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Outstanding features of a new Late Jurassic pachycormiform fish from the Kimmeridgian of Brunn, Germany and comments on current understanding of pachycormiforms

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Abstract

A new pachycormiform, †*Orthocormus roeperi* n. sp., is described from the upper Kimmeridgian of Brunn, Bavaria, Germany. The well-preserved specimen provides new information on features of the head, vertebral column and fins. The rostrodermethmoid bears a pair of straight, large paramedial teeth; the premaxilla is sutured with the rostrodermethmoid; there are small conical teeth on the upper jaw, a large tooth on the posterior part of the premaxilla, and both large and small teeth on the maxilla; the lower jaw carries large teeth anteriorly and smaller ones posteriorly; a dermosphenotic with a short anterior process forms only a portion of the complete dorsal margin of the orbit. The vertebral column is formed by a persistent notochord without chordacentra, but with well-developed, protruding arcocentra in the caudal region. The scythe-like pectoral fins possess rays with long bases, scarcely segmented, and finely branched distally; the characteristic Y-like branching pattern described for other pachycormiforms is apparently missing. The dorsal and anal fins present characteristic lateral expansions at their bases, possibly to facilitate water flow. The unpaired fins have numerous long and slender basal fulcra preceding the principal rays. There are more than 100 caudal rays, including 32 epaxial and 24 hypaxial principal rays. Large lateral processes are present on the lateral wall of the well-developed arch of the parhypural and on the hypural plate, suggesting the presence of a powerful hypochordal longitudinalis muscle. A protruding structure, named here the scaly caudal apparatus, covers laterally part of the hypural plate and the bases of the principal rays. This peculiar structure has not been previously reported in any pachycormiform. The scaly caudal apparatus, formed by large modified scales with a precise arrangement, is interpreted as an adaptation to fast swimming comparable to that of modern tunas and may occur in other pachycormiforms such as †*Sauropsis* as well.

The results of a survey of other pachycormiforms as well as of the literature suggest that incomplete knowledge of pachycormiform morphology can be explained by incomplete and poor preservation of many specimens. There has been a tendency to generalize the presence of structures based on few taxa. The fish described here is the best-preserved pachycormiform from Bavaria, Germany, as well as from the Upper Jurassic worldwide. It presents previously unknown characters and also characters that contradict some previous assumptions. Incomplete knowledge of most characters confounds the placement of Pachycormiformes within Neopterygii.

Introduction

Pachycormiformes comprise a group of actinopterygian fishes that are restricted to the Mesozoic, extending from the Early Jurassic (e. g., †*Pachycormus*, †*Sauropsis* and †*Hypsocormus* from the *Posidonia* shales, Toarcian, of Holzmaden, southern Germany; HAUFF & HAUFF 1981) to the Late Cretaceous (e. g., †*Protosphyraena* and †*Bonnerichthys* from the Niobrara Chalk of Western Kansas; STEWART 1988, FRIEDMAN et al. 2010). The group contains middle sized (e. g., †*Pachycormus* from 42 cm to 130 cm in HAUFF & HAUFF 1981; †*Orthocormus teyleri* from the Kimmeridgian of Cerin, France, 54 cm in LAMBERS 1992; and †*Orthocormus* *cornutus* from the Tithonian of Langenaltheim, Bavaria, Germany, 111 cm in WEITZEL 1930) to large fishes of many meters length (e. g., †*Bonnerichthys* of about 5 m in FRIEDMAN et al. 2010; †*Leedsichthys* from 8 to 16.5 m in LISTON this volume). In a broad sense they are interpreted as strong swimmers due to their hydrodynamic, elongate shapes, the possession of powerful fins, especially the pectoral fins with a scythe-like shape and the caudal fin with powerful rays oriented almost vertically, and an elongate, flexible body with a flexible vertebral column and lacking large and heavy scales (e. g., VIOHL 1996).

The general morphology, including the head, and the caudal skeleton, especially that of the largest pachycormiforms, is incompletely known. Part of this may be due to collecting methods and also the mounting of specimens in some collections. Many of the largest specimens deposited in museum collections are damaged (Fig. 1A, B). Many have been recovered in pieces and combined into one specimen afterwards, with possible loss of certain elements or misplacement of a few. It was a common practice previously to mount and fix the large pachycormiforms on museum walls (Fig. 1C), a practice that has made their study very difficult. Thus, it was a real surprise to discover, some years ago, in the Bürgermeister-Müller-Museum in Solnhofen, Bavaria, an extremely well-preserved specimen of †*Orthocormus* showing an unusual three-dimensional preservation of the caudal fin, a structure that resembles the caudal fin of certain phylogenetically unrelated forms, but also that of fast swimmers such as the Recent tunas.

The discovery of this beautifully preserved specimen of †*Orthocormus* initiated an extensive survey of other well-preserved pachycormiforms and other fishes identified as possible fast swimmers, such as some of the Jurassic and Cretaceous aspidorhynchiforms and ichthyodectiforms.

The goal of this contribution is to provide a taxonomic assignment for the new specimen and to describe some relevant morphological characters shown by the new species, especially the caudal region of fishes typically interpreted as fast swimmers (e. g., †*Orthocormus*) and discuss the potential functional and/or phylogenetic importance of some of these findings.

Locality

The new fish described herein (specimen BSPG 1993 XVIII-VFKO B16), was recovered near Brunn, a small town 25 km NW of Regensburg, Bavaria (see Fig. 2). The Brunn quarry is at the "Kohlstatt locality", between the villages of Brunn and Wischenhofen. Paleobiogeographically, the locality is part of the Plattenkalk deposits of the small Pfraundorf-Heitzenhofen-Basin (MÜLLER 1961, RÖPER et al. 1996). The age of the limestones of Brunn is interpreted as late Kimmeridgian, being in the lower part of the *beckeri* Zone, *subeumela* Subzone (RÖPER et al. 1996, RÖPER & ROTHGAENGER 1997, SCHWEIGERT 2007). The locality is stratigraphically older than the Fossillagerstätten of the Solnhofen area in Bavaria, older than Nusplingen in Baden-Württemberg but younger than Wattendorf in Northern Franconia, Bavaria (SCHWEIGERT 2007).

The deposits of Brunn are interpreted as shallow marine sediments with tidal influence and deposited close to the coast (RÖPER et al. 1996). Brunn has yielded numerous fossils, especially well-preserved fishes, many of which have been interpreted as belonging to the same genera found in the Tithonian of the Solnhofen Limestone (RÖPER et al. 1996), but they have not been investigated to confirm such assignments.

Material and methods

Institutional abbreviations

Specimens cited here are deposited in the following institutions: **AMNH,** American Museum of Natural History, New York, U.S.A.; **BSPG,** Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Bavaria, Germany; **BMM-S,** Bürgermeister-Müller-Museum, Solnhofen, Bavaria, Germany; **CM,** Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **KUVP,** Division of Vertebrate Paleontology, Natural History Museum, University of Kansas, Lawrence, Kansas, U.S.A.; **JM-E,** Jura-Museum Eichstätt (SOS indicates that the fish was recovered in the Solnhofen Limestone), Eichstätt, Germany; **MB,** Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; **SenkM**, Senckenberg-Museum, Frankfurt am Main, Germany; **SMS**, Department of Paleozoology, Naturhistoriska Riksmuseet, Stockholm, Sweden.

List of studied pachycormiforms

Although we studied many specimens deposited in different museums, only the most informative specimens are listed below.

†*Asthenocormus titanius* (WAGNER, 1863) – JM-E SOS 542, Upper Jurassic, Tithonian, Langenaltheim, Bavaria, Germany; JM-E SOS 3556, Upper Jurassic, Tithonian, Blumenberg near Eichstätt, Bavaria, Germany.

†*Euthynotus* sp. – SMS P 1037, Lower Jurassic, Toarcian, Holzmaden, Baden-Württemberg, Germany.

†*Hypsocormus insignis* WAGNER, 1860 – BSPG AS VI 4a, b (holotype), Upper Jurassic, Solnhofen Limestone, Bavaria, Germany (precise locality not known); SMS P 5698, Upper Jurassic, Tithonian, Solnhofen Limestone, Bavaria, Germany; SenkM 1863, Upper Jurassic, Solnhofen Limestone, Bavaria, Germany (precise locality not known).

†*Orthocormus cornutus* WEITZEL, 1930 – SenkM 1863 (holotype), Upper Jurassic, Tithonian, Langenaltheim, Bavaria, Germany; JM-E SOS 3460, Upper Jurassic, Solnhofen Limestone, Blumenberg, Bavaria, Germany; JM-E SOS 3571a-b, Upper Jurassic, Solnhofen Limestone, Birkhof, Bavaria, Germany.

†*Orthocormus roeperi* n. sp. – BSPG 1993 XVIII-VFKO B16, as permanent loan in BMM-S (published under catalogue number BSP 1933 I 22 [cast AMNH FF 19639] by FRIEDMAN et al. 2010, Suppl. materialonline: 36), Upper Jurassic, upper Kimmeridgian, Brunn, Bavaria, Germany.

†*Pachycormus* sp. – SMS P 6151 and SMS P 6152, Lower Jurassic, Toarcian, Holzmaden, Baden-Württemberg, Germany; MB 2349, Lower Jurassic, Toarcian, Bad Boll, Baden-Württemberg, Germany.

†*Protosphyraena tenuis* LOOMIS, 1900 – KUVP 49419, Upper Cretaceous, Niobrara Formation, Trego County, Kansas, U.S.A.

†*Protosphyraena* cf. *P. perniciosa* – KUVP 67877, Upper Cretaceous, Niobrara Formation, Trego County, Kansas, U.S.A.

†*Protosphyraena* sp. – KUVP 49418 and KUVP 55000, Upper Cretaceous, Niobrara Formation, Trego County, Kansas, U.S.A.

†*Pseudoasthenocormus retrodorsalis* (EASTMAN, 1914) – BSPG 1956 I 361, Upper Jurassic, Tithonian, Quarry "An der Schrandel", Langenaltheim, Bavaria, Germany.

†*Sauropsis depressus* EASTMAN, 1914 – CM 4766A/B (holotype), Upper Jurassic, Solnhofen Limestone, Bavaria, Germany (precise locality not known).

†*Sauropsis longimanus* (AGASSIZ, 1833) – BSPG AS VII 1089 (holotype), Upper Jurassic, Solnhofen Limestone, Bavaria, Germany (precise locality not known).

†*Sauropsis* sp. – JM-E SOS 3336a-b, Upper Jurassic, Solnhofen Limestone, Blumenberg, Bavaria, Germany; JM-E 2181a-b, Upper Jurassic, Solnhofen Limestone, Tithonian, Schernfeld, Bavaria, Germany; MB 2348, precise locality unknown, but possibly Lower Jurassic, Lias, Toarcian, Bad Boll, Baden-Württemberg, Germany. (Specimens preliminarily identified as †*Sauropsis* from different localities and ages are in need of revision.)

For a list of material used in comparative studies see ARRATIA (2008); however, specimens mentioned in the text and figures are identified by their catalogue numbers within the text. Detailed information on Upper Jurassic localities in Bavaria can be found in SCHWEIGERT (2007).

Due to their large size, the pachycormiform described here and others used in comparisons were studied using high magnification hand lens and by photographs of each complete specimen and of its particular details. The drawings were done based on the photographs and using stereomicroscopes depending on the size of the specimen, but each feature was checked under lens and stereomicroscope (when possible) to avoid misinterpretations of the photographs.

Terminology

Names of different elements of a vertebra and of different kinds of vertebral centra (e. g., chordacentra, arcocentra) follow SCHULTZE & ARRATIA (1986, 1989) and ARRATIA et al. (2001).

The displacement of the dorsal arcocentra often observed in the most posterior caudal region makes their identification difficult because the 1 : 1 alignment may be discontinued, especially in fishes with a pronounced inclination toward the body axis of the neural and haemal spines. Consequently, dorsal arcocentra and their corresponding ventral arcocentra of the preural vertebrae were identified from the beginning of the caudal region up to the end of the preural region. These identifications were used to label the endoskeletal structures such as the neural and haemal spines and corresponding arcocentra.

The names of specialized structures in pachycormiforms, e. g., rostrodermethmoid and temporal boss (= frontoparietal boss) follow LAMBERS (1992). When referring to the skull-roof bones we make a distinction between traditional terminology versus terminology based on homologization of bones (e. g., SCHULTZE 2008).

The identification of the different caudal fin rays, e. g., fulcra, procurrent (or precurrent) and principal rays, follows ARRATIA (2008).

Systematic paleontology

Actinopterygii COPE, 1887
†Pachycormiformes BERG, 1937
†Pachycormidae WOODWARD, 1895

†*Orthocormus* WEITZEL, 1930

Type species: †*O. cornutus* WEITZEL, 1930 (Fig. 3 A, B).

†*Orthocormus roeperi* n. sp.

(Figs. 4 A, B, 5A, 6–10, 12)

1996 *Orthocormus* – RÖPER et al.: 18, 84, fig. 114.
1996 *Orthocormus cornutus* WEITZEL – RÖPER et al.: fig. 85 (= colour pl. 10).
2010 †*Orthocormus cornutus* VETTER [sic] – FRIEDMAN et al., Suppl. materialonline: 36 [the given number BSP 1993 I 22 is incorrect, the locality is not "near Kallmünz" but Brunn, southern Bavaria].

Diagnosis (based on a unique combination of features)**:** Elongate, fusiform fish with a very small temporal boss not projecting forward onto the parietal region; dermosphenotic with short anterior process not forming the whole dorsal orbital margin; premaxilla with small teeth irregularly placed and one large tooth in its posterior half; maxilla with scattered and moderately large teeth; dentary with large procumbent conical teeth and lacking small lateral teeth; three large teeth anteriorly; unpaired fins with numerous rays; dorsal fin with more than 50 rays; anal fin with more than 67 rays; caudal fin with more than 100 rays [*]; unpaired fins with numerous and slender basal fulcra preceding principal rays; lateral expansion of distal region of proximal radials and of proximal region of dorsal rays forming a bilateral surface framing the base of dorsal fin [*]; lateral expansion of the proximal region of anal rays forming a bilateral surface framing the base of anal fin [*]; caudal fin with well-developed scaly caudal apparatus; intestine with spiral valve. (Characters identified with an asterisk [*] are unique.)

Holotype: BSPG 1993 XVIII-VFKO B16, a very well preserved, complete specimen (Fig. 4A) that is under permanent loan at the exhibit of the Bürgermeister-Müller-Museum, Solnhofen, Bavaria.

Horizon and locality: Upper Jurassic, upper Kimmeridgian, lower part of *beckeri* Zone, *subeumela* Subzone; Brunn, Bavaria, Germany.

Table 1.
Body proportions expressed as percent of standard length (SL) and counts of fin rays in species of †*Orthocormus*. The counts of fins rays include all elements forming the fin, e. g., basal fulcra and rays. Data for †*O. cornutus* and †*O. teyleri* are from LAMBERS (1992).

