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Plesiosaurs (Reptilia; Sauropterygia) from the Braunjura β (Middle Jurassic; late Aalenian) of southern Germany

Kurzfassung

Plesiosauria (Reptilia; Sauropterygia) aus dem Braunjura β (Mittlers Jura, Spätes Aalenian) Süddeutschlands.

Obwohl Meeresreptilien aus dem Braunen Jura β seit dem 19. Jahrhundert bekannt sind und in deutschen Sammlungen gelagert werden, wurden sie bisher nie detailliert beschrieben. In diesen Schichten kommen Plesiosaurier-, Thalattosuchier- und selten auch Ichthyosaurierreste vor. Sie sind alle als Fragmente erhalten, wahrscheinlich aufgrund eines flachmarinen, hochenergetischen Ablagerungsraums. Die Cervicalwirbel aus den Sammlungen des Staatlichen Museums für Naturkunde Karlsruhe, welche hier beschrieben werden sind die erste Nachweis elasmosaurider Plesiosaurier aus dem deutschen Dogger.

Abstract

Although known and housed in German institutions since at least the 19th century, until now marine reptiles from the Braunjura β have never been described in detail. The strata have yielded plesiosaur, thalattosuchian and rare ichthyosaur remains, all fragmentary, most likely due to their deposition in a shallow marine, high energy palaeoenvironment. Cervical vertebrae, which are housed in the Staatliches Museum für Naturkunde Karlsruhe (State Museum of Natural History in Karlsruhe), are described here and reveal the first elasmosaurid plesiosaurs reported to date from the German Dogger.

Résumé

Plésiosaures (Reptilia; Sauropterygia) du Braunjura β (Jurassique moyen, Aalénien supérieur) du sud de l'Allemagne.

Bien que connus et conservés dans des institutions allemandes depuis au moins le 19è siècle, les reptiles marins du Braunjura β n'ont jamais été décrits en détail. Cette Formation a livré des restes de plésiosaures, thalattosuchiens et ichthyosaures, tous fragmentaires probablement en raison d'un milieu de dépôt marin peu profond de haute énergie. Des vertèbres cervicales conservées au Staatliches Museum für Naturkunde Karlsruhe (Muséum d'Histoire Naturelle de Karlsruhe) décrites ici se révèlent être les premiers restes de plésiosaures élasmosaurides signalés à ce jour dans le Dogger allemand.

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Introduction

When the collections of the Geologisches Institut (Geological Institute) of the University of Freiburg were dispersed in the 1980s, part of the vertebrate teaching collections was transferred to the Staatliches Museum für Naturkunde Karlsruhe (SMNK). The original labels are now the only available data about these specimens (MUNK, pers. comm.).

The specimens described herein are part of the material transferred to the SMNK. According to the original labels they come from the 'Braun Jura β, Murchisonae Eisenoolith, Wasseralfingen, Württemberg', a unit dated to the late Aalenian (e.g. HILLER & KUNZE 1979, GEYER & GWINNER 1986). The matrix adhering to the vertebrae confirms this stratigraphic occurrence (MUNK, pers. comm.). According to the original labels, the specimens were donated to the Geologisches Institut in 1921 by a collector named VON KAPFF.

The Braunjura β in southern Germany was deposited under shallow marine conditions (GEYER & GWINNER 1986). It is exposed along the northern and north-western slopes of the Swabian Alb (DIETL 1977, GEYER & GWINNER 1986). The sequence comprises alternating layers of shale and sandstone; in the upper half of the sequence, series of oolitic limestone and sandy ironstone alternate with sandstone and sandy shale (DIETL 1977, DIETL & ETZOLD 1977). Around Aalen and Wasseralfingen two oolitic beds of the *Ludwigia murchisonae* Zone locally called 'Unteres Flöz' and 'Oberes Flöz' were mined for iron from at least the 14th century until the middle of the 20th century (RIEBBER 1977, DIETL & ETZOLD 1977). Both beds have yielded numerous invertebrate fossils, but vertebrate remains such as fishes, thalattosuchians, plesiosaurs and rare ichthyosaurs have been discovered only in the 'Oberes Flöz' (JAECKEL 1901, DIETL & ETZOLD 1977). These fragmentary remains of marine reptiles have never been studied in detail and are rarely mentioned (e.g. DIETL & ETZOLD 1977: 7, Pl. 2).

Elasmosaurid plesiosaurs are known from the Sinemurian of England, *Eretmosaurus rugosus* (OWEN 1840) representing the first certain member of the family (SEELEY 1874, BROWN & BARDET 1994, BARDET et al. 1999). GODEFROIT (1995) described indeterminate elasmosaurid remains from the Sinemurian of Belgium.

According to BARDET et al. (1999), the postcranium of *'Plesiosaurus' conybeari* Sollas, 1881 from the Sinemurian of England probably also belongs to an elasmosaurid. During the late Liassic the elasmosaurid genera *Microcleidus* and *Occitanosaurus* are known from England and France, respectively (BARDET et al. 1999). German specimens formerly referred to the genus *Plesiosaurus* are also elasmosaurs, close to *Occitanosaurus* (MAISCH & ANSORGE 2004, GROSSMANN in prep.). The vertebrae herein described document the first occurrence of elasmosaurid plesiosaurs in the early Dogger of Germany.

Material

The specimen bearing the former Freiburg accession number FS 39/170 comprises four cervical vertebrae and the proximal portion of a left femur (Figs 1-5). More ancient labels and stickers on the bones allocate number 2891 to the femur portion and numbers 2892 to 2895 to the vertebrae. There is no evidence that all elements come from a single individual (see below). The specimens now have different accession numbers in the SMNK collections. The femur bears number SMNK-PAL 3991 (Fig. 1), and the vertebrae numbers SMNK-PAL 3987 to 3990 (Figs 2-5; Table 1), while the phalanx previously labelled FS 39/166 and 3283 in the Freiburg collections now bears the number SMNK-PAL 3992 (Fig. 6).

From their size alone, the elements bearing following former Freiburg numbers (vertebrae SMNK-PAL 3987-3990 and femur SMNK-PAL 3991) could belong to a single individual. But the lateral-most portions of the corpus of vertebra SMNK-PAL 3989 are abraded and the spongiosa is exposed; in lateral aspect, the cranial and caudal abraded areas are connected by a linear band of exposed spongiosa, which most likely indicates that a keel, now abraded, was present at mid-height on the corpus (see Discussion). The abraded areas are partly covered with matrix (Fig. 4a-c). The vertebra was therefore abraded prior to embedding. A similar, although less clearly expressed abrasion is visible on the preserved lateral margins of vertebrae SMNK-PAL 3987 and 3990 (Figs 2c, 5c), and traces of the matrix are also present in these areas. The other bones show no abrasion. Without further data it is impossible to determine if these differences in preservation are actually due to different origins or merely to partial exposure prior to embedding of a single carcass. The identical origin and collector cannot be taken as indicating identical locality and circumstances, for among the former Freiburg specimens housed in the SMNK, at least a partial thalattosuchian rostrum bears the same indications, including donor and donation date. It is therefore unknown how many individuals the elements described herein belonged to.

