Eurycormus − *Eurypoma*, two Jurassic actinopterygian genera with mixed identity

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Abstract

Three Late Jurassic actinopterygian species are commonly placed in the genus *Eurycormus*: *E. egertoni*, *E. grandis* and *E. speciosus*. A detailed comparison supports an earlier assignment to two different genera, *Eurycormus* Wagner, 1863 (*speciosus*) and *Eurypoma* Huxley, 1866 (*E. egertoni* and *E. grande*). Systematically, the two genera are only distantly related; *Eurycormus* belongs to the Teleosteomorpha, whereas *Eurypoma* is a halecomorph closely related to or a member of the Caturoidea within the Amiiformes.

Schlüsselwörter: Actinopterygii, Oberer Jura, Süddeutschland, Morphologie, Systematik.

Zusammenfassung

Drei oberjurassische Actinopterygier-Arten, *egertoni*, *grandis* und *speciosus*, werden gewöhnlich zur Gattung *Eurycormus* gestellt. Ein detaillierter Vergleich der drei Arten bestätigt eine frühere Zuordnung zu zwei verschiedenen Gattungen, *Eurycormus* Wagner, 1863 (*speciosus*) und *Eurypoma* Huxley, 1866 (*E. egertoni* und *E. grande*), die zwei höheren Taxa innerhalb der Neopterygii zugeordnet werden: *Eurycormus* zu den Teleosteomorpha und *Eurypoma* zu den Amiiformes innerhalb der Halecomorphi, möglicherweise nahe oder innerhalb der Caturoidea.

Introduction

Agassiz (1843) named a Late Jurassic fish from Speeton, Yorkshire, England, *Macropoma egertoni*. The fish was described and figured by Egerton (1858) and placed within the coelacanths following Agassiz (1843). Huxley (1866) erected the new genus *Eurypoma* for that actinopterygian fish, which Woodward (1894, 1895) synonymized with *Eurycormus* Wagner, 1863. Wagner (1863; see Figs 1, 2B) described the type species *Eurycormus speciosus* from the Upper Jurassic of Bavaria, Germany. Woodward (1890) also placed another species, *E. grandis* (see Fig. 2A), from the Upper Jurassic of Cambridgeshire, England, within this genus. Heineke (1906; see Fig. 3A, and new specimen Fig. 3B) placed fishes from the Upper Jurassic (Kimmeridgian) of Nusplingen, Baden-Württemberg, Germany, in the latter species, however, he used *Eurypoma* as the genus. He correctly argued that the two English species, *Eurycormus egertoni* and *grandis*, belong in Huxley's genus *Eurypoma* and are quiet different from *Eurycormus speciosus*. Nevertheless the generic name *Eurypoma* disappeared from the literature due to the enormous influence of Woodward's authority.

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Zittel (1887–1890; also in his textbook) placed *Eurycormus* (*E. speciosus*) close to *Caturus*, a form with which Wagner (1863) compared *Eurycormus*. Woodward (1890, studying *E. grandis* and 1895) followed Zittel and placed *Eurycormus* in the family Eugnathidae (= Caturidae). Woodward (1890) noted many similarities shared with the extant amiiform *Amia*. Within the Caturidae (= Eugnathidae = Furidae), *Eurycormus* appeared in the many editions and translations of Zittel's textbook of vertebrate paleontology, as well as in Romer (1945, 1966), in Berg & Obruchev (1964), and Lehman (1966). Patterson (1973) restudied *E. speciosus* and concluded that *Eurycormus* is a pholidophorid (that similarity was reported previously by Wagner 1863 and Heineke 1906), after Lund (1967) had placed *E. speciosus* close to *Leptolepis*. Patterson's assignment was followed thereafter (Carroll 1988; Lambers 1992; Arratia & Lambers 1996; Grande & Bemis 1998), until Arratia (2000) placed *Eurycormus* in the *Siemensichthys*-group, a sister group of the teleosts.

In his reassignment of *Eurycormus*, Patterson (1973) specifically referred to the type species *E. speciosus* and left the other species as caturids. That returns us to Heineke (1906), who wrote that the two English species are different from *E. speciosus*. Therefore he assigned two fishes from the Upper Jurassic of Nusplingen, Baden-Württemberg, Germany, and the species *E. grandis* to the genus *Eurypoma* noting similarities to *Ionoscopus* species. Woodward (1890) already had observed features similar to *Amia* in *E.* (his *Eurycormus*) *grandis*.

Wenz (1968) described *Eurypoma* (her *Eurycormus*) *grande* from the Callovian of France and placed it between ("intermédiare") Furidae and Amiidae.

The synonymization of *Eurypoma* with *Eurycormus* by Zittel (1887–1890) and Woodward (1890, 1895) created a taxon with three species, which belong to two large groups of actinopterygians, halecomorphs and teleosts. The taxon *Eurycormus* was placed within halecomorphs, until one species, *Eurycormus speciosus*, was assigned to teleosts (Patterson 1973) or stem-group teleosts (Arratia
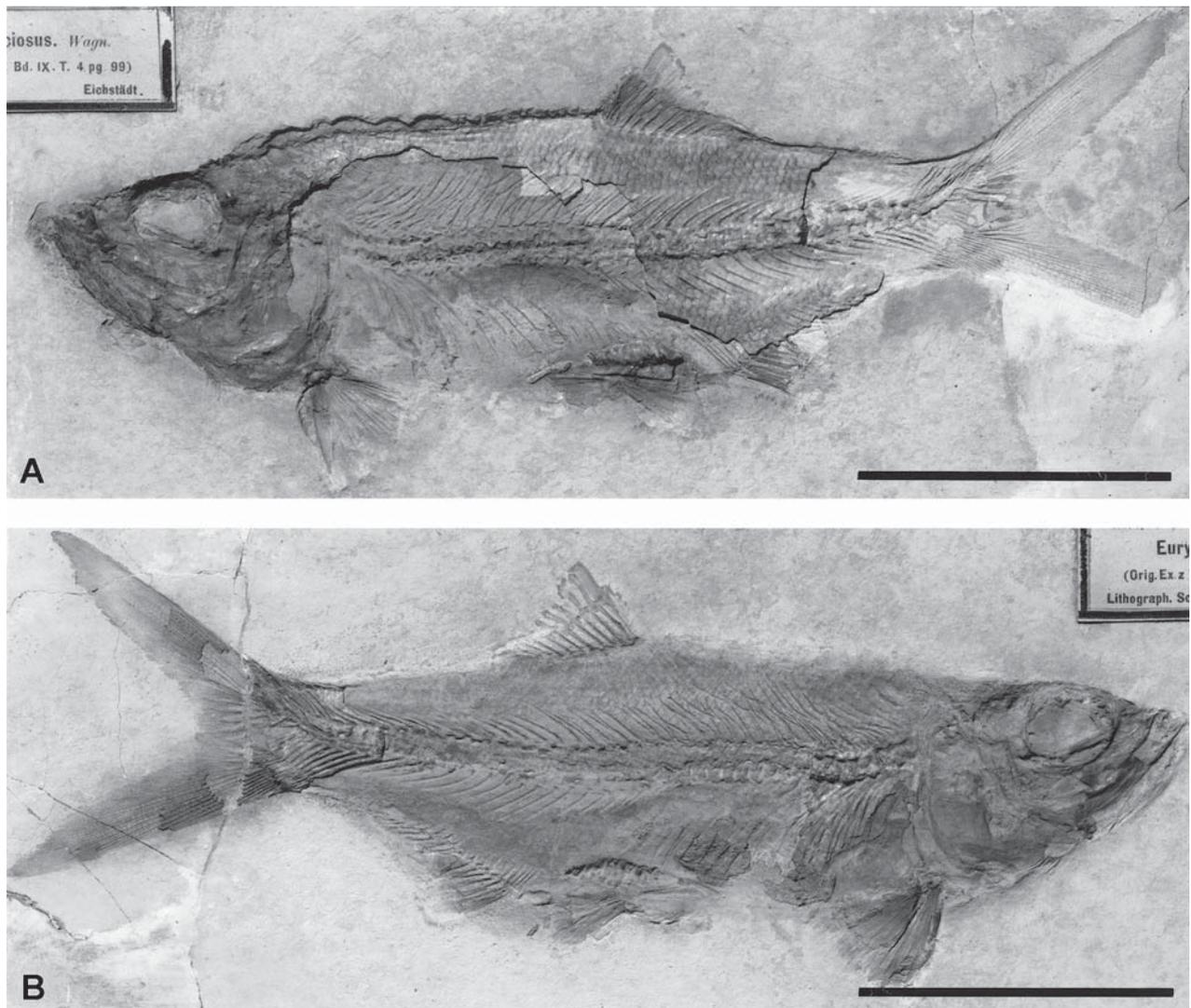
Fig. 1. Holotype of *Eurycormus speciosus* Wagner, 1863, BSP AS V510. Tithonian, Eichstätt, Bavaria. **A** – part; **B** – counterpart. Scale equals 5 cm.
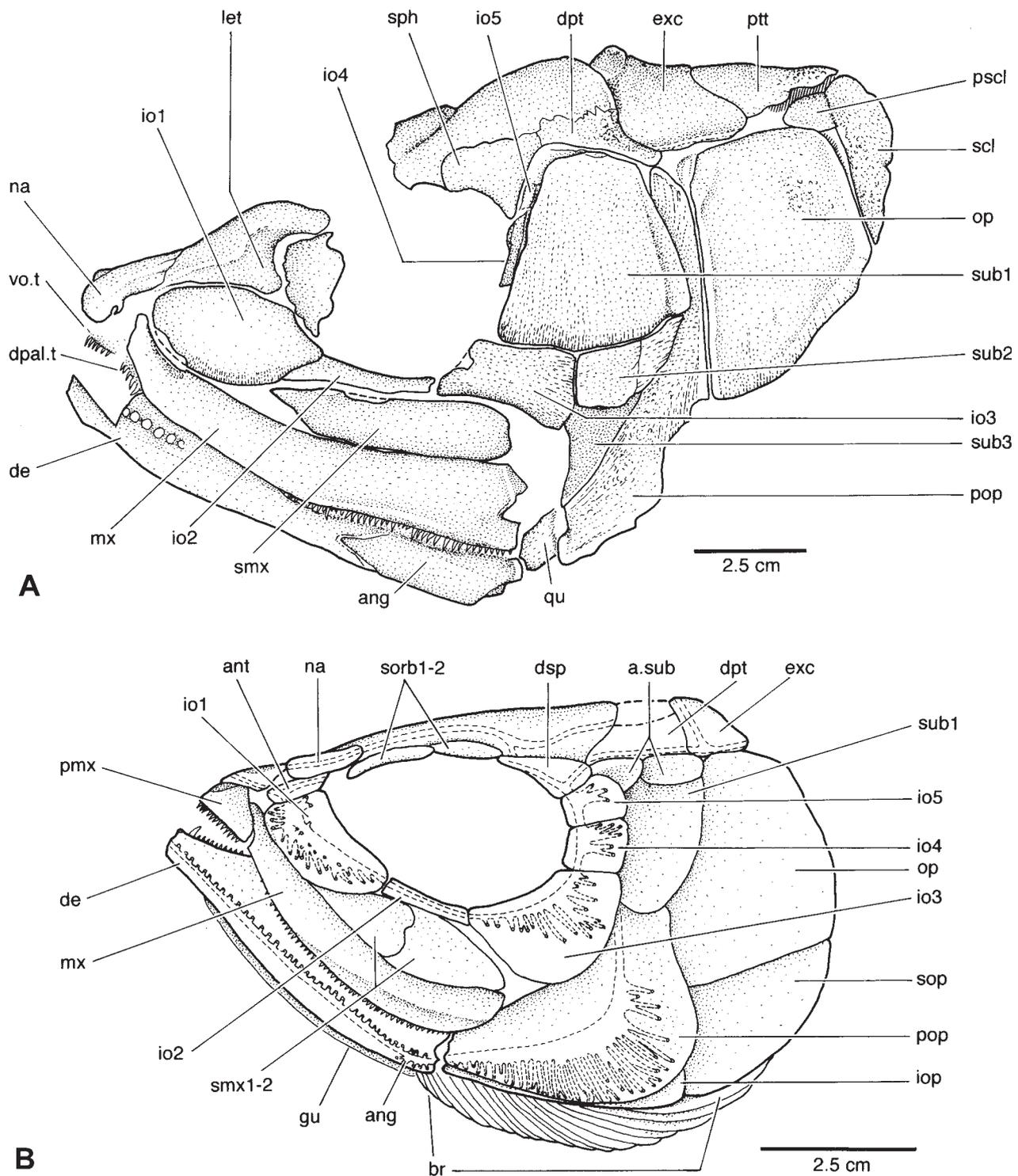
Fig. 2. Head of **A** − *Eurypoma grande* (Woodward, 1889), holotype, Kimmeridgian, Ely, Cambridgeshire (modified from Wood-ward 1890, pl. X, fig. 1); **B** − *Eurycormus speciosus* Wagner, 1863, Tithonian, Eichstätt and Zandt, Bavaria (modified from Grande & Bemis 1998, fig. 421C, based on JM SOS2341, JM SOS2339, and MB f.3840). Abbreviations: **ang** − angular; **ant** − antorbital bone; **a.sub** − accessory suborbital bones; **br** − branchiostegalia; **de** − dentary (= dentosplenial); **dpal.t** − dermopalatine teeth; **dpt** − dermopterotic (= supratemporotabular); **dsp** − dermosphenotic; **exc** − extrascapula; **gu** − gular; **io1** − infraorbital bone 1 (= lacrimal bone); **io2** − infraorbital bone 2 (= subinfraorbital bone of Grande & Bemis 1998); **io3** − infraorbital bone 3 (= jugal bone), **io4**, **io5** − infraorbital bones 4, 5 (= postorbital bones of Grande & Bemis 1998); **iop** − interoperculum; **let** − lateral ethmoid; **mx** − maxilla; **na** − nasal bone; **op** − operculum; **pmx** − premaxilla; **pop** − preoperculum; **pscl** − presu-pracleithrum; **ptt** − posttemporal; **qu** − quadrate; **scl** − supracleithrum; **smx1−2** − supramaxilla 1, 2; **sop** − suboperculum; **sorb1−2** − supraorbital bone 1, 2; **sph** − sphenotic; **sub 1, 2, 3** − suborbital bone 1, 2, 3; **vo.t** − vomerine teeth.
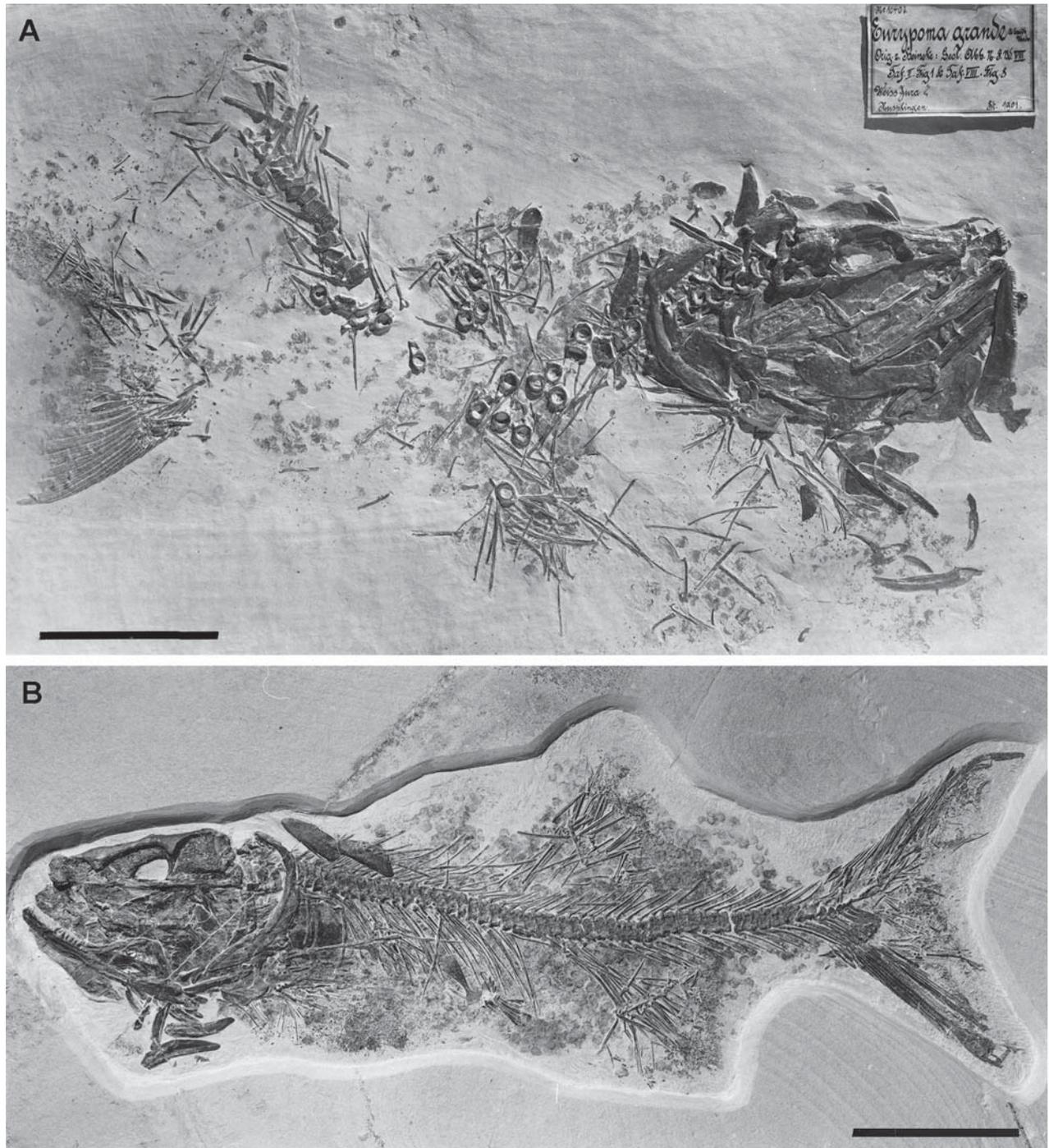
Fig. 3. *Eurypoma grande* in lateral view. Kimmeridgian, Nusplingen, Baden-Württemberg. **A** – SMNS 10402 (see Heineke 1906, pl. 2, fig. 1); **B** – SMNS 86901/38 (skull roof restored after SMNS 10402, years ago). Scales equal 10 cm.

