch ein „matter of debate" und hat daher nur provisorischen Charakter. Die Orthoptera lassen sich in zwei Gruppen unterteilen, die Ensifera und Caelifera. Die wichtigsten Merkmale der Ensifera sind lange, fadenförmige Antennen und ein aus den Vorderflügeln gebildeter Stridulationsapparat. In den Vordertibien bilden scolopidiale Sinneszellen ein Hörorgan, damit einher geht eine Umbildung der prothorakalen Tracheen zu „Hörrohren" Viele Arten sind nachtaktiv und omni- oder carnivor. Caelifera sind hingegen meist tagaktiv und herbivor. Die kauenden Mundwerkzeuge sind niemals besonders vergrößert. Die robusten Antennen sind kürzer als der Körper (Kurzfühlerschrecken). Bei den Acridoidea liegt das Hörorgan im 1. Abdominalsegment.

### Überordnung Ensifera

#### Familie Tettigoniidae

Unter den Tettigoniidae findet man mit die größten Insekten des Regenwaldes, Formen bis zu 15 cm Länge und 18 cm Flügelspannweite sind bekannt. Die Erfassung der amazonischen Tettigoniidenfauna steht erst am Anfang. Angesichts der bisher nur punktuellen Aufsammlungen ist unsere Kenntnis der Arten Nordwestamazoniens, insbesondere der endemischen Formen des Bergregenwaldes, gering. Einen wertvollen Schlüssel für die wichtigsten panamesischen Unterfamilien und Gattungen findet man bei NICKLE (1992a); die meisten der dort erwähnten Gattungen dürften auch in Nordwestamazonien vertreten sein. Eine gute Zusammenfassung der Biologie einiger neotropischer Arten gibt BELWOOD (1990). Die Nahrungsansprüche sind vielfältig, neben pflanzlicher Kost benötigen die meisten Arten stärker proteinhaltige Nährstoffe wie z.B. Pollen, so daß sie möglicherweise eine ökologische Funktion als Bestäuber erfüllen. Etliche Arten leben räuberisch und ernähren sich von kleineren Insekten. Umgekehrt sind die Tettigoniiden selber eine wichtige Nahrungsquelle für insektivore Wirbeltiere wie z.B. Krallenaffen oder Fledermäuse (BELWOOD & MORRIS 1987). Zahlreiche Charakteristika der Tettigoniiden können als Resultat eines evolutionären Wettrennens einer intensiven Räuber - Beute Beziehung interpretiert werden. So bietet die kryptische, meist blattähnliche Erscheinung der Unterfamilie Pseudophyllinae oder die Bates'sche Mimikry von bunten Wespen (Sphecidae) der tagaktiven Gattung *Aganacris* Schutz vor optisch orientierten Räubern. Charakteristisch ist auch „akustische Krypsis": nächtlich singende Tettigoniidae produzieren nur äußerst kurze Gesänge, um der Entdeckung durch Fledermäuse zu entgehen (BELWOOOD & MORRIS 1987). Lautaufnahmen ecuadorianischer Pseudophyllinae („false-leaf katydids") der Napo-Region zeigen, daß auch dort zahlreiche Arten kurze Laute in großen Abständen produzieren (MORRIS et al. 1989).

### Familie Gryllidae

Noch schlechter als die Tettigoniidae sind die Grillen (Gryllidae) bekannt, was wohl auf ihre nächtliche und versteckte Lebensweise sowie auf die hohe Zahl kleiner Arten zurückzuführen ist. Auch hier leistet ein Schlüssel von NICKLE (1992b) für panamesische Arten wertvolle Dienste. Während die Mehrzahl der Arten omnivor und nachtaktiv ist, sind einige Vertreter der Gattung *Eneoptera* (Eneopterinae) tagaktiv und herbivor. Die 3 cm große, unauffällig kaffeebraune Art *Eneoptera surinamensis* (BURMEISTER, 1838) besiedelt als Pionierart auch größere Sekundärformationen sowie Plantagen.

Grillen tragen ganz wesentlich zur Geräuschkulisse des Regenwaldes bei. Dabei bestehen alle bis jetzt bekannten Grillengesänge aus einer artspezifischen reinen Trägerfrequenz zwischen 2 und 10 kHz, die durch spezielle Resonatoren auf den Vorderflügeln erzeugt werden. Durch Tonaufnahmen können somit Artenzahlen sowie Abundanz und Aktivitätsrhythmus von Männchen bestimmt werden (RIEDE 1993a).

### Familie Gryllacrididae

Die Gryllacrididen werden aufgrund ihres wenig spezialisierten Geäders von Vorder- und Hinterflügel sowie fünfgliedrigen Tarsen als „ursprüngliche" Familie von anderen Orthopterengruppen abgegrenzt (KARNY 1937). Die Flügel besitzen keinen Stridulationsapparat, einige Arten stridulieren jedoch mit abdominalen Zirporganen oder den Mandibeln. Den meisten Arten fehlt ein Hörorgan, bei einigen findet man ein einfach gebautes, offenes Tympanum in den Vordertibien. Den größten Artenreichtum entfaltet diese Familie in der Alten Welt. KARNY (1937) beschreibt einige Gattungen aus Mittelamerika, die wahrscheinlich auch in Kolumbien und Ecuador zu finden sind.

## Unterordnung Caelifera

### Überfamilie Proscopioidea: Familie Proscopidae

Die Vertreter dieser auf Südamerika beschränkten Familie ähneln im Habitus den „Stabheuschrecken" (Phasmatoptera: Phasmidae), sind jedoch von diesen leicht durch ihr Sprungvermögen mittels spezialisierter Hinterbeine zu unterscheiden. Sie sind waldbewohnend und vorzugsweise auf alten Lichtungen und in Baumkronen zu finden. Der neueste Schlüssel stammt von MELLO-LEITÃO (1939), sie werden zur Zeit nicht systematisch bearbeitet.

### Überfamilie Tetrigoidea: Familie Tetrigidae

Im Habitus ähneln diese Tiere, die selten größer als 2 cm werden, kleinen Acridoidea, von denen sie sich jedoch durch ein lang ausgezogenes Pronotum und das Fehlen eines Tympanalorgans unterscheiden. Obwohl diese Gruppe ihren größten Artenreichtum in den Tropen der Alten Welt entfaltet, findet man einige Arten auch in Nordwestamazonien. Besonders interessant sind hierbei die baumbewohnenden Vertreter, die irisierend grün gefärbt sind und somit stark von den bisher bekannten Arten abweichen („...never green...tree climbing is rare": KEVAN 1982). Viele Tetrigidae ernähren sich von Algen und Moosen; epiphyllische Algen könnten auch die Nahrungsgrundlage baumbewohnender Formen darstellen.

### Überfamilie Eumastacoidea

Diese Überfamilie ist in Südamerika durch die Familie der Eumastacidae und in Nordwestamazonien hauptsächlich durch die Unterfamilie der Eumastacinae artenreich vertreten. Einige Arten sind kryptisch braun gefärbt, andere jedoch zeichnen sich durch auffällige Färbung aus, wobei vor allem Kopf und Hinterende oder die letzten Abdominalsegmente durch intensive blaue oder rote Färbung vom gelbbraunen Rest abgehoben sind. Die Tiere stellen die Sprungbeine seitlich ab, wodurch ihre typische „Pfeil-und-Bogen" Position entsteht (Taf. 1a). Die biologische Bedeutung dieser Beinstellung ist unbekannt.

### Überfamilie Acridoidea

Diese Gruppe zeichnet sich von den anderen Caelifera durch das im ersten Abdominalsegment gelegene Hörorgan (Tympanalorgan) aus. Diese größte Gruppe unter den Caelifera umfaßt weltweit 10 Familien (nach KEVAN 1982; verschiedene Autoren sind sehr unterschiedlicher Ansicht), von denen 4 in Nordwestamazonien zu finden sind. Die Acrididae bilden mit Abstand die größte Familie, unter der früher sämtliche anderen Familien als Unterfamilien zusammengefaßt wurden. Die systematische Einteilung der südamerikanischen Acridoidea wurde durch AMÉDÉGNATO (1974) unter Einbeziehung einer Vielzahl von Merkmalen neu vollzogen. Ein wichtiges systematisches Merkmal ist die komplizierte Anatomie der männlichen Genitalien, die in einigen Unterfamilien auch die Grundlage der Unterscheidung äußerlich sehr ähnlicher Arten bildet. Hierdurch erhielten die ehemaligen Romaleinae Familienstatus (Romaleidae mit Unterfamilien Romaleinae und Bactrophorinae), und die ehemals größte künstliche Gruppierung der „Catantopinae", die 57% der neotropischen Acrididae enthält, wurde in verschiedene, teilweise neu errichtete Unterfamilien aufgeteilt (AMÉDÉGNATO 1977).

Neben der systematischen Einteilung ist eine Aufteilung nach Lebensformtypen für zahlreiche ökologische und vergleichende physiologische Fragestellungen von großem Nutzen. Für Heuschrecken wurden bereits von UVAROV (1977) die wichigsten Lebensformtypen charakterisiert, diese Einteilung wurde von DESCAMPS (1976) erweitert und verfeinert. Der in den gemäßigten Zonen sowie tropischen Savannen weit verbreitete Typus der graminicolen Feldheuschrecke - in Mitteleuropa im wesentlichen durch die lautbegabte Unterfamilie Gomphocerinae vertreten - ist in tropischen Wäldern vergleichsweise selten zu finden.

Vor allem in den amazonischen Wäldern dominieren die baumbewohnenden Arten, die rund 40% der nordwestamazonischen Heuschreckenfauna ausmachen (DESCAMPS 1976). Im schwer zugänglichen Bereich der Kronenregion wurde eine große Zahl bisher unbekannter Taxa gesammelt (ROBERTS 1973, DESCAMPS 1976). Unterschiedliche Bereiche der Kronenregion werden von Vertretern der Unterfamilien Ommatolampinae, Bactrophorinae, Proctolabinae und Romaleinae bewohnt (AMÉDÉGNATO 1990). Der „dendrophile Lebensformtyp" (DESCAMPS 1976) zeichnet sich durch lebhafte Färbung, gedrungene Körperform, verkürzte, zum Flug meist untaugliche Flügel und gut entwickelte, hervorstehende Augen aus (Taf. 4b – d). Charakteristisch sind außerdem lange Hintertarsen sowie die für Kurzfühlerschrecken relativ langen Antennen. Nur die Romaleinae sind lautbegabt. Alle übrigen Unterfamilien können nicht stridulieren, besitzen aber durchaus funktionsfähige Hörorgane (RIEDE et al. 1990). Dagegen beobachtet man bei vielen Arten intraspezifische optische Kommunikation durch charakteristische, lautlose Winkbewegungen der auffällig gefärbten Antennen- und Hinterschenkel (RIEDE 1987). Die Fauna der Kronenregion ist in Westamazonien arten- und individuenreich vertreten, innerhalb Amazoniens sinkt die Artenzahl in östlicher Richtung (AMÉDÉGNATO & DESCAMPS 1982). In den angrenzenden subtropischen Waldgebieten ist dieser Lebensformtypus selten und in den gemäßigten Breiten überhaupt nicht zu finden. Die Fauna des peruanischen Amazoniens ist durch die Aufsammlungen von AMÉDÉGNATO & DESCAMPS (1980a) gut bekannt; ein großer Teil dieser Fauna ist auch in den unterhalb 500 m gelegenen Regionen des Napo (Limoncocha, Misahualli) und Aguarico (San Pablo de Kantesyia, Remolinos) zu finden (Abb. 1). Oberhalb von 500 m kommen jedoch andine Faunenelemente hinzu, und die Ergebnisse der eingangs erwähnten punktuellen Aufsammlungen in den Kronen frisch gefällter Bäume zeigen einen hohen Anteil neu zu beschreibender endemischer Arten und Gattungen (AMÉDÉGNATO, pers. Mitt.; siehe auch RIEDE 1990a).

DESCAMPS (1976) unterscheidet noch zahlreiche weitere Lebensformtypen. Hier ist insbesondere die reiche Fauna „thamnorhabdophiler" Arten zu erwähnen, die Büsche und junge Bäume in natürlichen Lichtungen („gaps") sowie kleinen anthropogenen Sekundärformationen wie verlassenen Indianerpflanzungen bewohnen. Dabei wechselt die Artenzusammensetzung in charakteristischer Weise mit der Sukzession der Sekundärformationen, wobei die Abundanz einzelner Arten vorübergehend beträchtlich ansteigen kann (AMÉDÉGNATO & DESCAMPS 1980b). Viele dieser Arten sind völlig flügellos und lebhaft gefärbt (Taf. 2e, 3a–e). Die weiter unten behandelten Farbvarianten (Chromotypen) der Unterfamilien Ommatolampinae und Rhytidochrotinae sind diesem Typus zuzuordnen.

### Familie Pyrgomorphidae

Die Mehrzahl der Arten dieser Familie bewohnt die Alte Welt, während sie in der Neuen Welt mit einigen Arten in Mexiko, in der Neotropis jedoch mit nur einer Art vertreten ist, der flügellosen *Omura congrua* WALKER, 1870.

### Familie Ommexechidae

Diese auf Südamerika beschränkte Familie erreicht ihre größte Artenvielfalt im südlichen Südamerika. Nur wenige Arten leben in Amazonien; entsprechend ihren Habitatpräferenzen sind sie auch in Nordwestamazonien insbesondere an Flußufern mit Geröll zu finden. So findet man die kryptische Art *Ommexecha brunneri* BOLIVAR, 1889 häufig am Oberlauf des Rio Napo.

### Familie Pauliniidae

Diese artenarme Familie bewohnt Wasserpflanzen der Gattungen *Salvinia* und *Eichhornia* und ist in allen aquatischen Lebensräumen Nordwestamazoniens zu finden, die die entsprechenden Schwimmpflanzen aufweisen. *Paulinia acuminata* (DE GEER, 1773) weist einige bemerkenswerte Anpassungen an dieses außergewöhnliche Habitat auf. Ruderförmig verbreiterte Hintertibien dienen zum Schwimmen und Tauchen (CARBONELL 1981). Durch ihre kryptische Färbung ist diese Art auf *Salvinia*-Pflanzen nur schwer zu entdecken. Rasterelektronenmikroskopische Untersuchungen zeigten außerdem eine bemerkenswerte Konvergenz zwischen wachsartigen Kristallen der Oberfläche von Heuschreckenlarven und ihrer Wirtspflanze (BARTHLOTT et al., im Druck).

### Familie Acrididae

Die weltweit verbreitete Familie der Acrididae tritt in Südamerika in 10 Unterfamilien auf (KEVAN 1982). Vier davon (Acridinae, Gomphocerinae, Oedipodinae, Cyrtacantharidinae) sind erst sehr spät aus dem Norden über Mittelamerika eingewandert. Auch die Melanoplinae sind holarktischen Ursprungs. Die restlichen

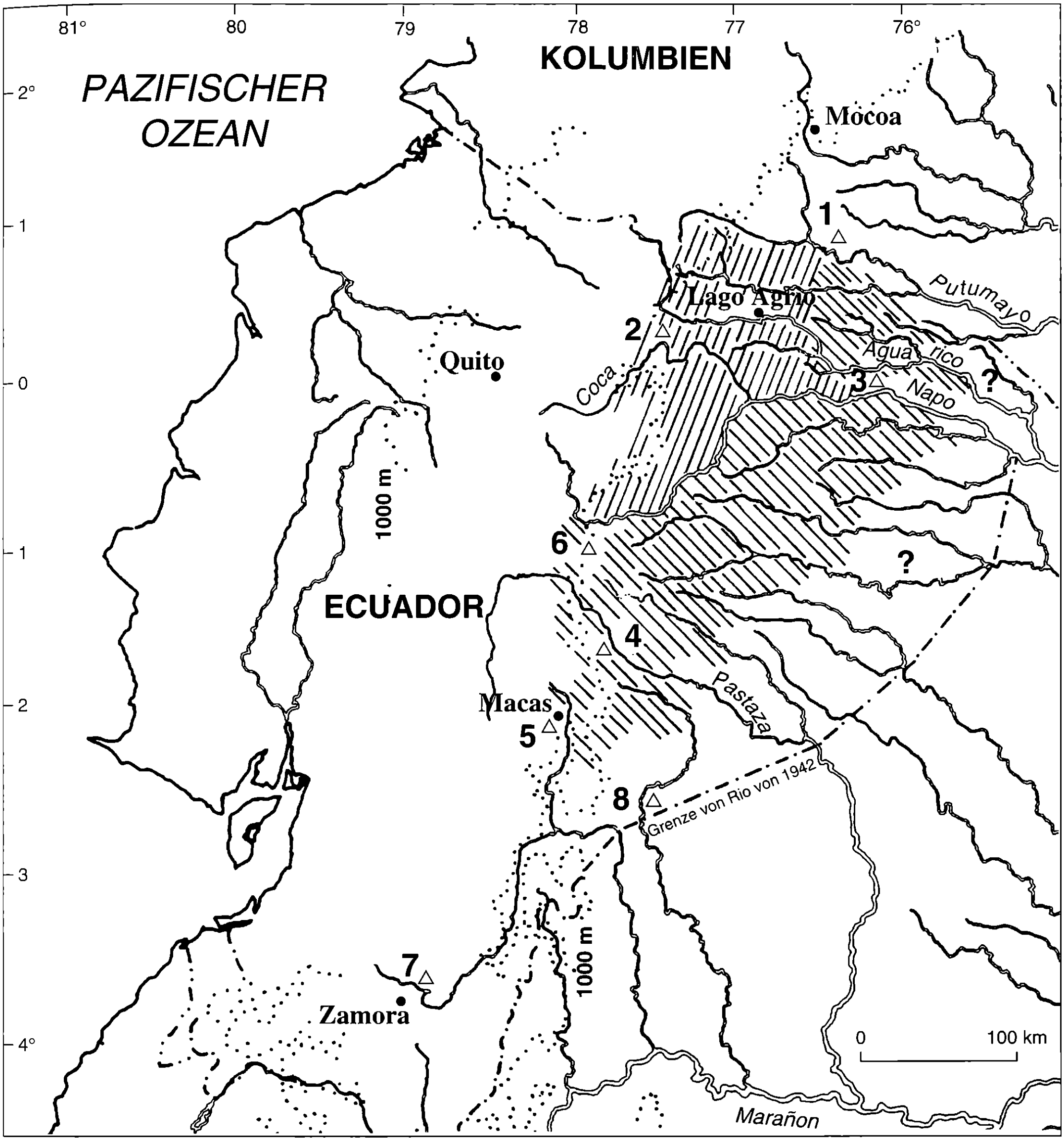

Abbildung 1. Geographische Variation bei *Psiloscirtus* (Ommatolampinae, Acrididae) in Ecuador und Südkolumbien (siehe Taf. 1). 1: Puerto Asis, Prov. Putumayo, Kolumbien; 2: Lumbaqui, Prov. Sucumbios, Ecuador; 3: Limoncocha, Prov. Sucumbios, Ec.; 4: Jibaría Shurupe, Prov. Morona Santiago, Ec.; 5: Macas, Prov. Morona Santiago, Ec.; 6: San José, Prov. Pastaza, Ec.; 7: Zamora, Prov. Zamora Chinchipe, Ec.; 8: Santiago, Prov. Morona Santiago, Ec.
Verbreitung zweier Chromotypen von *Galidacris variabilis* nach eigenen Daten. Nördliche Form (///): Rote Hinterfemora, südliche Form (\\\): Grüne Hinterfemora.

fünf Unterfamilien (Ommatolampinae, Leptysminae, Rhytidochrotinae, Proctolabinae und Copiocerinae) sind endemisch für Südamerika. Drei davon sind verwandtschaftlich eng miteinander verbunden (Ommatolampinae, Leptysminae, Rhytidochrotinae). Kein Vertreter dieser drei Unterfamilien ist zu Lautäußerungen fähig (RIEDE 1987). Sie bilden den Schwerpunkt unserer biogeographisch-systematischen Untersuchungen.

**Unterfamilie Leptysminae**

Von den Leptysminae sind bisher 22 Gattungen und 71 Arten (ROBERTS & CARBONELL 1980) beschrieben. Die Körperform ist im allgemeinen schmal und länglich, die meisten Arten sind flugfähig. Die männlichen Cerci sind stark in die Höhe gebogen (Ausnahmen: *Pseudoxyplepta*, *Xenismacris*, *Phryganacris*).

Die Mehrzahl der Arten lebt an Flußufern und in feuchten Habitaten, wo meist Monokotyledonen als Futterpflanzen dienen. Einige Leptysminae sind semiaquatisch. Die Larven verschiedener Formen leben gregär (cf. PFROMMER 1990) und unterscheiden sich stark in Farbe und teilweise in Form von den Adulttieren (Taf. 2b,c). Im Fall von *Tetrataenia surinama* (LINNAEUS, 1764) sind bei erwachsenen Tieren ebenfalls größere Verbände zu beobachten (RIEDE 1987). Der untypischen Leptysminenart *Chloropseustes brunneus* ROBERTS & CARBONELL, 1980 (Taf. 2d) fehlen Flügel und Tympana. Aus dieser Gattung sind aus Französisch-Guyana (ROBERTS & CARBONELL 1980) mehrere Farbvarianten beschrieben worden. Auch aus Ecuador konnten zwei Farbmorphen nachgewiesen werden (DUFFNER unveröff.).

**Unterfamilie Rhytidochrotinae**

Sämtliche Vertreter dieser Unterfamilie sind flügellos, wodurch das Mesonotum im allgemeinen völlig sichtbar wird. Nur in Ausnahmefällen sind Flügelreste vorhanden. Das Pronotum ist seitlich ohne Kiel. Die Genitalien der Männchen und Weibchen zeigen nur geringe interspezifische Unterschiede, so daß diese in der Systematik häufig so wichtigen Strukturen zur Unterscheidung der Arten wenig hilfreich sind (DESCAMPS & AMEDEGNATO 1972a,b).

Für die Anden Ecuadors und Kolumbiens werden fünf (*Rhytidochrota*, *Driphilacris*, *Opaonella*, *Muyscacris*, *Leopacris*), für die amazonischen Regenwälder zwei (*Galidacris*, *Paropaon*) und für die pazifischen Wälder von Costa Rica bis Ecuador sechs Gattungen (*Hylopedetes*, *Liparacris*, *Opaon*, *Parapiezops*, *Piezops*, *Trichopaon*) mit insgesamt 31 Arten aufgeführt (DESCAMPS & AMEDEGNATO 1972a).

Rhytidochrotinae besiedeln strauch- und gebüschreiche Randzonen aufgelassener Felder der Bergregenwälder, aber auch kleine Lichtungen und Flußufer des Tieflandregenwaldes. Hier können bemerkenswerte Individuenzahlen erreicht werden (RIEDE 1993b). Diese Unterfamilie entfaltet ihren höchsten Artenreichtum am Andenostabhang in Höhen zwischen 500 m und 1800 m. Die Vermutung liegt nahe, daß diese Artenvielfalt mit der dort zu beobachtenden explosiven Radiation strauchiger Futterpflanzen (z.B. *Anthurium*, *Piper*, cf. KUBITZKI 1985) zusammenhängt.

Wahrscheinlich ist die Anzahl der Spezies viel größer als bisher angenommen, wie beispielsweise der Fund der von RIEDE entdeckten neuen Gattung *Palandella* zeigt (Taf. 2e). Weitere bisher unbeschriebene Formen fand DUFFNER in den Bergregionen um Macas. Einige Arten existieren in Farbvarianten, deren systematische Stellung noch unklar ist - es könnte sich bei diesen „Chromotypen" durchaus um unterschiedliche Arten handeln. Biogeographisch interessant sind die Farbvarianten von *Galidacris variabilis* DESCAMPS & AMEDEGNATO, 1972 (Taf. 3a–c), deren Gesamtverbreitungsgebiet sich entlang der östlichen Andenabhänge und dem angrenzenden Tiefland von Südkolumbien bis Südecuador erstreckt. Aus Kolumbien beschrieben DESCAMPS & AMEDEGNATO (1972b) vier Chromotypen. Mindestens zwei davon sind auch in Ecuador vertreten: beide Farbvarianten sind am Körper glänzend grün mit schwarzen Flecken, während die Hinterbeine rot (Taf. 3a) bzw. grün (Taf. 3b) sein können. Zuchtexperimente zeigten, daß die Beinfarbe genetisch fixiert ist. Der Rio Napo bildet eine natürliche Barriere zwischen der rotbeinigen und der grünbeinigen Form (Abb. 1). Weiter nördlich verläuft die Grenze ohne erkennbares Hindernis quer durch den Regenwald, nur in einer sehr schmalen Kontaktzone von wenigen 100 m Breite konnten von DUFFNER Mischformen (Taf. 3c) gefunden werden. Beide *Galidacris* Varianten zeigen das gleiche komplexe Balzverhalten, bestehend aus charakteristischen Winkbewegungen der Hinterbeine (RIEDE 1987). Sowohl in der Kontaktzone als auch in Gefangenschaft balzen und kopulieren grün- und rotbeinige Exemplare miteinander. Die Fertilität der Hybride wird derzeit im Labor untersucht.

**Unterfamilie Ommatolampinae**

Wie die Rhytidochrotinae besitzen die Ommatolampinae ein eher untersetztes Erscheinungsbild. Viele Arten sind flügellos, bei etlichen sind noch Flügelreste vorhanden. Das Mesonotum ist in der Regel nicht oder nur der hintere Teil davon sichtbar. Bisher wurden 46 Gattungen beschrieben (AMÉDÉGNATO 1974). Ommatolampinae sind weit verbreitet in den andinen Amazonaswäldern und dem sich anschließenden Tiefland. Mitglieder dieser Gruppe bevorzugen die mittleren Schichten der Kronenregion, es werden aber auch kleine Lichtungen besiedelt.

Männchen der flügellosen Art *Psiloscirtus* sp. bilden je nach Standort verschiedene Chromotypen aus (Taf. 1), während die Weibchen einförmig braun und nicht voneinander zu unterscheiden sind (Taf. 2f). Alle Männchen besitzen seitlich einen gelben Fleck, zeigen aber in der Körper- und Augenfarbe eine sehr starke geographische Variation (Abb. 1). Auch hier müssen Kreuzungsexperimente zeigen, ob es sich um unterschiedliche Arten handelt.

*Hippariacris latona* (Taf. 3d) ist eine sehr weit verbreitete Art, die genau wie *Psiloscirtus* sp. starken Geschlechtsdimorphismus zeigt. *Ommatolampis quadrimaculata* (Taf. 3e) ist ein typischer Bewohner der mittleren Bergregenwälder des nördlichen Ecuador. Dort ist auch der Tribus Syntomacrini artenreich vertreten

(Taf. 3f), die systematische Revision dieser Gruppe steht allerdings noch aus (AMÉDÉGNATO, pers. Mitt.).

### Unterfamilie Proctolabinae

Angehörige dieser Unterfamilie stellen einen weiteren wichtigen Anteil der arboricolen Heuschreckenfauna. Einige Gattungen (*Poecilocleus*) sind charakteristisch für späte Sukzessionsstadien (cf. AMÉDÉGNATO 1990). Diese Gattungen haben hell gefärbte Antennenspitzen und es gibt Hinweise auf optische und vibratorische Kommunikation (RIEDE 1987). Die Arbeiten von DESCAMPS (1980) und AMÉDÉGNATO & POULAIN (1987) liefern eine Zusammenstellung amazonischer Gattungen, Bestimmungsschlüssel, sowie die Beschreibung neuer, in der Naporegion von RIEDE gesammelter Arten (*Cercoceracris tarapoana* AMÉDÉGNATO & POULAIN, *Poecilocleus napoana* AMÉDÉGNATO & POULAIN, *Dendrophilacris secoya* AMÉDÉGNATO & POULAIN).

### Unterfamilie Copiocerinae

Die Angehörigen dieser Unterfamilie ernähren sich von Palmblättern. Aufgrund ihrer guten Flugfähigkeit sind sie schwer zu fangen. Einen Bestimmungsschlüssel findet man bei DESCAMPS (1984), allerdings ist eine zuverlässige Bestimmung ohne eine umfangreiche Vergleichssammlung kaum möglich.

### Unterfamilie Gomphocerinae

Die in der Alten Welt wie auch in Nordamerika artenreich vertretenen Gomphocerinae sind erst nach der Bildung der mittelamerikanischen Landbrücke nach Südamerika eingewandert. Auffällig ist, daß keiner Art eine Anpassung an das Baumleben gelungen ist. Die wenigen Arten waldbewohnender Gomphocerinae sind nur auf kleinen Lichtungen oder in Uferregionen zu finden (Taf. 4a).

### Familie Romaleidae

Zu dieser typisch neotropischen Familie gehören die größten und auffälligsten Feldheuschrecken des Kontinents (z.B. *Tropidacris* mit einer Länge von ca. 15 cm). Besiedelt werden alle Schichten des Waldes vom Boden bis in die Baumkronen. Während die Romaleinae mehrheitlich in subtropischen Bereichen zu finden sind, gelten die Bactrophorinae als typische Pluvialwaldbewohner. Man kennt vier Verbreitungszentren der Romaleidae: Napo und Ucayali im Westen sowie Guyana und Madeira im Osten (AMÉDÉGNATO & DESCAMPS 1982). Als morphologische Gemeinsamkeit besitzen alle Mitglieder dieser Familie einen äußeren, apikalen Stachel an den Hintertibien.

### Unterfamilie Bactrophorinae

Die Vertreter dieser artenreichen Unterfamilie besiedeln vor allem die Kronenregion (cf. AMÉDÉGNATO 1990) und können am besten durch den eingangs erwähnten dendrophilen Lebensformtyp charakterisiert werden (Taf. 4b–d). Bactrophorinae sind leicht an ihrem sehr gedrungenem Körperbau und den bunten, oft streifigen Farbmustern zu erkennen. Die Antennen sind meist sehr breit, abgeplattet und relativ lang. Es existieren geflügelte und flügellose Arten. Diese Unterfamilie wird wiederum in drei Gruppen eingeteilt: Bactrophorini (hauptsächlich Zentralamerika), Taeniophorini (Nordanden) und die Ophthalmolampini (Zentralamerika, Anden, guyanisches Amazonien). Die Spezies der Bactrophorinae sind in nur begrenztem Maße in der Lage, größere Barrieren zu überwinden und haben daher oft kleine Verbreitungsgebiete (AMÉDÉGNATO & POULAIN 1986). Auch aus dieser Gruppe sind Chromotypen bekannt (DESCAMPS 1983).

Falls überhaupt Flügel vorhanden sind, ist deren Fläche im Verhältnis zum oft massigen Körper meist so gering, daß sie nicht zum aktiven Flug, sondern höchstens zum Gleiten ausreicht. Einige Arten bleiben nach Fällungen von Bäumen in „ihren“ Baumkronen sitzen und verlassen den Baum nicht einmal, wenn die Blätter welken. Die Tiere bilden dort kleine Populationen mit bis zu 50 Individuen, wobei unterschiedliche Entwicklungsstadien gemeinsam vorkommen.

### Unterfamilie Romaleinae

Mit Ausnahme des Tribus Trybliophorini verfügen die Romaleinae über einen Stridulationsapparat. Dabei wird beim Öffnen der Flügel eine Kante der Unterseite des Vorderflügels über einen Resonator der Hinterflügel bewegt, so daß ein breitbandiges Rauschen erzeugt wird (RIEDE 1987). So ist der lautstarke Gesang der Männchen von *Prionacris cantrix* DESCAMPS, 1981 an sonnigen Tagen ein wesentlicher Bestandteil der Geräuschkulisse des Tieflandregenwaldes.

Eine weitere auffällige und häufige Art ist *Chromacris icterus* (PICTET & SAUSSURE, 1887), die allerdings nicht durch ihren Gesang, sondern durch ihre kontrastreich gelb-grüne Färbung auffällt. Die jüngeren Larvenstadien sind jedoch schwarz und bilden dichte Verbände von bis zu 300 Tieren (PFROMMER 1990) auf ihren Futterpflanzen (bevorzugt Solanaceen). Die 6 - 8 cm großen Tiere sind häufig in dicht bewachsenen aufgelassenen Feldern in ganz Nordwestamazonien zu finden. Auf solchen Flächen ist auch die an den Hintertibien mit auffällig langen Stacheln bewehrte Art *Aeolacris octomaculata* Scudder, 1869 (Taf. 4e) zu finden.

Die stummen Vertreter des Tribus Trybliophorini (Gattung *Trybliophorus*) sind dendrophil, mit ähnlichen Lebensgewohnheiten wie Bactrophorinae, mit denen sie auch vergesellschaftet auftreten.

Eine interessante morphologische Konvergenz zu den Copiocerinae zeigen die Arten des Tribus Leguini, die außerdem ein ähnliches Futterpflanzenspektrum (Palmen) aufweisen (AMÉDÉGNATO & POULAIN 1986). Bei den gleichen Autoren findet man Nachweise von peruanischen Arten für Ecuador sowie Erstbeschreibungen der von RIEDE gesammelten Arten (*Pareusychius defurcus* AMÉDÉGNATO & POULAIN, 1987, Taf. 4f; *Xomacris riederi* AMÉDÉGNATO & POULAIN, 1986).

## 3. Diskussion und Ausblick

Während unsere Kenntnis der neotropischen Ensiferenfauna noch äußerst lückenhaft ist, sind die Kurzfühlerschrecken – insbesonders die Acridoidea – vergleichsweise gut bekannt. Zwar sind aus den Bergregenwäldern zwischen 500 und 1500 m Höhe eine Reihe bislang unbekannter Arten und sogar Genera zu erwarten (Taf. 2e), die wegweisenden Arbeiten von AMÉDÉGNATO (1977) sowie DESCAMPS (1976) erlauben jedoch eine gute Einordnung in ein solides systematisches Gerüst. Die vielfältigen offenen Fragen betreffen im wesentlichen Probleme der Ökologie (Habitat- und Nahrungspräferenzen) sowie der Autökologie und Verhaltensbiologie einzelner Arten. Völlig ungeklärt sind beispielsweise die Ursachen für das geklumpte Auftreten vieler dendrophiler Arten auf bestimmten Wirtsbäumen. Auf den ersten Blick können solche Verbände als Ansammlungen oligophager Arten auf „ihren" Futterbäumen gedeutet werden (cf. ROWELL 1978, 1987). Es gibt aber Hinweise, daß die meisten Arten ein größeres Nahrungsspektrum haben (AMÉDÉGNATO, pers. Mitt.). Möglicherweise wird das Vorkommen in Verbänden durch andere Faktoren wie Mikroklima, Prädatoren oder die Verfügbarkeit von Eiablageplätzen in Form von Humusansammlungen in der Kronenregion bestimmt. Schließlich könnte ein Zusammenhalt von Gruppen auch die Partnerfindung bei insgesamt geringer Populationsdichte erleichtern. Es stellt sich hierbei die Frage, wie die Besiedelung neuer „Nahrungsinseln" durch die meist nicht flugfähigen Arten erfolgt.

Im Zusammenhang mit Artbildungsprozessen scheint uns die Untersuchung der Verbreitungsmuster polytypischer „Arten" im oberen Amazonasgebiet besonders lohnend. Auf kleinsten Räumen kommt es zur Ausbildung von lokalen Farbvarianten, deren systematischer Status noch unklar ist. DESCAMPS (1983) beschreibt diesen Polytypismus auch bei amazonischen Bactrophorinae, wobei nur in wenigen Fällen Parapatrie nachgewiesen wurde. Die Chromotypen von *Galidacris variabilis* sind geographisch streng voneinander getrennt. Dabei bildet der Rio Napo eine natürliche Grenze zwischen den Populationen, während entlang der Kontaktzone (Abb. 1) geographische und ökologische Barrieren fehlen. HAFFER (1974) vermutet, daß für die Speziation neotropischer Vögel pleistozäne Refugien eine wichtige Rolle gespielt haben. In solchen „Rückzugsgebieten" könnten sich auch die vorliegenden Chromotypen der Acrididen entwickelt haben. Nach dem Wegfall klimatisch bedingter Barrieren (z.B. Savannen) konnten dann ehemals getrennte Populationen sekundär wieder in Kontakt treten. Dies ist auch im Fall von *Galidacris* denkbar. Hier bleibt durch Kreuzungsexperimente zu prüfen, wie weit die Artbildung fortgeschritten ist. Während die Übereinstimmung im Balzverhalten auf nur unwesentliche Unterschiede hinweist, läßt die geringe Ausdehnung der Kontaktzone auf Mechanismen schließen, die eine breite Vermischung beider Formen verhindern. Möglicherweise sind prä- oder postnatale Fertilitätsschranken wirksam. Hierzu sind weitere Laboruntersuchungen geplant.

Die Verbreitungsmuster der Chromotypen von *Psiloscirtus* lassen sich hingegen einfacher durch ein „umgekehrtes Refugienmodell" (cf. RIEDE 1990b) deuten. Die Vermutung liegt nahe, daß diese Art während der bekanntermaßen kühleren Klimaphasen Amazoniens auch im Tiefland verbreitet war. Die heutigen Bergregenwälder wären demnach voneinander isolierte, „aktuelle" Refugien für *Psiloscirtus*, in denen Artbildungsprozesse ablaufen. Vergleiche mit Farbmorphen von Schmetterlingen (BROWN 1982) könnten zeigen, ob ähnliche Verbreitungsgrenzen vorliegen.

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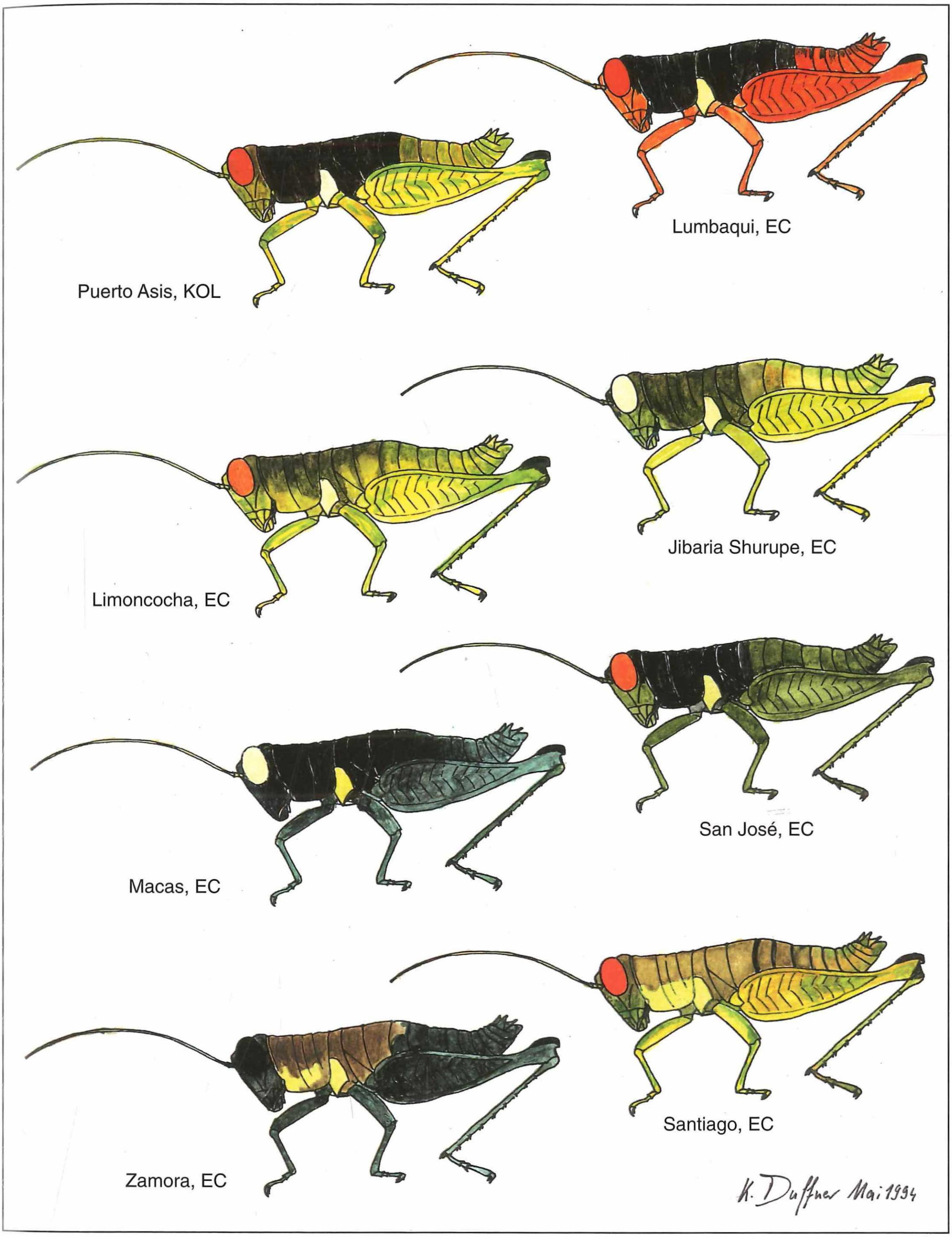
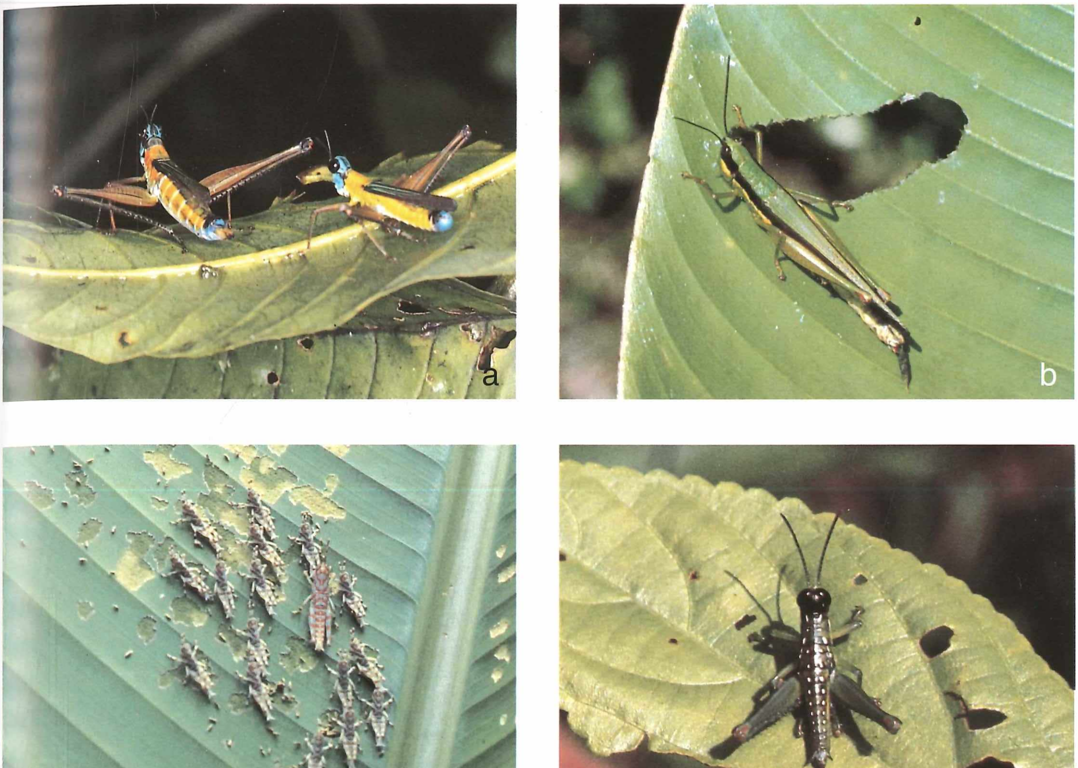
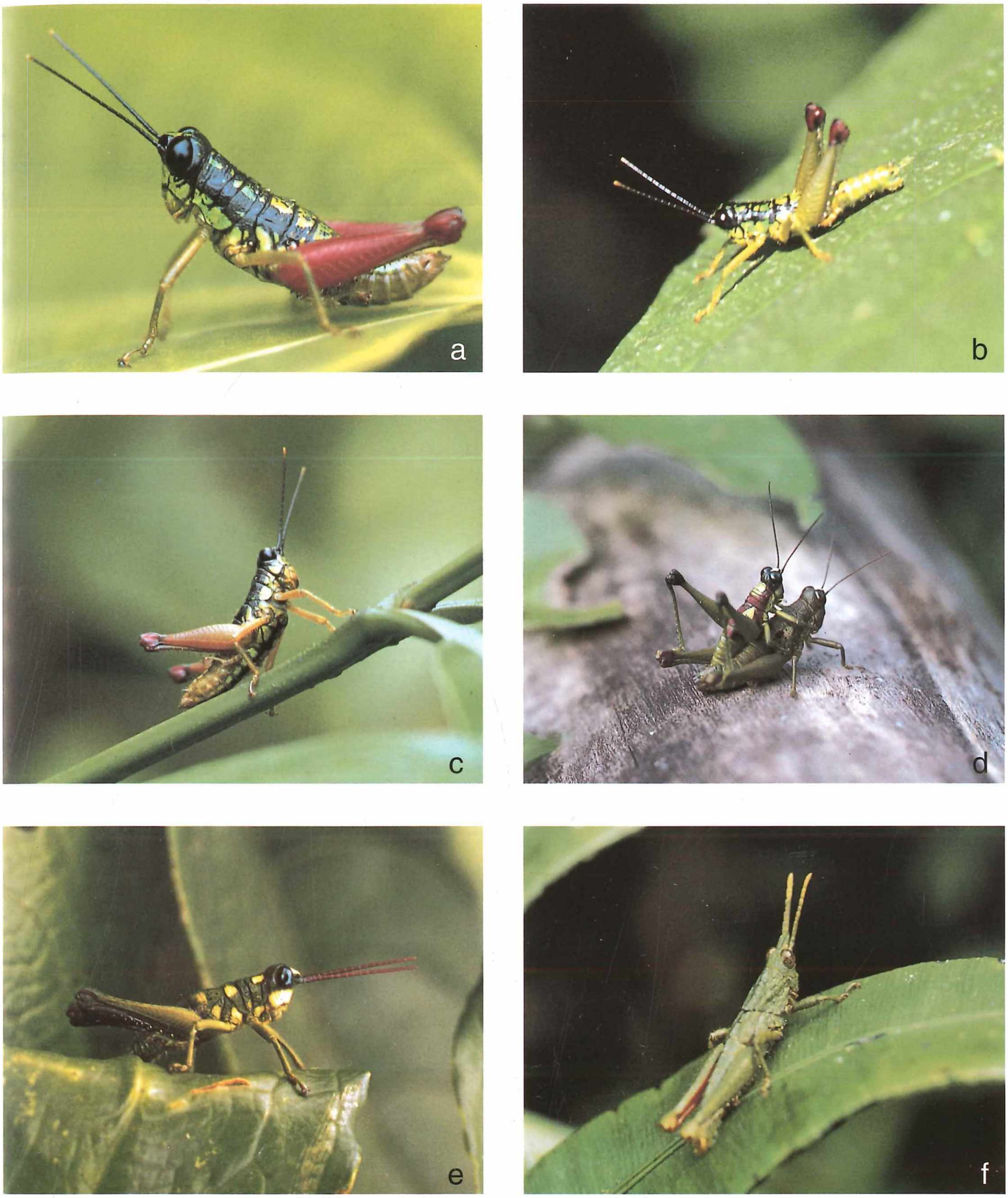


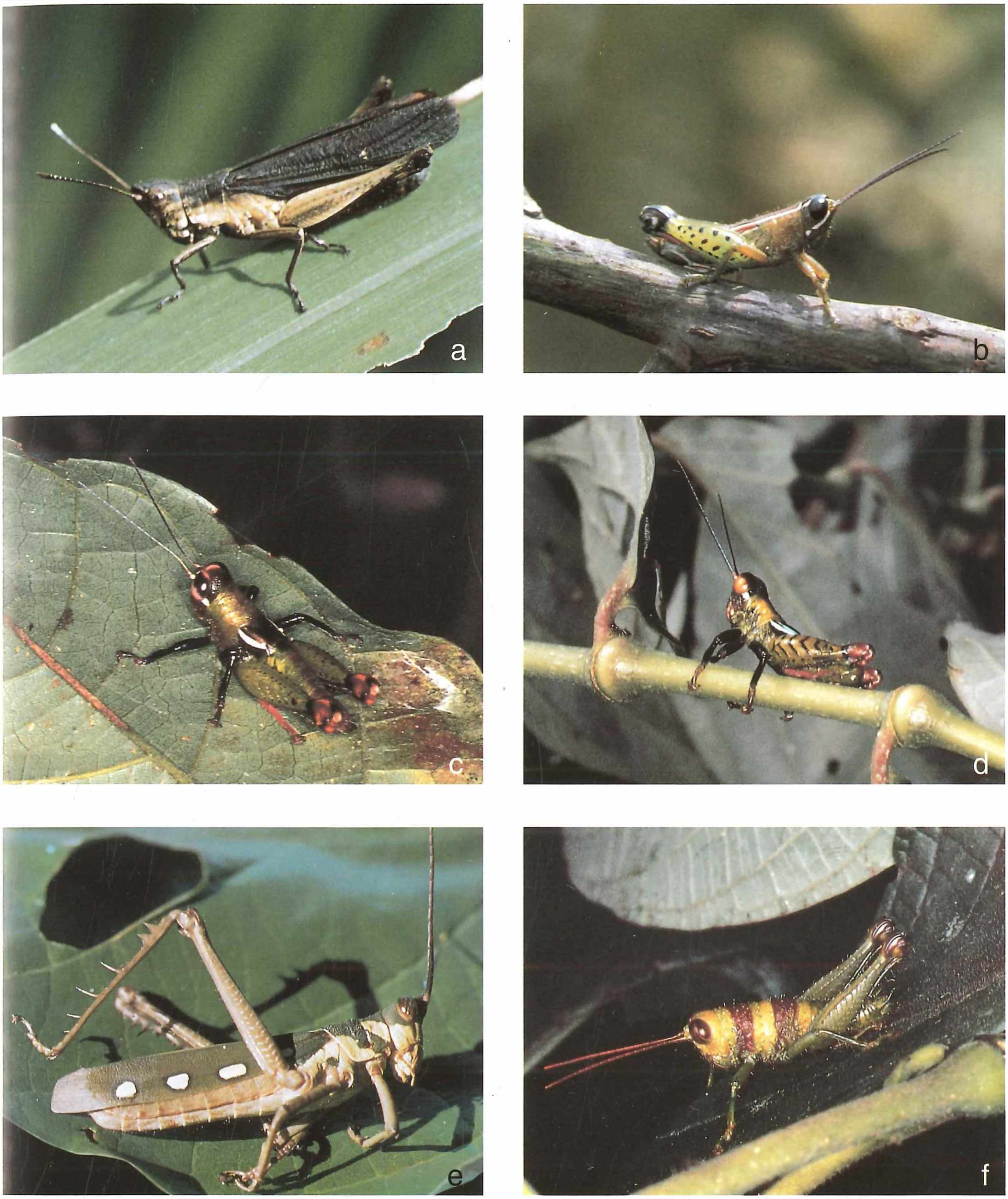
Tafel 1. Geographische Variation bei *Psiloscirtus* sp. (Ommatolampinae, Acrididae) in Ecuador und Südkolumbien (vergl. Verbreitungskarte Abb. 1). In Macas (5) tritt neben einer weißäugigen auch eine rotäugige Variante auf. Es ist anzunehmen, daß noch mehr geographische Varianten innerhalb dieser Gattung existieren; Zeichnung: K. DUFFNER.



