Postcranial morphology of a basal Pistosauroidea (Sauropterygia) from the Lower Muschelkalk of Winterswijk, The Netherlands

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RESEARCH PAPER

Postcranial morphology of a basal Pistosauroidea (Sauropterygia) from the Lower Muschelkalk of Winterswijk, The Netherlands

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Abstract Two partial postcranial skeletons from the Lower Muschelkalk (early Anisian) of Winterswijk, The Netherlands, are described in detail. The specimens were assigned to basal Pistosauroidea, presumably to cf. *Cymatosaurus* or a closely related taxon. *Cymatosaurus* is currently the earliest member of the Pistosauroidea and is only known from skull material. Taxonomical assignment is based on humerus morphology and histology, and on morphological differences from other Sauropterygia (Nothosauria and Pachypleurosauria).

Keywords Triassic Sauropterygia · *Cymatosaurus* · Early Anisian · Postcranial skeleton

Kurzfassung Zwei postcraniale Skelettreste aus dem Unteren Muschelkalk (frühes Anis) von Winterswijk (Niederlande) werden im Detail beschrieben. Die Stücke werden einem basalen Pistosauroidea, möglicherweise cf. *Cymatosaurus* oder einem nah verwandten Taxon, zugeordnet. *Cymatosaurus* ist der früheste Vertreter der Pistosauroidea und bislang nur von isolierten Schädelfunden bekannt. Die taxonomische Zuordnung basiert vor allem auf der Morphologie des Humerus und dessen knochenhistologischen Merkmalen, sowie auf morphologischen Unterschieden im direkten Vergleich mit anderen Sauropterygiern (Nothosauria und Pachypleurosauria).

Schlüsselwörter Triassische Sauropterygia · *Cymatosaurus* · Frühes Anis · Morphologie Postkranialskelett

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Institutional Abbrevations

NMNHL National Museum of Natural History (NCB Naturalis), Leiden, The Netherlands

Introduction

Sauropterygia is a diverse group of marine reptiles that first appear in the Germanic Basin in the early Middle Triassic (Rieppel and Hagdorn 1997). By the Lower Muschelkalk (early Anisian, Middle Triassic), Sauropterygia are very diverse and the fossil record contains many individuals from this group (summarized in Rieppel 2000; Klein 2010; Kelley et al. 2012). They can be divided into four major groups: the Placodontia, the Pachypleurosauria, the Nothosauria, and the Pistosauroidea (Rieppel 2000). The latter includes the Plesiosauria, the only sauropterygian clade that thrived until the end of the Cretaceous.

Cymatosaurus, a basal member of Pistosauroidea, is currently the geologically oldest diagnostic member of Pistosauroidea and Sauropterygia from the Germanic Basin (Rieppel 2000). It is known from the Lower to Middle

Muschelkalk of Central Germany and Western Poland (Rieppel and Hagdorn 1997). *Cymatosaurus* is restricted to the Anisian and is so far only known from isolated skulls (summarized in Rieppel 2000). Except for *Corosaurus* from the uppermost Lower Triassic from the Eastern Pacific faunal province (western USA) (Case 1936; Storrs 1991; Rieppel 2000), all other members of Triassic Pistosauroidea originate from stratigraphically younger horizons from the Tethys and its associated epicontinental seas. Additionally, the latter are only known from a few, often incomplete, specimens (e.g., Meyer 1839; Storrs 1991; Sander et al. 1997; Rieppel et al. 2002; Dalla Vecchia 2006; Cheng et al. 2006; Sato et al. 2010).

Sues (1987) and Rieppel (1997) had proposed that postcranial material of "*Proneusticosaurus*" as well as humeri from the Lower Muschelkalk localities of Freyburg, Central Germany, and Winterswijk, The Netherlands (Rieppel 1994, 1995) could possibly belong to *Cymatosaurus*. However, this was never confirmed due to the lack of diagnostic material such as skulls associated with postcranial bones, so these assignments remained hypothetical. Klein (2010) studied the morphology and histology of humeri of Sauropterygia from the Lower to Middle Muschelkalk, including those hypothetically assigned to *Cymatosaurus*. Unexpectedly, bone tissue types of these sauropterygian humeri turned out to be very diverse, comprising several histotypes and growth patterns, additionally implying that bone histology possibly contains a phylogenetic signal, at least in Triassic Sauropterygia. The humeri that Rieppel (1994, 1995) had suggested as belonging to *Cymatosaurus* and the humeri associated with the skeletons described below show a morphology, a histotype, and a growth pattern that are well separated from those of other eosauropterygians (Klein 2010). Furthermore, this characteristic histotype contains layers of fibrolamellar bone and a high radial vascular density (histotype A bone tissue; Klein 2010), a bone tissue which was, until recently, only seen in Sauropterygia in Cretaceous plesiosaurs (Wiffen et al. 1995). Krahl et al. (2009, in review), however, detected similar radial fibrolamellar bone tissue in the Upper Muschelkalk (late Anisian, Middle Triassic) pistosauroid *Pistosaurus*, the sister group of Plesiosauria (Fig. 1). This supports the possible presence of fibrolamellar bone in the entire clade of Pistosauroidea (Klein 2010), which would also include *Cymatosaurus*, its basalmost member. Humeri showing histotype A bone tissue were thus assigned to ?*Cymatosaurus* or a close relative (Klein 2010). Histotype A bone tissue always occurs together with a particular humerus morphology, which is useful for distinguishing it from those of nothosaurs and pachypleurosaurs (Klein 2010, see below).

The current paper describes, for the first time, the postcranial morphology of cf. *Cymatosaurus* or a closely related basal Pistosauroidea, based on two skeletons (NMNHL RGM 449487A and NMNHL RGM 445912) from the Lower Muschelkalk of Winterswijk, The Netherlands.

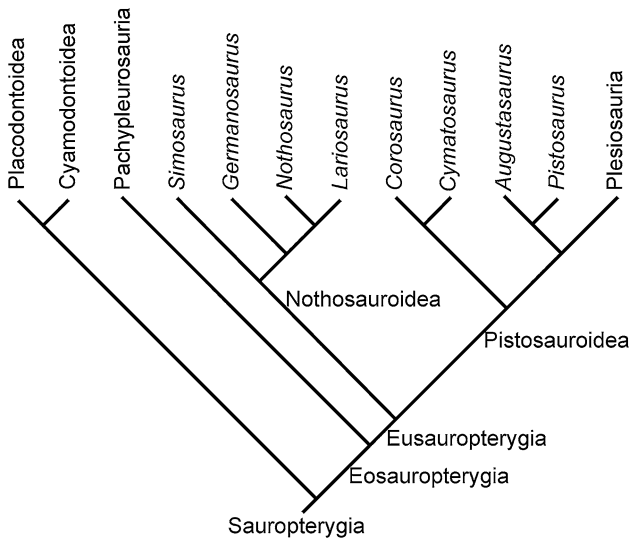


Fig. 1 Phylogenetic hypothesis for the major groups of Triassic Sauropterygia, after Rieppel (2000). Pachypleurosauroidea are monophyletic and form the sister group to the Eusauropterygia (Nothosauroidea and Pistosauroidea). *Simosaurus* is regarded as a basal nothosaur and *Corosaurus* forms the sister taxon to *Cymatosaurus*. Placodontoidea are regarded as the sister group to all other Sauropterygia

Material

The locality

The material studied here originates from the productive limestones in the locality of Winterswijk, The Netherlands (middle Lower Muschelkalk, early Anisian, Middle Triassic). Winterswijk is unique within the Germanic Basin due to its northwesternmost position in the basin as a vertebrate-producing locality but also because of its taphonomy (Klein 2009). Isolated bones, which are typical finds for the Germanic Basin, are very common in Winterswijk, but articulated and associated finds of marine reptiles also occur. On the other hand, thousands of footprints and tracks of terrestrial vertebrates are known from Winterswijk (Oosterink 2009). Ongoing research on the marine reptile fauna in Winterswijk has so far produced two species of *Nothosaurus* (Albers and Rieppel 2003; Albers 2005a; Klein and Albers 2009; Albers 2011), the pachypleurosaur *Anarosaurus heterodontus* (Rieppel and Lin 1995; Klein 2009, 2010, 2012), and at least four taxa of placodonts, of which two are restricted to Winterswijk (Albers 2005b; Neenan et al. 2013; Klein and Scheyer

2013). The bone histology of isolated femora from Winterswijk and the humerus of specimen NMNHL RGM 449487A revealed the presence of a basal member of the Pistosauroidea, most likely cf. *Cymatosaurus* or a close relative in Winterswijk (Klein 2010). Besides Sauropterygia, the prolacertiform *Amotosaurus rotfeldensis* (previously *Tanystropheus antiquus*; Wild and Oosterink 1984; Oosterink et al. 2003, 2013) and the enigmatic aff. *Eusaurosphargis* (listed as *Saurosphargis* in Klein 2009) have been unequivocally identified in Winterswijk.