2000). The systematic position of the other two species (of *Eurypoma*) is uncertain.

Our goals are to compare material previously assigned to *Eurycormus* and *Eurypoma*, and to describe and reassess morphological characters that demonstrate that these are two very different genera. Additionally, we will study the systematic position of these taxa within actinopterygians.

Institutional abbreviations. The material studied is deposited in the following institutions:

BMNH	The Natural History Museum, London, England
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
JM	Jura Museum, Eichstätt, Germany
MB f.	Paläontologische Sammlungen (fish collections), Museum für Naturkunde der Humboldt Universität zu Berlin, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
Tü	Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany
UMZC	University Museum of Zoology, Cambridge, Great Britain
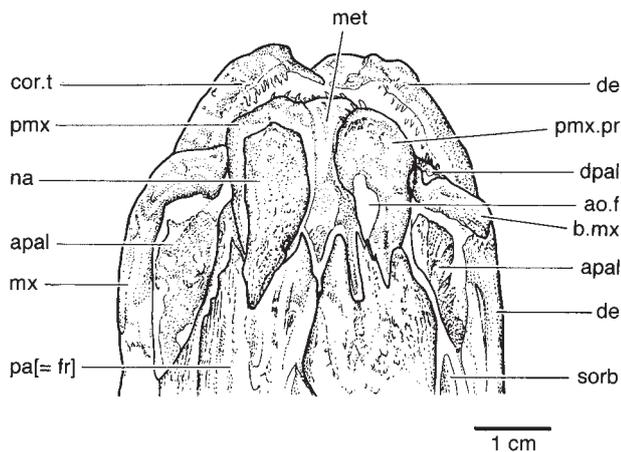
Fig. 4. *Eurypoma grande*, Callovian, Villers-sur-Mer, Calvados (modified from Wenz 1968, pl. 38, fig. B). Abbreviations: **ao.f** – olfactory foramen; **appal** – autopalatine; **b.mx** – broken part of anterior maxilla; **cor.t** – coronoid teeth; **de** – dentary (= dentosplenial); **dpal** – dermopalatine; **met** – mesethmoid; **mx** – maxilla; **na** – nasal bone; **pa [= fr]** – parietal bone (= "frontal" bone of traditional terminology); **pmx** – premaxila; **pmx.pr** – nasal process of premaxilla; **sorb** – supraorbital bone.

Comparison between *Eurypoma* and *Eurycormus*

Some relevant morphological characters of *Eurypoma* and *Eurycormus* are presented below in a comparative way. Most of these are cranial characters, but also features of the vertebral column and caudal skeleton distinguish the two genera as well.

P r e m a x i l l a. The premaxillary bone is different in both genera. The premaxilla (Figs 4, 5) of *Eurypoma* consists of two main parts. The anterior part is thick, laterally elongate, and bears a tooth row. The posterodorsal part, or nasal process, is thinner than the anterior part, broad and elongated posteriorly and perforated by a large opening, the olfactory foramen. Most of the nasal process is hidden by the large nasal bone that lies on the premaxilla (see Fig. 4), it sutures posteriorly with the parietal bone (so-called frontal bone of traditional terminology) in a zig-zag suture. Consequently, the premaxilla in *Eurypoma* is not a mobile bone. The description above fits very well to the premaxilla of *Amia*
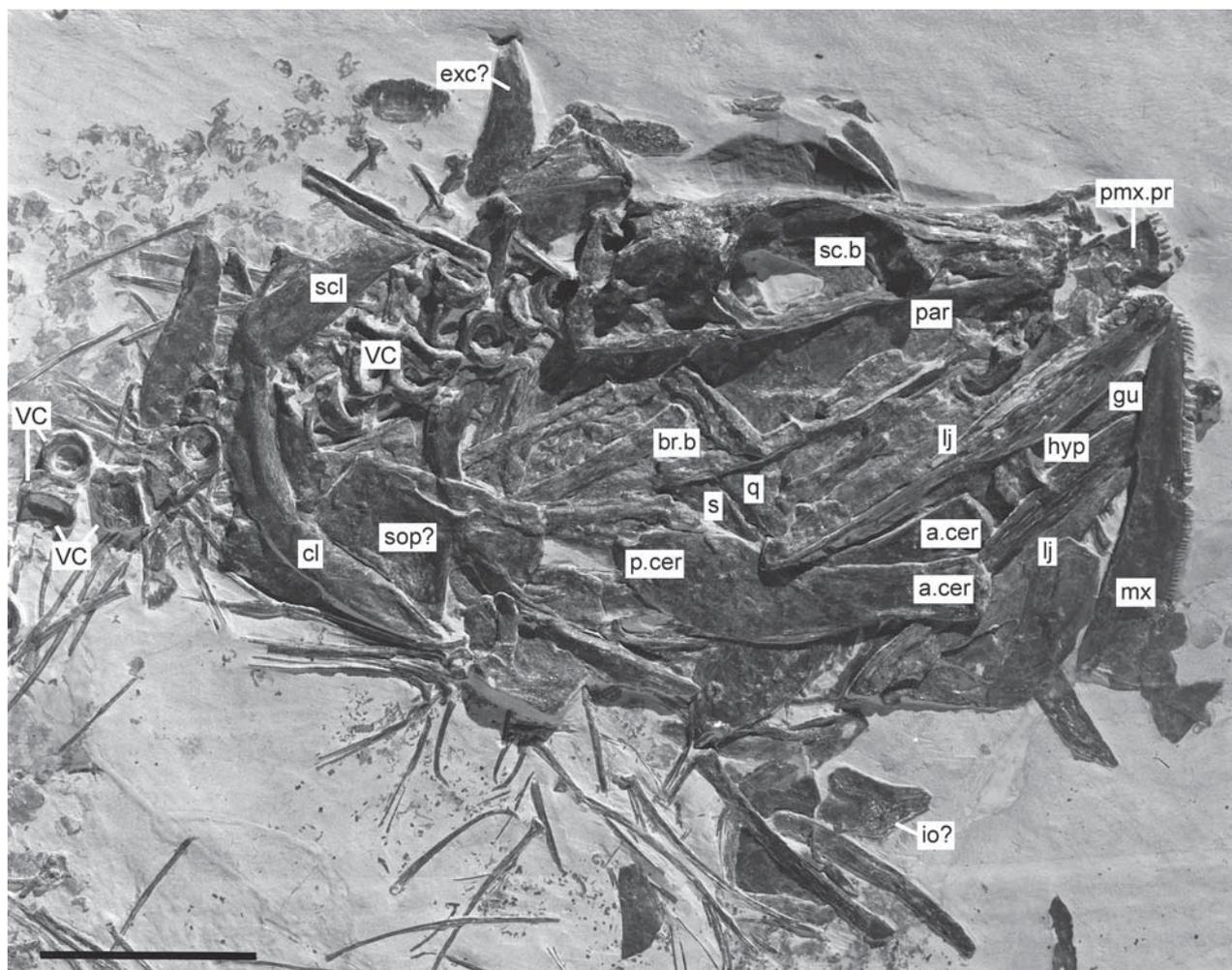
Fig. 5. *Eurypoma grande*, SMNS 10402, head in lateral view. Kimmeridgian, Nusplingen, Baden-Württemberg. Abbreviations: **a.cer** – anterior ceratohyal; **br.b** – unidentified branchial bone; **cl** – cleithrum; **exc?** – extrascapula?; **gu** – gular; **hyp** – hypohyals; **io?** – questionable infraorbital bone; **lj** – lower jaw; **mx** – maxilla; **par** – parasphenoid; **p.cer** – posterior ceratohyal; **pmx.pr** – nasal process of the premaxilla; **q** – quadrate; **sc.b** – sclerotic bone; **scl** – supracleithrum; **sop?** – questionable suboperculum; **s** – symplectic; **VC** – vertebral centrum. Scale equals 5 cm.

as already indicated by Wenz (1968). One significant difference is the development and position of the lateral part of the anterior portion of the premaxilla. In *Amia*, the anterior part is laterally elongate (see Grande & Bemis 1998, fig. 42A–D), whereas in *Eurypoma* the lateral part projects in an anterior, thick process (see Fig. 5).

A premaxilla bearing a well-developed nasal process is not unique to amiids and caturids; this feature is also found in other neopterygians such as *Acentrophorus* (Patterson 1975, fig. 136), *Perleidus* (Patterson 1975, fig. 138), *Watsonulus* (Olsen 1984, figs 6B, 7) and other parasemionotiforms (Patterson 1975, fig. 137), semionotiforms (Patterson 1975, fig. 135; Thies 1989, figs 2, 5; Olsen & McCune 1991, figs 5A, 7; Thies 1991, figs 10, 11; Thies & Zapp 1997) and *Dapedium* (Patterson 1975, fig. 134).

In contrast, the premaxilla of *Eurycormus* (Figs 2B, 6) is an almost triangular bone that lacks the nasal process present in *Eurypoma* and amiiforms, and it consequently is not sutured with the parietal bone. Due to the position and relationships of this type of premaxilla, it is expected that this bone in *Eurycormus* was mobile (Patterson 1973; Arratia 1999). A mobile premaxilla was interpreted as a synapomorphy of teleosts (including pachycormiforms and aspidorhynchiforms) by Patterson (1977), a synapomorphy of *Pholidophorus bechei*

plus more advanced teleosts by Arratia (1999, character 183), and as a synapomorphy of the *Siemensichthys*-group and *Pholidophorus bechei* plus more advanced teleosts by Arratia (2000, character 121). Pachycormiforms have a semi-mobile or immobile premaxilla (Wenz 1968; Patterson 1977; pers. observ.), and aspidorhynchiforms have a premaxilla sutured to the rostral bone and to the ethmoidal region (Brito 1992, 1997; pers. observ.).