Tafel 2. a) Pärchen der Unterfamilie Eumastacinae. Man beachte die auffällige Färbung und die typische „Pfeil-und-Bogen" Stellung der Hinterbeine. Diese Position unterscheidet sie deutlich von ihren altweltlichen Verwandten, deren Beine wie bei Heuschrecken angewinkelt sind, San Pablo, Prov. Sucumbios, Ecuador; b) *Cornops* sp. (Leptysminae, Acrididae) auf einem Bananenblatt, San Pablo, Prov. Sucumbios, Ecuador; c) Gregär lebende Larven von *Cornops* sp., San Pablo, Prov. Sucumbios, Ecuador; d) *Chloropseustes brunneus* ROBERTS & CARBONELL, 1980 (Leptysminae, Acrididae), San Pablo, Prov Sucumbios, Ecuador, eine eher untypische Form innerhalb der Leptysminae; e) *Palandella cardinalis* AMÉDÉGNATO & POULAIN, in prep. (Rhytidochrotinae, Acrididae), Palanda, Zamora Chinchipe, Ecuador; f) Weibchen von *Psiloscirtus* sp., Macas, Prov. Santiago Morona, Ecuador; Fotos a-e: K. RIEDE, Foto f: K. DUFFNER.



Tafel 3. *Galidacris variabilis* Descamps & Amédégnato, 1972 (Rhytidochrotinae, Acrididae). Es existieren mehrere Chromotypen, darunter eine a) mit roten Hinterbeinen, Sevilla, Prov. Sucumbios, Ecuador; und eine b) mit grünen Hinterbeinen, San Pablo, Prov. Sucumbios, Ecuador; im Kontaktgebiet beider Typen konnte c) eine Mischform gefunden werden. d) Kopula bei *Hippariacris latona* (Günther, 1940) (Ommatolampinae, Acrididae). Laborbeobachtungen haben gezeigt, daß die Kopula über 24 Stunden dauern kann. Wie bei *Psiloscirtus* (Taf. 1 & 2 f) herrscht auch bei dieser Gattung ein ausgeprägter Geschlechtsdimorphismus, Misahuallí, Prov. Napo, Ecuador; e) *Ommatolampis quadrimaculata* Carbonell & Descamps, 1978 (Ommatolampinae, Acrididae), Coca Falls, Prov Sucumbios, Ecuador; f) *Lysacris sylvestris* Descamps & Amédégnato, 1972 (Tribus Syntomacrini, Ommatolampinae, Acrididae), San Pablo, Prov. Sucumbios, Ecuador; Fotos a, c, d: K. Duffner; Fotos b, e, f: K. Riede.



Tafel 4. a) *Peruvia nigromarginata* (Scudder, 1875), Weibchen (Gomphocerinae, Acrididae). Die Männchen dieser Art zeigen eine komplexe Balz mit optischen und akustischen Elementen, bei der die weißen Antennenspitzen vor dem Weibchen bewegt werden. Limoncocha, Prov. Napo, Ecuador; b) *Adrolampis maculisnigris* Descamps, 1983 (Bactrophorinae, Romaleidae), Lumbaqui, Prov. Sucumbios, Ecuador; c) *Helolampis nigriceps* Descamps, 1983 (Bactrophorinae, Romaleidae), Limoncocha, Prov. Napo. Ecuador; d) *Helolampis coloniana* Descamps, 1983 (Bactrophorinae, Romaleidae), San Pablo, Prov. Sucumbios, Ecuador; e) *Aeolacris octomaculata* (Scudder, 1869) (Romaleinae, Romaleidae), San Pablo, Prov. Sucumbios, Ecuador; f) *Pareusychius defurcus* Amédégnato & Poulain, 1987 (Romaleinae, Romaleidae), San Pablo, Prov. Sucumbios, Ecuador; Fotos a, d, f: K. Riede; Fotos b, c, e: K. Duffner.

**andrias, 13:** 161-168, 3 Abb.; Karlsruhe, 30. 9. 1994

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# Untersuchungen zur Biologie dreier Laufkäferarten (Coleoptera, Carabidae, Harpalini) aus amazonischen Regenwäldern

**Kurzfassung**

Mit drei Laufkäferarten des Tribus Harpalini (Carabidae) aus zentralamazonischen Regenwäldern wurden Aufzuchtversuche mit unterschiedlichem Nahrungsangebot und Nahrungswahlversuche im Labor durchgeführt, sowie die Entwicklungsdauer bestimmt. Ergänzend wurden Mandibelgestalt von Larven und Käfern untersucht. Zwei der Käferarten (*Notiobia* sp. 1 und sp. 2) durchlaufen ihre präimaginale Entwicklung auf Feigenfruchtflächen (*Ficus* spp.) im Festlandregenwald bei Manaus (Amazonien, Brasilien). Die dritte Art *Athrostictus batesi* lebt in Weißwasser-Überschwemmungswäldern bei Manaus und wurde bisher nicht auf den Fruchtflächen des nichtüberschwemmten Regenwaldes beobachtet. *A. batesi* gehört im Gegensatz zu den *Notiobia*-Arten zu den weniger ausgeprägt spermophagen Harpalini. Ein Vergleich der Entwicklungsdauer aller drei Arten im Labor zeigte jedoch, daß die Spezialisierung der beiden Fruchtflächenarten auf ihre nur kurzfristig existierenden Habitate offenbar nicht zu einer Beschleunigung der präimaginalen Entwicklung geführt hat. Die Larven, aller drei Arten, zeigten in den Aufzuchtversuchen häufig Kannibalismus oder räuberisches Verhalten. Samen von Melastomataceen, die anderen *Notiobia*-Arten im Festlandregenwald als Nahrungsgrundlage dienen, wurden von den Adulten beider hier untersuchten *Notiobia* Arten gefressen, ihre Larven lehnten sie dagegen ab und entwickelten sich bei diesem Nahrungsangebot nicht. Die Käfer könnten eventuell Melastomataceen-Fruchtflächen als Trittsteinhabitate auf der Suche nach Feigen-Fruchtflächen nutzen. Eine gewisse Nischenaufteilung zwischen den beiden unterschiedlich großen *Notiobia*-Arten auf Feigenfruchtflächen deutet sich an: Larven des I. Stadiums der kleineren Art können größere Samen nicht öffnen, wodurch diese auf Fruchtflächen kleinsamiger Feigen beschränkt sein sollte.

**Abstract**

**Investigations on the biology of three carabid species (Coleoptera, Carabidae, Harpalini) from central Amazon rainforests**

For three carabid species of the tribe Harpalini (Coleoptera: Carabidae) from central Amazon rainforests we realized rearing experiments with different diets and food selection experiments in the laboratory. Duration of development, size of larval stages and the structure of mandibles of larvae and adults were also studied. Two species (*Notiobia* sp. 1 and sp. 2) pass their preimaginal development on fruit fall sites of figs (*Ficus* spp.) in an Amazon upland rainforest near Manaus (Brazil). The third species *Athrostictus batesi* lives in whitewater inundation forests near Manaus and was not observed on fruit fall sites in the non-inundated forest.

In contrast to the *Notiobia* species, *Athrostictus batesi* is a less pronounced spermophageous Harpalini. A comparison of the development times of the three species showed that the specialization of the two species of *Notiobia* to only temporarily existing fruit fall sites of figs did not result in an accelerated preimaginal development. The larvae of *A. batesi* and of both *Notiobia* species showed preference for animal diet and cannibalism or predatory behaviour in the experiments. Seeds of Melastomataceae, which serve other species of *Notiobia* in the same forest as food, were also eaten by imagines of the two species of *Notiobia* studied here. However, the larvae did not accept the seeds and they did not develop on this diet. The beetles might eventually use the fruit fall sites of Melastomataceae as stepping stone habitat during their search for fruit fall sites of figs. Niche partitioning between the two *Notiobia* species, which differ in size, is indicated: first instar larvae of the smaller species are incapable of opening larger seeds, and therefore its reproduction might be restricted to fruit fall sites of figs with small seeds.

**Resumo**

**Investigações sobre a biologia de três espécies de carabídeos (Coleoptera, Carabidae, Harpalini) de floresta tropical úmida na Amazônia central**

Fez-se observações da opção alimentar, experimentos de criação com ofertas alimentares diversas, identificação do tempo de desenvolvimento e do tamanho dos diferentes estádios, bem como observações concernentes a forma das mandíbulas de larvas e adultos, de duas espécies de carabídeos do gênero *Notiobia* (Coleoptera, Carabidae, Harpalini). O desenvolvimento pré-imaginal ocorre em áreas de queda de frutos de figueira (*Ficus* sp.) numa floresta tropical de terra firme. A fim de comparação, estudou-se a espécie *Athrostictus batesi*, espécie esta que ocorre numa floresta inundável da várzea, mas não em áreas de queda de figos. As áreas de origem de todas as espécies situam-se nos arredores da cidade de Manaus (Amazonas, Brasil).

*A. batesi* pertence aos Harpalini de pouco caráter espermófago, ao contrário das espécies do gênero *Notiobia*. Porém a especialização das duas espécies de *Notiobia* nas áreas apenas temporárias da queda de frutos, não conduziu à aceleração do desenvolvimento do estádio pré-imaginal, em comparação à espécie *A. batesi*. As larvas de *A. batesi*, bem como as das espécies de *Notiobia*, apresentam grande tendência para a alimentação animal e para o canibalismo ou predação. Sementes de melastomatáceas (Melastomataceae), que servem de base alimentar para outras espécies do gênero *Notiobia*, também foram aceitas pelos adultos das duas espécies de *Notiobia* aqui estudadas, não, porém, pelas suas larvas, que não se desenvolveram com este alimento. Os adultos das duas espécies eventualmente poderiam utilizar as áreas da queda dos frutos de melastomatáceas como „habitat de passada“ (stepping stone habitat), na procura de áreas adequadas de figueiras. Uma certa repartição de nichos entre as duas espécies *Notiobia* ocorrentes nas figueiras é suposta: larvas iniciais da menor das duas espécies teriam o seu desenvolvimento limitado às áreas de queda de figos de sementes diminutas.

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## 1. Einleitung

Im Laufkäfertribus Harpalini finden sich viele phytophage Arten, die besonders zur Spermophagie, dem Fressen von Samen, neigen (SKUHRAVY 1959, ALLEN 1979, FORSYTHE 1983). Von der Arbeitsgruppe BRANDMAYR wurden umfangreiche Untersuchungen zur Verbreitung der Spermophagie unter den italienischen Harpalini durchgeführt (Zusammenfassung bei BRANDMAYR 1990). Das Spektrum von Arten reicht von solchen mit fast ausschließlich räuberischer Lebensweise bis zu Arten mit reiner Spermophagie.
Im Gegensatz zu den meist flugunfähigen Laufkäfern der Waldbiotope gemäßigter Breiten, kann ein hoher Prozentsatz der Laufkäfer tropischer Regenwälder ausgezeichnet fliegen. Sie treten geklumpt auf Fruchtflächen auf, die oft nur wenige Wochen existieren. Dies zwingt sie zu einer ständigen Wanderung von Fruchtfläche zu Fruchtfläche (ERWIN 1979). Spermophagie dürfte unter diesen Carabiden eine große Rolle spielen.
In Rahmen des Forschungsprojektes „Mechanismen des Diversitätserhalts bei tropischen Laufkäfern" ist ein Hauptthemenbereich das Studium der Carabidengemeinschaften auf Fruchtflächen. Zum Verständnis von Zusammensetzung und Dynamik dieser Gemeinschaften ist es wichtig, das Nahrungsspektrum von Larven und Imagines der verschiedenen Arten zu kennen. Um dies festzustellen, wurden die Larven mit unterschiedlichem Futter aufgezogen und der Entwicklungserfolg ermittelt. Beobachtungen zur Nahrungswahl von Larven und Käfern sollten die dadurch gewonnenen Ergebnisse ergänzen. Von Untersuchungen der Mandibelmorphologie erwarteten wir weitere Hinweise auf die Ernährungsweise.
Die dominanten Käferarten der bisher untersuchten Fruchtflächengemeinschaften unter Feigenbäumen (Gattung *Ficus*, Moraceae) und unter verschiedenen Baumarten der Familie Melastomataceae gehören zur Gattung *Notiobia* (Harpalini). NOONAN (1973), der die nord- und mittelamerikanischen Arten dieser Gruppe bearbeitet hat, macht keine Angaben über die Lebensweise der Larven. Leider ist die Taxonomie der südamerikanischen Vertreter dieser Gattung noch nicht ausreichend bearbeitet.
Zu Beginn der Untersuchungen standen in Deutschland zwei *Notiobia*-Arten von Feigenfruchtflächen aus Amazonien zur Verfügung. Aus Freilanduntersuchungen war bekannt, daß beide Arten ihre präimaginale Entwicklung auf diesen Fruchtflächen durchlaufen (PAARMANN & ADIS, unveröff.). Als Vergleichsart aus dem Tribus Harpalini zogen wir *Athrostictus batesi* BATES, 1878 heran, die bisher nicht auf Fruchtflächen gefunden wurde.

## 2. Versuchstiere und Methoden

### 2.1 Versuchstiere

Die Käfer für die Laborzuchten (*Notiobia* sp. 1 und *Notiobia* sp. 2) stammen aus einem Primärwald (terra firme), der Reserva Florestal A. Ducke (vgl. PENNY & ARIAS 1982), 26 km nördlich von Manaus. Adulti und Larven kommen auf den Fruchtflächen noch unbestimmter Feigenarten („Gameleira", *Ficus sp.*) vor. Sie wurden im Juli/August 1991 und im Februar/März 1992 gefangen. Die Imagines beider Arten sind nachtaktiv, flugfähig und verbringen den Tag im oberen Bodenhorizont.
Die Elterngeneration der Versuchstiere von *Athrostictus batesi* wurden als Imagines auf der Ilha de Marchantaria, einer Insel im Rio Solimões-Amazonas, ca. 15 km oberhalb des Zusammenflusses mit dem Rio Negro, im Februar/März 1992 gesammelt. Sie lebten in der Laubstreu eines Weißwasser-Überschwemmungswaldes (vgl. ADIS et al. 1990, ADIS 1992). Die Imagines sind ebenfalls nachtaktiv, flugfähig und verstecken sich tagsüber im Boden.

### 2.2 Haltung und Zucht

Imagines und Larven der drei Laufkäferarten wurden unter kontrollierten Bedingungen in Thermoschränken (10 h 27 °C / 14 h 21 °C; 12 h Licht (06 - 18 Uhr); 100 % Luftfeuchte) gehalten. Käfer aller drei Arten lebten in feuchtem Torf in abgedeckten 1 l-Weckgläsern (= Haltungsgläser). Die Larven wurden einzeln in offenen Schnappdeckelgläschen (50 ml) aufgezogen, die zur Hälfte mit feuchtem Torf gefüllt waren und in abgedeckte Kühlschrankschalen gestellt wurden. Larven und Adulti der beiden *Notiobia*-Arten bekamen zerdrückte Kiwisamen ohne Fruchtfleisch als Ersatzfutter für die amazonischen Feigenfrüchte, mit denen im getrockneten Zustand die Larvenaufzucht in Deutschland nicht gelungen ist, sowie zerteilte Mehlwurmstücke. *Athrostictus batesi* wurde mit zerteilten Mehlwurmstücken und Fischtrockenfutter „TetraMin" gefüttert (TetraMin-Zusammensetzung: Fischmehl, Trockenhefe, brauner Reis, Krabbenmehl, Stärke, trockene Kartoffelprodukte, Hafermehl, Sojabohnenmehl und Öl, Algenmehl, Sorbitol, Lecithin, Gelatin, natürliche und künstliche Farbstoffe, Ethoxyquin (Antibiotikum zur Schimmelvorbeugung), sowie L-ascorbyl-2-polyphosphate als Vitaminzugabe; min. Rohprotein 45 %, min. Rohfett 5 %, max. Rohfaser 2 %, max. Feuchtigkeit 6 %).
Alle Imagines und Larven der drei *Harpalini*-Arten wurden dreimal pro Woche mit frischem Futter versorgt und frischgeschlüpfte Larven aus den Haltungsgläsern der Käfer in Schnappdeckelgläschen überführt.
Für die Aufzuchtversuche von Larven zu Imagines mit unterschiedlicher Nahrung wurden nur junge Larven des ersten Stadiums ausgesucht. Kiwisamen hatten sich als Ersatzfutter an Stelle der amazonischen Feigenfrüchte bewährt, weshalb

sie auch den Larven in unzerdrückter und zerdrückter Form (da größer als Feigenfrüchte) angeboten wurden. *Bellucia dichotoma*-Samen wurden gefüttert, da andere *Notiobia*-Arten ihre Entwicklung auf Fruchtflächen dieser Art durchlaufen (PAARMANN & ADIS, unveröff.). Die weiteren Futtervarianten sind den Tabellen 3, 4 und 5 zu entnehmen.

## 2.3 Video-Nachtaufnahmen

In Nachtversuchen sollten Nahrungswahl und Freßverhalten beobachtet werden. Hierfür wurden drei Futtervarianten in einer offenen, runden Glasschale (Ø 50 mm), auf feuchtem Filterpapier und im Dreieck angeordnet angeboten: ein Stück eines zerteilten Mehlwurms, zerdrückte Kiwikerne sowie TetraMin. Die Eingewöhnungszeit der Tiere in den Glasschälchen vor Versuchsbeginn betrug ca. 5 Min. Die Beobachtungsdauer pro Versuch, wenn nicht anders vermerkt, betrug 5 ± 1 Min. Die Versuche wurden, entsprechend der Hauptaktivitätsphase der Tiere im Freiland zwischen 18:30 und 22:00 Uhr durchgeführt.

Die Nachtaufnahmen der Nahrungswahlversuche wurden im verdunkelten Labor bei ca. 23 °C Raumtemperatur mit einer Videokamera (S -VHS 625 Panasonic) über einen Restlichtverstärker (Hamamatsu, „Night viewer" C 3100) und eine CCD-Kamera mit einem 105 mm Macro-Fotoobjektiv (Pentax) erstellt. Die Video-Bandaufnahmen wurden über einen Video-Farbdrucker (Hitachi VY-150 E) ausgedruckt und schwarzweiß abfotografiert.

Folgende Versuchsserien wurden mit *Notiobia* sp. 1, *Notiobia* sp. 2 und *Athrostictus batesi* durchgeführt:

I. Beobachtung einzelner Larven im I. Stadium
II. Beobachtung von 5 Larven des I. Stadiums zusammen
III. Beobachtung von 5 Larven des II. Stadiums zusammen
IV. Beobachtung einer Larve des I. bzw. II. Stadiums zusammen mit einem Käfer
V. Beobachtung von 2-4 Larven des I. Stadiums zusammen mit 2-4 Larven des II. oder III. Stadiums
VI. Beobachtung von Larven des I. Stadiums beider *Notiobia*-Arten gemeinsam
VII. Beobachtung von *Notiobia*-Larven (I. Stadium) zusammen mit Käfern der anderen *Notiobia*-Art bzw. von *Athrostictus batesi*

Zusätzlich zu diesen Versuchen wurden Video-Nachtaufnahmen von Käfern beider *Notiobia*-Arten gemacht, denen entweder nur das Stück eines zerteilten Mehlwurms oder unzerdrückte Kiwikerne (mittlere Länge x Breite: 2,33 x 1,57 mm) angeboten wurden (Versuch VIII) sowie von Larven des I. Stadiums von *Notiobia* sp. 1 und *Notiobia* sp. 2, denen ausschließlich unzerdrückte Kiwikerne als Futter zur Verfügung standen (Versuch IX).

Mit Käfern der beiden *Notiobia*-Arten wurden noch 5 weitere Versuche durchgeführt, in denen folgendes Futter angeboten wurde:

1. zerdrückte Kiwikerne & ganze Kiwikerne
2. große Feigensamen (mittlere Länge x Breite: 1,50 x 1,04 mm) & kleine Feigensamen (mittlere Länge x Breite: 0,83 x 0,69 mm)
3. kleine Feigensamen & *Bellucia dichotoma* (Melastomataceae)-Samen (mittlere Länge x Breite: 0,77 x 0,49 mm), (Papierausstrich), aufgeweicht
4. getötete Drosophila-Fliegen
5. Bellucia dichotoma (Melastomataceae)-Samen (Papierausstrich), aufgeweicht, nach 10 Tagen ohne Fütterung

Tabelle 1. Körperlängen der Imagines.

| | *Notiobia* sp. 1 | *Notiobia* sp. 2 | *Athrostictus batesi* |
|---|---|---|---|
| ♂♂ | n = 19 | n = 11 | n = 13 |
| | 12,0-13,2 mm | 9,0-10,0 mm | 8,2-9,0 mm |
| $\bar{x}$ | 12,70 ± 0,38 | 9,60 ± 0,30 | 8,55 ± 0,27 |
| ♀♀ | n = 14 | n = 20 | n = 17 |
| | 11,0-13,0 mm | 9,0-10,0 mm | 8,0-10,0 mm |
| $\bar{x}$ | 12,30 ± 0,54 | 9,80 ± 0,27 | 9,05 ± 0,58 |

Tabelle 2. Eimaße, Dauer der Embryonalentwicklung sowie Länge von Kopfkapsel und Körper der Larvenstadien bzw. Puppen.

| | *Notiobia* sp. 1 | *Notiobia* sp. 2 | *Athrostictus batesi* |
|---|---|---|---|
| Ei-Länge [mm] | 2,4 | 2,1 | 1,6 |
| Ei-Breite [mm] | 1,4 | 1,0 | 1,1 |
| Dauer der Embryonalentwicklung | 6-8 Tage | 6-8 Tage | 4-8 Tage |
| Kopfkapsellänge [mm]: | | | |
| Stadium I. | 1,1 -1,6 (n = 27) | 0,6 -1,2 (n = 32) | 0,4 -0,8 (n = 23) |
| | ($\bar{x}$ = 1,3 ± 0,14) | ($\bar{x}$ = 0,93 ± 0,17) | ($\bar{x}$ = 0,6 ± 0,16) |
| Stadium II. | 1,6 -1,9 (n = 15) | 1,2 -1,5 (n = 41) | 0,8 -1,3 (n = 42) |
| | ($\bar{x}$ = 1,7 ± 0,11) | ($\bar{x}$ = 1,3 ± 0,13) | ($\bar{x}$ = 1,1 ± 0,11) |
| Stadium III. | 1,9 -2,3 (n = 37) | 1,6 -1,7 (n = 31) | 1,3 -1,7 (n = 37) |
| | ($\bar{x}$ = 2,1 ± 0,14) | ($\bar{x}$ = 1,64 ± 0,04) | ($\bar{x}$ = 1,5 ± 0,14) |
| Körperlänge [mm]: | | | |
| Stadium I. | 4,9 -6,6 (n = 23) | 3,8 -6,0 (n = 38) | 2,9 -5,1 (n = 33) |
| | ($\bar{x}$ = 5,9 ± 0,60) | ($\bar{x}$ = 5,4 ± 0,71) | ($\bar{x}$ = 4,4 ± 0,40) |
| Stadium II. | 7,1 -10,2 (n = 31) | 7,5 -8,9 (n = 28) | 5,4 -7,7 (n = 41) |
| | ($\bar{x}$ = 8,9 ± 0,86) | ($\bar{x}$ = 8,7 ± 0,40) | ($\bar{x}$ = 7,1 ± 0,60) |
| Stadium III. | 10,5 -14,5 (n = 38) | 9,2 -12,5 (n = 31) | 8,0 -11,8 (n = 38) |
| | ($\bar{x}$ = 12,9 ± 1,10) | ($\bar{x}$ = 10,8 ± 1,13) | ($\bar{x}$ = 10,4 ± 1,10) |
| Puppe | 6,5-8,5 (n = 9) | 5,5-7,5 (n = 9) | 5,0-7,0 (n = 9) |

Larven von *Notiobia* sp. 1 wurde noch in zwei weiteren Versuchen folgendes Futter angeboten:

1. getötete Drosophila-Fliege
2. *Bellucia dichotoma* (Melastomataceae)-Samen (Papierausstrich), aufgeweicht

## 3. Ergebnisse

### 3.1 Morphometrische Daten und postembryonale Entwicklung

Von den drei untersuchten Arten sind die Imagines von *Notiobia* sp. 1 mit durchschnittlich 12,7 mm die größten (Tab. 1).

Morphometrische Daten zur Eigröße, Körperlänge der Larval- und Pupalstadien sowie zur Kopfkapsellänge der Larven aller drei Arten sind in Tabelle 2 dargestellt.

Die Dauer der embryonalen- sowie der postembryonalen Entwicklung war bei allen drei Arten recht ähnlich. Die postembryonale Entwicklungsdauer von *Notiobia* sp. 1 bis zur Verpuppung betrug 24-29 Tage (N = 25) und bis zur Imago 32-40 Tage (N = 23). Die frischgeschlüpften weißen Larven des I. Stadiums bildeten innerhalb von 1-1,5 Stunden ihr schwarzes Pigment aus. Das I. Larvenstadium dauerte 5-6 Tage, das II. Larvenstadium 13-15 Tage. Die postembryonale Entwicklungsdauer von *Notiobia* sp. 2 bis zur Verpuppung betrug 23-26 Tage (N = 21) und bis zur Imago 32-36 Tage (N = 21). Nach 5-6 Tagen häuteten sich die Erstlarven zum II. Larvenstadium und nach 13-15 Tagen zum letzten Stadium. Die postembryonale Entwicklungsdauer von *A. batesi* bis zur Verpuppung betrug 22-26 Tage (N = 31) und bis zur Imago 31-35 Tage (N = 29). Das I. Larvenstadium dauerte 5-7 Tage und das II. Larvenstadium 14-15 Tage.

### 3.2 Aufzucht von Larven mit unterschiedlicher Nahrung

Die Versuchsergebnisse sind in den Tabellen 3, 4 und 5 zusammengestellt. Das Nahrungsspektrum beider *Notiobia*-Arten ist im Versuch sehr ähnlich. Vor allem Mehlwürmer und Kiwikerne ermöglichen eine Entwicklung. TetraMin ist, trotz der ausgewogenen Kombination tierischer und pflanzlicher Komponenten, offenbar nicht als Nahrung geeignet, ebensowenig die Samen von *Bellucia dichotoma* und das Kiwifruchtfleisch. Auffallend ist, daß es auch keine erfolgreiche Entwicklung bei Fütterung mit getrockneten Feigensamen gab. Im Gegensatz zu *Notiobia* sp. 1 entwickelt sich *Notiobia* sp. 2 beim Füttern mit ganzen Kiwikernen nicht bis zum Käfer. Bei *Notiobia* sp. 1 verlief die Entwicklung am schnellsten mit „Mehlwurm & zerdrückte Kiwikerne" sowie mit „TetraMin & ganze Kiwikerne" und „ganze Kiwikerne". Bei Larven von *Notiobia* sp. 2 mit „Mehlwurm", „Mehlwurm & zerdrückte Kiwikerne" und „Mehlwurm & TetraMin".

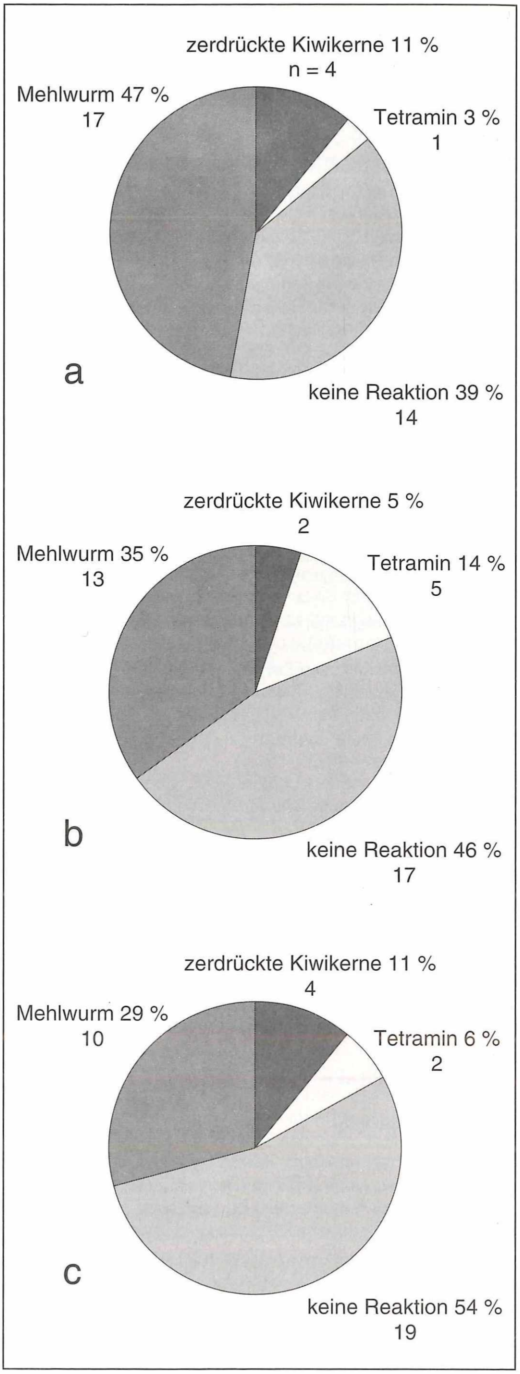

Abbildung 1. Prozentualer Vergleich der Nahrungswahl in den Versuchen mit Video-Nachtaufnahmen bei Larven von a) *Notiobia* sp. 1 (n = 36), b) *Notiobia* sp. 2 (n = 35) und c) *A. batesi* (n = 37).

Tabelle 3. *Notiobia* sp. 1: Ergebnisse der Aufzucht von Larven mit unterschiedlicher Nahrung.

| Versuch | Versuchstiere | tote Larven | tote Puppen | geschlüpfte Käfer | Entwicklungserfolg |
|---|---|---|---|---|---|
| Mehlwurm & zerdrückte Kiwikerne (Standardfutter) | 16 | 5 | 1 | 10 | 62 % |
| Mehlwurm | 13 | 4 | 0 | 9 | 70 % |
| Mehlwurm & TetraMin | 8 | 2 | 1 | 5 | 67 % |
| TetraMin | 5 | 5 | 0 | 0 | 0 % |
| TetraMin & ganze Kiwikerne | 8 | 4 | 0 | 4 | 50 % |
| zerdrückte Kiwikerne | 15 | 6 | 0 | 9 | 60 % |
| ganze Kiwikerne | 16 | 3 | 5 | 8 | 50 % |
| Kiwi-Fruchtfleisch | 6 | 6 | 0 | 0 | 0 % |
| grüne Feige (zerriebene Frucht, trocken) | 7 | 7 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, trocken) | 8 | 8 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, aufgeweicht) | 8 | 8 | 0 | 0 | 0 % |

Tabelle 4. *Notiobia* sp. 2: Ergebnisse der Aufzucht von Larven mit unterschiedlicher Nahrung.

| Versuch | Versuchstiere | tote Larven | tote Puppen | geschlüpfte Käfer | Entwicklungserfolg |
|---|---|---|---|---|---|
| Mehlwurm & zerdrückte Kiwikerne (Standardfutter) | 16 | 5 | 2 | 9 | 56 % |
| Mehlwurm | 13 | 8 | 1 | 4 | 31 % |
| Mehlwurm & TetraMin | 17 | 5 | 1 | 11 | 65 % |
| TetraMin | 5 | 5 | 0 | 0 | 0 % |
| TetraMin & ganze Kiwikerne | 5 | 5 | 0 | 0 | 0 % |
| zerdrückte Kiwikerne | 12 | 6 | 3 | 3 | 25 % |
| ganze Kiwikerne | 13 | 13 | 0 | 0 | 0 % |
| Kiwi-Fruchtfleisch | 5 | 5 | 0 | 0 | 0 % |
| grüne Feige (zerriebene Frucht, trocken) | 6 | 6 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, trocken) | 8 | 8 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, aufgeweicht) | 8 | 8 | 0 | 0 | 0 % |

Tabelle 5. *Athrostictus batesi* -Ergebnisse der Aufzucht von Larven mit unterschiedlicher Nahrung.

| Versuch | Versuchstiere | tote Larven | tote Puppen | geschlüpfte Käfer | Entwicklungserfolg |
|---|---|---|---|---|---|
| Mehlwurm & TetraMin ( Standardfutter) | 16 | 8 | 0 | 8 | 50 % |
| Mehlwurm | 16 | 9 | 0 | 7 | 44 % |
| Mehlwurm & zerdrückte Kiwikerne | 12 | 5 | 1 | 6 | 50 % |
| TetraMin | 16 | 13 | 3 | 0 | 0 % |
| TetraMin & ganze Kiwikerne | 8 | 4 | 0 | 4 | 50 % |
| zerdrückte Kiwikerne | 10 | 9 | 1 | 0 | 0 % |
| ganze Kiwikerne | 5 | 5 | 0 | 0 | 0 % |
| Kiwi-Fruchtfleisch | 5 | 5 | 0 | 0 | 0 % |
| grüne Feige (zerriebene Frucht, trocken) | 5 | 5 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, trocken) | 5 | 5 | 0 | 0 | 0 % |
| *B. dichotoma* (Melastomataceae)-Samen (Papierausstrich, aufgeweicht) | 5 | 5 | 0 | 0 | 0 % |

Tabelle 6. Zusätzliche Nahrungswahlversuche bei den *Notiobia*-Arten

| Nahrungsangebot | Reaktion | | |
|---|---|---|---|
| | *Notiobia* sp.1 (Imagines) | *Notiobia* sp.2 (Imagines) | *Notiobia* sp.1 *(Larven)* |
| A) zerdr. Kiwikerne | 7x | 7x | |
| B) ganze Kiwikerne | 2x | 1x | |
| keine Reaktion | 1x | 2x | |
| | (n = 10) | (n = 10) | |
| A) große Feigensamen | 6x | | |
| B) kleine Feigensamen | 6x | 8x | |
| keine Reaktion | | 2x | |
| | (n = 12) | (n = 10) | |
| A) kleine Feigensamen | 10x | 3x | |
| *B) B. dichotoma* -Samen (Papierausstrich, aufgeweicht) | 1x | 1x | |
| keine Reaktion | 1x | 1x | |
| | (n = 12) | (n = 5) | |
| A) getötete Drosophila | 8x | 4x | 4x |
| keine Reaktion | 2x | 2x | 4x |
| | (n = 10) | (n = 6) | (n = 8) |
| A) *B. dichotoma* -Samen (Papierausstrich, aufgeweicht), nach 10 Tagen ohne Fütterung | 6x | 4x | |
| keine Reaktion | 4x | 2x | 8x |
| | (n = 10) | (n = 6) | (n = 8) |

Nur bei vier Futtervarianten gelang die Aufzucht von *Athrostictus batesi* von der Larve bis zum Käfer: Mehlwurm & TetraMin (die schnellste Entwicklung), Mehlwurm, Mehlwurm & zerdrückte Kiwikerne, TetraMin & ganze Kiwikerne.

### 3.3 Nahrungswahl bei Larven und Imagines (Video-Nachtaufnahmen)

In den Nahrungswahlversuchen I-VII (vgl. 2.3) wurden insgesamt 36 Larven von *Notiobia* sp. 1 beobachtet. 14 ließen während des Beobachtungszeitraums die Nahrung unberührt, 17 wählten das Mehlwurmstück, 4 die zerdrückten Kiwikerne und eine Larve das TetraMin.
Von den insgesamt 35 beobachteten Larven von *Notiobia* sp. 2 berührten 19 das Futter nicht, 10 Larven wählten das Mehlwurmstück, vier die zerdrückten Kiwikerne und zwei das TetraMin (Abb. 1; vgl. Vanicek 1993 für Einzelversuche). Zwar ist der Anteil der Larven, die keine Reaktion zeigten bei *Notiobia* sp. 2 höher als bei *Notiobia* sp. 1, in der Nahrungspräferenz sind sich die Arten aber sehr ähnlich. Auffallend ist die starke Bevorzugung der tierischen Nahrung.
Käfer beider *Notiobia*-Arten fraßen sowohl vom Mehlwurm bzw. knackten und fraßen ganze Kiwikerne, wenn kein anderes Futter zur Verfügung stand (Versuch VIII). Mit Versuch IX konnte gezeigt werden, daß nur die Larven des I. Stadiums von *Notiobia* sp. 1 in der Lage sind, ganze Kiwikerne zu knacken und zu fressen, nicht aber Erstlarven von *Notiobia* sp. 2. Larven und Käfer beider Arten haben am häufigsten vom Mehlwurm gefressen (Abb. 1). In Versuchen mit Einzelhaltung haben die Larven öfter gefressen als bei gemischter Haltung, bei der sie eine größere Aktivität zeigten.
Bei *Athrostictus batesi* haben von insgesamt 37 Larven in den Nahrungswahlversuchen I-VII (vgl. 2.3) 17 Larven keine Nahrung aufgenommen. 13 Larven fraßen am Mehlwurm, 5 am TetraMin und zwei an zerdrückten Kiwikernen (Abb. 1).
Bei vielen *Notiobia*-Larven wurde interspezifisches Konkurrenzverhalten und Kannibalismus beobachtet. Die Käfer dagegen haben weder Larven der eigenen Art noch der anderen Arten gefressen.
Während der Video-Nachtaufnahmen mit Larven wurden folgende Angriffe mit anschließendem Kannibalismus beobachtet: Bei *Notiobia* sp. 1 hat eine Larve im II. Larvenstadium (LII) eine LI-Larve gefressen, eine LIII-Larve hat eine LI-Larve und eine zweite LIII-Larve hat eine dritte LIII-Larve gefressen. Bei *Notiobia* sp. 2 hat eine LII-Larve zwei LI-Larven gefressen und eine im LIII-Larve eine LII-Larve.
Bei Larven von *Athrostictus batesi* wurden während der Video-Nachtaufnahmen zwar Angriffe mit anschließender Tötung beobachtet, aber kein Kannibalismus. Eine LII-Larve hat eine LI-Larve angegriffen und eine LII-Larve hat mit einer weiteren LII-Larve gekämpft.

### 3.4 Mandibelmorphologie der drei Arten

Die Larven-Mandibeln der *Notiobia*-Arten sind nur wenig gekrümmt, haben eine breite Basis und ein spitzes Ende. An der Innenbasis befinden sich ein paar Borsten, davor ein medianwärts vorspringender spitzer Zahn, das Retinaculum, und vor ihm vier kleinere, höckerartige Zähne auf dem Terebralkamm. Der Retinaculumzahn und die ventrale Rinne der Mandibeln ist bei *Notiobia* sp. 1 stärker ausgeprägt als bei *Notiobia* sp. 2 (Abb. 2a, b).
Larven von *Athrostictus batesi* haben mehr sichelförmig gekrümmte Mandibeln mit einer schärferen Spitze als bei den *Notiobia*-Arten. Auf dem Terebralkamm befinden sich keine Zähne (Abb. 2c).
Bei Imagines von *Notiobia* sp. 1 und *Notiobia* sp. 2 sind die Mandibeln nur wenig länger als breit und enden in einer stumpfen Spitze. Bei *Notiobia* sp. 1 findet man eine stärker ausgeprägte ventrale Rinne und einen kleineren Retinaculumzahn als bei *Notiobia* sp. 2 (Abb. 3a, b).

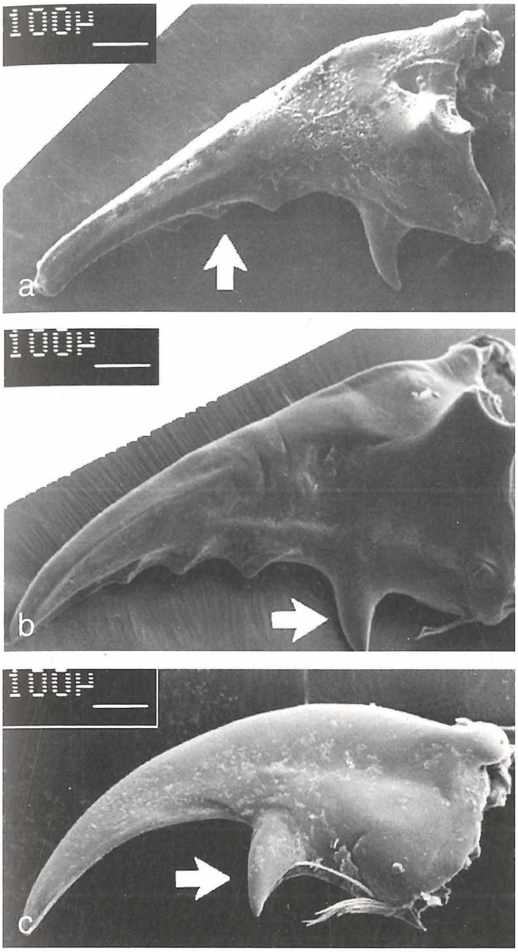

Abbildung 2. a) *Notiobia* sp. 1: Rechte Mandibel (dorsal, REM) der LIII-Larve. Pfeil = Terebralkamm; b) *Notiobia* sp. 2: Rechte Mandibel (dorsal, REM) der LIII-Larve. Pfeil = Retinaculumzahn; c) *Athrostictus batesi*: Rechte Mandibel (dorsal, REM) der LIII-Larve. Pfeil = Retinaculumzahn.

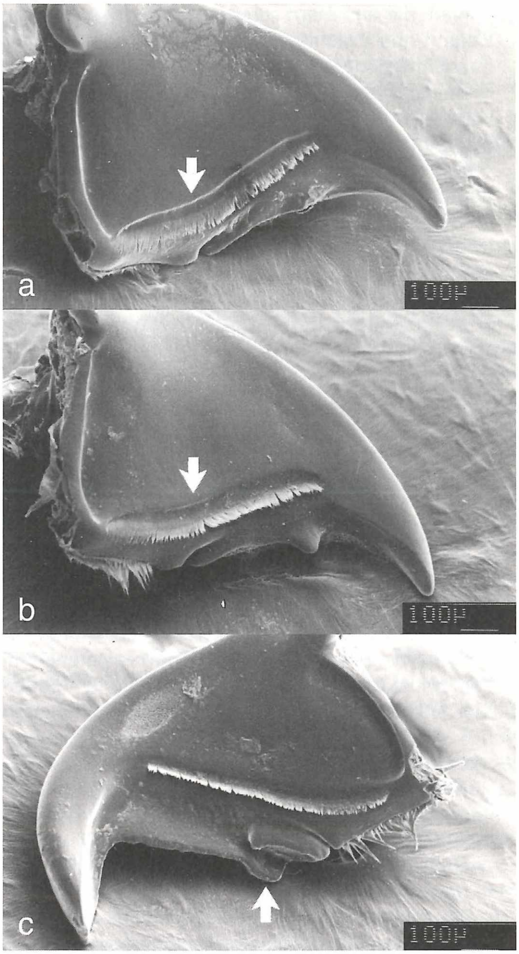

Abbildung 3. a) *Notiobia* sp. 1: Rechte Mandibel (ventral, REM) der Imago. Pfeil = ventrale Rinne; b) *Notiobia* sp. 2: Rechte Mandibel (ventral, REM) der Imago. Pfeil = ventrale Rinne; c) *Athrostictus batesi*: Linke Mandibel (ventral, REM) der Imago. Pfeil = Retinaculumzahn.