	†*O. cornutus*	†*O. teyleri*	†*O. roeperi* n. sp.
Total length			±50 cm
Standard length (SL)	±106 cm	±54 cm	±43 cm
Head length/SL	±21 %	±25 %	±23 %
Prepelvic length/SL	±36 %	±41 %	±39 %
Predorsal length/SL	±57 %	±55 %	±57 %
Preanal length/SL	±64 %	±67 %	±66 %
Pectoral rays	±22	±37	>30
Pelvic rays	±22	±28	>15
Dorsal rays	±40	±48	>52
Anal rays	±60	±50	>67
Caudal rays	±80	±93	>100
Dorsal caudal lobe	±40	±50	>54
Ventral caudal lobe	±40	43	±50

Etymology: The species name honors Dr. Martin RÖPER, who collected the specimen in 1992 during an extensive program of excavation and study of the Plattenkalk of Brunn that he began in 1990, and for willingness to develop paleontological studies at the Bürgermeister-Müller-Museum in Solnhofen, Bavaria.

Comments: The new species is without question a member of the genus †*Orthocormus* according to the diagnostic characters provided by LAMBERS (1992). Currently, †*Orthocormus* contains two species, †*O. cornutus* WEITZEL, 1930, from the Tithonian of Langenaltheim, Bavaria and †*O. teyleri* LAMBERS, 1988, from the Kimmeridgian of Cerin, France. The new species appears closer to †*O. teyleri* than to

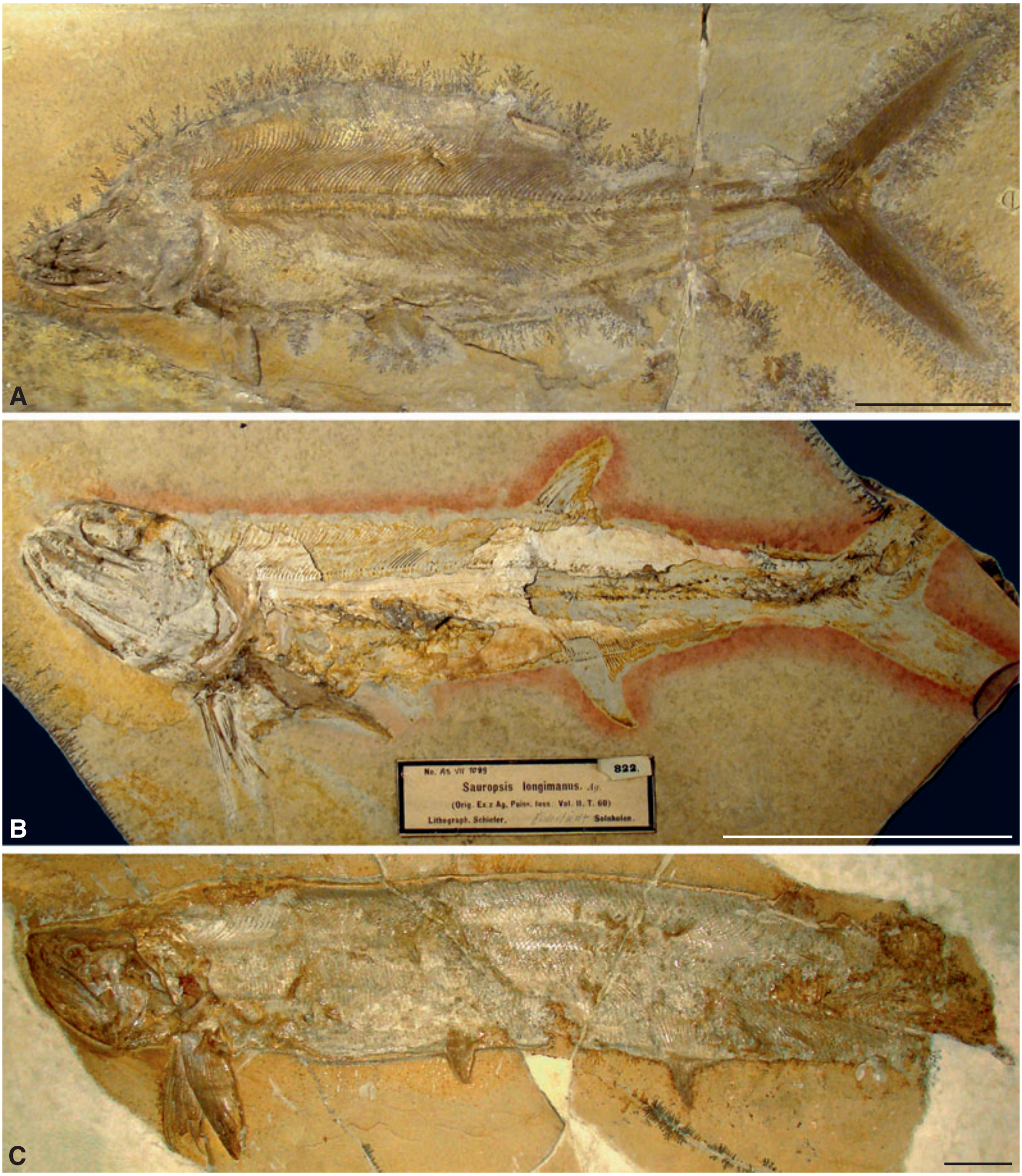


Fig. 1.
Examples of typical preservation and mounting of important specimens of pachycormiforms. **A,** †*Hypsocormus insignis* WAGNER, 1860, Solnhofen Limestones, Bavaria (holotype BSPG AS VI 4a). **B,** †*Sauropsis longimanus* (AGASSIZ, 1833–1843) Solnhofen Limestones, Bavaria (holotype BSPG AS VII 1089). **C,** †*Pseudoasthenocormus retrodorsalis* (EASTMAN, 1914) Tithonian, Langenaltheim, Bavaria (BSPG 1956 I 361). The specimen is mounted on the wall on the stairs to the third floor in the Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Scales = 10 cm.

†*O. cornutus* on the basis of just a few characters. For instance, both species share the presence of three large, almost vertical teeth on the anterior part of the dentary, close to the mandibular symphysis; a dentary

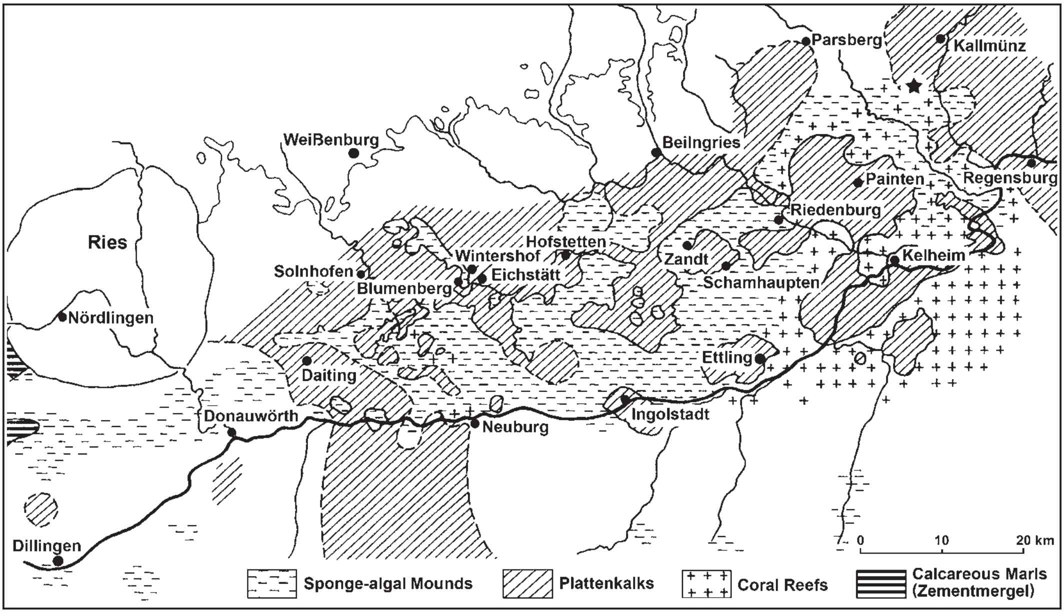


Fig. 2.
Distribution of Plattenkalk basins and reef areas in the southern Franconian Alb during Kimmeridgian–Tithonian times (slightly modified from VIOHL 1996). The new pachycormid species was recovered in Brunn, about 25 km northwest of Regensburg, Bavaria (indicated with a star).

with large procumbent conical teeth, and the presence of basal fulcra in the unpaired fins. Both species present a large number of rays in the unpaired fins, but those of the new species are even more numerous (see Table 1). †*Orthocormus teyleri* possesses small teeth lateral to the large series of dentary teeth; the small teeth are lacking in the new species. The close similarity to †*O. teyleri* is also in agreement with the argument of RÖPER et al. (1996: 98) that the sedimentology, flora and fauna of Brunn are closely comparable with those of Cerin ("Brunn – ein kleines Cerin im Oberpfälzer Jura"). In addition, both localities are of the same age, late Kimmeridgian. The new species resembles †*O. cornutus* in the presence of only one large tooth in the posterior half of the premaxilla in contrast to three teeth present in †*O. teyleri.*

A major difference between the three species is the small temporal boss (compare Fig. 3B with 4B) in †*Orthocormus roeperi* n. sp., that is restricted to the temporal region and does not project anteriorly onto the parietal region (of traditional terminology), which gives the new species a smooth dorsal profile between the anterior tip of the snout and the dorsal fin. To the best of our knowledge, a scaly caudal apparatus, as described below, and the lateral projections at the bases of the dorsal and anal fins are reported for the first time for pachycormiforms.

Anatomical description

The description presented below is restricted to the diagnostic features and certain structures that are interpreted as important for the swimming capabilities of the fish.

The fish has an elongate, fusiform body and a narrow caudal peduncle (Fig. 4A). Its maximum body depth is about 18 % of the standard length. The head lacks the large, protruding elevation at the back of the skull (compare Fig. 3B and 4B) that is present in the other two species of †*Orthocormus*. The temporal or frontoparietal boss may be well developed (e. g., †*Orthocormus cornutus*), poorly developed (e. g., †*Protosphyraena*) or absent (e. g., †*Sauropsis*) in pachycormiforms. A well-developed temporal boss is not present in all species of †*Orthocormus*; the new species possesses a very small boss restricted to the temporal region. The dorsal profile of the head and of the predorsal region in the new species is continuously smooth due to the small size of the temporal boss.

The head is moderately large; its length is about 23 % of SL. The orbit (Figs. 4B, 5A) is small, oval and in a dorsal position on the lateral aspect of the head. The pectoral fins (Fig. 4A,B) are placed close to the ventral margin of the body, but are incompletely preserved. The pelvic fins (Fig. 4A) are almost triangular; the posterior most rays are considerably shorter than the anterior rays. The dorsal fin is placed posterior to the mid-body length, while the anal fin is more posteriorly positioned with its anterior margin caudal to the level of the dorsal fin base. The pelvic fins are closer to the pectoral fins than to the anal fin, and placed anterior to the origin of the dorsal fin (Table 1).

The fish has a long body cavity (Fig. 4A) that extends to the beginning of the posteriorly placed anal fin. A portion of the intestine is preserved closer to the place where the anus was likely located. The intestine shows the presence of a spiral cololite (Fig. 6; see below).

Rostrodermethmoid, jaws and teeth. A well-developed, heavily ossified rostrodermethmoid (Figs. 4B, 5A) forms the antero-dorsal border of the mouth. The rostrodermethmoid has a median projection extending anteriorly beyond the level of the symphysis of the lower jaw. It bears a pair of large paramedial teeth that are almost straight, in contrast to the condition present in †*Orthocormus cornutus* (Fig. 3B) and †*O. teyleri*, in both of which the teeth are directed obliquely forward. The premaxilla is tightly sutured to the rostrodermethmoid medially, so it is unlikely that this element was movable.

The premaxilla (Figs. 4B, 5A) bears a series of small conical teeth irregularly placed on the oral margin and one large conical tooth in its posterior half.

The anterior part of the maxilla is partially destroyed, whereas its posterior half is preserved but broken at its distal tip. The bone (Figs. 4B, 5A) is markedly curved, with a concave oral margin in its distal half. There is one row of scattered, conical teeth of variable size that are smaller than the dentary teeth, but not as small as the premaxillary teeth situated in the anterior half of the bone, or the small conical teeth positioned between the large maxillary teeth (Fig. 5A); the maxillary teeth are similar to those found in †*Hypsocormus leedsi* (see WOODWARD 1895: pl. XI, figs. 3, 5). Teeth of the oral margin reach the posterior tip of the maxilla, like those of †*Hypsocormus insignis* (Fig. 5B). A supramaxilla is not observed and there is no indication of its presence at the dorsal margin of the maxilla or caudally as described for some pachycormiforms (LAMBERS 1992: figs. 1, 7, 17).

The powerful lower jaw (Figs. 4B, 5A) has a similar shape to that of †*Orthocormus cornutus* (Fig. 3B) and †*O. teyleri*, with the dentary as its main component. There are large teeth anteriorly, close to the symphysis, that are almost straight and vertical, not obliquely directed anteriorly as in †*O. cornutus* (see Fig. 3B) and *O. teyleri* (see LAMBERS 1992: 192, fig. 2b). The remaining dentary teeth are slightly smaller than the anterior ones and slightly procumbent as in †*O. teyleri*. Small lateral teeth are lacking. It is unclear whether some of the mandibular teeth are coronoid teeth or not, like those present in the lower jaw of †*Hypsocormus leedsi* (see WOODWARD (1895: pl. XI, fig. 5a), †*Hypsocormus insignis* (Fig. 5B,C), and †*Australopachycormus hurleyi* (KEAR 2007: fig. 1J).

Dermosphenotic. The dermosphenotic (Figs. 4B, 5A) is positioned at the postero-dorsal corner of the orbit. The bone has a moderately acute and short anterior process, a broad and slightly rectangular posterior region, and a slightly rounded latero-ventral process. The shape of the bone resembles Pattern 1f (= T-shaped) of POPLIN (2004). The bone sutures with the parietal bone (= frontal of traditional terminology) antero-medially and with the dermopterotic posteriorly. It is unclear how the bone relates to the dorsal most posterior infraorbital. The trajectory of sensory canals is not observed and we suggest that the canals were sunk deeply in the bone.

Vertebral column. The vertebral column (Figs. 4A, 6, 7A,B) is represented by a persistent and unconstricted notochord that apparently does not form chordacentra or ossified centra in any region of the body. The shape and size of the notochord are indicated by the well-ossified neural arches dorsally and haemal arches and ribs ventrally. The notochord has a more or less consistent diameter in the abdominal region but decreases gradually in diameter in the caudal region. Small scales and lateral line scales are preserved above the notochord.

It is difficult to count the total number of vertebral elements (as represented by the arcocentra), mainly due to the displacement of some of the paired neural arches and spines in the abdominal region and because of damage to a small section of the abdominal region (Figs. 4A, 7A). The total number of dorsal arcocentra is at least 124. Of these, 76 bear paired neural spines; the number could be slightly higher considering the possibility that the fish has more neural elements in the region just behind the cranium, which is covered by the supracleithrum, and in the damaged section (interpreted as formed by 10 arcocentral elements).