Maxilla. The maxilla in *Eurypoma* is a long, massive bone, with a slight curvature about mid-length (Fig. 2A) or the bone may be almost straight (Figs 5, 7A, B; Egerton 1858, pl. 10, fig. 2). The posterior margin of the maxilla is at the level of the posterior end of the lower jaw. The dorsal margin presents a broad supramaxillary process in the specimen from Villers-sur-Mer (Calvados, France) studied by Wenz (1968; see Fig. 7A, B), whereas the process is smaller and sharp in the material from Nusplingen (Germany) (see Fig. 5) and bears a notch where the supramaxilla abuts. The maxilla becomes slightly narrower rostrad and deeper caudad. Its posterior end bears a notch that is clearly shown in Figs 2A, 7A, B (also in Egerton 1858, pl. 10, fig. 2; Woodward 1890, pl. 10, fig. 1; Wenz 1968, pl. 38, fig. D). The posterior end of the maxilla of specimen SMNS 10402 from Nusplingen (Fig. 5) is covered by other bony elements, so that
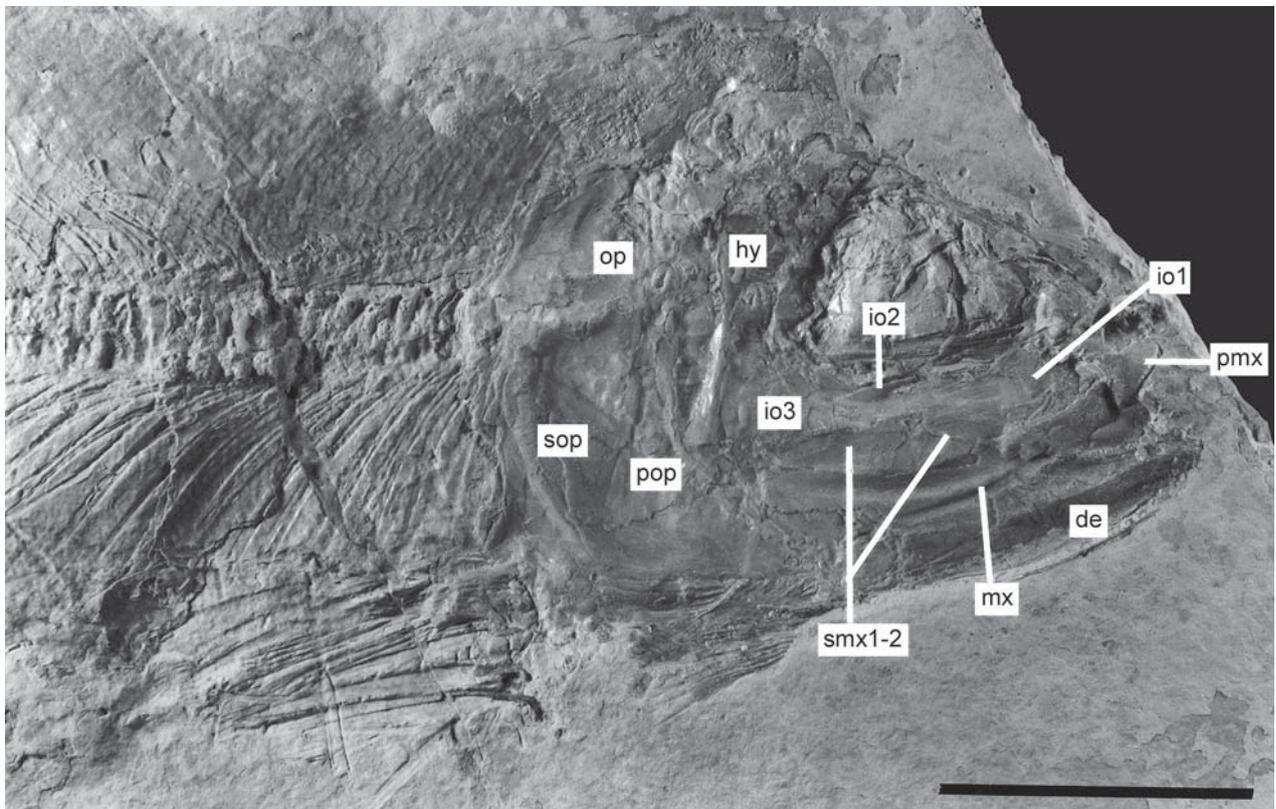
Fig. 6. *Eurycormus speciosus*, MB f.3840, head in lateral view. Tithonian, Eichstätt, Bavaria. Abbreviations: **de** – dentary (= dentosplenial); **hy** – hyomandibula; **io1** – infraorbital bone 1 (= lacrimal bone); **io2** – infraorbital bone 2 (= subinfraorbital bone of Grande & Bemis 1998); **io3** – infraorbital bone 3 (= jugal bone); **mx** – maxilla; **op** – operculum; **pmx** – premaxilla; **pop** – preoperculum; **smx1–2** – supramaxilla 1, 2; **sop** – suboperculum. Scale equals 5 cm.
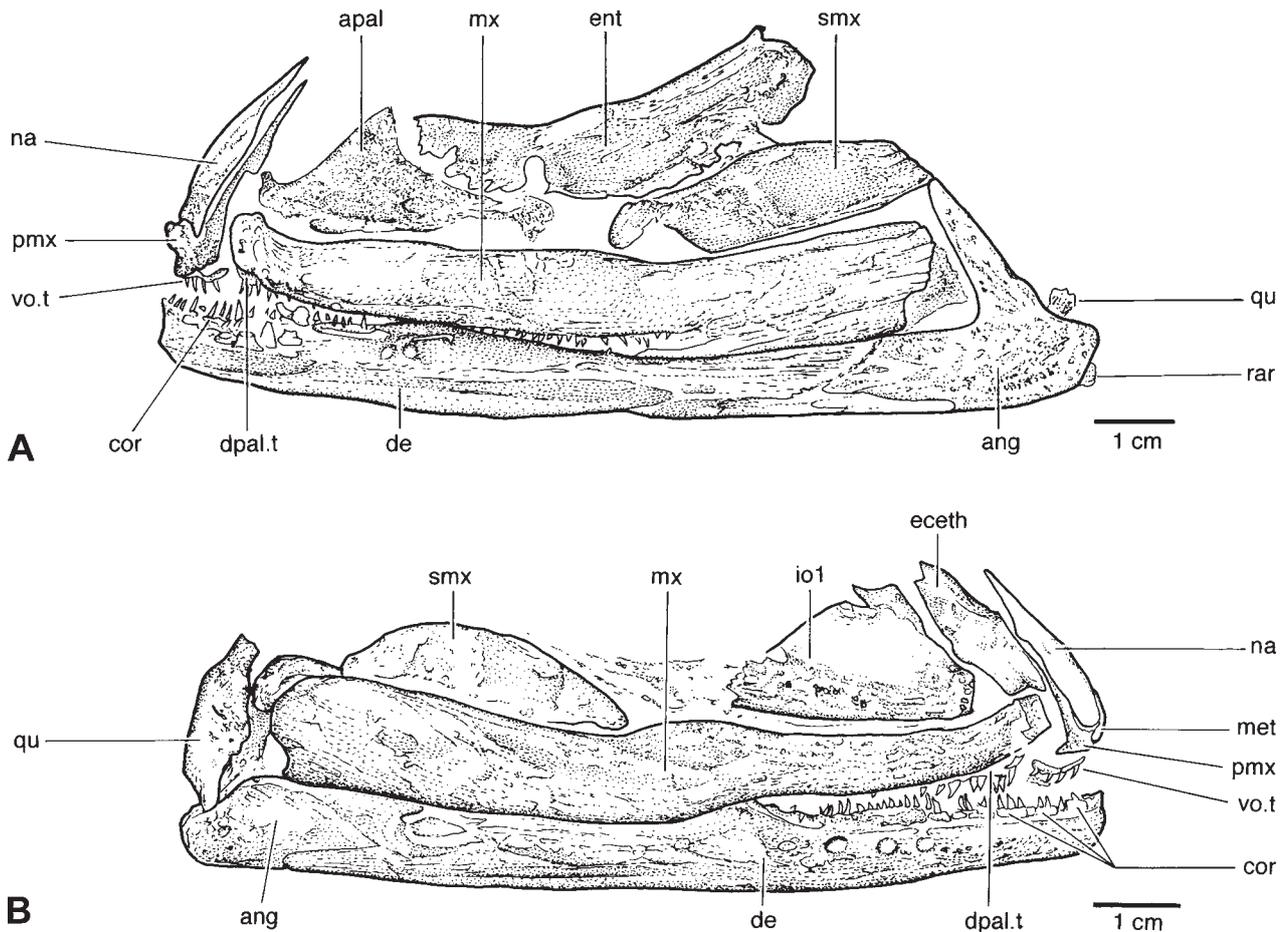
Fig. 7. *Eurypoma grande*, Callovian, Villers-sur-Mer, Calvados, lower part of head in lateral view. **A** — left side (modified from Wenz 1968, pl. 38, fig. C); **B** — right side (modified from Wenz 1968, pl. 38, fig. D). Abbreviations: **ang** — angular; **apal** — auto-palatine; **cor** — coronoid; **de** — dentary (= dentosplenial); **dpal.t** — dermopalatine teeth; **eceth** — ecethmoid; **ent** — entoptery-goid; **io1** — infraorbital bone 1 (= lacrimal bone); **met** — mesethmoid; **mx** — maxilla; **na** — nasal bone; **pmx** — premaxilla; **qu** — quadrate; **rar** — retroarticular; **smx** — supramaxilla; **vo.t** — vomerine teeth.

the notch cannot be observed. The maxilla has a strong broad articular process at the anterior end in the material from France (Fig. 7A, B), whereas the process is longer in the material from England studied by Woodward (1890; see Fig. 2A). There is one row of maxillary teeth (Egerton 1858, pl. 10, fig. 2). The teeth are conical and some small teeth alternate with larger teeth (Fig. 2A; also Egerton 1858, pl. 10, fig. 2). There are teeth along the whole ventral margin of the maxilla, except on the anterior articulatory process.

The maxilla of *Eurypoma* presents some features important for the placement of the genus within neopterygians. For instance: (1) The presence of a notch at the posterior margin of the maxilla is considered a halecomorph synapomorphy (Grande & Bemis 1998). (2) The presence of the supramaxillary process and a notch where the supramaxilla abuts, is interpreted as another halecomorph synapomorphy by Arratia & Herzog (submitted). Wenz (1968) suggested that the presence of the anterior articular process of the maxilla and other features of this bone such as the size and shape are indications of a possible relationship with amiids. Cer-

tainly, as shown above, there are similarities between the maxilla of *Eurypoma* and that of amiids.

The maxilla of *Eurycormus* differs from that of *Eurypoma* (compare Fig. 2A with 2B). In *Eurycormus*, the maxilla is gently curved, has a similar depth along the maxillary blade, and its posterior margin is rounded. The anterior articular process is elongated and is partially covered by the premaxilla (Figs 2B, 6). A row of minuscule, conical teeth covers most of the ventral margin of the maxilla.

Maxillae similar to that in *Eurycormus* are found in many of the so-called pholidophoriforms, as well as basal teleosts (see for instance Nybelin 1966, figs 1, 3, 1974, figs 1, 4, 13, 15, 18, 23, 29, 34, 35; Arratia 1997, figs 5, 47, 51; Arratia 2000, fig. 1).

Supramaxilla. Neopterygians may have one or two supramaxillary bones at the dorsal margin of each maxilla, or the bone may be absent. *Eurypoma* bears only one supramaxillary bone (Figs 2A, 7A, B; Egerton 1858, pl. 10, fig. 1; Wenz 1968, pl. 38, figs C, D) at the dorsal margin of the maxilla. The bone is large and massive and is at least as long as half the length of the maxilla (Egerton

1858, pl. 10, fig. 1). The supramaxilla of *Eurypoma grande* illustrated in Fig. 2A and Fig. 7A is missing the anterior part, whereas the supramaxilla illustrated in Fig. 7B is missing its posterior part. The supramaxilla is not preserved in the specimens from Nusplingen (Figs 3, 8), but the presence of the supramaxillary process in the maxilla of SMNS 10402 is a good indication of the length of the supramaxilla. A large supramaxilla is also present in some amiiforms, e.g., *Amia calva* and *A. pattersoni* (see Grande & Bemis 1998). Within teleosteomorphs, the species of *Siemensichthys* are characterized by the presence of a large supramaxilla sitting on most of the dorsal margin of the maxilla. The presence of one large supramaxilla, as long as the maxillary blade, is a synapomorphy of the genus (Arratia 2000).

The presence of one supramaxilla is currently interpreted as an halecomorph synapomorphy (Grande & Bemis 1998); however, this is a homo-plastic feature also found in some of the potential stem-group teleosts such as pachycormiforms and aspidorhynchiforms as well as semionotiforms among others. In pachycormiforms and aspido-rhynchiforms at least, the so-called supramaxilla has a very different position to that of halecomorphs where it lies on the dorsal margin of the maxilla (Arratia 1999).

In contrast to *Eurypoma*, two supramaxillary bones (Figs 2B, 6) lie on the dorsal margin of the maxilla in *Eurycormus*. They are named supramaxilla 1 and supramaxilla 2. Two supramaxillary bones are commonly present in most basal teleosts, e.g., *Pholidophorus bechei* (Nybelin 1966, figs 1, 3), *Leptolepis coryphaenoides*, *Ascalabos*, and others (see Arratia 1997, figs 5, 47, 51).