Bei Imagines von *Athrostictus batesi* sind die Mandibeln stärker gebogen und enden in einer scharfen Spitze. Der Retinaculumzahn ist gut ausgebildet (Abb. 3c).

## 4. Diskussion

Aus den Ergebnissen der Aufzuchtversuche (Tab. 3, 4, 5) und der Untersuchungen zur Mandibelgestalt von Larven und Käfern schließen wir, daß *A. batesi* nicht zu den ausgeprägt spermophagen Harpalini-Arten gehört. Dies war zu erwarten, da diese Art, im Gegensatz zu den *Notiobia*-Arten, nicht auf den nur kurzfristig existierenden Fruchtflächen beobachtet wurde. Unerwartet ist dagegen der Befund, daß sich die Dauer der Entwicklungszeiten von *A. batesi* und den beiden *Notiobia*-Arten im Labor nicht unterscheiden (Tab. 2, 3, 4). Wir nehmen an, daß die gesamte Entwicklungsdauer vom Ei bis zur Imago bei den *Notiobia*-Arten mindestens so lange dauert wie die Mehrzahl der Feigenfruchtfälle oder länger (PAARMANN et. al., unveröff.). Für die *Notiobia*-Arten ergeben sich dadurch zwei Probleme:

1. Jungkäfer schlüpfen auf einer Fruchtfläche, die von Samen weitgehend leergeräumt ist. Sie können sich somit durch Samen keine Fettreserven für die Wanderung zur nächsten Fruchtfläche anfressen.

2. Larven, die aus Eiern schlüpfen, die nicht gleich zu Beginn des Fruchtfalls abgelegt wurden, können ihre Entwicklung nicht mittels Samenfraß bis zum Ende des Fruchtfalls abschließen. Für diese Larven wäre die beobachtete Fähigkeit, sich bei ausschließlicher Ernährung mit Insekten (Mehlwurm) entwickeln zu können (Tab. 3, 4), von großer Bedeutung. Der beobachtete Kannibalismus der größeren an den kleineren Larven könnte dazu beitragen, daß die Larven, deren Entwicklung schon am weitesten fortgeschritten ist, ihre Entwicklung auch bei Mangel an Früchten abschließen.

Freilanduntersuchungen (PAARMANN & ADIS, unveröff.) ergaben, daß die Larven durchaus ihre gesamte Entwicklung bei alleiniger Fütterung mit Samen bestimmter Feigenarten durchlaufen können. Die in den Aufzuchtversuchen angebotenen Feigenfrüchte stammen offenbar von Baumarten, deren Früchte den Käfern auf ihrer Wanderung zwar als Nahrung dienen mögen, aber keine Entwicklung der Larven zulassen. Auf Melastomataceen-Fruchtflächen entwickeln sich drei weitere *Notiobia*-Arten (PAARMANN & ADIS, unveröff.). Die Käfer der beiden *Notiobia*-Arten von Feigen-Fruchtflächen fressen zwar die Melastomataceensamen, die Larven von *Notiobia* sp. 1 aber nicht (Tab. 6). Larven von *Notiobia* sp. 2 wurden daraufhin nicht untersucht. Jedenfalls ist eine erfolgreiche Entwicklung der Larven beider Arten bei ausschließlicher Fütterung mit Samen von *B. dichotoma* nicht möglich (Tab. 3, 4). Dies deutet darauf hin, daß neben Feigen auch bestimmte Melastomataceen-Bäume durch ihr Fruchtangebot den Käfern auf ihren Wanderungen als Trittsteinhabitate dienen können.

Zwischen den beiden Feigenkäferarten deutet sich eine gewisse Nischenaufteilung an: *Notiobia* sp. 1 ist deutlich größer als *Notiobia* sp. 2 (Tab. 1). Auf Grund dieser Körpergrößenunterschiede, kann *Notiobia* sp. 1 sich deutlich größere Samen als Nahrungsquelle erschließen, als *Notiobia* sp. 2. Diese Vorstellung wird durch die Ergebnisse der Nahrungswahlversuche (Tab. 6) bestätigt: Käfer von *Notiobia* sp. 1 zeigten bei gleichzeitigem Angebot von kleinen und großen Samen keine Bevorzugung eines Samentyps, während die Käfer von *Notiobia* sp. 2 ausschließlich die kleinen Samen wählten.

Aus den Fütterungsversuchen (Tab. 3, 4) ergab sich, daß die kleinere Art (*N.* sp. 2), im Gegensatz zu der größeren (*N.* sp. 1), sich nicht entwickeln kann, wenn unzerstörte Kiwisamen als Futter angeboten werden. Die Larven des I. Stadiums von *Notiobia* sp. 2 sind offensichtlich nicht in der Lage, die vergleichsweise großen Kiwisamen zu öffnen.

Im Lebensraum der Käfer dürften die geschilderten Unterschiede zwischen den Arten dazu führen, daß *Notiobia* sp. 2 optimale Ernährungsbedingungen nur auf Fruchtflächen von kleinfrüchtigen Feigen (= kleinsamig; PAARMANN et al., unveröff.) findet, *Notiobia* sp. 1 dagegen ein breiteres Spektrum an Ernährungsbedingungen vorfindet, da ihre Erstlarven auch Feigen mit größeren Samen nutzen können.

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# Diversität von Interaktionen zwischen Ameisen und Pflanzen im südostasiatischen Regenwald

**Kurzfassung**
Assoziationen von Ameisen mit Pflanzen (und oft noch mit pflanzensaugenden Insekten als drittem Partner) dürften eine Ursache des Artenreichtums und der hohen Abundanzen tropischer Formicidae sein. Die von den Ameisen genutzten Pflanzen bieten entweder Nahrung an, über extraflorale Nektarien und/oder Nährkörperchen, oder aber - bei den eigentlichen Myrmekophyten - Nistraum und z.T. auch Nahrung. Diese Beziehungen zeichnen sich durch unterschiedliche Nutzungsweisen und Nutzungsintensitäten und damit stark differierende Abhängigkeit der Partner voneinander aus. Ein besonders breites Spektrum von Ameisen-Pflanzen-Assoziationen finden wir in der paläotropischen Baumgattung *Macaranga* (Euphorbiaceae), die sich daher als Modellsystem für vergleichende Untersuchungen hervorragend eignet.
Die Grundfrage unserer Untersuchungen an diesem System lautet: Verläuft aufgrund der ausgeprägt mosaikartigen Verteilung der von den myrmekophilen Pflanzen angebotenen Nahrungs- und Nistraumressourcen die Neu- und Wiederbesiedlung von Habitaten durch die Ameisen in Form von Zufallsprozessen? Oder werden, im Gegenteil, durch diesen Umstand Spezialisierungen seitens der Ameisen gefördert und die Zusammensetzung der Lebensgemeinschaften dadurch stärker deterministisch geprägt?
Unsere bisherigen Untersuchungen zeigen, daß beide Prinzipien wirken. Bei der alleinigen Nutzung von Nahrungsressourcen fehlen spezialisierte Beziehungen weitgehend und stochastische Ereignisse dürften sehr häufig die Pflanzen-Ameisen-Assoziation bestimmen. Bei den eigentlichen Myrmekophyten hingegen ist die Auswahl der assozierten Ameisen viel stärker determiniert, ganz besonders dann, wenn der Wohnraum, den die Pflanze offeriert, nur durch aktives Öffnen seitens der Ameisen erschlossen werden kann.

**Abstract**
**Diversity of ant-plant interactions in south-east Asian rain forests**
Associations of ants with plants can be regarded as one reason for the high abundance and diversity of ants in the tropics. The plants either provide food as extrafloral nectar and/or food bodies or, in the true myrmecophytes, nesting space and partly also food. These associations are characterized by very different forms and intensities of use of the plant resources and, therefore, also varying mutual dependency of the partners. A broad spectrum of different ant-plant associations is found in the paleotropical tree genus *Macaranga* (Euphorbiaceae) which is therefore especially suited as a model system for a comparative investigation. The central question of our studies is: Does the mosaic character of the spatial distribution of food and nesting resources provided by the myrmecophilous plants rather favour stochastic processes during colonization of habitats by ants? Or does it, on the contrary, preferentially lead to strong specializations in the ants? Our investigations show that both principles are realized. In interactions where ants only use the food resources, specific relationships are lacking and stochastic events direct the associations. In obligate myrmecophytes, however, the colonization largely follows deterministic principles, especially when nesting space inside the plant actively has to be made accessible by the ants.

Mit Unterstützung der Deutschen Forschungsgemeinschaft im Rahmen des Schwerpunktprogramms „Mechanismen der Aufrechterhaltung tropischer Diversität“

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## 1. Einleitung

Ameisen stellen die nach Biomasse und Individuenzahl dominierende Tiergruppe in der Vegetation tropischer Regenwälder dar. Ihre Verbreitung wird dabei vornehmlich von ihren Nahrungsbedürfnissen und ihren Ansprüchen an die Nistmöglichkeiten bestimmt. Zwar können Ameisen pflanzliches Blattmaterial nicht - wie Herbivore - direkt als Nahrung verwerten, wohl aber z.B. zuckerhaltige Pflanzensäfte. Diese erhalten sie entweder direkt von den Primärproduzenten oder indirekt über Nährsymbiosen mit Pflanzensaft saugenden Insekten. In beiden Fällen kommt es manchmal zu sehr engen mutualistischen Beziehungen zwischen Ameisen und ihren Futterpflanzen und/oder ihren Symbionten. Der in den Tropen besonders hohe Artenreichtum der Ameisenunterfamilien Formicinae, Dolichoderinae und teilweise der Myrmicinae dürfte zu einem wesentlichen Teil auf diesen durch Nährsymbiosen verkürzten Anschluß an die Primärproduktion zurückzuführen sein (MASCHWITZ 1992).
Assoziationen zwischen höheren Pflanzen und Ameisen haben sich in großer Vielfalt in den tropischen Regenwäldern entwickelt. Die Ameisen, die ihre Nahrung direkt von den Primärproduzenten beziehen, nutzen z.B. extraflorale Nektarien (EFN) (Taf. 1a). EFN haben keine Funktion in Zusammenhang mit Pollinationsprozessen. Sie zeichnen sich durch eine große strukturel-

Tabelle 1. Vorläufige Liste der Ameisen an extrafloralen Nektarien in 4 Untersuchungsgebieten

| | Primärwald | | Sekundärhabitat | |
|---|---|---|---|---|
| | Pasoh | Belum | Gombak | Kepong |
| Ponerinae | | | | |
| *Diacamma rugosum* | | | | |
| *Gnamptogenys* sp. | | | | |
| *Odontomachus rixosus* | | | | |
| Pseudomyrmecinae | | | | |
| *Tetraponera* sp. | | | | |
| Myrmicinae | | | | |
| *Cataulacus* sp. | + | | | |
| *Crematogaster inflata* | + | | | |
| *Crematogaster* | 5(+)spp. | 4(+)spp. | 5(+)spp. | 5(+)spp. |
| *Meranoplus mucronatus* | + | + | + | + |
| *Myrmicaria* cf. *birmana* | + | | + | + |
| *Pheidole* sp. | | + | + | |
| unident. Arten | 1 spp. | 2 spp. | 4 spp. | 3 spp. |
| Dolichoderinae | | | | |
| *Dolichoderus* (*Hypoclinea*) | 2 spp. | 2 spp. | 2 spp. | 2 spp. |
| *Philidris* sp. | + | | | |
| *Technomyrmex* | 3 spp. | + | 2 spp. | + |
| unident. Arten | 2 spp. | 1 spp. | 2 spp. | 3 spp. |
| Formicinae | | | | |
| *Anoplolepis longipes* | | | + | + |
| *Camponotus* | 6 spp. | 3 spp. | 5 spp. | 3 spp. |
| *Echinopla* sp. | + | | + | |
| *Oecophylla smaragdina* | | + | + | |
| *Polyrhachis (Hemioptica)* sp. | + | + | | |
| *Polyrhachis* | 6 spp. | 3 spp. | 5 spp. | 3 spp. |

le Variabilität aus und sind besonders bei Pflanzen der Subtropen und Tropen häufig. Seltener (und kaum im Detail untersucht) produziert der pflanzliche Symbiosepartner kohlehydrat-, protein- und/oder lipidreiche sogenannte Nährkörperchen. Ameisenpflanzen (Myrmekophyten) im engeren Sinn, die gleichzeitig Nahrung und Nistraum bieten, sind nur aus den Tropen bekannt geworden. Die Myrmekophyten profitieren von ihren Ameisen durch Nährstoffbereitstellung und Schutz, wobei aber im Fall der EFN die mutualistische Funktion der Ameisen immer noch kontrovers diskutiert wird. Es überwiegen aber die Befunde, die überzeugend Schutzeffekte der Ameisen gegenüber Herbivoren belegen (Überblick z.B. bei Koptur 1992).

In den letzten Jahren haben wir in mehreren Projekten begonnen, die Diversität und Relevanz der Interaktionen von Ameisen und Pflanzen in tropischen Habitaten zu erfassen und zu analysieren. Die Palette der Beziehungen reicht von unspezifischen Myrmekophytiesystemen bis zu Symbiosen, bei denen zumindest ein Partner existentiell vom anderen abhängt (Fiala & Maschwitz 1991, 1992, Maschwitz et al. 1991, 1992, 1994, Fiala et al. 1994 und unveröff.).

Hauptgesichtspunkte unserer Untersuchungen an Ameisen-Pflanzen-Interaktionen sind die Nutzung der pflanzlichen Nahrungsressourcen (extrafloraler Nektar, Nährkörperchen) und bei den eigentlichen Myrmekophyten zusätzlich der Aspekt der Nistressource. Als Modellsystem für die vergleichende Bearbeitung von unspezifischen Interaktionen bis hin zu engen Symbiosen ist die paläotropische Baumgattung *Macaranga* besonders geeignet, da sich bei den Arten dieser Gattung viele deutlich unterschiedliche Zustände in den Interaktionen mit Ameisen finden.

Unsere Grundfrage lautet: Sind bei der Nutzung pflanzlicher Nahrungs- und Nistraumressourcen durch Ameisen Zufallsprozesse vorherrschend bei weitgehender Nischenüberlappungen der Nutzerarten, oder werden, im Gegenteil, starke Spezialisierungen gefördert? Im folgenden soll ein Einblick in einige unserer Arbeitsschwerpunkte gegeben werden.

Tabelle 2. Relative Häufigkeit der einzelnen Ameisentaxa an extrafloralen Nektarien (ohne Berücksichtigung der Individuenzahl/Pflanze; n = Anzahl Sichtungen).

| Pasoh |  | Gombak |  | Kepong |  |
|---|---|---|---|---|---|
| n = 398 |  | n = 297 |  | n = 255 |  |
| *Gnamptogenys* sp. | 28% | *Crematogaster* spp. | 21% | *Crematogaster* spp. | >60% |
| *Crematogaster* spp. | 23% | *Diacamma rugosum* | 11% | *Anoplolepis longipes* | 12% |
| *Polyrhachis* spp. | 13% | *Camponotus* spp. | 10% | *Camponotus* spp. | 11% |
| *Camponotus* spp. | 10% | *Polyrhachis* spp. | 8% | *Polyrhachis* spp. | 7% |
| sonstige | <8% | sonstige | <8% | sonstige | <7% |

## 2. Nutzung von Nahrungsressourcen

Diese Interaktionen zwischen Ameisen und Pflanzen wurden bisher als unspezifisch betrachtet, d.h. viele Ameisenarten besuchen dieselbe Nahrungspflanze, und die Ameisen nutzen verschiedene Pflanzenarten. Wenige Arbeiten untersuchten bisher vergleichend verschiedene Ameisenzönosen und Pflanzengesellschaften im unterschiedlichen ökologischen Kontext. Es existieren auch nur wenige Studien (meist aus der Neotropis) zur Verbreitung und Abundanz von EFN in verschiedenen Pflanzentaxa und Vegetationstypen.

Da aus Südostasien bisher fast keine Informationen über das Vorkommen von Pflanzen mit EFN und die assoziierte Ameisenfauna vorlagen, haben wir - vor der Analyse der Bedeutung der EFN - erstmals eine gründliche Bestandsaufnahme des Vorkommens und der Häufigkeit von Pflanzen mit EFN (beschränkt auf Sträucher und Bäume) und der assoziierten Ameisenfauna in einem südostasiatischen Primärwald durchgeführt. Untersuchungsgebiet war Pasoh Forest Reserve, ein Tiefland-Dipterocarpaceen-Wald in West Malaysia. In einem Gebiet von ca. 100 ha überprüften wir 741 Baumarten (bei einem Artenbestand von insgesamt 814 Baumarten, KOCHUMMEN et al. 1990) aus allen sechs Unterklassen der Magniolopsida. EFN waren besonders häufig in den Familien Euphorbiaceae, Fabaceae und Rosaceae. Interessant war ihr häufiges Vorkommen bei Keimlingen der in Südostasien wichtigen Nutzholzfamilie der Dipterocarpaceae (FIALA & LINSENMAIR unveröff.). 83 (=11,2%) der insgesamt untersuchten Baumarten wiesen EFN auf. Dies ist einer der niedrigsten Werte, der bisher in der Literatur für tropische Vegetationsformen dokumentiert wurde (Übersicht bei OLIVEIRA & OLIVEIRA-FILHO 1991). Ein Vergleich unserer Daten mit denen aus dem einzigen weiteren bisher untersuchten - neotropischen - Waldgebiet (Barro Colorado Island, Panama, SCHUPP & FEENER 1991) zeigt eine relativ große Übereinstimmung in der taxonomischen Zugehörigkeit der Pflanzen mit EFN: Von 43 in beiden Regionen vorkommenden Familien weisen 32 Vertreter mit EFN auf, bzw. fehlen EFN-Pflanzen in den entsprechenden Taxa in beiden Gebieten. Nur in 11 Familien differiert das Vorkommen von EFN, d.h. kommen EFN-Pflanzen entweder nur in Pasoh oder in Barro Colorado vor.

Die Häufigkeit von EFN in Primärwaldgebieten scheint deutlich unter den Werten stärker gestörter Habitate zu liegen. So ergaben unsere Studien in weiteren Tieflandprimärwaldgebieten, Belum (Perak, Westmalaysia) und Lambir (Sarawak, Borneo) als durchschnittliche Werte 7% bzw. 8,5% (in Lagen <300 m ). Im Gegensatz dazu lag die Häufigkeit von EFN-Arten in den untersuchten Sekundärhabitaten bei 22% (Ulu Gombak, Malaysia) und 23,5% (Kepong, Malaysia). Somit bestätigen sich die Ergebnisse ähnlicher Untersuchungen aus der Neotropis (OLIVEIRA & OLIVEIRA-FILHO 1991).

In Pasoh wurden bislang an den EFN mindestens 37 Ameisenarten aus 17 Gattungen als Besucher festgestellt. Arten aus fast allen in Malaysia vorkommenden Formiciden-Unterfamilien sind vertreten (Tab. 1). Dies entspricht durchschnittlich etwa 28,9% der in Pasoh auf der niederen Vegetation gesammelten Arten (Bestandsaufnahme der Ameisenfauna in Pasoh von K. ROŚCISZEWSKI, Karlsruhe, in Vorb.) Unsere Beobachtungen ergaben in keinem Fall Hinweise auf enge, spezifische Beziehungen zwischen Pflanze und Ameisen. Allein auf der detaillierter untersuchten Art *Macaranga lowii* z.B. ließen sich 18 Ameisenarten nachweisen.

Ähnliche Ergebnisse, zumindest auf Gattungsebene, deuten sich für das zweite von uns untersuchte Tieflandprimärwaldgebiet Belum (Tab. 1) an. Allerdings wäre ein Vergleich der Artenzahlen der Ameisen von Belum mit den anderen Gebieten aufgrund der geringen Datenmenge verfrüht, da wir in Belum bislang nur wenige Tage verbringen konnten. (In dieser kurzen Zeit konnten wir bereits 20% der Pflanzenarten mit EFN finden, die wir in Pasoh festgestellt hatten.) Auch die taxonomische Zusammensetzung der Ameisenfauna an EFN in den zwei Sekundärhabitatgebieten in Ulu Gombak und Kepong ähnelt der der Primärwaldgebiete, wie ebenfalls erste Untersuchungen zeigen (Tab. 1); es kommen jedoch typische Störanzeiger wie *Anoplolepis longipes* hinzu.

Unterschiedlich war jedoch die relative Häufigkeit der einzelnen Taxa in den verschiedenen Habitaten

(Tab. 2), wobei Arten der Gattungen *Crematogaster*, *Camponotus* und *Polyrhachis* überall mit am häufigsten auftraten. Eine quantitative Auswertung für Belum wird aufgrund der kurzen Untersuchungszeit ausgeklammert. Die bisherigen Befunde sprechen jedoch ebenfalls für eine ähnliche Zusammensetzung der Ameisenfauna mit einer deutlichen Dominanz von *Crematogaster* spp., *Camponotus* spp., *Polyrhachis* spp. und *Gnamptogenys* sp. Hinzu kam auffällig häufig *Meranoplus mucronatus*, die in den anderen Gebieten wesentlich seltener auftrat (Belum 10%, Pasoh 2%, Ulu Gombak 3%, Kepong 2%).

Die Nutzung der EFN durch Ameisen war in Pasoh relativ schwach, durchschnittlich fanden sich nur auf 29,8% der kontrollierten Pflanzen mit EFN Ameisen (10-100%, je nach Pflanzenart). Jede dieser Arten wurde im Mittel von 3,7 Ameisenarten besucht (1-10; n=535 überprüfte Pflanzen <2 m, n pro Art = 8-60). Die Zahl der Ameisen, die pro Kontrolle auf einer Pflanze gesichtet wurde, war relativ niedrig. So fanden sich z.B. auf den regelmäßig kontrollierten Arten (je nach Art 2-94 kontrollierte Pflanzen) bei 30 tageszeitlich verschiedenen Kontrollgängen durchschnittlich 5,1 Ameisen pro Pflanze (1-8), meist nur auf den jüngsten 2 Blättern. Ausnahmen bildeten die Baumsturzlücken-Besiedler *Endospermum diadenum* und *Leea indica* mit $\overline{x}$=15,5 bzw. 17,5 Ameisen. Die Präsenz von Ameisen auf den EFN-Pflanzen war lokal sehr unterschiedlich, möglicherweise als Folge mosaikartiger Siedlungsweise der Ameisen. Die Artenüberlappung zwischen den einzelnen Flächen war recht gering, vielmehr fanden wir eine recht wechselnde Artenzusammensetzung. Manche Ameisenarten wurden an 50 Köderstellen nur 1-2mal angetroffen, während andere an bis zu 60% aller Stellen auftauchten (z.B. *Philidris* sp. bzw. *Gnamptogenys* sp.).

Die Ameisenaktivität auf der niedrigeren Vegetation (<2m) des Waldbestands in Pasoh war generell relativ gering. Bei 20 abgesuchten Transekten war im Pasoh-Primärwald durchschnittlich nur jede 15. Pflanze (6,5% von n=1249 Pflanzen) von Ameisen belaufen, meist von einzelnen Arbeiterinnen. Regelmäßig auf der Vegetation zu sehen, waren vor allem Vertreter der Gattungen *Crematogaster*, *Dolichoderus*, *Camponotus*, *Polyrhachis* sowie *Diacamma rugosum* und *Gnamptogenys* sp. Im zweiten von uns untersuchten Primärwaldgebiet, Belum, ergaben sich ähnliche Werte: Im geschlossenen Waldbestand wurde durchschnittlich jede 17 Pflanze mit Ameisen angetroffen (5,9% von n=1250 Pflanzen). In gaps und an sehr offenen, gestörten Standorten hingegen waren in Pasoh durchschnittlich auf jeder 6. Pflanze Ameisen zu finden (16,6% von n=132 untersuchten Pflanzen), in Belum auf jeder 11. Pflanze (9,1% von n=321). In den relativ gestörten Habitaten in Ulu Gombak und Kepong trafen wir Ameisen auf 17,8% aller Pflanzen (n=588) bzw. auf 14,2% (n=449) an.

Die generell schwache Ameisenaktivität auf der Vegetation in Pasoh wurde auch durch Köderversuche bestätigt. Es dauerte meist recht lange, bis die ersten (Honig- und Fleisch-) Köder entdeckt wurden: je nach Standort (n=24) durchschnittlich 36-64 Minuten. Der Prozentsatz überhaupt entdeckter Köder im Beobachtungszeitraum von 2,5 Stunden lag bei 35%. In Ulu Gombak wurden in der gleichen Zeitspanne jedoch 44% aller Köder entdeckt. Die Köderversuche bestätigten das Bild eines stark mosaikartigen Siedlungsmusters der Ameisen. Durchschnittlich wurden in Pasoh 4,8±1,9 Ameisenarten pro Köderstandort gefunden (1-8 Arten), in Ulu Gombak 2,8±1,3 (1-6 Arten).

Alle Ameisenarten, die wir an EFN fanden, gingen bei Köderversuchen auch an Fleischnahrung und sind daher als Generalisten zu betrachten. Offensichtlich liegt für die EFN eine opportunistische Nahrungsnutzung vor, und die EFN haben möglicherweise zu verschiedenen Jahreszeiten eine unterschiedlich hohe Bedeutung als Nahrungsressource und werden dementsprechend von den Ameisen unterschiedlich intensiv genutzt. Hier sind unbedingt mehr Beobachtungen zu verschiedenen Jahreszeiten nötig.

Bisher waren aus südostasiatischen Waldgebieten kaum Informationen über Artenzahl und -zusammensetzung der Ameisenfauna bekannt, während die Ameisenfauna der Neotropis wesentlich besser bearbeitet ist. Unsere Ergebnisse können daher nur mit neotropischen Regionen verglichen werden. Ein solcher Vergleich (OLIVEIRA & BRANDÃO 1991) weist auf gewisse Übereinstimmungen in generellen Grundprinzipien der Ameisen-Pflanzen-Interaktionen in beiden Tropenregionen hin. Auch in der Neotropis sind die Beziehungen von Ameisen zu EFN-Pflanzen eher unspezifischer Natur. Die meisten EFN-besuchenden Arten gehörten in der Neotropis und in unseren Untersuchungsgebieten zu den Myrmicinen. Ponerinen waren am seltensten, Dolichoderinen und Formicinen wiesen einen etwa gleich großen Anteil in beiden Regionen auf.

## Fazit

Unsere Befunde haben uns einen ersten, notwendigerweise kursorischen Einblick in die Vielfalt dieser Ameisen-Pflanzen-Beziehungen gegeben und eine sehr variable Nutzung der EFN demonstriert. Während der Nutzen, den die Ameisen aus dieser Interaktion ziehen, sehr klar erkennbar ist, blieben viele weitere Fragen vorerst offen. Warum werden die EFN nicht intensiver genutzt? Gibt es wesentliche qualitative Unterschiede im Nektarangebot, oder ein zeitlich nur sehr eingeschränktes, bei dem sich eine Nutzung für die Ameisen wirklich lohnt? Wesentlich unklarer und vermutlich viel unterschiedlicher sind jedoch die Vorteile, die die Pflanzen aus den unspezifischen Interaktionen gewinnen (z.B. BECERRA & VENABLE 1989, FIALA 1990). Einen eindeutigen Nachweis positiver Wirkung der Ameisenbesucher auf Pflanzen mit EFN konnten wir bereits in zwei Fällen in Sekundärhabitaten erbringen: 1. Schutzfunktion gegen Fraßschäden für *Macaranga tanarius* (Nicht-Myrmekophyt mit EFN) und *M. hosei* durch zunächst unspezifische Ameisenbesuche an EFN und spätere spezifische Besiedlung durch *Crematogaster* sp. (FIALA et al. 1994). 2. Schutz der Blütenknospen der Liane *Thunbergia grandiflora* durch EFN-besuchende *Dolichoderus thoracicus* vor Befall und quantitativer Zerstörung durch Schmetterlingsraupen (FIALA et al. in Vorb.).

In sehr vielen Fällen bleibt der Nutzen für die Pflanze vorerst fraglich. Nur sehr viele detaillierte, langfristige Studien, die verschiedenste, auch die jüngsten Altersklassen der Pflanzen einschließen, werden zeigen können, wann eine intensivere Nutzung stattfindet, ob bestimmte Altersklassen profitieren, EFN-besitzende Pflanzen interspezifisch konkurrieren - und inwieweit und warum pflanzensaugende Insekten von den Ameisen - zum Nachteil der Pflanzen - bevorzugt werden.

## 3. Nutzung von Nistraum

Für Myrmekophyten (Pflanzen mit Nistraum für Ameisen) haben wir inzwischen eine Reihe von Hinweisen, daß die Struktur der diese Pflanzen besiedelnden Ameisengemeinschaft weitgehend durch deterministische Prinzipien bestimmt wird. Um die Datenbasis für diese Annahme zu erweitern, wollten wir einen möglichst umfassenden Überblick über die Besiedlung dieser Pflanzen erhalten und haben nach weiteren Myrmekophyten gesucht.

Dabei haben wir uns einige bekannte, aber bisher mangelhaft beschriebene Assoziationen von Myrmekophyten und ihren Ameisen näher angeschaut und konnten zudem neue ameisenbesiedelte Pflanzenarten entdecken. Alle untersuchten Arten bieten Nistraum in hohlen, z.T. angeschwollenen Internodien, unterscheiden sich aber darin, wie der Zugang der Ameisen zu diesem Nistraum erfolgt.

Bei zwei Arten (*Ficus borneensis*, Moraceae und *Clerodendrum fistulosum*, Verbenaceae) öffnen sich die Höhlungen (= Domatien) spontan, ohne äußere Einwirkung (Abb. 1). Beide Pflanzenarten bieten den Ameisen extrafloralen Nektar als Nahrung. Die Domatien wurden von einer Vielzahl arborealer Ameisen bewohnt (z.B. *Cataulacus* sp., *Crematogaster* spp., *Tetramorium* sp., *Technomyrmex* spp., *Camponotus* spp., *Camponotus* (*Colobopsis*) sp.). Enge spezifische Interaktionen konnten wir in beiden Fällen nicht feststellen (MASCHWITZ et al. im Druck a, b).

Im Gegensatz dazu konnten wir zwei weitere, sehr spezifische Systeme entdecken. Die Domatien der beteiligten Pflanzen (*Neonauclea cyrtopoda* aus Sumatra und *N. celebica* aus Sulawesi) werden ebenfalls durch Degeneration des Sproßmarks hohl, entwickeln aber keine Eingangslöcher. Diese müssen von den besiedelnden Ameisen (zwei verschiedene *Crematogaster*-Arten aus zwei unterschiedlichen Subgenera) selbst gebissen werden. Beide Assoziationen erweisen sich als hochentwickelt und spezifisch, und in beiden Fällen waren nach unseren Befunden stets trophobiotische Pseudococciden beteiligt. Blattfressende Insekten und pflanzliche Konkurrenten (wie Kletterpflanzen) wurden von den auf der Pflanzenoberfläche aktiven Ameisen heftig attackiert (MASCHWITZ, FIALA & LINSENMAIR eingereicht).

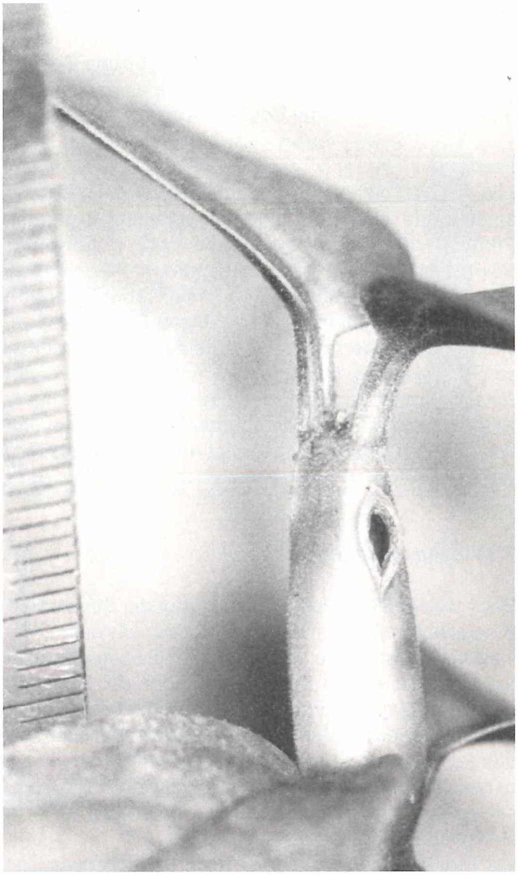

Abbildung 1. Domatium von *Clerodendrum fistulosum* mit spontan entstandener Öffnung.

Neben den Pflanzen, bei denen die Domatien von sich aus hohl werden (wobei z.T. Öffnungen von selbst entstehen, z.T. von den Ameisen geschaffen werden müssen), gibt es auch solche, wo die Ameisen die Domatien aufbeissen und das Mark aushöhlen müssen. Dies ist z.B. bei allen Pflanzenassoziationen mit Beteiligung von Ameisen aus der Gattung *Cladomyrma* der Fall. Auf der Pflanzenseite sind Vertreter aus 5 verschiedenen Pflanzenfamilien beteiligt (A. MOOG et al.

in Vorb.). Manche der Pflanzen erzeugen distinkte, von außen gut erkennbare Domatienstrukturen. In jedem Fall handelt es sich um sehr spezifische Besiedlungen, die wir in verschiedenen Gebieten der malaysischen Halbinsel und auf Borneo wiederfinden konnten.

### Fazit

Alle unseren bisherigen Befunde zeigen, daß es dann zu sehr spezifischen Interaktionen kommt, wenn die Pflanzen den Ameisen außer Nahrung in Form der Sekrete extrafloraler Nektarien und/oder Futterkörperchen auch Wohnraum bieten, dieser aber nicht von der Pflanze selbst in der endgültigen Form bereitgestellt wird, sondern von den Ameisen aktiv erschlossen werden muß. Offensichtlich haben die jeweiligen Ameisenarten nur für eine oder wenige, ähnliche Pflanzenarten die entsprechenden Techniken evoluiert, und die Besiedlung erfolgt in deterministischer Weise.

## 4. Modellsystem *Macaranga*

Nach welchen Prinzipien entsteht nun die Struktur der Ameisengemeinschaft in unserem Modellsystem *Macaranga*? Bestimmen bei den myrmekophytischen Arten ebenfalls starke Spezialisierungen der Ameisen die Besiedlung? Aus der Vielzahl bearbeiteter Fragen wollen wir hier nur den Aspekt der Wirtsspezifität herausgreifen. Welche der beteiligten Ameisenarten verhalten sich wirtsspezifisch und unter welchen ökologischen Bedingungen? Handelt es sich dabei z.T um Habitatspezifität?
Zur Erhellung dieser Fragen haben wir in jüngster Zeit bei mehreren Feldaufenthalten verstärkt nach isolierten Wuchsorten von *Macaranga*-Pflanzen gesucht, und zwar bevorzugt in Regionen, wo möglichst viele Arten sympatrisch vorkommen, um Daten zur Wirtsspezifität auch unter stark mosaikartiger und heterogener Ressourcenverteilung gewinnen zu können. Unsere besondere Aufmerksamkeit fanden spezielle Waldstandorte, wie Flußufer und Baumsturzlücken (gaps), die als die ursprünglichen Habitate der *Macaranga*-Arten vermutet werden (WHITMORE 1973). Baumsturzlücken im Primärwald weisen eine inselhafte Verteilung auf, ihre Entstehung ist räumlich und zeitlich unvorhersehbar, die darin im häufig dichten Unterwuchs versteckten kleinen *Macaranga-K*eimlinge stellen für die sie besiedelnden Ameisenköniginnen nochmals wesentlich stärker isolierte Kleinsthabitate dar. Eine unserer zentralen Fragen war, ob diese insuläre Lage zufällige Besiedlung besonders fördert, indem die Pflanzen opportunistisch durch Ameisen (aus einem breiten Spektrum von in Frage kommenden Arten) genutzt werden, die die Ressource als erste entdecken, oder ob hier ebenfalls ganz spezielle Fähigkeiten bestimmter Ameisenarten die Besiedlung determinieren.
Die Suche nach solchen gaps haben wir hauptsächlich in Pasoh, Belum, Lambir (Tieflandwälder) sowie im Kinabalu National Park (Sabah, Bergwald) entlang von Transekten durch Primär- und Sekundärwaldgebiete durchgeführt. Ergänzende Studien konnten wir in einem Waldgebiet nahe Balikpapan in Kalimantan (Borneo) durchführen, hier waren jedoch nur noch winzige Primärwaldreste vorhanden, und wir arbeiteten meist in 10-25 Jahre altem, relativ gut regeneriertem Sekundärwald.
Die Zusammensetzung der Myrmekophytenflora in diesen Gebieten war sehr unterschiedlich, so daß es möglich sein sollte, eine eventuell vorhandene Habitatspezifität gut zu erkennen. Die Habitate sollten möglichst natürlich entstanden sein, da nur in diesen Fällen eine lückenhafte Verteilung der *Macaranga*-Arten gewährleistet ist. Sie können nämlich an sehr lichten Standorten (wie Kahlschläge und Straßenränder) extrem häufig werden, und die Distanzen zwischen den einzelnen Exemplaren wären dann zur Untersuchung der o.g. Fragestellung zu gering. Bisher haben wir 50 Standorte auswerten können, die die Bedingung erfüllten, daß Jungpflanzen verschiedener Arten syntop vorkamen. Unsere Ergebnisse zeigen eine sehr starke Wirtsspezifität auf: Nur an sieben Standorten kam unspezifische Besiedlung vor, d.h. an diesem Standort waren eine oder mehrere Arten nicht von ihrer „typischen" sondern einer Ameisenart besiedelt, die ansonsten für eine andere *Macaranga*-Art an diesem Standort spezifisch war. Zweimal war der normalerweise gefundene Besiedler am Standort nicht vorhanden. Diese relativ seltenen Fälle von „Fehlbesiedlung" scheinen meistens „korrigiert" zu werden, da wir sie bisher selten in großen Bäumen gefunden haben, sondern hauptsächlich in Jungpflanzen. (Dies würde auf ein völlig deterministisches System deuten.) Maximal kamen in unseren Studiengebieten fünf verschiedene *Macaranga*-Arten auf kleinem Raum nebeneinander vor. Mehrfach fanden wir in einem gap direkt nebeneinander in bis zu vier verschiedenen *Macaranga*-Arten entsprechend auch bis zu vier der für sie spezifischen Ameisenarten, was auf sehr differenzierte Wirtsselektions- und effektive Findemechanismen der besiedelnden Königinnen schließen läßt. Auch in sehr insulären Lagen wurde die Spezifität der Assoziation fast immer aufrecht erhalten. Wir wissen allerings noch wenig darüber, ob hier Konkurrenz die entscheidende Rolle spielt oder ob möglicherweise die wechselseitigen Spezialisierungen so stark sind, daß Fehlbesiedlungen nur selten zur Reproduktion der Ameisenkolonie führen.
Neben den ursprünglichen Standorten haben wir auch die Sekundärstandorte untersucht, in denen *Macaranga*-Pflanzen in viel größerer Abundanz und auch in anderen Artenkombinationen auftreten. Unsere bisherigen Daten - bislang hatten wir >1500 Pflanzen von 18 myrmekophytischen *Macaranga*-Arten aus ver-

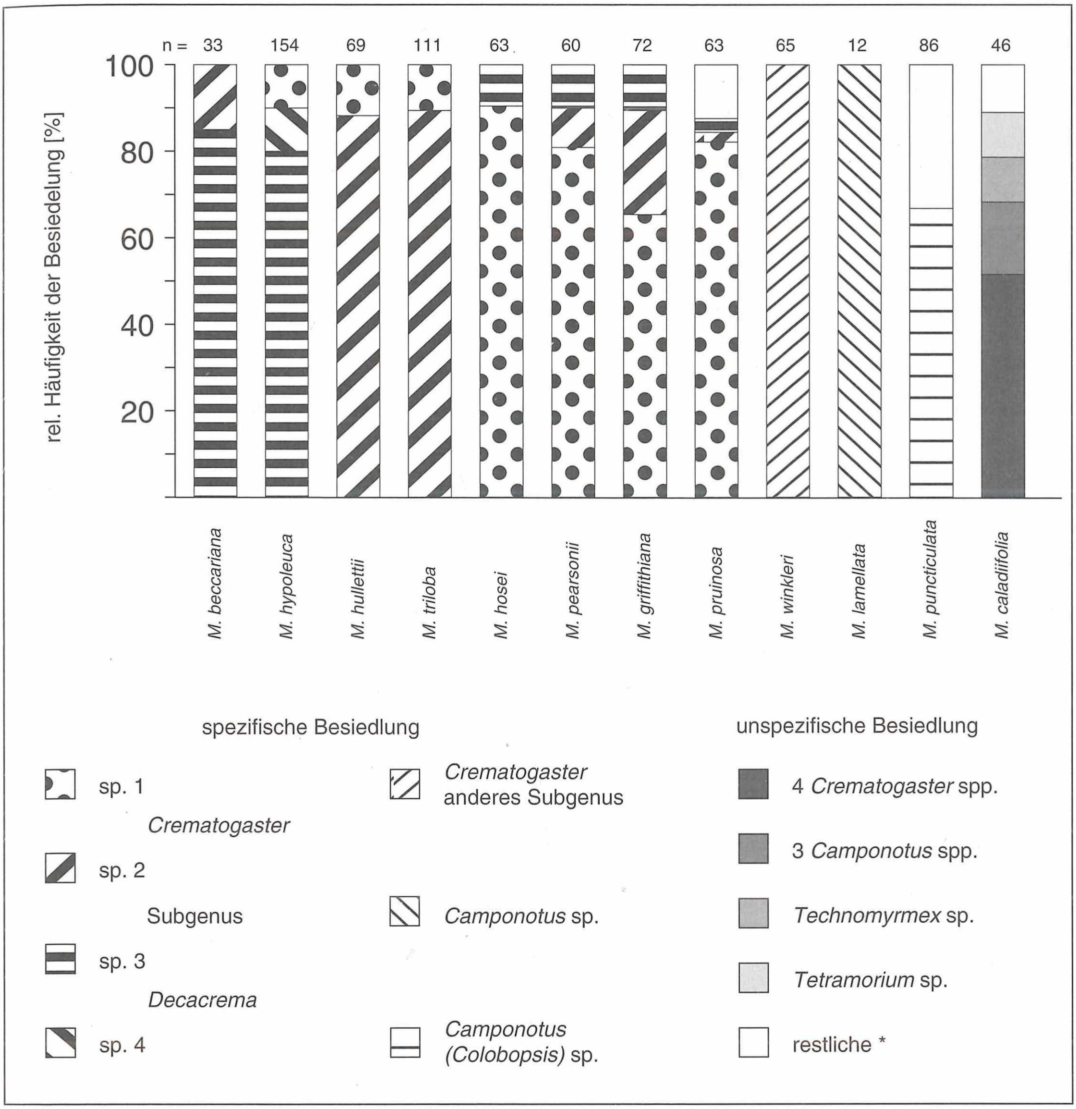

Abbildung 2. Ameisenbesiedlung verschiedener *Macaranga*-Arten. (Darstellung anhand des bisher ausgewerteten Materials.)
* restliche Arten wurden aus Gründen der Übersichtlichkeit nicht aufgeschlüsselt. *M. pruinosa:* 6 weitere Arten aus 4 Gattungen; *M. puncticulata*: 35 Arten aus 14 Gattungen; *M. caladiifolia:* 7 Arten aus 5 Gattungen.

schiedenen geographischen Gebieten auf ihre Ameisenpartner überprüft - ließen generell auf eine recht hohe Spezifität des Beziehungsgefüges auch in anthropogen veränderten Habitaten schließen. Um diesen Datenumfang noch zu erweitern, haben wir zusätzliche qualitative und quantitative Aufsammlungen an Standorten verschiedener Höhenlage und unterschiedlicher anthropogener Störung durchgeführt: in verschiedenen Regionen der Halbinsel Malaysia (Sumpf- bis Gebirgswald), auf Borneo (Sabah, Sarawak, Kalimantan), Sumatra, Java, Bali, Sulawesi und in Thailand. Die Daten zur Besiedlung sind noch nicht vollständig ausgewertet, was neben der großen Materialfülle hauptsächlich auf die taxonomischen Probleme zurückzuführen ist, die sich vor allem bei der Zuordnung der taxonomisch nicht revidierten und z.T. unbeschriebenen Arten der Gattung *Crematogaster* ergeben.

Unsere bisherigen Untersuchungen lassen vermuten, daß die meisten myrmekophytischen *Macaranga*-Arten zu hohem Prozentsatz mit einer spezifischen Ameisenart assoziiert sind (vergl. Abb. 2). Überwiegend handelt es sich um Arten der Gattung *Crematogaster* (meist Untergatt. *Decacrema*). *Macaranga*-Arten, die aufgrund von morphologischen Merkmalen bisher als vermutlich nah verwandt betrachtet werden, weisen anscheinend identische Ameisenspezies auf. Auf diesem Feld gibt es aber noch viele ungeklärte Fragen sowohl hinsichtlich der Pflanzen- als auch der Ameisentaxonomie, und für die Zukunft sind begleitende molekularbiologische Arbeiten geplant.

**Übergangsarten**

Völlig ungeklärt waren die Besiedlungsverhältnisse bei den bisher als Übergangsarten bezeichneten Pflanzenspezies, die hinsichtlich ihres Besiedlungsgrads und ihrer morphologischen Charakteristika von den eindeutigen Myrmekophyten differieren: So besitzen z.B. einige Arten markerfüllte Internodien, die von den Ameisen ausgehöhlt werden müssen; z.T. sind die bei obligaten Myrmekophyten reduzierten EFN noch vorhanden, und die Lokalisation der Nahrungskörper ist wenig konzentriert. Auch sind weniger Individuen dieser Arten oder nur Teilbereiche von ihnen besiedelt, während „echte" Myrmekophyten nach dem Jungpflanzenstadium praktisch immer vollständig bewohnt sind. Nach unserem bisherigen Wissensstand hatten wir z.B. *M. caladiifolia*, *M. puncticulata* und *M. pruinosa* in diese Kategorie eingeordnet (FIALA & MASCHWITZ 1991, 1992). Alle genannten Arten kommen an relativ nährstoffarmen Standorten vor, *M. puncticulata* und *M. pruinosa* syntop in den Sumpfwäldern Westmalaysias.