The bones are three-dimensionally preserved. They are partly prepared; however, matrix remains in the neural canal of all vertebrae except SMNK-PAL 3989 (Fig. 4a, b). Additionally, the matrix adhering to the cranial articular surface of vertebra SMNK-PAL 3988 (Fig. 3c, d) and covering most of the pre- and postzygapophyses (Figs 2a-d, 3a, b, 5b, c) indicates that the vertebrae, even if belonging to a single individual, must have been disarticulated prior to embedding. The ribs were not fused to the corpora, for matrix still partly covers the apophyses (Figs 2c, 3b, c, 4c, d, 5c). All neural arches are poorly preserved. All neural spines are broken due to recent damage (Figs 2-5). The right prezygapophysis of vertebra SMNK-PAL 3987 was broken prior to embedding, for its remains are covered with matrix (Fig. 2a, c).

The neural arches are fused to the corpora but, although no suture line is visible, its former course is marked by a distinct swelling of the bone surface (Figs 2c, 3b, 4c, 5c). All vertebrae thus represent a young adult *sensu* BROWN (1981).

The femur is represented only by its proximal-most portion (Fig. 1). The poor condition of the compacta hints at recent damage, maybe during collecting. Some matrix is still present especially on the articular surfaces (Fig. 1).

The phalanx is free from matrix except on its distal articular surface, where the partial shell of an unionid bivalve (MUNK, pers. comm.) and some matrix were left adhering to the bone (Fig. 6).

Systematic Palaeontology

Sauropterygia OWEN, 1860
Plesiosauria DE BLAINVILLE, 1835
Plesiosauria indet.

Table 1. List of the specimens described in the text, their actual and former accession numbers, identification and illustration in this paper.

Specimen	Former Freiburg accession number	Identification	Figure in this paper
SMNK-PAL 3987	FS 39/170; 2892	Elasmosauridae indet., cervical vertebra	Fig. 2
SMNK-PAL 3988	FS 39/170; 2893	Elasmosauridae indet., cervical vertebra	Fig. 3
SMNK-PAL 3989	FS 39/170; 2894	Elasmosauridae indet., cervical vertebra	Fig. 4
SMNK-PAL 3990	FS 39/170; 2895	Elasmosauridae indet., cervical vertebra	Fig. 5
SMNK-PAL 3991	FS 39/170; 2891	Plesiosauria indet., proximal portion of femur	Fig. 1
SMNK-PAL 3992	FS 39/166; 3283	Plesiosauria indet., phalanx	Fig. 6

SMNK-PAL 3991 (Fig. 1)
Material: Proximal portion of a femur.
Description: In proximal aspect, the femur head is almost symmetrical (Fig. 1d). The oval capitulum is confluent with the subquadrangular trochanter articular surface. In proximal view, when the long axis of the trochanter articular surface is oriented dorsally, the longest axis of the capitulum is oriented slightly craniocaudoventrally.
The capitulum is gently convex, while the trochanter articular surface is almost flat (Fig. 1a-c). These structures form sharp margins with the shaft. In cranial and caudal aspects, the capitulum and trochanter articular surface form together an angle of approximately 120° (Fig. 1a, b).

SMNK-PAL 3992 (Fig. 6)
Material: One phalanx.
Description: In dorsal and ventral aspects the phalanx is hour-glass shaped (Fig. 6d, e). It is 32 mm in proximodistal dimension. Its craniocaudal extent is 19 mm proximally and a maximum of 21 mm distally. It is narrowest around midshaft, where it is 11 mm in length. Its dorsal and ventral margins are almost parallel in cranial and caudal aspects, their proximal- and distal-most portions being only slightly expanded dorsoventrally (Fig. 6a, b).
The proximal articular surface is gently convex and in proximal aspect exhibits four foramina which are almost aligned craniocaudally (Fig. 6c). The dorsoventral height of the proximal surface is 10 mm. Most of the distal articular surface is nearly flat, while its caudalmost 4 mm is inclined dorsocaudally (Fig. 6d, e). The height of the distal surface is also 10 mm.

Plesiosauroidea WELLES, 1943
Elasmosauridae COPE, 1869
Elasmosauridae indet.
Specimens SMNK-PAL 3987-3990 (Figs 2-5)
Material: Four fragmentary cervical vertebrae.
Description: The corpora are shallowly amphicoelous to platycoelous; all are longer than high (Figs 2-5). The dimensions of the corpora are given in Table 2.

Table 2. Dimensions of the corpora in mm.

Specimen	Length	Maximal width	Minimal height	Maximal height
SMNK-PAL 3987	40	40	25	27
SMNK-PAL 3988	36	50	30	33
SMNK-PAL 3989	50	41	27	30
SMNK-PAL 3990	39	46	31	34

The central portion of the ventral surface of the corpora is flat. The lateral surfaces of the corpora are shallowly concave (Figs 2-5).
In cranial and caudal aspects, the ventral margin of the articular surfaces of the corpora is horizontal. Their lateral margins are gently convex; their dorsal margin is depressed at the level of the neural canal (Figs 2a, b, 3a, 4a, b, 5a, b). The outer margins of the articular surfaces are rounded, forming poorly expressed lips toward the lateral and ventral surfaces of the corpora (Figs 2c, d, 3b-d, 4c, d, 5c, d).
On either side of the midline the ventral surface of the corpora exhibits a pair of foramina, the foramina subcentralia. The foramina are longitudinally oval, of a similar size on either side of each corpus (Figs 2d, 3c, 4d, 5d).
A single rib facet is visible on the left side of vertebra SMNK-PAL 3987, although this could be due to poor preservation of the bone surface dorsal to the facet (Fig. 2c, d). All other rib facets are double, diapophysis and parapophysis being distinct and separated by a sulcus (Figs 2d, 3b, c, 4c, d, 5c, d). The diapophysis and parapophysis of each vertebra are of similar size and shape. They are longitudinally oval, located on the ventral-most portion of the lateral surface of the vertebrae and slightly raised compared to the lateral surface of the corpus. The apophyses of SMNK-PAL 3989 are more dorsoventrally depressed and more pointed cranially and caudally than the apophyses of the other vertebrae (Fig. 4c, d). In lateral aspect, the apophyses are located at the midpoint of the length of the corpora.
The corpus of SMNK-PAL 3987 shows on both sides a longitudinal keel situated in height around the dorsal two-thirds of the corpus (Fig. 2c). SMNK-PAL 3989 most likely had a similar keel situated around midheight of the corpus in lateral aspect, which is now abraded (Fig. 4c; see Material).
In lateral aspect, the contact between corpus and neural arch is ventrally convex. The neural arch inserts from 2 mm caudal to the cranial margin of the corpus to nearly its caudal margin (Figs 2c, 3b, 4c, 5c).
The maximal width of the neural arch represents approximately one half of the width of the corpus (Figs 2a, b, 3a, d, 5a, b). The neural arch appears proportionally wider in vertebra SMNK-PAL 3989, which could be due to abrasion of the lateral surfaces of the corpus (Fig. 4a, b; see Material).
The neural canal is free from matrix only in SMNK-PAL 3989 (Fig. 4a, b), where it has the shape of a vertical oval 10 mm in width ventrally and 15 mm in height.
The articular surface of the prezygapophyses of SMNK-PAL 3989 is inclined about 35° to the horizontal in cranial aspect (Fig. 4a). In SMNK-PAL 3988, almost the entire prezygapophysis projects cranial to the cranial articular surface of the corpus (Fig. 3b). In SMNK-PAL 3989, only the cranial half of the prezygapophysis projects cranial to the cranial articular surface of the corpus (Fig. 4c). The postzygapohyses are damaged on all vertebrae. In SMNK-PAL 3988 they are transversely broken and the visible section in caudal aspect indica-