L o w e r j a w. The lower jaw of *Eurypoma grande* (Figs 2A, 5, 8) is similar to that of amiiforms (see for instance Lambers 1992, fig. 23b; Grande &
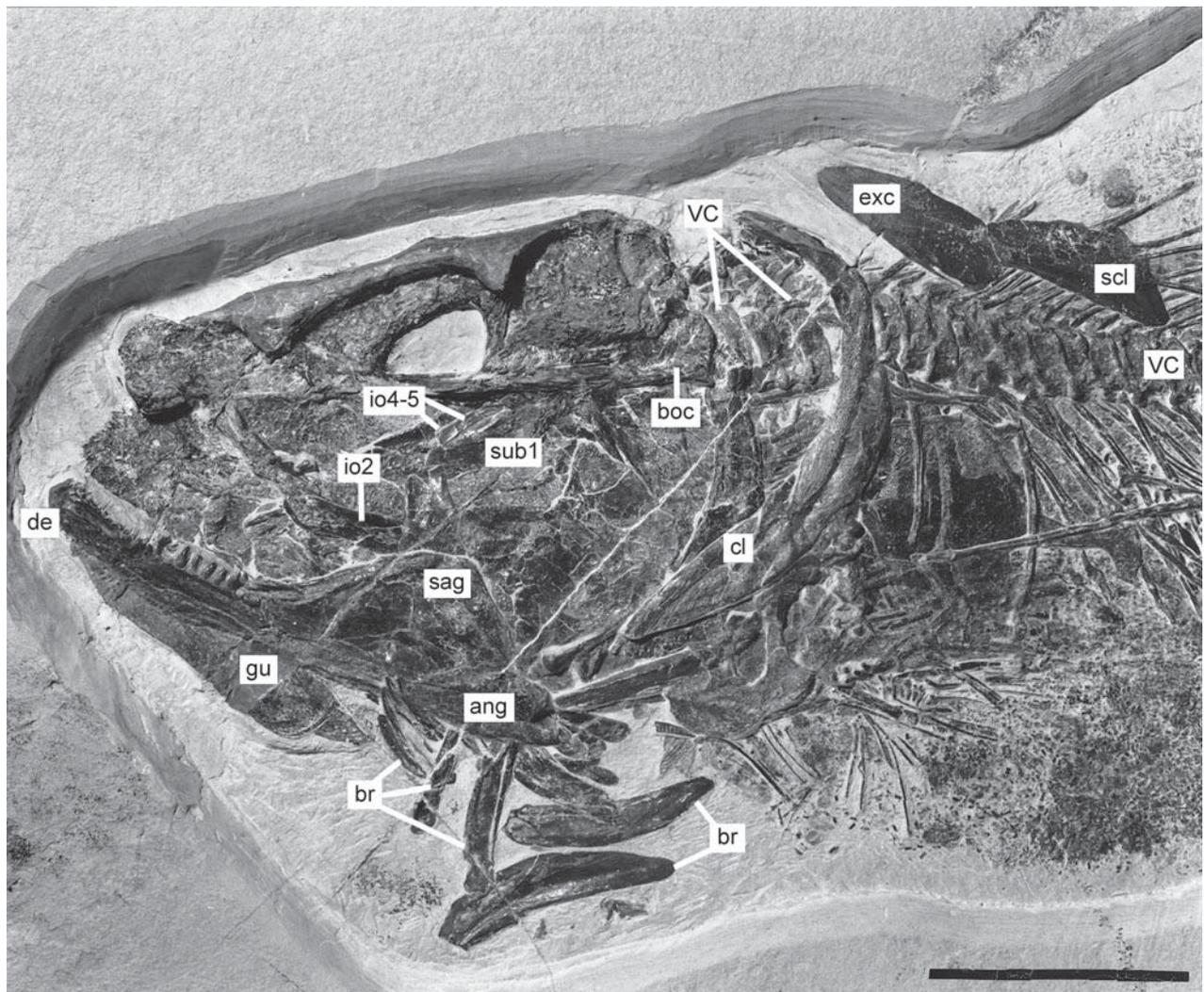
Fig. 8. *Eurypoma grande*, SMNS 86901/38, head and anterior part of body. Kimmeridgian, Nusplingen, Baden-Württemberg. Abbreviations: **ang** – angular; **boc** – basioccipital; **br** – branchiostegals; **cl** – cleithrum; **de** – dentary (= dentospleniall); **exc** – extrascapula; **gu** – gular; **io2** – infraorbital bone 2 (= subinfraorbital bone of Grande & Bemis 1998); **io4–5** – infraorbital bone 4, 5 (= postorbital bones of Grande & Bemis 1998); **sag** – surangular; **scl** – supracleithrum; **sub1** – suborbital bone 1; **VC** – vertebral centrum. Scale equals 5 cm.

Bemis 1998, figs 43, 104, 123, 148, 151, 184, 280B, C, 337, 360, 383, 390). The jaw of *Eurypoma* is narrow in its anterior part, whereas it is deep posteriorly, at the level of the coronoid process (see Figs 5, 8). The jaw in lateral view is formed by the dentary bone (= dentosplenial bone), angular, and supraangular or surangular (Figs 2A, 3B, 7A, B, 8). Other bones are seen in medial view, as for instance, coronoid bones (Fig. 7A, B), prearticular, two ossifications of the articular, and retroarticular (Fig. 5). The largest element is the dentary, with a ventral margin that is almost straight. The dorsal margin bearing teeth is also straight in the anterior part; the margin ascends dorso-posteriad to form part of the rounded coronoid process. There is one row of dentary teeth of different sizes (Fig. 8). The anteriormost teeth are smaller than the posterior ones, that are thick, large, and conical. Eight large teeth are counted in SMNS 86901/38, and there are two large sockets at the end of the row, so that the jaw bears about 10 large teeth (see Fig. 8). The specimen from France (Fig. 7B; Wenz 1968, pl. 38, fig. D) also shows the difference in size between anterior and posterior teeth in *Eurypoma grande*. The holotype of *Eurypoma grande* (Woodward 1890, pl. 10, fig. 1) shows only five sockets for large teeth, small teeth cannot be seen, because the anterior part of the lower jaw is not preserved. Numerous coronoid bones bearing teeth are placed medial to the dentary (Fig. 7A, B). The angular extends rostrad, cone-shaped, into the dentary bone in *Eurypoma grande* (Woodward 1890, pl. 10, fig. 1; Wenz 1968, pl. 38, figs C, D; figs 2A, 7A, B). The posterior part of the lower jaw is covered in *Eurypoma egertoni* (Egerton 1858, pl. 10, fig. 2), in the holotype (Woodward 1890, pl. 10, fig. 1) and the French specimen (Wenz 1968, pl. 38, figs C, D), so that its shape is not visible. Specimen SMNS 86901/38 shows only the deep posterior part of the lower jaw (Fig. 8), mainly formed by angular and surangular. Another important feature to be mentioned is that the lower jaw presents two articulatory facets, one for the quadrate and another for the symplectic (see Fig. 5). The openings of the mandibular sensory canal are represented by a few foramina on the lower part of the lower jaw (Wenz 1968).

The lower jaw of *Eurycormus* is poorly known and only in lateral view. Thus, comparison with the lower jaw of *Eurypoma* is limited. The lower jaw (Figs 1A, B, 2B, 6) of *Eurycormus* has a slightly curved ventral margin, whereas the anterior dorsal margin of the dentary ascends progressively, so that the dentary is deeper in its anterior and middle part than that of *Eurypoma*. *Eurycormus* has one large conical tooth on the oral margin of the dentary that is followed by small conical teeth. It is unknown if *Eurycormus* has coronoid bones or not. The mandibular sensory canal produces many small pores that mark the path of the canal along the jaw. With age, the branching of the canal increases and there are many small pores at the posterior part of the angular, giving the erroneous idea of an ornamented jaw. A similar feature has been observed in the "pholidophoriform" *Siemensichthys* (Arratia 2000).

Infraorbital series of bones. The information on the infraorbital bones of *Eurypoma* is incomplete, but what is preserved shows remarkable features. There is a large infraorbital bone 1 (= lacrimal bone), followed by a narrow infraorbital bone 2, and a slightly dumb-bell shaped infraorbital bone 3 (Fig. 2A = jugal bone, also Woodward 1890). SMNS 86901/38 has preserved infraorbital bone 2 and part of infraorbital bone 3. Infraorbital bones 4 and 5 are very narrow, rectangularly-shaped, and bear a section of the infraorbital canal (Figs 2A, 8, and see Egerton 1858, pl. 10, fig. 1). Pores of the infraorbital sensory canal open near the margin of infraorbital bone 1 (Fig. 7B). There is no available information on the dermosphenotic and antorbital bone.

In *Eurycormus*, the infraorbital series consists of a rectangularly-shaped antorbital bone, a large infraorbital bone 1, a narrow infraorbital bone 2, a large infraorbital bone 3 partially covering the anterior margin of the preoperculum, infraorbital bones 4 and 5 that are almost square and with their posterior margins overlying suborbital bones, and a slightly triangular dermosphenotic (Fig. 2B). The infraorbital canal produces numerous tubules on infraorbital bones 1 and 3, that end in small pores. The branching of the tubules increases with age, so that large specimens have more sensory pores than small, young specimens. The infraorbital canal extends rostrad onto the antorbital and rostral bones. It bifurcates in the dermosphenotic.

Supraorbital bones. The number of supraorbital bones is unknown in *Eurypoma*. Wenz (1968: pl. 38, fig. D) illustrated one supraorbital bone. *Eurycormus* has two elongated supraorbital bones (Fig. 2B).

Suborbital bones. *Eurypoma grande* has a posterior series of three suborbital bones. The largest suborbital bone (Figs 2A, 8), identified here as suborbital bone 1, almost covers the whole cheek region. Anteriorly, suborbital bone 1 contacts the narrow infraorbital bones 4 and 5; dorsally it reaches the lateral margin of the skull roof (dermopterotic region); posteriorly, it overlaps the anterior region of the preoperculum, and ventrally it contacts infraorbital bone 3 and an elongated triangular suborbital bone 2. Suborbital bone 3, a triangularly shaped bone, contacts infraorbital bone 3 and suborbital bone 2. The bone lies on the anteroventral part of the preoperculum. The large size of suborbital bone 1 is uncommon among actinopterygians. *Ionoscopus cyprinoides*, an ionoscopiform, has a
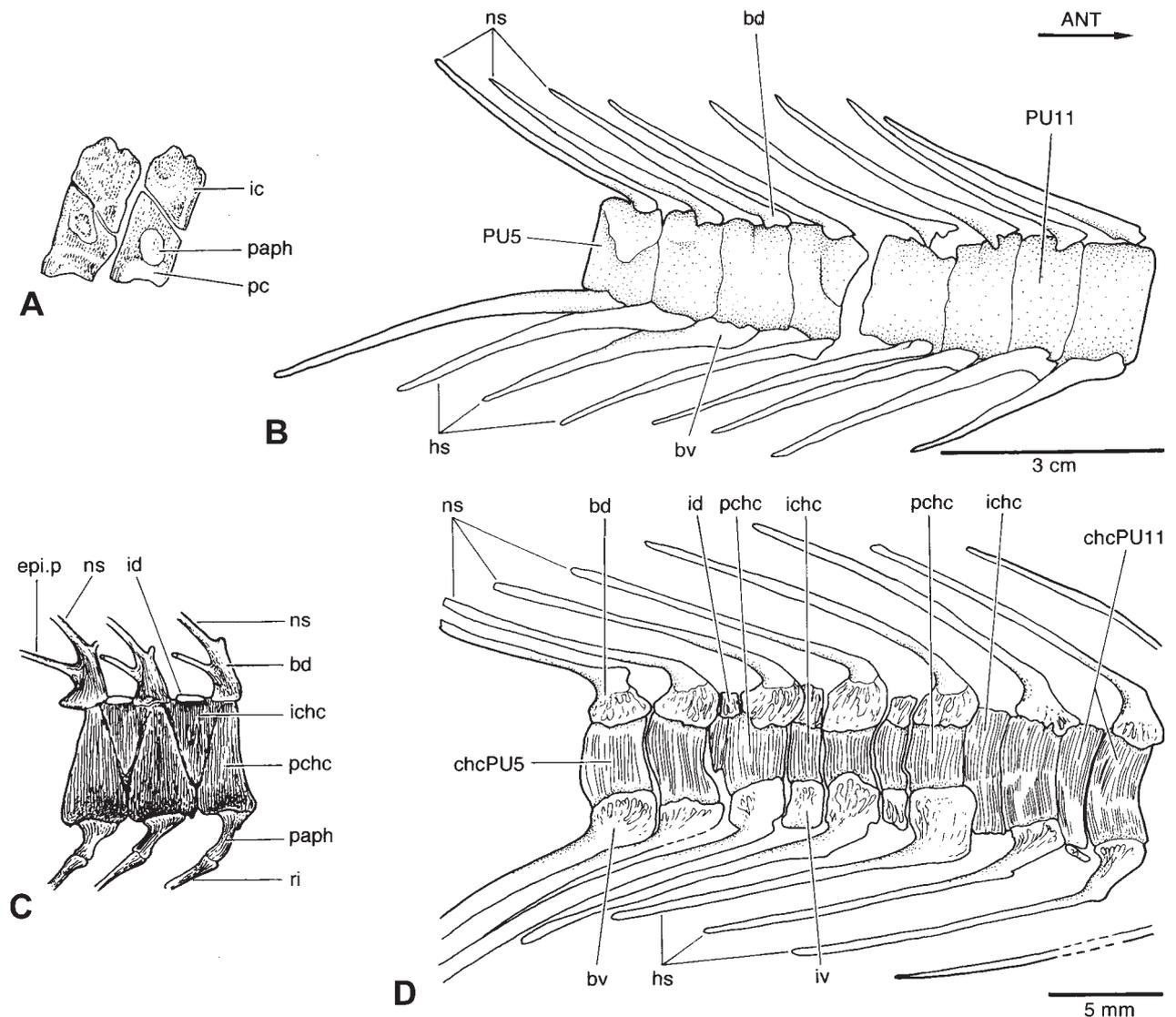
Fig. 9. Vertebrae of **A**, **B** – *Eurypoma grande*; **A** – holotype, Kimmeridgian, Ely, Cambridgeshire, diagrammatic representation of two monospondylous abdomial vertebrae (modified after Woodward 1890, pl. X, fig. 2); **B** – SMNS 86901/38, Kimmeridgian, Nusplingen, Baden-Württemberg, caudal region between monospondylous preural vertebrae 5 and 12; and of **C**, **D** – *Eurycormus speciosus*, Tithonian; **C** – BSP AS V510, Eichstätt, Bavaria, diagrammatic representation of four monospondylous abdominal vertebrae (modified from Zittel 1887−1890, fig. 242); **D** – JM SOS2341, Zandt, Bavaria, caudal region between diplospondylous preural vertebrae 5 and 11. Abbreviations: **ANT** – anterior; **bd** – basidorsal (dorsal arcocentrum); **bv** – basiventral (ventral arcocentrum); **chcPU5**, **11** – chordacentrum(a) of preural vertebra 5, 11; **epi.p** – epineural process; **hs** – haemal spine; **ic** – intercentrum; **ichc** – intercentral chordacentrum; **id** – interdorsal; **iv** – interventral; **ns** – neural spine; **paph** – parapophysis; **pc** – main centrum; **pchc** – main chordacentrum; **PU5**, **11** – preural vertebra 5, 11; **ri** – rib.

large suborbital bone, but not as large as the bone in *Eurypoma*.