Bei den genaueren Untersuchungen stellten wir nun fest, daß sich diese Arten in ihrer Besiedlung stark unterscheiden.

*M. caladiifolia* und *M. puncticulata* haben hohle Domatien. Überraschenderweise öffnen sich die von *M. caladiifolia* durch Wachstumsprozesse der Pflanze von selbst: Es entstehen zunächst schlitzförmige, später ovale Öffnungen direkt unterhalb der Internodien. Bei der morphologisch sehr ähnlichen *M. puncticulata* - die von WHITMORE (1975) sogar mit *M. caladiifolia* synonymisiert wurde - ist dies hingegen nicht der Fall, die Eingangsöffnungen müssen bei dieser Art vielmehr von den Ameisen selbst gebissen werden. Beide Pflanzen verfügen im Gegensatz zu anderen myrmekophytischen *Macaranga*-Arten über kohlenhydrathaltige Flüssigkeiten sezernierende EFN an den Blatträndern. Futterkörperchen können bei beiden Arten über die gesamte Pflanzenoberfläche verteilt sein.

Eine ganz anderes Erscheinungsbild findet sich bei *M. pruinosa*. Sie ist markhaltig und muß von den Ameisen ausgehöhlt werden (Taf. 1b), bietet EFN nur auf ganz jungen, dann stets noch unbesiedelten Pflanzen und produziert die Nährkörperchen hauptsächlich konzentriert an den Stipeln.

Lassen sich die Besiedlungsverhältnisse bei diesen Pflanzen mit diesen morphologischen Unterschieden korrelieren? Die markhaltige *M. pruinosa* ist in geringerem Maß besiedelt als viele der anderen obligaten *Macaranga*-Myrmekophyten (85% versus 92-98%; FIALA et al. 1991). In manchen Teilen Borneos und Sumatras wird sie überhaupt nicht von Ameisen kolonisiert. Ihre Besiedlung ist jedoch sehr spezifisch: 84% aller besiedelten Pflanzen waren von *Crematogaster* (*Decacrema)* sp. 1 bewohnt. In geringen Prozentsätzen (alle <4%) fanden wir sechs weitere Internodienbesiedler: die „unspezifisch" nistende, arboreale Ameise *Tetraponera* sp., 2 weitere *Crematogaster*-Arten (nicht Subgenus *Decacrema)*, 1 *Pheidole* sp. und 2 *Camponotus (Colobopsis)* spp. Außer der *Tetraponera* waren alle Besiedler durch bereits vorhandene Öffnungen in die Internodien gelangt.

Die syntop vorkommende *M. puncticulata* war ebenfalls hochspezifisch kolonisiert, allerdings von *Camponotus* (*Colobopsis*) sp. (nahe *saundersi*). Im Unterschied zu den Symbiosen fast aller anderen untersuchten myrmekophytischen *Macaranga*-Arten handelt es sich hier um ein Zweipartnersystem, der sonst übliche 3. Partner - trophobiotische Schildläuse - fehlt. Die hohlen Internodien dieser Art wurden außerdem von einer ganzen Reihe (36 Arten) opportunistischer Ameisenarten bewohnt, die alle durch bereits bestehende Öffnungen (zum großen Teil Verletzungsstellen an den Pflanzen) eingedrungen waren.

Obwohl die normale Besiedlung dieser beiden *Macaranga*-Arten in hohem Maß spezifisch zu sein scheint, bleibt jeweils eine ganze Reihe von Pflanzen gänzlich unbesiedelt bzw. nur teilweise besiedelt, so daß arborealen Ameisen, die opportunistisch verschiedenste Hohlräume zum Nisten nutzen können, mehr Möglichkeit geboten ist, diese Pflanzen zu bewohnen, als dies bei den meisten anderen *Macaranga*-Myrmekophyten der Fall ist.

Auf nochmals völlig andere Verhältnisse stießen wir bei *M. caladiifolia*. Bei den in Bako, Sarawak, untersuchten Pflanzen haben wir bisher keine spezifische Besiedlung feststellen können. Vielmehr wurden die Internodien mit den spontan entstandenen Öffnungen gänzlich unspezifisch von einer Reihe verschiedenster Ameisen besiedelt (14 Arten aus 8 Gattungen und 3 Unterfamilien), wobei aber nur eine Pflanze von zwei verschiedenen Arten bewohnt war. Meist handelte es sich um kleine Kolonien, die nur ein Internodium besetzten.

Auch *M. caladiifolia* wies nie Schildläuse im Innern auf, es handelt sich abweichend zu den *Macaranga*-*Crematogaster*-Assoziationen nur um ein Zweipartnersystem. Die *Crematogaster*-Arten in *Macaranga* waren immer mit trophobiotischen Schildläusen vergesellschaftet. Die beobachteten Schildläuse waren in

Tafel 1. a) *Polyrhachis* sp. an extrafloralen Nektarien von *Leea indica.*

Tafel 1. b) *Crematogaster*-Königin beim Aushöhlen eines Domatiums von *Macaranga pruinosa.*

der Regel spezifisch für *Macaranga* und zeigten eine unerwartet hohe Artenvielfalt: Bisher haben wir 18 verschiedenen Arten gefunden, die z.T. noch unbeschrieben sind. Hier bedarf es noch einer genauen Analyse, ob es sich um spezifische Bindungen zu den Ameisen-Pflanzen-Assoziationen handelt oder eher um Habitatspezifitäten.

Eine weitere Form einer Assoziation konnten wir bei *M. lamellata* in Sarawak entdecken. Diese Art wird ebenfalls spezifisch von einer *Camponotus*-Art (jedoch nicht aus der Untergattung *Colobopsis*) kolonisiert, und sie kommt syntop mit einer Reihe anderer *Macaranga*-Arten vor, die von den „typischen" *Crematogaster*-Spezies besiedelt werden. Im Gegensatz zu der *Camponotus* (*Colobopsis*) auf *M. puncticulata* ist diese *Camponotus* auch wieder mit Schildläusen assoziert. Hier vermuten wir, daß im Unterschied zu den sogenannten „Übergangsarten" wie *M. pruinosa* (und der ähnlichen *M. hosei)* eine bereits voll spezialisierte myrmekophytische *Macaranga*-Art von einer Ameise aus einer ganz anderen systematischen Kategorie als Wirtspflanze übernommen worden ist.

Auch in diesem Fall zeigte sich wieder, daß die Spezifität der Ameisen-Pflanzen-Interaktion dann besonders ausgeprägt ist, wenn der Wohnraum aktiv erschlossen werden muß.

Völlig unklar ist vorerst die biologische Basis der Spezifität der Besiedlung - und zwar sowohl auf der Ebene der unmittelbaren wirkenden Mechanismen wie der zugrundeliegenden Ursachen. Es ist anzunehmen, daß chemischen Signalen entscheidende Bedeutung bei der Wirtsfindung zukommt. Nach wie vor völlig unbekannt ist, was die Ameisen daran hindert, andere als die von ihnen normalerweise bewohnten *Macaranga*-Arten zu besiedeln, bzw. was sie möglicherweise - beim Versuch der Besiedlung - den anderen auf die jeweiligen *Macaranga*-Arten spezialisierten Ameisenarten in der Konkurrenz unterlegen macht. Unklar ist auch, ob beide Partner in gleicher Weise von der exklusiven Bindung profitieren oder ob die Vorteile vor allem auf einer Seite liegen, von der dann auch der höhere Selektionsdruck auf die Beibehaltung dieser spezifischen Beziehung kommen dürfte. Wir haben inzwischen begonnen, diesen Fragen in Freiland- und Laborversuchen nachzugehen, z.B. durch Besiedlungsexperimente an nachgezogenen *Macaranga*-Arten, genetische Analysen der beteiligten Partner zur Aufklärung der phylogenetischen Verwandschaftsverhältnisse sowie durch chemische Analysen sekundärer Inhaltsstoffe und Nährstoffanalysen der Futterkörperchen.

## Fazit

*Macaranga* kann in vielfacher Weise als Analogon zu der neotropischen Baumgattung *Cecropia* betrachtet werden, in der ebenfalls zahlreiche Assoziationen mit Ameisen vorkommen. *Cecropia* weist ebenfalls überwiegend schnellwüchsige Pionierarten auf und besiedelt meist lichtreiche Sekundärhabitate. Auch bei *Cecropia* wird durch neueste Untersuchungen immer deutlicher, daß die Assoziationen mit Ameisen sehr vielfältig sind und eine Reihe verschiedener Ameisenarten und -gattungen einbeziehen. Dominierend sind jedoch Arten der Dolichoderine *Azteca*. Da in diese Gattung im Gegensatz zu *Crematogaster* inzwischen einiges taxonomische Licht gebracht wurde (LONGINO 1991), liegen bereits umfangreiche Daten zu Spezifität der Assoziationen und auch zu Standorteinnischungen vor. Es bestehen sehr viele Ähnlichkeiten zu den Ameisenassoziationen in *Macaranga,* doch es zeigen sich auch überraschende Differenzen zu diesem System. So ist z.B. anscheinend bei *Macaranga* bewohnenden Ameisen eine viel höhere Wirtsspezifität verwirklicht, während bei *Cecropia* Habitatspezifität eine große Rolle zu spielen scheint (HARADA & BENSON 1988, LONGINO 1989). Da die evolutive Geschichte symbiotischer Ameisen-Pflanzen-Systeme anscheinend weitgehend unabhängig in den biogeographischen Regionen verlaufen ist (DAVIDSON & MCKEY 1993), können Vergleiche zwischen den Kontinenten generelle Einsichten in die evolutionäre Dynamik solcher Systeme liefern.

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KRZYSZTOF ROŚCISZEWSKI & ULRICH MASCHWITZ

# Prey specialization of army ants of the genus *Aenictus* in Malaysia

**Abstract**
Army ants of the genus *Aenictus* in the investigation area Pasoh Forest Reserve (Malaysia, Negeri Sembilan) are specialized on other ants as food source. This is also true for *A. gracilis* EMERY und *A. laeviceps* (F. SMITH), for which a much wider food spectrum is known from the Philippines. Prey could be taken off in 9 of 11 species (4 of them hitherto undescribed) found in the area. The different prey spectrum of each *Aenictus* species indicates resource partitioning, which is shown in preference of particular taxa, strata and prey size. These factors are described and discussed. A list of the prey species is included. An attack of *Aenictus dentatus* FOREL on a *Pheidole* species is described in detail.

**Kurzfassung**
**Beutespezialisierung der Treiberameisen der Gattung *Aenictus* in Malaysia**
Im Untersuchungsgebiet Pasoh Forest Reserve (Malaysi Negeri Sembilan) lebende Treiberameisen der Gattung *Aenictus* sind auf andere Ameisen als Nahrungsquelle spezialisiert. Dies gilt auch für *A. gracilis* EMERY und *A. laeviceps* (F. SMITH), für die von den Philippinen ein viel breiteres Nahrungsspektrum bekannt ist. Bei 9 von insgesamt 11 gefundenen Arten – von denen 4 bislang unbeschrieben sind – konnte Beute entnommen und identifiziert werden. Das für jede *Aenictus*-Art unterschiedliche Artenspektrum von Beuteobjekten deutet auf eine Ressourcen-Teilung hin. Sie äußert sich in Bevorzugung bestimmter Taxa, Strata und Beutegröße. Dieses wird beschrieben und diskutiert. Eine Liste der Beutearten ist aufgeführt. Ein Überfall von *Aenictus dentatus* FOREL auf eine *Pheidole*-Art wird detailliert beschrieben.

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## 1. Introduction

The genus *Aenictus* occurs both in the Indo-Australian region and in tropical Africa, with its centre of distribution in South-East Asia. WILSON (1964) in his revision listed 34 species for the Indo-Australian region. In the last years three new species from Sumatra were described (TERAYAMA & YAMANE 1989), and additional three from Thailand and Vietnam (TERAYAMA & KUBOTA 1993). It is supposed, that all members of this genus are predominantly or exclusively specialized on other ants as prey (CHAPMAN 1964, GOTWALD 1976, 1978, 1982, SCHNEIRLA & REYES 1966, WILSON 1964). However, the extent of the specialization on particular ant species is not known. Solely for *A. gracilis* and *A. laeviceps* some data exist. Both species were investigated by CHAPMAN (1964) and SCHNEIRLA & REYES (1966) in the Philippines. According to these autors, both species have very wide prey spectra, including many arthropodes (spiders, wasps), as well as other invertebrates (earthworms), with other ants being the most common prey. Both species hunt similar prey, that of *A. gracilis* being in general smaller than that of *A. laeviceps*, but with a wide degree of overlapping (SCHNEIRLA & REYES 1966). CHAPMAN (1964) gives a list of ant species taken as prey by both *Aenictus* species in the Philippines (tab. 1), without differentiating between *A. gracilis* and *A. laeviceps*.

Eleven species of *Aenictus* were found in the investigated area in Pasoh Forest Reserve. We presumed resource partitioning as one way to maintain sympatric occurrence of them. We investigated therefore more closely the prey spectra of the Aenictus species recorded in this area.

## 2. Study sites and methods

Most of the observations were made in Pasoh Forest Reserve, a primary lowland rain forest in the state Negeri Sembilan, managed by the Forest Research Institute of Malaysia (FRIM). In the results are also included data gained in the environs of Ulu Gombak and (in one case of *A. camposi*) of Sekinchan, both in the state Selangor.

Pasoh Forest Reserve is one of the few remaining fragments of the primary lowland rain forest in Peninsular Malaysia. It lies about 140 km south-east of Kuala Lumpur (2°59' N, 102°19' E) and consists of a core area of 650 ha of a primary lowland mixed dipterocarp forest surrounded by another 650 ha of buffer zone of partly regenerated and partly virgin forest. A further about 1000 ha of primary hill dipterocarp forest rises to about 600 m a.s.l. to the east. Except for this slope, the terrain is relatively flat with an altitude of 90 m (MANOKARAN & KOCHUMMEN 1990, MANOKARAN et al. 1990). The soils are mainly loamy or sandy clay, the pH is 4,3-4,8 (ALLBROOK 1973). Climate data were recorded between 1970 and 1974 (SOEPADMO 1978, AOKI et al., 1978). The annual rainfall varied between 1728 mm and 3112 mm with a mean value of 2054 mm. The months April-May and November-December were relatively wet (250-300 mm rainfall), February-March and July-August relatively dry (30-100 mm rainfall). Somewhat different are data from the nearest meteorological station at Kuala Pilah (about 25 km distance). A mean annual rainfall of 1850 mm is recorded with rain fairly evenly distributed throughout the year,

Table 1. Ant species taken as prey by *Aenictus gracilis* and *A. laeviceps* in the Philippines (CHAPMAN 1964).

Ponerinae
*Ponera* sp.

Myrmicinae
*Crematogaster* sp.
*Ischnomyrmex longipes* EMERY
*Myrmicaria brunnea*
    subsp. *subcarinata* EMERY
*Pheidole* sp.
*Pheidologeton diversus* JERDON
*Pristomyrmex* sp.
*Tetramorium* sp.

Dolichoderinae
*Dolichoderus bituberculatus* MAYR

Formicinae
*Acropyga molucca* MAYR
*Acantholepis chapmani* WHEELER
*Anoplolepis longipes* JERDON
*Camponotus carin* EMERY
*Camponotus leonardi* EMERY
*Camponotus* sp.
*Echinopla* sp.
*Paratrechina longicornis* LATR.
*Polyrhachis armata* LEGUILLOU
*Polyrhachis bihamata* DRURY
*Polyrhachis* (*Myrma*) sp.
*Polyrhachis* sp.

except that monthly rainfall is less than 100 mm in June (MANOKARAN & KOCHUMMEN 1990). Monthly mean temperature in Pasoh 3 m above the ground was 23,0 °C (range 17,5-29,7 °C) in the forest and 24,8 °C (range 19,6-35,9 °C) at the base camp (SOEPADMO 1978, AOKI et al. 1978).

The second locality, Ulu Gombak Field Studies Centre, is a research station of the University of Malaya near Kuala Lumpur (3°19' N, 101°45' E) at an altitude of 220 m. The area is covered with secondary lowland dipterocarp forest. At various locations bamboos were dominant as a result of previous logging (MASCHWITZ et al. 1989).

The third locality (one observation only) is a peat swamp forest near Sekinchan, Selangor, at the west coast of the peninsula (about 3°30' N, 101° E).

To investigate the prey spectra of the army ants their raids were observed whenever encountered, and the visible booty items were picked out. To lesser extent this was done also during emigrations, as probably all encountered *Aenictus* colonies were in the migratory phase and transported the food to new bivouac sites. Almost all of the booty items were taken off from the columns of *Aenictus*. Especially attention was paid to the imagines of prey species. Some were collected directly from attacked colonies, when it was clear, that imagines of these colonies were taken as prey by the army ants (i.e. they were killed and transported away).

The field work was done by K. R. Specimens are deposited in Staatliches Museum für Naturkunde Karlsruhe, Germany, and in the entomological collection of the Forest Research Institute of Malaysia (FRIM), Kepong, Kuala Lumpur. The new species of *Aenictus* will be described elsewere.

## 3. Results

In the investigated area (about 25 ha) in Pasoh Forest Reserve a total of 11 species of *Aenictus* was found, four of them undescribed (TERAYAMA, personal com.). They are: *A. aratus* FOREL, *A. camposi* WHEELER & CHAPMAN, *A. cornutus* FOREL, *A. dentatus* FOREL, *A. gracilis* EMERY, *A. hottai* TERAYAMA & YAMANE, *A. laeviceps* (F. SMITH), *Aenictus* sp. n. [near *laeviceps*], *Aenictus* sp. n. 2, *Aenictus* sp. n. 3, *Aenictus* sp. n. 5. This is somewhat less than 30% of the known species number of this genus, and quite a high number of army ants for the small area, though the nomadic habit and comparatively long collecting period (6,5 months) must be considered.

Booty of 9 species of *Aenictus* could be collected. They all seem to be specialized on other ants as food. From 1062 prey items taken off only 4 were no ants. (1 small spider in *A. laeviceps*, 1 leaf hopper in *Aenictus* sp. n. [near *leaviceps*], and 2 unidentified larvae in *Aenictus* sp. 2). However, it was observed, that during an attack of *Aenictus* sp. n. 3 on a nest of *Acropyga acutiventris* and *A. gracilis* on *Acropyga* sp. 3, trophobiontic Homoptera which have been within the prey species' nest, were taken, too.

53 ant species were found as prey of *Aenictus* spp. According to our observations both brood and imagines are taken as prey. All prey species listed in table 2 were determinated by the imagines, solely *Odontomachus* sp. was recognized by the heads of the pupae.

The prey spectrum of each *Aenictus* species is clearly different. This is also true for the three epigeicly foraging species *A. gracilis*, *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*] – species from which the highest numbers of food items were taken off.

Some specialization of the *Aenictus* species can be noticed. Particularly, species of the four most epigeic species *cornutus*, *gracilis*, *laeviceps* and sp. n. [near *laeviceps*] possess, despite of quite a wide prey spectrum, at most one prey species in common. Noticeable is also the difference between *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*], especially the „predilection" of the last for *Pseudolasius*. In 10 of 13 raids *Pseudolasius* was stated as prey, in seven raids *Pseudolasius* sp. 5. On the contrary, none of the *Pheidole* species was stated, although they occurred with great constancy as prey of *A. laeviceps* (in 5 of 8 raids). Whether *A. aratus* may be specialized on *Pheidole* spp. as prey, as suggested by the few data, must be proofed by more observations. Taxonomic preferences at the subfamily level are recognizable in *A. camposi* (small Formicinae) and *A. gracilis* (Formicinae and Dolichoderinae).

Looking closely to the prey species it seems, that some of them are especially suitable as prey. For example *Technomyrmex* sp. 8 and *Camponotus* sp. 4 were taken by three *Aenictus* species.

Table 2. Ant species found as prey for the respective *Aenictus* species (marked with a „+"). Frequency of occurrence and locality (if different than Pasoh) of the prey species is indicated in parentheses, G: Gombak, S: Sekinchan. *Aenictus* species numbers refer to the following species: 1-*aratus*, 2-*camposi*, 3-*cornutus*, 4-*dentatus*, 5-*gracilis*, 6-*hottai*, 7-*laeviceps*, 8-sp. n. [near *laeviceps*], 9-sp. n. 3. The number of raids (or emigrations after a raid) of which booty was taken off, is indicated in parentheses below the species numbers. Included are raids from Gombak (*Aenictus aratus*: 1; *camposi*: 1; *dentatus*: 1; *gracilis*: 12; *laeviceps*: 1, sp. n. [near *laeviceps*]: 1; and Sekinchan (*camposi*: 1).

| | *Aenictus*-species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| prey species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| | (3) | (6) | (2) | (7) | (12) | (1) | (8) | (13) | (1) |
| Ponerinae | | | | | | | | | |
| *Hypoponera* sp.3 | | | | | | | | +(1) | |
| *Odontomachus* sp. | | | | | | +(1) | | | |
| Myrmicinae | | | | | | | | | |
| *Crematogaster* sp.5 | | | | | | | +(1) | | |
| *Crematogaster* sp.8 | | | +(1) | | | | | | |
| *Crematogaster* sp.19 | | | | | | | | +(1) | |
| *Pheidole longipes* | | | | +(1) | | | +(2) | | |
| *Pheidole comata* | | | | +(1) | | | | | |
| *Pheidole* sp.3 | | | | +(2) | | | | | |
| *Pheidole* sp.4 | +(1:G) | | | +(2) | | | | | |
| *Pheidole* sp.6 | | | | +(2) | | | | | |
| *Pheidole* sp.8 | +(2) | | | | | | | | |
| *Pheidole* sp.17 | | | | +(1) | | | | | |
| *Pheidole* sp.18 | | | | | | | +(1) | | |
| *Pheidole* sp.19 | | | +(1) | | | | +(1) | | |
| *Pheidole* sp.G-1 | | | | | | | +(1:G) | | |
| Dolichoderinae | | | | | | | | | |
| *Technomyrmex* sp.1 | | | | +(1) | | | | +(1) | |
| *Technomyrmex* sp.4 | | | | | +(1:G) | | | | |
| *Technomyrmex* sp.7 | | | | | +(4:G) | | | | |
| *Technomyrmex* sp.8 | | | +(1) | +(1:G) | +(5:G) | | | | |
| *Technomyrmex* sp.9 | | | +(2) | | | | | | |
| *Technomyrmex* sp.G-1 | | | | | +(6:G) | | | | |
| *Technomyrmex* sp.G-2 | | | | | +(2:G) | | | | |
| *Technomyrmex* sp.G-3 | | | | | +(3:G) | | | | |
| Formicinae | | | | | | | | | |
| *Acropyga acutiventris* | | | | | | | | | +(1) |
| *Acropyga* sp.3 | | | | | +(2:G) | | | | |
| *Euprenolepis procera* | | | | +(2,1:G) | | | | +(1) | |
| *Euprenolepis* sp.2 | | | | +(1) | | | | | |
| *Paratrechina* sp.1 | | +(3) | | | +(2:G) | | | | |
| *Paratrechina* sp.2 | | +(2,1:S) | | | | | | | |
| *Paratrechina* sp.4 | | +(2) | | | | | | | |
| *Paratrechina* sp.7 | | +(2) | | | | | | | |
| *Paratrechina* sp.8 | | +(1) | | | | | | | |
| *Paratrechina* sp.G-1 | | | | | +(1:G) | | | | |
| *Paratrechina* sp.G-2 | | | | | +(1:G) | | | | |
| *Prenolepis naoroji* | | +(1:G) | | | | | | +(1) | |
| *Prenolepis* sp.2 | | | | | +(3:G) | | +(1:G) | | |
| *Pseudolasius* sp.4 | | | | | | | | +(1) | |
| *Pseudolasius* sp.5 | | | | | | | | +(7,1:G) | |
| *Pseudolasius* sp.6 | | | | | | | | +(1) | |
| *Camponotus* sp.4 | | | | +(1) | | | +(1:G) | +(1) | |
| *Camponotus* sp.19 | | | | | | | +(2) | | |

| prey speci | *Aenictus*-species<br>1<br>(3) | <br>2<br>(6) | <br>3<br>(2) | <br>4<br>(7) | <br>5<br>(12) | <br>6<br>(1) | <br>7<br>(8) | <br>8<br>(13) | <br>9<br>(1) |
|---|---|---|---|---|---|---|---|---|---|
| *Camponotus* sp.25 | | | | | | | +(1) | | |
| *Camponotus* sp.29 | | | | | | | | +(1) | |
| *Camponotus* sp.30 | | | | | | | +(1) | | |
| *Polyrhachis bicolor* | | | | | | | +(2) | | |
| *Polyrhachis rufipes* | | | | | | | +(1) | | |
| *Polyrhachis schang* | | | | | | | +(1) | | |
| *Polyrhachis striata* | | | | | | | | +(1) | |
| *Polyrhachis* sp.13 | | | | | | | +(1) | | |
| *Polyrhachis carbonaria* | | | | | | | +(1) | | |
| *Polyrhachis* sp.27 | | | | | | | +(1) | | |
| *Polyrhachis* sp.29 | | | +(1) | | | | | | |
| *Polyrhachis* sp.31 | | | | | | | +(1) | | |

Table 3. Nest sites of prey species in Pasoh: A: ground stratum (soil, litter and dead wood on the ground), B: low arboreal stratum (hanging dead wood, tree trunks, silk- and carton nests etc. up to approx. 3 m height), C: high arboreal stratum (from approx. 3 m height up to the top of the canopies).

| prey species | stratum | nest site (n) |
|---|---|---|
| Ponerinae | | |
| *Hypoponera* sp.3 | A[2] | |
| *Odontomachus* sp. | A[2] | |
| Myrmicinae | | |
| *Crematogaster* sp.5 | B | under bark (1) |
| *Crematogaster* sp.8 | ? | |
| *Crematogaster* sp.19 | | |
| *Pheidole longipes* | A | dead wood (3) |
| *Pheidole comata* | A | soil (2) |
| *Pheidole* sp.3 | A | dead wood (4) |
| *Pheidole* sp.4 | ? | |
| *Pheidole* sp.6 | A | soil (2) |
| *Pheidole* sp.8 | A | dead wood, litter (9) |
| *Pheidole* sp.17 | ? | |
| *Pheidole* sp.18 | | |
| *Pheidole* sp.19 | | |
| *Pheidole* sp.G-1 | | |
| Dolichoderinae | | |
| *Technomyrmex* sp.1 | A | dead wood, litter (3) |
| *Technomyrmex* sp.4 | B | dead wood, under bark (3) |
| *Technomyrmex* sp.7 | B[1] | foliage (1) |
| *Technomyrmex* sp.8 | ? | |
| *Technomyrmex* sp.9 | | |
| *Technomyrmex* sp.G-1 | | |
| *Technomyrmex* sp.G-2 | | |
| *Technomyrmex* sp.G-3 | | |
| Formicinae | | |
| *Acropyga acutiventris* | A | dead wood (3) |
| *Acropyga* sp.3 | A | soil (1) |
| *Euprenolepis procera* | A | dead wood, leaf litter (7) |
| *Euprenolepis* sp.2 | A | soil (1) |
| *Paratrechina* sp.1 | A | dead wood, litter (9) |
| *Paratrechina* sp.2 | ? | |
| *Paratrechina* sp.4 | | |
| *Paratrechina* sp.7 | A | dead wood (1) |
| *Paratrechina* sp.8 | B | epiphyte (1) |
| *Paratrechina* sp.G-2 | ? | |
| *Prenolepis naoroji* | | |
| *Prenolepis* sp.2 | | |
| *Pseudolasius* sp.4 | A[2] | |
| *Pseudolasius* sp.5 | A[2] | |
| *Pseudolasius* sp.6 | A[2] | |
| *Camponotus* sp.4 | A | litter (1) |
| *Camponotus* sp.19 | C | foliage (silk nest) (3) |
| *Camponotus* sp.25 | ? | |
| *Camponotus* sp.29 | | |
| *Camponotus* sp.30 | C | dead wood |
| *Polyrhachis bicolor* | BC | foliage (silk nest) (2) |
| *Polyrhachis rufipes* | B | dead wood (2) |
| *Polyrhachis schang* | BC | foliage (silk nest) (2) |
| *Polyrhachis striata* | A | dead wood, litter, soil (4) |
| *Polyrhachis* sp.13 | ? | |
| *Polyrhachis carbonaria* | AB | dead wood, soil (2) |
| *Polyrhachis* sp.27 | ? | |
| *Polyrhachis* sp.29 | | |
| *Polyrhachis* sp.31 | B | foliage (silk nest) (5) |

[1] One colony was found in approx. 3 m height between leaves.

[2] No nests of these species were found, but all representatives of these genera were found in Pasoh in the ground stratum.

Table 4. Body size of *Aenictus* spp. and their prey species (total lengths). Data behind the diagonal stroke refer to soldiers. A horizontal stroke marks polymorphic species without a differentiate soldier caste.

| *Aenictus* sp. (length [mm]) | prey sp. | length [mm] |
|---|---|---|
| *aratus* (3.8) | *Pheidole* sp.4 | 3.0/5.0 |
| | *Pheidole* sp.8 | 1.9/3.0 |
| *camposi* (2.5) | *Paratrechina* sp.1 | 2.2 |
| | *Paratrechina* sp.2 | 1.4 |
| | *Paratrechina* sp.4 | 1.3 |
| | *Paratrechina* sp.7 | 1.6 |
| | *Paratrechina* sp.8 | 2.0 |
| | *Prenolepis naoroji* | 2.9 |
| *cornutus* (4.3) | *Crematogaster* sp.8 | 3.0 |
| | *Pheidole* sp.19 | /3.4 |
| | *Technomyrmex* sp.8 | 3.1 |
| | *Technomyrmex* sp.9 | 4.4 |
| | *Polyrhachis* sp.29 | 5.8 |
| *dentatus* (4.7) | *Pheidole longipes* | 5.5/7.5 |
| | *Pheidole comata* | 5.0/7.5 |
| | *Pheidole* sp.3 | 3.0/5.0 |
| | *Pheidole* sp.4 | 3.0/5.0 |
| | *Pheidole* sp.6 | 3.0/6.2 |
| | *Pheidole* sp.17 | /3.2 |
| | *Technomyrmex* sp.1 | 3.0 |
| | *Technomyrmex* sp.8 | 3.1 |
| | *Euprenolepis procera* | 4.5-6.0 |
| | *Euprenolepis* sp.2 | 4.2-5.8 |
| | *Camponotus* sp.4 | 9.5/12.8 |
| *gracilis* (4.0) | *Technomyrmex* sp.4 | 2.4 |
| | *Technomyrmex* sp.7 | 4.1 |
| | *Technomyrmex* sp.8 | 3.1 |
| | *Technomyrmex* sp.G-1 | 2.5 |
| | *Technomyrmex* sp.G-2 | 2.6 |
| | *Technomyrmex* sp.G-3 | 2.6 |
| | *Acropyga* sp.3 | 2.0 |
| | *Paratrechina* sp.1 | 2.2 |
| | *Paratrechina* sp.G-1 | 3.2 |
| | *Paratrechina* sp.G-2 | 1.9 |
| | *Prenolepis* sp.2 | 3.9 |
| *hottai* (5.2) | *Odontomachus* sp. | 10.0[1] |
| *laeviceps* (4.1) | *Crematogaster* sp.5 | 2.3-4.9 |
| | *Pheidole longipes* | 5.5/7.5 |
| | *Pheidole* sp.18 | /3.2 |
| | *Pheidole* sp.19 | /3.4 |
| | *Pheidole* sp.G-1 | 2.3 |
| | *Prenolepis* sp.2 | 3.9 |
| | *Camponotus* sp.4 | 9.5/12.8 |
| | *Camponotus* sp.19 | 5.2 |
| | *Camponotus* sp.25 | 4.8 |
| | *Camponotus* sp.30 | 7.4/9.0 |
| | *Polyrhachis bicolor* | 6.2 |
| | *Polyrhachis rufipes* | 6.4 |
| | *Polyrhachis schang* | 6.2 |
| | *Polyrhachis* sp.13 | 6.8 |
| | *Polyrhachis* sp.20 | 6.5 |
| | *Polyrhachis* sp.27 | 6.0 |
| | *Polyrhachis* sp.31 | 4.3 |
| sp. n. [near *laeviceps*] (4.2) | *Hypoponera* sp.3 | 2.6 |
| | *Crematogaster* sp.19 | 1.7 |
| | *Technomyrmex* sp.1 | 3.0 |
| | *Euprenolepis procera* | 4.5-6.0 |
| | *Prenolepis naoroji* | 2.9 |
| | *Pseudolasius* sp.4 | 3.3/5.1 |
| | *Pseudolasius* sp.5 | 3.5/4.9 |
| | *Pseudolasius* sp.6 | /4.4 |
| | *Camponotus* sp.4 | 9.5/12.8 |
| | *Camponotus* sp.29 | 8.5/11.5 |
| | *Polyrhachis striata* | 10.8 |
| sp. n.3 (2.9) | *Acropyga acutiventris* | 3.8 |

Both species of *Odontomachus* found in Pasoh Forest Reserve (*O. rixosus* F. SMITH and *O. simillimus* F. SMITH) have a total length of about 10 mm.

Beside of preferences for certain taxa as prey, spatial distribution of the army ants and their prey species may also have an influence of the prey spectrum of *Aenictus*. With regard to their extranidal activities the observed species of *Aenictus* can be divided in two groups. The first group are epigeic active species, to which belong *A. cornutus*, *gracilis*, *laeviceps* and sp. n. [near *laeviceps*]. The raids and emigrations are proceeded by them on the soil, litter, and wood. To the second group – hypogeic active species – belong all other representatives of this genus. They perform raids and emigrations below roots, in subterranean cavities, and under the litter and usually appear on the surface for short distances, only. This separation does not hold comparing foraging behavior, at the front of the raids. The epigeic species are active then also under the litter, searching for prey, and at least some hypogeic *Aenictus* pursue their prey also quite high on tree trunks. Thus, for example, *A. hottai* was seen at a height of about 3 m on a tree stem, apparently foraging, whereas *A. dentatus* likewise pursued fleeing *Pheidole* several meters high on a tree trunk. In this context the nesting sites of the prey ants are interesting. They are shown in table 3.

As expected all registered prey ants of the hypogeic group of *Aenictus* nest in the ground stratum. In contrast the epigeic active *Aenictus* species seem to prefer distinct strata to forage. It seems to be least pronounced in *A. gracilis*. Successful foraging of this spe-

Table 5. Body size of *Aenictus* spp. and their prey species: total lengths of *Aenictus* spp., arithmetic means of the total lengths of prey species (± standard deviation [SD], soldiers omitted, species without differentiated soldiers averaged), and ratio between the two quantities. Data ordered after increasing size of the *Aenictus* spp.

| *Aenictus* sp. | *Aenictus* length [mm] | prey length ($\bar{x}$ ± SD [mm]) | ratio prey length/ *Aenictus* length |
|---|---|---|---|
| *camposi* | 2.5 | 1.9 ± 0.6 | 0.76 |
| sp. n.3 | 2.9 | 3.8 | 1.31 |
| *aratus* | 3.8 | 2.5 ± 0.8 | 0.66 |
| *gracilis* | 4.0 | 2.8 ± 0.7 | 0.70 |
| *laeviceps* | 4.1 | 5.6 ± 1.7 | 1.37 |
| sp. n. [near *laeviceps*] | 4.2 | 5.1 ± 3.3 | 1.21 |
| *cornutus* | 4.3 | 4.1 ± 1.3 | 0.95 |
| *dentatus* | 4.7 | 4.5 ± 2.1 | 0.96 |
| *hottai* | 5.2 | 10.0 | 1.92 |

cies was observed as well in the litter as on tree trunks and lianas in the B-stratum. *A. laeviceps* showed a distinct preference of the arboreal strata, whereas *Aenictus* sp. n. [near *laeviceps*] was obviously restricted to the ground stratum while foraging. Data relating to foraging behavior are unfortunately lacking for *A. cornutus*. The foraging activity is apparently not restricted to particular nest sites of the prey species, but rather to a particular stratum as whole.

Another factor which may influence the prey selection of *Aenictus* is the body size. According to SCHNEIRLA & REYES (1966) the prey of (somewhat smaller) *A. gracilis* is in general smaller than that of *A. laeviceps*. Prey ants of the neotropical Ecitoninae range up to 1.5 times the length of the largest army ant workers (RETTENMEYER et al. 1983). Table 4 gives a survey about the total lengths of *Aenictus* and their prey species. The length was measured on single, apparently average specimens in dorsal view from the tip of the mandibles to the end of the gaster. If the specimens were not outstretched, measurements were made in two or three planes and the results were summed.

Arithmetic means of the body size of the prey species and their ratio to the body size of *Aenictus* spp. are shown in table 5.

It seems, that generally the larger species of *Aenictus* take indeed bigger prey on average than smaller ones. However, the correlation is rather poor. The correlation coefficient is significant if all *Aenictus* species are taken into account ($r = 0.735$, $P < 0.05$), but not significant if both species with single observations (*Aenictus* sp. n. 3 and *A. hottai*) are omitted ($r = 0.705$, n.s.). Noticeable is the difference between *A. gracilis* and *A. laeviceps*, the average prey size of the latter being two times bigger than of the former species. Compared with its own length *A. gracilis*, beside of *A. aratus* and *A. camposi*, take the smallest prey species. Generally the prey species are smaller or only slightly longer than their predators (see tab. 4 and 5). However, in some cases the prey's length is more than two times the length of the *Aenictus*: *Polyrhachis striata* and *Camponotus* sp. 4 in *Aenictus* sp. n. [near *laeviceps*], and *Camponotus* sp. 4 in *A. laeviceps*.

Though specialized on ants, *Aenictus* species did not take all ant species as prey. They ignored many species, showed avoidance behavior, particularly against other army ants, and sometimes became prey themselves, as show the following observations:

1. Ignoring of other ants during a raid or emigration:
   - *Dolichoderus* sp. 1, *Crematogaster* sp. 3, and *Meranoplus* sp. were completely ignored by *A. gracilis* during a raid, although their trails intersected with the trails of the other ant species.
   - Individuals of *Polyrhachis* sp. and *Diacamma* sp. went repeatedly on the same branches as *A. gracilis*, without provoking any attack.
   - The same observation was also made for *Polyrhachis* sp. 16 and *A. laeviceps.*
   - An unidentified ant male fell in a column of *A. gracilis*, but could withdraw without difficulties.
   - A single worker of *Odontomachus rixosus*, which was tentatively placed into a raid of *A. hottai*, was not attacked and could retire without difficulties. (In one case brood of *Odontomachus* was found to be booty of *A. hottai*. Possibly the imagines of this species are not regarded as prey, at least outside of the nest area. This is also known from other investigated species of *Aenictus* in Afrika; GOTWALD 1976, 1982).
   - An emigration column of *A. cornutus* ran partly on the same route as a trail of *Cataulacus insularis*. No aggression was observed, although single *Cataulacus* went into the *Aenictus* column.

Plate 1. a) Encounter of two army ant raids: *Aenictus camposi* (yellow) and *Aenictus* sp. n. [near *laeviceps*] (black). The raids have been temporarily interrupted but no hostilities occurred. Eventually both species changed the routes and continued their raids; Photograph: ROŚCISZEWSKI.

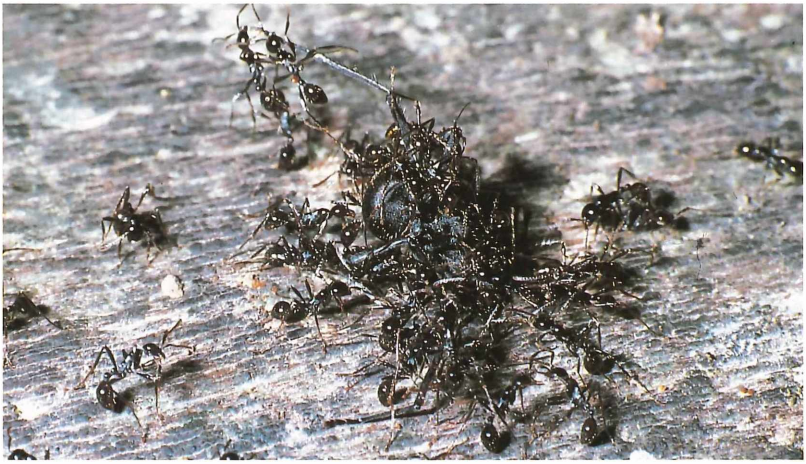

Plate 1. b) *Aenictus* sp. n. [near *laeviceps*] killing during a raid a worker of *Polyrhachis striata*, one of the prey species; Photograph: ROŚCISZEWSKI.

Plate 1. c) Nest evacuation of a prey species (apparently belonging to the tribe Prenolepidini: *Paratrechina* sp., *Prenolepis* sp. or *Euprenolepis* sp.) after detection of their nest by *Aenictus;* Photograph: MASCHWITZ.

2. Ignoring of other ants despite of disturbances caused by them:
   - A raid of *A. gracilis*, as well as one of *Aenictus* sp. n. [near *laeviceps*] was disturbed by *Lophomyrmex bedoti*, which stood on both sides of the *Aenictus* trail. Occasionally short fights with the *Aenictus* „guards" setting against them occurred, but generally the army ants behaved very passive.
   - In similar way a raid of *A. gracilis* was disturbed by *Gnamptogenys* sp.
3. Avoidance behavior:
   - A raid of *Aenictus* sp. n. [near *laeviceps*] was forced by *Paratrechina* sp. 8 to change its route by gathering and blocking the stretch. The same species of *Paratrechina* was found to be the prey of *A. camposi*.
   - During a contact of a raid of *A. hottai* with an emigration column of *Leptogenys* cf. *borneensis* there were no hostilities: The ants of both colonies got out of the way after short hesitation.
   - During an encounter between raid columns of *A. camposi* and *Aenictus* sp. n. [near *laeviceps*] no agressions were observed. Both species changed their trails in such a way, that these did not intersect (*Aenictus* sp. n. [near *laeviceps*] used a „bridge" of litter, whereas *A. camposi* continued on the soil: plate 1a).
4. *Aenictus* as prey of other ants:
   - Workers of *Oecophylla smaragdina* (mostly several individuals) were repeatedly observed picking out single workers of *A. gracilis* from the trail, killing, and carrying them to the nest.
   - *Odontoponera transversa* picked up single individuals from the trails of *A. hottai* and *A. cornutus*.

CRAWLEY (1924, cited after CHAPMAN 1964) describes an attack of *A. aitkeni* var. *dentata* FOREL (= *dentatus* FOREL: WILSON 1964) on a colony of *Pheidole plagearia* F. SMITH nesting in the roof of a house. According to him only brood was taken as prey, but no imagines. This does not at all agree with our observations. We therefore describe here an attack of *A. dentatus* on two nests of *Pheidole comata* F. SMITH, which took place on February 13, 1990 from 11 until 13 o'clock:
The *Aenictus* ran preferably below, but sometimes also on the litter – searching for the prey in the litter. Under the roots of a joung tree they discovered a nest of *Pheidole*, which fled with their brood upwards. The *Aenictus* pursued them approx. 2 m high. On this occasion several *Pheidole* were killed. The gaster of the soldiers were cut off and taken as booty, otherwise also whole imagines, but mainly brood. Several metres apart of the tree the *Aenictus* discovered in the litter some individuals of the prey species and killed them, too. At the time, some *Pheidole* ants from another nest, which was also located under tree roots 1-2 m apart, ran out with their brood. They also fled on the tree trunk upwards, parts of the brood were robbed by *Bengalia* flies. (*Bengalia* flies, family Calliphoridae, are known to rob prey and brood from different ant species; MASCHWITZ & SCHÖNEGGE 1980. In Pasoh they could be regularly observed robbing prey from columns of epigeic active *Aenictus* species during the day.) The *Aenictus*, however, did not become aware of the *Pheidole* and passed the tree. The *Pheidole* returned slowly into their nest. We guided now the *Aenictus* raid to the *Pheidole* nest by offering them some prey ants on suitable places. The army ants soon discovered the nest of the prey and came on, whereas the *Pheidole* fled again with their brood on the trunk upwards. They were pursued by *Aenictus* workers several metres high and offered no resistance, many dropped on the ground and were killed there. After approx. 15 minutes the *Aenictus* slowly descended the trunk, followed hesitatingly by the *Pheidole*, mainly soldiers. They snapped occasionally at the *Aenictus* and sometimes short fights happened, but the opponents separated always from each other after a short time. During the next 15 minutes the *Aenictus* entirely drew back from the tree and remained only at the robbed nest. Occasionally individual *Pheidole* soldiers which ventured to approach too close, were still seized and killed. A lot of booty was carried off: whole brood, parts of brood, whole imagines of the minor workers, and gaster of the soldiers; seldom other parts of the soldiers. About 1 hour after the beginning of the attack, the army ants abandoned definitely the robbed nest, and the *Pheidole* returned slowly. However, the raid of *Aenictus* continued, branched out, and a part of the troop came back from the other side of the trunk. The *Pheidole* fled again upwards – several were seized and killed. But this time the *Aenictus* pursued them only approx. 1 m high on the trunk and did not enter the robbed nest once more. Finally, after about 1.5 hour the *Pheidole* moved back to their nest with the rescued brood. The queen was not seen.
In a similar pattern *A. dentatus* proceeded an attack on a colony of *Pheidole longipes* (F. SMITH). Also in that case the prey left their nest in time, and would probably have remained undiscovered by the *Aenictus* without the intervention of the observer. In the case of the subterranean *Acropyga acutiventris* ROGER many imagines fled with brood being attacked by *Aenictus* sp. 3. Though the nest got robbed, the colony survived, as the *Aenictus* did not pursue them on the ground surface.

## 4. Discussion

Our observations allow the following conclusions:
1. All species of *Aenictus* in the investigated area take ants as prey and at least some are apparently fully specialized on other ants as food resource. This is also true for *A. gracilis* and *A. laeviceps* – species

which tend to be food generalists in the Philippines (CHAPMAN 1964, SCHNEIRLA & REYES 1966).