tes an angle of about 25° to the horizontal (Fig. 3a). In SMNK-PAL 3988 and 3989 the dorsomedial surface of the prezygapophysis is divided into two areas by a faint ridge running laterally and slightly caudally. The area cranial to this ridge is matte and rugose and covers the cranial-most two thirds of the dorsomedial surface of the prezygapophysis. The area caudal to the ridge is bright and smooth and gradually merges with the neural spine (Fig. 3d). The cranial-most area is most likely the contact surface with the postzygapophysis.

In lateral aspect, as far as can be judged from only partial preservation, the articular surfaces of the pre- and postzygapophyses appear slightly inclined cranioventrally (Figs 3b, 4c, 5c).

A horizontal, sharp ridge joins the dorsal margin of the prezygapophysis of SMNK-PAL 3987 to the ventral margin of its postzygapophysis (Fig. 2c). In SMNK-PAL 3988, 3989 and 3990 the area between pre- and postzygapophyses exhibits no ridge but is slightly laterally convex (Figs 3d, 4c, 5c).

The neural spine gently tapers in width dorsally. It is the widest at its base, immediately dorsal to the level of the pre- and postzygapophyses (Figs 2a, b, 3a, d, 5a, b).

In cranial aspect, the base of the neural arches in SMNK-PAL 3987, 3988 and 3990 exhibits a subtriangular recessus dorsal to the prezygapophyses (Figs 2a, 5a). In SMNK-PAL 3988, the summit of the recessus extends until 10 mm dorsal to the dorsal-most point of the prezygapophyses, while in SMNK-PAL 3987, the summit of this recessus only reaches the level of the dorsal-most point of the prezygapophyses (Fig. 2a). The summit of the recessus of SMNK-PAL 3990 is missing due to breakage of the neural spine. As preserved, it extends until 12 mm dorsal to the dorsal-most point of the prezygapophyses (Fig. 5a).

Dorsal to the recessus in SMNK-PAL 3988 the cranial margin of the neural spine is a sharp, cranially convex blade in lateral aspect (Fig. 3b).

In caudal aspect the base of the neural spine exhibits a lenticular recessus. In SMNK-PAL 3988 it extends from the ventral-most extent of the postzygapophyses and is 25 mm high. A median ridge 2 mm tall is present dorsal to the recessus until the broken dorsal edge of the specimen, as if the caudal margin of the neural spine also were blade-like more dorsally (Fig. 3a).

Discussion

Identification and comparisons

The preserved portion of femur and the phalanx are typically plesiosaurian, but not diagnostic below ordinal level (see e.g. BROWN 1981).

The foramina subcentralia, together with the general morphology of the vertebrae, are characteristic of Plesiosauria. Because the apophyses are situated in the ventrolateral-most portion of the corpora all vertebrae are clearly cervicals (e.g. TARLO 1960, BROWN 1981). Among Plesiosauria, the longer than high and depressed cervical corpora with platycoelous or shallowly amphicoelous articular surfaces characterise elasmosaurids (WELLES 1943, 1952, 1962, BROWN 1981, BARDET et al. 1999). It is noteworthy that elasmosaurids here are taken as defined by the elongation of the neck through elongation of the individual vertebrae and increase in number of cervical vertebrae, reaching a climax in the Late Cretaceous genus *Elasmosaurus* COPE, 1868 (WELLES 1952, PERSSON 1963, BROWN 1981, O'KEEFE 2001). The vertebrae described here document a clear trend toward elongation of the cervical vertebrae, justifying their identification as elasmosaurid for biomechanical reason, regardless of the recent cladistic-based revisions of the taxonomy of Plesiosauria (e.g. O'KEEFE 2001, GASPARINI et al. 2003, GROSSMANN & MAISCH in prep., MAISCH pers. comm.). In particular, the current debate about the taxa to be included in the families Cryptoclididae and Elasmosauridae (GASPARINI et al. 2003, O'KEEFE & WAHL 2003, O'KEEFE 2004, GROSSMANN & MAISCH in prep., MAISCH pers. comm.) is a matter of differences in the cladistic approach to different specimens, which is not considered here.

The elongation of the corpora is especially visible in vertebrae SMNK-PAL 3987 and 3989 (Figs 2, 4). The corpora SMNK-PAL 3988 and 3990 are shorter compared to their height (Figs 3, 5, Table 1). According to the measurements given by WELLES (1943: Tables 4, 10, 1952: Tables 1, 3, 6, 7) and BARDET et al. (1999: Table 2), the ratio of length to height of the cervical corpora is variable when measured along the neck of a single individual. On average the caudal-most corpora tend to be shorter compared to their height than the cranial-most corpora. Owing to the ventral location of the apophysis in corpora of SMNK-PAL 3988 and 3990 (Figs 3b, c, 5c, d) these do not represent caudal cervical corpora, but the ratio does not decrease regularly along the neck (WELLES 1943: Tables 4, 10, 1952: Tables 1, 3, 6, 7, BARDET et al. 1999: Table 2). Therefore the relative shortness of the corpora of SMNK-PAL 3988 and 3990 does not contradict their otherwise clearly elasmosaurid morphology.

The lateral keel visible on SMNK-PAL 3987 (Fig. 2c) and abraded on SMNK-PAL 3989 (Fig. 4c) is also present in some cervical vertebrae of elasmosaurids and members of the genus *Plesiosaurus* (see Introduction); it probably marks the insertion of an aponeurosis correlated with the elongation of the neck (BROWN 1981, BARDET et al. 1999, O'KEEFE 2001).

The vertebrae are not diagnostic below familial level.

Plesiosaurs of the Middle Jurassic of southern Germany.