The specimens

NMNHL RGM 449487A

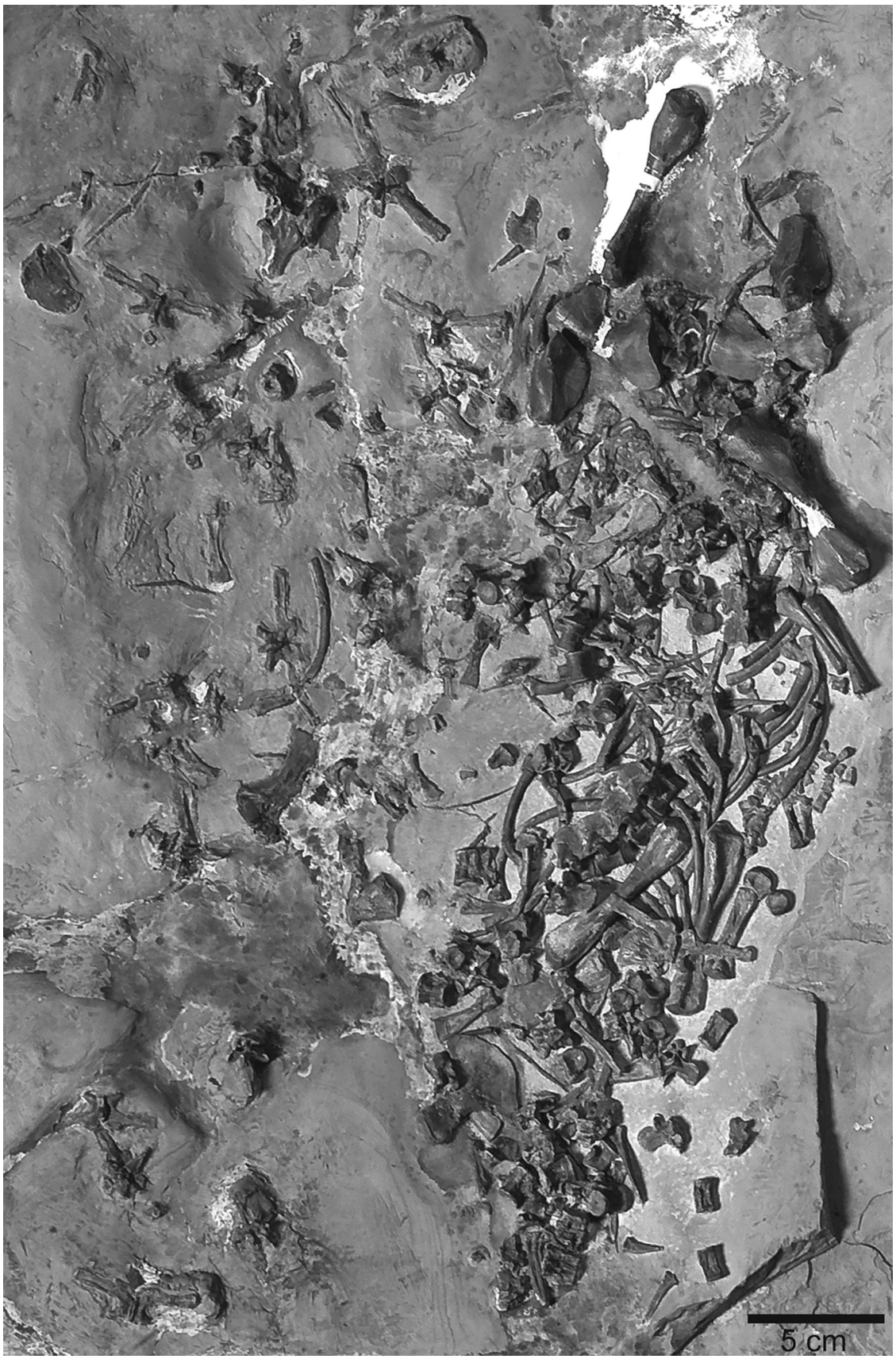
NMNHL RGM 449487 is a postcranial skeleton associated with disarticulated remains of the enigmatic marine reptile *Eusaurosphargis* and a skull of *Anarosaurus heterodontus* on a matrix block bearing the accession number NMNHL RGM 449487 (Figs. 2, 3). We designate the partially articulated postcranial skeleton here NMNHL RGM 449487A and the *Anarosaurus* skull NMNHL RGM 449487B, with further letters of the alphabet reserved for the as-yet unstudied aff. *Eusaurosphargis* material. NMNHL RGM 449487 is the main matrix block of a bone accumulation that was found in 1999 between layers 4 and 9 of the still active quarry 3 at Winterswijk (Oosterink 1986). Other parts of the bone accumulation were collected on several smaller slabs. The beds hosting the bone accumulation are assigned to the Vossenveld Formation, which is equivalent to the Wellenkalk Fazies in the center of the Muschelkalk Basin (SKPT 2008; Hagdorn and Simon 2010). The bone assemblage contains several individuals of different taxa, which seem to have accumulated by the water in a slight depression on the surface of a carbonate mudflat. This kind of accumulation of skeletons is rather typical of the Winterswijk locality, with disarticulated remains of several intertwined individuals often seen. The additional slabs associated with NMNHL RGM 449487 contain numerous bones and pieces of bony armor of several individuals, mainly aff. *Eusaurosphargis*. Other previously identified bones belong to fishes (e.g., cf. *Saurichthys*), *Amotosaurus* (cervical vertebra), placodontids, and a variety of eosauropterygians. However, these will be the topic of another publication. Due to the fairly complete nature of skeleton NMNHL RGM 449487A, it is not very likely that the additional slabs contain further diagnostic bones of this individual that would be essential to the description of basal Pistosauroidea described in detail below.

The skeleton NMNHL RGM 449487A (Figs. 2, 3, 6, 7, 8) is decayed to a certain degree and was moved (most likely by water) before fossilization. As a result, the bones are exposed in various views. The missing skull as well as the incomplete neck and tail region may also be the result of movement by water. The pattern of skeleton preservation is suggestive of an originally slightly curved position of the carcass. It measures along its vertebral column approximately 40.0 cm (posterior neck region to the postsacral region). The total body length is estimated to have been 100–120 cm, depending on the lengths of the missing parts (skull, neck, and tail length). Zygopodia and autopodia are incomplete. The measurements and ratios of the bones are given in Table 1.

Based on its morphology, the skull roof associated with specimen NMNHL RGM 449487A, labeled NMNHL RGM 449487B (Figs. 2, 3), can be assigned to the pachypleurosaur *Anarosaurus heterodontus* (Klein 2009). This incomplete skull does not belong to the skeleton NMNHL RGM 449487A. Besides its morphology, which is typical of *A. heterodontus* (Klein 2009), a plot of skull length versus humerus length for various eosauropterygians clearly shows that the skull roof does not lie on the regression line for pachypleurosaurs and nothosaurs (Fig. 4). Furthermore, an assignment of the postcranial skeleton NMNHL RGM 449487A to *A. heterodontus* can be excluded based on its morphology (Klein 2012) as well as its long-bone histology (Klein 2010).