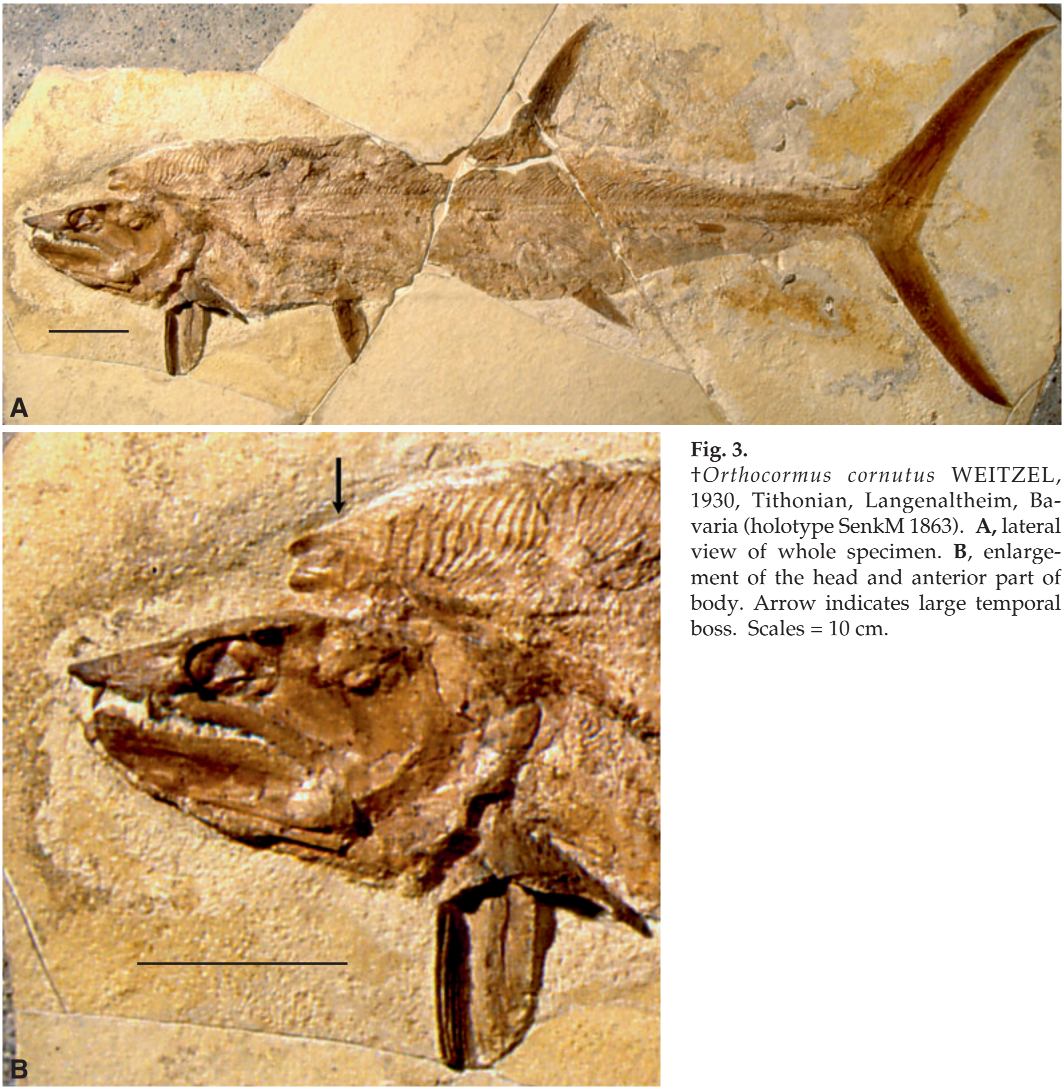


Fig. 3.
†*Orthocormus cornutus* WEITZEL, 1930, Tithonian, Langenaltheim, Bavaria (holotype SenkM 1863). **A,** lateral view of whole specimen. **B**, enlargement of the head and anterior part of body. Arrow indicates large temporal boss. Scales = 10 cm.

However, we believe that the given total number (76) of paired spine-bearing dorsal arcocentra is a close approximation. The abdominal region is considerably longer than the caudal region. The abdominal dorsal arcocentra have short neural arches that bear a short anterior process probably dorsal to the neural cord. Each dorsal arcocentrum continues in a short neural spine that is gently inclined toward the horizontal. A further forty-three or forty-four arcocentra have unpaired neural spines. The identification of the first caudal element is unclear because it is almost impossible to determine, with certainty, which is the first element bearing a haemal arch (Fig. 4A). However, it is possible to establish that the fish has at least 42 or 43 unquestionable caudal arcocentra whose haemal arches and unpaired spines extend from anterior to the first anal pterygiophore posteriorly.

Fig. 4.
†*Orthocormus roeperi* n. sp. in lateral view, upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). **A,** †*Orthocormus roeperi* n. sp. in lateral view. **B,** Head and pectoral fin in lateral view. Scales = 10 cm.

▷


A
B

No ossified, independent parapophyses are observed. There is no indication whether the parapophyses were cartilaginous or not because there is no remnant of cartilage or spongy bone (Figs. 6, 7A,B) at the articular heads of the ribs. One possibility could be that the parapophyses are fused with the ribs, forming their rod-like, well-developed proximal region. The ribs, long and slightly curved in the anterior part of the body cavity, become progressively inclined toward the horizontal, and seeming to transition smoothly into the haemal spines so that it is difficult to separate the last ribs (except by their inclination) from the first haemal arch and its spine. The position and length of ribs versus haemal arches and spines may explain some published restorations where both the ribs and the haemal arches plus their spines, are shown as a continuous series (e. g., *Hypsocormus insignis* in WOODWARD 1895: fig. 40).

The caudal arcocentra (Figs. 4A, 6, 8A,B, 9) have their neural and haemal spines curved posteriorly and strongly inclined toward the horizontal. The inclination is more pronounced in the preural region (see below). No interhaemal elements have been observed in the anterior caudal region.

Intermuscular bones. Long, narrow, sigmoidal supraneurals (Fig. 7A,B) extend between the distal tips of the neural spines, filling almost all the gaps between the neural spines. It is unclear whether the first neural spines just behind the occiput and supraneurals are separate elements because only one continuous element is observed, not two. Supraneurals and neural spines positioned posterior to the supracleithrum are two distinct elements. Most supraneurals are missing their distal tips; therefore, they are expected to be much longer than the preserved portions shown by the specimen. The last few supraneurals are short and extend in between the first dorsal pterygiophores (Fig. 7B).

Epineural processes or epineural bones are absent as are epipleural bones.

Dorsal fin. The length of the base of the dorsal fin (Figs. 4, 6) is about half that of the anal fin. The dorsal fin rays are supported by a series of pterygiophores that are about a third the depth of the longest rays. The dorsal fin is triangular, with the first principal rays being the longest and the last ones being the shortest. The last four rays are about the same size.

The dorsal fin contains 13 or 14 slender basal fulcra, the first four being the shortest, 3 procurrent rays with few, long segments, and 33 principal rays. (At least three more basal fulcra are expected to be present; the elements associated with the first pterygiophore are damaged.) Each slender basal fulcrum ends in an expanded tip, which is triangular, similar to those found at the leading margins of the other unpaired fins. A few elongate fringing fulcra, with lancet-shaped or triangular distal tips like those of the caudal basal fulcra (see below), are observed between the distal tips of the basal fulcra and the procurrent rays, and on the first principal ray. The first principal rays have scarce segmentation and few branches whereas the posterior rays are finely branched.

Forty-one narrow, elongate pterygiophores are preserved. The anterior-most ones support a variable number of basal fulcra and rays, but the posterior ones, except the last one, support only one ray each. The bases of the basal fulcra and of the rays and the distal portions of the proximal radials expand laterally, producing a characteristic lateral extension (Figs. 4A, 6, 7B) of the base of the dorsal fin.

Apparently, a small scute precedes the dorsal basal fulcra.

Anal fin. The anal fin (Fig. 6) is similar to the dorsal fin, but its posterior part, formed by short rays, is considerably longer than that of the dorsal fin. The general shape of the fin can be described as falcate, with the first few principal rays being the longest and the last ones being the shortest: a fin resembling this description is present in ichthyodectiforms.

The anal fin has preserved 12 slender basal fulcra and about 55 principal rays. (One or two more basal fulcra are expected anteriorly, but this region is not easy to observe.) Each slender basal fulcrum ends in an expanded tip, triangular or lancet-like, similar to those found at the leading margins of all other unpaired fins. It is unclear if a few fringing fulcra with distal tips similar to those of the basal fulcra are present between the distal tips of the basal fulcra, but at least one elongate fringing fulcrum is placed between the last basal fulcrum and the first ray. The anterior, long and slender principal rays have scarce segmentation and few branches, whereas the posterior, short 35 rays have about the same size as each other, are not segmented, but are finely branched.

Thirty-nine narrow, elongate rod-like pterygiophores are preserved. The first one is the longest. As in the dorsal fin, the distal portion of the pterygiophores expands laterally, and the bases of the basal fulcra and of the rays also expand laterally producing a protruding lateral extension of the base of the anal fin (Figs. 4A, 6).

It is unclear whether a very small scute precedes the anal basal fulcra.

Caudal fin and endoskeleton. The large caudal fin (Figs. 4A, 8A,B) is deeply forked, with two slightly asymmetric-shaped lobes that form an angle of about 120° between them. The distal tip of the dorsal lobe is not preserved. The rays form an angle of about 60° degrees with respect to the horizontal; the proximal tips of most dorsal and ventral principal rays almost meet lateral to the hypural plate.

As far as can be observed, there are about 10 or 11 preural centra whose haemal spines support the hypaxial basal fulcra and rays. The preural vertebrae are formed by well-developed dorsal and ventral arcocentra and their heavily ossified neural and haemal spines, which are strongly inclined toward the horizontal. The unpaired neural spines of preural vertebrae 8 to 1 and the haemal spines of preural vertebrae 10 to 1 are laterally expanded, protruding in such a way that they produce a characteristic expansion dorsolateral and ventrolateral to the notochord. The posterior part of the caudal endoskeleton (Figs. 8A,B, 9) is partially covered by large, characteristically shaped, modified scales forming the scaly caudal apparatus, numerous small scales that are incompletely preserved, and the bases of the middle principal rays.

The neural spine (Figs. 8A,B, 9) of preural vertebra 5, which is slightly displaced, shows clearly that this element is not an uroneural, but an expanded spine that protrudes laterally, producing a well-developed and thick lateral margin. The neural spine of preural vertebra 4 is slightly displaced below the neural spine of preural vertebra 3. All these spines are broken proximally so that their arcocentra are missing. Neural spines of preural vertebrae 2 and 1 are partially hidden by the ventral arcocentra and the hypural plate. All these spines (Fig. 9) produce the characteristic lateral thick margin and give the misleading impression that they are uroneurals. This specimen has no uroneurals.

The proximal regions of four massive, rod-like epurals (Figs. 8A,B, 9) are observed. It is expected that more epurals were present.

The ventral arcocentra are massive (Figs. 8A,B, 9) and together with the spines protrude laterally. Arcocentra of preural centra 3 and 2 are considerably developed, especially that of preural centrum 2, which exhibits laterally a well-developed process or hypurapophysis-like for insertion of muscles. The arcocentrum of preural centrum 1 is comparatively narrower than those of the preceding vertebrae but exhibits a well-developed hypurapophysis. There is a well-ossified hypural plate, with lateral projections in the form of crests that are interpreted here as additional lateral processes for insertion of the hypochordal longitudinalis. The bases of the principal rays cover laterally the dorsal hypural region so that it is impossible to provide more information on the hypurals.

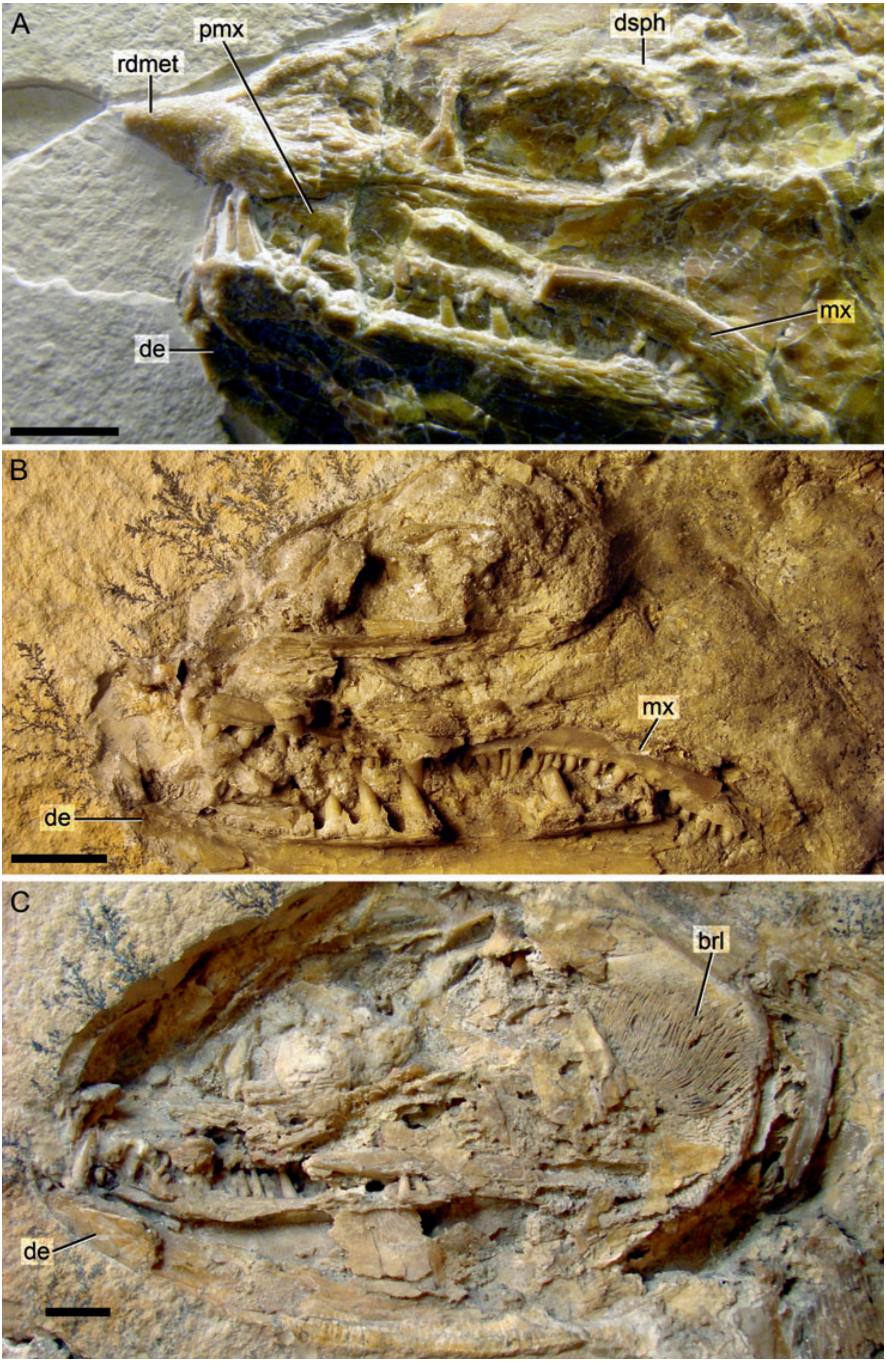
The caudal fin presents a large number of rays. Most rays are heavily ossified and slender except for some rays as explained below. We count 97 rays, but the number is still larger because we are missing in the count a few of the smallest basal fulcra placed at the anterior edges of the fin.

The dorsal lobe is formed by at least 54 rays. Its anterior-most edge (Fig. 9) is formed by five small, fusiform-like, paired epaxial basal fulcra, which are followed by 14 slender basal fulcra that increase in length caudally. Each slender epaxial fulcrum ends distally in a characteristically expanded tip (see Fig. 10), a pattern also observed in the hypaxial basal fulcra. No fringing fulcra are present.