During the Early Jurassic, both southern and northern Germany were covered by epicontinental seas connected to one another via a strait between the emergent Rhenic and Bohemian Massifs (e.g. GEYER & GWINNER 1986, GODEFROIT 1994, MAISCH & ANSORGE 2004).

During the Middle Jurassic, the Rhenic and Bohemian Massifs coalesced into a continuous land mass; the connection between the northern and southern German Basins was lost, and southern Germany became a shallow marginal basin of the Tethys (e.g. GEYER & GWINNER 1986).

Marine reptiles are relatively abundant and well preserved from the Lower Jurassic sea (e.g. GODEFROIT 1994, HAUFF 1997, BARDET et al. 1999, MAISCH & ANSORGE 2004), while they are rare and fragmentary in the Middle Jurassic of southern Germany (WELLNHOFER 1970). It has never been investigated whether the scarceness of marine reptiles preserved in the Middle Jurassic sediments of southern Germany reflects the actual scarceness of marine reptiles there at that time or is merely due to sedimentation conditions with poor preservation potential for articulated skeletons.

Until now, elasmosaurid plesiosaurs from the Dogger of southern Germany were never mentioned in literature. Published reports of plesiosaurs from the Dogger of southern Germany were listed by WELLNHOFER (1970). None of these remains comprises elements that can be compared with the elements described here. *'Plesiosaurus' suevicus* QUENSTEDT, 1858 was defined on caudal vertebrae from Frittlingen, Württemberg, and a femur from Hagenbuch, Württemberg, all deriving from the Braunjura α (von HUENE 1923, WELLNHOFER 1970). An additional isolated vertebra from the Braunjura δ of Zillhausen, Württemberg, was referred to *Plesiosaurus* sp. (QUENSTEDT 1858); the original description is insufficient to certify that the remains are actually plesiosaurian (WELLNHOFER 1970). *Thaumatosaurus oolithicus* von MEYER, 1856 and the remains attributed by von HUENE (1934) to *Pliosaurus* [sic] (*Liopleurodon*) *ferox* SAUVAGE, 1873 both comprise vertebrae and skull fragments that allow referral to Pliosauridae (von HUENE 1934, WELLNHOFER 1970). WELLNHOFER (1970) additionally described plesiosaur remains from the Opalinuston (Braunjura α) of Amberg, Bavaria. The material comprises a pectoral vertebra, a tibia, a fibular, a metatarsal and a phalanx, all probably from the same individual, and was referred to *Plesiosaurus* sp. (WELLNHOFER 1970). The phalanx much resembles the one described here, but among plesiosaurs phalanx morphology is of no taxonomic import. The pectoral corpus is slightly longer than high, shallowly amphicoelous and its ventral margin is strongly convex (WELLNHOFER 1970: 265, Fig. 1). However, the pectoral vertebrae of elasmosaurs do not appear to show characteristic features like cervical vertebrae do (WELLES 1943, 1952, 1962, BROWN 1981, BARDET et al. 1999, O'KEEFE 2001).

The genus *Plesiosaurus* has long been a wastebasket taxon that recently received partial clarification (STORRS 1997, MAISCH & RÜCKLIN 2000, BARDET et al. 1999) but is still in need of revision (MAISCH & ANSORGE 2004, GROSSMANN in prep., MAISCH pers. comm.). As noted in the introduction, some of the members of the genus appear to be elasmosaurids (GROSSMANN in prep.). The material described by WELLNHOFER (1970), according to the current understanding of plesiosaurian anatomy and systematics, is undiagnostic below superfamilial level. Similarly, the material described herein was also assigned to *Plesiosaurus* sp. according to the Freiburg labels. Re-examination of such ancient material, especially when including cervical vertebrae, will surely yield more long-necked plesiosaurs and help clarifying the status and stratigraphic and palaeogeographic range of elasmosaurids. Moreover, a systematic examination of the remains of thalattosuchians and ichthyosaurs would provide a better view of the marine reptile assemblage of the German Dogger and might help explain the rarity of its preservation.

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References

BARDET, N., GODEFROIT, P. & SCIAU, J. (1999): A new elasmosaurid plesiosaur from the Lower Jurassic of Southern France. – Palaeontology, **42**: 927-952.

BLAINVILLE, H. D. DE (1835): Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpetologie et d'Amphibiologie. – Nouv. Ann. Mus. Nat. Hist. nat., Paris, **3**(4): 233-296.

BROWN, D. S. (1981): The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. – Bull. Br. Mus. (Nat. Hist.), Geol., **35** (4): 253-347

BROWN, D. S. & BARDET, N. (1994): *Plesiosaurus rugosus* Owen, 1840 (currently *Eretmosaurus rugosus*; Reptilia, Plesiosauria): proposed designation of a neotype. – Bull. Zool. Nomencl., 51: 247-249.

COPE, E. D. (1869): Synopsis of the extinct Batrachia, Reptilia and Aves of North America. –

Trans. Amer. Phil. Soc., n. s., **14**: 1-252.

DIETL, G. (1977): The Braunjura (Brown Jurassic) in Southwest Germany. – Stuttgarter Beitr. Naturk., B, **25**: 1-41.

DIETL, G. & ETZOLD, A. (1977): The Aalenian at the type locality. – Stuttgarter Beitr. Naturk., B, **30**: 1-13.

GASPARINI, Z., BARDET, N., MARTIN, J. E. & FERNANDEZ, M. (2003): The elasmosaurid plesiosaur *Aristonectes* Cabrera from the latest Cretaceous of South America and Antarctica. – J. Vert. Pal., **23**(1): 89-103.

GEYER, O. F. & GWINNER, M. P. (1986): Geologie von Baden-Württemberg. – 3. Aufl., 472 S.; Stuttgart (E. Schweizerbart'sche Verlagbuchhandlung).

GODEFROIT, P. (1994): Les reptiles marins du Toarcien (Jurassique inférieur) belgo-luxembourgeois. – Mem. Expl. Cartes géol. min. Belgique, **39**: 1-98.

GODEFROIT, P. (1995): Plesiosauria (Reptilia) sinémuriens de Lorraine belge. – Bull. Inst. r. Sci. nat. Belgique, **65**: 165-178.

HAUFF R. B. (1997): Urwelt-Museum Hauff. Leben im Jura Meer. – 37 S.; Holzmaden (Urwelt-Museum Hauff).

HILLER, D. & KUNZE, T. (1979): Der Braune Jura β (Ober-Aalenium) zwischen Nürtingen und Owen (Württemberg). – Arb. Inst. Geol. Paläont. Univ. Stuttgart, N.F., **74**: 141-163.

HUENE, F. VON (1923): Ein neuer Plesiosaurier aus dem oberen Lias Württembergs. – Jh. Ver. vaterl. Naturk. Württemberg, **79**: 1-21.

HUENE, F. VON (1934): Ein großer *Pliosaurus* aus dem schwäbischen Ornatenton. – Jh. Ver. Vaterl. Naturk. Württemberg, **90**: 31-46.