In addition to specimens NMNHL RGM 449487A and NMNHL RGM 449487B, bones of aff. *Eusaurosphargis* are also present on the slab. In order to clarify which of the intimately associated bones of the skeleton NMNHL RGM 449487A and those of aff. *Eusaurosphargis* belong to which taxon, a brief description of the bones of the aff. *Eusaurosphargis* on the matrix block is necessary. The bones of aff. *Eusaurosphargis* are easy to distinguish because they have a different morphology from those of NMNHL RGM 449487A and NMNHL RGM 449487B and because of the generally crushed and flattened appearance of the long bones, which probably results from a very thin cortex (Figs. 2, 3).

Aff. *Eusaurosphargis* was unequivocally identified on the basis of several scattered cervical vertebrae, the neural arches, which are capped by pointed osteoderms, and by its dorsal vertebrae, which carry characteristic elongated transverse processes (Figs. 2, 3; Huene 1936; Nosotti and Rieppel 2003). In addition to their characteristic shape, aff. *Eusaurosphargis* vertebrae also have their neural arch fused to the centrum, as opposed to the eosauropterygian skeleton, where the centrum and neural arch are most often found to be isolated due to unossified neurocentral sutures. The centra of aff. *Eusaurosphargis* vertebrae are spindle-shaped and amphicoelous but not notochondral. In addition to the pointed triangular osteoderms, the cervicals show a short, stocky prezygapophysis that is not well set off from the centrum, and a long postzygapophysis. The form of the


5 cm

◀ **Fig. 2** Overview photograph of slab NMNHL RGM 449487. The skeleton of the basal pistosaur (NMNHL RGM 449487A) is concentrated in the *right half of the figure*. The preserved trunk region is disarticulated, but the main parts are still associated, including the partially preserved hind and forelimbs. The *left half of the figure* shows the left ilium and the incomplete pubis of NMNHL RGM 449487A that have drifted away from the other bones, as well as an isolated skull roof of the pachypleurosaur *A. heterodontus* (NMNHL RGM 449487B) and isolated vertebrae of aff. *Eusaurosphargis*

osteoderm varies depending on its anatomical position but it is generally oval-oblong with a broader socket as the basis. Its surface is always pitted. Isolated osteoderms are found in addition to those still attached to the cervical vertebrae. Altogether, 26 vertebrae of the neck and trunk region as well as five very flat limb bones and one presumed coracoid are identified as belonging to aff. *Eusaurosphargis* (Figs. 2, 3).

Fig. 3 Overview sketch of slab NMNHL RGM 449487. The different taxa are marked by different shades of *gray*: *dark gray* denotes the bones belonging to the skeleton of cf. *Cymatosaurus* (NMNHL RGM 449487A), except for the ribs and gastralia, which are only shown in outline. *Medium gray* denotes the flattened long bones and the characteristic vertebrae assigned to aff. *Eusaurosphargis*. Note that a few bones of this taxon have been omitted for clarity. The isolated skull roof of the pachypleurosaur *A. heterodontus* (NMNHL RGM 449487B) is marked in *light gray*. *as* astragalus, *c* caudal, *ca* calcaneus, *co* coracoid, *cr* caudal rib, *cv* cervical vertebra, *dv* dorsal vertebra, *Euco Eusaurosphargis* coracoid, *Eudv Eusaurosphargis* dorsal vertebra, *Eu?is Eusaurosphargis* ?ischium, *Euhu Eusaurosphargis* humerus, *Eufe Eusaurosphargis* femur, *Eulb Eusaurosphargis* lower limb bone, *Euv Eusaurosphargis* vertebra, *fe* femur, *hu* humerus, *il* ilium, *is* ischium, *isd* distal part of right ischium, *isp* proximal part of right ischium, *mt* metatarsalia, *ph* phalanges, *pu* pubis, *ra* radius, *sc* scapula, *sr* sacral rib, *sv* sacral vertebra, *ti* tibia, *ul* ulna

Table 1 Measurements, numbers, and ratios of the basal eosauropterygian skeletons NMNHL RGM 449487A and NMNHL RGM 445912

Measurements	RGM 449487	RGM 445912
Length of neck vertebrae	c. 0.8–1.2	–
Width of neck vertebrae	c. 1.6–2.0	–
Length of dorsal vertebra	1.2	0.9
Width of dorsal vertebra	2.15	1.9
Trunk length	c. 40.0	>20.0
Length of tail vertebra	1.2	–
Width of tail vertebra	1.7	–
Length of sacral rib	2.7	–
Clavicula length	–	c. 5.1
Clavicula width	–	c. 1.6
Scapula length	4.9	c. 4.5
Scapula ventral width/length	2.1/3.65	c. 1.75/3.55
Coracoid length	5.2	–
Coracoid prox. width	2.8	–
Coracoid shaft	1.3	–
Coracoid distal width	3.2	–
Ilium length	2.1	–
Ilium width	1.7	–
Pubis length	4.2	–
Pubis prox. length	–	–
Pubis distal length	2.55	–
Ischium length	4.15	–
Ischium prox. width	4.2	–
Ischium shaft width	1.1	–
Ischium distal width	1.55	–
Humerus length	7.9	7.2
Humerus prox. width/length	c. 1.6/1.7	1.2/1.65
Humerus shaft width/length	0.8/0.6	0.95/0.85
Humerus distal width/length	2.35/0.9	c. 1.8/0.8
Radius length	4.2	–
Ulna length	3,85	3.2
Femur length	7.35	–
Femur prox. width/length	1.25	–
Femur shaft width/length	0.5	–
Femur distal width/length	1.2	–
Tibia length	3.6	–
Fibula length	c. 2.9	–
Number of presacral vert.	min. 30	>18
Number of tail vertebrae	min. 15	–
Number of carpalia	2–3	–
Number of tarsalia	2 (+?)	–
Standard length (Sander 1989)	4.5	c. 4.2
Neck vert. length/width	0.5–0.57	–
Dorsal vert. length/width	0.57	0.47
Tail vertebra length/width	0.7	–
Humerus/femur	1.07	–
Humerus/clavicula	–	1.44
Humerus/scapula	1.6	1.6
Humerus/ulna	2.5	2.25
Humerus/radius	1.8	–
Humerus/coracoid	1.52	–
Humerus/tibia	2.19	–
Humerus/pubis	1.9	–
Humerus/ischium	1.9	–
Humerus/standard length	1.75	1.7
Femur/tibia	2.04	–
Femur/standard length	1.63	–
Scapula/standard length	1.09	1.07
Clavicula/standard length	–	1.19
Ulna/standard length	0.85	0.76
Radius/standard length	0.93	–
Tibia/standard length	0.8	–

min., minimal; c., circa

Whereas the long bones of aff. *Eusaurosphargis* are difficult to identify, the coracoid (Figs. 2, 3) exactly matches the round form with the open notch of the coracoid foramen of *Eusaurosphargis* as described by Nosotti and Rieppel (2003). Another girdle bone (Fig. 3, Eugb) is interpreted as an ischium (Nosotti and Rieppel 2003).

NMNHL RGM 445912

The second specimen on which this study is based on is a partial postcranial skeleton preserved in dorsolateral view (Fig. 5). Due to the relatively undisturbed preservation, there is no evidence of scavenger feeding or water transport for this skeleton. NMNHL RGM 445912 arrived in the museum collection of the University of Delft in 1966 through Prof. F. J. Faber, who was at that time employed as advisor to the Winterswijk quarry. Later, the entire Delft collection was taken over by the NMNHL. The specimen NMNHL RGM 445912 was found in the now inactive quarry 2 at Winterswijk, but no further stratigraphical or taphonomical information was recorded. NMNHL RGM 445912 consists of an anterior trunk region of an incomplete but articulated specimen in ventral view (Fig. 5) that exhibits a badly preserved and incomplete vertebral column, a few mostly incomplete ribs, the distal part of a left interclavicle and the proximal part of a left clavicle, a left scapula, a left humerus, a left ulna, three carpal elements, one metacarpal, and some gastral ribs. The skeleton measures c. 25.0 cm (posterior neck to praesacral region) along the preserved vertebral column. The body length of the individual was not more than approximately 90 cm, again depending on the length of the missing skull, neck, and tail.