Three slender segmented rays (Fig. 10) follow the series of epaxial basal fulcra. The first ray has only one segment but its distal region is obscured by other rays. The second segmented ray has a long base followed by a long segment distally. The third ray has the longest base of the three, and has two segments, the distal one the longest. It is unclear whether the first two rays or all three rays are epaxial rudimentary rays (by comparison with †*Sauropsis* sp., with two epaxial rudimentary rays; see Fig. 11A,B and below) because the extent of their bases cannot be observed owing to the prominent scaly caudal apparatus covering them.

According to our counts there are 32 principal rays in the dorsal lobe, including two of the middle principals with expanded bases. Since a diastema is not present, it is difficult to establish the limits between hypurals 2 and 3 (see SCHULTZE & ARRATIA this volume). The first principal ray is comparatively short and much shorter than the second. It has a long base and is as thin and slender as the basal fulcra.

The second principal ray has a base that is slightly shorter than that of the first principal ray. It has only one simple segment followed by the bifurcation of the ray in its second segment (Fig. 10). The following 10–12 principal rays are irregularly segmented and branched and show a characteristic entwined pattern that makes it difficult to follow the trajectory of a single ray. The segmentation diminishes in the following rays, but they become extensively and finely branched distally. The rays are oriented obliquely until the 28th principal ray, covering the hypural plate. Rays 28–30 have very short bases, and the angle of the branched portion is almost parallel to the axis of the body, but the short bases are markedly bent, forming the last part of the bases of the dorsal principal rays (Fig. 9). Rays 31 and 32 are short and with a fine and extensive branching, and their bases are broad and crenulated (Fig. 9). The anterior portion of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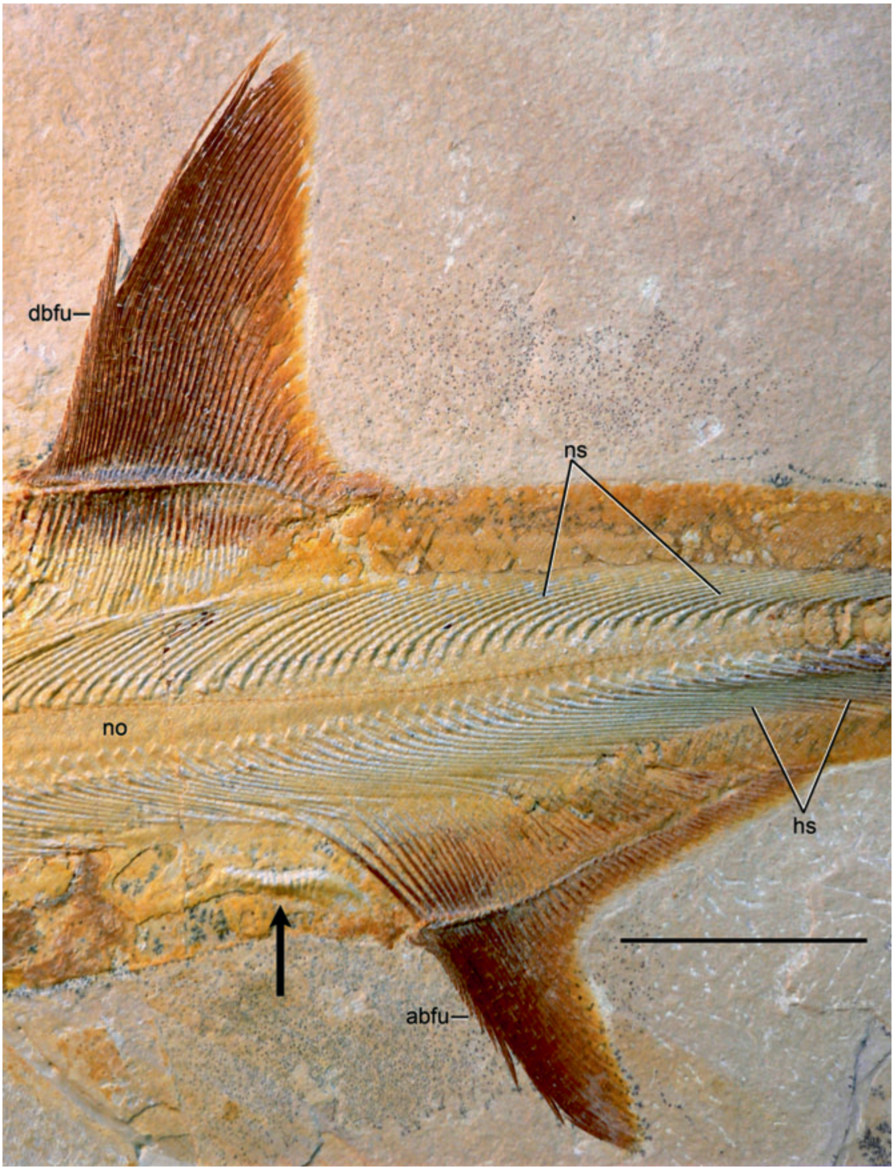

Fig. 6.
Mid-posterior region of the trunk of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria illustrating the dorsal and anal fins and their relationships with supporting elements (holotype BSPG 1993 XVIII-VFKO B16). Note the preserved section of the intestine showing the spiral cololite (arrow) and the lateral expansions at the base of the dorsal and anal fins. Abbreviations: **abfu**, basal fulcra of anal fin; **dbfu**, dorsal basal fulcra; **hs**, haemal spines; **no**, notochord; **ns**, neural spines. Scale = 5 cm.

◁ **Fig. 5.**
Details of the head in pachycormiforms. **A,** detail of rostrodermethmoid, dermosphenotic, and dentition in †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). **B, C,** detail of jaws and dentition in †*Hypsocormus insignis*, Solnhofen Limestones, Bavaria (BSPG ASVI 4a and b, respectively). Figure C reversed (for comparison). Abbreviations: **brl**, branchial lamellae; **de**, dentary; **dsph**, dermosphenotic; **mx**, maxilla; **pmx**, premaxilla; **rdmet**, rostrodermethmoid. Scales = 1 cm.

the bases is broken but presumably they were longer than preserved, covering laterally the bases of other principal rays.

The epaxial basal fulcra, the so-called rudimentary rays, and at least the first three principal rays form the dorsal leading margin of the caudal fin. Since the distal tip of the dorsal lobe is broken, we are unable to give a more precise description, but a similar pattern was described by ARRATIA (2008: 78) for †*Sauropsis* sp.

The ventral lobe has about 50 rays including 24 long and slender principal rays and more than 20 slender basal fulcra. There are additional fringing fulcra irregularly placed between the distal tips of the basal fulcra. The anterior-most basal fulcra are damaged and not included in this count. The hyapaxial basal fulcra (Figs. 8A,B, 9, 12) increase in length progressively, and each fulcrum ends in a typical, slightly expanded tip giving the impression that the margin is formed by a series of fringing fulcra. The few accessory fringing fulcra also have similar distal tips to those of the basal fulcra, sometimes making their identification difficult. Small scales are preserved on the proximal portions of the basal fulcra.

The caudal hypaxial principal rays, like those of the dorsal lobe, have long bases and scarce segmentation. The rays forming the middle region of the tail branch profusely (Fig. 8A,B). All hypaxial basal fulcra and principal rays have their proximal regions (Figs. 8A,B, 9, 12) oriented in a similar way, almost forming a straight line, and covering a considerable portion of the haemal spines of the preural vertebrae.

The ventral leading margin of the caudal fin is formed mainly by the long epaxial basal fulcra, and partly by the first principal rays. Unlike the dorsal margin, accessory fringing fulcra are irregularly present.

A long and strong dorsal scute, incompletely preserved, lies in front of the series of epaxial basal fulcra. The anterior tip of the scute (Figs. 4A, 8A,B, 9) reaches the level of preural vertebra 17 or 18 (counting from preural vertebra 1 anteriorly). The surface of the scute has longitudinal grooves. The scute expands slightly anteriorly and posteriorly. A similar long scute was illustrated for †*Sauropsis* sp. by ARRATIA (2008: fig. 18) and observed in other specimens of †*Sauropsis* (e. g., JM-E 2181b). The dorsal scute has a position similar to a large bony structure described for †*Orthocormus teyleri* as formed anteriorly by "a bundle of five slender, flattened rays that passes into a stout joint from which again a bundle of about five flattened rays projects towards the caudal lobe" (LAMBERS 1992: 203). The enlarged dorsal scute with its longitudinal grooves is considered to have a stiffening function and facilitate the flow of water. A small, oval ventral scute (Fig. 12) is placed anterior to the hypaxial basal fulcra.

Scaly caudal apparatus. The caudal fin of †*Orthocormus roeperi* n. sp. has an unusual structure that is positioned lateral to the long bases of the epaxial basal fulcra and epaxial principal rays. The unusual structure was called "Seitenruder" by ROEPER et al. (1996: 84). This structure, named here as the **scaly caudal apparatus**, is formed by a series of highly modified scales that protruded laterally at the base of the caudal fin in a semicircle (Figs. 8A,B, 9) but are preserved folded dorsally against the base of the caudal fin. The scales seem to be covered by a layer of ganoine. The series is formed by at least 30 modified scales that change from approximately rectangular scales to large, upside-down L-shaped scales. The mid region of the scaly caudal apparatus is covered by small, thin scales of different shapes and sizes, some of which are illustrated in Figure 9. In the holotype, the left scaly caudal apparatus is almost complete, and the laterally protruding right scaly caudal apparatus is partially preserved (see Figs. 8A,B, 9). We interpret this paired structure as a specialization of a fast swimmer (see below).

Scales. The fish, as far as preservation permits, seems to have been covered by small, thin scales on trunk and on rays of the unpaired fins. The scales lack ganoine (in contrast to the scales of the scaly apparatus) as already described by SCHULTZE (1966: fig. 36a,b) for †*Sauropsis latus* and †*Pachycormus curtus*.

Comparisons and discussion

Analysis of some unusual morphological features

Temporal (= frontoparietal) boss. The presence of a temporal (= frontoparietal) boss is unique to pachycormiforms among actinopterygians; however, the boss is missing in some pachycormiforms, and it seems to be formed by different skull roof bones in different pachycormiforms (see comments in LAMBERS 1992: 272–273). The boss is very small in †*O. roeperi*.

The temporal boss projects anteriorly over the parietal region of the skull in pachycormiforms such as †*Orthocormus cornutus* (see Fig. 3A), †*O. teyleri* (LAMBERS 1992: 189, pl. 1c), and †*'Hypsocormus' macrodon*. The presence of this boss is remarkable because it brings other major changes: the vertebral column and the epaxial series of bones, e. g., supraneurals and neural spines, acquire a more dorsal position in comparison with the placement of these bones in †*Orthocormus roeperi* n. sp. (compare Figs. 3A,B with 4A,B). The dorsal profile of the head and predorsal region of the body in the new species resembles the generalized condition among holosteans as well as stem group teleosts, and it can be interpreted here as the primitive condition among pachycormiforms.

The temporal boss, together with the pointed rostrodermethmoid in †*Orthocormus cornutus*, was interpreted as an efficient water cutting device (i. e., a cutwater) by WEITZEL (1930).

Dermosphenotic. According to our review of the literature, the dermosphenotic is known only from a few pachycormiforms (e. g., †*Pachycormus macropterus*: LEHMAN 1949, 1966; †*Euthynotus incognitus*: WENZ 1968; †*Bonnerichthys gladius* and †*Protosphyraena* spp.: FRIEDMAN et al. 2010) due to incomplete preservation of the cranium, especially of elements framing the orbit (see for instance Figs. 3B, 5B,C). LEHMAN (1949) interpreted the bone as a compound structure ("supraorbito-dermosphenotic"). The dermosphenotic of †*Pachycormus* and †*Euthynotus* has a long anterior process that frames the dorsal margin of the orbit. This type of dermosphenotic was classified as Pattern 1b (= extended more or less over the orbit) by POPLIN (2004) who based this identification on WENZ (1968).

†*Orthocormus* spp. (including the new species here reported) was erroneously identified as possessing a dermosphenotic forming the dorsal margin of the orbit (FRIEDMAN et al. 2010, Suppl. materialonline: p. 24, 41, character 32). †*Orthocormus roeperi* has a more or less T-shaped dermosphenotic, with a short anterior process (see Figs. 4B, 5A). The condition is still unknown in †*O. cornutus* (e. g., Fig. 3B) and †*O. teyleri* (LAMBERS 1988: fig. 2; 1992: 192, fig. 2a,b).

Vertebral centra. A vertebra, as defined by ARRATIA et al. (2001), includes the centrum plus neural arch with spine, parapophysis, and haemal arch with spine depending on the body region. All actinopterygians have at least ossified dorsal and ventral arches with spines, even those members with a persistent notochord and lack of vertebral centra as support of dorsal and ventral elements. To understand the evolution of the vertebral centra in actinopterygians requires an understanding of the differences between arcocentra (formed by extension of the ossification of the arches around the chordal sheaths present in all actinopterygians), chordacentra (mineralized middle chordal sheath variously present in different actinopterygians) and autocentra (ossified part of the vertebral centrum outside the chorda sheaths characteristic of teleosts) (see SCHULTZE & ARRATIA 1986, 1988, 1989; ARRATIA et al. 2001). †*Orthocormus roeperi* n. sp. as well as other pachycormiforms (Figs. 1A,B, 3A,B, 4A,B, 6–9) do not have ossified centra; all their vertebral centra, especially those of the caudal vertebrae, are represented by well-developed arcocentra that become even larger caudally and constitute the main vertebral element (Figs. 8A,B, 9; ARRATIA & LAMBERS 1996: figs. 1–3A, 4A,B, 7, 7, 8, 10B, 11, 13A). †*Orthocormus roeperi* as well as other species of †*Orthocormus* do not form chordacentra (Figs. 1A,B, 3B, 4A, 6–9). However, chordacentra have been reported and/or illustrated in †*Euthynotus* (e. g., LAMBERS 1992, ARRATIA & LAMBERS 1996: fig. 8), †*Sauropsis*, †*Pachycormus* and †*Saurostomus* (LAMBERS 1992: 285, table 1, character 15). Pachycormiforms do not have autocentra such as those present in †*Leptolepis*, †*Tharsis*, *Elops* (e. g., *E. hawaiensis*) and *Hiodon alosoide*s (see SCHULTZE & ARRATIA 1988: figs. 1, 10, 12, 17, 19–21). In contrast, the elements described for certain pachycormiforms by LAMBERS (1992: 277–278) are chordacentra. Chordacentra are mineralized elements formed in the middle sheath of the notochord as shown by histological studies of SCHULTZE & ARRATIA (1986, 1988: figs. 12, 19, 20; present volume) and ARRATIA & SCHULTZE (1992: figs. 10, 16, 17). Chordacentra, then, are not bone like the autocentra, and consequently they cannot be coded as ossified vertebrae as done by FRIEDMAN et al. (2010, Suppl. material online: 27, character 72), based on a misinterpretation of LAMBERS (1992: 277–278, his character 15) who clearly made the distinction that the elements present in some pachycormiforms are chordacentra.