JAECKEL, O. (1901): Über jurassiche Zähne und Eier von Chimäriden. – N. Jb. Min., Beil.-Bd., **14**: 540-564.

MAISCH, M. W. & ANSORGE, J. (2004): The Liassic ichthyosaur *Stenopterygius* cf. *quadriscissus* from the lower Toarcian of Dobbertin (northeastern Germany) and some considerations on Lower Toarcian marine reptile palaeobiogeography. – Paläont. Zeitschr., **78**(1): 161-171.

MAISCH, M. W. & RÜCKLIN, M. (2000): Cranial osteology of the sauropterygian *Plesiosaurus brachypterygius* from the Lower Toarcian of Germany. – Palaeont., **43**(1): 29-40.

O'KEEFE, F. R. (2001): A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). – Acta Zool. Fennica, **213**: 1-63.

O'KEEFE, F. R. (2004): On the cranial anatomy of the polycotylid plesiosaurs, including new material of *Polycotylus latipinnis* Cope from Alabama. – J. Vert. Pal., **24**(2): 326-340.

O'KEEFE, F. R. & WAHL, W. (2003): Current taxonomic status of the plesiosaur *Pantosaurus striatus* from the Upper Jurassic Sundance Formation, Wyoming. – Paludicola, **4**(2): 37-47.

OWEN, R. (1840): Report on British fossil reptiles, Part I. – Rep. Brit. Ass. Adv. Sci., 1839, **9**: 153-166.

OWEN, R. (1860): On the orders of fossil and recent Reptilia, and their distribution in time. – Rep. Brit. Ass. Adv. Sci., 1859, **29**: 153-166.

PERSSON, P. O. (1963): A revision of the classification of the Plesiosauria, with a synopsis of the stratigraphical and geographical distribution of the group. – Lunds Universitets Arsskrift, N.F. Avd. 2, **59**: 1-59.

QUENSTEDT, F. A. (1858). Der Jura. – 842 S.; Tübingen (Laupp).

RIEBER, H. (1977): Remarks to the Aalenian of the Swabian Alb. – Stuttgarter Beitr. Naturk., B, **29**: 1-5.

SAUVAGE M. H. E. (1873): Notes sur les reptiles fossiles. – Bull. Soc. géol. France, **3**(1): 365-380.

SEELEY, H. G. (1874): Note on some generic modifications of the plesiosaurian pectoral arch. – Q. J. Geol. Soc., London, **30**: 436-449.

STORRS, G. W. (1997): Morphological and taxonomic clarification of the genus *Plesiosaurus*. – In: CALLAWAY, J. M. & NICHOLLS, E. L. (Eds.): Ancient Marine Reptiles: 145-190; San Diego (Academic Press).

SOLLAS, W. J. (1881): On a new species of *Plesiosaurus* (*P. Conybeari*) from the Lower Lias of Charmouth; with observations on *P. Megacephalus*, Stutchbury, and *P. Brachycephalus* Owen. – Q. J. Geol. Soc., **37**: 439-483.

TARLO, L. B. (1960): A review of Upper Jurassic Pliosaurs. – Bull. Brit. Mus. Nat. Hist. Geol., **4** (5): 145-189.

WELLES, S. P. (1943): Elasmosaurid plesiosaurs with a description of new material from California and Colorado. – Mem. Univ. Calif., **13**(3): 125-215.

WELLES, S. P. (1952): A review of the North American Cretaceous elasmosaurs. – Univ. Calif. Publs geol. Sci., **29**(3): 47-144.

WELLES. S. P. (1962): A new species of Elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. – Univ. Calif. Publs Geol. Sci., **44**(1): 1-96.

WELLNHOFER, P. (1970): Plesiosaurier-Reste aus dem Opalinuston von Amberg (Opf.). – Mitt. Bayer. Staatssamml. Paläont. u. hist. Geol., **10**: 261-270.