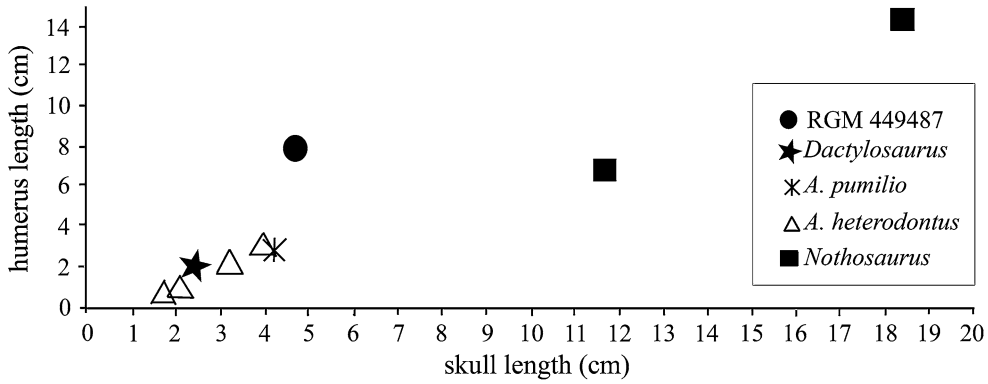


Fig. 4 Plot of skull length vs. humerus length for some eosauropterygians. The graph shows clearly that the skull NMNHL RGM 449487B does not belong to the skeleton NMNHL RGM 449487A. The morphology of the skull roof (NMNHL RGM 449487B) is identical to that of *A. heterodontus* (Klein 2009). The length of the skull was reconstructed on the basis of complete skulls known to originate from *A. heterodontus* (Klein 2009). Measurements were taken from the original specimens and from the literature. The assignment of NMNHL RGM 449487A to cf. *Cymatosaurus* or a basal pistosauroid is based on its humerus morphology and histology

This estimation is based on a comparison with the bone dimensions of other more complete eosauropterygian skeletons (e.g., Schröder 1914; Klein 2012).

Due to the preservation of the specimens in a block of matrix and the frequent superposition of elements in specimen NMNHL RGM 449487, it was, unfortunately, not possible to figure all bones adequately, or to obtain detailed measurements of many elements. Additionally, in the case of NMNHL RGM 445912, many of the bones from the trunk region are not originally preserved; only their imprints remain.

Systematic paleontology

Sauropterygia Owen 1860
Eosauropterygia Rieppel 1994
Pistosauroidea Baur 1887–90
Cymatosaurus Fritsch 1894

Diagnosis

See Fritsch (1894: 273–302) for the original description. See Rieppel (1997, 2000) for diagnosis of skull morphology: small- to medium-sized eosauropterygians with moderately depressed skulls; snout constricted; postorbital skull distinctly elongated; occiput deeply concave; supraoccipital vertically oriented and in loose connection with the dermatocranium; distinctly reduced nasals; frontals paired; posterolateral process of frontal closely approaches upper temporal fossa and may enter its anteromedial margin; parietals incompletely or completely fused; jugal enters posterior margin of the orbit and remains excluded from upper temporal arch; quadratojugal absent.

Included species

C. fridericianus Fritsch 1894 from the Upper Buntsandstein (earliest Anisian) form Halle-Nietleben, Saxony-Anhalt, Germany. *C. latifrons* Gürich 1884 from the Lower Muschelkalk of Gogolin, Upper Silesia, Poland. *C. minor* Rieppel and Werneburg 1998 from the Lower Muschelkalk of Hetschburg, Thuringia, Germany. *C. multidentatus* Huene 1958 from the earliest Anisian from the Krabachmasse, Trittwangkopf, NNW Stuttgarter Hütte, Lechtaler Alps (Arlberg), Austria. All species are only known from isolated skulls.

Referred specimens

NMNHL RGM 449487A, a partially articulated skeleton with a nearly complete trunk region, including some limb and girdle bones preserved (Figs. 2, 3, 6, 7, 8). NMNHL RGM 445912, a partial postcranial skeleton preserved as natural molds and original bones of articulated ribs and vertebrae from the trunk region, shoulder girdle bones, and a humerus (Figs. 5, 8d). Both specimens originate from the locality of Winterswijk, The Netherlands (Middle Triassic, early Anisian, Lower Muschelkalk, Vossenfeld Formation). For a detailed discussion of preservation see above; for measurements see Table 1.

Description

Axial skeleton

No atlas-axis complex was identified. For the disarticulated specimen NMNHL RGM 449487A, 30 presacral vertebrae, 2 sacral vertebrae, and 15 caudal vertebrae were counted,

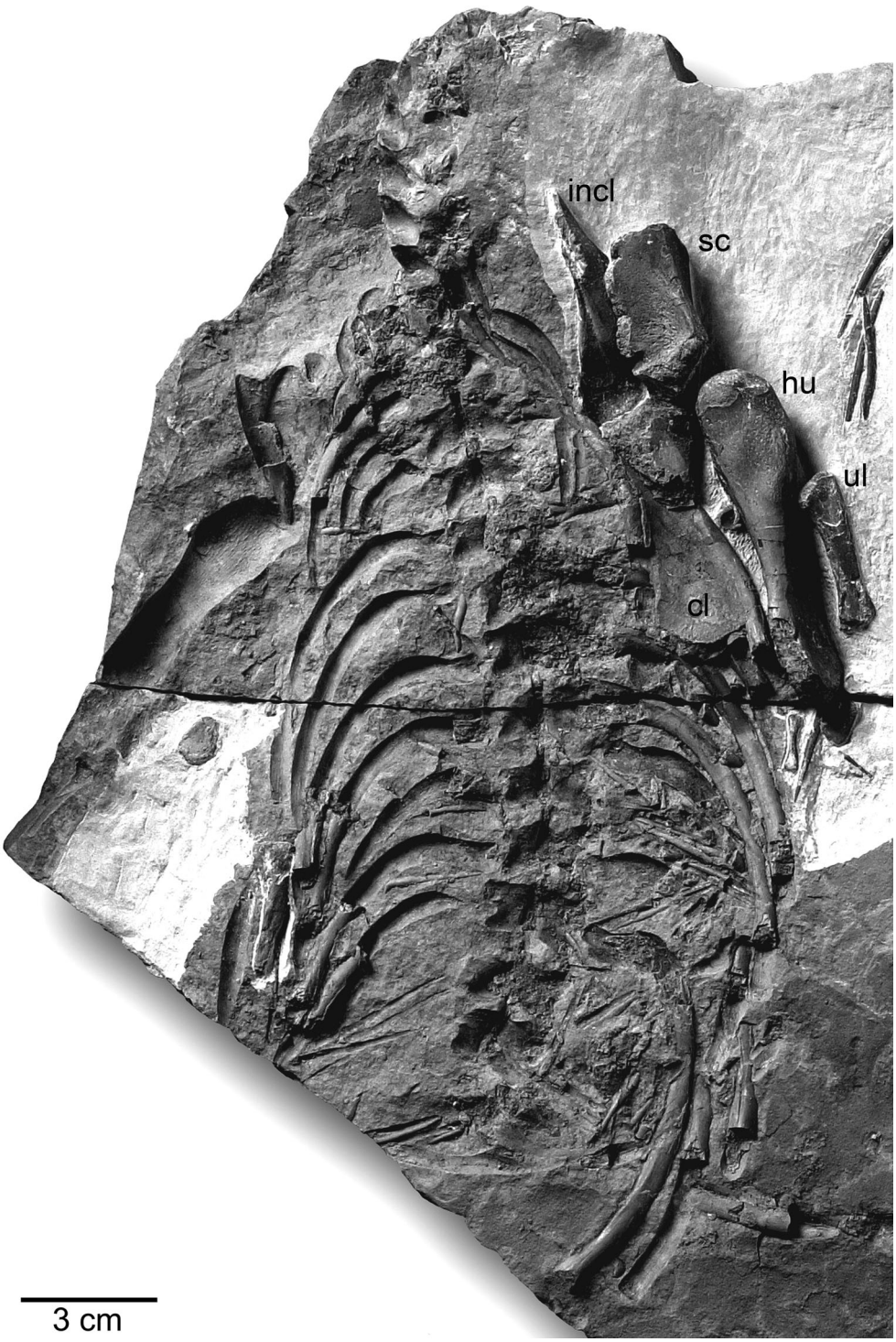


Fig. 5 Overview photograph of slab NMNHL RGM 445912. Most of the bones in this partially preserved skeleton are only represented by natural molds. Original bones comprise just a few articulated ribs and vertebrae from the trunk region, as well as some bones from the left shoulder girdle and forelimb. The assignment of NMNHL RGM 445912 to cf. *Cymatosaurus* is based on its humerus morphology. *cl* clavicle, *hu* humerus, *incl* interclavicle, *sc* scapula, *ul* ulna

which most likely does not represent their full original counts due to losses before and during the fossilization processes. Specimen NMNHL RGM 445912 shows impressions of 17 or 18 presacral vertebrae.