Consequently, chordacentra and autocentra are different elements by origin; they cannot be interpreted as homologous since both are occurring together in fishes such as fossil (e. g., ARRATIA 1991: pl. 4A–C; 1997: fig. 89) and extant teleosts (e. g., SCHULTZE & ARRATIA 1988: figs. 9A–C, 10A–C, 18, 19A, 20A,B; ARRATIA & SCHULTZE 1992: figs. 10, 12, 16, 17, 26; see also ARRATIA 2010). Furthermore, †*Caturus* (e. g., GRANDE & BEMIS 1998; pers. obser.), †*Euthynotus* (LAMBERS 1992, ARRATIA & LAMBERS 1996), †*Orthocormus* (Fig. 3A,B; LAMBERS 1992), †*Pholidophorus bechei* (PATTERSON 1968; pers. observ.), and †*Watsonulus* (based on the available literature and specimens) do not have ossified centra as they are coded in FRIEDMAN et al. (2010, Suppl. materialonline: 27, character 72).

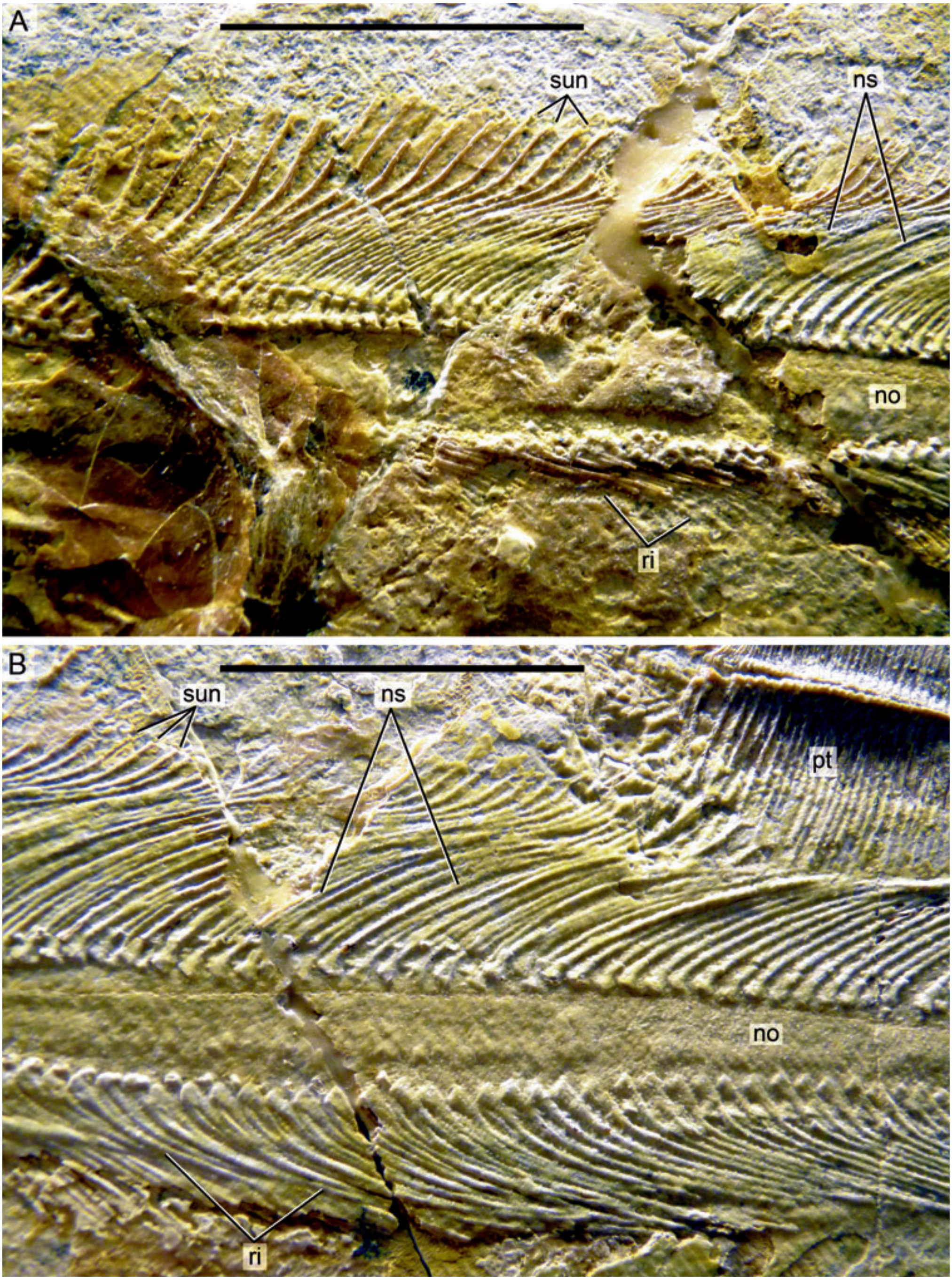

Fig. 7.
Different sections of the trunk of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). **A,** anterior section, just posterior to the head showing anterior abdominal vertebrae, ribs and supraneurals. **B,** middle-section of the abdominal vertebral column, in front of the pelvic fin and beginning of dorsal fin. Note the lateral expansion at the base of the dorsal fin. Abbreviations: **no**, notochord; **ns**, neural spines; **pt**, dorsal pterygiophores; **ri**, ribs; **sun,** supraneurals. Scales = 5 cm.

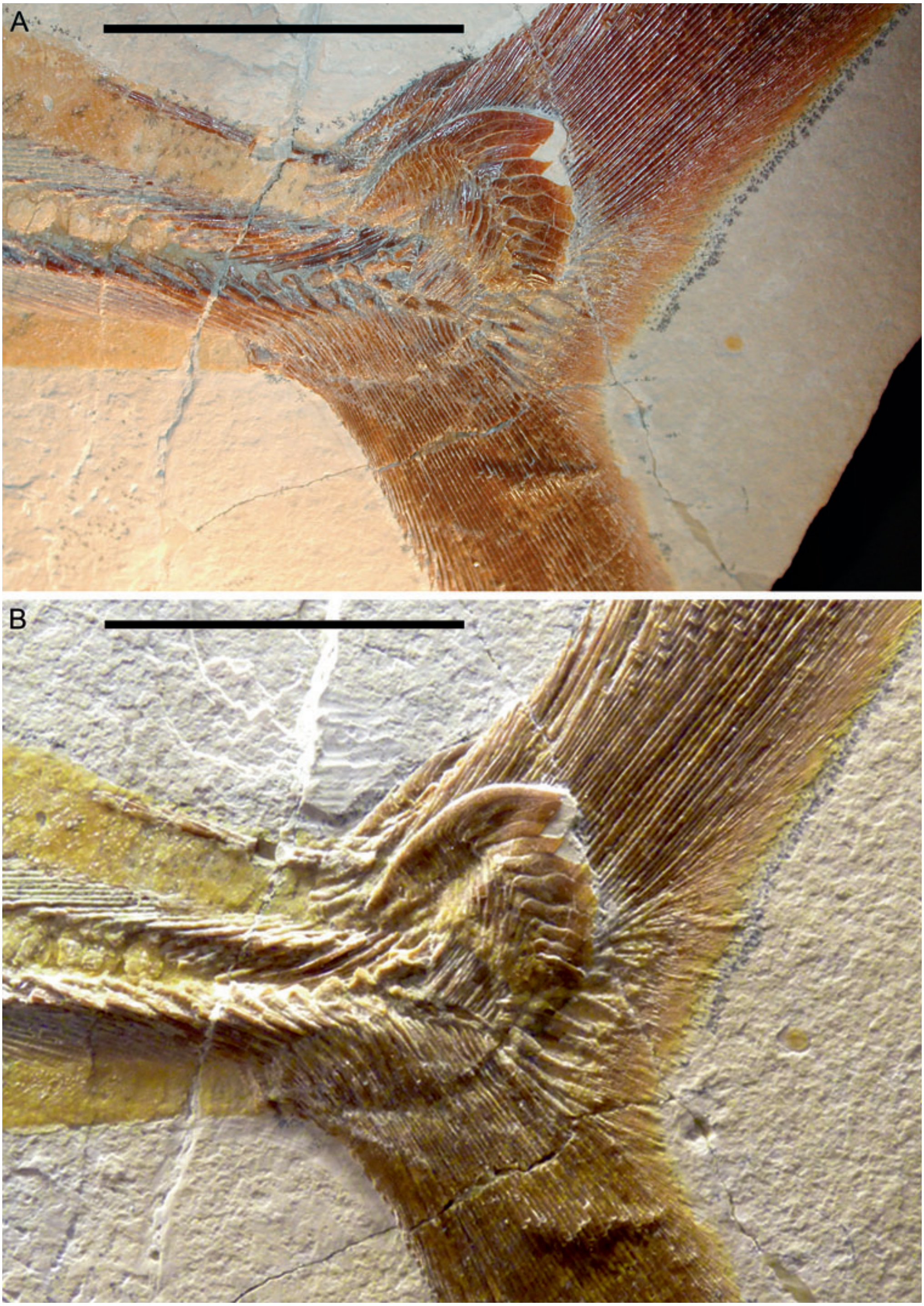

Fig. 8.
A, caudal endoskeleton and fin of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). **B,** the same view as in A but the light is directed in a different angle. Scales = 5 cm.

Shape of fins. Pachycormiforms have elongate, fusiform, hydrodynamic bodies, a body shape interpreted as an adaptation to fast swimming. The shapes of the fins are also interpreted as adaptations of a fast swimmer.

Shape of a fin and type of segmentation of its rays are two different characters and should be treated separately. For instance, all pachycormiforms share a derived scythe-like pectoral fin. However, some scythe-like pectoral fins have rays only segmented distally (e. g., †*Orthocormus*), whereas others lack segmentation (e. g., †*Protosphyraena*), or both segmentation and lack of segmentation may be variably present in †*Sauropsis* and †*Pachycormus*. By treating the two characters as one, all pachycormiforms appear to share a scythe-like pectoral fin with lepidotrichia segmented distally (see FRIEDMAN et al. 2010, Suppl. materialonline: 29, character 85, where all pachycormiforms are coded with the derived character state "1"). In fact, the presence and absence of segmentation of the rays are different states found among various pachycormiform taxa.

Pectoral fin. The pectoral fins of pachycormiforms are scythe-like (see for instance †*Pachycormus macropterus* in WENZ 1968: fig. 60; †*Orthocormus teyleri* in LAMBERS 1992: 192, fig. 2a,b; Figs. 1B,C, 4A,B, 13A herein); this feature is considered as uniquely derived for the group. The lateral, leading-edge portion of the pectoral fin is considerably longer than the medial, trailing edge portion, which has very short rays. As far as can be observed, †*O. roeperi* n. sp. has similar fin shapes to other pachycormiforms, including the pectoral fin.

Caudal fin. The shape of the caudal fin and the position of the dorsal and ventral rays differ in pachycormiforms. For instance, in the Early Jurassic †*Euthynotus*, unlike in other pachycormiforms, both lobes are inclined toward the horizontal and the epaxial principal rays are almost horizontally extending lateral to the hypural plate (see fig. 8A,B in ARRATIA & LAMBERS 1996). The epaxial principal rays in the Late Jurassic †*Sauropsis* sp. are also slightly inclined toward the horizontal (Fig. 11A). In the Early Jurassic †*Pachycormus* and in the Late Jurassic †*Orthocormus*, both lobes are more vertically oriented and the epaxial principal rays cover the hypural plate at a more oblique angle (see figs. 4A, 5A in ARRATIA & LAMBERS 1996) (Figs. 3A, 4A). We assume that the shape of the caudal fin and the orientation and position of the principal rays are adaptations of a fast swimmer. A similar fin shape and position of the principal rays is also observed in large Cretaceous ichthyodectiforms (e. g., †*Xiphactinus*, KUVP 103; †*Ichthyodectes ctenodon*, KUVP 68102). A somewhat similarly enlarged and shaped caudal fin is present in modern tunas, which are fast swimmers of the open sea. In contrast, †aspidorhynchids also have a deeply forked caudal fin, but the principal rays are weakly supported by endoskeletal elements (e. g., MAISEY 1991: 173; BRITO 1997: fig. 45, 1999: figs. 3, 4; ARRATIA 2008: fig. 21).

Fin rays. Most fin rays in pachycormiforms have scarce segmentation, a feature also present in †*Orthocormus roeperi* (Figs. 3B, 4A,B, 6, 10, 12). †*Euthynotus* seems to be an exception in having more segments in the principal caudal rays than other Jurassic pachycormiforms (see fig. 8A,B in ARRATIA & LAMBERS 1996). Lack of segmentation has been reported for certain pachycormiforms such as †*Asthenocormus titanius* (Fig. 14; LAMBERS 1992), †*Leedsichthys,* and †*Martillichthys* (LISTON 2007).

As discussed above, the pectoral rays of pachycormiforms may be scarcely segmented or not. However, an asymmetrical Y-type pattern of bifurcation of the pectoral rays seems to be unique for pachycormiforms. The condition is unclear in †*Orthocormus roeperi* because the lateral longer rays have long bases and they seem to be only segmented at their distal tips, without showing a special pattern.

Some of the principal caudal rays in †*O. roeperi* are entwined (Fig. 10), showing a pattern that apparently is unique. It could be the case that this pattern is also present in other pachycormiforms, but has not been reported due to the condition of preservation of the rays.

The unpaired fins in pachycormiforms have long and slender basal fulcra and some of them also have fringing fulcra (e. g., Figs. 6, 10–12; ARRATIA 2008: fig. 18A,B). †*Orthocormus roeperi* n. sp. shows that the distal tips of the slender basal fulcra and also those of the fringing fulcra are slightly expanded in a characteristic triangular or lancet shape, producing characteristic leading margins of the unpaired fins that can be interpreted as efficient water cutting devices. The anterior-most caudal epaxial and hypaxial basal fulcra in †*Euthynotus* are considerably shorter than those in †*Orthocormus*, †*Sauropsis* and †*Pachycormus*. In some specimens with the external surface of rays poorly preserved, it is impossible to distinguish between basal fulcra and principal rays (Fig. 14).