Eurycormus has three suborbital bones (Fig. 2B) whose features differ markedly from those in *Eurypoma*. The slightly oval-shaped suborbital bone 1 is placed posteriorly to infraorbital bones 3, 4, and 5. Posteriorly the bone covers the dorsal limb of the preoperculum and extends onto the operculum. There are two accessory suborbital bones dorsal to suborbital bone 1 and posterior to infraorbital bone 5 and the dermosphenotic. They are oval-shaped and run along the lateral margin of the skull roof (dermopterotic region).

Sensory canals. In *Eurypoma*, as far as it can be seen in the available material, the cephalic sensory canals run deeply within the thick bone. In contrast, bones are comparatively thinner in *Eurycormus* and the path of the sensory canals, of the sensory tubules, and the pores are easily observed, especially the numerous branching in the infraorbital bones and preoperculum. There are many minuscule pores in *Eurycormus*, whereas the sensory pores of the lower jaw in *Eurypoma* are few in number.

Vertebral column. The vertebral column of *Eurypoma* consists of about 47 monospondylous
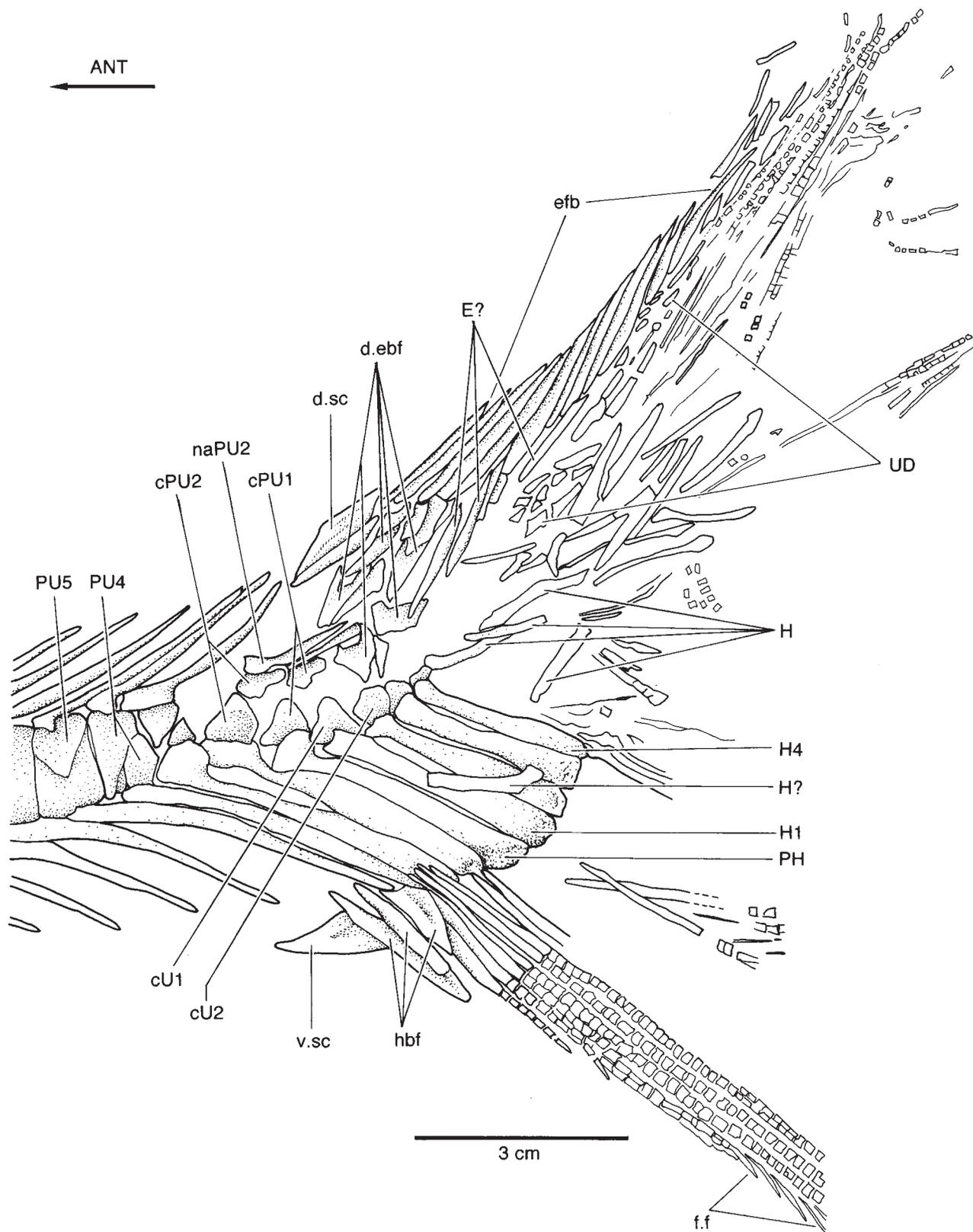
Fig. 10. *Eurypoma grande*, SMNS 86901/38, caudal skeleton. Kimmeridgian, Nusplingen, Baden-Württemberg. Abbreviations: **cPU1, 2** – dorsal and ventral chordacentrum of preural centrum 1 and 2; **cU1**, **2** – ventral chordacentrum of ural centrum 1; **d.ebf** – displaced epaxial basal fulcra; **d.sc** – dorsal scute; **E?** – epurals?; **efb** – epaxial basal fulcra; **f.f** – fringing fulcra; **H1**, **4**, **?** – hypural 1, 4 and ?; **hbf** – hypaxial basal fulcra; **naPU2** – neural arch of preural centrum 2; **nsPU3−2** – neural spine of preural centrum 3, 2; **PH** – parhypural; **PU4, 5** – preural centrum 4, 5; **UD** – urodermal; **v.sc** – ventral scute.

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vertebrae, with smooth surfaces. The abdominal and first caudal centra are slightly obliquely oriented, whereas the most posterior caudal centra have an almost straight orientation with respect to the long axis of the fish (see Fig. 3B). Each centrum is pierced by a large notochordal canal (see Figs 3A, 5). Each centrum is massive and the chordacentral elements seem to be covered by perichondral ossification. However, this assumption should be tested with histological sections (a future project by the authors).

In *Eurypoma*, the structure of the centra varies between abdominal and caudal vertebrae. The abdominal centra (Figs 3B, 8) are narrow and deep, and almost rectangularly-shaped. Each abdominal centrum is formed by two elements, the dorsal intercentrum and the ventral main centrum (Fig. 9A). Both, intercentrum and main centrum are separated by an oblique suture. The basidorsal element (or dorsal arcocentrum or neural arch) lies on the dorsal surface of the intercentrum, whereas the basiventral element or parapophysis is placed on the ventro-lateral part of the main centrum. The caudal centra (Figs 3B, 8, 9B, 10, 11) are approximately square or rectangularly-shaped and longer than the first abdominal centra. Most caudal centra are compact elements that result from fusion between the intercentrum and main centrum. Incomplete lines of suture can be observed in some of the centra. Centra such as preural centra 3−1 are formed by dorsal and ventral hemichordacentra (Fig. 10).

In *Eurypoma*, the dorsal arcocentra are autogenous as are the ventral arcocentra of the caudal region. The dorsal arcocentra lie closer to the anterior margin of the centrum. Neural spines of the abdominal vertebrae are double, but both halves of

Fig. 11. Caudal vertebrae and caudal skeleton of *Eurypoma grande*, SMNS 86901/38. Kimmeridgian, Nusplingen, Baden-Württemberg. See Fig. 10 for identification of structures. Scale equals 5 cm.

each arch seem to be fused just above the neural canal. The neural spines of the caudal region are single, a feature found in actinopterygians with the exception of *Polypterus* and Acipenseriformes (Arratia et al. 2001). Most neural and hemal spines are narrow, with the exception of the hind-most which are slightly expanded (Fig. 9). The neural and hemal spines are inclined toward the horizontal in the caudal region.

The vertebral column of *Eurycormus* is formed by about 44 or 45 vertebrae that have a delicate appearance in comparison with those of *Eurypoma*. In *Eurycormus*, the abdominal region is formed by monospondylous centra (Fig. 9C) and the caudal region by diplospondylous centra (Fig. 9D), a major difference with those in *Eurypoma*. In *Eurycormus*, the centra are of chordacentral type. Each abdominal centrum is composed of (1) a dorsal, almost triangularly-shaped intercentrum whose larger region is dorsally placed and (2) the main chordacentrum that also is triangularly-shaped but its larger region

is ventrally placed. Small, often partially ossified, interdorsal elements are present on the dorsal region of the intercentra, between two dorsal arcocentra. The basidorsal elements (= dorsal arcocentra = neural arches) are small in the abdominal region; both halves of each arch are separated such that the neural spines are double. Elongate epineural processes are associated with the dorsal arcocentra of the abdominal region. There are well-developed parapophyses associated with the ventro-lateral regions of the centra; they form the articulations for the ribs.

The caudal vertebrae of *Eurycormus* are formed by the main chordacentrum that bears dorsal and ventral arcocentra (Fig. 13). Posterior to the main chordacentrum lies a narrower intercentral chordacentrum. Dorsal and ventral arcocentra are large and expanded, and their proximal portions retained cartilage in different stages of ossification, even in large specimens. The intercentral chordacentra may be associated with interdorsal and interventral ele-
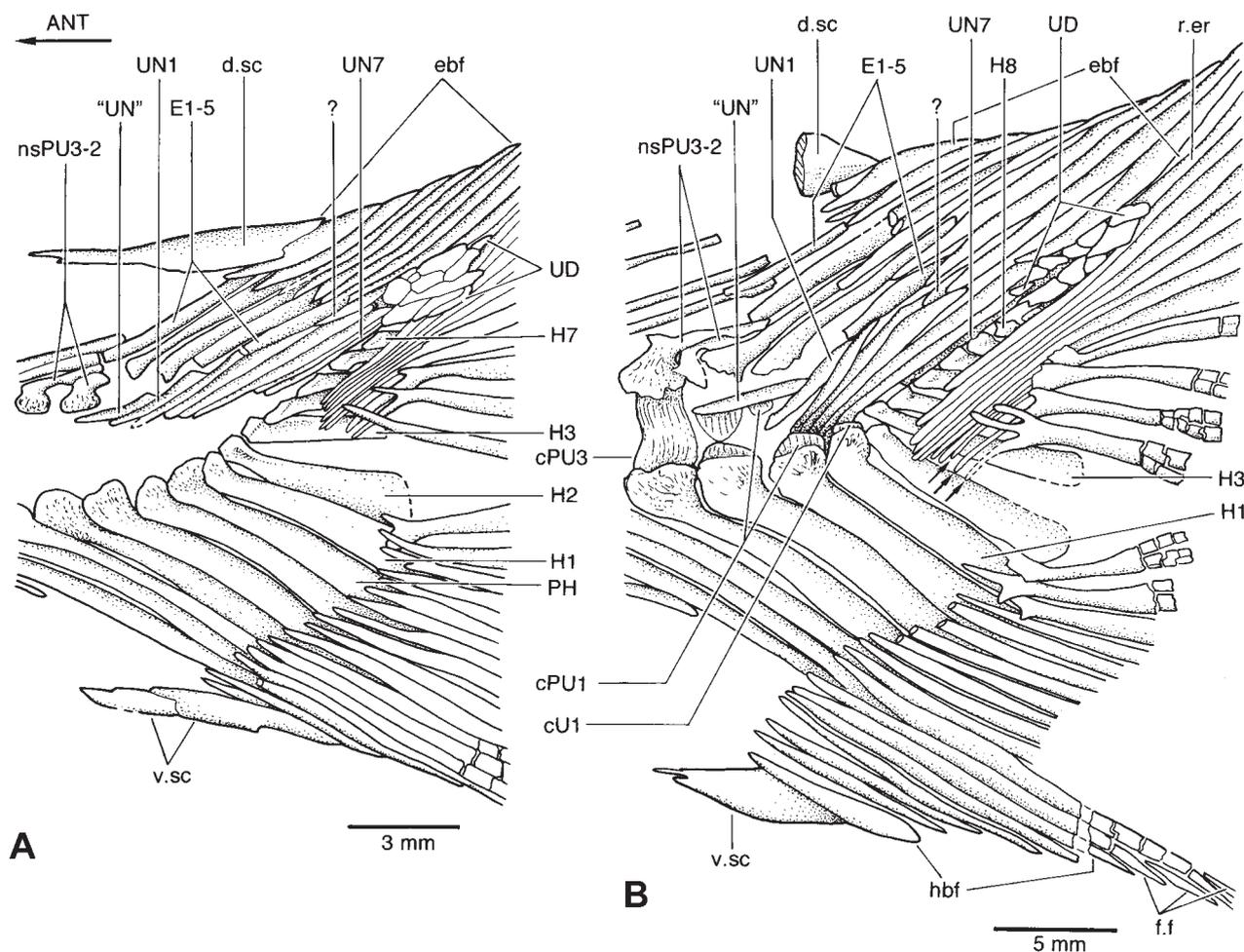
Fig. 12. *Eurycormus speciosus*, Tithonian, Zandt, Bavaria, caudal skeleton (both reversed to the left). **A** – JM SOS 2339, juvenile specimen (modified from Arratia & Lambers 1996, fig. 14A); **B** – JM SOS 2341, adult specimen (modified from Arratia 1999, fig. 15). Small arrows point to the elongate processes of the inner principal rays of the dorsal lobe. Abbreviations: **cPU1, 3** – chordacentrum of preural centrum 1 and 3; **cU1** – ventral chordacentrum of ural centrum 1; **d.sc** – dorsal scute; **E1–5** – epural 1–5; **ebf** – epaxial basal fulcra; **f.f** – fringing fulcra; **H1, 2, 3, 7, 8** – hypural 1, 2, 3, 7 and 8; **hbf** – hypaxial basal fulcra; **nsPU3–2** – neural spine of preural centrum 1; **PH** – parhypural; **r.er** – rudimentary epaxial ray; **UD** – urodermal; **"UN"** – uroneural-like element of preural centrum 1; **UN1, 7** – uroneural 1 and 7; **v.sc** – ventral scute.

ments that usually are incompletely ossified and do not form arches. The diplospondylous condition is lost in the preural region where the centra are monospondylous chordacentra. The neural and hemal spines of the caudal region (except for the first preural vertebrae) are narrow, long, and inclined toward the horizontal.