Many of the vertebrae of NMNHL RGM 449487A are separated along their neurocentral suture into neural arch and centrum (Figs. 2, 3), presenting the typical "sauropterygian cross" on the dorsal centrum surface. The "sauropterygian cross" is formed by a "butterfly-shaped or cruciform facet" (Rieppel 2000, p. 12; Fig. 5) in which the "body" is represented by the neural canal. The weak connection between neural arch and centrum is typical of eosauropterygians, irrespective of their ontogenetic stage.

The vertebrae are generally all weakly amphicoelous. The centra are constricted and not pachyostotic. The neural arches are generally wider than the length of the centra.

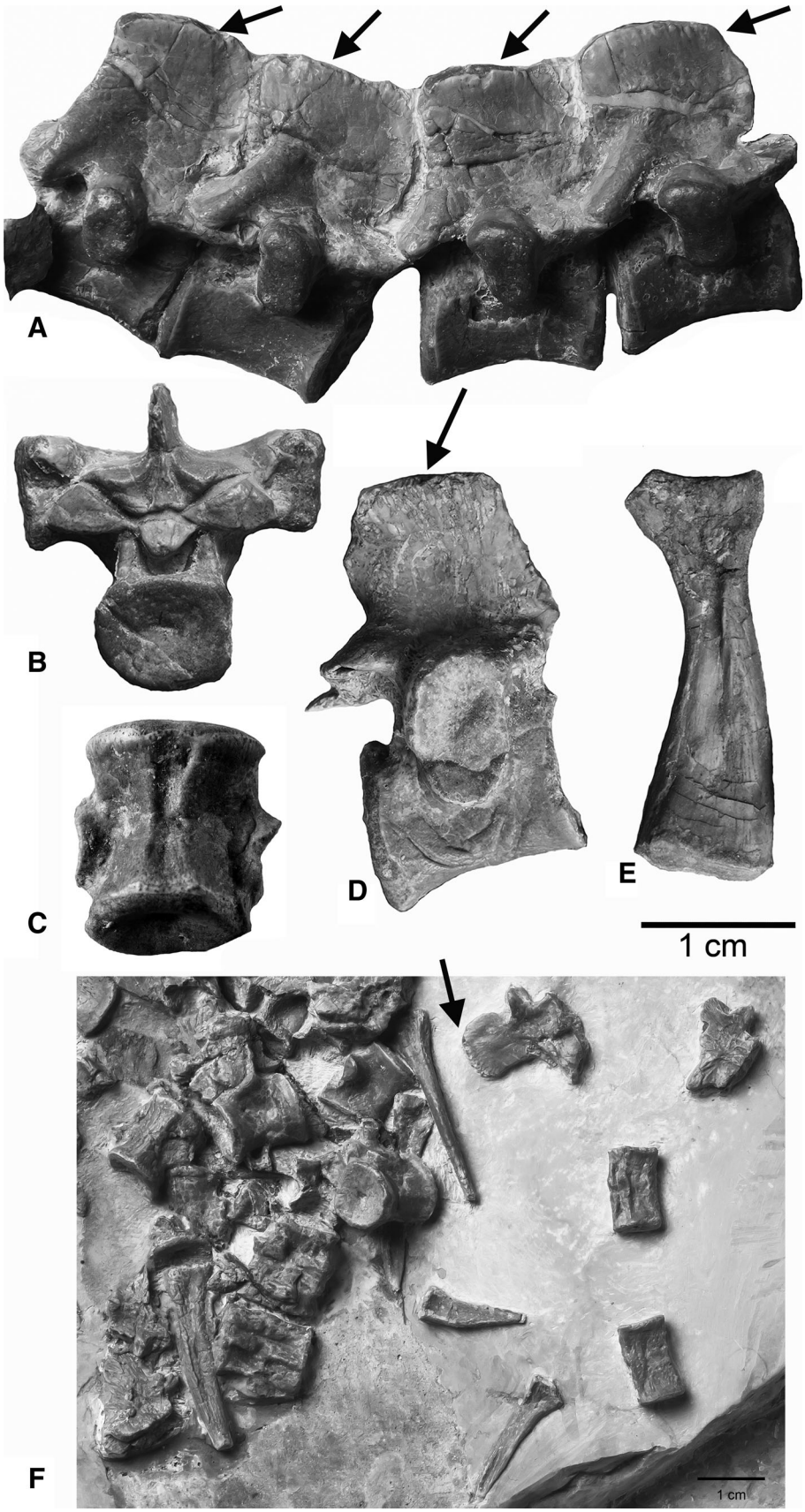
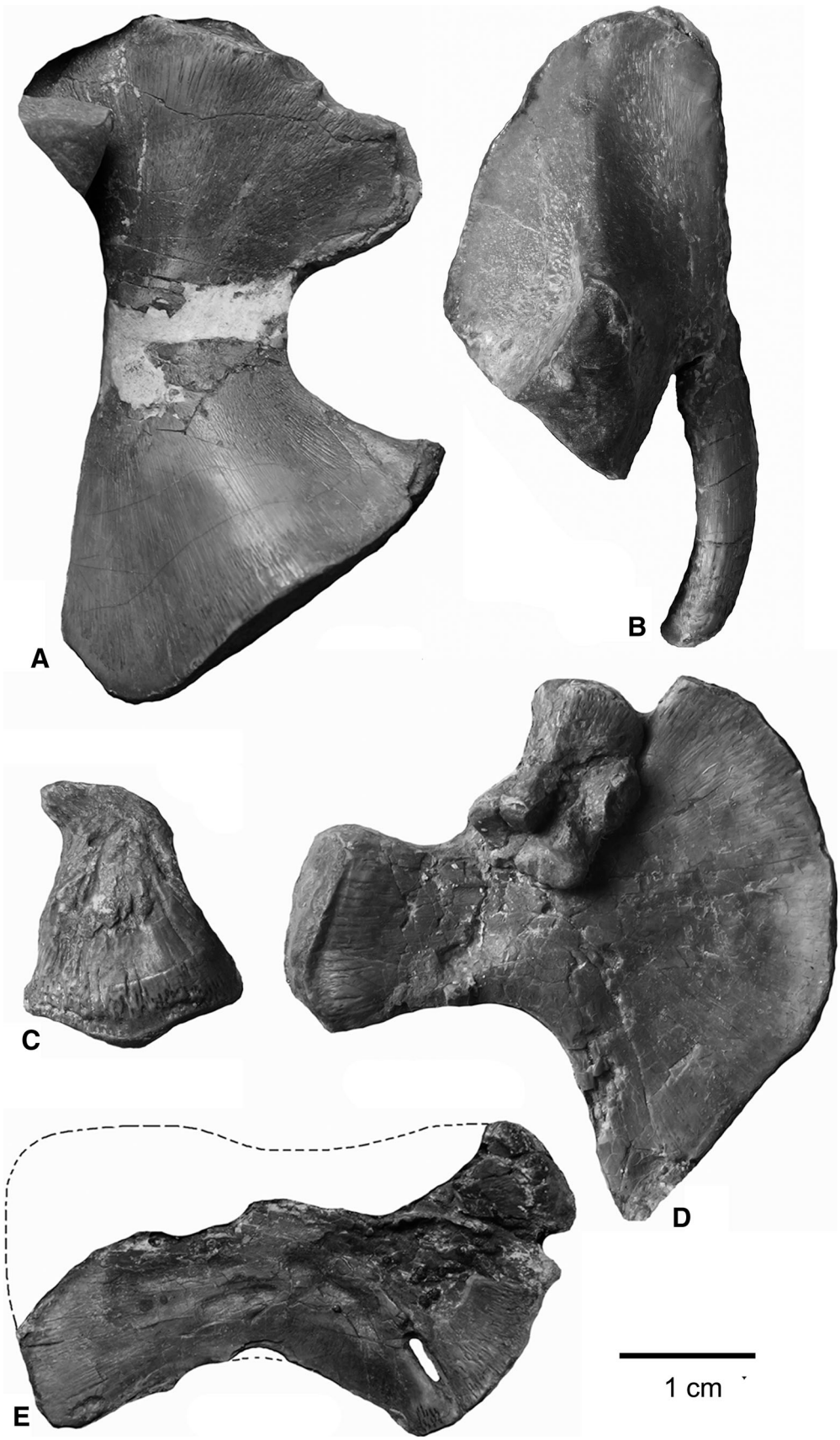