Currently, it is difficult to evaluate the literature concerning the fulcra and their types in pachycormiforms, because fulcra are not usually mentioned, or when they are mentioned it is unclear whether the author is referring to basal or fringing fulcra. The genera †*Orthocormus* and †*Asthenocormus* were diagnosed as lacking fulcra in all fins (LAMBERS 1992: 188, 207). However, as far as preservation permits, slender

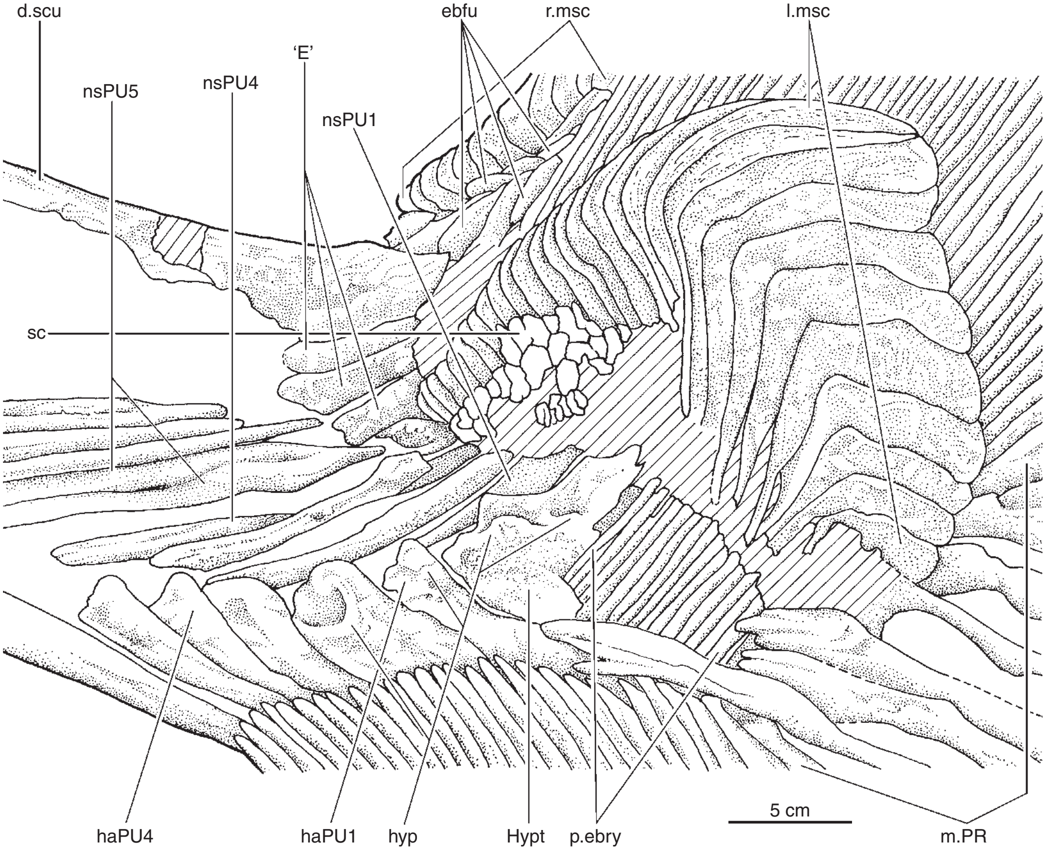

Fig. 9.
Details of the caudal endoskeleton and proximal regions of basal fulcra and rays of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). Abbreviations: **d.scu**, dorsal caudal scute; **'E'**, epurals; **ebfu**, epaxial basal fulcra; **haPU1–haPU4**, haemal arch of preural vertebrae 1 and 4; **hyp**, hypuraphophyses; **Hypt**, hypural plate; **l.msc**, scaly caudal apparatus of left side; **m.PR**, principal rays of the middle region of the tail; **nsPU1, PU4, PU5**, neural spines (the so-called 'uroneurals' in pachycormiforms) of preural vertebrae PU1, PU2, and PU5; **p.ebry**, proximal region of epaxial basal fulcra and epaxial rays; **r.msc**, scaly caudal apparatus of right side; **sc**, scales.

and deep basal fulcra are present in the unpaired fins of †*Orthocormus*. The presence or absence of basal fulcra should be revised in †*Asthenocormus* (Fig. 14) when better-preserved specimens will be available for study. Basal and fringing fulcra probably could be used as taxonomic tools characterizing certain taxa when these structures are clearly defined (ARRATIA 2008, 2009), but again, all depends on the degree of preservation of the different fulcra and rays.

As far as the available information permits, the presence of the especially slender and deep basal fulcra present in the unpaired fins seems to be a pachycormiform character among actinopterygians.

Leading margins of caudal fin. In "true" teleosts (e.g., †*Leptolepis coryphaenoides* plus more advanced teleosts in ARRATIA's 1999, 2000, 2008 phylogenetic hypothesis), the dorsal and ventral leading margins of the caudal fin are formed by the first and last principal ray (segmented but not branched), respectively. However, in fishes such as 'pholidophoriforms' and aspidorhynchiforms, the leading margins are not formed uniquely by the first and last principal ray, but by the addition of other principal rays (see ARRATIA 2008: figs. 10, 11, 18, 19, 21). Pachycormiforms seem to be unique in that many long basal fulcra and more than one marginal principal ray form the epaxial and hypaxial leading margins of the caudal fin (e.g., Figs. 10, 11, 12, 14; ARRATIA 2008) unlike the condition found in "true" teleosts.

Scaly caudal apparatus. The series of highly modified scales or scaly caudal apparatus (Figs. 8A,B, 9) present in †*Orthocormus roeperi* n. sp. is apparently a structure described for the first time for a pachycormiform.We have checked the caudal region of numerous pachycormiforms, but unfortunately, the region is commonly poorly preserved, so that we are uncertain if this feature has been preserved in †*O. roeperi* because of its excellent preservation, or if it is a specialization of certain species or a feature that may be a synapomorphy of the group. According to our survey, *Pachycormus* sp. (SMS P.6152) from the Lower Jurassic of Holzmaden, Germany, presents dorsal remains of something that might be a scaly caudal apparatus, and the structure appears at the same place as in †*O. roeperi*. EASTMAN (1914) described and figured the holotype of †*Sauropsis depressus*, which poorly preserves some large modified scales on the caudal ragion (see Fig. 13B). Unlike the condition found in *O. roeperi*, the scaly apparatus in †*S. depressus* apparently is larger, covering also the last preural vertebrae (compare Figs. 8A,B, 9 with Fig. 13B). Remnants of the scaly apparatus, which apparently is larger than in †*O. roeperi*, were observed in other specimens of †*Sauropsis* (e. g., MB 2348). Although the preservation is not the best, these are the structures most closely resembling the scaly apparatus of †*O. roeperi* that we could find.

A comparison with other fast-swimming fishes shows that recent tunas possess modified, elongate acicular scales of different sizes (Fig. 15; MONOD 1968: figs. 770–772) that are positioned lateral to the caudal skeleton and possibly reduce drag as the scaly caudal apparatus possibly did.

We suggest the scaly caudal apparatus as another feature channeling the flow of water and the swimming capabilities of the fish.

Endoskeletal caudal structures. The morphology of the posterior region of the vertebral column and of the caudal fin of †*Orthocormus roeperi* n. sp. also points to that of a fast swimmer.

Arcocentra and hypurapophyses. In pachycormiforms, the arcocentra of the last caudal vertebrae (e. g., Figs. 8A,B, 9; ARRATIA & LAMBERS 1996: figs. 1, 2, 3A, 4A,B, 5A,B, 8A,B, 9) – especially the ventral arcocentra–are greatly laterally expanded as are their corresponding neural spines. These structures are placed one next to each other with almost no space between them, similar to the situation observed in the last caudal vertebrae of modern tunas (Fig. 16; MONOD 1968: e. g., figs. 752, 755, 762, 766, 773, 775, 776, 779; POTTHOFF 1975: fig. 13), in which heavily ossified centra have laterally expanded neural and haemal spines.

The new fossil fish has a well-developed, expanded arcocentrum of the parhypural, and the arcocentrum possesses a prominent lateral process or hypurapophysis (Figs. 8A,B, 9). The parhypural is followed by a hypural plate formed by an unknown number of hypurals and having additional lateral projections or hypurapophyses-like at its base to increase the area of insertion of the hypochordal longitudinalis muscle. Based on the considerable development of these hypurapophyis-like projections, the hypochordal longitudinalis must have been a large and powerful muscle. Recent tunas have a powerful, platform-like lateral hypurapophysis (Fig. 16; MONOD 1968: e. g., figs. 752, 756–758, 775, 777–779) for the insertion of the hypochordal longitudinalis muscle.

The lateral expansion of the arcocentra and of the neural spines (uroneural-like; see below) of the preural vertebrae are interpreted as specializations to increase the stiffness of the tail and consequently to facilitate fast movements.

Neural spines versus uroneurals. †*Orthocormus roeperi* has a series of powerfully developed and laterally expanded median neural spines bearing parts of their arcocentra at their proximal regions. These modified and enlarged neural spines belong to preural vertebrae (Figs. 8A,B, 9), with none of these elements corresponding to an ural vertebra. However, these elements have been named “uroneural of a peculiar type” by PATTERSON (1973), and “ural neural arches modified as uroneural” by PATTERSON (1977). In contrast, LAMBERS (1992) and ARRATIA & LAMBERS (1996) named them “uroneural-like” elements.

Uroneurals are **modified paired ural neural arches** (PATTERSON 1968). In other words, they are not preural elements, but ural elements. As far as can be determined from ontogenetic series – and also, as the caudal skeleton of adult teleosts shows – the true uroneurals only arise as modified neural arches of the ural region. It is unclear if all elements named uroneurals in Figure 17 belong to the preural region because, as PATTERSON (1973: 275) recognized, “it is difficult to decide which of them are ural neural arches, but if it is assumed that the normal one-to-one relationship [with hypurals] exists, there are seven pairs of ural neural arches (as in pholidophorids and leptolepids: Patterson, 1968), all of which have grown forward well beyond their point of origin, like the uroneurals in teleosts. I therefore interpret these structures as uroneurals of a peculiar type which differ from those of other teleostean relatives in grading into unmodified pre-ural neural arches anteriorly, with no real boundary between the two types of structure.”

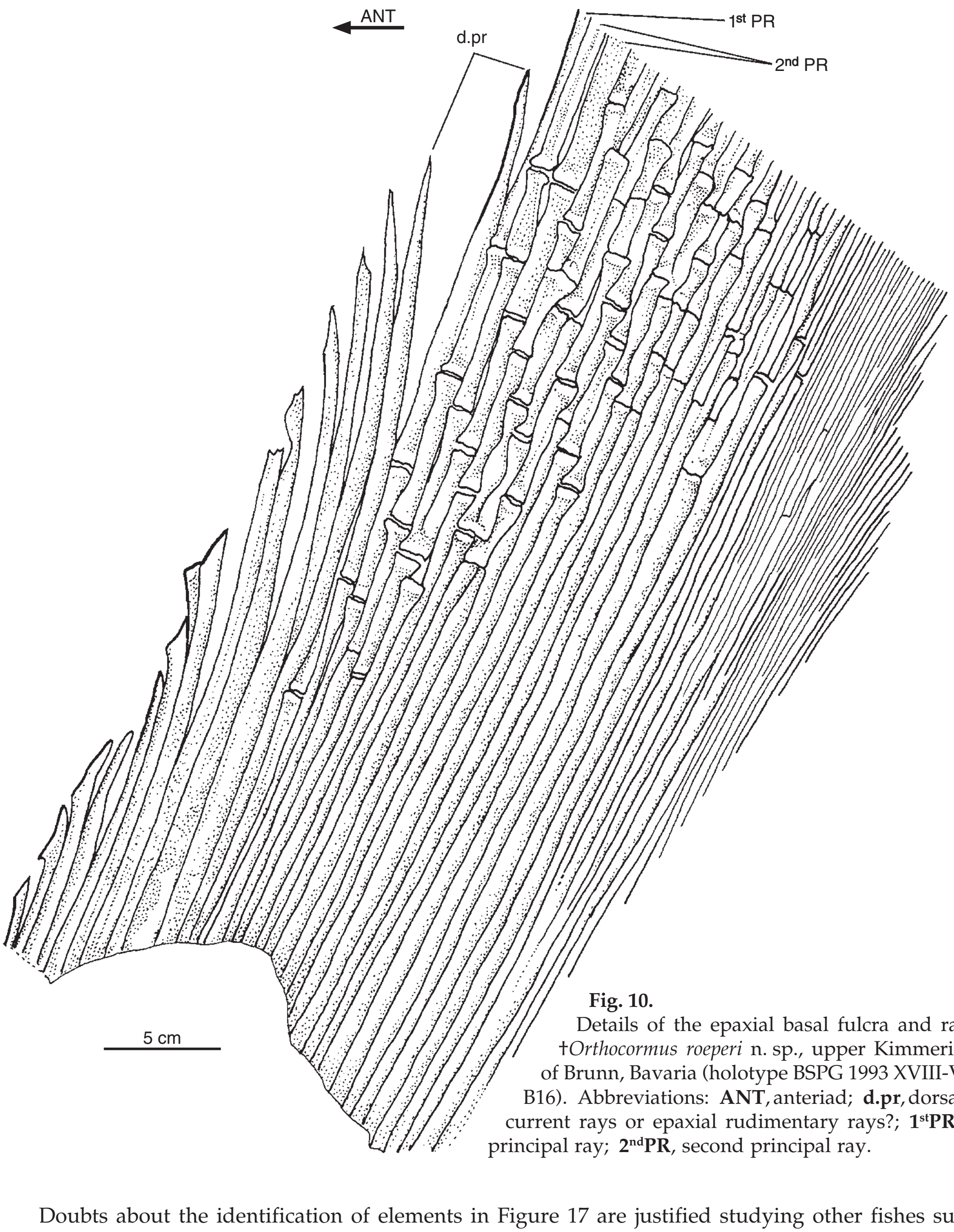

Fig. 10.
Details of the epaxial basal fulcra and rays of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). Abbreviations: **ANT**, anteriad; **d.pr**, dorsal procurrent rays or epaxial rudimentary rays?; **1stPR**, first principal ray; **2ndPR**, second principal ray.

Doubts about the identification of elements in Figure 17 are justified studying other fishes such as †*Orthocormus roeperi*, where all the uroneural-like elements are unquestionably neural spines of the preural region, not the ural region. Other pachycormiforms studied by ARRATIA & LAMBERS (1996) also show this pattern. The "normal" one-to-one relationship described by PATTERSON (1968), and used to support his arguments in 1973, is unjustified because a one-to-one relationship is lacking in pholidophorids and basal teleosts including leptolepids with more than seven hypurals (ARRATIA 1991: figs. 5, 7, 9, 11, 13; 1999: figs. 13, 15; ARRATIA & SCHULTZE 2007: fig. 12B). Such one-to-one relationship (together with other teleostean synapomorphies) is also missing in aspidorhynchiforms, interpreted as basal teleosts by PATTERSON (1977: fig. 19), with less than seven uroneurals and even fewer hypurals (e.g., †*Vinctifer*,

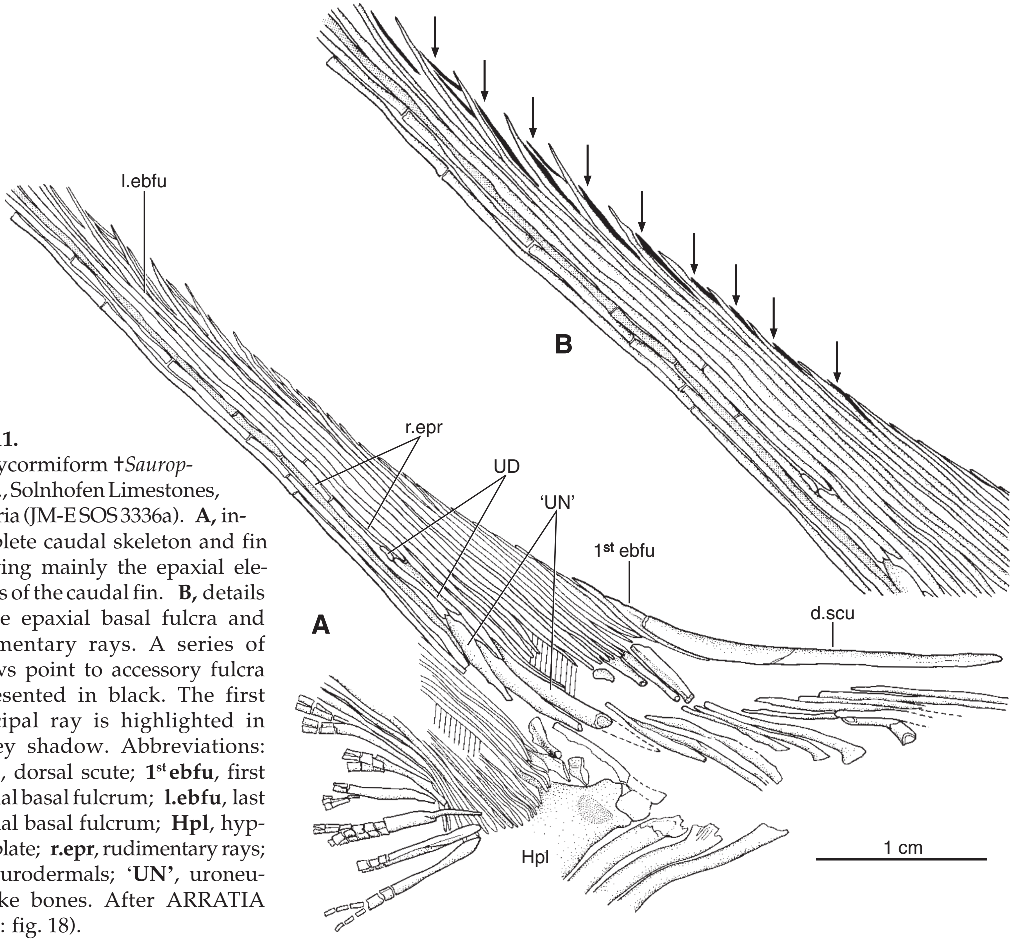

Fig. 11. Pachycormiform †*Sauropsis* sp., Solnhofen Limestones, Bavaria (JM-E SOS 3336a). **A,** incomplete caudal skeleton and fin showing mainly the epaxial elements of the caudal fin. **B,** details of the epaxial basal fulcra and rudimentary rays. A series of arrows point to accessory fulcra represented in black. The first principal ray is highlighted in a grey shadow. Abbreviations: **d.scu**, dorsal scute; **1st ebfu**, first epaxial basal fulcrum; **l.ebfu**, last epaxial basal fulcrum; **Hpl**, hypural plate; **r.epr**, rudimentary rays; **UD**, urodermals; **'UN'**, uroneural-like bones. After ARRATIA (2008: fig. 18).