2. The different prey spectrum indicates resource partitioning. The observed factors are:
   - Preference of particular taxa (*A. camposi*: Formicinae, mainly *Paratrechina* spp.; *A. aratus* and partly *A. dentatus*: *Pheidole* spp.).
   - Foraging in different strata (e.g. *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*]).
   - Preference of particular prey size (*A. gracilis* and *A. camposi*: small prey; *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*]: also bigger prey – see plate 1b and tab. 4 and 5).
3. Both brood and imagines are taken as prey. This was observed in 8 of 9 species. No imagines as prey were noticed in the only occasion in which *A. hottai* could be observed. Thus, for this species a definitive statement is not possible. The preponderance of the juvenile stages in other investigations (CHAPMAN 1964, MIRENDA et al. 1980) could be a result of the higher mobility of the imagines (flight). It is more likely, however, that the immobile, nutrient-rich brood is preferred, but not exclusively taken.
4. The flight reaction of some prey species (*Pheidole longipes*, *Pheidole comata*) can be interpreted as a specific behavior pattern.
5. Ant species which do not belong to the prey spectrum of particular *Aenictus* species are ignored or avoided.
6. *Aenictus* species seem not to take congenerics, and probably also no other ants with army ant habits (e.g. *Leptogenys*) as prey. To our knowledge fights between *Aenictus* colonies have never been observed. CHAPMAN (1964) succeeded even in mixing of workers of two different species. The phenomenon of avoiding conflicts between army ant colonies is also known from the neotropis. No one species of Ecitoninae has been seen to injure or capture other ants of the subfamily (RETTENMEYER et al. 1983).

According to RETTENMEYER et al. (1983) about 20 sympatric species of army ants can be expected in a lowland moist tropical forest in the neotropis. This number could be true for the Pasoh Forest Reserve, too. Beside of the 11 *Aenictus* species (almost certainly some representatives of this genus remainded undiscovered) several more species of ants with army ant life habits have been found in this locality: *Dorylus laevigatus* F. SMITH, *Leptogenys crassicornis* EMERY, *L. distinguenda* (EMERY), *L. mutabilis* (F. SMITH), and *Pheidologeton silenus* (F. SMITH). However, all of them can be regarded as generalists (MASCHWITZ et al. 1989, MASCHWITZ & STEGHAUS-KOVAC 1991, MOFFETT 1988, WEIßFLOG & MASCHWITZ unpublished data). Ant adults are reported to be prey of *Pheidologeton silenus*, but only as a minor diet component (MOFFETT 1988). Thus *Aenictus* species seem to be the only army ants of this region specialized in ants as prey. Ants of the genus *Cerapachys*, of which 13 species were found in Pasoh Forest Reserve, are also, as far as it is known, specialized ant predators. However, because of their solitary scouting and group recruitment to the discovered prey nests, they are not regarded as army ants (HÖLLDOBLER 1982, HÖLLDOBLER & WILSON 1990).

Leaving the nest in time or an immediate flight in the case of detection of the nest by *Aenictus* seems to be a quite succesful strategy for a prey species to avoid the total extinction of the colony (plate 1c). At least a part of the brood and the imagines keep alive and occupy their nest again. A repeated attack on the nest robbed just short time ago seems unlikely, as the *Aenictus* went on after the raid. One can suppose, that for the army ants it is more efficient to search for other prey nests which offer concentrated food supply in form of motionless brood, as to catch the dispersed fleeing ants. Such flight reaction was described also for two species of relatively large *Pheidole*, prey of *Neivamyrmex nigrescens* (MIRENDA et al. 1980). This American army ant is like the *Aenictus* species a column raider, has a comparable colony size (up to approx. 100000 individuals), and is specialized on other ants (and some species of termites) as prey. A very strong reaction shows *Camponotus festinatus*, one of the prey species of *N. nigrescens*. Already one single worker, which takes notice of the army ants, can cause the flight of the whole colony, including the queen. The ants stay for several hours in the vegetation outside of the nest. This reaction is of the all-or-none type, and can not be caused by mechanical disturbances or blowing into the nest. Hence, it is possibly a specific reaction against the threat by the army ants (LAMON & TOPOFF 1981). Mass evacuation as a reaction on the odour of single crushed worker of *Eciton hamatum* shows also *Dolichoderus rugosus* (RETTENMEYER et al. 1983). Nest defence as an alternative reaction on the presence of *N. nigrescens* occurs in smaller species of *Pheidole* (MIRENDA et al. 1980) and some *Camponotus* species (LAMON & TOPOFF 1981).

The prey spectrum of army ants depends probably on the composition and availability of the ant fauna (or of the potential prey generally) in space and time. This suggest the results of the investigations of MIRENDA et al. (1980) for *Neivamyrmex nigrescens*. Also the different prey spectrum of *A. gracilis* and *A. laeviceps* on the Philippines and in Pasoh Forest Reserve, is an indication of this assumption. According to CHAPMAN (1964), and SCHNEIRLA & REYES (1966) neither prey specialization nor resource partitioning between the two species is existing (except that prey of *A. gracilis* is in general smaller then prey of *A. laeviceps*). Both species take almost any invertebrate that they can find and overcome, and their prey lists overlap widely (SCHNEIRLA & REYES 1966). As ant prey the authors mention representatives of the genera *Polyrhachis*, *Camponotus*, *Formica*, *Crematogaster* and *Pheidole*, without citing a detailed list of species. On contrary, our data show clear differences in prey spectra of the two species and specialization on other ants as prey.

Looking on our results for these two species two factors must be taken into consideration:

- The still relative small number of prey registered (53 raids in all).
- Different sampling localities – Gombak for *A. gracilis*, mainly Pasoh for *A. laeviceps*.

We expect little differences in the ant fauna composition between both localities because of their relative similarity (about 150 km distance, about 130 m altitude difference, mostly similar vegetation structure). However, such differences cannot be fully ruled out and it is still possible, that the prey spectrum of *A. gracilis* in Pasoh differs in some way from that in Gombak.

Also other unknown factors may play a role in prey selection of army ants. *Eciton hamatum* is a neotropical army ant which feeds largely on ant brood. Rettenmeyer et al. (1983) reported differences in prey spectrum of *E. hamatum* in two localities, though the composition of ant faunas was at least partly similar in both areas. Attine ants are common in Panama, as well as in Ecuador, but are commonly raided by the army ant in the first, and rarely in the second locality. It is likely, however, that both ant faunas differ in their species composition and relative abundance of species. Thus, their similarity may be in fact superficially.

Considering the poor data material to our opinion nothing can be stated about a prey specialization of *A. hottai* and *Aenictus* sp. 3. The presumption expressed by Gotwald (1978, 1982), that the hypogeic foragers are usually trophic specialists, whereas the epigeic foragers become general predators, is not supported by our data. It may be simply a result of greater difficulties in observing of the former.

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ROSAMARY SILVA VIEIRA & HUBERT HÖFER

# Prey spectrum of two army ant species in central Amazonia, with special attention on their effect on spider populations

**Abstract**

During six months of field work in a terra firme rainforest near Manaus in the central Amazon we collected prey fragments from 28 colonies of the large swarm-raiding army ant species *Eciton burchelli* and from 9 colonies of the smaller swarm-raiding ant *Labidus praedator*. Regarding the presence of prey fragments from 20 arthropod orders in samples of both army ant species, these might be considered generalist predators. But relative abundances of the prey fragments showed that only four arthropod orders made up 89 % of the prey of *Eciton burchelli* and nine arthropod orders 95 % of the prey of *Labidus praedator*. Spiders made up 13 % respectively 17 % of the prey. Identification of the spider fragments on the morphospecies level showed that *Eciton burchelli* hunted principally on spiders of one genus (*Ctenus*), which is represented by seven species in the study area. Comparison of preliminary density data for these spiders from the same site with the extrapolated number of spiders, caught during one day by a colony of *Eciton burchelli*, points out that the army ants have a high effect on *Ctenus* populations. *Labidus praedator* hunted on a wider variety of spiders, but *Ctenus* fragments were also found. We conclude, that repeated hunting of the two army ant species in the same area, which was observed in another site near Manaus, can have a very high impact on ground living spider assemblages.

**Kurzfassung**

**Das Beutespektrum zweier Treiberameisen-Arten in Zentralamazonien, unter besonderer Berücksichtigung ihres Einflußes auf Spinnenpopulationen**

Während sechsmonatiger Feldarbeiten in einem nicht-überschwemmten Regenwald bei Manaus in Zentralamazonien wurden Beutefragmente von 28 Kolonien der schwarmjagenden Treiberameisenart *Eciton burchelli* und von 9 Kolonien der ebenfalls schwarmjagenden Art *Labidus praedator* gesammelt. In den Aufsammlungen beider Arten waren Beutefragmente aus 20 Arthropodenordnungen zu finden, so daß diese Treiberameisen als Generalisten zu bezeichnen wären. Allerdings zeigen die relativen Abundanzen ein differenzierteres Bild. Nur vier Arthropodenordnungen stellten im Mittel 89 % der Beute von *Eciton burchelli* und neun Arthropodenordnungen im Mittel 95 % der Beute von *Labidus praedator*. Spinnen stellten mit 13 % bzw. 17 % für beide Ameisenarten eine wichtige Beutegruppe dar. Identifizierung der Spinnenfragmente bis auf Morphospezies-Ebene zeigte, daß *Eciton burchelli* hauptsächlich Spinnen der Gattung *Ctenus* jagte, einer Gattung, die im Untersuchungsgebiet mit 7 Arten vertreten ist. Ein Vergleich vorläufiger Daten zur Dichte dieser Spinnen im selben Gebiet mit der extrapolierten Zahl der Spinnen, die pro Tag von den Treiberameisen erbeutete wurden, weist auf einen hohen Effekt der Ameisen auf die Spinnenpopulation hin. *Labidus praedator* erbeutet eine größere Varietät von Spinnen, darunter auch *Ctenus*. Aufgrund von Beobachtungen in einem zweiten Waldgebiet bei Manaus, die zeigen, daß *Eciton burchelli* und *Labidus praedator* innerhalb eines Jahres wiederholt in den gleichen Flächen jagen, schließen wir auf einen beträchtlichen Einfluß der Treiberameisen auf die Struktur von Spinnenpopulationen und -assoziationen des Waldbodens.

**Resumo**

**Espectro de presas de duas espécies de formigas de correição na Amazônia central, com ênfase no efeito das formigas sobre as populações de aranhas**

Durante seis meses de trabalho de campo numa floresta de terra firme na Amazônia central perto de Manaus coletamos fragmentos de presas de 28 colónias de *Eciton burchelli* e de 9 colónias de *Labidus praedator*, ambas espécies de formigas de correição predando em forma de enxame. Através da presência de 20 ordens de artrópodos nas coletas de presa das duas espécies de formigas, estas poderiam ser consideradas predadores generalistas. Pórem as abundâncias relativas dos fragmentos de presa mostraram que somente quatro ordens de artrópodos forneceram 89 % da presa de *Eciton burchelli* e nove ordens 95 % da presa de *Labidus praedator*. Aranhas representaram 13 % e 17 % da presa, respectivamente. A identificação dos fragmentos de aranhas até o nível de espécie mostrou que *Eciton burchelli* caçou principalmente aranhas de um só gênero (*Ctenus*), o qual está representado por sete espécies na área estudada. A comparação de dados préliminares sobre a densidade destas aranhas da mesma área com o número de aranhas capturado por *Eciton burchelli* - extrapolado para um dia inteiro de caça, indica que as formigas de correição prejudicam fortemente as populações de *Ctenus*. *Labidus praedator* caçou uma variedade mais ampla de aranhas, incluindo *Ctenus*. Nos concluímos que caçadas repetidas das duas espécies de formigas de correição na mesma área, o que foi observado numa outra reserva perto de Manaus, podem afetar fortemente populações e associações de aranhas errantes do chão.

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## 1. Introduction

Much of the recent discussion in community ecology has focused on the importance of predation versus competition in structuring communities (CONNELL 1983, SCHOENER 1983, SIH et al. 1985). For tropical areas a greater predatory pressure than in temperate areas has been hypothesized as a mechanism of maintaining high species diversity (CONNELL 1975, 1978; PAINE 1966). Intense predation in the tropics has been shown mostly in marine environments and by herbivores on trees (CONNELL 1971, 1975; JANZEN 1970), but seldom in terrestrial invertebrate communities.

Ants are among the most abundant and species rich invertebrate predators in the tropics, and it has been shown that the rate of predation by ants on wasps increases towards the tropics (JEANNE 1979). Especially army ants could be expected to have a substantial impact on the ground fauna because they are not only carnivorous predators, but, due to their nomadic lifestyle, they forage over a vast area during their activity cycle (SCHNEIRLA 1971). Unlike most of the other neotropical army ants of the tribe Ecitonini, *Eciton burchelli* and *Labidus praedator* are swarm-raiding ants and prey on a wide variety of arthropods (HÖLLDOBLER & WILSON 1990, RETTENMEYER et al. 1983, SCHNEIRLA 1971).

During studies on spider communities in central Amazon rain forests, repeated movements of *E. burchelli* and *L. coecus* were observed within a 400 m² experimental plot (GASNIER & HÖFER, unpublished data). An apparently low density of spiders and a decline of spider abundance during one year within the experimental area led to the hypothesis that predation by army ants could affect spider populations and influence the structure of spider assemblages in leaf litter. To evaluate such effects, we initiated a field study on the ecology of two army ant species, with special emphasis on the prey spectrum of these ants. In this paper, we present a preliminary analysis of the prey item data of two species of army ants and estimate the effect of army ants on spider populations.

## 2. Study area and Methods

The study was conducted between June and November 1993 in a terra firme rainforest (reserve 1501) of the „Biological Dynamics of Forest Fragments Project“ (BDFFP, INPA/Smithsonian Institution), approximately 80 km north of Manaus, in central Amazonia (2° 25' S, 59° 48' W). The reserve, which has been described in detail by LOVEJOY (1980) and LOVEJOY et al. (1983), has a grid of trails with interdistances of 100 meters.

*Eciton burchelli* colonies were located by walking the trails during the morning (7:00 - 14:00) until ants were detected visually or audibly (by listening for the typical noises of antbirds, RETTENMEYER 1963, WILLIS 1967). When the raid column was found, it was followed in the opposite direction in order to locate the bivouac. The sampling of prey items was done from a point (usually regular surfaces such as tree trunks or open soil), where the collector had a sufficient view on the main column of ants returning to the nest. Depending on the position of the bivouac, the sampling point was at different distances from the nest.

*Labidus praedator* colonies were not easily found in the forest due to the smaller size of the ants and their more hypogeic lifestyle. Consequently we searched along a dirt road and prey items were collected from the columns crossing the road.

Army ants carry prey under their body and secure them firmly even when disturbed. We collected prey items by using tweezers to pick up the ants which carried prey and putting them into 80 % alcohol for preservation. This was done during periods of two hours. Unfortunately the ants run so fast, that is was not possible to collect every ant passing with prey. We checked the efficiency of our samples by counting *Eciton* ants passing with prey during 40 periods of 10 seconds each and compared the resulting median number of prey items for two hours with the median number of prey items we were able to collect during our samples. The number of ants carrying food in the 10 second samples was similar to that given in the literature (see below). Thus we calculated an efficiency of 4.4 % for our samples of *Eciton* prey. No measurement of the efficiency was taken for samples of *Labidus* prey.

In the laboratory, all prey fragments were separated from ants and sorted to taxonomic orders. So far only spiders were sorted to morphospecies. Due to our experience in identifying Amazon spiders, we were often able to identify a genus or species even with incomplete (prosomas) and juvenile material (e.g. *Ctenus*). Each prosoma in the sample was counted as one individual spider. The number of individual spiders of the genus *Ctenus* in our samples was used to estimate the number of *Ctenus* spiders caught by the ant colony during a whole day (Iday, tab. 3). This was done by the following formula: Iday = Is * ef * tf, where Is is the number of individual *Ctenus* spiders in our samples, ef the factor adjusting to an efficiency of 100 % (= 100/4.4) and tf the time factor, adjusting the number of individual spiders in two hour samples to a daily eight hour period (= 4).

The effect of ants preying on *Ctenus* spiders was expressed as the proportion of the *Ctenus* population which would have been caught by the ants during one day by using Iday and data for the density of *Ctenus* in 40 areas of 160 m² in the same reserve (median 15 *Ctenus*/160 m², GASNIER unpubl.), extrapolated to a hunting area of 1000 m². *Ctenus* densities were studied by searching spiders at night with the aid of headlamps. Only spiders with a body size (length of prosoma and abdomen) of about 1 cm or more were considered. We made no attempt to measure the hunting area of *Eciton burchelli*, but instead used a mean of 1000 m², which seems to us as a realistic mean of the many values for width and length of the daily hunting area, given in literature (see appendix).

As most of the data are not expected to be normally distributed we calculated the median instead of the mean, and present the lower and upper quartile (lQ, uQ) together with the interquartile range/2 in percent of the median (IQ %) to give an idea of the relative variability (LAMPRECHT 1992).

## 3. Results and Discussion

### 3.1 *Eciton burchelli*

### 3.1.1 Prey spectrum of *Eciton burchelli*

Twenty-eight colonies of *Eciton burchelli* were found and thirty-one prey item samples (2 hours each) were

Table 1. Prey spectrum of *Eciton burchelli*: absolute numbers of prey fragments in two hour-samples (Ara-Araneae, Sco-Scorpionida, Opi-Opilionida, Amb-Amblypygi, Uro-Uropygi, Schiz-Schizomida, Aca-Acari, Chilo-Chilopoda, Isopo-Isopoda, Thys-Thysanura, Derm-Dermaptera, Blatt-Blattodea, Isopt-Isoptera, Ortho-Orthoptera, Het-Heteroptera, Dipt-Diptera, Col-Coleoptera, Hym-Hymenoptera, Form-Formicidae, Lep-Lepidoptera, Rept-Reptilia, n. i.-not identified; IQ-lower quartile, uQ-upper quartile, IQ%-half of interquartile in % of median; sample no. 30 was a 4-hour sample and thus divided).

| sample | | Systematic category | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| no. | date | Ara | Sco | Opi | Amb | Uro | Schiz | Aca | Chilo | Isopo | Thys | Derm | Blatt | Isopt | Ortho | Het | Dipt | Col | Hym | Form | Lep | Rept | n.i. | sum |
| 1 | 07-Jul | 46 | 4 | 0 | 3 | 18 | 0 | 0 | 1 | 0 | 1 | 1 | 56 | 0 | 1 | 0 | 0 | 0 | 0 | 49 | 0 | 1 | 2 | 183 |
| 2 | 20-Jul | 43 | 1 | 0 | 1 | 0 | 0 | 2 | 4 | 0 | 0 | 0 | 67 | 0 | 12 | 0 | 0 | 0 | 0 | 43 | 0 | 0 | 6 | 179 |
| 3 | 21-Jul | 44 | 3 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 2 | 0 | 115 | 0 | 12 | 2 | 0 | 0 | 0 | 41 | 4 | 1 | 3 | 243 |
| 4 | 22-Jul | 60 | 5 | 0 | 4 | 0 | 0 | 0 | 14 | 0 | 1 | 0 | 85 | 0 | 22 | 1 | 0 | 2 | 0 | 21 | 0 | 0 | 3 | 218 |
| 5 | 13-Aug | 26 | 4 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 57 | 0 | 16 | 0 | 1 | 3 | 2 | 65 | 0 | 0 | 15 | 196 |
| 6 | 14-Aug | 24 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 71 | 0 | 25 | 1 | 0 | 4 | 3 | 107 | 1 | 0 | 7 | 250 |
| 7 | 15-Aug | 89 | 11 | 0 | 0 | 2 | 0 | 0 | 9 | 0 | 0 | 0 | 70 | 0 | 41 | 0 | 1 | 3 | 2 | 129 | 1 | 0 | 13 | 371 |
| 8 | 17-Aug | 99 | 6 | 0 | 1 | 1 | 0 | 1 | 4 | 0 | 2 | 0 | 144 | 0 | 35 | 0 | 0 | 1 | 6 | 37 | 1 | 0 | 1 | 339 |
| 9 | 17-Aug | 21 | 1 | 0 | 0 | 2 | 0 | 0 | 6 | 0 | 0 | 0 | 27 | 0 | 2 | 0 | 0 | 1 | 7 | 16 | 0 | 0 | 3 | 86 |
| 10 | 18-Aug | 74 | 13 | 0 | 2 | 22 | 0 | 0 | 3 | 1 | 0 | 0 | 111 | 0 | 17 | 1 | 1 | 1 | 5 | 102 | 2 | 1 | 10 | 366 |
| 11 | 18-Aug | 23 | 5 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 80 | 0 | 22 | 2 | 0 | 3 | 2 | 21 | 2 | 0 | 6 | 172 |
| 12 | 26-Aug | 68 | 9 | 0 | 0 | 2 | 0 | 0 | 7 | 0 | 3 | 0 | 60 | 0 | 7 | 0 | 0 | 0 | 8 | 105 | 0 | 0 | 9 | 278 |
| 13 | 27-Aug | 47 | 9 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 91 | 0 | 29 | 0 | 1 | 1 | 0 | 27 | 0 | 0 | 7 | 225 |
| 15 | 15-Sep | 33 | 13 | 0 | 6 | 9 | 0 | 0 | 14 | 0 | 0 | 1 | 76 | 0 | 44 | 10 | 0 | 3 | 0 | 240 | 0 | 0 | 4 | 453 |
| 17I | 16-Sep | 96 | 13 | 0 | 9 | 1 | 0 | 0 | 5 | 0 | 2 | 0 | 84 | 0 | 73 | 7 | 1 | 2 | 2 | 118 | 1 | 1 | 9 | 424 |
| 17III | 16-Sep | 51 | 14 | 0 | 9 | 3 | 0 | 0 | 6 | 0 | 0 | 0 | 51 | 6 | 52 | 6 | 0 | 1 | 0 | 140 | 1 | 0 | 9 | 349 |
| 17V | 16-Sep | 18 | 25 | 0 | 12 | 1 | 0 | 0 | 14 | 0 | 0 | 0 | 37 | 5 | 23 | 4 | 0 | 5 | 9 | 305 | 1 | 0 | 3 | 462 |
| 18 | 21-Sep | 61 | 12 | 0 | 3 | 21 | 2 | 0 | 24 | 0 | 3 | 6 | 144 | 0 | 58 | 6 | 2 | 1 | 1 | 174 | 0 | 1 | 18 | 537 |
| 19 | 06-Okt | 111 | 46 | 0 | 14 | 6 | 0 | 0 | 0 | 0 | 1 | 2 | 163 | 1 | 72 | 0 | 0 | 20 | 3 | 283 | 0 | 0 | 53 | 775 |
| 20 | 21-Okt | 72 | 5 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 10 | 0 | 82 | 0 | 50 | 2 | 0 | 2 | 1 | 219 | 1 | 0 | 7 | 453 |
| 22 | 05-Nov | 35 | 10 | 0 | 1 | 3 | 0 | 0 | 8 | 1 | 6 | 0 | 77 | 0 | 51 | 3 | 0 | 1 | 5 | 35 | 0 | 2 | 10 | 248 |
| 23 | 07-Nov | 26 | 24 | 0 | 0 | 8 | 0 | 0 | 7 | 0 | 3 | 0 | 117 | 0 | 56 | 1 | 0 | 1 | 2 | 47 | 0 | 2 | 10 | 304 |
| 24 | 09-Nov | 40 | 8 | 0 | 3 | 11 | 0 | 0 | 7 | 0 | 0 | 0 | 81 | 0 | 56 | 3 | 0 | 1 | 2 | 72 | 1 | 1 | 26 | 312 |
| 25 | 17-Nov | 13 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 8 | 0 | 58 | 1 | 45 | 0 | 1 | 1 | 0 | 52 | 0 | 0 | 3 | 186 |
| 26 | 20-Nov | 28 | 5 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 127 | 0 | 62 | 3 | 0 | 1 | 0 | 107 | 5 | 0 | 26 | 367 |
| 27 | 21-Nov | 26 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 15 | 0 | 73 | 0 | 56 | 0 | 2 | 0 | 0 | 50 | 0 | 4 | 4 | 235 |
| 28 | 22-Nov | 11 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 22 | 0 | 11 | 1 | 0 | 0 | 0 | 350 | 0 | 1 | 0 | 404 |
| 29 | 23-Nov | 29 | 26 | 0 | 0 | 2 | 0 | 0 | 13 | 0 | 1 | 2 | 120 | 0 | 114 | 1 | 0 | 0 | 0 | 209 | 3 | 3 | 4 | 527 |
| 30 | 24-Nov | 29.5 | 1.5 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 | 7 | 0 | 82.5 | 1 | 56 | 1 | 0 | 1 | 0.5 | 64 | 0.5 | 5 | 10.5 | 271.5 |
| 30 | 24-Nov | 29.5 | 1.5 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 | 17 | 0 | 82.5 | 1 | 56 | 1 | 0 | 1 | 0.5 | 64 | 0.5 | 5 | 10.5 | 271.5 |
| 31 | 25-Nov | 35 | 12 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 8 | 0 | 51 | 0 | 58 | 4 | 0 | 3 | 1 | 113 | 1 | 2 | 16 | 305 |
| sum | | 1408 | 292 | 2 | 86 | 120 | 2 | 3 | 174 | 2 | 110 | 16 | 2562 | 15 | 1234 | 60 | 10 | 63 | 62 | 3405 | 26 | 30 | 308 | 9990 |
| median | | 35 | 6 | 0 | 1 | 1 | 0 | 0 | 4 | 0 | 2 | 0 | 80 | 0 | 44 | 1 | 0 | 1 | 1 | 72 | 0.5 | 0.0 | 7.0 | 304.0 |
| IQ | | 9 | 4 | 0 | 1 | 1 | 0 | 0 | 3 | 0 | 2 | 0 | 22 | 0 | 27 | 1 | 0 | 0 | 1 | 29 | 0.5 | 0.0 | 4.0 | 79.0 |
| uQ | | 26 | 7 | 0 | 3 | 2 | 0 | 0 | 4 | 0 | 3 | 0 | 31 | 0 | 12 | 2 | 1 | 2 | 2 | 68 | 0.5 | 1.0 | 3.5 | 100.0 |
| IQ% | | 50 | 91.7 | | 200 | 150 | | | 87.5 | | 125 | | 33.1 | | 44.3 | 150 | | 100 | 150 | 67.4 | 100.0 | | 53.6 | 29.4 |

Table 2. Prey spectrum of *Eciton burchelli*: relative numbers of fragments in two hour-samples.

| sample | date | Systematic category | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Araneae | Blattodea | Orthoptera | Formicidae | not id. | sum | others |
| 1 | 07-Jul | 25.14 | 30.60 | 0.55 | 26.78 | 1.09 | 84.2 | 15.8 |
| 2 | 20-Jul | 24.02 | 37.43 | 6.70 | 24.02 | 3.35 | 95.5 | 4.5 |
| 3 | 21-Jul | 18.11 | 47.33 | 4.94 | 16.87 | 1.23 | 88.5 | 11.5 |
| 4 | 22-Jul | 27.52 | 38.99 | 10.09 | 9.63 | 1.38 | 87.6 | 12.4 |
| 5 | 13-Aug | 13.27 | 29.08 | 8.16 | 33.16 | 7.65 | 91.3 | 8.7 |
| 6 | 14-Aug | 9.60 | 28.40 | 10.00 | 42.80 | 2.80 | 93.6 | 6.4 |
| 7 | 15-Aug | 23.99 | 18.87 | 11.05 | 34.77 | 3.50 | 92.2 | 7.8 |
| 8 | 17-Aug | 29.20 | 42.48 | 10.32 | 10.91 | 0.29 | 93.2 | 6.8 |
| 9 | 17-Aug | 24.42 | 31.40 | 2.33 | 18.60 | 3.49 | 80.2 | 19.8 |
| 10 | 18-Aug | 20.22 | 30.33 | 4.64 | 27.87 | 2.73 | 85.8 | 14.2 |
| 11 | 18-Aug | 13.37 | 46.51 | 12.79 | 12.21 | 3.49 | 88.4 | 11.6 |
| 12 | 26-Aug | 24.46 | 21.58 | 2.52 | 37.77 | 3.24 | 89.6 | 10.4 |
| 13 | 27-Aug | 20.89 | 40.44 | 12.89 | 12.00 | 3.11 | 89.3 | 10.7 |
| 15 | 15-Sep | 7.28 | 16.78 | 9.71 | 52.98 | 0.88 | 87.6 | 12.4 |
| 17I | 16-Sep | 22.64 | 19.81 | 17.22 | 27.83 | 2.12 | 89.6 | 10.4 |
| 17III | 16-Sep | 14.61 | 14.61 | 14.90 | 40.11 | 2.58 | 86.8 | 13.2 |
| 17V | 16-Sep | 3.90 | 8.01 | 4.98 | 66.02 | 0.65 | 83.5 | 16.5 |
| 18 | 21-Sep | 11.36 | 26.82 | 10.80 | 32.40 | 3.35 | 84.7 | 15.3 |
| 19 | 06-Okt | 14.32 | 21.03 | 9.29 | 36.52 | 6.84 | 88.0 | 12.0 |
| 20 | 21-Okt | 15.89 | 18.10 | 11.04 | 48.34 | 1.55 | 94.9 | 5.1 |
| 22 | 05-Nov | 14.11 | 31.05 | 20.56 | 14.11 | 4.03 | 83.9 | 16.1 |
| 23 | 07-Nov | 8.55 | 38.49 | 18.42 | 15.46 | 3.29 | 84.2 | 15.8 |
| 24 | 09-Nov | 12.82 | 25.96 | 17.95 | 23.08 | 8.33 | 88.1 | 11.9 |
| 25 | 17-Nov | 6.99 | 31.18 | 24.19 | 27.96 | 1.61 | 91.9 | 8.1 |
| 26 | 20-Nov | 7.63 | 34.60 | 16.89 | 29.16 | 7.08 | 95.4 | 4.6 |
| 27 | 21-Nov | 11.06 | 31.06 | 23.83 | 21.28 | 1.70 | 88.9 | 11.1 |
| 28 | 22-Nov | 2.72 | 5.45 | 2.72 | 86.63 | 0.00 | 97.5 | 2.5 |
| 29 | 23-Nov | 5.50 | 22.77 | 21.63 | 39.66 | 0.76 | 90.3 | 9.7 |
| 30 | 24-Nov | 10.87 | 30.39 | 20.63 | 23.57 | 3.87 | 89.3 | 10.7 |
| 30 | 24-Nov | 10.87 | 30.39 | 20.63 | 23.57 | 3.87 | 89.3 | 10.7 |
| 31 | 25-Nov | 11.48 | 16.72 | 19.02 | 37.05 | 5.25 | 89.5 | 10.5 |
| median | | 12.8 | 26.5 | 12.9 | 23.7 | 2.6 | 89.3 | 10.7 |
| lQ | | 1.2 | 2.0 | 5.3 | 4.6 | 1.0 | 2.5 | 2.6 |
| uQ | | 2.3 | 1.0 | 1.9 | 11.1 | 0.4 | 2.6 | 2.5 |
| IQ% | | 13.9 | 5.6 | 27.9 | 33.1 | 25.9 | 2.9 | 23.8 |

taken. *Eciton burchelli* ants immobilize their prey and depending on prey size, carry it whole or cut into pieces (GOTWALD 1982, DA SILVA 1972). For large prey (generally >1cm length) legs, wings, and antennas are cut off at the insertion point or at articulations, and heads or prosomas are separated from abdomens. Most items were large, the samples, therefore, consist of few complete individuals and a large number of fragments of arthropods. The number of prey fragments collected during the two hour-sampling periods varied from 86 to 775, with a median of 304 and an IQ of 29.4 % (tab. 1). To check the efficiency of our own samples, we counted the number of ants passing by with prey during periods of 10 seconds. The median number was 9.5 ants in 10 seconds (n = 40, IQ = 24.5 %), which is similar to other reported values (FRANKS 1990). Thus a total of 27360 prey fragments would have been collected during 8 hours of foraging. FRANKS (1990) calculated 29000 prey fragments/colony/day from studies in Panama.

Altogether the 31 samples contained 9990 fragments, which were sorted into Reptilia and 20 arthropod orders belonging to Arachnida, Crustacea, Myriapoda and Insecta (tab. 1). We were unable to identify 308 fragments. Cockroaches (Blattodea) were the most abundant group with a median of 26.5 %, followed by ants (Formicidae) with 23.7 % (including adults, eggs, larvae and pupae), grasshoppers (Orthoptera) with

12.9 % (including a few mantids) and spiders (Araneae) with 12.8 %. All remaining groups made up 10.7 %, and no individual group more than 2 % of the median (tab. 2). None of these remaining groups made up more than 8 % of any single sample. Maximum values for the relative portion of the four major prey groups for single samples were 29 % for spiders, 47 % for cockroaches, 24 % for grasshoppers and 87 % for ants (tab. 2).

Published data on prey spectrum of *Eciton burchelli* (Rettenmeyer 1963, Schneirla 1971, Da Silva 1972, Willis 1967) show Formicidae, Blattodea, Orthoptera and Araneae as the most important groups, but no study reports absolute or relative numbers. One exception is Franks (1990), who showed that social Hymenoptera (adults and larvae) represent 55 % of the dry weight of all prey, whereas crickets and cockroaches make up 34 % in the rainy season and 30 % in the dry season, other arthropods constituting the remaining 12 and 15 % of the prey.

In this study, the four most abundant prey groups (Blattodea, Formicidae, Orthoptera, Araneae) also showed the lowest IQ % values, indicating that they were also the most regularly sampled prey. This is especially true for these four groups as a whole, which had a minimum of 80 % of every sample (median 89.3) and show very low variation (IQ 2.9 %) compared with the single groups (tab. 2). However, variation of both absolute and relative number of prey fragments was higher for ants than for cockroaches and spiders (tab. 1, 2), reflecting the more uneven distribution of ants as social insects (nests with many individuals), compared with the individually living arthropods.

In studies of ground living arthropods in the Manaus area, Formicidae, Orthoptera, Blattodea and Arachnida are among the dominant groups, their relative abundances changing only slightly, depending on the sampling method (pitfall traps or quadrat sampling, Adis & Schubart 1984, Malcolm 1991, Morais 1985). Arthropod orders which were not represented in the prey spectrum of *Eciton burchelli* in proportion to their availability in the leaf litter are termites (Isoptera), and insects and arachnids of very small size, such as Diplura, Symphyla, Pauropoda, Protura and Pseudoscorpiones.

### 3.1.2 Spiders as prey of *Eciton burchelli*

A median of 35 spider fragments was collected from *Eciton* ants during the two-hour samples (minimum 11, maximum 111, IQ = 50 %, table 3). Spiders were most often cut in ten fragments (prosoma, abdomen, eight legs), only a few small spiders appeared intact in the samples. Consequently, the ratio between fragments and individuals should be close to 10. When using prosomas as indicative of individual spiders in our samples this ratio is clearly below 10 (median 4.9; IQ 33 %, table 3), which means that legs and abdomens are underrepresented. Because legs carried by ants are even more visible for the collector than prosomas we suppose that principally legs and sometimes abdomens get lost on the way to the bivouac. Thus prosomas represent the best basis to calculate the total number of spider individuals caught during one day. The median number of individual spiders, based on the number of prosomas in the two hour-samples, was 9 (minimum 2, maximum 24, IQ = 50 %, table 3).

Most of the 312 individual spiders could be identified to family and some to genera and species. Species iden-

Table 3. Spiders as prey of *Eciton burchelli* in two hour-samples (frag-spider fragments, ind-number of fragments representing individual spiders, Is-number of *Ctenus* individuals in two hour-samples, Iday-extrapolated number of *Ctenus* caught by the ants per day).

| sample | date | frag | ind | frag/ind | Is | Iday |
|---|---|---|---|---|---|---|
| 1 | 07-Jul | 46 | 5 | 9.2 | 3 | 272.7 |
| 2 | 20-Jul | 43 | 5 | 8.6 | 5 | 454.5 |
| 3 | 21-Jul | 44 | 6 | 7.3 | 6 | 545.5 |
| 4 | 22-Jul | 60 | 11 | 5.5 | 10 | 909.1 |
| 5 | 13-Aug | 26 | 5 | 5.2 | 4 | 363.6 |
| 6 | 14-Aug | 24 | 3 | 8.0 | 1 | 90.9 |
| 7 | 15-Aug | 89 | 9 | 9.9 | 9 | 818.2 |
| 8 | 17-Aug | 99 | 24 | 4.1 | 21 | 1909.1 |
| 9 | 17-Aug | 21 | 3 | 7.0 | 2 | 181.8 |
| 10 | 18-Aug | 74 | 21 | 3.5 | 19 | 1727.3 |
| 11 | 18-Aug | 23 | 7 | 3.3 | 6 | 545.5 |
| 12 | 26-Aug | 68 | 14 | 4.9 | 14 | 1272.7 |
| 13 | 27-Aug | 47 | 21 | 2.2 | 21 | 1909.1 |
| 15 | 15-Sep | 33 | 4 | 8.3 | 4 | 363.6 |
| 17I | 16-Sep | 96 | 18 | 5.3 | 16 | 1454.5 |
| 17III | 16-Sep | 51 | 10 | 5.1 | 8 | 727.3 |
| 17V | 16-Sep | 18 | 6 | 3.0 | 4 | 363.6 |
| 18 | 21-Sep | 61 | 14 | 4.4 | 12 | 1090.9 |
| 19 | 06-Okt | 111 | 21 | 5.3 | 20 | 1818.2 |
| 20 | 21-Okt | 72 | 18 | 4.0 | 16 | 1454.5 |
| 22 | 05-Nov | 35 | 13 | 2.7 | 10 | 909.1 |
| 23 | 07-Nov | 26 | 14 | 1.9 | 12 | 1090.9 |
| 24 | 09-Nov | 40 | 7 | 5.7 | 4 | 363.6 |
| 25 | 17-Nov | 13 | 2 | 6.5 | 2 | 181.8 |
| 26 | 20-Nov | 28 | 9 | 3.1 | 8 | 727.3 |
| 27 | 21-Nov | 26 | 9 | 2.9 | 5 | 454.5 |
| 28 | 22-Nov | 11 | 3 | 3.7 | 1 | 90.9 |
| 29 | 23-Nov | 29 | 9 | 3.2 | 8 | 727.3 |
| 30 | 24-Nov | 29.5 | 7 | 4.2 | 6 | 545.5 |
| 30 | 24-Nov | 29.5 | 7 | 4.2 | 6 | 545.5 |
| 31 | 25-Nov | 35 | 7 | 5.0 | 5 | 454.5 |
| median | | 35.0 | 9.0 | 4.9 | 6.0 | 545.5 |
| IQ | | 9.0 | 4.0 | 1.6 | 2.0 | 181.8 |
| uQ | | 26.0 | 5.0 | 1.6 | 6.0 | 545.5 |
| IQ% | | 50.0 | 50.0 | 33.1 | 66.7 | 66.7 |

Table 4. Species list of spiders, preyed by *Eciton burchelli*.

| family | morphospeci | sum | % |
|---|---|---|---|
| Clubionidae | *Elaver* sp. | 1 | 0.3 |
| Clubionidae ? | sp. | 1 | 0.3 |
| Corinnidae | *Corinna* sp. | 10 | 3.2 |
| Ctenidae | *Ctenus manauara* | 5 | 1.6 |
| Ctenidae | *„Ctenus"* cf. *auberti* | 27 | 8.7 |
| Ctenidae | *Ctenus amphora* | 8 | 2.6 |
| Ctenidae | *Ctenus crulsi* | 2 | 0.6 |
| Ctenidae | *Ctenus* spp. | 221 | 70.8 |
| Ctenidae | *Enoploctenus* sp. | 1 | 0.3 |
| Ctenidae | gen.? sp. | 3 | 1.0 |
| Deinopidae | *Deinopis* sp. | 1 | 0.3 |
| Heteropodidae | Sparianthinae sp. | 7 | 2.2 |
| Mygalomorphae | spp. | 18 | 5.8 |
| Pholcidae | sp. | 2 | 0.6 |
| Salticidae | pluridentatae sp. | 2 | 0.6 |
| Theraphosidae | sp. | 2 | 0.6 |
| Zodariidae | sp. | 1 | 0.3 |
| sum | | 312 | 100 |

tification was possible only in the case of adult male and female fragments of spiders of the genus *Ctenus* and some juveniles with the typical abdominal design (e.g. *„Ctenus"* cf. *auberti*). The genus *Ctenus* represented 84 % of all spiders in the samples, and 4 species of *Ctenus* were identified. Most mygalomorphs could not be identified to family, but most probably belong to Dipluridae or Theraphosidae. In total, 18 morphospecies are represented in the samples (tab. 4).

The spider prey spectrum represented only a fraction of the total spider availability in the area (HÖFER, BRESCOVIT, GASNIER unpubl.; VIEIRA unpubl. data). *Eciton burchelli* almost never preyed upon web-building spiders (Araneidae, Pholcidae, Pisauridae, Theridiidae) and very small spiders (Anapidae, Ochyroceratidae, Oonopidae), and never caught the abundant but cryptic and motionless remaining spiders of the genus *Paratropis* (Paratropididae). The fact that some abundant wandering spiders which are slightly smaller than *Ctenus* spiders are not or underrepresented in the prey samples (e.g. Caponiidae, Heteropodidae, Pisauridae, Salticidae, Zodariidae) suggests that *Eciton burchelli* prefers medium sized spiders of 1-2 cm body length. In reserve 1501, this size class is represented mainly by adults of two smaller species of *Ctenus* (*C. manauara*, *C.* n.sp.) and juveniles of *Ctenus amphora*, *Ctenus crulsi*, *„Ctenus"* cf. *auberti* and *C. tapereba* (see HÖFER et al. 1994, this volume). The ants seem not to be able to prey on larger ctenid and pisaurid spiders (*Ctenus villasboasi*, *Phoneutria* spp., *Ancylometes* spp.), nor to catch the burrowing mygalomorphs (Actinopodidae, Nemesiidae, Theraphosidae).

The number of *Ctenus* prosomas in the two hour-samples (minimum 1, maximum 21, median 6, IQ = 66.7, table 3) was extrapolated by the formula above to a number of *Ctenus* individuals theoretically caught by the ants during eight hours. Thus, a median of 545 *Ctenus* individuals would have been caught by a colony during one day (Iday in table 3: minimum 91, maximum 1909, IQ = 66.7 %).

### 3.2 *Labidus praedator*

### 3.2.1 Prey spectrum of *Labidus praedator*

Nine colonies of *Labidus praedator* were found and one sample of two hours was taken from each. *Labidus praedator* preys in the same manner as *Eciton burchelli*, but individual prey usually is smaller or is cut into smaller pieces (SCHNEIRLA 1949, cited in RETTENMEYER 1963). This makes identification of fragments more difficult, resulting in a higher portion of unidentified fragments (229 fragments = 5.2 %, table 5, 6). The number of prey fragments collected during two hours varied from 73 to 339, with a median of 177 and an IQ of 75 % (tab. 5). A total of 1911 fragments was collected from the ants, including fragments of 20 arthropod orders and of reptiles (tab. 5). Cockroaches (Blattodea) were the most abundant prey with a median of 31.6 %, followed by spiders (Araneae, 17 %), centipedes (Chilopoda, 5.5 %), larvae of Lepidoptera (4.3 %), and whip scorpions (Holopeltidia, 3.5 %). Ants (Formicidae) had low representation with a median of 3 %, as well as grasshoppers (Orthoptera) and scorpions (Scorpionida) with 2.7 % (tab. 5). Together with earwigs (Dermaptera, 2.3 %) and the unidentified fragments, these 9 arthropod groups represented 94.5 % (median), the remaining 11 groups accounting for only 5.5 % (median, table 6). Maximum values for relative abundance of the major prey groups in a single sample were 24.7 % for spiders, 19.7 % for whip scorpions, 16.7 % for earwigs, 39.2 % for cockroaches. Only cockroaches and spiders showed IQ values below 50 % (20,8 and 42.2 respectively) and thus were the most regularly sampled prey (tab. 6).

*Labidus praedator* is also considered to be a generalist arthropod predator (RETTENMEYER 1963, DA SILVA 1972). In our prey samples of *Labidus* the same number of arthropod orders is present as in samples of *Eciton*. Differences in the representation of prey groups include the absence of Amblypygi and Hymenoptera (excl. ants) and the presence of Protura and Neuroptera in the prey samples of *Labidus*. Regarding the relative abundance of arthropod groups in the prey samples *Labidus* seems to make use of a wider spectrum than *Eciton burchelli* (tab. 2 vs. 6). Hunting in the same habitats and strata and consequently having the same prey spectrum available, *Labidus* caught relatively more Arachnids (spiders, scorpions and whipscorpions), centipedes and larvae of Lepidoptera. Ants were less important.

Table 5. Prey spectrum of *Labidus praedator*: absolute numbers of fragments in two hour-samples (for abbreviations see table 1; Prot-Protura, Neuro-Neuroptera).

| sample | | Systematic category | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| no. | date | Ara | Sco | Opi | Uro | Schiz | Aca | Chilo | Isopo | Prot | Derm | Blatt | Isopt | Neuro | Ortho | Thys | Het | Dipt | Col | Form | Lep | Rept | n.i. | sum |
| 1 | 24-Jun | 63 | 1 | 6 | 7 | 2 | 1 | 11 | 0 | 1 | 12 | 65 | 0 | 0 | 2 | 3 | 9 | 0 | 6 | 4 | 29 | 0 | 62 | 284 |
| 2 | 24-Jun | 18 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 4 | 27 | 0 | 0 | 9 | 0 | 1 | 0 | 1 | 1 | 6 | 0 | 2 | 73 |
| 3 | 03-Aug | 13 | 4 | 0 | 10 | 0 | 0 | 28 | 0 | 0 | 1 | 68 | 0 | 0 | 3 | 1 | 2 | 2 | 4 | 6 | 2 | 0 | 56 | 200 |
| 5 | 16-Aug | 63 | 9 | 5 | 12 | 2 | 5 | 18 | 10 | 0 | 16 | 107 | 1 | 0 | 27 | 4 | 21 | 1 | 5 | 15 | 11 | 1 | 6 | 339 |
| 6 | 26-Aug | 32 | 12 | 0 | 37 | 0 | 0 | 5 | 0 | 0 | 0 | 16 | 2 | 1 | 0 | 0 | 0 | 0 | 5 | 12 | 2 | 0 | 64 | 188 |
| 7 | 14-Sep | 10 | 5 | 1 | 3 | 0 | 0 | 15 | 0 | 0 | 1 | 39 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 8 | 10 | 0 | 10 | 107 |
| 8 | 15-Sep | 19 | 0 | 0 | 20 | 0 | 0 | 21 | 9 | 0 | 5 | 85 | 0 | 0 | 9 | 4 | 2 | 0 | 4 | 12 | 22 | 0 | 5 | 217 |
| 9 | 22-Nov | 37 | 7 | 0 | 5 | 0 | 2 | 24 | 0 | 0 | 2 | 47 | 0 | 0 | 14 | 14 | 3 | 0 | 3 | 3 | 4 | 2 | 7 | 174 |
| 10 | 25-Nov | 40 | 24 | 4 | 30 | 0 | 1 | 18 | 0 | 0 | 55 | 99 | 0 | 0 | 9 | 2 | 1 | 0 | 9 | 5 | 14 | 1 | 17 | 329 |
| sum | | 295 | 62 | 16 | 125 | 4 | 9 | 143 | 19 | 1 | 96 | 553 | 3 | 1 | 75 | 28 | 41 | 3 | 38 | 66 | 100 | 4 | 229 | 1911 |
| median | | 32 | 5 | 0 | 10 | 0 | 0 | 18 | 0 | 0 | 4 | 65 | 0 | 0 | 9 | 2 | 2 | 0 | 4 | 6 | 10 | 0 | 10 | 177 |
| lQ | | 16.5 | 4.5 | 0 | 6 | 0 | 0 | 10 | 0 | 0 | 3 | 32 | 0 | 0 | 7 | 2 | 1 | 0 | 2 | 2.5 | 7 | 0 | 4.5 | 98 |
| uQ | | 19.5 | 5.5 | 4.5 | 15 | 1 | 1.5 | 4.5 | 4.5 | 0 | 10 | 27 | 0.5 | 0 | 2.5 | 2 | 4 | 0.5 | 1.5 | 6 | 8 | 1 | 49 | 168 |
| IQ% | | 56.3 | 100 | | 105 | | | 40.3 | | | 162.5 | 45.4 | | | 52.8 | 100 | 125 | | 43.8 | 70.8 | 75 | | 267.5 | 75.1 |

### 3.2.2 Spiders as prey of *Labidus praedator*

A median of 32 fragments of spiders was collected with *Labidus* ants during two hours (minimum 10, maximum 63, IQ = 56 %, table 7). Most of the larger spiders (Ctenidae, Heteropodidae, Mygalomorphae) were in smaller pieces than in the samples from *Eciton* (e.g. parts of the prosoma), but many smaller spiders were found intact or only with a few legs cut off. This resulted in a very low ratio between fragments and individuals (median 1.7; IQ 13 %, table 7). As in the *Eciton* samples prosomas were counted as individual spiders and a median of 16 spiders was present in the two hour samples (minimum 6, maximum 39, IQ = 72 %, table 7). Because of the rapid movement of the small *Labidus* ants no efficiency test was executed and thus, no extrapolation of the data to the amount of prey taken during one day could be made.