Fig. 6 Vertebrae and a sacral rib of skeleton NMNHL RGM 449487A. **a** Four articulated dorsal vertebra in lateral view; **b** dorsal vertebra in anterior view; **c** caudal vertebra in ventral view; **d** sacral vertebra in lateral view; **e** sacral rib in posterior view; **f** disarticulated caudal vertebrae and caudal ribs. *Arrows* indicate the typical rugosities on the dorsal neural spines


A
B
C
D
E
1 cm

◀ **Fig. 7** Girdle bones of the skeleton NMNHL RGM 449487A. **a** Left coracoid in dorsal view; **b** left scapula in ventral view; **c** left ilium in medial view; **d** left ischium in ventral view; **e** left incomplete pubis in ventral view

They carry distinct protruding neural spines, which are located slightly posterior compared to their centrum. The dorsoventral height of the neural spines clearly increases towards the trunk and anterior tail region, indicating a kind of back keel. The neural spines of the dorsal vertebrae show at their outermost top a weak longitudinal rugosity, mainly in the form of striations, which is probably the area of attachment of the spinalis muscle. The anterior margin of the neural spine in the mid-dorsal vertebrae is straighter and longer than its posterior margin. The anterior dorsal vertebrae have similar lengths of the margins of both neural spines. The anterior margin of the neural spines in the dorsal vertebrae close to the sacral vertebrae remains straight or becomes slightly concave and increases again in length (Fig. 6a). The posterior margin of the neural spine is straight in cervical vertebrae and in anterior dorsal vertebrae but is straight to convex in the more posterior dorsal vertebrae (Fig. 6a). Most of the neural arches show a distinct ridge that runs anteroposteriorly and separates the ventral part of the neural arch from the neural spine (Fig. 6a).

The pre- and postzygapophyses are oriented horizontally in the cervical and anterior dorsal vertebrae. In the posterior dorsal vertebrae, the postzygapophyses are located more ventrally compared to the prezygapophyses. The zygapophyses are generally short, the prezygapophysis does not exceed the anterior margin of the centrum, and the postzygapophysis only just reaches beyond the posterior margin of the centrum. Laterally, the prezygapophyses and the postzygapophyses extend beyond the width of the centrum, and the latter are distinctly wider. The vertebrae show zygosphen and zygantrum facets. The transverse processes are stubby but generally project beyond the zygapophyses (Fig. 6b).

The transverse processes are not divided into diapophysis and parapophysis but show a single large articulation facet. This articulation facet is usually oblong, but in some it is slightly constricted in the middle part, with the dorsal part then becoming more prominent. Some dorsal vertebrae show a posteriorly oriented dorsal tip of the articulation facet. In the sacral vertebrae, this articulation facet is round to oval and very prominent: three times the size of that in other vertebrae (Fig. 6d). In the posterior cervical and dorsal vertebrae, only the neural arch carries the transverse processes; in the sacral vertebrae, the ventralpart of the transverse process is carried by the centrum. In the caudal vertebrae, this articulation facet again decreases in size, until finally only a tiny and short transverse process remains. The centrum keeps carrying the ventral part of the articulation facet. The form of the articulation facet in the caudal vertebrae is triangular-round. The caudal vertebrae carry two parallel ridges on their ventral bodies (Fig. 6c, f), but it is unclear if such a feature occurs on the presacral vertebrae due to preservation and view.

Cervical ribs seem to have developed only in the posterior neck region. It cannot be established whether or not the cervical ribs are double-headed. The dorsal ribs are unicipital with a constricted articulation facet. The dorsoventrally oblong head of the rib is very massive and constricted near its proximal basis. It shows a distinct ridge before the rib broadens distinctly. Then the rib circumference decreases and its shaft starts to point backwards, leaving the entire rib distinctly curved. The shaft ends in a simple unfinished, possibly incomplete, distal end. There is very light striation on the rib shaft. The ribs are not pachyostotic.

The short, massive sacral ribs differ from all the other ribs (Fig. 6e). They are not curved or anteroposteriorly compressed but they are broad in the dorsoventral direction. According to the articulation facet on the sacral vertebrae, their heads are large and oval. The shaft has a round oval form proximally but expands distally to a predominantly oblong oval form. The distal end is distinctly expanded. Only two sacral ribs were identified.

Five distally pointed and disarticulated caudal ribs were preserved (Fig. 6f).

The gastralia have the typical broad-shanked form with a variable angle and a distinct anterior pointing process. The angle enclosed by the median gastral ribs seems to be wider in the anterior trunk region than in the posterior region. The number of elements that compose one gastral rib could not be clarified.

The pectoral girdle

Only the left distal half of the interclavicle is preserved in NMNHL RGM 445912 (Fig. 5). This is a slender lateral process that is in solid contact with a well-developed groove on the posteroventral side of the proximal clavicle. The clavicle is also incomplete but laterally expanded.

The scapula is divided into a broad ventrally expanded part that posteriorly carries the glenoid, and a slender posterodorsal process (Fig. 7b). The ventrally expanded part has a laterally concave side, whereas the medial side is convex. The ventral side is divided into two areas: a large, centrally located and oval-shaped depression, which is visually offset by a sharp ventrolaterally pointing keel. This depression is surrounded by the second part of the scapula, which ends proximally in a pointed slender margin but expands medially and distally in a two-part articulation surface. The distal part contacts the coracoid and the more