†*Aspidorhynchus* and †*Belonostomus*; see MAISEY 1991: 187; BRITO 1997: figs. 35, 45; 1999: figs. 1–5; ARRATIA 1999: fig. 16A, 2008: fig. 21).

Pachycormiforms should not be coded as having teleostean uroneurals (= modified ural neural arches) because these are preural elements. Examples include PATTERSON (1977: character 1), GARDINER et al. (1996: character 35, where †*Pachycormus* and Recent *Elops* are coded as "1"), HURLEY et al. (2007: character 60, where extant *Elops* and *Hiodon* are coded as "1" like †*Pachycormus* and †*Pholidophorus*), FRIEDMAN et al. (2010, Suppl. materialonline: p. 28, character 74, where extant *Elops hawaiensis* and *Hiodon alosoides* are coded as "1" like †*Pholidophorus bechei* and the pachycormiforms †*Euthynotus*, †*Orthocormus*, †*Pachycormus*, and †*Protosphyraena*).

Spiral valve in intestine. The specimen described here possesses a spiral structure (Figs. 4A, 6) in the preserved posterior portion of the intestine close to the anus. This is not an isolated finding because one specimen of †*Asthenocormus* studied first by VETTER (1881) and illustrated later by NEUMAYER (1919) was interpreted as containing a spiral valve; however, this structure was interpreted as a calcified air bladder by EASTMAN (1914) because of the small diameter of the tube and the tapering of the structure past the anal fin. We have not seen evidence of the body cavity extending past the anal fin in any of the studied pachycormiforms; therefore, we interpret the structure as a spiral cololite being expelled through the anus. Spirale cololites form behind the spiral valve (MCALLISTER 1985: 4–6) and are moved through the colon. Expelled, the spirale cololite becomes a spirale coprolite.

The spiral valve is a spiral fold of the mucous membrane in the middle intestine of some fishes that

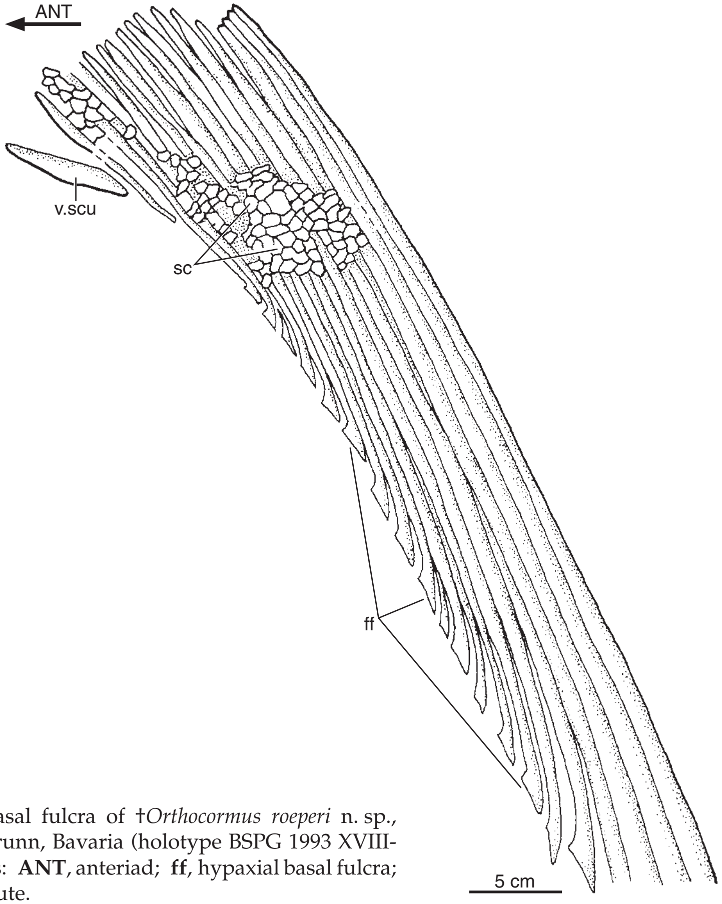

Fig. 12.
Details of the hypaxial basal fulcra of †*Orthocormus roeperi* n. sp., upper Kimmeridgian of Brunn, Bavaria (holotype BSPG 1993 XVIII-VFKO B16). Abbreviations: **ANT**, anteriad; **ff**, hypaxial basal fulcra; **sc**, scales; **v.scu**, ventral scute.

increases the surface area for absorption of nutrients. An intestine with a spiral valve has been reported from agnathans, chondrichthyans, possibly acanthodians (e. g., PARKER 1885, MCALLISTER 1984, 1985, HENNIGSEN et al. 2005), sarcopterygians (e. g., MCALLISTER 1984, 1985, MILLOT et. al. 1978, HASSANPOUR & JOSS 2009), and primitive actinopterygians (polypterids, acipenserids, polyodontids, lepisosteids, *Amia*, caturids; MCALLISTER 1984, CATALDI et al. 2002, PETERMAN & PETRIE-HANSON 2006). A spiral valve has not been reported from aspidorhynchiforms and "pholidophoriforms" (ARRATIA pers. observ.); a spiral valve is unknown in Recent teleosts (RAUTHER 1940, HARDER 1964, MCALLISTER 1984).

The position and structure of the intestinal spiral valve varies among the fishes where it has been described. For instance it is present in the lower portion of the intestine in some sharks, rays and skates. Several morphological patterns have been identified, such as distinguishing the scroll valve (valvula voluta) from the "true" spiral valve (valvula spiralis); the latter has been divided into four types (PARKER 1885, MCALLISTER 1984). The most common spiral valve is Type D, found in most fish groups and interpreted as the primitive state by MCALLISTER (1984). Type D occurs when the infolding mucosa has a size/development greater than those of the lumen, and the mucosa forms spiralling cones; the apices of the cones are directed anteriorly.

It is unclear whether pachycormiforms have spiral valve type D or not. The presence and distribution of the valve in certain actinopterygians indicate that the structure may be not homologous with the valve present in other fish groups. However, the presence of the spiral valve in pachycormiforms is not a character shared with primitive teleosts but with certain holosteans such as *Lepisosteus*, *Amia,* and caturids.

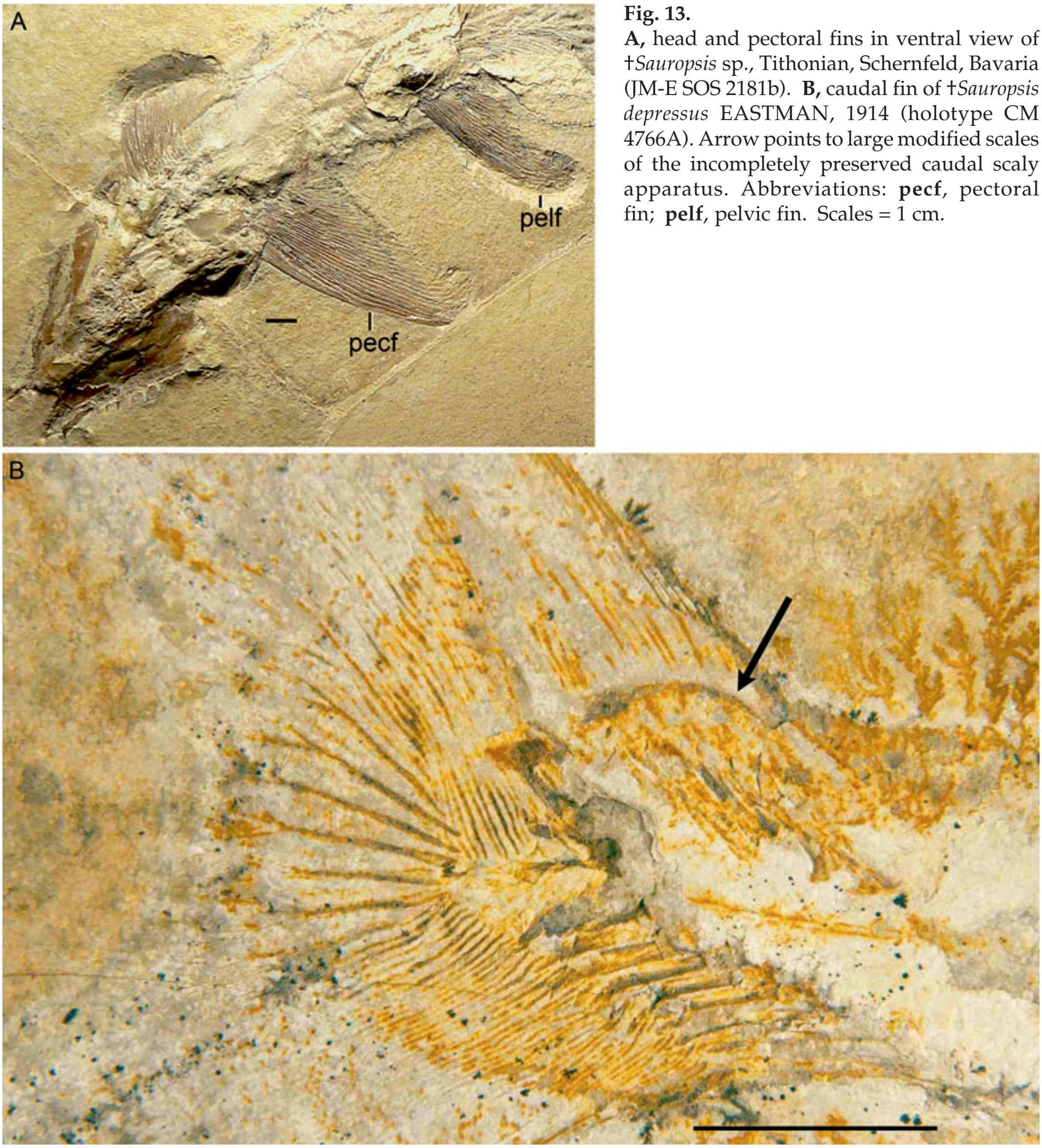

Fig. 13.
A, head and pectoral fins in ventral view of †*Sauropsis* sp., Tithonian, Schernfeld, Bavaria (JM-E SOS 2181b). **B,** caudal fin of †*Sauropsis depressus* EASTMAN, 1914 (holotype CM 4766A). Arrow points to large modified scales of the incompletely preserved caudal scaly apparatus. Abbreviations: **pecf**, pectoral fin; **pelf**, pelvic fin. Scales = 1 cm.

Taxonomic assignment of †*Orthocormus roeperi* n. sp.

Is †*Orthocormus roeperi* a pachycormiform?

Certain features have been traditionally interpreted as unique for pachycormiforms, despite different names sometimes used in the past, e.g., “ethmoid fused with vomer and forming a prominent rostrum” (WOODWARD 1895: 374) (= rostrodermethmoid). The following features have been traditionally considered unique for pachycormiforms:

1) median rostrodermethmoid separating the premaxillary bones (e.g., WOODWARD 1895, BERG 1940, WENZ 1968, MAINWARING 1978, LAMBERS 1988, 1992, KEAR 2007, FRIEDMAN et al. 2010);
2) pectoral-fin scythe-like (e.g., WENZ 1968, MAINWARING 1978, LAMBERS 1988, 1992, KEAR 2007, FRIEDMAN et al. 2010);

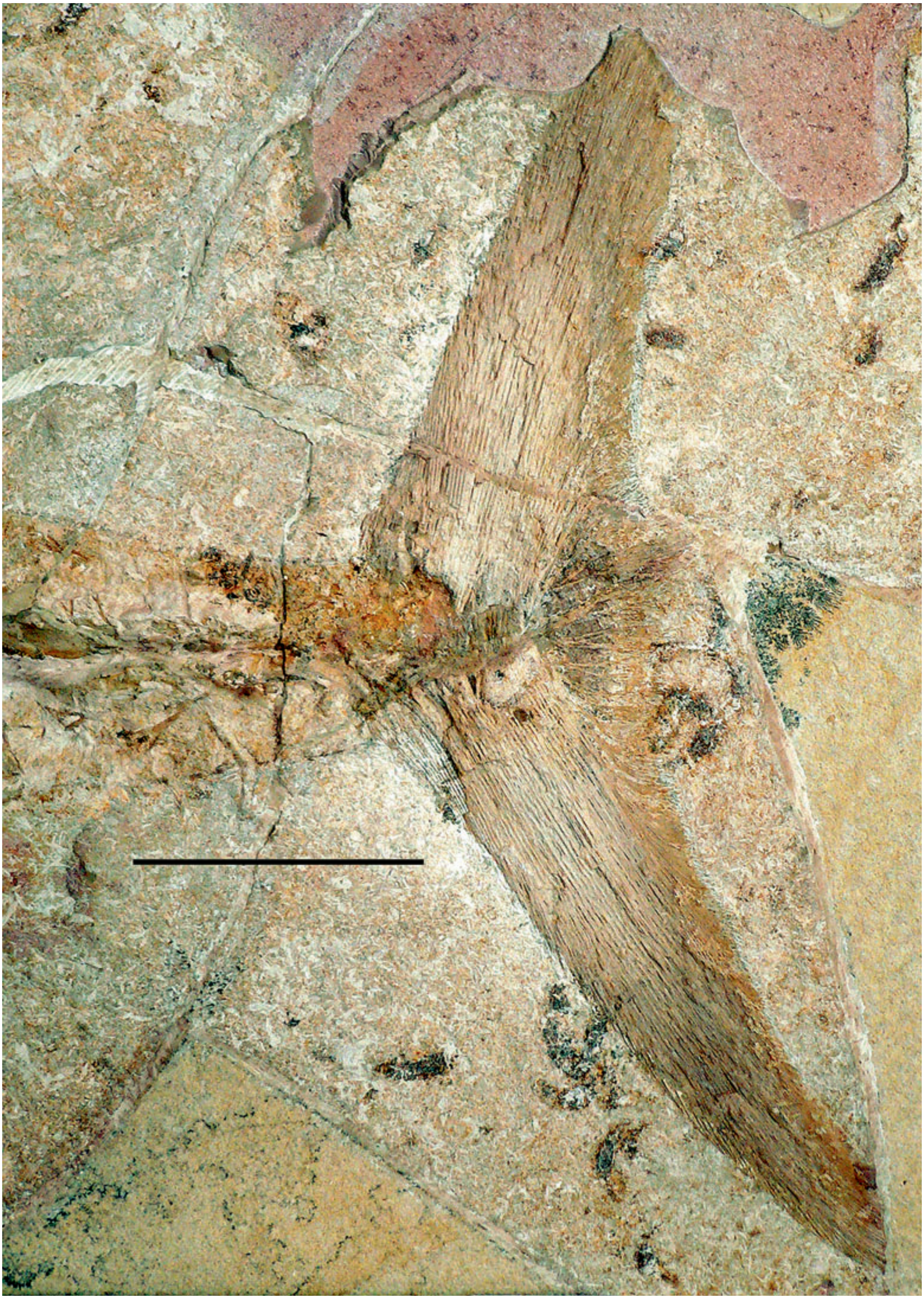

Fig. 14.
Caudal fin of †*Asthenocormus titanius* (WAGNER, 1863), Tithonian, Langenaltheim, Bavaria (JM-E SOS 542). Scale = 10 cm.