From a total of 173 individual spiders collected, 28 morphospecies could be identified (tab. 8). Fragments of Ctenidae were most abundant with 27 %, followed by Salticidae (19.1 %) and Dipluridae (12.7 %).

The sampled *Labidus* colonies preyed upon a wider variety of spiders than *Eciton*, including web spiders (Araneidae, Deinopidae, Mysmenidae, Pholcidae, Uloboridae), a large number of the small wandering spider mentioned above and the medium sized *Ctenus* spiders (tab. 8).

## 4. Conclusion

Both *Eciton burchelli* and *Labidus praedator* have been considered polyphagous predators (generalists), in comparison to other army ant species of the tribe Ecitonini (GOTWALD 1982, RETTENMEYER et al. 1983). However, our data show that four arthropod groups dominate the prey spectrum of *Eciton burchelli*. Arthropod representation in the prey samples seems to be dependent partly on the availability (relative abundance and frequence) of these arthropods in the habitat. However, some small-sized arthropods and termites, very abundant in the leaf litter, were rare in the prey samples of *Eciton burchelli*. The ants might prefer some prey (e.g. larvae) or avoid others (aggressive, distasteful, smooth and armoured) and fail to detect cryptic motionless animals, but this will only be visible below the level of orders. Among spiders *Eciton burchelli* shows preference for wandering spiders of the genus *Ctenus*, which in fact might be a preference for a certain size class.

*Labidus praedator* showed a higher evenness in the prey spectrum, both on the level of arthropod orders and in spiders. They also seem to make use of some of the smaller arthropod groups. However, overlap with the prey spectrum of *Eciton burchelli* is considerably high.

The extrapolation of our samples resulted in a median number of 545 *Ctenus* spiders, caught by a colony of

Table 6. Prey spectrum of *Labidus praedator*: relative numbers of fragments in two hour-samples (for abbreviations see table 1).

| sample | date | Systematic category | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| no. | | Ara | Sco | Uro | Chilo | Derm | Blatt | Ortho | Form | Lep | | sum | others |
| 1 | 24-Jun | 22.2 | 0.4 | 2.5 | 3.9 | 4.2 | 22.9 | 0.7 | 1.4 | 10.2 | 21.8 | 90.1 | 9.9 |
| 2 | 24-Jun | 24.7 | 0.0 | 1.4 | 4.1 | 5.5 | 37.0 | 12.3 | 1.4 | 8.2 | 2.7 | 97.3 | 2.7 |
| 3 | 03-Aug | 6.5 | 2.0 | 5.0 | 14.0 | 0.5 | 34.0 | 1.5 | 3.0 | 1.0 | 28.0 | 95.5 | 4.5 |
| 5 | 16-Aug | 18.6 | 2.7 | 3.5 | 5.3 | 4.7 | 31.6 | 8.0 | 4.4 | 3.2 | 1.8 | 83.8 | 16.2 |
| 6 | 26-Aug | 17.0 | 6.4 | 19.7 | 2.7 | 0.0 | 8.5 | 0.0 | 6.4 | 1.1 | 34.0 | 95.7 | 4.3 |
| 7 | 14-Sep | 9.3 | 4.7 | 2.8 | 14.0 | 0.9 | 36.4 | 1.9 | 7.5 | 9.3 | 9.3 | 96.3 | 3.7 |
| 8 | 15-Sep | 8.8 | 0.0 | 9.2 | 9.7 | 2.3 | 39.2 | 4.1 | 5.5 | 10.1 | 2.3 | 91.2 | 8.8 |
| 9 | 22-Nov | 21.3 | 4.0 | 2.9 | 13.8 | 1.1 | 27.0 | 8.0 | 1.7 | 2.3 | 4.0 | 86.2 | 13.8 |
| 10 | 25-Nov | 12.2 | 7.3 | 9.1 | 5.5 | 16.7 | 30.1 | 2.7 | 1.5 | 4.3 | 5.2 | 94.5 | 5.5 |
| median | | 17.0 | 2.7 | 3.5 | 5.5 | 2.3 | 31.6 | 2.7 | 3.0 | 4.3 | 5.2 | 94.5 | 5.5 |
| IQ | | 8.0 | 2.5 | 0.9 | 1.5 | 1.6 | 6.6 | 1.6 | 1.5 | 2.6 | 2.6 | 6.4 | 1.5 |
| uQ | | 4.7 | 2.9 | 5.6 | 8.4 | 2.8 | 5.2 | 5.3 | 3.0 | 5.5 | 19.7 | 1.5 | 6.4 |
| IQ % | | 42.2 | 125 | 167 | 91.6 | 225 | 20.8 | 166 | 91.1 | 99.8 | 275 | 4.2 | 100.6 |

*Eciton burchelli* during one day. Assuming a daily hunting area of 1000 m$^2$ and a mean density of 94 *Ctenus* spiders per 1000 m$^2$ (Gasnier unpubl.) the ants would have an efficiency of 580 %. Using the maximum density in Gasnier's samples, 175 *Ctenus* spiders per 1000 m$^2$, they still would have an efficiency of 311 %. Obviously the ants cannot kill more prey than actually exists and so estimates of >100 % are biased. There is a series of possible sources for such bias. First, daily hunting area and daily hunting time were not measured for every ant colony, but instead were generalized from information in the literature. Next, the hunting efficiency of the army ants fluctuates during the day (Schneirla 1971) and a linear extrapolation from two hour-samples to eight hours might cause an error. During the morning the ants set up booty caches, where they retain prey fragments and they make a midday break (Rettenmeyer et al. 1983). The activity cycle of the ants consists of a migratory and a statary phase, which influences hunting effort (Schneirla 1971), and we do not know in which phase our sampled colonies were. We also do not know the size of the colony which was observed hunting. Another possible source of error lies in the assumption that we collected 4,4 % of all actual prey taken by the ants. The probability to loose the smallest prey fragments is certainly higher and thus, the efficiency for the large spider fragments could be higher than the overall efficiency. However, most of the above mentioned sources of error should be partially eliminated by using 30 samples, which were taken from different colonies, at different times of the day.

On the other hand our field experience leads us to the assumption that ants are much better collectors of *Ctenus* than we are, principally because they are searching every centimeter of the forest floor and the lower vegetation, and even enter in burrows and crevices. They should encounter close to 100 % of the *Ctenus* spiders. *Ctenus* densities attained by visual censusing of large areas (160 m$^2$) by men are certainly underestimates. Spider density also fluctuates considerably with area and army ants are supposed to adjust their foraging behavior to prey densities (Chadab & Rettenmeyer 1975). Using a probably more realistic density of 1 *Ctenus*/m$^2$, the ants would still prey on 54 % of them. This estimation for *Ctenus* spiders is not contradicted by the numerous observations of several workers that many spiders flee from the advancing raid, because these „spiders“ were never identified. We assume that mostly larger spiders (see above) are frequently observed escaping at the front of the raids.

A more reliable estimate of the effect on prey populati-

Table 7 Spiders as prey of *Labidus praedator* in two hour-samples (frag-spider fragments, ind-number of fragments representing individual spiders).

| sample no. | date | frag | ind | frag/ind |
|---|---|---|---|---|
| 1 | 24-Jun | 63 | 39 | 1.6 |
| 2 | 24-Jun | 18 | 12 | 1.5 |
| 3 | 03-Aug | 13 | 8 | 1.6 |
| 5 | 16-Aug | 63 | 31 | 2.0 |
| 6 | 26-Aug | 32 | 16 | 2.0 |
| 7 | 14-Sep | 10 | 6 | 1.7 |
| 8 | 15-Sep | 19 | 7 | 2.7 |
| 9 | 22-Nov | 37 | 30 | 1.2 |
| 10 | 25-Nov | 40 | 24 | 1.7 |
| median | | 32.0 | 16.0 | 1.7 |
| IQ | | 16.5 | 8.5 | 0.15 |
| uQ | | 19.5 | 14.5 | 0.3 |
| IQ % | | 56.3 | 71.9 | 13.2 |

Table 8. Species list of spiders, preyed by *Labidus praedator.*

| family | morphospecies | sum | % |
|---|---|---|---|
| Araneidae | spp. | 5 | 2.9 |
| Araneidae | *Hypognatha* sp. | 1 | 0.6 |
| Caponiidae | *Nops* sp. | 2 | 1.2 |
| Clubionidae | sp. | 2 | 1.2 |
| Corinnidae | spp. | 16 | 9.2 |
| Ctenidae | *Ctenus* spp. | 47 | 27.2 |
| Deinopidae | *Deinopis* sp. | 1 | 0.6 |
| Dipluridae | spp. | 22 | 12.7 |
| Gnaphosidae | gen.? sp. | 3 | 1.7 |
| Heteropodidae | sp. | 1 | 0.6 |
| Heteropodidae | sp.f | 3 | 1.7 |
| Lycosidae | sp. | 1 | 0.6 |
| Mygalomorphae | spp. | 8 | 4.6 |
| Mysmenidae | sp. | 2 | 1.2 |
| Pholcidae | *Blechroscelis* sp. | 1 | 0.6 |
| Pholcidae | gen.? sp. | 1 | 0.6 |
| Pisauridae | cf. *Dossenus* sp. | 1 | 0.6 |
| Pisauridae | sp. | 1 | 0.6 |
| Salticidae | spp. | 33 | 19.1 |
| Scytodidae | *Scytodes* sp. | 1 | 0.6 |
| Uloboridae | *Miagrammopes* sp. | 1 | 0.6 |
| Zodariidae | sp. | 5 | 2.9 |
| Zoridae ? | sp. | 8 | 4.6 |
| indet. | | 7 | 4.0 |
| sum | | 173 | 100 |

ons should involve the measurement of spider availability in the same area where army ants forage, before and after the hunt. This was done by OTIS et al. (1986), and they reported that spider populations were not at all affected by *Eciton burchelli* raids, whereas pseudoscorpion density was significantly reduced. In their study, however, they were only able to collect two quadrats of 1 m$^2$ in front and behind each raiding swarm, and the non-homogeneous distribution of arthropods on the forest floor resulted in a very high variability. *Ctenus* spiders are not even expected to be captured by this method; for these relatively large spiders reliable density measurements are not rapidly made and because the hunting area of the ants is not predictable, such measurements cannot be made in advance (e.g. before army ants pass), at least not in sufficiently high numbers to allow statistically significant results.

In another rainforest reserve near Manaus (Reserva Ducke) we were able to mark an area of 30 m$^2$ during the day, when *Eciton burchelli* hunted, and came back to count spiders in this area at night and we did not count even one spider.

We conclude from our data that *Eciton burchelli* can have a high direct effect (mortality) on *Ctenus* populations. Also, by prefering certain *Ctenus* species (by prefering a certain size class) over others, they might have a considerable effect on the structure of this guild of wandering spiders. This is strengthened by our observations on foraging frequence within a certain area. In an experimental plot in Reserva Ducke, during each of three sampling periods of four weeks within one year *Eciton burchelli* was caught in pitfall traps, making it highly probable that they hunted there at least three times in one year.

*Labidus* makes use of a larger portion of the existing spider assemblage and consequently should have a smaller effect on single species populations. On the other hand, observations in Panguana, Peru (VERHAAGH pers. comm.) and our own studies in Reserva Ducke indicate that *Labidus* colonies stay much longer in the same area. Samples of arboreal funnel traps (2 m above ground) have shown that the flushing effect of *Labidus praedator* on large and medium sized spiders is high (GASNIER & HÖFER unpublished). The flushing effect on spiders (and other arthropods) from the litter during foraging, exposes them to other predators like ant following ant-birds and woodcreepers (WILLIS & ONIKI 1978), monkeys (RYLANDS et al. 1989), and parasites like Tachinidae and Conopidae (RETTENMEYER 1961). This indirect impact may be higher than the direct impact by the ants (FRANKS 1982, FRANKS & BOSSERT 1983). Therefore repeated foraging by *Labidus*, in addition to foraging of *Eciton burchelli* in the same area within a short period should lead to a substantial impact on spider assemblages.

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## Appendix:

| Author | measurements of hunting area of *Eciton burchelli* | | |
|---|---|---|---|
| | width | distance | area |
| FRANKS 1982 | | 105 m | |
| FRANKS 1990 | | | 500 m$^2$/day |
| FRANKS & BOSSERT 1983 | | 116 m (migratory fase)<br>89 m (statary fase) | |
| FRANKS & FLETCHER 1983 | | 105 m | |
| FRANKS et al. 1991 | | | 1000 m$^2$/day |
| SCHNEIRLA 1971 | > 15 m (max. 25 m) | 70-140 m | 1050-2100 m$^2$/day |
| DA SILVA 1972 | | 89 m (migratory fase)<br>76 m (statary fase) | |
| WILLIS 1967 | < 15 m (mean 6 m) | | |

**andrias, 13:** 199-214; Karlsruhe, 30. 9. 1994 199

Manfred Verhaagh & Krzysztof Rościszewski

# Ants (Hymenoptera, Formicidae) of forest and savanna in the Biosphere Reserve Beni, Bolivia

**Abstract**

During an expedition to Bolivia in 1993 ants have been collected in different habitats (terra firme forest, inundation savanna, and forest islands in savanna) in the Biosphere Reserve „Estación Biológica del Beni“ Intense, mainly hand collecting yielded a total of 188 ant species within seven days. 121 species were collected from forest islands, 74 from terra firme forest and 59 from savanna. 21 species and one genus are recorded for the first time from Bolivia. Most diverse ant genera were *Camponotus* (28 spp.), *Pheidole* (25 spp.) and *Pseudomyrmex* (20 spp.). A comparison of the ant faunas of the three examined habitats showed highest similarity in species composition between different forest islands (Sørensen quotient: S > 40%). Similarity between the ant faunas of forest islands and terra firme forest, respectively forest islands and savanna (including savanna trees) was between S = 30-40%, each. Lowest similarity (S = 10-20%) showed the ant faunas of forest islands and, especially, of terra firme forest with the one of the ground and grass stratum of the savanna (without trees).

**Kurzfassung**

**Ameisen (Hymenoptera, Formicidae) aus Wald und Savanne des Biosphärenreservats Beni in Bolivien**

Während einer Expedition nach Bolivien im Jahre 1993 wurden in verschiedenen Biotopen des Biosphärenreservats Beni (terra firme-Regenwald, Überschwemmungssavanne und Waldinseln in der Savanne) Ameisen gesammelt. Insgesamt konnten innerhalb von sieben Tagen 188 Arten überwiegend durch Handfang nachgewiesen werden, und zwar 121 aus Waldinseln, 74 aus terra firme-Wald und 59 aus der Savanne. Die Funde von 29 Arten und einer Gattung stellen Erstnachweise für Bolivien dar. Die artenreichsten Gattungen waren *Camponotus* (28 spp.), *Pheidole* (25 spp.) und *Pseudomyrmex* (20 spp.). Ein Vergleich der in den drei untersuchten Biotopen gefangenen Ameisenarten zeigte, daß die Faunen der Waldinseln sich untereinander am stärksten ähnelte (Sørensen Quotient: S > 40%). Waldinseln und terra firme-Wald, bzw. Waldinseln und Savanne (einschließlich Savannenbäume) wiesen eine Faunenähnlichkeit von S = 30-40% auf. Die mit S = 10-20% geringsten Gemeinsamkeiten im Artenbestand zeigten Waldinseln und besonders der terra firme-Wald im Vergleich mit dem Boden und Grasstratum der Savanne (ohne Savannenbäume).

**Resumen**

**Hormigas (Hymenoptera, Formicidae) de bosque y sabana en la Reserva de la Biósfera „Estación Biológica del Beni“, Bolivia**

Durante una expeditión a Bolivia en el año 1993 coleccionamos hormigas en varios biótopos (bosque de tierra firme, sabana de inundación y islas forestales en la sabana) de la Reserva de la Biósfera „Estación Biológica del Beni“ En total cogimos - mayormente manualmente - 188 especies durante siete dias: 121 en islas forestales, 74 en bosque de tierra firme y 59 en la sabana. 29 especies y un género fueron encontrados por la primera vez en Bolivia. Los géneros los mas ricos en especies fueron *Camponotus* (28 spp.), *Pheidole* (25 spp.) y *Pseudomyrmex* (20 spp.). La comparación de los tres biotopos monstró que la fauna de las islas forestales entre sí fue la mas similar (Sørensen cociente: S < 40%). Islas forestales y bosque de tierra firme o sea islas forestales y sabana (incluido arboles) monstraron una similitud de S = 30-40%. Islas forestales y bosque de tierra firme se parecieron lo menos (S = 10-20%) en la composición de su fauna al suelo y estrato graminal de la sabana (sin arboles).

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## 1. Introduction

In July 1993 the second author had the opportunity to participate in an expedition to Bolivia organized under a convention between the Staatliches Museum für Naturkunde Karlsruhe (SMNK) and the Colleción Boliviana de Fauna La Paz (CBF) (for details see Höfer & Brescovit 1994, this volume). The main purpose of the journey was to collect animals in different ecoregions of Bolivia to broaden the still poor faunistic knowledge about this country. Here we present a species list of ants collected around the Biological Station of the Biosphere Reserve Beni (Estación Biológica del Beni - El Porvenir).

## 2. Locality and methods

### Locality

Sampling was conducted around the Estancia El Porvenir, northeast of San Borja, Departamento Beni, at the Estación Biológica del Beni (EBB; 66°38' W 14°30' S midpoint, 175 - 190 m a.s.l.), a biosphere reserve with a surface of 135,000 ha situated at the southwestern edge of the Beni savannas. A description of landscape, climate and vegetation of the area is given by Hanagarth (1993). The whole region is an ecotone of forests and (seasonal) wet areas of which about 70% are inundated for several months every year (duration and height of inundation depending on the relief). Beside low inundation forests (mainly 10 - 15 m high), poor in tree species, there exist evergreen as well as seasonal evergreen high forests

Table 1. Pattern of standardized sampling in different habitats at EBB with daytime and date; FI 1-3: Forest islands in savanna; Sav: Inundation savanna; P: single trees, *Pseudobombax marginatum*, in the savanna; BS: *Ficus* tree at the Biological station in savanna; Tf: Terra firme forest near Trapiche, 8 km from the Biological Station; down: - searching for 2 h. on the ground, including litter, roots, and rotten wood; up: - searching for 1 h. (the same area as „down") the lower vegetation stratum including foliage, twigs, hanging rotten wood and the bark of trees.

| | FI 1 | | FI 2 | | FI 3 | | Sav | P | BS | Tf | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | down | up | down | up | down | up | | | | down | up |
| day: | | | | | | | | | | | |
| date | 21.7.93 | 21.7.93 | 21.7.93 | 21.7.93 | 22.7.93 | 22.7.93 | 23.7.93 | 23.7.93 | 20.7.93 | 26.7.93 | 26.7.93 |
| time | 10-12 | 12-13 | 14:30-16:30 | 16:30-17:30 | 10-12 | 12-13 | 9:30-11:30 | 12-13 | 12-13 | 9:30-11:30 | 11:30-12:30 |
| | | | | | | | 24.7.93 | | 20.7.93 | | |
| | | | | | | | 9:30-11:30 | | 17-18 | | |
| night: | | | | | | | | | | | |
| date | 22.7.93 | 22.7.93 | 23.7.93 | 23.7.93 | | | | | | | |
| time | 19-21 | 21-22 | 19-21 | 21-22 | | | | | | | |

(terra firme) of 30 - 40 m height. Especially around El Porvenir inundation savannas are dominating the landscape with interspersed forest islands of different size (see HANAGARTH 1993, and HÖFER & BRESCOVIT 1994 for photographic illustration of the area).

## Sampling sites

1. Terra firme forest (= Tf) near Trapiche, about 8 km from El Porvenir, moderately influenced by human activities and cattle.
2. Forest islands (= FI) in inundation savanna near the Estancia El Porvenir, in a distance of approx. 1 km from one each other.
   a. Forest island 1 (FI 1), about 0.05 ha
   b. Forest Island 2 (FI 2), about 0.05 ha
   – c. Forest Island 3 (FI 3), about 1.5 ha

FI 1 and FI 2 were strongly influenced by cattle, but not FI 3; this forest island had much undergrowth.

The whole area of FI 1 and FI 2 was searched for ants completely, in FI 3 ants were collected in a plot of equivalent size. From a fourth forest island (FI 4) a litter sample was included in the results.

3. Inundation savanna (= Sav), between FI 1 - FI 2 and FI 2 - FI 3, respectively, and several small solitary trees, *Pseudobombax marginatum*, Bombacaceae (= Sav-tr) at different sites in the savanna.
4. Stem of a big *Ficus* tree, Moraceae (at 1-3 m height) at the research station in savanna vegetation (= Sav-tr).

## Methods

Ants were mainly hand collected between 20-27 July 1993 (7 sampling days) according to methods proposed by CODDINGTON et al. (1991) for spiders but modified in order to collect ants - and further called „standardized sampling" - in the following scheme (see tab. 1):

„looking down": a careful examination (on the knees) of the ground layer including the litter, roots, and rotten wood (2 h.).

„looking up": a search in about the same area as in „looking down" but of the lower vegetation stratum above the knee up to a height of 2 - 2.5 m including foliage, twigs, hanging rotten wood, and bark of the tree stems (1 h.).

The aim of such a sampling procedure is not to pick up every ant encountered but to detect as much different species as possible. Thus, just some voucher specimens of each assumed assemblage or colony were taken and not much time was spent when a nest was found.

Terra firme forest and forest islands were sampled 3 hours during the day, 2 h. on the ground, 1 h. in the vegetation. In the savanna we searched for ants 2 times 2 h. during the day, on the *Ficus* tree 2 times 1 h., and on the *Pseudobombax* trees 1 h. FI 1 and FI 2 were sampled for another 3 hours during the night (2 h. ground, 1 h. vegetation). In the savanna we did not collect at night, because the vegetation was completely wet.

Beside this standardized sampling some more random hand collecting was done during the day and, in the forests, at night as well. Additionally, from each of the four forest islands (FI 1 - FI 4) 2 $m^2$ litter were collected and searched for ants. The complete sample number ( samples ranging from a single ant to part of a nest) was 495, with 313 from forest islands (143 FI 1, 96 FI 2, 64 FI 3, 10 FI 4), 93 from terra firme forest, and 88 from savanna (62 from low vegetation and ground, 26 from trees). 1 sample (*Solenopsis saevissima*) from the station's kitchen was counted as savanna sample. 407 of all samples were collected during the day, 8 a.m. to 6 p.m. and 88 at night from 7 to 10 p.m.

For comparison of species similarity in two habitats we used the SØRENSEN quotient:

$$S = 2j/(a+b) \times 100(\%)$$

where j is the number of species common (joint) to the two habitats compared and a and b are respectively the total number of species in each habitat (SOUTHWOOD 1978). We made no efforts to test significance for different values of S in habitat comparisons as we think that the ant fauna could not be sampled sufficiently within the 7 days we spent at EBB.

Species determination was done by the first author and is, if not otherwise stated, based on workers. Beside the actual taxonomic literature some species were identified by direct comparisons with species of the ant collection of the SMNK which were formerly cross-checked with material in the ant collection of the Museum of Comparative Zoology, Cambridge. New records for Bolivia are mainly based on the catalogues of neotropical ants of KEMPF (1972) and BRANDÃO (1991). Specimens are deposited in the collections of SMNK and CBF.

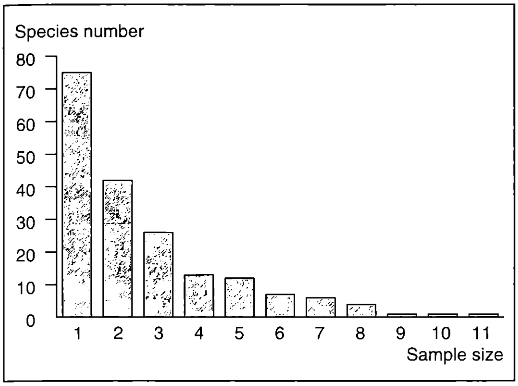

Figure 1. Relation between sampling frequency (sample size) and species number for all 188 species collected at EBB.

## 3. Results and Discussion

During the 7-day-expedition to EBB we found a total of 188 ant species representing 43 genera from 6 subfamilies (tab. 7, see comments on some species in the appendix). 5 species were only represented by single dealated queens, or males (*Gnamptogenys* sp. [*rastrata*-group], *Pseudomyrmex* sp. 3, *Procryptocerus* sp., *Apterostigma* sp., and *Labidus coecus*). 148 species were found during 25 h. of standardized sampling (tab. 1, tab. 8), another 40 species by additionally hand sampling and litter searching. Only six species were exclusively found in the litter samples (*Apterostigma* sp., *Strumigenys eggersi*, *Pheidole* sp. 25, *Monomorium floricola*, *Solenopsis* (*Diploropthrum*) sp. 3, *Iridomyrmex* sp. 1), and one species, *Solenopsis saevissima*, was only collected in the kitchen of the station.

129 species were collected exclusively during the day, 41 species during night and day, and 18 species at night only (in the majority *Camponotus* species). As many species (62,2 %) were found only one or two times (fig. 1) it cannot be stated in many cases whether a species is definitely diurnal or nocturnal.

Many species - so far determination was possible - are widespread in the neotropics and typical elements of the Amazonian ant fauna. Most abundant were the Myrmicinae with 80 species, followed by Formicinae (36 spp.), Ponerinae (31 spp.), Pseudomyrmicinae (20 spp.), Dolichoderinae (17 spp.), and at last 4 species of Ecitoninae (tab. 3, 7). 29 species and 1 genus represent new records for Bolivia (tab. 2). The collection in its proportional composition and dominance ranking is highly similar to the hitherto species richest known ant fauna of the neotropics, the one of Panguana in central Amazonian Peru (tab. 3) which was assessed during 27 months field work and comprised both forest and open habitats (pastures, plantations; VERHAAGH 1990, 1991 and unpubl. results). Thus, the collecting methods used in Bolivia seem to be highly effective for a quick assessment of the relative composition of the ant fauna. There are two main exceptions: Ecitoninae and small Dacetini (*Strumigenys*, *Smithistruma* a. o. genera) were not well represented in this collection with 2.1, respectively 1.6%, of the whole fauna when compared with the fauna of Panguana, where, both Ecitoninae and Dacetini, each had a portion of 4.8% of the whole fauna. Reasons for the former are in our opinion their nomadic habits which makes longer study periods necessary to find more species. For the latter, their cryptic life style requires intense sampling by extraction methods (BERLESE, WINKLER etc.). For the same reason, other small cryptic living ants with small colony size of different genera and

Table 2. Species recorded for the first time from Bolivia

Ponerinae
*Platythyrea angusta* FOREL 1901
*Hypoponera opaciceps* (MAYR 1887)
*Hypoponera parva* (FOREL 1909)
*Pachycondyla* (= *Neoponera*) *apicalis* (LATREILLE 1802)
*Pachycondyla* (= *Mesoponera*) *constricta* (MAYR 1883)
*Pachycondyla* (= *Neoponera*) *obscuricornis* (EMERY 1890)
*Pachycondyla* (= *Neoponera*) *unidentata* (MAYR 1862)

Ecitoninae
*Eciton vagans* (OLIVIER 1791)

Pseudomyrmicinae
*Pseudomyrmex dendroicus* (FOREL 1904)
*Pseudomyrmex ethicus* (FOREL 1911)
*Pseudomyrmex filiformis* (FABRICIUS 1804)
*Pseudomyrmex maculatus* (F. SMITH 1855)
*Pseudomyrmex simplex* (F. SMITH 1877)

Myrmicinae
*Cyphomyrmex major* FOREL 1901
*Cyphomyrmex minutus* MAYR 1862
*Mycetarotes parallelus* (EMERY 1905)
- first record of the genus from Bolivia
*Eucryptocerus placidus* (F. SMITH 1860)
*Strumigenys cordovensis* MAYR 1887
*Nesomyrmex asper* (MAYR 1887)
*Nesomyrmex echinatinodis* (FOREL 1886)
*Monomorium floricola* (JERDON 1852)
*Solenopsis bondari* SANTSCHI 1925

Formicinae
*Camponotus* (*Myrmaphaenus*) *novogranadensis* MAYR 1870
*Camponotus* (*Myrmobrachys*) *burtoni* MANN 1916
*Camponotus* (*Myrmothrix*) *femoratus* (FABRICIUS 1804)
*Camponotus* (*Tanaemyrmex*) *abuanus* MANN 1916
*Camponotus* (*Tanaemyrmex*) *hagemanni* FOREL cit. apud SANTSCHI 1922
*Dendromyrmex chartifex* (F. SMITH 1860)
*Paratrechina longicornis* (LATREILLE 1802)

Table 3. a) Comparison of the ant fauna of EB Beni, Bolivia and Panguana, Peru (VERHAAGH 1990, 1991 and unpubl.). Number of species [n] and relative portion [%]. b) Comparison of the 10 most diverse ant genera of EB Beni and Panguana, number of species [n] and relative portion of the total species number [%].

| a) | EBB, Bolivi | | Panguana, Peru | |
|---|---|---|---|---|
| | n | % | n | % |
| Ponerinae | 31 | 16.5 | 92 | 17.7 |
| Ecitoninae | 4 | 2.1 | 25 | 4.8 |
| Pseudomyrmicinae | 20 | 10.6 | 33 | 6.3 |
| Myrmicinae | 80 | 42.6 | 242 | 46.5 |
| Dolichoderinae | 17 | 9.0 | 47 | 9.0 |
| Formicinae | 36 | 19.1 | 81 | 15.6 |
| Σ | 188 | | 520 | |

b)

| EBB, Bolivia | | % | Panguana, Peru | | % |
|---|---|---|---|---|---|
| *Camponotus* | 28 | 14.9 | *Pheidole* | 57 | 11.0 |
| *Pheidole* | 25 | 13.3 | *Camponotus* | 52 | 10.0 |
| *Pseudomyrmex* | 20 | 10.6 | *Pseudomyrmex* | 33 | 6.3 |
| *Solenopsis* | 12 | 6.4 | *Gnamptogenys* | 23 | 4.4 |
| *Crematogaster* | 10 | 5.3 | *Solenopsis* | 23 | 4.4 |
| *Pachycondyla* | 9 | 4.8 | *Crematogaster* | 22 | 4.2 |
| *Zacryptocerus* | 9 | 4.8 | *Pachycondyla* | 21 | 4.0 |
| *Dolichoderus* | 8 | 4.3 | *Dolichoderus* | 21 | 4.0 |
| *Gnamptogenys* | 6 | 3.2 | *Azteca* | 18 | 3.5 |
| *Hypoponera* | 6 | 3.2 | *Strumigenys* | 18 | 3.5 |
| Σ | 133 | 70.8 | | 288 | 55.3 |

subfamilies (Ponerinae, Myrmicinae, Formicinae) are believed to be underrepresented, too. On the other hand, Formicinae and Pseudomyrmicinae were relatively highly represented in the samples of EBB, in comparison to Panguana. This might be due to the collecting method biased towards epigeic and arboreal species, or to a real difference in the composition of the ant faunas of EBB and Panguana. Approx. 60% of the collected ant species can probably be regarded as at least partly arboreal or living in vegetation. In Panguana the proportion was about 50%.

## 3.1 Comparison of the faunal composition in different habitats

Most species were found in the forest islands, primarly, due to the longer time spent in these habitats but also due to higher species numbers than in the other habitats as revealed by comparison of species numbers after the same sampling time (tab. 8). 66 species (35.1%) were exclusively recorded from these forest islands in contrast to 39 (20.7%) from terra firme forest and 25 (13.3%) from the savanna. Only 8 species were common to all three habitats.

### Forest islands

In the forest islands ant species of all subfamilies but Ecitoninae were well present. Especially species rich in these habitats were *Pheidole*, *Camponotus*, *Pseudomyrmex*, *Crematogaster* and *Zacryptocerus*. The standardized sampling showed on the average within a single forest island the following degrees of similarity: $S(\bar{x}) = 43.2\%$ (ground ant fauna) and 25.0% (vegetation ant fauna) in a comparison day versus night, and 23.5% (day) and 30.0% (night) in a comparison between ground versus vegetation ant fauna (tab. 4). The least similar samples were the nocturnal ones from the ground compared with those from the vegetation during the day ($\bar{x} = 10.2\%$).

The similarities between the different islands FI 1, FI 2 and FI 3 (tab. 4) were also higher in the ground fauna ($S = 29.0 - 47.7\%$, $\bar{x} = 38.7\%$) than in the fauna found in the vegetation ($S = 8.2 - 36.8\%$, $\bar{x} = 22.3\%$). The two smaller islands FI 1 and FI 2 (0.05 ha each) seemed to be more similar to each other in their faunal composition than to the larger (1.5 ha) forest island FI 3 (tab. 4 and 8).

### Terra firme forest

The most striking feature of the terra firme forest ant fauna was the relatively high proportion of Ponerinae and *Camponotus* species as well as the occurrence of all four army ant species (Ecitoninae) encountered during this study. Similarity between ground and vegetation fauna was low ($S < 20\%$). We assume that this is the least completely sampled habitat in the study.

### Savanna

Very conspicuous was the dissimilarity between the ant fauna found on the ground and in the grass layer of the savanna and the ants on the savanna trees. The two examined savanna areas situated between forest islands FI 1 - FI 2 and FI 2 - FI 3 - showed a high level of species overlap ($S = 45.5\%$, tab. 4). In contrast, similarity with the savanna tree fauna was very low in the standardized samples (tab. 4, 5) as well as regarding overall sampling ($S = 12.7\%$, tab. 6). The total number of 39 species found in the savanna (not regarding savanna trees) seems to be very low and may be in part due to methodical reasons: We did not collect at night, and collecting in general was difficult in the grass layer of the savanna. The only ant genera better represented in this habitat were *Pseudomyrmex*, *Pheidole* and *Camponotus* whereas we did not find any dolichoderine species.

Of the few trees examined, most species (20 out of 24) were found on the stem of a single *Ficus* at the biologi-

Table 4. Species similarity between habitats (standardized sampling). Indicated are SØRENSEN quotients (in %) and species numbers common to both habitats compared. Fl 1 - Fl 3. = Forest islands; Tf = Terra firme forest; Sav1 + 2 = Savanna between Fl 1-Fl 2 respectively Fl 2-Fl 3, without trees; Sav-tr = Trees in savanna; gro = ground, veg = vegetation, d = day, n = night; species number of habitats in ().

| | Fl1 gro n (27 spp) | Fl1 veg d (27 spp) | Fl1 veg n (20 spp) | Fl2 gro d (42 spp) | Fl2 gro n (20 spp) | Fl2 veg d (16 spp) | Fl2 veg n (9 spp) | Fl3 gro d (27 spp) | Fl3 veg d (22 spp) | Tf gro d (18 spp) | Tf veg d (13 spp) | Sav1 d (21 spp) | Sav2 d (23 spp) | Sav-tr d (24 spp) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fl1 gro d (46 spp) | 41.1%-15 | 35.6%-13 | 24.2%-8 | 47.7%-21 | 21.2%-7 | 16.1%-5 | 14.5%-4 | 35.6%-13 | 26.5%-9 | 18.8%-6 | 13.6%-4 | 9.0%-3 | 5.8%-2 | 22.9%-8 |
| Fl1 gro n (27 spp) | | 3.7%-1 | 25.5%-6 | 34.8%-12 | 42.6%-10 | 4.7%-1 | 22.2%-4 | 25.9%-7 | 4.1%-1 | 17.8%-4 | 5.0%-1 | 8.3%-2 | 16.0%-4 | 3.9%-1 |
| Fl1 veg d (27 spp) | | | 34.0%-8 | 23.2%-8 | 0 | 23.3%-5 | 0 | 0 | 8.2%-2 | 0 | 10.0%-2 | 4.2%-1 | 4.0%-1 | 51.0%-13 |
| Fl1 veg n (20 spp) | | | | 3.2%-1 | 15.0%-3 | 0 | 20.7%-3 | 8.5%-2 | 4.8%-1 | 5.3%-1 | 12.1%-2 | 4.9%-1 | 4.7%-1 | 27.3%-6 |
| Fl2 gro d (42 spp) | | | | | 45.2%-14 | 10.3%-3 | 15.7%-4 | 29.0%-10 | 34.4%-11 | 20.0%-6 | 18.2%-5 | 12.7%-4 | 21.5%-7 | 21.2%-7 |
| Fl2 gro n (20 spp) | | | | | | 16.7%-3 | 34.5%-5 | 29.8%-7 | 14.3%-3 | 26.3%-5 | 6.1%-1 | 14.6%-3 | 23.3%-5 | 0 |
| Fl2 veg d (16 spp) | | | | | | | 16.0%-2 | 14.0%-3 | 36.8%-7 | 11.8%-2 | 34.5%-5 | 0 | 5.1%-1 | 30.6%-6 |
| Fl2 veg n (9 spp) | | | | | | | | 22.2%-4 | 25.8%-4 | 22.2%-3 | 18.2%-2 | 0 | 6.3%-1 | 6.1%-1 |
| Fl3 gro d (27 spp) | | | | | | | | | 24.5%-6 | 26.7%-6 | 10.0%-2 | 0 | 4.0%-1 | 3.9%-1 |
| Fl3 veg d (22 spp) | | | | | | | | | | 20.0%-4 | 17.1%-3 | 4.7%-1 | 8.9%-2 | 17.4%-4 |
| Tf gro d (18 spp) | | | | | | | | | | | 19.4%-3 | 5.1%-1 | 4.9%-1 | 0 |
| Tf veg d (13 spp) | | | | | | | | | | | | 0 | 0 | 0 |
| Sav 1 d (21 spp) | | | | | | | | | | | | | 45.5%-10 | 8.9%-2 |
| Sav 2 d (23 spp) | | | | | | | | | | | | | | 12.8%-3 |

cal station. They were mostly *Pseudomyrmex*, Cephalotini and *Camponotus* species. Ponerinae, Ecitoninae, Attini, Dacetini, Leptothoracini, Pheidolini and Solenopsidini were not found on the stems of the examined trees.

### 3.2 Comparison between the habitats

#### Forest islands and terra firme forest

Similarity quotients of the different standardized sampling in forest islands and in terra firme forest during the day were between 0 and 34.5%, with an average of only 16.7% (tab. 4). The quotients were higher (between 20 and 30%) when collections of ants from the ground and vegetation were taken together (tab. 5). Highest similarity (S = 35.3%) resulted when all samples of the habitats collected during the day were recognized (tab. 6). Regarding all samples, both habitats had 32 species in common.

#### Forest islands and savanna

Comparison of single standardized samples (tab. 4) resulted in average similarity quotients of 8.8% (2 h. collections of the ground of forest islands versus 2 h. savanna collections excluding trees) and 4.5% for vegetation collections of forest islands (1 h.) versus savanna collections (2 h.). Much higher were the SØRENSEN quotients when samples from ground or vegetation of forest islands were compared with those from the few examined savanna trees (*Ficus* and *Pseudobombax*): $\bar{x}$ = 16.0, respectively 32.8%, with a top similarity of 51.0% between ants from savanna trees and vegetation of Fl 1 (tab. 4). These direct comparisons between standardized collections yielded a total mean of only 12.6%. Higher quotients resulted from combined data of diurnal sampling on the ground and in the vegetation of the forest islands, respectively grass stratum and trees in the savanna: up to 39.6% in standardized sampling (tab. 5) and 38.7% regarding all samples (tab. 6). A look

Table 5. Species similarity between habitats (standardized sampling). Species found on the ground or in the vegetation are taken together for forest islands and terra firme forest. Indicated are SØRENSEN quotients (in %) and species number common to both habitats compared. Fl 1 - Fl 3. = Forest islands; Tf = Terra firme forest; Sav1 + 2 = Savanna between Fl 1-Fl 2 respectively Fl 2-Fl 3, without trees; Sav-tr = Trees in savanna; d = day, n = night; species number of habitats in (), n.d. = not determined.

| | Fl 1 n (40 spp) | Fl 2 d+n (54 spp) | Fl 2 d (44 spp) | Fl 2 n (23 spp) | Fl 3 d (44 spp) | Sav1 + Sav-tr d (41 spp) | Sav2 + Sav-tr d (42 spp) | Sav1+2 d (34 spp) | Sav-tr d (24 spp) | Tf d (28 spp) |
|---|---|---|---|---|---|---|---|---|---|---|
| Fl 1 d+n (79 spp) | n.d. | 49.6%-33 | n.d. | n.d. | 34.1%-21 | 31.6%-19 | 31.4%-19 | 15.9%-9 | 31.1%-16 | 20.6%-11 |
| Fl 1 d (60 spp) | 42.2%-23 | n.d. | 46.2%-24 | 21.7%-9 | 36.5%-19 | 39.6%-20 | 39.2%-20 | 12.8%-6 | 38.1%-16 | 22.7%-10 |
| Fl 1 n (40 spp) | | n.d. | 28.6%-12 | 41.3%-13 | 23.8%-10 | 19.8%-8 | 22.0%-9 | 13.5%-5 | 18.8%-6 | 14.7%-5 |
| Fl 2 d+n (54 spp) | | | n.d. | n.d. | 44.9%-22 | 25.3%-12 | 29.2%-14 | 25.0%-11 | 20.5%-8 | 29.3%-12 |
| Fl 2 d (44 spp) | | | | 41.8%-14 | 38.6%-17 | 23.5%-10 | 27.9%-12 | 23.1%-9 | 20.6%-7 | 27.8%-10 |
| Fl 2 n (23 spp) | | | | | 32.8%-11 | 12.5%-4 | 18.5%-6 | 21.1%-6 | 4.3%-1 | 27.5%-7 |
| Fl 3 d (44 spp) | | | | | | 11.8%-5 | 14.0%-6 | 7.7%-3 | 8.8%-3 | 27.8%-10 |
| Sav1+ Sav-tr d (41 spp) | | | | | | | n.d. | n.d. | n.d. | 5.8%-2 |
| Sav2+ Sav-tr d (42 spp) | | | | | | | | n.d. | n.d. | 2.9%-1 |
| Sav1+2 d (34 spp) | | | | | | | | | 10.3-3 | 6.5%-2 |
| Sav-tr d (24 spp) | | | | | | | | | | 0 |

on the combined samples shows that the ant fauna from the trees is responsible for the higher quotients. Without the fauna of savanna trees similarity of forest islands and savanna remains low (S < 20%) even when all samples are considered. Similar results were reported by VERHAAGH (1991) from pastures in Panguana, Peru, where also the total number of species in the grassland strongly depended on the presence of trees.

### Terra firme forest and savanna

Both habitats were extremely dissimilar in the samples taken. Most samples of these habitats had none or just a single species in common, therefore the average SØRENSEN quotient was extremely low (S = 1.7%). The quotients remained low in combined standardized samples (tab. 5) and reached only 16.5% in the comparison of all collections (tab. 6) when savanna trees were included, and 8.8% (or just 5 species common to both habitats) when not. Thus, terra firme forest and savanna showed the lowest overlap in species composition of the three examined habitats.

## 4. Conclusions

The collection of 188 ant species in 7 days is certainly far away from a complete species inventory of the examined habitats. Nevertheless, the intense search resulted in a collection that is very similar in its relative taxonomic composition to the better known Amazonian ant fauna of Panguana, Peru (VERHAAGH 1990, 1991 and unpubl.). The standardized method yielded 148 species in 25 collecting hours but duration of sampling was to short as shown by increasing SØRENSEN quotients when more samples were included in the comparisons. The quotient, however, depends also on the question whether compared units were collected under similar conditions (collecting duration, day time of collecting, strata etc.).

In spite of the limits set by short collecting time some preliminary conclusions can be drawn regarding the three compared habitats:

1. The ant faunas of the forest islands show greatest similarity among each other especially those of the

Table 6. Species similarity between habitats regarding all - standardized and additional - samples from ground, litter and vegetation. Indicated are SØRENSEN quotients (in %) and species numbers common to both habitats compared. FI = Forest islands (FI 1-4); Sav = Savanna between FI 1-FI 2 respectively FI 2-FI 3, without trees; Sav-tr = Trees in savanna; Tf = Terra firme forest; d = day; species number of habitats in (); n.d. = not determined.

| | Sav total + Sav-tr (59 spp) | Sav total (39 spp) | Sav-tr (24 spp) | Tf total (74 spp) |
|---|---|---|---|---|
| FI total (121 spp) | 34.4%-31 | 18.8%-15 | 26.2%-19 | 32.8%-32 |
| FI d (96 spp) | 38.7%-30 | 17.8%-12 | 20.0%-18 | 35.3%-30 |
| Sav total + Sav-tr (59 spp) | | n.d. | n.d. | 16.5%-11 |
| Sav total (39 spp) | | | 12.7-4 | 8.8%-5 |
| Sav-tr (24 spp) | | | | 10.2%-5 |

two smaller islands.

2. The combined ant faunas of the forest islands seem to be almost equally similar to the ant faunas of the terra firme forest and the savanna when savanna trees are included.
3. Low similarity seems to exist between the faunas of forest islands and that of the ground and the grass stratum of the savanna (excluding trees), and, especially, between the savanna ant fauna and that of terra firme forest.

An explanation for these results may be that forest islands and terra firme forest show a lot of structural similarities thus offering a similar spectrum of nesting sites. But both forest types differ considerably in their physical settings and therefore in their ecological conditions. The small forest islands should be characterized by a warmer climate because radiation is higher inside than in the continous terra firme forest. This could result, for example, in an unability for heat sensible army ants to colonize these islands permanently.