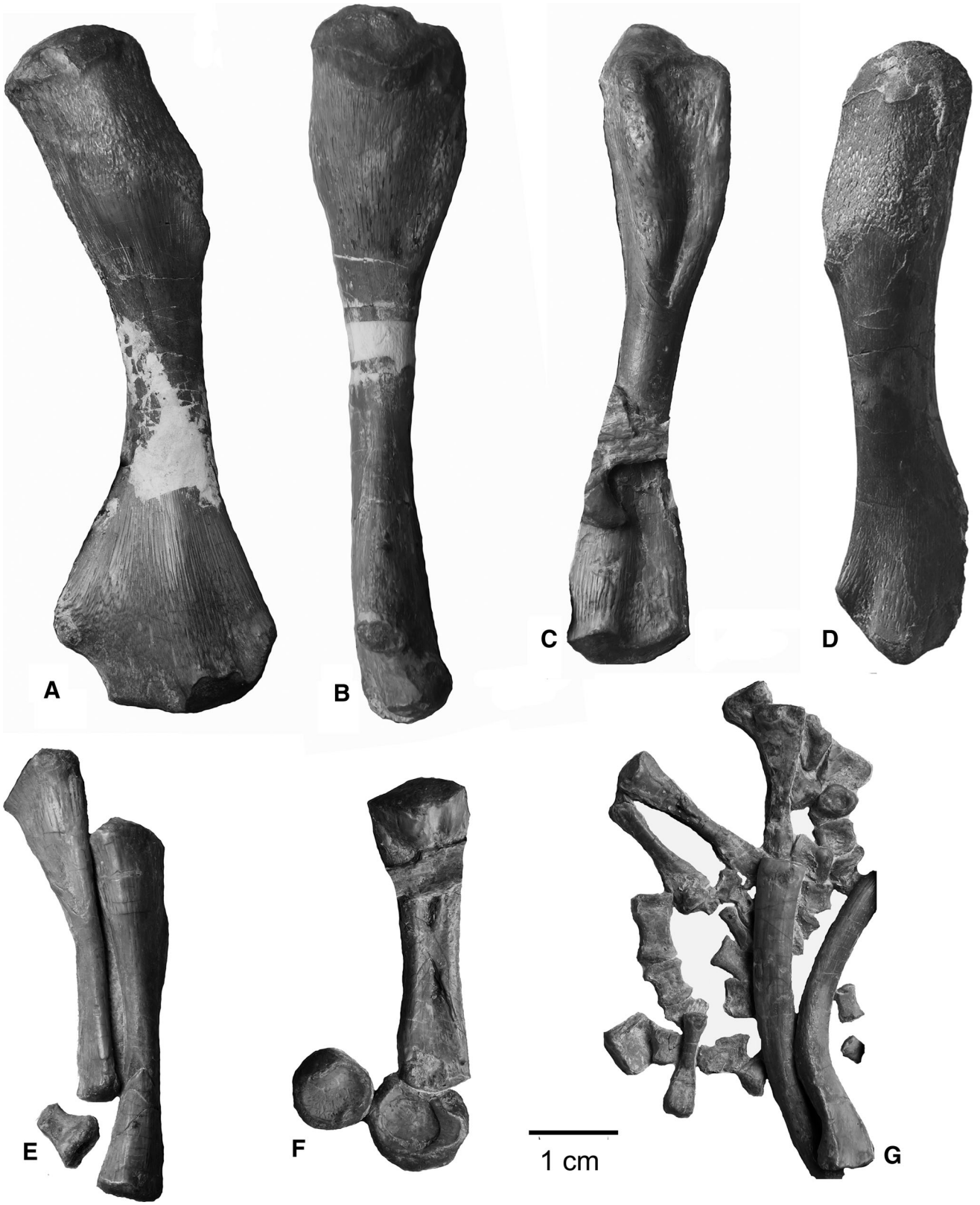


Fig. 8 Limb bones of the skeleton NMNHL RGM 449487A. **a** Right humerus in dorsal view; **b** left humerus in medial view; **c** right femur; **d** left humerus NMNHL RGM 445912 in dorsal view; **e** right radius and ulna in dorsal view; **f** left tibia, astragalus, and calcaneum in ventral view; **g** incomplete pes partially covered by two incomplete ribs

proximal part of the humerus. Above the articulation surface to the coracoid, the medial margin carries a deep, half-round groove, which together with the anterior coracoid forms the coracoid foramen. The ventral part of the scapula has a straight to slightly convex medial margin and an expanded convex lateral margin. The dorsal process of the scapula is thin and slender. In the left scapula of NMNHL RGM 449487A it is slightly curved.

An anterior, a middle (=shaft), and a posterior or symphyseal part of the flat coracoid can be distinguished, with the shaft being clearly indented (Fig. 7a). The ventral surface of the coracoid is smooth, whereas its dorsal surface is more structured. The medial margin is distinctly concave and short compared to the nearly straight and long lateral margin. The anterior part is divided into three parts. The lateral and middle part makes up 2/3 of the anterior margin and contacts the humerus and the scapula. The transition to the medial part is clearly set off, concave, and carries the other half of the coracoid foramen, which is less deep than that part on the scapula. The medial part points without any articulation into the large fenestra built by the shoulder girdle bones. The posterior part is divided into a long and straight symphyseal margin and a distinctly shorter posterior margin. The connection between them can be angled or round. The symphyseal margin bulges.

The pelvic girdle

In medial view, the flat ilium looks like a stout cone that is constricted in its upper third (Fig. 7c). An iliac blade is not developed but there is a short process that points anterodorsally. The medial surface is essentially flat but has at least one large articulation facet for a sacral rib. Additionally, the medial surface is slightly convex, structured with striations, and pitted with grooves. The lateral side presents ventrally a roughly oval but well-developed articulation facet, the supra-acetabular buttress, which contacts the femur. The ilium is broader anteriorly than posteriorly. The anterior margin is dorsally concave and ventrally straight in medial view. The entire posterior margin is concave.

The flat pubis has a broad lateral margin, and the posterior margin is distinctly curved. The anterior margin is not preserved, and only the posterior end is visible from the medial part (Fig. 7e). The nearly closed obturator foramen lies posterior to the contact with the ischium. However, in spite of the relatively large size and the non-juvenile status of the individual (Klein 2010), the obturator foramen is not enclosed by bone; both involved margins touch each other, leaving a drop-shaped obturator foramen, implying that it was open earlier during the ontogeny of the individual. The concave posterior margin is symmetrical, broad-shanked (inverse U), and indicates a large thyroid fenestra. The posterior medial end is convex but it is not clear if it is longer than the anterior medial part, and it forms a kind of prepubis process as in *N. marchicus* (Schröder 1914).

The flat ischium has a slender lateral part, which passes smoothly into the short shaft, whereas the medial part distinctly broadens, like a fan (Fig. 7d). The ventral surface is flat and smooth, whereas the dorsal surface is slightly concave. The acetabular articulation surface is tripartite, like a triangle with rounded edges. The articulation facet to the acetabulum and to the proximal femur occurs ventrally. Dorsally, the anterior articulation surface points to the pubis and the posterior one extends to the ilium. The anterior margin is more deeply curved than the posterior, and forms, together with the pubis, a large thyroid fenestra. The proximal fan-like end has a straight anterior margin, representing the contact with its counterpart, and a slightly convex posterior margin. The ischia do not have a notch where they meet the obturator foramen of the pubis.

The forelimb

In NMNHL RGM 449487A, the right humerus is in dorsal view and the left one in postaxial view preserved (Fig. 8a–b). The preaxial proximal side forms a planar, near-rectangular surface that slightly descends towards the dorsal side. The dorsal proximal end carries a distinct deltopectoral crest. The postaxial proximal side of the left humerus carries slight dorsal and ventral channels, each extending down from the proximal head. The right humerus exhibits a rhombic indentation ventrally on the preaxial proximal shaft, which is most likely the attachment site of the pectoralis muscle. The shaft region of both humeri is slender and clearly constricted due to the concave forms of the pre- and postaxial margins. The cross-section of the midshaft is round to oval. The distal end broadens distinctly and shows a complex morphology, which entails a proximally shifted entepicondyle and a capitulum that is located on the preaxial half of the bone. The capitulum is postaxially followed by a distinct ectepicondylar groove and a proximally located small ectepicondyle. The proximal preaxial side of the right humerus carries a sculpture dominated by slight grooves, whereas the opposite side and the distal end are dominated by striations in both humeri. A histological midshaft sample from the left humerus was studied in detail and revealed histotype A bone tissue (Klein 2010; Fig. 12a–c). This characteristic type of bone tissue was assigned to the pistosauroid *Cymatosaurus* or a close relative (Klein 2010).

The left humerus is preserved in NMNHL RGM 445912. It was completely prepared out of the sediment and is thus visible from all sides (Fig. 8d). The bone histology of the humerus of NMNHL RGM 445912 was not established, but it is morphologically identical to the other

studied "?*Cymatosaurus*" humeri (Klein 2010). It is distally incomplete and proximally somewhat dorsopreaxially compressed. Nevertheless, it shares with the humeri of NMNHL RGM 449487A the same proximal and shaft morphology, including striation patterns. In contrast to the humeri of NMNHL RGM 449487A, it carries a small central foramen at the distal postaxial side of the proximal head. However, the distal morphology differs from that of the humeri of NMNHL RGM 449487A. Although incomplete, the distal end of NMNHL RGM 445912 has steeply angled preaxial and postaxial margins in dorsoventral view. This results from a proximal shift of the ectepicondyle and entepicondyle. The almost centrally located capitulum is prominent and distally protruding. The proximal end is twisted (mainly in postaxial view) when compared to the distal end.

The humeri of NMNHL RGM 449487A and the humerus of NMNHL RGM 445912 are classified into two different morphotypes after Klein (2010) based on differences in distal humerus morphology. These most likely represent different sexual morphs or closely related taxa of a basal Pistosauroidea.