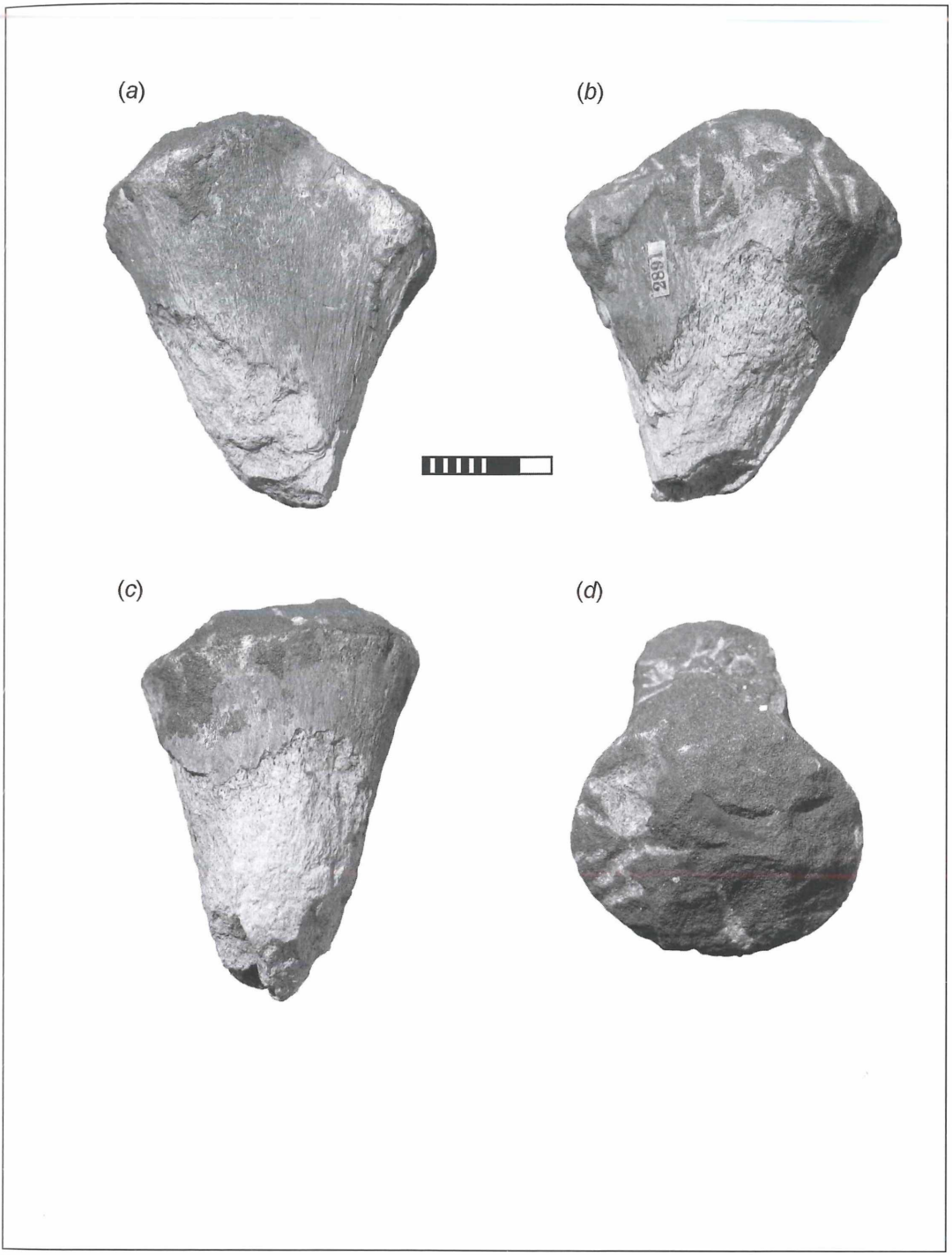

Figure 1. SMNK-PAL 3991, Plesiosauria indet., proximal portion of femur in (*a*) cranial, (*b*) caudal, (*c*) ventral and (*d*) proximal views. Scale bar 20 mm.

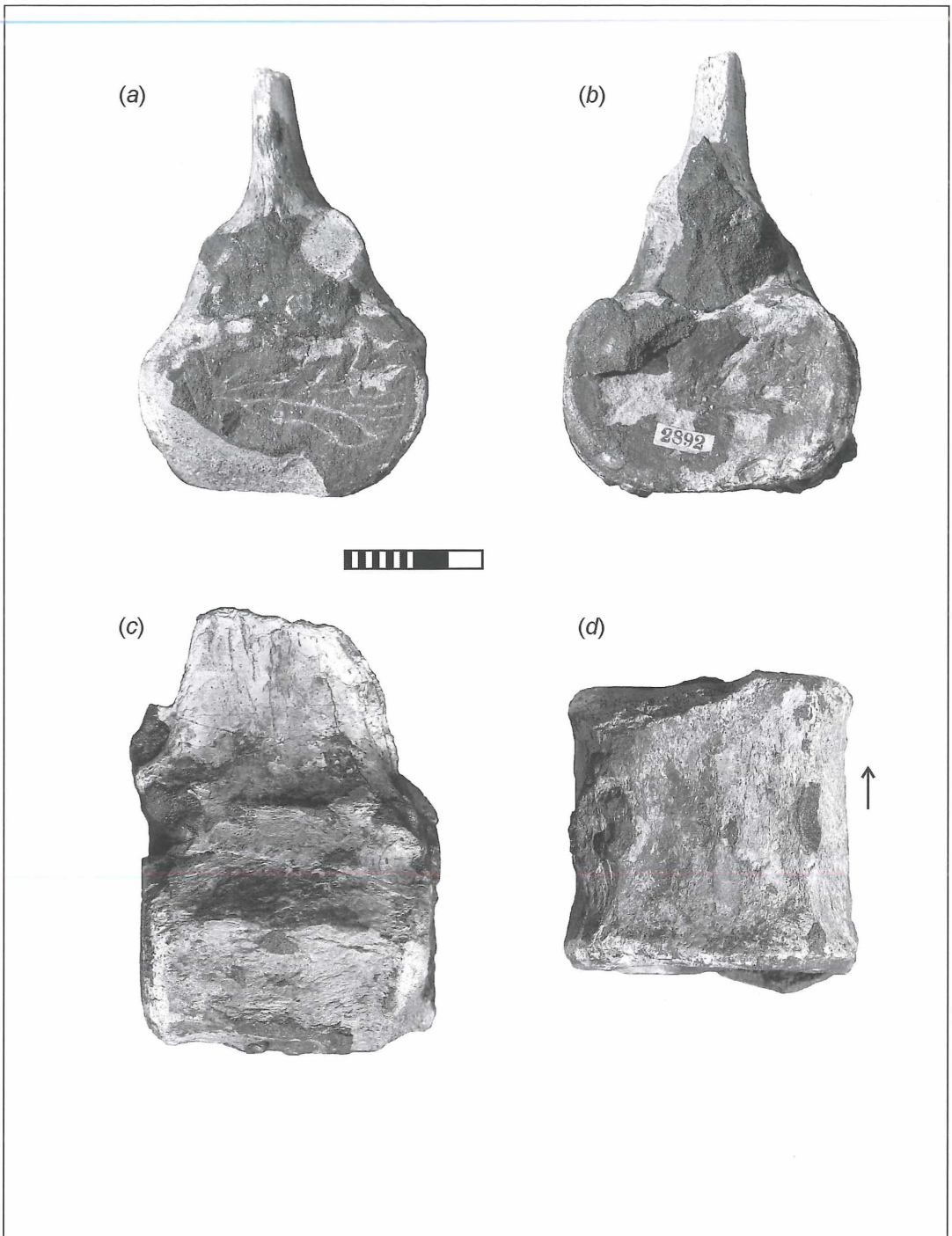

Figure 2. SMNK-PAL 3987, Elasmosauridae indet., cervical vertebra in (*a*) cranial, (*b*) caudal, (*c*) right lateral and (*d*) ventral views. Arrow in (*d*) points cranially. Scale bar 20 mm.