Even more severe consequences for terrestrial, especially hypogeic ant species should result from the annual flooding of the savanna for several months which effects the forest islands, too. Therefore the preponderance of at least partly arboreal species that we found in the samples is possibly not exclusively a methodical one but can be explained by ecological reasons. The Estación Biológica del Beni is apparently an exellent area for comparative studies on habitat choice, competition and ecological effects of physical stress in a tropical ant fauna.

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## Appendix

Table 7. Occurrence of ant species around EBB - El Porvenir according to different habitats and daytime; Fl-lit = from litter samples of forest islands Fl 1-4; Fl-gro = from ground stratum of forest islands (looking down); Fl-veg = from lower vegetation stratum of forest islands (looking up); Sav = from soil surface and grass stratum of inundation savanna; Sav-tr = from trees in savanna, P = *Pseudobombax marginatum*, BS = *Ficus* sp. at the Biological Station; Tf-gro = from ground stratum in terra firme forest; Tf-veg = from lower vegetation stratum in terra firme forest; d = capture between 8.00 and 18.00, $x^{lit}$ = species represented by litter sample only; n = capture between 19.00 and 22.00; sa = number of samples; q/$^{q}$ = species represented by a single dealated queen only, $^{aq}$ = including a single alated female, m/$^{m}$ = species represented by a single male only; $^{ki}$ = species collected only in the kitchen of the station; $^{hyp}$ = species found in the soil (hypogeicly); $^{n}$ = located nest.

| | Fl-lit | Fl-gro | Fl-veg | Sav | Sav-tr | Tf-veg | Tf-gro | d | n | sa |
|---|---|---|---|---|---|---|---|---|---|---|
| Species number | 31 | 89 | 65 | 39 | 24 | 46 | 36 | 170 | 59 | |
| Ponerinae (31) | | | | | | | | | | |
| Amblyoponini (1) | | | | | | | | | | |
| *Prionopelta* sp. | | x | | | | | | x | | 1 |
| Ectatommini (9) | | | | | | | | | | |
| *Ectatomma edentatum* ROGER 1863 | $x^{\text{Fl 3}}$ | x | | x | | | | x | x | 4 |
| *Ectatomma quadridens* (FABRICIUS 1793) | $x^{\text{Fl 1}}$ | x | | | | | | x | | 3 |
| *Ectatomma tuberculatum* (OLIVIER 1791) | | | | x | | | | x | | 1 |
| *Gnamptogenys* cf. *tornata* (ROGER 1861) | | x | | x | | | | x | | 2 |
| *Gnamptogenys* cf. *rustica* (SANTSCHI 1929) | | x | | | | | x | x | x | 2 |
| *Gnamptogenys* cf. *sulcata* (F. SMITH 1858) | | | x | | | | | x | | 1 |
| *Gnamptogenys teffensis* (SANTSCHI 1929) | | x | | | | | | x | x | 2 |
| *Gnamptogenys* sp. | | | | | | | x | x | | 1 |
| *Gnamptogenys* sp. (*rastrata*-group) (q) | | | | | | | x | $x^{q}$ | | 1 |
| Platythyreini (1) | | | | | | | | | | |
| *Platythyrea angusta* FOREL 1901 | | | | | | x | | x | | 2 |
| Ponerini (19) | | | | | | | | | | |
| *Anochetus mayri* EMERY 1884 | | | | x | | | | x | | 1 |
| *Hypoponera distinguenda* (EMERY 1890) | $x^{\text{Fl 3,4}}$ | x | | | | | | x | | 3 |
| *Hypoponera opaciceps* (MAYR 1887) | | | | | | | x | x | | 1 |
| *Hypoponera parva* (FOREL 1909) | $x^{\text{Fl 3}}$ | $x^{aq}$ | | | | | | x | | 3 |
| *Hypoponera* cf. *trigona* (MAYR 1887) | $x^{\text{Fl 2}}$ | x | | | | | | x | | 3 |
| *Hypoponera* sp. (near *opaciceps*) | | | | x | | | $x^{hyp}$ | x | | 3 |
| *Hypoponera* sp. 1 | | x | | | | | | | x | 1 |
| *Odontomachus brunneus* (PATTON 1894) | $x^{\text{Fl 2}}$ | x | | x | | | x | x | x | 5 |
| *Odontomachus haematodus* (LINNAEUS 1758) | | $x^{n}$ | x | | | x | x | x | x | 8 |
| *Odontomachus minutus* EMERY 1894 | | x | | | | | x | x | x | 6 |
| *Pachycondyla (=Neoponera) apicalis* (LATREILLE 1802) | | x | x | | | | | x | | 4 |
| *Pachycondyla* (=*Mesoponera*) constricta (MAYR 1883) | | x | | x | | | | x | x | 4 |
| *Pachycondyla crassinoda* (LATREILLE 1802) | | | | | | | $x^{n}$ | x | | 2 |
| *Pachycondyla* (=*Neoponera*) *crenata* (ROGER 1861) | | x | | | | x | | | x | 2 |
| *Pachycondyla harpax* (FABRICIUS 1804) | $x^{\text{Fl 1}}$ | x | | | | | | x | x | 4 |
| *Pachycondyla* (=*Neoponera*) *obscuricornis* (EMERY 1890) | | | | | | | x | x | | 1 |
| *Pachycondyla* (=*Trachymesopus*) *stigma* (FABRICIUS 1804) | | x | | | | | | x | | 2 |
| *Pachycondyla* (=*Neoponera*) *unidentata* (MAYR 1862) | | | | | | x | | x | | 1 |
| *Pachycondyla* (=*Neoponera*) *villosa* (FABRICIUS 1804) | | x | x | | | x | x | x | x | 9 |
| Typhlomyrmicini (1) | | | | | | | | | | |
| *Typhlomyrmex pusillus* EMERY 1894 | | | | | | | $x^{hyp}$ | x | | 1 |

| | Fl-lit | Fl-gro | Fl-veg | Sav | Sav-tr | Tf-veg | Tf-gro | d | n | sa |
|---|---|---|---|---|---|---|---|---|---|---|
| Ecitoninae (4) | | | | | | | | | | |
| *Eciton drepanophorum* (F. Smith 1858) | | | | x | | | x | x | | 2 |
| *Eciton vagans* (Olivier 1791) | | | | | | | x | x | | 1 |
| *Labidus coecus* (Latreille 1802) (m) | | | | | | | x | $x^{m}$ | | 1 |
| *Neivamyrmex gradualis* Borgmeier 1953 | | | | | | | x | x | | 2 |
| Pseudomyrmicinae (20) | | | | | | | | | | |
| *Pseudomyrmex curacaensis* (Forel 1912) | | x | $x^{n}$ | | | | | x | | 4 |
| *Pseudomyrmex dendroicus* (Forel 1904) | | | | | | $x^{n}$ | | x | | 2 |
| *Pseudomyrmex eduardi* (Forel 1912) | | x | x | | $x^{BS}$ | x | | x | | 5 |
| *Pseudomyrmex elongatus* (Mayr 1870) | | x | x | | | | | x | | 3 |
| *Pseudomyrmex ethicus* (Forel 1911) | | | x | | | x | x | x | | 3 |
| *Pseudomyrmex filiformis* (Fabricius 1804) | | | x | | | | | x | | 1 |
| *Pseudomyrmex gracilis* (Fabricius 1804) | | x | x | $x^{n}$ | $x^{BS}$ | | | x | | 7 |
| *Pseudomyrmex laevifrons* Ward 1989 | | | | | $x^{BS}$ | | | x | | 1 |
| *Pseudomyrmex maculatus* (F. Smith 1855) | | x | x | | | | | x | | 3 |
| *Pseudomyrmex oculatus* (F. Smith 1855) | | x | x | | | x | | x | | 5 |
| *Pseudomyrmex sericeus* (Mayr 1870) | | | x | | | | | x | | 1 |
| *Pseudomyrmex simplex* (F. Smith 1877) | | x | x | x | $x^{BS}$ | | | x | | 5 |
| *Pseudomyrmex tenuis* (Fabricius 1804) | $x^{Fl\,4}$ | x | x | | | x | x | x | | 7 |
| *Pseudomyrmex tenuissimus* (Emery 1906) | | x | x | | $x^{BS}$ | | | x | | 5 |
| *Pseudomyrmex termitarius* (F. Smith 1855) | | | | x | | | | x | | 3 |
| *Pseudomyrmex triplarinus* (Wedell 1849) | | | | | | x | | x | | 1 |
| *Pseudomyrmex* sp. 1 (*pallidus*-group) | | | | x | | | | x | | 3 |
| *Pseudomyrmex* sp. 2 (*pallidus*-group) | | | | $x^{n}$ | $x^{BS}$ | | | x | | 3 |
| *Pseudomyrmex* sp. 3 (q) | | | | x | | | | $x^{q}$ | | 1 |
| *Pseudomyrmex* sp. 4 (*viduus*-group) | | | | | | $x^{n}$ | | x | | 1 |
| Myrmicinae (80) | | | | | | | | | | |
| Attini (11) | | | | | | | | | | |
| *Acromyrmex subterraneus* Forel 1893 | | | | | | | x | x | | 1 |
| *Apterostigma* sp. (m) | $x^{Fl\,3}$ | | | | | | | $x^{lit/m}$ | | 1 |
| *Atta cephalotes* (Linnaeus 1758) | | | | | | | $x^{n}$ | x | | 1 |
| *Atta sexdens* (Linnaeus 1758) | | x | | | | | x | x | | 3 |
| *Cyphomyrmex major* Forel 1901 | | | | x | | | | x | | 2 |
| *Cyphomyrmex minutus* Mayr 1862 | $x^{Fl\,2,3}$ | $x^{n}$ | | | | | | x | x | 7 |
| *Cyphomyrmex rimosus* (Spinola 1853) | | x | x | | | | | x | | 3 |
| *Mycetarotes parallelus* (Emery 1905) | | | | x | | | | x | | 1 |
| *Mycocepurus smithi* Forel 1893 | | x | | | | | | x | | 3 |
| *Sericomyrmex* sp. | | x | | | | | | x | | 1 |
| *Trachymyrmex* sp. | | x | | | | | | x | | 2 |
| Cephalotini (12) | | | | | | | | | | |
| *Cephalotes atratus* (Linnaeus 1758) | | x | x | | $x^{BS}$ | x | | x | | 6 |
| *Eucryptocerus placidus* (F. Smith 1860) | | | | | | x | | x | | 1 |
| *Procryptocerus* sp. (q) | | | | x | | | | $x^{q}$ | | 1 |
| *Zacryptocerus conspersus* (F. Smith 1867) | | | x | | | | | x | | 1 |
| *Zacryptocerus depressus* (Klug 1824) | | | | x | | | | x | | 3 |
| *Zacryptocerus grandinosus* (F. Smith 1860) | | | $x^{n}$ | | $x^{BS}$ | | | x | | 3 |
| *Zacryptocerus maculatus* (F. Smith 1876) | | | x | | | | | x | | 1 |
| *Zacryptocerus minutus* (Fabricius 1804) | | x | x | | $x^{BS}$ | x | | x | x | 7 |
| *Zacryptocerus pallens* (Klug 1824) | | | x | | $x^{BS}$ | | | x | x | 3 |
| *Zacryptocerus pusillus* (Klug 1824) | | | x | | $x^{P}$ | | | x | | 2 |
| *Zacryptocerus simillimus* (Kempf 1951) | | x | x | | | x | | x | | 3 |
| *Zacryptocerus umbraculatus* (Fabricius 1804) | | | | | $x^{BS}$ | | | x | | 1 |

| | Fl-lit | Fl-gro | Fl-veg | Sav | Sav-tr | Tf-veg | Tf-gro | d | n | sa |
|---|---|---|---|---|---|---|---|---|---|---|
| Crematogastrini (10) | | | | | | | | | | |
| *Crematogaster* sp. 1 | $x^{\text{Fl 4}}$ | | x | | $x^{\text{BS}}$ | | | x | | 4 |
| *Crematogaster* sp. 2 | | x | x | | $x^{\text{BS}}$ | | | x | x | 4 |
| *Crematogaster* sp. 3 | | | | x | | | | x | | 2 |
| *Crematogaster* sp. 4 | | x | x | | $x^{\text{P}}$ | | | x | x | 4 |
| *Crematogaster* sp. 5 | $x^{\text{Fl 4}}$ | x | x | | | | | x | x | 5 |
| *Crematogaster* sp. 6 | | x | | | | | x | x | | 2 |
| *Crematogaster* sp. 7 | | | x | | | | | | x | 1 |
| *Crematogaster* sp. 8 | $x^{\text{Fl 2,3}}$ | x | x | | | x | x | x | x | 11 |
| *Crematogaster* sp. 9 (cf. *levior* Forel 1911) | | | | | | $x^{\text{n}}$ | | x | | 1 |
| *Crematogaster* sp. 10 | | | | x | | | | x | | 2 |
| Dacetini (3) | | | | | | | | | | |
| *Daceton armigerum* (Latreille 1802) | | x | x | | | x | | x | x | 6 |
| *Strumigenys cordovensis* Mayr 1887 | | | | | | | x | x | | 1 |
| *Strumigenys eggersi* Emery 1890 | $x^{\text{Fl 1}}$ | | | | | | | $x^{\text{lit}}$ | | 1 |
| Leptothoracini (4) | | | | | | | | | | |
| *Nesomyrmex asper* (Mayr 1887) | | | x | | | | | x | | 1 |
| *Nesomyrmex echinatinodis* (Forel 1886) | | | x | | | | | x | | 1 |
| *Nesomyrmex spininodis* (Mayr 1887) | | x | | x | | | | x | | 2 |
| *Nesomyrmex* sp. | | | | x | | | | x | | 1 |
| Myrmicini (1) | | | | | | | | | | |
| *Hylomyrma* sp. | | | | | | | x | x | | 1 |
| Pheidolini (25) | | | | | | | | | | |
| *Pheidole cephalica* F. Smith 1858 | | x | | | | x | x | x | x | 3 |
| *Pheidole* sp. 1 | | x | x | | | | | x | x | 6 |
| *Pheidole* sp. 2 | | x | | | | | | x | x | 3 |
| *Pheidole* sp. 3 | | x | | | | | | x | | 2 |
| *Pheidole* sp. 4 | | x | | | | | | x | x | 2 |
| *Pheidole* sp. 5 | | x | | | | | | x | x | 2 |
| *Pheidole* sp. 6 | | x | | | | | | x | x | 2 |
| *Pheidole* sp. 7 | | | x | | | | | x | | 1 |
| *Pheidole* sp. 8 | | x | x | x | | | | x | x | 5 |
| *Pheidole* sp. 9 | $x^{\text{Fl 1}}$ | x | | $x^{\text{n}}$ | | | x | x | x | 8 |
| *Pheidole* sp. 10 | $x^{\text{Fl 3}}$ | x | x | | | | | x | x | 4 |
| *Pheidole* sp. 11 | | x | | | | | | x | | 1 |
| *Pheidole* sp. 12 | | x | x | | | x | | x | | 4 |
| *Pheidole* sp. 13 | | x | | | | | | x | | 1 |
| *Pheidole* sp. 14 | | | | | | | x | x | | 1 |
| *Pheidole* sp. 15 | | x | | | | | | | x | 1 |
| *Pheidole* sp. 16 | $x^{\text{Fl 2}}$ | | | x | | | | x | | 2 |
| *Pheidole* sp. 17 | $x^{\text{Fl 3}}$ | x | | | | | x | x | x | 5 |
| *Pheidole* sp. 19 | | x | | | | | | x | | 1 |
| *Pheidole* sp. 20 | | x | | | | | | x | | 1 |
| *Pheidole* sp. 21 | | | | | | | x | x | | 1 |
| *Pheidole* sp. 22 | | | | | | | x | x | | 1 |
| *Pheidole* sp. 23 | | | | x | | | | x | | 1 |
| *Pheidole* sp. 24 | | | | x | | | | x | | 3 |
| *Pheidole* sp. 25 | $x^{\text{Fl 4}}$ | | | | | | | $x^{\text{lit}}$ | | 1 |
| Solenopsidini (13) | | | | | | | | | | |
| *Monomorium floricola* (Jerdon 1852) | $x^{\text{Fl 1}}$ | | | | | | | $x^{\text{lit}}$ | | 1 |
| *Solenopsis bondari* Santschi 1925 | $x^{\text{Fl 2,4}}$ | x | | | | | x | x | x | 7 |
| *Solenopsis saevissima* (F. Smith 1855) | | | | $x^{\text{ki}}$ | | | | | x | 1 |

| | Fl-lit | Fl-gro | Fl-veg | Sav | Sav-tr | Tf-veg | Tf-gro | d | n | sa |
|---|---|---|---|---|---|---|---|---|---|---|
| *Solenopsis* (*Diploropthrum*) sp. 1 | | x | x | | | $x^{n}$ | | x | | 3 |
| *Solenopsis* (*Diploropthrum*) sp. 2 | | | | $x^{n}$ | | | | x | | 2 |
| *Solenopsis* (*Diploropthrum*) sp. 3 | $x^{Fl\ 3}$ | | | | | | | $x^{lit}$ | | 1 |
| *Solenopsis* (*Diploropthrum*) sp. 4 | | x | x | | | | | x | x | 2 |
| *Solenopsis* (*Diploropthrum*) sp. 5 | | | | x | | | | x | | 1 |
| *Solenopsis* (*Diploropthrum*) sp. 6 | $x^{Fl\ 1,3,4}$ | x | | | | | | x | x | 5 |
| *Solenopsis* (*Diploropthrum*) sp. 7 | | x | | | | | | x | | 1 |
| *Solenopsis* (*Diploropthrum*) sp. 8 | | x | | | | | | x | x | 2 |
| *Solenopsis* (*Diploropthrum*) sp. 9 | | | | | | x | | x | | 1 |
| *Solenopsis* (*Diploropthrum*) sp. 10 | | x | | x | | | | x | | 2 |
| Myrmicinae incertae sedis (1) | | | | | | | | | | |
| *Wasmannia auropunctata* (Roger 1863) | $x^{Fl\ 1,4}$ | $x^{n}$ | | x | | x | x | x | x | 10 |
| Dolichoderinae (17) | | | | | | | | | | |
| Dolichoderini (8) | | | | | | | | | | |
| *Dolichoderus attelaboides* (Fabricius 1775) | | | | | | x | | x | | 1 |
| *Dolichoderus bispinosus* (Olivier 1792) | | | | | | x | | x | | 1 |
| *Dolichoderus debilis* Emery 1890 | | x | x | | | | | x | | 2 |
| *Dolichoderus ghilianii* (Emery 1894) | | | | | | x | | | x | 1 |
| *Dolichoderus imitator* Emery 1894 | | | x | | | | | | x | 1 |
| *Dolichoderus lamellosus* (Mayr 1870) | | | x | | | x | | x | x | 2 |
| *Dolichoderus lutosus* (F. Smith 1858) | | | $x^{n}$ | | $x^{BS}$ | | | x | x | 3 |
| *Dolichoderus quadridenticulatus* (Roger 1862) | | | | | $x^{BS}$ | x | | x | | 2 |
| Tapinomini (9) | | | | | | | | | | |
| *Azteca* sp. 1 | | | x | | | | | x | x | 2 |
| *Azteca* sp. 2 | | x | x | | $x^{P}$ | | | x | | 4 |
| *Azteca* sp. 3 | | | x | | | | | x | | 1 |
| *Azteca* sp. 4 | | | x | | | x | | x | | 2 |
| *Iridomyrmex* sp. 1 | $x^{Fl\ 1-4}$ | | | | | | | $x^{lit}$ | | 4 |
| *Iridomyrmex* sp. 2 | | x | | | | | | | x | 1 |
| *Iridomyrmex* sp. 3 | | | | | | | x | x | | 1 |
| *Tapinoma* sp. 1 | | | x | | | | | | x | 1 |
| *Tapinoma* sp. 2 | | x | x | | | | | | x | 3 |
| Formicinae (36) | | | | | | | | | | |
| Camponotini (29) | | | | | | | | | | |
| *Camponotus* (*Myrmaphaenus*) *novogranadensis* Mayr 1870 | | x | x | | $x^{BS}$ | x | | x | x | 6 |
| *Camponotus* (*Myrmaphaenus*) sp. 1 | | | | | | x | | x | | 1 |
| *Camponotus* (*Myrmaphaenus*) sp. 2 | | x | x | | $x^{P}$ | | | x | | 5 |
| *Camponotus* (*Myrmaphaenus*) sp. 3 | | | | x | | | | x | | 2 |
| *Camponotus* (*Myrmaphaenus*) sp. 5 | | x | | | | x | | x | x | 3 |
| *Camponotus* (*Myrmaphaenus*) sp. 6 | | | | x | | | | x | | 2 |
| *Camponotus* (*Myrmobrachys*) *burtoni* Mann 1916 | | x | x | | | x | | x | | 4 |
| *Camponotus* (*Myrmobrachys*) cf. *crassus* Mayr 1862 | | x | x | x | | x | | x | | 8 |
| *Camponotus* (*Myrmobrachys*) sp. 8 | | x | $x^{n}$ | | $x^{BS}$ | | | x | | 6 |
| *Camponotus* (*Myrmobrachys*) sp. 9 | | | x | | | | | x | | 2 |
| *Camponotus* (*Myrmobrachys*) sp. 11 | | | | | | x | | x | | 1 |
| *Camponotus* (*Myrmobrachys*) sp. 12 | | x | | | | x | | x | | 2 |
| *Camponotus* (*Myrmobrachys*) sp. 13 | | | | | | x | | x | | 2 |
| *Camponotus* (*Myrmocladoecus*) cf. *sanctaefidei* Dalla Torre 1892 | | x | x | | | | | x | | 2 |
| *Camponotus* (*Myrmocladoecus*) *latangulus* Roger 1863 | | | | | | x | | x | | 1 |
| *Camponotus* (*Myrmocladoecus*) sp. 16 | | x | x | | | x | | x | | 5 |
| *Camponotus* (*Myrmothrix*) *abdominalis* (Fabricius 1804) | | | | | | | $x^{n}$ | x | | 1 |

| | Fl-lit | Fl-gro | Fl-veg | Sav | Sav-tr | Tf-veg | Tf-gro | d | n | sa |
|---|---|---|---|---|---|---|---|---|---|---|
| *Camponotus* (*Myrmothrix*) *femoratus* (FABRICIUS 1804) | | | | | | $x^{n}$ | | x | | 2 |
| *Camponotus* (*Myrmothrix*) *renggeri* EMERY 1894 | $x^{Fl\ 1}$ | x | x | x | $x^{BS}$ | | | x | x | 5 |
| *Camponotus* (*Tanaemyrmex*) *abuanus* MANN 1916 | | | x | | | | | | x | 1 |
| *Camponotus* (*Tanaemyrmex*) *hagemanni* FOREL cit. apud SANTSCHI 1922 | | | | | $x^{BS}$ | | | x | | 1 |
| *Camponotus* (*Tanaemyrmex*) sp. 22 | | | x | | | | | | x | 1 |
| *Camponotus* sp. 23 | | | | | | x | | | x | 1 |
| *Camponotus* sp. 24 | | x | x | | | | | | x | 2 |
| *Camponotus* sp. 25 | | | | x | | | | | x | 1 |
| *Camponotus* sp. 26 | | | | | | x | | | x | 2 |
| *Camponotus* sp. 27 | | x | | | | | | | x | 1 |
| *Camponotus* sp. 28 | | | | | | x | | | x | 1 |
| *Dendromyrmex chartifex* (F. SMITH 1860) | | | | | | x | | x | | 1 |
| Myrmelachistini (2) | | | | | | | | | | |
| *Brachymyrmex* sp. 1 | $x^{Fl\ 2}$ | x | x | | | | | x | x | 8 |
| *Brachymyrmex* sp. 2 | | | | x | | | | x | | 1 |
| Prenolepidini (5) | | | | | | | | | | |
| *Paratrechina longicornis* (LATREILLE 1802) | $x^{Fl\ 1}$ | | | | $x^{BS}$ | | | x | | 3 |
| *Paratrechina* sp. 1 | | | | | | x | x | x | | 2 |
| *Paratrechina* sp. 2 | $x^{Fl\ 3}$ | $x^{n}$ | | | | | | x | x | 7 |
| *Paratrechina* sp. 3 | $x^{Fl\ 4}$ | x | | | | | | x | | 3 |
| *Paratrechina* sp. 4 | $x^{Fl\ 4}$ | x | x | x | | | | x | x | 6 |
| Σ samples | | | | | | | | | | 495 |

Table 8. Occurrence of ant species in different habitats during standardized sampling (see tab. 1). 1 - 4 Forest island I (Fl 1); 5 - 8 Forest island II (Fl 2), 9 -10 Forest island III (Fl 3), 11 - 12 Inundation savanna, without trees (Sav), 13 - 15 Savanna trees (Sav-tr), 16 - 17 Terra firme forest (Tf): 1, 5, 9, 16 - vegetation, day (1 h.); 2, 6 - vegetation, night (1 h.); 3, 7, 10, 17 - ground, day (2 h.); 4, 8 - ground, night (2 h.); 11, 12 - savanna, day (2 h.); 13, 14 - *Ficus* tree at the station, day (1 h.); 15 - *Pseudobombax* trees in savanna, day (1 h.).

| | Fl 1 | | | | Fl 2 | | | | Fl 3 | | Sav | | Sav-tr | | | Tf | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| Number of samples | 30 | 20 | 47 | 28 | 16 | 9 | 42 | 20 | 23 | 29 | 23 | 23 | 15 | 7 | 4 | 13 | 18 |
| Species number | 27 | 20 | 46 | 27 | 16 | 9 | 42 | 20 | 22 | 27 | 21 | 23 | 15 | 7 | 4 | 13 | 18 |
| Ponerinae | | | | | | | | | | | | | | | | | |
| *Prionopelta* sp. | | | | | | | | | | x | | | | | | | |
| *Ectatomma edentatum* | | | | | | | | x | | x | | x | | | | | |
| *Ectatomma quadridens* | | | x | | | | x | | | | | | | | | | |
| *Gnamptogenys* cf. *tornata* | | | | | | | x | | | | | x | | | | | |
| *Gnamptogenys* cf. *rustica* | | | | | | | | | | x | | | | | | | |
| *Gnamptogenys* cf. *sulcata* | | | | | | | | | x | | | | | | | | |
| *Gnamptogenys teffensis* | | | | | | | x | x | | | | | | | | | |
| *Platythyrea angusta* | | | | | | | | | | | | | | | | x | |
| *Anochetus mayri* | | | | | | | | | | | | x | | | | | |
| *Hypoponera distinguenda* | | | | | | | | | | x | | | | | | | |
| *Hypoponera opaciceps* | | | | | | | | | | | | | | | | | x |
| *Hypoponera parva* | | | | | | | | | | x | | | | | | | |
| *Hypoponera* cf. *trigona* | | | x | | | | | | | x | | | | | | | |
| *Hypoponera* sp. (near *opaciceps*) | | | | | | | | | | | x | x | | | | | |
| *Hypoponera* sp. 1 | | | | x | | | | | | | | | | | | | |
| *Odontomachus brunneus* | | | | | | | x | x | | | x | | | | | | |
| *Odontomachus haematodus* | | x | x | x | | x | | | | x | | | | | | x | x |

| | Fl 1 | | | | Fl 2 | | | | Fl 3 | | Sav | | Sav-tr | | | Tf | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| *Odontomachus minutus* | | | x | x | | | x | x | | x | | | | | | | |
| *Pachycondyla apicalis* | | | x | | | | x | | x | x | | | | | | | |
| *Pachycondyla constricta* | | | | x | | | x | x | | | | x | | | | | |
| *Pachycondyla crenata* | | | | x | | | | | | | | | | | | | |
| *Pachycondyla harpax* | | | x | x | | | | | | x | | | | | | | |
| *Pachycondyla stigma* | | | x | | | | x | | | | | | | | | | |
| *Pachycondyla villosa* | | | x | | x | x | x | x | x | x | | | | | | | x |
| Pseudomyrmicinae | | | | | | | | | | | | | | | | | |
| *Pseudomyrmex curacaensis* | x | | x | | | | | | | | | | | | | | |
| *Pseudomyrmex eduardi* | | | | | x | | x | | x | | | | x | | | | |
| *Pseudomyrmex elongatus* | x | | x | | | | x | | | | | | | | | | |
| *Pseudomyrmex ethicus* | | | | | | | | | x | | | | | | | | x |
| *Pseudomyrmex filiformis* | x | | | | | | | | | | | | | | | | |
| *Pseudomyrmex gracilis* | x | | | | | | x | | | | x | x | x | | | | |
| *Pseudomyrmex laevifrons* | | | | | | | | | | | | | x | | | | |
| *Pseudomyrmex maculatus* | x | | x | | | | x | | | | | | | | | | |
| *Pseudomyrmex oculatus* | x | | | | x | | x | | | | | | | | | x | |
| *Pseudomyrmex sericeus* | x | | | | | | | | | | | | | | | | |
| *Pseudomyrmex simplex* | | | | | x | | x | | x | | | x | x | | | | |
| *Pseudomyrmex tenuis* | | | x | | | | x | | x | x | | | | | | | x |
| *Pseudomyrmex tenuissimus* | x | | x | | x | | x | | | | | | x | | | | |
| *Pseudomyrmex termitarius* | | | | | | | | | | | x | x | | | | | |
| *Pseudomyrmex* sp. 1 (*pallidus*-group) | | | | | | | | | | | x | x | | | | | |
| *Pseudomyrmex* sp. 2 (*pallidus*-group) | | | | | | | | | | | x | x | x | | | | |
| *Pseudomyrmex* sp. 3 (q) | | | | | | | | | | | x | | | | | | |
| Myrmicinae | | | | | | | | | | | | | | | | | |
| *Atta sexdens* | | | | | | | x | | | x | | | | | | | |
| *Cyphomyrmex major* | | | | | | | | | | | x | x | | | | | |
| *Cyphomyrmex minutus* | | | x | x | | | x | | | x | | | | | | | |
| *Cyphomyrmex rimosus* | | | | | x | | x | | x | | | | | | | | |
| *Mycetarotes parallelus* | | | | | | | | | | | x | | | | | | |
| *Mycocepurus smithi* | | | x | | | | x | | | x | | | | | | | |
| *Sericomyrmex* sp. | | | x | | | | | | | | | | | | | | |
| *Trachymyrmex* sp. | | | x | | | | x | | | | | | | | | | |
| *Cephalotes atratus* | x | | | | x | | x | | | | | | x | | | | |
| *Procryptocerus* sp. (q) | | | | | | | | | | | x | | | | | | |
| *Zacryptocerus conspersus* | | | | | x | | | | | | | | | | | | |
| *Zacryptocerus depressus* | | | | | | | | | | | x | | | | | | |
| *Zacryptocerus grandinosus* | x | | | | | | | | | | | | x | | | | |
| *Zacryptocerus maculatus* | | | | | x | | | | | | | | | | | | |
| *Zacryptocerus minutus* | x | x | x | | | | | | x | | | | x | | | | |
| *Zacryptocerus pallens* | x | x | | | | | | | | | | | | x | | | |
| *Zacryptocerus pusillus* | x | | | | | | | | | | | | | | x | | |
| *Zacryptocerus simillimus* | | | | | x | | x | | | | | | | | | x | |
| *Zacryptocerus umbraculatus* | | | | | | | | | | | | | x | | | | |
| *Crematogaster* sp. 1 | x | | | | | | | | | | | | x | x | | | |
| *Crematogaster* sp. 2 | x | x | x | | | | | | | | | | | x | | | |
| *Crematogaster* sp. 3 | | | | | | | | | | | | x | | | | | |
| *Crematogaster* sp. 4 | x | x | x | | | | | | | | | | | | x | | |
| *Crematogaster* sp. 5 | x | x | x | x | | | | | | | | | | | | | |
| *Crematogaster* sp. 6 | | | x | | | | | | | | | | | | | | x |
| *Crematogaster* sp. 7 | | x | | | | | | | | | | | | | | | |

| | Fl 1 | | | | Fl 2 | | | | Fl 3 | | Sav | | Sav-tr | | | Tf | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| *Crematogaster* sp. 8 | | | | | x | x | x | x | x | x | | | | | | x | x |
| *Crematogaster* sp. 10 | | | | | | | | | | | x | x | | | | | |
| *Daceton armigerum* | x | x | x | | | | | | | | | | | | | x | |
| *Strumigenys cordovensis* | | | | | | | | | | | | | | | | | x |
| *Nesomyrmex asper* | | | | | | | | | x | | | | | | | | |
| *Nesomyrmex echinatinodis* | | | | | | | | | x | | | | | | | | |
| *Nesomyrmex spininodis* | | | x | | | | | | | | x | | | | | | |
| *Nesomyrmex* sp. | | | | | | | | | | | | x | | | | | |
| *Hylomyrma* sp. | | | | | | | | | | | | | | | | | x |
| *Pheidole cephalica* | | | | | | | | | | x | | | | | | | x |
| *Pheidole* sp. 1 | | | x | x | x | | x | x | | x | | | | | | | |
| *Pheidole* sp. 2 | | | x | x | | | x | | | | | | | | | | |
| *Pheidole* sp. 3 | | | x | | | | | | | x | | | | | | | |
| *Pheidole* sp. 4 | | | x | x | | | | | | | | | | | | | |
| *Pheidole* sp. 5 | | | x | x | | | | | | | | | | | | | |
| *Pheidole* sp. 6 | | | x | x | | | | | | | | | | | | | |
| *Pheidole* sp. 8 | | x | | x | | | | x | | | x | x | | | | | |
| *Pheidole* sp. 9 | | | | x | | | x | x | | | x | | | | | | x |
| *Pheidole* sp. 10 | | x | | | | | | x | | x | | | | | | | |
| *Pheidole* sp. 11 | | | | | | | x | | | | | | | | | | |
| *Pheidole* sp. 12 | | | | | x | | x | | x | | | | | | | x | |
| *Pheidole* sp. 13 | | | | | | | x | | | | | | | | | | |
| *Pheidole* sp. 14 | | | | | | | | | | | | | | | | | x |
| *Pheidole* sp. 15 | | | | | | | | x | | | | | | | | | |
| *Pheidole* sp. 16 | | | | | | | | | | | | x | | | | | |
| *Pheidole* sp. 17 | | | | | | | | x | | x | | | | | | | x |
| *Pheidole* sp. 19 | | | | | | | | | | x | | | | | | | |
| *Pheidole* sp. 20 | | | | | | | | | x | | | | | | | | |
| *Pheidole* sp. 21 | | | | | | | | | | | | | | | | | x |
| *Pheidole* sp. 23 | | | | | | | | | | | x | | | | | | |
| *Pheidole* sp. 24 | | | | | | | | | | | x | x | | | | | |
| *Solenopsis bondari* | | | x | x | | | x | x | | | | | | | | | x |
| *Solenopsis* (*Diploropthrum*) sp. 1 | x | | x | | | | | | | | | | | | | x | |
| *Solenopsis* (*Diploropthrum*) sp. 2 | | | | | | | | | | | x | | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 4 | | x | x | | | | | | | | | | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 5 | | | | | | | | | | | | x | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 6 | | | | x | | | | | | x | | | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 7 | | | | | | | | | | x | | | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 8 | | | | x | | | x | | | | | | | | | | |
| *Solenopsis* (*Diploropthrum*) sp. 9 | | | | | | | | | | | | | | | | x | |
| *Solenopsis* (*Diploropthrum*) sp. 10 | | | x | | | | | | | | x | | | | | | |
| *Wasmannia auropunctata* | | | x | x | | | x | x | | | | x | | | | | x |
| Dolichoderinae | | | | | | | | | | | | | | | | | |
| *Dolichoderus debilis* | | | | | | | | | x | x | | | | | | | |
| *Dolichoderus imitator* | | x | | | | | | | | | | | | | | | |
| *Dolichoderus lamellosus* | | x | | | | | | | | | | | | | | | |
| *Dolichoderus lutosus* | x | x | | | | | | | | | | | | x | | | |
| *Dolichoderus quadridenticulatus* | | | | | | | | | | | | | x | | | | |
| *Azteca* sp. 1 | x | x | | | | | | | | | | | | | | | |
| *Azteca* sp. 2 | x | | x | | | | | | | | | | | | x | | |
| *Azteca* sp. 3 | x | | | | | | | | | | | | | | | | |
| *Azteca* sp. 4 | x | | | | | | | | | | | | | | | | |
| *Iridomyrmex* sp. 2 | | | | x | | | | | | | | | | | | | |

| | Fl 1 | | | | Fl 2 | | | | Fl 3 | | Sav | | Sav-tr | | | Tf | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| *Iridomyrmex* sp. 3 | | | | | | | | | | | | | | | | | x |
| *Tapinoma* sp. 1 | | x | | | | | | | | | | | | | | | |
| *Tapinoma* sp. 2 | | x | | x | | x | | | | | | | | | | | |
| Formicinae | | | | | | | | | | | | | | | | | |
| *Camponotus* (*Myrmaphaenus*) *novogranadensis* | | | x | | | x | | | x | x | | | x | | | | |
| *Camponotus* (*Myrmaphaenus*) sp. 2 | x | | x | | x | | x | | | | | | | | x | | |
| *Camponotus* (*Myrmaphaenus*) sp. 3 | | | | | | | | | | | | x | | | | | |
| *Camponotus* (*Myrmaphaenus*) sp. 5 | | | | | | | x | x | | | | | | | | | |
| *Camponotus* (*Myrmaphaenus*) sp. 6 | | | | | | | | | | | | x | | | | | |
| *Camponotus* (*Myrmobrachys*) *burtoni* | | | x | | | | | | x | | | | | | | x | |
| *Camponotus* (*Myrmobrachys*) cf. *crassus* | | | x | | | | x | | x | | x | x | | | | | |
| *Camponotus* (*Myrmobrachys*) sp. 8 | x | | x | | x | | x | | | | | | x | | | | |
| *Camponotus* (*Myrmobrachys*) sp. 9 | x | | | | | | | | x | | | | | | | | |
| *Camponotus* (*Myrmobrachys*) sp. 12 | | | x | | | | | | | | | | | | | | |
| *Camponotus* (*Myrmobrachys*) sp. 13 | | | | | | | | | | | | | | | | x | |
| *Camponotus* (*Myrmocladoecus*) cf. *sanctaefidei* | | | x | | | | | | x | | | | | | | | |
| *Camponotus* (*Myrmocladoecus*) sp. 16 | | | | | x | | x | | x | | | | | | | x | |
| *Camponotus* (*Myrmothrix*) *renggeri* | | x | | x | | | | | | | | | | x | | | |
| *Camponotus* (*Tanaemyrmex*) *abuanus* | | x | | | | | | | | | | | | | | | |
| *Camponotus* (*Tanaemyrmex*) *hagemanni* | | | | | | | | | | | | | | x | | | |
| *Camponotus* (*Tanaemyrmex*) sp. 22 | | | | | | x | | | | | | | | | | | |
| *Camponotus* sp. 24 | | | | | | x | | x | | | | | | | | | |
| *Camponotus* sp. 27 | | | | x | | | | | | | | | | | | | |
| *Brachymyrmex* sp. 1 | | x | x | x | | x | x | x | x | | | | | | | | |
| *Brachymyrmex* sp. 2 | | | | | | | | | | | x | | | | | | |
| *Paratrechina longicornis* | | | | | | | | | | | | | x | x | | | |
| *Paratrechina* sp. 1 | | | | | | | | | | | | | | | | x | x |
| *Paratrechina* sp. 2 | | | x | x | | | x | x | | x | | | | | | | |
| *Paratrechina* sp. 3 | | | x | x | | | | | | | | | | | | | |
| *Paratrechina* sp. 4 | | | | x | | x | x | x | | | | x | | | | | |

## Biological and taxonomical remarks on some species

*Hypoponera parva*
An alated queen on July 27 on the ground of a forest island.

*Odontomachus haematodus*
A soil nest under rotten wood in a forest island.

*Pachycondyla crassinoda*
A nest in rotten wood on the ground in terra firme forest.

*Eciton vagans*
Workers of this species carried workers and pupae of *Odontomachus brunneus* as prey during a raid in the litter of terra firme forest.

*Pseudomyrmex curacaensis*
A nest in a rotten twig hanging in a height of 1.8 m in the vegetation.

*Pseudomyrmex dendroicus*
We found a colony on an undetermined tree of 8 m height in the terra firme forest. So far known this species is an obligate inhabitant of trees of the genus *Triplaris* (WARD 1989).

*Pseudomyrmex gracilis*
A nest in the dry stalk of a savanna plant.

*Pseudomyrmex* sp. 2 (*pallidus*-group)
A nest in a blade of grass in savanna. The three yellow species of the *pallidus*-group we found during this

study (*Pseudomyrmex* sp. 1, sp. 2, and *P. simplex*) are very similar in their morphology. In the savanna all three species were collected several times nearby each other, but only *P. simplex* could also be detected in forest islands.

*Pseudomyrmex* sp. 4 (*viduus*-group)
We found a colony of this species on an undetermined tree of 6 m height in terra firme forest. Species of the *viduus*-group are mainly associated with trees of the genera *Tachigali* and *Triplaris* (WARD 1989).

*Atta cephalotes*
A big nest of this species was found in terra firme forest with workers carrying leaves during the day. Leaf cutting ants have been considered enlarging forest islands in the Beni savannas by modifying the soil relief with their nesting activities (HANAGARTH 1993).

*Crematogaster* sp. 8
A number of workers was encountered together with a dealated queen on lianas in the largest of the forest islands. In Panguana, Peru, colonies of several *Crematogaster* species could be observed in budding processes, during which part of the workers leave the nest together with young dealated queens to a new nesting site (VERHAAGH unpubl.).

*Crematogaster* sp. 9
This species was found in a carton nest in the terra firme forest together with *Camponotus femoratus* and belongs to the *C. limata parabiotica*-complex. Already SWAIN (1980) had the suspicion that the *Crematogaster* species living in „parabiosis" with *Camponotus femoratus,* respectively *Dolichoderus* (=*Monacis*) *debilis* may represent two different species. B. BOLTON discovered morphological differences between both (cit. apud SWAIN 1980). Also during the study of the ant fauna of Panguana, Peru (VERHAAGH unpubl.), two morphospecies of *Crematogaster* were encountered in these interspecific associations, and the morphological differences between them are the same found by BOLTON. The one living with *D. debilis* (and sometimes also found together with *D. bispinosus*) is on the average larger and darker than the species found with *C. femoratus* and characterized by several prominent longitudinal rugulae on the lateral parts of the promesonotum. In the species occurring together with *C. femoratus* the promesonotum is almost completely smooth and shining. With regards to published names the larger and darker of the two morphospecies agrees with the description of *Crematogaster limata parabiotica* FOREL 1904 (also originally described as living in parabiosis with *D. debilis*), and the smaller and lighter species with *Crematogaster limata parabiotica* var. *levior* FOREL 1911. Of course, only a thorough revision of the whole *limata*-complex will clear the status of the two morphs.

*Cyphomyrmex major*
The taxonomy of the *Cyphomyrmex rimosus*-group, having been for a long time in a confusing state, was elucidated recently by SNELLING & LONGINO (1992). Following their revision, *C. major* is only known so far from the type series from Guatemala. The authors believe that specimens from the state São Paulo, Brazil, published later by FOREL under this name are probably not conspecific. The morphology of the specimens from EBB agrees well with the characters given by SNELLING & LONGINO (1992) for this species.

*Cyphomyrmex minutus*
After SNELLING & LONGINO (1992), *C. minutus* is widespread throughout the Carribean and ranges from Texas and Florida to northern South America (Venezuela, Colombia). Thus, the record from the Beni savannas enlarges the geographical range of the species considerably. The species has been found in Panguana, central Peru, too (VERHAAGH unpubl.). In EBB we found a nest on the ground under rotten wood in a forest island.

*Zacryptocerus grandinosus*
A nest in a rotten twig in a height of 1.50 m in a forest island.

*Pheidole sp. 9*
A soil nest in the savanna.

*Solenopsis* (*Diploropthrum*) sp. 1
A nest in a rotten twig hanging in a height of approx. 1.80 m in the vegetation.

*Solenopsis* (*Diploropthrum*) sp. 2
A nest in the savanna grass.

*Wasmannia auropunctata*
A nest in the soil of a forest island.

*Camponotus* (*Myrmobrachys*) sp. 8
A nest in a rotten twig hanging in a height of approx 1.80 m in the vegetation of a forest island.

*Camponotus* (*Myrmothrix*) *abdominalis*
A nest in rotten wood on the ground of terra firme forest.

*Dolichoderus quadridenticulatus*
One worker was collected with a 7-8 mm large fly between the mandibles.

**andrias, 13:** 215-224, 1 Fig., 1 Colour Plate; Karlsruhe, 30. 9. 1994

MANFRED VERHAAGH

# *Pachycondyla luteola* (Hymenoptera, Formicidae), an inhabitant of *Cecropia* trees in Peru

## Abstract

Biological data of the rarely collected ponerine ant *Pachycondyla luteola* (ROGER, 1861) are presented. The „locus typicus" of this ant is corrected to Sarayacu, a mission at the Río Ucayali, Peru. The present known geographical distribution of the ant is limited to preandine lowland and submontane regions in Peru covered by evergreen and seasonal-evergreen tropical rain forest.

Ant colonies and colony founding queens were only found in the hollow stems of *Cecropia* trees and seedlings. The ants feed exclusively on Müllerian bodies produced by the plants in high numbers in special hair pads (trichilia) at the base of petioles of young leaves. Ant queens already colonize very young plants. The older colony is supposed to be functional polygynous, because in one examined nest three physogastric queens were found together. This social status has been rarely encountered in ponerine ants, and certainly has been evolved in context with the unusual nest habit. The species build up colonies which belong to the largest known for ponerine species in the world (several thousands of workers, possibly even between 10,000 and 100,000).

The benefits to the plants seem to consist primarily in a good protection against herbivores, not only insects but also vertebrates, because the ant is armed with a powerful sting. The pain of its stings in humans lasts longer than known from any other ant, and any other Hymenoptera as well. It is concluded that the protection against large herbivores is an advantage especially for *Cecropia* trees that grow slowly in small forest gaps at low light intensities.

## Kurzfassung

### *Pachycondyla luteola* (Hymenoptera, Formicidae), eine Bewohnerin von Cecropien in Peru

Die selten gesammelte Ponerine *Pachycondyla luteola* (ROGER, 1861) ist bisher nur aus immergrünen bis saisonal-immergrünen Regenwäldern des vorandinen Tieflandes und der submontanen Zone Perus bekannt geworden. Als „Locus typicus" dieser Ameise wird Sarayacu, eine Missionsstation am Río Ucayali in Peru bestimmt.