The radius has a prominent rectangular proximal end, a constricted thin shaft, and a small, rounded distal end (Fig. 8e). The proximal head is slightly concave and the lateral connection to the ulna is provided by a straight and short margin. The flat ulna is distally slightly shorter than the radius. The ulna is not broader than the radius and its proximal and distal ends have a simple round morphology. The shaft is constricted, with a nearly straight lateral and a slightly concave medial margin. The proximal end of the left ulna of NMNHL RGM 445912 is somewhat broader than its distal end.

The hind limb

Both femora are preserved in ventral view on slab NMNHL RGM 449487A (Fig. 8c). They resemble the typical sauropterygian condition, with a prominent proximal head, a long, straight, and slender shaft, and a distal division into simple symmetrical condyles, pointing postaxially. The protruding and rounded articulation surface of the proximal head has a process extending horizontally to distally, the possible insertion of the iliofemoralis muscle. Below this process, on the dorsal side, is a shallow concave groove. The ventral side of the proximal head is divided by the deep intertrochanter fossa, which reaches far down along the shaft. The proximal and distal ends are about the same width, but the distal end is flat. The shaft is straight and constricted, with a rounded triangular cross-section. The dorsal shaft margin is straight, but the ventral shaft margin is slightly concave. In dorsal view, the postaxial margin is straight and the preaxial margin is slightly concave. The condyles are equally in size.

The tibia is a rectangular bone that is broader and thicker proximally than distally (Fig. 8f). The postaxial margin is slightly convex. The proximal articulation surface is oval with a pointed postaxial side and a broad preaxial one. The distal end is rather flat. Two-thirds of the distal articulation surface is convex and fits into a facet of the large astragalus (Fig. 8f), whereas the remaining distal margin is straight. The tibia is only 45 % of the length of the femur. The fibula is shorter (37 % of the femur length) and more slender than the tibia. Its postaxial margin is strongly curved. The proximal head is thick and massive, but towards the shaft and the distal end the fibula becomes continously thinner. The distal end is badly preserved and appears only as a knobby elongation of the shaft.

An ulnare, an intermedium, an astragalus, and a calcaneum of the left half of the body can be identified in NMNHL RGM 449487A, all of which are well ossified (Fig. 8g). The disarticulated carpals are round and the intermedium is approximately twice the size of the ulnare.

The astragalus is around 1/3 larger than the calcaneum. The astragalus is still articulated to the distal tibia in NMNHL RGM 449487A, forming here a concave facet, whereas the rest of the element is round (Fig. 8f). The round calcaneus has a short, straight connection to the astragalus. All elements are dorsoventrally biconcave.

The postcranial skeletons NMNHL RGM 449487A and NMNHL RGM 445912 most likely represent cf. *Cymatosaurus* or a close relative and show the following combination of characters: vertebral centra are constricted and not pachyostotic; distally expanded sacral ribs; long slender dorsal scapula process; medial part of coracoid is deeply concave/indented; dorsal part of ilium is a simple dorsal process, which points anterodorsally; pubis with an obturator foramen; rather symmetrical ischium with a broad, fan-shaped medial part and a shaft-like lateral part; humerus with a constricted shaft, a roundish massive proximal and a flattened distal end, and a plesiomorphic (terrestrial) distal morphology; humerus histology reveals histotype A bone tissue (see Klein 2010) with a high number of radial vascular canals and fibrolamellar bone; ulna not distinctly broadened but constricted; femur slender with a protruded proximal end; tibia rectangular; femur/humerus ratio is 1.07.

Comparison

Assignment of the skeletons NMNHL RGM 449487A and NMNHL RGM 445912 to a nothosaur or a pachypleurosaur can be excluded for several morphological reasons (i.e., humerus and pubis morphology—compare, e.g., Schröder 1914; Rieppel and Wild 1996; Lin and Rieppel 1998; Rieppel 2000; Klein 2010, 2012).

In the following, NMNHL RGM 449487A and NMNHL RGM 445912 are compared to postcranial material of "*Proneusticosaurus*" (Volz 1902), which has also been proposed to belong to *Cymatosaurus* (Sues 1987; Rieppel 1997, 2000). "*Proneusticosaurus*" was described from the Lower Muschelkalk of Gogolin and Sacrau, Poland. The two specimens each consist of mainly the trunk region with partially preserved extremities; additionally, in the large specimen (body length estimated >1 m) from Gogolin, the pelvic region is preserved. Only a part of one specimen survived the bombing during World War II and was redescribed in detail by Rieppel and Hagdorn (1997). The material was not studied first-hand for the current study; the descriptions and figures of Volz (1902) are adequate and informative.

Although the overall morphology of the vertebrae and ribs in "*Proneusticosaurus*" is similar to the corresponding morphologies for the two skeletons from Winterswijk, the vertebrae are barrel-shaped in "*Proneusticosaurus*," whereas the vertebral centra are clearly constricted in the Winterswijk specimens. "*Proneusticosaurus*" and the Winterswijk skeletons share two parallel ridges on the ventral side of the caudal vertebral centra. However, those ridges on the ventral side of the caudal vertebrae are also known for other Sauropterygia (Rieppel 2000; Klein 2012). The radius and ulna are difficult to compare due to the different preserved views of each, but in the Winterswijk skeletons they are even more slender and elongated than in the Polish specimens. In "*Proneusticosaurus*," the distal femur is also more slender and straight than the distally slightly expanded femur in NMNHL RGM 449487A. The pubis of "*Proneusticosaurus*" lacks a distinct prepubis, a feature that is unclear in NMNHL RGM 449487A and not known for NMNHL RGM 445912. However, they differ in overall pubis morphology. The pubis in "*Proneusticosaurus*" is rectangular and stout, and the round obturator foramen is open, which contrasts with the slit-shaped and closed obturator foramen in the mediolaterally elongated pubis of NMNHL RGM 449487A. The ischium in "*Proneusticosaurus*" is hatchet-shaped with a long and straight medial margin and a rounded and protruding distal margin. In NMNHL RGM 449487A, the ischium is fan-shaped with equally sized medial and distal margins and pointed corners. The ilium in "*Proneusticosaurus*" has a dorsal process pointing anterior and lying parallel to the ventral surface (Volz 1902; Fig. 17), whereas the ilium in NMNHL RGM 449487A has a dorsal process that points anterodorsally (Fig. 7c). Additionally, the ventral articulation facets are morphologically more structured in "*Proneusticosaurus*" when compared to NMNHL RGM 449487A.

In conclusion, the morphology of "*Proneusticosaurus*" differs from those of the Winterswijk skeletons beyond mere ontogenetic variation. It is unclear if these differences represent intraspecific variation (including sexual dimorphism), or are related to species or even genus level. Too little is known about variations in early eosauropterygians, so this cannot be clarified without new diagnostic finds.

Discussion

The alpha taxonomy of Triassic Sauropterygia from the Germanic Basin is largely based on skull morphology (e.g., Rieppel 2000). Phylogenetic analyses of Triassic Sauropterygia have been optimized for both cranial and postcranial characters (e.g., Neenan et al. 2013). However, due to the lack of skull material, and because the postcranial skeletons NMNHL RGM 449487A and NMNHL RGM 445912 are incomplete, including them in a phylogenetic analysis would not clarify phylogenetic relationships.

The assignment of the skeletons NMNHL RGM 449487A and NMNHL RGM 445912 to basal Pistosauroidea is based solely on humerus morphology (*Cymatosaurus* in Rieppel 1994) and histology (histotype A bone tissue according to Klein 2010). Although the phylogenetic information content of bone histology is generally difficult to evaluate (Cubo et al. 2005; de Ricqlés et al. 2008), bone histology (i.e., bone tissue type and growth pattern) carries a phylogenetic signal in Triassic Sauropterygia, at least at the major clade level (Klein 2010; Krahl et al. 2009, in review).

Since *Cymatosaurus*, which is well known from several isolated skulls but not from any postcranial bone, is the only basal Pistosauroidea known so far from the early Middle Triassic of the Germanic Basin, it is very likely that NMNHL RGM 449487A and NMNHL RGM 445912 represent individuals of that taxon. The problem remains, however, that no skulls of *Cymatosaurus* have been found in Winterswijk (Oosterink et al. 2013).

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