E p i n e u r a l   b o n e s. *Eurypoma* does not have epineural bones, an absence also found in various neopterygians including halecomorphs. The neural arches of the abdominal vertebrae of SMNS 10402 and SMNS 86901/38 (Figs 3A, B, 8) do not have any process or thin bones associated with them that could be interpreted as epineural elements.

The neural arches of the abdominal vertebrae of *Eurycormus* present epineural processes (Fig. 9C). Each arch bears a long, thin, posterior bony process, the so-called epineural bone. The presence of long, thin, bony epineural processes is interpreted as a synapomorphy of "true" teleosts (*Leptolepis coryphaenoides* and more advanced forms) (Arratia 1999, 2000). However, this feature is homoplastic

and found also in *Eurycormus* among the *Siemensichthys*-group.

C a u d a l   s k e l e t o n. To our best knowledge, the caudal skeleton of *Eurypoma* is only preserved in specimens from Nusplingen. Specimen SMNS 86901/38 (Figs 10, 11) has the best-preserved caudal skeleton, whereas SMNS 10402 has displaced elements belonging to the caudal endoskeleton (Fig. 3A). Six or seven preural vertebrae (Fig. 10) are associated with dermal elements such as scutes, basal fulcra, and rays. Preural centrum 3 is formed by two hemichordacentra. Neural spine 3 is as long as spines 4 and 5, and hemal spine 3 is slightly broader than spines 4 and 5. Preural centrum 2 is also formed by two hemichordacentra. Its neural arch and spine are comparatively smaller than those of preural centrum 3. The neural spine of preural centrum 2 is short, about half the length of neural spines of anterior preural vertebrae. The hemal spine of preural centrum 2 is broader than preceding spines. Preural centrum 1 is formed by two hemichordacentra. Neural spine 1 is the shortest of the whole series of preural spines. The par-
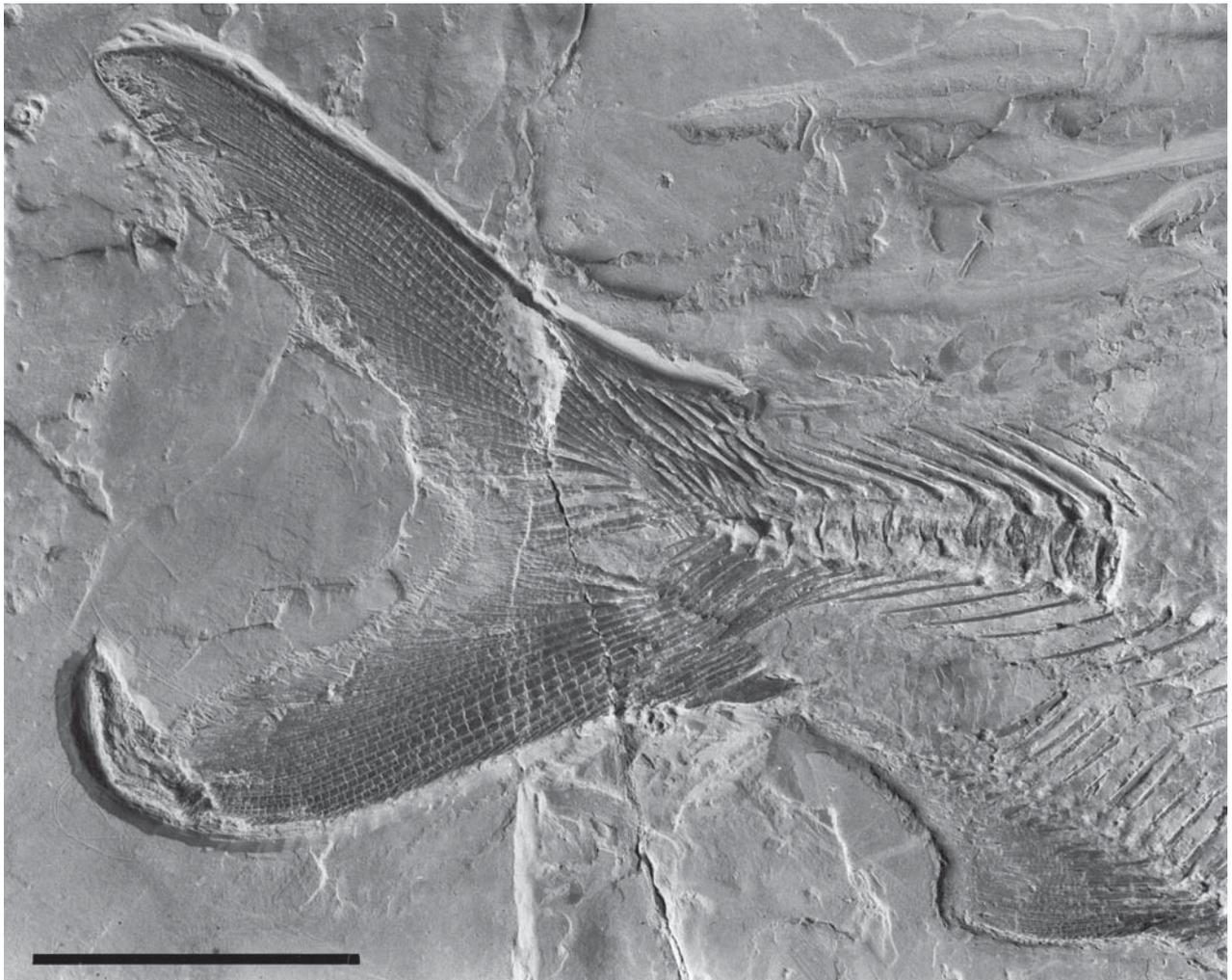
Fig. 13. *Eurycormus speciosus* Wagner, 1863, JM SOS 2341, caudal skeleton. Tithonian, Zandt, Bavaria. See Fig. 12B for identification of structures. Scale equals 5 cm.

hypural is as broad as the hemal spine of preural centrum 2 and hypural 1. There are four additional ventral hemichordacentra preserved at the bases of hypurals 1 to 4. They are ural centra 1–4. Consequently, *Eurypoma* has a polyural caudal skeleton. There are at least five displaced elements that, judging from their shape, could be hypurals. However, the total number of hypurals is unknown. There are four incomplete, elongated dorsal elements that are interpreted here as epurals. There are numerous displaced basal fulcra, rays, and broken rays, that make it impossible to identify all elements.

Eurypoma has a large number of urodermals that cover an elongated area ventral to the epaxial series of fulcra and the bases of the dorsal fins rays. The last urodermals are very small ovoid or rhombic elements. The epaxial basal fulcra and probably the hypaxial basal fulcra, are unpaired elements bifurcated proximally. It is unclear if the last epaxial basal fulcra are paired or single elements. Epaxial and hypaxial fringing fulcra are present. The caudal
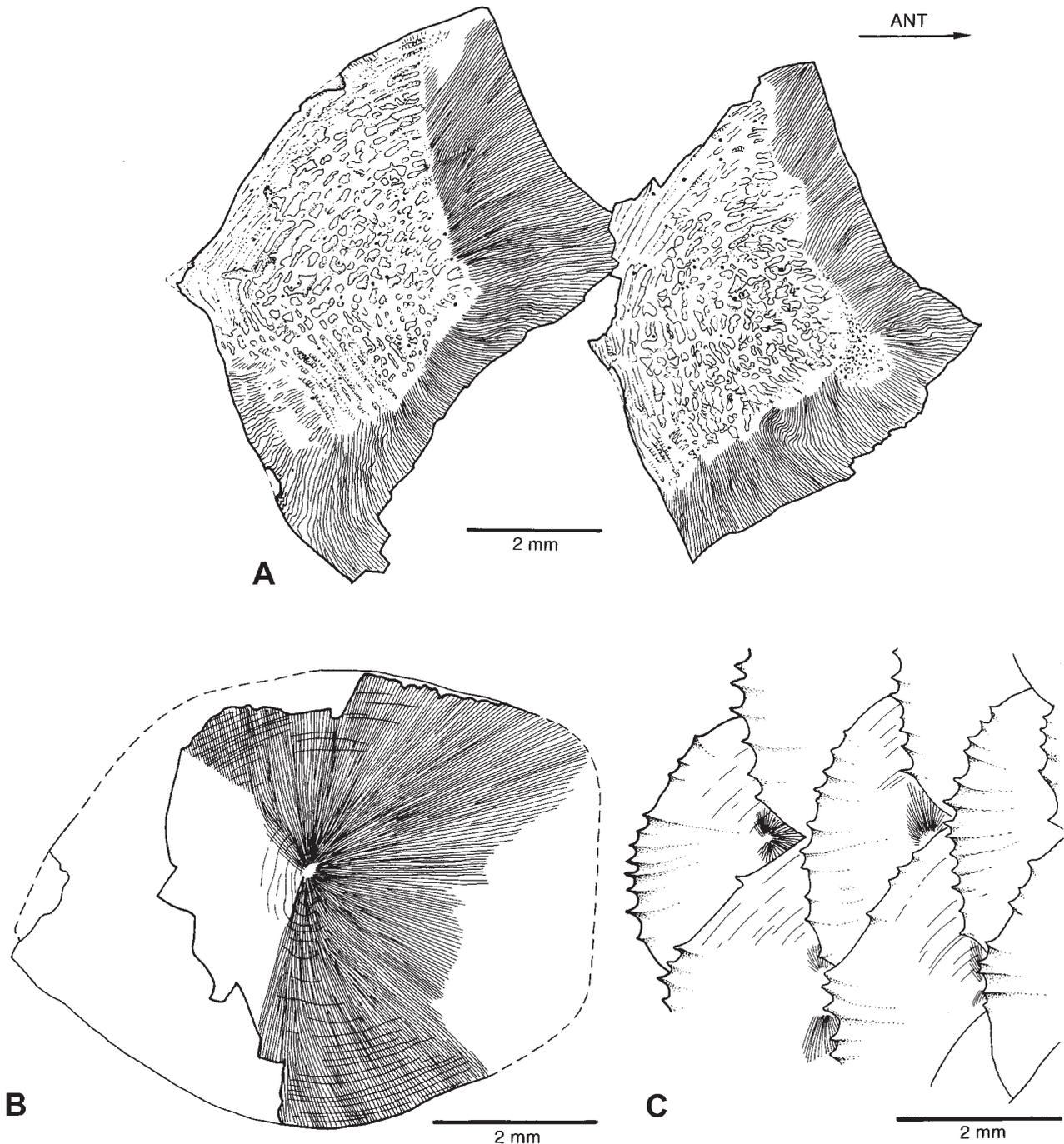
Fig. 14. Scales of **A** – *Eurypoma egertoni*, holotype, BMNH P6912, Callovian, Peterborough, Huntingdonshire, short behind the head; **B** – *Eurypoma grande*, Tü 17577, Kimmeridgian, Nusplingen, Baden-Württemberg, anterior part of body; **C** – *Eurycormus speciosus*, holotype, BSP AS V510, Tithonian, Eichstätt, Bavaria, in front of dorsal fin. **ANT** – arrow points in direction of head.

rays appear to have short bases, and are formed by many small segments. Some rays, close to their distal ends, show a Z-like or step-like segmentation.

The caudal skeleton of *Eurycormus* is better known than that of *Eurypoma*. Although both are of polyural type and share some general similarities such as the presence of scutes, basal and fringing fulcra, etc., there are major differences separating them. For instance, *Eurycormus* lacks a neural arch and spine on preural centrum 1 (Figs 12A, B, 13); the neural spines of preural centra 3 and 2 are short, whereas the neural spine of preural centrum 3 is long in *Eurypoma*. *Eurycormus* has five epurals and at least 9 hypurals. The total number of epurals and hypurals is unknown in *Eurypoma*. *Eurycormus* has a series of eight dorsal elongated paired elements. The first is uroneural-like, a modification of the neural arch of preural centrum 1, and the other seven are interpreted as uroneurals or modified ural neural arches (Patterson 1973, Arratia & Lambers 1996, Arratia 1999). This is a major difference between these taxa, and an indication of relationship of *Eurycormus* with teleosts. There are numerous scale-like urodermals covering the base of the last epaxial basal fulcra and the first dorsal rays. However, there are fewer urodermals in *Eurycormus* than in *Eurypoma* (compare Fig. 12A, B with Fig. 10).

Unfortunately, a comparison between fulcra and rays of *Eurypoma* and *Eurycormus* is difficult due to conditions of preservation. Still, there are some significant differences that can be noted. For instance, the bases of the rays in *Eurycormus* are comparatively longer than those of *Eurypoma*. About 10 or 11 epaxial basal fulcra are present in *Eurycormus*. In contrast, *Eurypoma* has a longer series of epaxial basal fulcra (more than 15 fulcra). The bases of the inner principal caudal rays have processes in *Eurycormus* (Fig. 12B); the ventral most is long and placed in the same position as the principal rays so that the bases of the principal rays and the elongate processes form a continuous series. We have not seen these processes in the available material of *Eurypoma*. Finally, *Eurypoma* seems to have small dorsal and ventral scutes preceding the basal fulcra, whereas the scutes are longer and larger in *Eurycormus*.

S c a l e s. Both genera, *Eurycormus* and *Eurypoma*, have amioid scales (Schultze 1996). This means that the anterior, covered field of the scales is marked by radial ridges. The scales of *Eurycormus* (Fig. 14C) are thin and the free field is smooth except for weak ridges reaching from the serration of the posterior margin. The serration of the posterior margin is characteristic of *Eurycormus* scales. In contrast, the scales of *Eurypoma* are thick and have an unserrated posterior margin, which ends in a median point. The free field of the scales of *Eury-*

poma egertoni (Fig. 14A) is sculptured with irregular tubercles, which are arranged along the growth lines of the free field. The surface of the scales of *Eurypoma grande* (Fig. 14B) is smooth and shiny.

Result of the comparison

According to the comparison presented above, *Eurycormus* and *Eurypoma* differ sufficiently that we interpret them as two separate genera. Furthermore, the morphological characters of these genera place them in different large clades of Neopterygii. *Eurycormus* is close to the teleosts, and *Eurypoma* lies within the halecomorphs.