Die Kolonien und koloniegründenden Königinnen der Ameise wurden nur in hohlen Stämmen von Cecropien-Bäumen und ihren Jungpflanzen gefunden. Die Ameisen fressen ausschließlich Müllersche Körperchen, die die Pflanzen in großer Zahl in speziellen Haarpolstern (Trichilien) an der Basis junger Blattstiele produzieren. Die Ameisen-Königinnen besiedeln junge Cecropien bereits in einem sehr frühen Stadium. Die ältere Kolonie ist wahrscheinlich funktionell polygyn, da in einem näher untersuchten Nest drei physogastrische Königinnen zusammen lebten. Diese Form sozialer Organisation ist bei Ponerinen selten gefunden worden und scheint im Zusammenhang mit der ungewöhnlichen Lebensweise entstanden zu sein. *P. luteola* baut Koloniestärken auf, die zu den größten unter den Ponerinen überhaupt gehören (mehrere tausend Arbeiterinnen, wahrscheinlich sogar zwischen 10.000 und 100.000).

Der Nutzen für die Pflanzen liegt offenbar in einem guten Schutz gegenüber Herbivoren, Insekten wie Wirbeltieren, denn die Ameisen sind mit einem kräftigen Stachel ausgerüstet, dessen Stich eine längere Wirkung erzielt, als von irgendeiner anderen Ameise oder Hymenoptere bekannt ist. Der Schutz gegen große Herbivoren scheint ein Vorteil speziell für langsam wachsende Cecropien in kleinen Baumsturzlücken im Innern des Waldes zu sein.

## Resumen

### *Pachycondyla luteola* (Hymenoptera, Formicidae), un habitante de *Cecropia* en Peru

Se presenta datos biológicos de la hormiga *Pachycondyla luteola* (ROGER, 1861). Como „locus typicus" de la hormiga esta fijado Sarayacu, una misión al lado del Río Ucayali en Peru. La distributión conocida se limite a bosques siempre verdes y estacional siempre verdes de la región preandina baja y submontañosa en Peru.

Las colonias de la hormiga y reinas colonizadoras fueron encontradas solamente dentro de troncos huecos de arboles y arbolitos de *Cecropia*. Las hormigas se alimentan exclusivamente de los corpúsculos de Müller que las plantas producen a las bases des pecíolos entre cojines de pelos especiales (trichilia) en grandes cantidades. Reinas ya colonizan cecropias muy pequeñas. Presuntamente la colonia establecida es funcionalmente polygyna, porque en un nido examinado vivieron tres reinas fisogastricas juntas. Este modo de organización social es raramente encontrado en Ponerinae y paracе ser evolucionado en relación con el tipo de nido. Las colonias de esta especie forman parte de las mas grandes conocidas en hormigas de la subfamilia Ponerinae (unas millares de trabajadoras, probablemente 10.000-100.000).

Las plantas aprovechan de una buena protección contra animales herbívoros sea insectos o vertebrados porque las hormigas tienen una lanceta muy efectiva. El dolor de las picaduras dura mas tiempo que en cada otra especie de hormiga o de cualquier otra Hymenoptera conocida. Esta concluido que la protección contre herbívoros grandes es una ventaja especial para una especie de *Cecropia* que crece despacio en el interior del bosque con poca luz.

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Dedicated to the memorial of Dr. MARIA KOEPCKE, one of the founders of the biological station Panguana,who first reported on the *Pachycondyla-Cecropia*-association.

## 1. Introduction

The biology of most of the hitherto approx. 2500 described neotropical ant species (Kempf 1972) is poorly known or even not at all. This holds true even for larger species and includes such basic information as the nest site and nest type.

An astonishing example in this respect was, until recently, the ponerine *Pachycondyla luteola*. More than 1 cm in size, it apparently got known to science for the second time 115 years after its discovery (leg. L. Pena 1962). Koepcke (1972) reported for the first time that its colonies occupy a *Cecropia* and that two species of Icteridae (*Clypicterus oseryi* and *Ocyalus latirostris*) build their nests at leaves and petioles of *Cecropia* trees colonized by these ants. They are part of an interesting neotropical ant-plant-association and obviously build up the largest colonies among neotropical ponerines, probably even outnumbering the populous colonies of nomadic *Leptogenys* species of South-East Asia (Maschwitz et al. 1989). But nothing in detail was known about their biology up to the late 80s when Davidson and co-workers started publishing results of their comparative work on ant-*Cecropia*-associations in south-eastern Peru (Davidson et al. 1988, 1989, 1991, Davidson & Fisher 1991, Davidson & McKey 1993).

The observations on *P. luteola* presented here were made during a two-year-field study (1983 1985) about the ant fauna at the biological station of Panguana/Peru.

## 2. Taxonomy and Distribution

### Taxonomy

Roger described this ponerine ant in the year 1861 from seven specimens under the name *Ponera luteola* in such a good manner that it can be recognized with great certainty already from his description. Very typical is the reddish brown or rusty color of the workers. Callow specimens are even yellow-red, hence the name. Workers are about 1.2 cm in size (combined head, thorax, petiolus and gaster length), the queens between 1.6 to more than 1.8 cm, and dark brown coloured. In the original description Roger missed the weakly developed carina on the cheeks between the insertion of the mandibels and the compound eyes. This structure is better developed only in queens, and Emery (1890) was the first to mention it. This character sets the species between the species of the pantropical genus *Pachycondyla* (Smith, 1858) (=species without cheek carina) and the pure neotropical genus *Neoponera* (Emery, 1901) (=species with clearly developed carina), hence explaining its taxonomic history:

*Ponera luteola* Roger, 1861
*Pachycondyla luteola* (Roger 1863, Dalla Torre 1893)
*Neoponera luteola* (Emery 1901, 1911, Kempf 1972)

Kempf (1964) already had profound doubts about the generic distinctness of *Neoponera* and *Pachycondyla*, and Brown (1973) proposed the synonymy of *Neoponera* and other ponerine genera with *Pachycondyla*. Hölldobler & Wilson (1990) followed Brown's opinion in their standard work.

### Locus typicus

Roger (1861) closed his description as follows: „7 ☿ in der Kaiserl[ichen]. Sammlung zu Paris stammen von der Mission Sareyacu (Pampa del Sacramento) in Südamerika, von wo sie Mr. de Castelnau mitgebracht."

The spelling of the location is wrong. The name should be correctly the Quechua word „sarayacu" (sara = maiz, yacu = water). The true position of this locality was never identified in the past. Roger (1863) himself believed it to be in Uruguay, Emery (1890) in Brazil (1911: Rio de Janeiro, Brazil), and Kempf (1972) in Bolivia. All interpretations turned out to be wrong shown at once by the label of a syntype in the Museum of Comparative Zoology at Harvard: „Perou, Pampas del Sacramento, De Castelnau 1847". This label must have been unknown to Roger and other myrmecologists.

In modern maps of Peru the mentioned pampas are not found, but in a map added to the book of Portillo (1901). Stiglich (1922) wrote about them: „Sacramento, chico y grande Hdas. en la Montaña de Paucartambo, Prov. de Pasco, Dist. de Ninacaca. Las Pampas del Sacramento son las vastas llanuras que se extienden al N y al E de la cuenca del Pachitea y en ella estan los salvajes cashibos....." Stephens & Traylor (1983) defined this not sharply limited area according to the „Map of Hispanic America (MHA), American Geographical Society, New York, 1922-1952" as „SACRAMENTO, PAMPA DEL; Loreto/San Martin ca. 400-500 m in plain E of Cordillera Azul, leftbank of Rio Ucayali drainage." Ortiz (1974) gave a report about the discovery of this vast plain (=pampa), completely covered with forest, by some Franciscan friars on Corpus Christi Day (=dia del sacramento) in 1726.

The mission Sarayacu was founded in 1791 by the Franciscan Francisco Girbal on the left bank of the Ucayali. It is situated at the northern border of the Pampas del Sacramento on a little elevation (165 m a.s.l.) on the right side of a little affluent (Caño Sarayacu) about 10 km apart from the Ucayali itself (Stiglich 1922). The next larger settlement is Orellana about 20 km to the south. Stephens & Traylor (1983) gave the coordinates with 6°44'S, 75°06'W and the altitude of 125 m a.s.l. according to the MHA. That is probably the altitude of the mouth of the caño into the Ucayali. Ortiz (1974) reported the arrival of de Castelnau to the mission (tome I: 304): „El año 1846 recibe [el padre Plaza] en Sarayacu al expedicionario frances Castelnau..."

### Distribution of *Pachycondyla luteola*

*P. luteola* is known only from the following locations in Peru: Sarayacu, Dep. Loreto (165 m); Panguana, Dep. Huánuco (220 m); Pozuzo, Dep. Cerro de Pasco (600 m), leg F. Gestr IV. 1985 and donated to the author; Cocha Cashu, Manu, Dep. Madre de Dios (400 m), leg. D. Davidson XI. 1985 (see also Davidson et al. 1991, Davidson & Fisher 1991); Quincemil, Dep. Cusco (750 m), leg L. Pena XI. 1962 and IX. 1967; and Tambopata (200 m), Dep. Madre de Dios (Davidson et al. 1991, Davidson & Fisher, 1991). Thus, the geographical distribution of *P. luteola* so far known is confined to evergreen and seasonal-evergreen tropical rain forest of the lowland and submontane region of preandine Amazonian Peru (fig. 1).

Specimens are deposited in Musée d' Histoire Naturelle, Paris, Museum of Comparative Zoology, Cambridge, Mass., and Staatliches Museum für Naturkunde Karlsruhe.

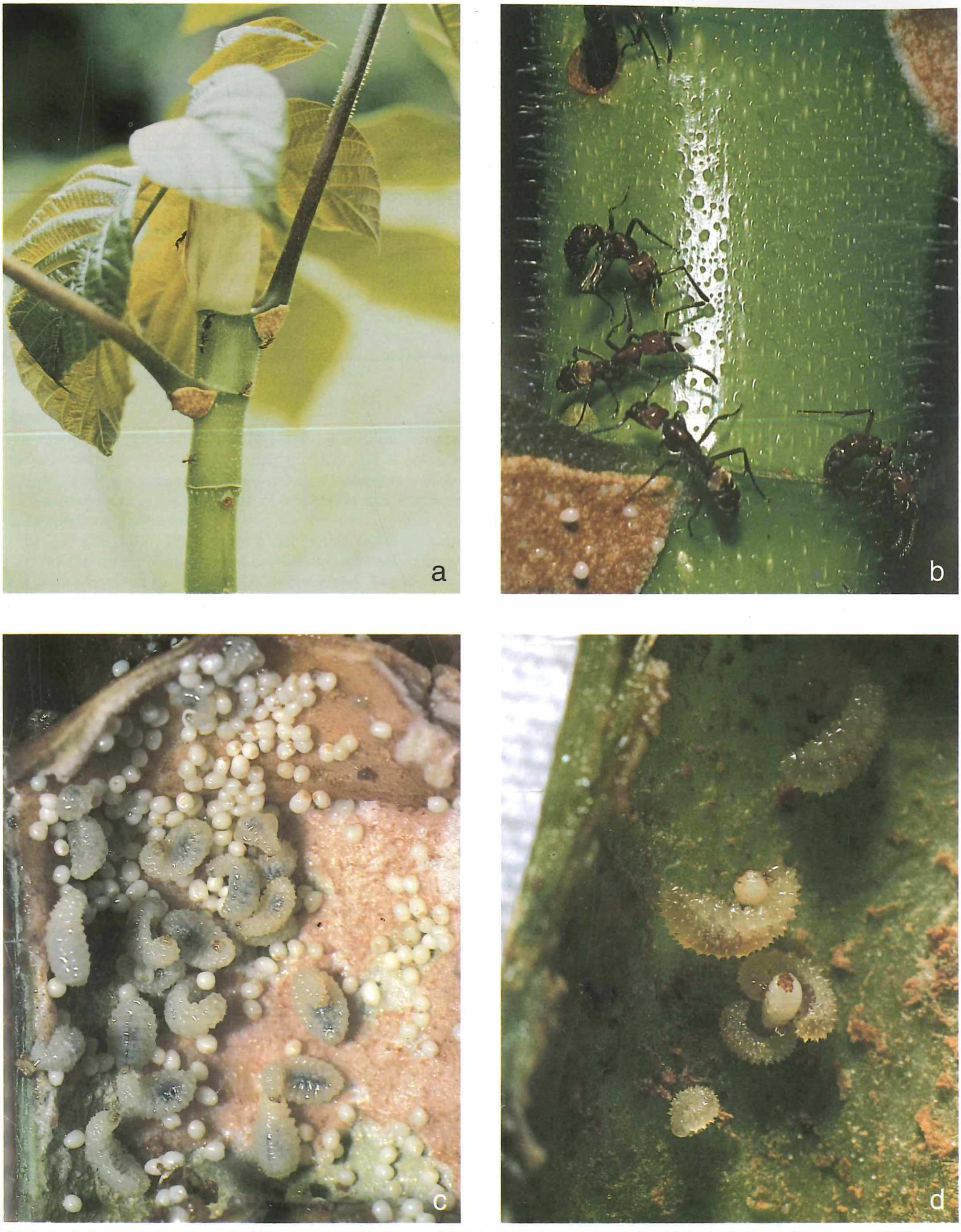

Plate 1. a) *Cecropia tessmannii* with a colony of *Pachycondyla luteola* in the garden of the biological station Panguana. b) Workers of *P. luteola* on the stem of the host *Cecropia*. Note Müllerian bodies (M.b.) in trichilium at the base of petiole (bottom), the worker with a recently harvested M.b. between the mandibles (middle), and the entrance of the nest (top). c) Look in the interior of an internodium of the *C. tessmannii* with numerous M.b. and larvae between them. d) Single larva feeding on M.b.

## 3. Study site and Material

### Study site

The biological station Panguana (9°37'S, 74°56'W, Departamento Huánuco) is situated at 220 m a.s.l. at the left bank of the Río Yuyapichis, an affluent of the Río Pachitea. The average rainfall (7 years measurement) is 2403 mm (minimum 1998 mm, maximum 3004 mm), with 80% falling during the rainy season between October and April. The mean annual temperature at the forest border (station) is approx. 25 °C. For further details about the climate and soil types of Panguana see HANAGARTH (1981) and RÖMBKE & VERHAAGH (1992).

The vegetation zone at Panguana is classified as preandine hylaea (HUECK 1966); the region is naturally covered by seasonal-evergreen tropical rain forest (terra firme) and, to a small degree, by different inundation vegetation types (matorrales, HANAGARTH 1981). There are different anthropogeic biotopes (pastures, plantations, and secondary forests in different stages of succession) near the station, too.

### Material

The results presented here are based on 6 collected or observed colonies, 8 colony-founding queens and 6 solitary queens. Voucher specimens are deposited under the indicated field numbers in the collection of the Staatliches Museum für Naturkunde Karlsruhe.

VFor 237 (25.7.83): 25 ☿☿ from a colony on a 4-5 m high *Cecropia* in a recent clearing of primary forest (total colony size was estimated to at least 2000 individuals). The ants remained on the cut *Cecropia* for approx. one week then disappeared with the whole brood. Whether they left the host plant with their brood or were eaten by animals is not known.

VFor 225 (5.10.83): 1 dealated ♀, solitary on a scrub in the garden behind the station.

VFor 433 (4.4.84): 1 ☿ from a colony in dense, 3-year-old secondary growth with numerous *Cecropia*.

VFor 456 (17.4.84): 1 alated ♀, at the station hut before noon.

VFor 489 (29.5.84): 1 dealated ♀ with two larvae and 6 eggs in the topmost internodium of a 70 cm high *Cecropia* in a secondary growth (no Müllerian Bodies, M.b. inside, but some in leaf trichilia). The internodium below contained a young nest of a *Camponotus* (*Tanaemyrmex*) species.

90/335 C-P (9.7.84): 1 dealated ♀ with 7 pupae, 7 larvae and 9 eggs in 45 cm height in a young *Cecropia* in secondary growth. Three internodia (total length 7 cm) were connected by holes in the nodial septa, a 6 x 3 mm large entrance was in the topmost internodium; no M.b. were found inside.

VFor 940a (3.4.85): 1 dealated ♀ at 6 p.m. at the stem of a *Cecropia* in the garden of the station (see VFor 940c). Held permanently contact with some workers through antennation. Also mutual oral contact was observed but no exchange of regurgitated food.

VFor 940b (19.4.85): 2 dealated ♀♀ (one of them still with wing remains) in close vicinity to the *Cecropia* in the garden but hidden in a rotten palm stem from which the *Cecropia* grew. One of them left the hiding-place loudly stridulating when disturbed.

VFor 940c (19.4.85): Complete nest from a 1.60 m high *Cecropia* (plate 1a, the same plant as VFor 940a,b) in the garden of the station (the plant was cut, put in a plastic bag and then poisened): 3 dealated physogastric ♀♀, 230 +/- 5 ☿☿, 1 not yet fully coloured ♂, 163 pupae, 241 larvae, 347 eggs, approx. 5800 M.b. (tab. 1), remains of an alien ant male and of a tree hopper (Membracidae), 1 living mite (Galumnidae, Oribatei). The bottom 80 cm of the plant were small, woody and uninhabited. The wider, inhabited 18 internodia (tab. 1) were all connected by holes in the nodial septa. The youngest internodium at the peak was still empty. The actual entrance was in the topmost inhabited chamber, but the lower ones still showed the pits of the former entrances, and occasionally the plant had two entrances. This slowly growing *Cecropia* had been colonized at least since a height of 50 cm.

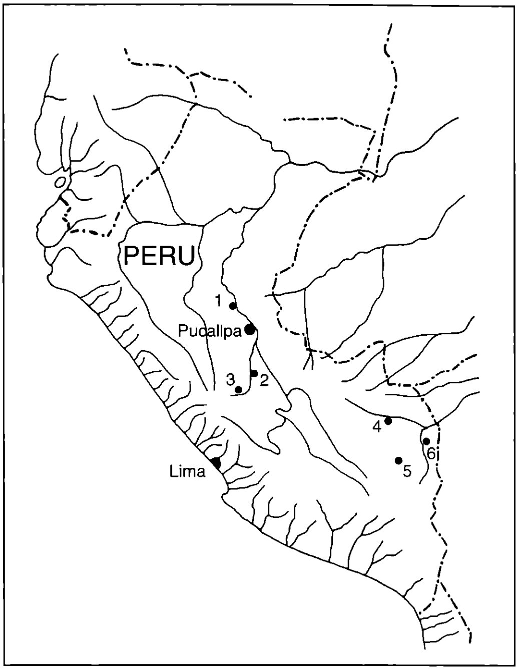

Figure 1. Geographical distribution of *Pachycondyla luteola* in Peru: 1 – Sarayacu (Río Ucayali); 2 – Panguana (Río Yuyapichis), 3 – Pozuzo; 4 – Cosha Cashu, Manu Park; 5 – Quincemil; 6 – Tambopata Reserve.

VFor 1033a-d (12.5.85): 4 dealated ♀♀ from one 20 cm high *Cecropia* with only 5 internodia from a small gap in a 20-year-old secondary forest; only the internodia 2 and 3 were interconnected by holes in the nodial septa:

a) In internodia 2 and 3 (counted from the bottom), 1 ♀ with 1 pupa, 9 larvae and 5 eggs. The larvae fed on M.b.; there were numerous mites (deuteronymphs of Tyroglyphidae, Acaridiae, Sarcoptiformes) inside the nest.

b) In the internodium above, 1 ♀ without brood and M.b.

c) In the top most internodium, 1 ♀ without brood but 4 M.b.; there were also some mites (Tyroglyphidae) in this internodium. All three ♀♀ had an entrance to the *Cecropia* for their own, in which often the head or antennae were seen. Knocking at the *Cecropia* occasionally caused them to leave the interior.

d) A fourth ♀ sat in front of the *Cecropia* on the forest ground and was stridulating. This specimen carried several phoretic Tyroglyphidae on the body.

VFor 1034 (12.5.85): 1 dealated ♀ with 9 pupae, 13 larvae and 12 eggs, but no M.b. in a 35 cm high *Cecropia* close to VFor 1033. The 4 topmost internodia were interconnected by holes in the nodia. The entrance (in the topmost internodium) was closed by a plug of soft material (chewed parenchym?).

Table 1. Distribution of brood and Müllerian bodies (M.b.) in the internodes (IN) of *Cecropia tessmannii* inhabited by *Pachycondyla luteola* (nest VFor 940). Numbers of internodes (IN) from top to bottom; magnitudes for M.b.: I = 1-100, II = 101-1,000; III = 1,001-2,000; size of larvae arbitrarily divided into large, middle sized, and small.

| IN | M.b. | brood | remarks |
|---|---|---|---|
| 1 | II | | inner ø=3.3 cm, 4 cm long |
| 2 | II | none | |
| 3 | III | none | IN 1/3 filled |
| 4 | II | large larvae | |
| 5 | II | large larvae | |
| 6 | I | large larvae/pupae | |
| 7 | I | large larvae/pupae | |
| 8 | I | large larvae/pupae | IN nearly filled |
| 9 | I | large larvae/pupae | IN nearly filled |
| 10 | I | large larvae/pupae | IN nearly filled |
| 11 | I | large larvae/pupae | IN nearly filled |
| 12 | I | large larvae/pupae | IN nearly filled |
| 13 | I | large larvae/pupae | IN nearly filled |
| 14 | II | small/middle sized larvae | |
| 15 | III | eggs | |
| 16 | I | eggs/small larvae | |
| 17 | I | eggs/small larvae | |
| 18 | I | few small larvae | water in IN; inner ø=1.8 cm, 4.5 cm long |

VFor 1043 (12.5.85): 1 dealated ♀ without brood nor M.b. in the middle of three internodiums of a 20 cm high *Cecropia* in river bank vegetation (matorral) with the up to 11 m high grass *Gynerium sagittatum*. In the bottom internodium with closed entrance a dealated ♀ of *Azteca* sp. with eggs was found.

VFor 1045 (11.5.85): 1 ☿ from a colony on *Cecropia* in primary forest in a small gap caused by numerous colonies of *Myrmelachista* sp. on *Cordia* and *Duroia* trees.

VFor 1056 (14.5.85): 1 dealated ♀ without brood but some M.b. in a 1 m high *Cecropia* at the transition of matorral and terra firme forest.

VFor 1251 (1.7.85): 56 ☿☿, 69 pupae and 45 larvae from a nest (the rest of the completely sampled nest got lost) on a 2.5 m high *Cecropia* in primary forest in a nearly overgrown gap with *Cordia* and *Duroia* trees. Nesting scheme similar to that described from VFor 940c. Entry to the nest was in the topmost inhabited internodium. Brood was separated in pupae, larvae and eggs, too. There was no hint to other food than M.b. in the interior of the *Cecropia*. One worker held the head of a worker of *Cephalotes atratus* between its mandibles.

A further colony inside the primary forest could be shortly observed during a forest walk. The stem of the approx. 10 m high *Cecropia* was densely covered by workers. I estimate that this colony might have reached a number of approx. 10,000 workers.

## 4. Results and Discussion

### Nest, and colony founding

*Pachycondyla luteola* was regularly found in the vicinity of Panguana, although it was never especially searched for. Koepcke (1972) examined 6 colonies in Panguana. The ant colonies lived exclusively on *Cecropia* trees (plate 1). Whether this was only one *Cecropia* species or more could not be verified as *Cecropia* seedlings often resemble each other. As far as noted, the young colonized *Cecropia* trees were densely covered by rather long, stiff hairs (plate 1b). The local people know both the ant and the *Cecropia* on which it lives as „pungara“ According to Ferreyra (1970), the *Cecropia* called „pungara“ in Peru is *Cecropia tessmannii* Mildbr., but this still lacks confirmation. Berg (1978) questioned the specific distinctness of *C. tessmannii* from *C. membranacea* Trécul. *P. luteola* is also not uncommon in the vicinity of Cosha Cashu, Manu Park, and the Tambopata Reserve, as Davidson and co-workers examined 28 established colonies on *C. tessmannii* and 42 foundresses or incipient colonies on *C. tessmannii*, respectively 18 on *C. membranacea* (Davidson et al. 1991, Davidson & Fisher 1991). According to these authors, *C. tessmannii* and *C. membranacea* look very similar but have different ecological demands, *C. tessmannii* being a shade-tolerant, very slowly growing species typical for small forest gaps and edges of forest swamps (aguajales) of which only seedlings can be found in clearings and riverine vegetation. In contrast, *C. membranacea*, is a fast growing, light-demanding species of stream and river bank disturbances and clearings which cannot survive under light limited conditions. In comparison with *C. membranacea*, *C. tessmannii* has shorter internodes, larger Müllerian bodies (0.16 mg dry weight versus 0.09 mg), starts earlier with production of M.b. (on the average with the 6th leaf when seedling still has not reached 10 cm height versus *C. membranacea* that on average starts production of M.b. with the 16th leaf; Davidson et al. 1991, Davidson & McKey 1993). These authors found larger, established colonies only on *C. tessmannii* that grew in small forest gaps. Foundresses of *P. luteola* on *C. membranacea*, however, either died (possibly because of limited food supply) or were replaced by faster growing *Azteca* colonies on the same plant. In their investigation 90% of established *C. tessmannii* were colonized by *P. luteola* and 10% by *Camponotus balzani*, but both species excluded each other on the same tree. Davidson et al. conclude that the long stiff hairs on the stem and, especially, the urticating hairs around the large prostomata favour large-bodied *P. luteola* queens over smaller-sized *Azteca* queens in *C. tessmannii*. But *C. membranacea* exhibits the same traits and is regularly occupied by *Azteca alfari*, *A. xanthochroa* and *Camponotus balzani* as are other rapidly growing *Cecropia* species, too (DAVIDSON et al. 1989, 1991, DAVIDSON & FISHER 1991, DAVIDSON & McKEY 1993).

Keeping these results in mind, most likely the *Cecropia* trees in Panguana colonized by *P. luteola* were indeed *C. tessmannii*, and probably only a few *C. membranacea* (e.g. VFor 489, and 90/335 C-P from secondary growth, and VFor 1043 and VFor 1056 from the matorral). Only in two of the examined *Cecropia* other ants were found besides *P. luteola* (once *Camponotus* sp. and once *Azteca* sp., both in presumed *C. membranacea*). The young trees were already colonized by the foundresses when only few (4-5) internodes were present, and it happened that several queens colonized the same plant. Ant queens shed their wings after mating and search for a young *Cecropia* with still uninhabited internodes. Some also obviously seek reception in yet established colonies, and it seems reasonable to speculate that they even do this in the mother nest.

In all cases observed, the young queens entered the internodium through the prostoma, a thin preformed spot in the wall of each internodium, that is easily gnawed by the ants to make a round or elliptical (up to 6 x 3 mm) entrance (plate 1b). Queens primarly colonized only one internodium and normally did not close the prostoma as do *Azteca* queens with chewed parenchyma (however, see the observation with VFor 1034). They harvested M.b. very early and fed them to the young larvae and certainly consumed them theirselves (see VFor 1033 a,c). Queens of ponerine species have to nourish themselves during colony founding because they are not supplied with great amounts of reserve material as queens of many myrmicine, formicine and dolichoderine species are. Colony founding queens of *Pseudomyrmex ferruginea* also regularly leave the swollen thorns of acacias to collect Beltian bodies (JANZEN 1967). The observations on foundresses of *P. luteola* made by DAVIDSON et al. (1991) and DAVIDSON & FISHER (1991) were similar to the results from Panguana. They state that colony growth is very slow and possibly depends on the production of M.b. They found colonies with as few as 2 - 4 workers a full year after colonization. Colony growth might also depend on the rate of parasitation of the pupae by parasitoids (Chalcidoidea) that have easy access to the brood because of the unclosed prostoma (DAVIDSON & FISHER 1991).

**Polygyny**

Multiple colonization of young trees of different *Cecropia* species by queens of one or several different ant species is not uncommon, but normally only one colony survives with one queen (e.g. in *Azteca*). Deadly fights between the colony foundresses are indicated by the carcasses of *Azteca* or queens of other species often found inside the internodia. Obviously, *P. luteola* queens avoid deadly fights among each other - carcasses or body parts were never found. Possibly, the young colonies on the same *Cecropia* later fuse, as it is known from the obligate *Acacia* inhabitant *Pseudomyrmex venefica*, too (JANZEN 1973). The result would be a polygynous colony.

The strongest hint pointing to a polygynous colony form are three dealated queens found in the completely examined colony on a *C. tessmannii* in the garden of the station (VFor 940c, plate 1). All three queens were physogastric. Because of the tubular construction of the 3rd and 4th abdominal segment this is indicated in ponerine ants by the telescopically spreading of the abdominal segments and the protruding of the intersegmental membranes. Physogastry was especially distinct in comparison with virgin not egg laying alated or dealated queens showing a „normal", non-physogastric abdomen. The dissection of two of the three physogastric queens revealed that the ovaries were fully developed and mature eggs were present. As the third, not dissected, queen showed an identical enlarged abdomen I assume that the colony had three reproductive queens at the time of examination. Unfortunately, it cannot be stated whether the queens stayed together or separately in the nest. All internodia of the *Cecropia* were interconnected by holes in the nodal septa, and eggs were found in three neighbouring internodia (tab. 1).

The observation at this nest on April 3rd, 1985 of a dealated queen communicating by antennal and oral contact with workers on the *Cecropia* stem may have been part of an adoption process of an alien queen. The colony did not yet produce queens on its own (there was only a single callow male inside when the nest was examined). Two other dealated queens were observed at the base of the same *Cecropia* on April 19 and April 20, 1985, possibly indicating that such adoption processes occur regularly.

Besides these observations, there are good theoretical reasons why *P. luteola* colonies are likely to be polygynous.Functional polygyny (facultative or obligatory one, for definitions see BUSCHINGER 1974) in which all queens of a colony contribute to the reproduction of alates can be achieved in different ways within an ant colony (HÖLLDOBLER & WILSON 1977, 1990):

- Several queens found a new colony together (= pleometrosis and primary polygyny).
- Queens found colonies independent from one each other, and later colonies adopt alien or own fertilized queens (= haplometrosis and secondary polygyny).
- Fertilized queens leave the nest with a number of workers for new nesting sites (= budding). Often, the daughter-colonies stay in contact with the mother-colony, thus resulting polydomous colonies.

Pleometrosis and primary polygyny have been interpreted in several cases to maximize fitness during the difficult period of colony founding, but often only one queen survives the fights which start later when colonies grow (see e.g. TSCHINKEL & HOWARD 1983, RISSING & POLLOCK 1987). Transitions from primary to secondary polygyny are observed in species in which queens found colonies independently but young colonies soon fuse and later adopt additional queens, too. This is the case, for example, in *Pseudomyrmex venefica* living on bull-horn acacia (JANZEN 1973).

In most cases of permanent, i.e. secondary polygyny a selective advantage for the colony as a whole is supposed (group selection; OSTER & WILSON 1978) which surpasses the importance of the kin selection (e.g. BUSCHINGER 1974, HÖLLDOBLER & WILSON 1977, NONACS 1988). That means, the adoption of new, mostly alien queens must have advantages for the established colony and for the queens seeking adoption, as well. For the foundresses the chance for reproduction seems to be better in an established colony because nest sites, i.e. young *Cecropia* are limited in number. For colonies, in general, a number of ecological reasons are discussed in which a polygynous social organization is favored (see e.g. WILSON 1963, 1971, 1974 JANZEN 1973, BUSCHINGER 1974, HÖLLDOBLER & WILSON 1977, 1990, WARD 1983, VARGO 1988). For *P. luteola* the following reasons are likely to be important:

1. While the reproductive capacity of most ponerine queens is rather limited (in comparison to ant species from other subfamilies) polygyny enables a ponerine species to increase its colony size rapidly enough which, on the other hand, is necessary for complete occupation and defense of the steadily growing nest (=*Cecropia* tree).
2. Polygyny prolongs the lifetime of a colony independently of the individual lifetime of the single queen. Thus, a *Cecropia* can be colonized by the same colony over several decades.
3. The *Cecropia* trees occupied by *P. luteola* are long-living nest sites but unpredictable in space and limited in number.
4. The effective breeding size of the population increases which is especially important for rare species and those limited to very special or rare habitats.

At present it is not known whether the supposed polygyny in *P. luteola* is an obligatory or a facultative one, in the latter case being a plastic response to a different resource availability (i.e. amount of production of M.b.) or competiton (i.e. for limited *Cecropia* number) as observed in several plant-ants (see literature in DAVIDSON & MCKEY 1993).

The estimated number of up to 10,000 or more workers within colonies on adult *Cecropia* trees is very unusual for ponerines. DAVIDSON & MCKEY (1993) even estimate colony sizes up to 100,000 workers on mature *C. tessmannii* trees that reach a stature of 30 - 35 m after several or even many decades. Thus, they constitute the largest ponerine colonies in the neotropis, possibly even in the world, rivaling with nomadic *Leptogenys* colonies in South-East Asia (MASCHWITZ et al. 1989). Reasons for the normally small colony size (several dozens to some hundreds; WILSON 1971, HÖLLDOBLER & WILSON 1990) in ponerines are:

1. Colonies most frequently are monogynous (for exceptions see e.g. WARD 1981, PEETERS & CREWE 1985).
2. Queens most often do not differ very much in size from that of the workers and are often replaced by ergatogynes or gamergates (= reproductive individuals with worker-like habits; e.g. PEETERS & CREEWE 1985, WILDMAN & CREWE 1988).
3. Ponerine species are mainly predacious and often restricted in their diet (see overwievs in BRIAN 1983 and HÖLLDOBLER & WILSON 1990).
4. Hunting and prey transport is mainly done by single workers or by just some few after tandem recruitment. Group and mass recruitment are seldom developed (e.g. in *Megaponera*, *Pachycondyla*, *Leptogenys*, *Ectatomma*) and is often associated with a special diet (e.g. very large prey, or other social insects) and/or nomadic behaviour (WHEELER 1936, WILSON 1958, 1971, HÖLLDOBLER & WILSON 1990).

The first two points limit the egg production, the third and fourth the food supply for the brood. All points together result in small to medium colony sizes. Exceptions like nomadic monogynous *Leptogenys* species (MASCHWITZ et al. 1989) are certainly not food restricted, and in *P. luteola*, possibly all four points do not match: Colonies are supposingly polygynous, queens and workers differ quite much in size, the ants feed exclusively on a plant product which is always available (see below), and the ants must not hunt but just collect M.b. from the plant.

## Nutrition

Obviously, *P. luteola*'s diet consists exclusively of Müllerian bodies (M.b.), which are produced in special hair pads (trichilia) at the base of the petioles (plate 1b). Analyses of M.b. of *Cecropia peltata* revealed that, in contrast to other cells of *Cecropia* containing starch as reserve carbohydrate, they are rich in glycogen that is stored in plastid derivates (RICKSON 1971). Because M.b. also contain protein and lipids, *Cecropia* trees offer their ants a complete diet, which makes them independent of other nutritional resources.

M.b. produced by *Cecropia tessmannii* are white and average 1.0 x 1.3 mm in size (plate 1c,d). They weigh on average 0.16 mg, i.e. they have double or triple the size of those of most other *Cecropia* species mainly colonized by *Azteca* ants. More than 50% of the trichilia of a plant were actively producing M.b. in greenhouse experiments, and production was declining with leaf age (DAVIDSON et al. 1991, DAVIDSON & FISCHER 1991). Therefore, it is not surprising that the ants always shift the nest entrance to the topmost internodia close to the most productive trichilia. For *P. luteola* foundresses it might even be vital to stay outside the plant as short time as possible.

Workers of *P. luteola* pull the M.b. with their mandibles out of the trichilia as soon as they are ripe and project from the hairs. Sometimes they even try to pull them out when they still deeply stick in the trichilia (same observations were made for *Azteca* by BEQUAERT 1922). The workers carry the M.b. immediately into the interior of the *Cecropia* (plate 1b). In the complete examined nest (VFor 940) they were stored in the first three internodes and distributed to the other internodia with brood (tab. 1, plate 1c). The whole plant contained approx. 5800 M.b., i.e. on average, 12 per adult ant or larva.

During the opening of nests, several times larvae were found feeding directly on M.b. (plate 1d). The larvae are of the pogonomyrmecoid type with ectatommoid mandibles and have a very distinct „neck", giving the head much mobility. (This is a character believed to be typical for *Pachycondyla* species and to separate them from *Neoponera* species, WHEELER & WHEELER 1976). There were few hints in the nests on possible other food than M.b. taken by *P. luteola*: In nest VFor 940 remnants of a treehopper (Membracidae) and of a male ant were found; and one worker (in nest VFor 1251) held the head of a *Cephalotes atratus* ant between the mandibles. But except for one worker that was found sitting 20 cm apart from the base of a *Cecropia* cleaning itself (after it had fallen from the plant?) workers never could be observed away from their host plant. Additionally, DAVIDSON & FISHER (1991) found out that *P. luteola* rejected standard ant baits like tuna and cheese. Thus, it seems more likely that workers kill other insects because they had invaded the *Cecropia* rather than to feed on them. In contrast to *Cecropia* trees occupied by *Azteca,* scale insects were never encountered inside the plants.

## Mutualistic advantages

Mutualistic advantages in plant-ant-associations are known from many cases (see for recent reviews e.g. BEATTIE 1984, JOLIVET 1986, HUXLEY & CUTLER 1991, DAVIDSON & MCKEY 1993).

The relationship between *P. luteola* and *C. tessmannii* obviously is obligatory for the ant and of great advantage: The plant offers a nest site that grows with increasing colony size and plenty of food. On the other hand, the plant is protected by hyperaggressive ants, which are easy to stimulate and very vigilant. Access to abundant carbohydrate-rich food is apparently often linked with an increased colony size and aggression in ants (DAVIDSON & MCKEY 1993). During the day workers always patrol over the stem and in lower number over the leaves. At the slightest disturbance they get excited searching the whole surface of the plant for the source of the disturbance. This is already the case when somebody approaches the plant. The ants seem to be able to detect the human smell (and probably that of other vertebrates, too). JANZEN (1967) supposed the same for *Pseudomyrmex ferruginea*. The reaction of the ants is stronger and lasts longer if the plant is touched. Also at night, there are always some workers sitting on top of the plant and close to the entrance, which react and alert nestmates at the slightest disturbance.

Corresponding to the high aggression and vigilance of *P. luteola* the rate of damage by herbivores on colonized *C. tessmannii* is low. Two intensely examined trees showed no leaf damage. While sampling the *Cecropia* nest VFor 940 only two arthropods could be detected on the leaves: a small salticid spider, and a small beetle. Also in the study of DAVIDSON & FISHER (1991), *C. tessmannii* presented the lowest number of herbivorous insects on the leaves among all examined *Cecropia* species.

*P. luteola* offers its host plant not only a good protection against phytophagous insects but, in contrast to *Cecropia* colonizing *Azteca* species, also against phytophagous vertebrates by means of its powerful sting. The stings of *P. luteola* are very painful for humans as I could learn by own experience. The skin burned and swelled, the intense pain lasted in one case (sting in the belly) 2 hours, in another case about half an hour. More interesting than the acute pain, that is known from other ponerines as well (SCHMIDT 1986), is the long lasting residual pain. The sting in the belly was felt for a whole week. KOEPCKE (1972) reported a two weeks lasting pain. Thus, the sting has a longer effect than of any other ant known to the author including several other species of *Pachycondyla*, *Odontomachus*, *Pseudomyrmex*, and even *Paraponera clavata*, the most painful of all. According to SCHMIDT (1986, tab. 16), the pain even lasts for a longer time than in any other hymenopteran so far known.

*Cecropia* trees colonized by *Azteca* ants have been observed to suffer damage from monkeys and sloths (BEQUAERT 1922, WHEELER & BEQUAERT 1929, WHEELER 1942, BERG 1978, JOLIVET 1986). Whereas *Azteca* workers defend their colony only by biting and chemical repellents, which seem to be tolerable at least for some time for larger animals with dense fur or thick skin, the sting of *P. luteola* is strong enough to penetrate vertebrate skin not protected by dense fur. The pain of the sting should repell every animal intending to climb the *Cecropia*, and the pain lasts long enough to accelerate a learning process to avoid this „dangerous tree" in the future. DAVIDSON states that the stings reinforce vertebrate learning for a period of 7 to 10 weeks (DAVIDSON & MCKEY 1993).

JANZEN (1967) already made the observation that large mammals like deers (*Mazama*), donkeys and cattle avoid to browse on *Acacia*, which are colonized by painful stinging *Pseudomyrmex ferruginea*. In Africa, *Tetraponera* living on *Barteria fistulosa* defend their trees also with stings against big herbivores and are successful even against elefants (JANZEN 1972).

During his study on *Acacia* ants JANZEN (1967) observed that the herbivores learned the intensive, for a human even in 3 m distance still detectable odour of rancid onions that is part of the alarm pheromone of *P. ferruginea*, and avoided the colonized *Acacia* even at night. A similar displeasant odour is released by the *Tetraponera* on *Barteria*, too. *P. luteola* does not possess such a smell, but a similar function may have the striking stridulation of the workers. Even for the human ear it is audible up to a distance of several decimeters. The workers are stridulating nearly all the time while patroling over the plant or harvesting Müllerian bodies, but immediately intensify it, if they feel a disturbance by a mecanical stimulus or just by detecting a strange odour.

Ponerine ants stridulate with the abdominal tergites III and IV, and 48% of examined ponerine species possess the necessary structures (MARKL 1973, 1983, 1985). In most cases the stridulation of ants is not audible for humans because the frequences are too high, and sound energy and range are too low. This is also the reason why ants certainly cannot detect air conducted sound but only receive vibrations through direct contact or a substrate (e.g. MARKL et al. 1977, STUART & BELL 1980, MARKL 1983, 1985). Some large ponerine ants, however, produce sounds similar to chirping that are audible for humans, too (SHARP 1893, HOWSE 1984, and own observations). Stridulation in ants has been observed in a whole array of situations e.g. when movements were restricted, when ants got burried alive, in fights with other ants, in queens after copulation to keep males away, when capturing large prey, during recruitment, while feeding other ants (trophallaxis), during nest movements, and other „stress" situations (see e.g. MARKL 1967, SPANGLER 1967, MARKL et al. 1977, ZHANTIEV & SULKANOV 1977, MARKL & HÖLLDOBLER 1978, STUART & BELL 1980). In *Megaponera foetens*, a large African ponerine, stridulation has been interpretated as aposemantic signal against predators (MASTERS 1979, HOWSE 1984). These communication signals have a low intensity, a low range, and a low capacity to provoke a specific reaction (=low range signals). However, they can be precisely tuned, are not energy expensive, only effective as long they are directly practised, do not immediately alert to many nestmates, and cannot be used by enemies. Thus they are especially suited to function as alarm system respectively as trigger and/or amplifier of other communication systems in the often highly compartmented nests of social insects (MARKL 1983, 1985). In *P. luteola* at least two functions of the stridulation seem to be obvious:

1. As alarm system via a substrate, such as the stem and leaves of a *Cecropia*. Possibly, the hollow stem of the plant additionally amplifies these signals. An analogous alarm system is known from several *Camponotus* species that „knock" with the tip of their abdomen or with the mandibels against the thin wooden walls of their nests in trees (FUCHS 1976) or against the walls of their silk nests (*Camponotus senex*, pers. observation). In such strongly compartmented nests vibrations as communication form are possibly more effective and better tunable than chemical substances. The same seems to be plausible for the *Cecropia* nest, a hypothesis worth to be tested.
2. As aposemantic acoustical signal against vertebrates which approach the host plant. This could be important against terrestrial herbivores and any bigger animal able to damage young *Cecropia* trees mechanically, but especially against arboreal herbivores like iguanas, coendus, monkeys or sloths. Although *Cecropia* trees contain considerable amounts of tannins (DAVIDSON & FISHER 1991) and are often densely covered by stiff hairs their leaves are consumed by different mammals, e.g. the primates *Alouatta* and *Ateles* (HLADIK & HLADIK 1969) or the three-toed sloths *Bradypus variegatus* and *B. tridactylus*. The latter are known to consume leaves of *Cecropia* trees regularly (the Brazilian name „imbauba" for *Cecropia* means „sloth tree", WHEELER 1942) and stay sometimes for several day in a single tree (BEEBE 1922, SUNDQUIST & MONTGOMERY 1973, HUSSON 1978: 251). It is not known whether sloths also consume leaves of *Cecropia* inhabited by *P. luteola*. An acoustical warning signal which vertebrates are likely to learn quickly would be especially valuable against nocturnal herbivores such as coendus, two-toed sloths and partly three-toed sloths.

At last, it should be mentioned that according to DAVIDSON et al. (1988) *P. luteola* facultatively prunes vines and other plants that got attached to the host tree. The authors could observe this behaviour when other ants, especially predacious or behaviourally competing species, occurred on these plants. In Panguana, workers of the examined nest in the garden neither showed any interest to vines experimentally brought in contact with the *Cecropia* nor to a winding *Pueraria phaseoloides* (Fabaceae) which was climbing the stem of the *Cecropia*. As most *C. tessmannii* grow under shaded conditions, vines that climb over them are expected to be rare anyway.

## 5. Conclusion

*Pachycondyla luteola* is one of the very few ponerine ant species known to nest regularly in myrmecophytes DAVIDSON & MCKEY (1993). In *P. luteola* several life traits are uncommon for a ponerine ant: The nest site, the completely vegetarian diet in form of glycogen rich Müllerian bodies that *Cecropia tessmannii* produces in abundance, and also the presumed functional polygyny. It is concluded that these traits enable the species to build up the most populous ponerine colonies in the world. For the *Cecropia* species colonized by this ant there seems to be an additional advantage compared to associations of *Cecropia* trees and *Azteca* ants. Besides pruning vines and eliminating herbivorous insects as do *Azteca* species, *P. luteola* also protects its host plant effectively against herbivorous vertebrates because of its powerful sting which produces a long residual pain. Certainly, the birds nesting on *Cecropia* trees colonized by *P. luteola* profit from fewer predators in these trees (KOEPCKE 1972).

Thus, the possession of this ant is likely to facilitate *C. tessmannii* to grow, though slowly, even at localities, where other *Cecropia* species cannot survive, like very small gaps in the primary forest. Because protection of myrmecophytes by ants is often far from being perfect (see e.g. VERHAAGH 1988), at such places where low light intensities limit the growth of a plant, the loss of photosynthetic active (leaf) surface is certainly more disastrous compared with a place with plenty of light. Light flooded forest edges or river banks are sites where most of the fast growing *Cecropia* species live with *Azteca* ants as inhabitants. DAVIDSON et al.(1991) and DAVIDSON & MCKEY (1993) therefore conclude that it is advantageous for slowly growing, shade tolerant myrmecophytes to invest early during their development in biological protection, i.e. ants, against herbivores. Such an association is likely to be species-specific, as in *C. tessmannii* and *P. luteola*. In contrast, associations between rapidly growing *Cecropia* species and *Azteca* ants often seem to be habitat-specific (HARADA & BENSON 1988, LONGINO 1989, DAVIDSON et al. 1991, DAVIDSON & FISHER 1991, DAVIDSON & MCKEY 1993).

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