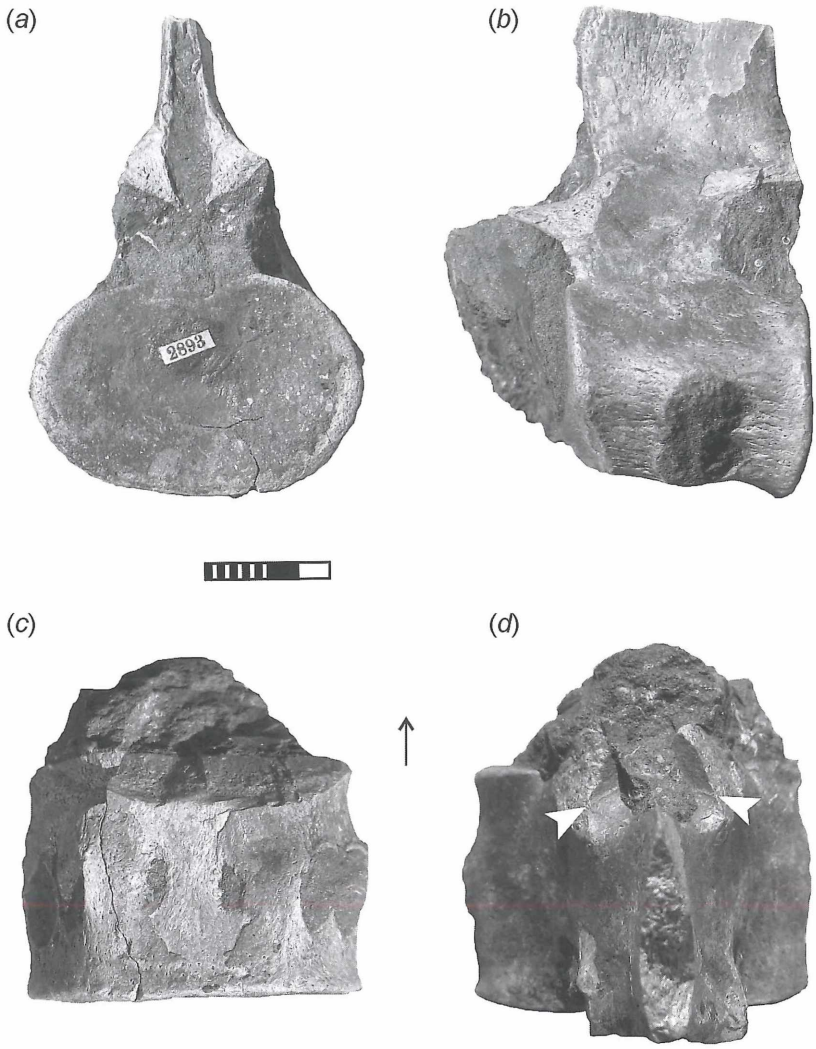

Figure 3. SMNK-PAL 3988, Elasmosauridae indet., cervical vertebra in (*a*) caudal, (*b*) left lateral, (*c*) ventral and (*d*) craniodorsal views. Black arrow in (*c*) and (*d*) points cranially. White arrows in (*d*) point at the ridge marking a change in texture on the dorsomedial surface of the prezygapophysis (see text). Scale bar 20 mm.

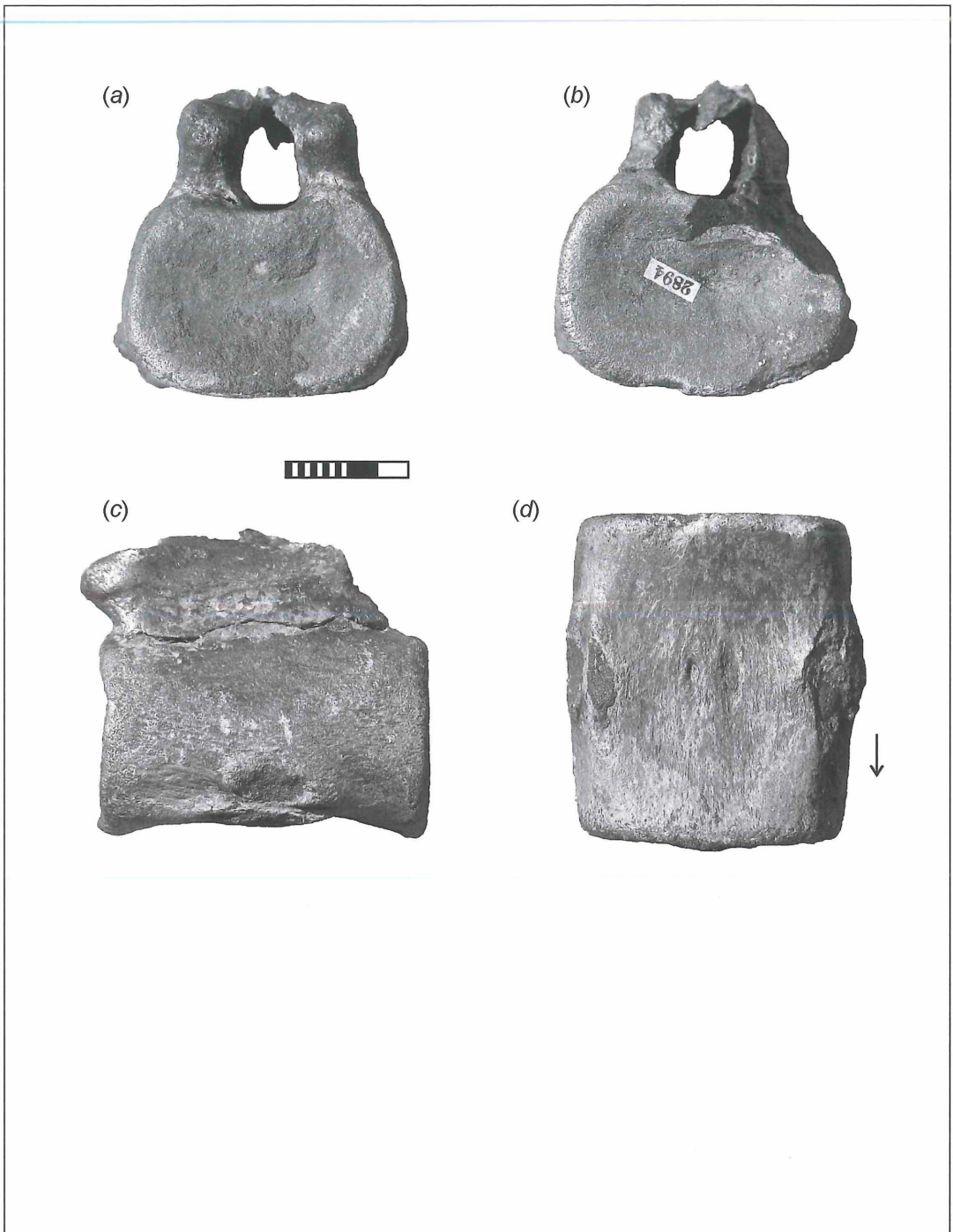

Figure 4. SMNK-PAL 3989, Elasmosauridae indet., cervical vertebra in (*a*) cranial, (*b*) caudal, (*c*) left lateral and (*d*) ventral views. Arrow in (*d*) points cranially. Scale bar 20 mm.