E u r y c o r m u s and the teleosts. *Eurycormus* shares with other teleosts a mobile premaxilla, two supramaxillae, a posteroventral process on the quadrate, a pectoral propterygium fused with the first pectoral ray, four pectoral radials, dorsal processes of the bases of the innermost principal rays present, ural neural arches modified as uroneurals, and all uroneurals inclined toward the horizontal, one beside the other (Arratia 2000). Other teleostean synapomorphies, such as number of hypohyals and absence of coronoid bones, are unknown because of incomplete preservation. Other features that are considered teleostean synapomorphies, such as cycloid scales, first two hypurals supported by a single ural centrum, are absent in *Eurycormus* (Arratia 2000).

Schultze (1966) placed *Eurycormus* (based on all three species, not stated in the paper) into forms with amioid scales. Consequently, Patterson (1973, p. 266), using this information, stated that amioid scales occur within teleosts. The taxon Teleostei of Patterson (1973) included stem-teleostean taxa, whereas the taxon Teleosteomorpha of Arratia (2001) includes Teleostei and the stem-teleostean taxa. Cycloid scales are restricted to Teleostei in the sense of Pinna (1996) and of Arratia (2001) above *Pholidophorus germanicus*, including *Leptolepis coryphaenoides* and all more advanced teleosts. *Eurypoma egertoni* and *E. grande* have amioid scales.

Patterson (1973) included *Eurycormus* within Pholidophoriformes based on some shared characters with some 'pholidophoriforms', and without performing a phylogenetic analysis. However, as demonstrated later, the order Pholidophoriformes is not a monophyletic group and the so-called pholidophoriforms occupy different phylogenetic positions (see Patterson 1977, fig. 19 and Arratia 2000, figs 20, 21). According to Arratia (2000), *Eurycormus* stands at the basal position of the *Siemensichthys*-group that includes at least *Siemensichthys macrocephalus* (= *Pholidophorus macrocephalus*) and *Siemensichthys siemensi* and species of *Ankilo-*

phorus from the Kimmeridgian of Cerin, France. (For details see Arratia 2000).

E u r y p o m a and the halecomorphs. *Eurypoma* shares with halecomorphs the following synapomorphies: presence of a single supramaxillary bone, a notch or concavity in the posterior margin of the maxilla, and an elongated symplectic forming part of the double articulation with the lower jaw (Grande & Bemis 1998). Additionally, *Eurypoma* presents the supramaxillary process on the maxilla, a halecomorph synapomorphy proposed by Arratia & Herzog (submitted).

To clarify the phylogenetic position of *Eurypoma*, we added *Eurypoma* to the data matrix (69 characters) of halecomorphs by Grande & Bemis (1998) adding or leaving off a hypothetical ancestor. We performed phylogenetic analyses with PAUP 4.0b10 (all characters unordered). With or without the hypothetical ancestor, we received the same tree (shortest tree with hypothetical ancestor 125 steps, without hypothetical ancestor 120 steps) as Grande & Bemis (1998) did, with *Eurycormus* close to teleosts. In both analyses, *Eurypoma* stands as the sister taxon to [Caturidae + Liodesmidae]. The characters of Caturoidea in Grande & Bemis (1998) unite Caturidae and Liodesmidae in our analyses as well. *Eurypoma* is joined to the Caturoidea only by one reversal (relatively long postparietal length) and one homoplastic chararacter (strongly inclined preural hemal and neural spines). Nevertheless, the genus clearly belongs to the Amiiformes within the Halecomorphi based on the following unique characters: a long and narrow preoperculum, two or fewer ossified ural neural arches (none identified in *Europoma*), symplectic distal end articulates with articular; the fourth unique character (shape of rostral bone) could not be checked because the bone is not preserved in the studied material.

Systematic Paleontology

Subdivision **Teleosteomorpha** Arratia, 2001
***Siemensichthys*-group**
Family **indet.**

Eurycormus **Wagner, 1863**

1863   *Eurycormus* Wagner, 1863: 707.
1881   *Eurycormus*. – Vetter: 113.
1887–1890 *Eurycormus*. – Zittel: 230.
1895   *Eurycormus*. – Woodward: 352.
1906   *Eurycormus*. – Heineke: 203.
1945   *Eurycormus*. – Romer: 581.
1964   *Eurycormus*. – Berg & Obruchev: 385.
1966   *Eurycormus*. – Lehman: 140.
1966   *Eurycormus*. – Romer: 354.
1966   *Eurycormus*. – Schultze: 271, 273.

1968   *Eurycormus* (parte). – Wenz: 177-184.
1973   *Eurycormus*. – Patterson: 264-266.
1988   *Eurycormus*. – Carroll: 603.
1988   *Eurycormus*. – Bartsch: 174, 176, 179.
1998   *Eurycormus*. – Grande & Bemis: 572, 574, 618.
1999   *Eurycormus*. – Arratia: 304.

D i a g n o s i s. (Based on a unique combination of primitive and advanced characters. (*) = supposedly a unique character). Elongate, slightly fusiform fishes with pointed snout (*) and orbit dorso-laterally placed. Dorsal and pelvic fins inserted slightly behind mid-point of standard length. Dorsal fin and pelvic fin origin almost at the same level. Dorsal and anal fins slightly acuminate. Dorsal fin with 16 to 18 rays. Long anal fin with about 17 or 18 rays. Homocercal caudal fin deeply bifurcated. Triangularly-shaped premaxilla without nasal process. Lower jaw deep, "leptolepid"-like, with one large conical tooth anteriorly, followed by minuscule conical teeth (*). One large suborbital bone covering dorsal limb of preoperculum. Two small, oval accessory suborbital bones present. Long, gently curved maxilla bearing one row of minuscule teeth. Two supramaxillae. Cephalic sensory canals with numerous sensory tubules mainly on infraorbital bones, preoperculum and lower jaw. Vertebral column with a combination of monospondylous abdominal and diplospondylous caudal centra. Thin, long epineural processes present, last epineural process on vertebra below posterior part of dorsal fin. Epipleural bones absent. Neural arches of preural centra 3 and 2 bearing short neural spines. Neural arches of preural centrum 1 and ural centra absent. Five long epurals present. One or two uroneural-like bones followed by seven uroneurals. About a dozen urodermals. About 10 or 11 long, well-developed epaxial basal fulcra present. Dorsal-most principal caudal rays of dorsal lobe of caudal fin obliquely crossing the hypurals, and ventrally reaching hypurals 2 or 3 (*). Inner principal rays of dorsal lobe with elongated processes; the ventral-most ray extending ventrad, parallel to the bases of the dorsal-most principal rays. Unpaired fins bearing fringing fulcra. Caudal fin with both dorsal and ventral fringing fulcra. Amioid-type, thin scales, deeply overlapping with serrated posterior margins.

C o m m e n t s. Some of the features used by Wagner (1863) to characterize his new genus, *Eurycormus*, are still valid. For instance: (1) presence of a short, anteriorly pointed head; (2) orbit high on the head; (3) long anal fin with 17 rays; (4) first tooth on the lower jaw longer than the posterior ones. Wagner also mentioned that the dorsal fin is long, with 10 rays. However, a fin with 10 rays is not long in comparison with numerous Jurassic teleosts, which typically have more than 10 rays in the dorsal fin (see Arratia 1997).

One interesting aspect to be mentioned is that Wagner (1863) discussed some features present in *Eurycormus* and suggested its possible relationships. For instance: (1) scales similar to those found in the amiiform *Caturus* (amioid-type), as well as similarity in the shape of the body, and a long anal fin. However, he mentioned that the shape of the head and the position of the neural spines differ between both taxa. (In *Caturus*, both the neural spines and hemal spines of caudal vertebrae are inclined markedly toward the horizontal.) (2) Shape of the skull similar to that of *Pholidophorus* as well as the structure of the vertebral column (Wagner 1863 compared with vertebrae of *Pholidophorus*, that would mean presence of hemichordacentra or

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complete chordacentra) and position of the neural spines in the caudal region. However, both taxa differ in the structure of the scales [amioid-type in *Eurycormus*; ganoid-type in *Pholidophorus*.] (3) Shape of the skull and length of the anal fin similar to those in the ichthyodectiform *Thrissops*. However, *Thrissops* has "solid" vertebral centra [autocentral type of vertebra] in contrast to those in *Eurycormus*, and in addition lacks fulcra in the unpaired fins. Wagner (1863) placed *Eurycormus* together with *Caturus*.

The diagnosis of *Eurycormus* given by Woodward (1895, p. 352) is a composite between *Eurycormus* (e.g., snout obtusely pointed, and maxilla laterally compressed, with a convexly arched dentigerous border; fulcra comparatively small in the unpaired fins; dorsal fin small and triangular, opposed to the pelvic pair; anal fin with somewhat extended base) and *Eurypoma* (e.g., external head bones and opercular bones very feebly ornamented with rugae and tuberculations; maxilla gradually deepened behind; teeth large in a single series occupying the anterior half of dentary; scales delicate, very finely tuberculated). Woodward (1895) placed his mixed genus *Eurycormus* within the family Eugnathidae together with *Eugnathus*, *Heterolepidotus*, *Allolepidotus*, *Ptycholepis*, *Caturus*, *Neorhombolepis*, and *Lophiostomus*. *Ptycholepis* is a palaeoniscoid. *Furo* (= *Eugnathus*), *Heterolepidotus*, *Allolepidotus*, and *Neorhombolepis* are usually placed together with *Caturus* in Caturidae (Eugnathidae, Furidae), that means within halecomorphs, whereas *Lophiostomus* is considered a 'pholidophoriform'. Grande & Bemis (1998) placed *Neorhombolepis*, *Heterolepidotus*, and *Furo* (= *Eugnathus*) "probably" in the Ophiopsidae, a family within the order Ionoscopiformes, one order within halecomorphs. All these assignments are not certain, because a modern analysis including these genera has not been performed.

Occurrence. Upper Jurassic; central Europe.

Type and only species. *Eurycormus speciosus* Wagner, 1863
Figs 1, 2B, 6, 9C, D, 12, 13, 14C

1863   *Eurycormus speciosus* Wagner, 1863: 709, pl. 4.
1881   *Eurycormus dubius* Vetter, 1881: 113, pl. 2, fig. 7.
1887−1890   *Eurycormus speciosus.* − Zittel: 230, fig. 242.
1895   *Eurycormus speciosus.* − Woodward: 352.
1906   *Eurycormus speciosus.* − Heineke: 203−205, pl. V, figs 2−4.
1963   *Eurycormus speciosus.* − Nybelin: 503, figs 13−14.
1963   "*Eurycormus*" *dubius.* − Nybelin: 504, fig. 15.
1964   *Eurycormus speciosus.* − Berg & Obruchev: fig. 85.
1967   *Eurycormus speciosus.* − Lund: 211.
1968   *Eurycormus speciosus.* − Wenz: 177.
1973   *Eurycormus speciosus.* − Patterson: 265, figs 14, 15.

1988   *Eurycormus speciosus.* − Bartsch: fig. 33C.
1991   *Eurycormus speciosus.* − Frickhinger: 452, fig. on p. 452.
1992   *Eurycormus speciosus.* − Lambers: 303, pl. 6, fig. C.
1994   *Eurycormus speciosus.* − Frickhinger: 228, fig. 478.
1996   *Eurycormus speciosus.* − Arratia & Lambers: fig. 14A.
1996   *Eurycormus.* − Arratia & Lambers: 212.
1998   *Eurycormus speciosus.* − Grande & Bemis: 11, 574, 627, fig. 421A−D.
1999   *Eurycormus speciosus.* − Arratia: fig. 15.
1999   *Eurycormus speciosus.* − Arratia: 270, 291, fig. 6B, C, 310, fig. 15.
2000   *Eurycormus.* − Arratia: 136, fig. 21.

Diagnosis. As for the genus.

Holotype. BSP AS V510 (complete fish, Wagner 1863, pl. 7; Zittel 1887−90, fig. 242; Nybelin 1963, fig. 13; Grande & Bemis 1998, fig. 421A−B; figs 1A, B, 9C, 13, 14C).

Additional material. BMNH 37031 (Patterson 1973, fig. 15; Grande & Bemis 1998, fig. 421D), BSP 824 (Nybelin 1963, fig. 14; Bartsch 1988, fig. 42E), JM SOS2341 (Frickhinger 1991, fig. on p. 452; Frickhinger 1994, fig. 478; Arratia 1999, fig. 15 [wrong identification as SOS2339]; Figs 2B, 9D, 12B), JM SOS2339 (Nybelin 1963, fig. 15; Arratia & Lambers 1996, fig. 14A; figs 2B, 12A), JM SOS4614, JM SOS4615, MB f.3840 (figs 2B, 6), UMZC GN480 (Patterson 1973, fig. 14).

Occurrence. Kimmeridgian − Tithonian, Upper Jurassic; Nusplingen (Baden-Württemberg), Eichstätt, Kehlheim, Solnhofen, Zandt (Bavaria), southern Germany.

Subdivision **Halecomorphi** Cope, 1872
Order **Amiiformes** Hay, 1929
Superfamily **Caturoidea** Owen, 1860
Family **indet.**

Eurypoma Huxley, 1866

1843 *Macropoma* (parte). − Agassiz: 174.
1858 *Macropoma* (parte). − Egerton: 1.
1866 *Eurypoma* Huxley, 1866: 32.
1894 *Eurycormus.* − Woodward: 214.
1895 *Eurycormus.* − Woodward: 352.
1906 *Eurypoma.* − Heineke: 209.
1968 *Eurycormus* (parte). − Wenz: 177−184.

Diagnosis. (Based on a unique combination of primitive and advanced characters. (*) = supposedly a unique character). Elongate, fusiform fishes with homocercal tail deeply bifurcated. Thick, massive bones with scarce ornamentation represented by some rugae and tubercles. Premaxilla with nasal process. Anterior thickened oral part of premaxilla with an antero-lateral process (*). Large and deep supramaxillary bone. External row of large conical teeth on about half of dentary; numerous conical teeth on coronoid bones. Infraorbital bones 4 and 5 narrow, rectangularly-shaped bones (*). Infraorbital bone 3 completely separated from preoperculum by suborbital bone 1 (*). Large, almost square suborbital bone 1, aligned with two postero-ventral suborbital bones (*). Gular plate present. Monospondylous, massive vertebrae. Abdominal centra composed of intercentrum and main centrum bearing parapophyses. Caudal centra (except preurals) formed by only one element. Smooth lateral surface of centra. Centra with large notochordal foramen. Epineurals and epipleurals absent. Preural centra 2 and 1 with short neural spines. Polyural caudal skeleton. Fifteen or more well-devel-

oped epaxial basal fulcra (*). Few hypaxial basal fulcra. Many urodermals of different shapes and sizes extending below of at least two-thirds of epaxial basal fulcra (*). Amioid-type of scales with smooth posterior margin ending in one pointed tip.

O c c u r r e n c e. Callovian − Kimmeridgian, Jurassic; Europe.

Type species. *Eurypoma egertoni* (Egerton, 1858)
Fig. 14A

1843   *Macropoma Egertoni* Agassiz, 1843: 174, 180 (name only).
1858   *Macropoma Egertoni*. − Egerton: 1−3, pl. X.
1859   *Palaeoniscus Egertoni*. − Leckenby: 9.
1866   *Eurypoma Egertoni*. − Huxley: 32.
1894   *Eurycormus egertoni*. − Woodward: 214.
1895   *Eurycormus egertoni*. − Woodward: 353.
1968   *Eurycormus egertoni*. − Wenz: 177−178.

D i a g n o s i s. Deep, short and massive posterior maxillary blade with a deep notch at the posterior margin. Triangularly shaped supramaxilla as long as the posterior maxillary blade. Zig-zag suture between dentary and angular bones. Skull bones coarsely rugose with tuberculation on skull roofing bones. Surface of scales covered with irregular tubercles, arranged around the growth center or radiating from the center (*).

H o l o t y p e. BMNH P569 (head with anterior body, Egerton 1858, pl. X, figs 1−3).

A d d i t i o n a l   m a t e r i a l. BMNH P6912 (head with some scales, Fig. 14A).

O c c u r r e n c e. Oxfordian − Kimmeridgian, Upper Jurassic; Peterborough (Huntingdonshire), Speeton (Yorkshire), England.

Eurypoma grande (Woodward, 1889)
Figs 2A, 3, 4, 5, 7, 8, 9A, B, 10, 11, 14B

1889   *Eurycormus grandis* Woodward, 1889: 449.
1890   *Eurycormus grandis*. − Woodward: 292, pl. X, figs 1−8.
1895   *Eurycormus grandis*. − Woodward: 354.
1906   *Eurypoma grande*. − Heineke: 209, pl. 2, fig. 1, pl. 8, figs 8, 13, 14.
1968   *Eurycormus grandis*. − Wenz: 177−183, figs 76, 77, pl. 38, pl. 39, fig. D.
1999   *Eurycormus speciosus*. − Arratia: fig. 6A (after Wenz 1968, fig. 77B).
2001   *Eurypoma* aff. *grande*. − Dietl & Schweigert: fig. 108.
2002   *Eurypoma* aff. *grande*. − Dietl et al.: pl. 6.

D i a g n o s i s. Elongate, feebly arched maxilla with a slightly concave notch posteriorly. Massive, rectangularly-shaped supramaxilla about half the length of the maxillary blade. V-shaped suture between dentary and angular bones. Cranial bones smooth or covered sparsely with small tubercles. Surface of scales smooth and shiny.

H o l o t y p e. Woodwardian Museum, Cambridge (head, vertebrae and single bones, Woodward 1890, pl. X, fig. 1−8; Figs 2A, 9A).

A d d i t i o n a l   m a t e r i a l. SMNS 10402 (complete specimen, Heineke 1906, pl. 8, figs 8, 13, 14; Figs 3A, 5), SMNS 86901/

38 (complete specimen, Figs 3B, 8, 9B, 10, 11), Tü 17577 (Fig. 14B), specimen in the collection Nicolet (partial head, Wenz 1968, figs 76, 77, pl. 38, figs A−D, pl. 39, fig. D; Figs 4, 7A, B).

O c c u r r e n c e. Callovian − Kimmeridgian; Villers-sur-Mer (Calvados), France, Ely (Cambridgeshire), Weymouth (Dorsetshire), England, Nusplingen (Baden-Württemberg), southern Germany.

Conclusion

The comparison of *Eurycormus speciosus* Wagner, 1863 with *Eurypoma grande* (Woodward, 1889) demonstrates clearly that we are dealing with two distinct Late Jurassic actinopterygian genera as Heineke (1906) stated. The two genera are distinct in body and head morphology, in bones of the cheek region and the jaws, in the vertebral column and in the composition of the caudal skeleton. It is easy to separate the two genera after the composition and shape of bones of the cheek region.

Eurycormus speciosus belongs to the *Siemensichthys*-group within Teleosteomorpha, whereas *Eurypoma egertoni* and *E. grande* are members of the Amiiformes within Halecomorphi, probably most closely related to the Caturidae.

References

Agassiz, L. 1833−43. Recherches sur les Poissons fossiles. Tome II, part 2: 336 pp., Petitpierre, Neuchâtel et Soleure.

Arratia, G. 1997. Basal teleosts and teleostean phylogeny. – Palaeo Ichthyologica **7**: 5–168.

– 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. – *In* Arratia, G. & Schultze, H.-P. (eds). Mesozoic Fishes 2 – Systematics and Fossil Record: 265–334, Verlag Dr. Friedrich Pfeil, München.

– 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the 'pholidophoriforms'. – Paläontologische Zeitschrift **74**: 113–143.

– 2001. The sister-group of Teleostei: Consensus and Disagreement. – Journal of Vertebrate Paleontology **21** (4): 767–773.

Arratia, G. & Herzog, A. (submitted). A new halecomorph fish from the Middle Triassic of Switzerland and its systematic implications. – Journal of Vertebrate Paleontology.

Arratia, G. & Lambers, P. 1996. The caudal skeleton of pachycormiforms: Parallel evolution? – *In* Arratia, G. & Viohl, G. (eds). Mesozoic Fishes – Systematics and Paleoecology: 191–218, Verlag Dr. Friedrich Pfeil, München.

Arratia, G., Schultze, H.–P. & Casciotta, J. 2001. Vertebral Column and Associated Elements in Dipnoans and Comparison with other Fishes: Development and Homology. – Journal of Morphology **250**: 101–172.

Bartsch, P. 1988. Funktionelle Morphologie und Evolution des Axialskelettes und der Caudalis ursprünglicher Knochenfische. – Palaeontographica A **204**: 117–226.

Berg, L. S. & Obruchev, D. V. 1964. Order Amiida. – *In* Obruchev, D. V. (ed.). Osnovy paleontologii. Vol. XI. Agnatha, Pisces: 380–386, Nauka, Moscow. (In Russian)

Brito, P. 1992. L'endocrâne et la moulage endocrânienne de *Vinctifer comptoni* (Actinopterygii – Aspidorhynchiformes) du Cretacé inferieur du Brésil. – Annales de Paléontologie (Vertébrés – Invertébrés) **78**: 129–157.

– 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoque: ostéologie et relations phylogénétiques, données environnementales et biogéographique. – Geodiversitas **19** (4): 681–772.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. – XIV + 698 pp., W. H. Freeman a. Co., New York.

Cope, E. D. 1872. Observations on the systematic relations of fishes. – Proceedings of the American Association for the Advancement of Science **20**: 317–343.

Dietl, G. & Schweigert, D. 2001. Im Reich der Meerengel. – Der Nusplinger Plattenkalk und seine Fossilien. – 144 pp.; Dr. Friedrich Pfeil Verlag, München.

Dietl, G., Schweigert, G. & Hugger, R. 2002. Der Nusplinger Plattenkalk (Weisser Jura) – Grabungskampagne 2001. – Jahreshefte der Gesellschaft für Naturkunde in Württemberg **158**: 49–69.

Egerton, P. de M. G. 1858. *Macropoma egertoni*. – Memoirs of the Geological Survey of the United Kingdom. Figures and Descriptions illustrative of British Organic Remains. Decade **IX**: 3pp.

Frickhinger, K. A. 1991. Fossilien Atlas Fische. – 1088 pp., Mergus, Melle, Germany.

– 1994. Die Fossilien von Solnhofen. Dokumentation der aus den Plattenkalken bekannten Tiere und Pflanzen. – 333 pp., Goldschneck-Verlag, Korb, Germany.

Grande, L. & Bemis, W. E. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. – Memoir **4**, Supplement to Journal of Vertebrate Paleontology **18** (1): X + 690 pp.

Hay, O. P. 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. – Carnegie Institution of Washington, Publication **390**: 1–2003.

Heineke, E. 1906. Die Ganoiden und Teleostier des lithographischen Schiefers von Nusplingen. – Geologische und Palaeontologische Abhandlungen, Neue Folge **8**: 159–214.

Huxley, T. H. 1866. Illustrations of the structure of the crossopterygian ganoids. – Memoirs of the Geological Survey of the United Kingdom. Figures and Descriptions illustrative of British Organic Remains. Decade **XII**: 44 pp.

Lambers, P. 1992. On the Ichthyofauna of the Solnhofen Lithographic Limestone (Upper Jurassic, Germany). – Proefschrift, Wiskunde en Natuurwetenschappen, Rijksuniversiteit Groningen: X + 336 pp.

Leckenby, J. 1859. Note on the Speeton clay of Yorkshire. – The Geologist **2**: 9–11.

Lehman, J.–P. 1966. Actinopterygii. – *In* Piveteau, J. (ed.). Traité de Paléontologie, Tome IV, **3** Actinoptérygiens, Crossoptérygiens, Dipneustes: 1–244, Masson et Cie., Paris.

Lund, R. 1967. An analysis of the propulsive mechanisms of fishes, with reference to some fossil actinopterygians. – Annals of Carnegie Museum **39**: 195–218.

Nybelin, O. 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. – Arkiv för Zoologi, Serie 2, **15**: 485–516.

– 1966. On certain Triassic and Liassic representatives of the family Pholidophoridae s.str. – Bulletin of the British Museum of Natural History, Geology **11**: 351–432.

Olsen, P. E. 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena group of Madagascar, with comments on the relationships of the holostean fishes. – Journal of Vertebrate Paleontology **4** (3): 481–499.

Olsen, P. E. & McCune, A. R. 1991. Morphology of the *Semionotus elegans* species group from the Early Jurassic part of the Newark Supergroup of eastern North America with comments on the family Semionotidae (Neopterygii). – Journal of Vertebrate Paleontology **11** (3): 269–292.

Owen, R. 1860. Palaeontology; or, a Systematic Summary of Extinct Animals and their Geological Remains. – 420 pp., A. and C. Black, Edinburgh.

Patterson, C. 1973. Interrelationships of holosteans. – *In* Greenwood, P. H., Miles, R. S. & Patterson, C. (eds). Interrelationships of Fishes. – Zoological Journal of the Linnean Society **53**, Supplement No. 1: 233–305.

– 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. – Philosophical Transactions of the Royal Society, London **269B**: 275–579.

– 1977. Contribution of paleontology to teleostean phylogeny. *In* Hecht, M. K., Goody, P. C. & Hecht, B. M. (eds). Major Patterns in Vertebrate Evolution. – NATO Advanced Study Institute Series, A Life Sciences **14**: 579–643.

Pinna, M. de 1996. Teleostean monophyly. – *In* Stiassny, M. L. J., Parenti, L. R. & Johnson, G. D. (eds). Interrelationships of Fishes: 147–162, Academic Press, San Diego.

Romer, A. S. 1945. Vertebrate Paleontology. 2nd edition. IX + 687 pp., The University of Chicago Press, Chicago, Illinois.

– 1966. Vertebrate Paleontology. 3nd edition. IX + 468 pp., The University of Chicago Press, Chicago and London.

Schultze, H.-P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen **126**: 232–314.

– 1996. The scales of Mesozoic actinopterygians. – *In* Arratia, G. & Viohl, G. (eds). Mesozoic Fishes – Systematics and Paleoecology: 83–93. Verlag Dr. Friedrich Pfeil, München.

Thies, D. 1989. *Lepidotes gloriae*, sp. nov. (Actinopterygii: Semionotiformes) from the Late Jurassic of Cuba. – Journal of Vertebrate Paleontology **9** (1): 18–40.

— 1991. The osteology of the bony fish *Tetragonolepis semicincta* Bronn 1830 (Actinopterygii, †Semionotiformes) from the Early Jurassic (Lower Toarcian) of Germany. — Geologica et Palaeontologica **25**: 251−297.

Thies, D. & Zapp, M. 1997. Ein *Lepidotes* (Actinopterygii, † Semionotiformes) aus den Plattenkalken (Oberjura, oberes Kimmeridgium) bei Schamhaupten (Süddeutschland). — Archaeopteryx **15**: 11−26.

Vetter, B. 1881. Die Fische aus dem lithographischen Schiefer im Dresdener Museum. — Königlich mineralogisch-geologisches und prähistorisches Museum Dresden, Mittheilungen **4**: VIII + 118 pp.

Wagner, J. A. 1863. Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns. Zweite Abtheilung. — Abhandlungen der mathematisch-naturwissenschaftlichen Abtheilung der königlichen bayerischen Akademie der Wissenschaften **9** (3): 611−748.

Wenz, S. 1968. Compléments à l'étude des poissons actinoptérygiens du Jurassique français. 276 pp., Cahiers de Paléontologie, Centre national de la Recherche Scientifique, Paris.

Woodward, A. S. 1889. Preliminary notes on some new and little-known British Jurassic fishes. — Geological Magazine, New Series, decade III **6**: 448−455.

— 1890. On a head of *Eurycormus* from the Kimmeridge Clay of Ely. — Geological Magazine, New Series, decade III **7**: 289−292.

— 1894. On a Second British Species of the Jurassic Fish *Eurycormus*. — Geological Magazine, New Series, decade IV **1**: 214−216.

— 1895. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part III. Containing the actinopterygian Teleostomi of the Orders Chondrostei (concluded), Protospondyli, Aetheospondyli, and Isospondyli (in part): XLIII + 544 pp. British Museum (Natural History), London.

Zittel, A. 1887−1890. Handbuch der Palaeontologie. I. Abtheilung. Palaeozoologie. III. Band, Vertebrata (Pisces, Amphibia, Reptilia, Aves). XII + 900 pp., R. Oldenbourg, München und Leipzig.

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