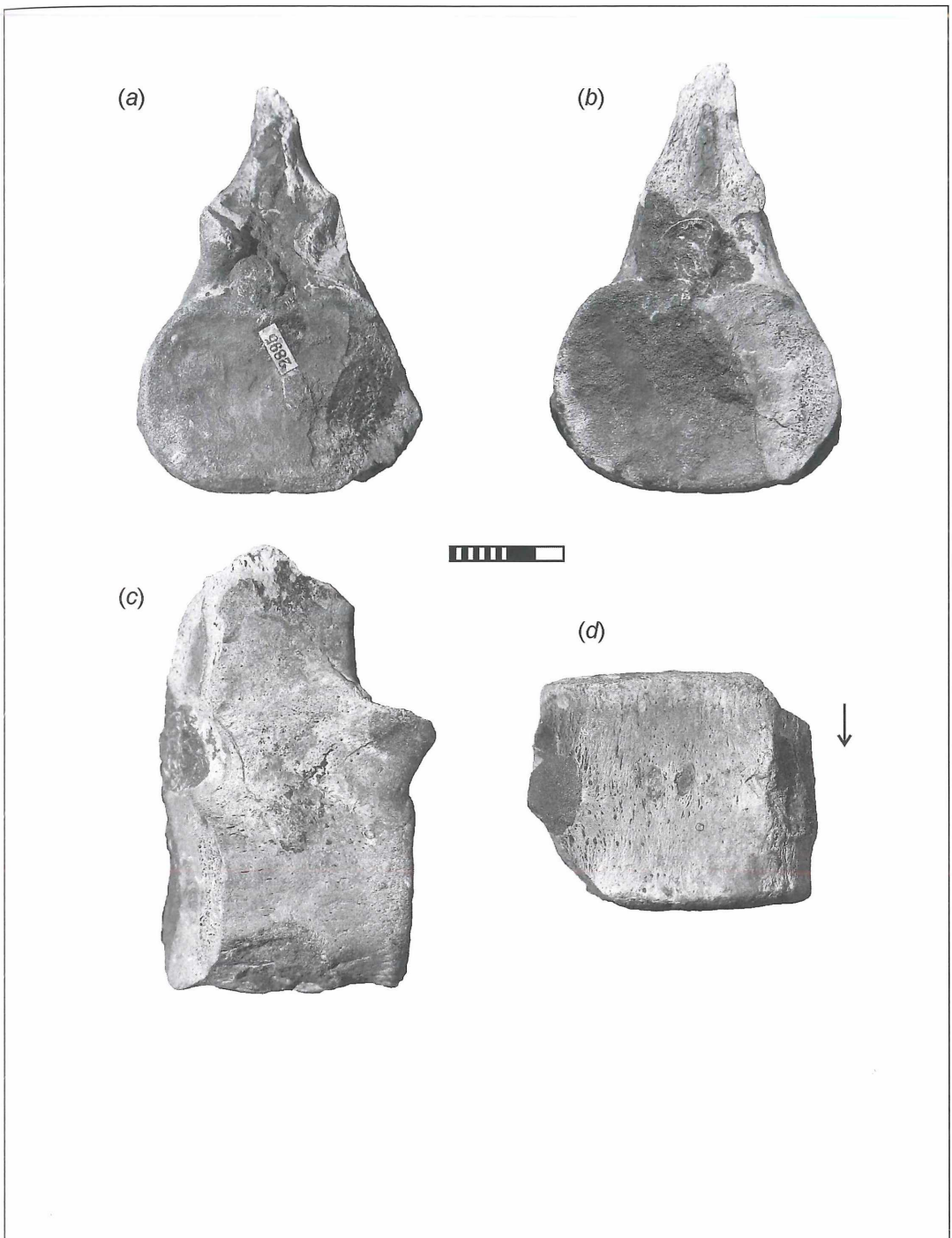

Figure 5. SMNK-PAL 3990, Elasmosauridae indet., cervical vertebra in (*a*) cranial, (*b*) caudal, (*c*) right lateral and (*d*) ventral views. Arrow in (*d*) points cranially. Scale bar 20 mm.

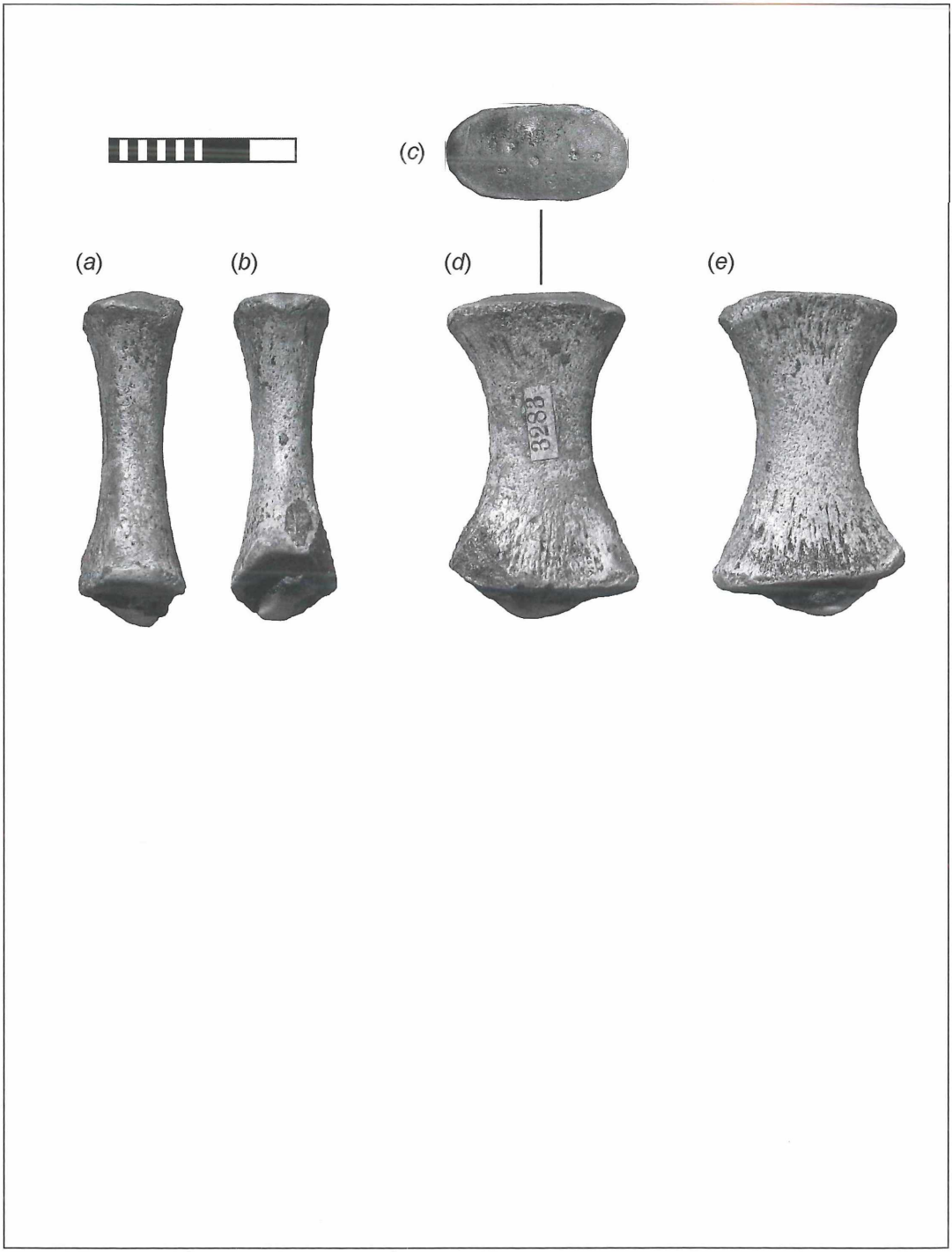

Figure 6. SMNK-PAL 3992, Plesiosauria indet., phalanx in (*a*) cranial, (*b*) caudal, (*c*) proximal and (*d*) and/or (*e*) dorsal and ventral views. Scale bar 20 mm..