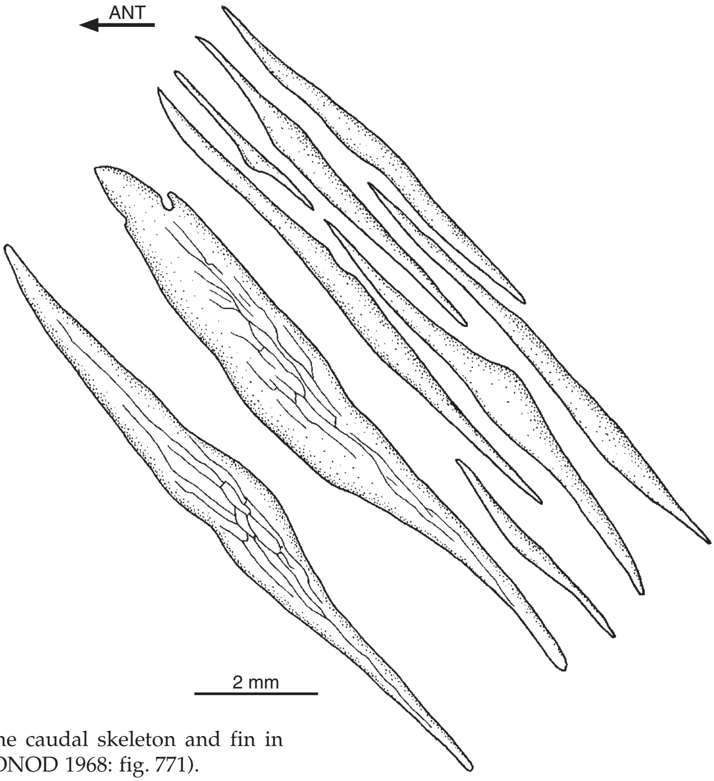

Fig. 15.
Modified scales present lateral to the caudal skeleton and fin in Recent *Neothunnus albacora* (after MONOD 1968: fig. 771).

3) pectoral rays branched distally (e. g., WENZ 1968, MAINWARING 1978, LAMBERS 1988, 1992, KEAR 2007, FRIEDMAN et al. 2010);
4) pectoral rays with Y-type bifurcation (e. g., LAMBERS 1992, FRIEDMAN et al. 2010);
5) hypural plate (e. g., WENZ 1968, PATTERSON 1973, LAMBERS 1992, FRIEDMAN et al. 2010).

†*Orthocormus roeperi* n. sp. shares characters 1, 2, 3, and 5 with other pachycormiforms. The pectoral rays apparently do not branch in a Y-fashion (ch. 4) in the new species. A hypural plate (ch. 5) is present in †*O. roeperi*, it includes hypural 1 plus an unidentified number of hypurals. Pachycormiforms have traditionally been interpreted with a hypural plate including hypural 2+n (see WENZ 1968: 130, figs. 63, 69; PATTERSON 1973: fig. 19), an interpretation that should be revised in the future because the element interpreted as hypural 1 by WENZ (1968) and PATTERSON (1973) has a well developed arch, so that it is not a hypural, but is the last vertebra (preural 1 plus its parhypural) with a developed haemal arch where the caudal blood vessels exit.

According to the most recent study of pachycormiforms (FRIEDMAN et al. 2010, Suppl. materialonline: p. 52) the monophyly of the group is supported by numerous characters, five of which are cited above. Other characters are listed below.

6) posterior margin of vagal foramen formed by outgrowths of intercalar;
7) anterior myodome absent;
8) dermosphenotic forms dorsal margin of orbit;
9) supraorbitals absent;
10) more than six infraorbitals behind orbit;
11) supramaxilla placed posterodorsal to maxilla;
12) dorsal and ventral caudal fin ray bases symmetric;
13) pectoral radials with broad distal radials and narrow proximal stack (paddle-shaped);
14) pectoral fin rays without segmentation;
15) pelvic fin placed anterior to midpoint between anal and pectoral fins.

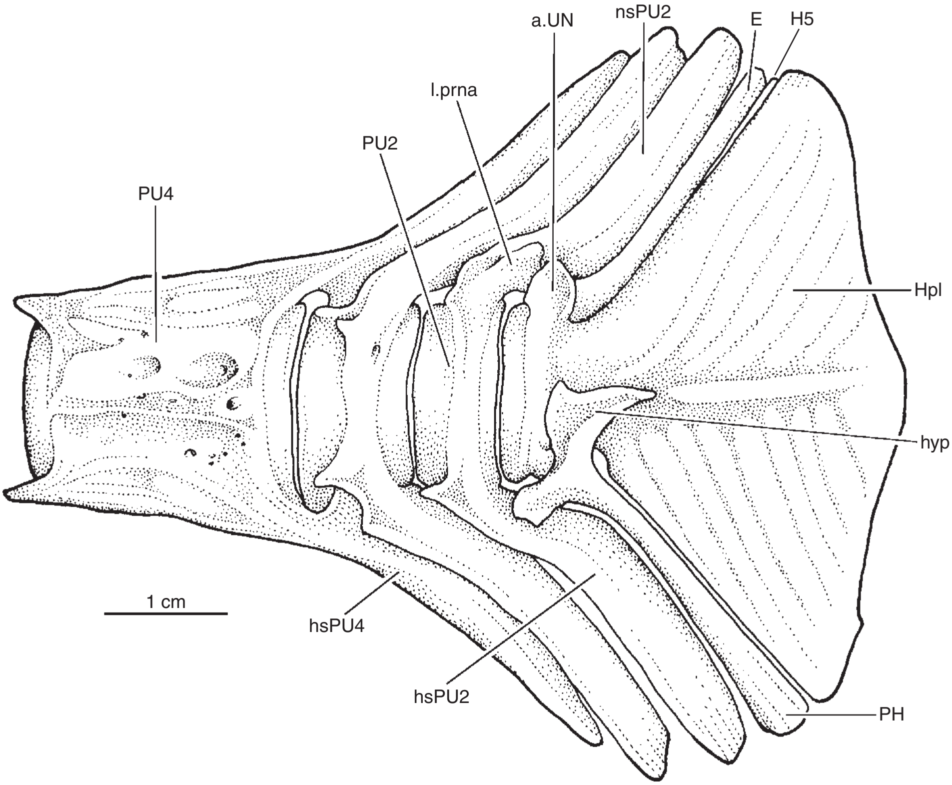

Fig. 16.
Caudal skeleton of the Recent *Thunnus atlanticus* of 504 mm SL (modified from POTTHOFF 1975). Abbreviations: **a.UN**, an atrophic uroneural according to POTTHOFF 1975 that it is more correctly interpreted as a lateral process of the compound terminal centrum; **E**, epural; **H5**, hypural 5; **hsPU2**, **hs PU4**, haemal spine of preural centrum 2 and 4; **hyp**, hypurapophysis; **Hpl**, hypural plate fused with preural centrum 1, an unknown number of ural centra, and probably one uroneural; **l.prna**, lateral process of the neural arch; **PH**, parhypural; **PU2**, **PU4**, preural centrum 1, 4.

Among the listed characters, †*Orthocormus roeperi* n. sp. shares characters 9 and 15 with other pachycormiforms, whereas characters 6, 7, 10, and 13 are unknown (due to conditions of preservation) in the new species. The new species reveals different conditions for characters 8, 12, and 14. See below.

Dermosphenotic (ch. 8). In †*Orthocormus roeperi* the dermosphenotic partially forms the postero-lateral margin of the orbit (see Figs. 4B, 5A) contrary to the condition illustrated by LEHMAN (1949: fig. 2) for †*Pachycormus macropterus* and WENZ (1968: fig. 67) for †*Euthynotus incognitus*, in which a large dermosphenotic forms the whole dorsal orbital margin. LEHMAN (1966), WENZ (1968), and others have followed LEHMAN's (1949) interpretation later.

†*Orthocormus* spp. was coded by FRIEDMAN et al. (2010, Suppl. materialonline: taxon-by-character matrix, character 32) as having a dermosphenotic forming the dorsal margin of the orbit. Such coding is based on AMNH FF 19639 (a cast of the holotype of †*O. roeperi* and on specimen descriptions in HOLMGREN & STENSIÖ (1936), RAYNER (1948) and LAMBERS (1988, 1992) (FRIEDMAN et al. 2010, Suppl. materialonline: 36). However, the descriptions and illustrations of these authors do not support this coding because the dermosphenotic is not illustrated or described, but the autosphenotic (see HOLMGREN & STENSIÖ 1936: fig. 366; RAYNER 1948: fig. 17, 18, LAMBERS 1988: figs. 1, 2, pl. 2, figs. A,B; 1992: p. 191, 192). The holotype of †*O. roeperi* (see Figs. 4B, 5A) does not have a long dermosphenotic forming the dorsal orbital margin. According to the available information, the condition is unknown for †*O. cornutus* and †*O. teyleri*, and †*O. roeperi* has a short anterior process of the dermosphenotic. Consequently, the coding of †*Orthocormus* spp. in FRIEDMAN et al. (2010) is mistaken.

Bases of principal rays (ch. 12). The bases of the principal epaxial and hypaxial caudal rays in the new species are not symmetrical (see Figs. 8A,B, 9). We should hardly expect to see a symmetrical pattern in species with different numbers of epaxial and hypaxial principal caudal rays as usually observed in pachycormiforms (see comparisons above, LAMBERS 1992 and ARRATIA & LAMBERS 1996).

Segmentation in pectoral rays (ch. 14). The pectoral rays in the new species show scarce segmentation in some of the longest rays. Scarcely segmented pectoral rays have also been reported by LAMBERS (1992: 262) for †*'Hypsocormus' macrodon*, †*Sauropsis*, and †*Pachycormus*. Thus, not all pachycormiforms lack segmentation in the pectoral rays.

Although †*Orthocormus roeperi* does not share with other pachycormiforms all synapomorphies cited for the group, we interpret the new species as a pachycormiform. Phylogenetic analyses that include pachycormiforms usually present a high number of unknown states ("?"). For instance, the synapomorphies cited above are listed in a matrix comprising 13 pachycormiform taxa, where 44.6 % of the characters are coded with a question mark and 4 % are coded with "–" as a logical impossibility or inapplicable character (FRIEDMAN et al. 2010, Suppl. materialonline: 20–30, taxon-by-character matrix). The number of question marks may be too high to support robust interpretations. For instance, the framing of the vagal foramen is coded with a question mark in 10 of the 13 taxa and the condition of the anterior myodome is coded with a question mark in 11 of the 13 pachycormiforms studied by FRIEDMAN et al. (2010, Suppl. materialonline: 40). Thus, in many characters the parsimony analysis interpreted them as synapomorphies supporting different nodes, although their states are almost unknown in pachycormiforms.

Generic position of †*Orthocormus roeperi* n. sp.

†*Orthocormus roeperi* n. sp. is included within †*Orthocormus* because it presents the diagnostic characters given by LAMBERS (1992: 187–188) in the most recent revision of the genus, with the mentioned exceptions:

1) The presence of a well-developed rostrodermethmoid bearing a pair of large, laterally compressed teeth, directed obliquely forward (e. g., LAMBERS 1992: 191, fig. 1A,B). However, in †*Orthocormus roeperi* the well-developed rostrodermethmoid bears a pair of vertically oriented teeth (see Figs. 4B, 5A).
2) Pronounced, anteriorly directed boss in the parietal region (of traditional terminology), the so-called temporal boss (LAMBERS 1992: 272–273). According to LAMBERS (1992), in †*Hypsocormus* the boss mainly comprises the posttemporal with a small contribution from the supratemporal; the boss also includes the parietal bone (of traditional terminology) in †*Pachycormus*, but the main element is the posttemporal. The presence of a temporal boss is not unique to †*Orthocormus* because the structure is also found in a variety of pachycormiforms such as †*Hypsocormus* (Fig. 1A), †*Pachycormus*, and †*Protosphyraena*. The temporal boss is very well developed in †*O. cornutus* (see WEITZEL 1930: figs. 13–14; Fig. 3A herein), whereas it is small in the new species and does not project anteriorly over the parietal region. The temporal boss is apparently absent in †*Saurostomus* (WOODWARD 1916), but a small temporal boss was observed in some well-preserved skulls by MAINWARING (1978). The temporal boss is small in the new species and it does not project anteriorly over the parietal region. †*Euthynotus* and †*Sauropsis* apparently lack a temporal boss (LAMBERS 1992).

   The presence of a temporal boss is interpreted here as a homoplastic character among pachycormiforms, and its reduction as a unique feature of †*Orthocormus roeperi* n. sp. within the genus †*Orthocormus*.
3) The lower jaw has a row of large, medial procumbent teeth and small lateral teeth. However, the small lateral teeth are missing in †*Orthocormus roeperi* (see Figs. 4B, 5A). There is no evidence of small teeth or sockets for small teeth in the oral margin of the jaw.

Despite these absences, we assign the new fish described here to †*Orthocormus* because of the shared diagnostic characters proposed by LAMBERS 1992 (elongated, fusiform trunk; temporal boss; rostrodermethmoid reaching anterior to symphysis of lower jaw; rostrodermethmoid with pair of large, laterally compressed teeth; premaxilla with large teeth; maxilla with small teeth; mandible with row of large, medial, procumbent teeth; large pelvic fin closer to pectoral than anal fin; large dorsal fin behind middle of trunk; dorsal fin completely in front of anal fin; base of anal fin extended; caudal fin with long, slender lobes and more than 40 rays). (See Comments, p. 90). Within †*Orthocormus*, the erection of a new species is justified because of differences in the temporal boss and shape of the head, in the size and number of jaw teeth, in the higher number of rays in the unpaired fins, especially of the caudal rays (see Table 1), in the lateral expansions of the base of the dorsal and anal fins, and in the presence, structure, and position of the scaly caudal apparatus (formed by large rectangular-turning into reversed L-shaped scales), unique to the new species.

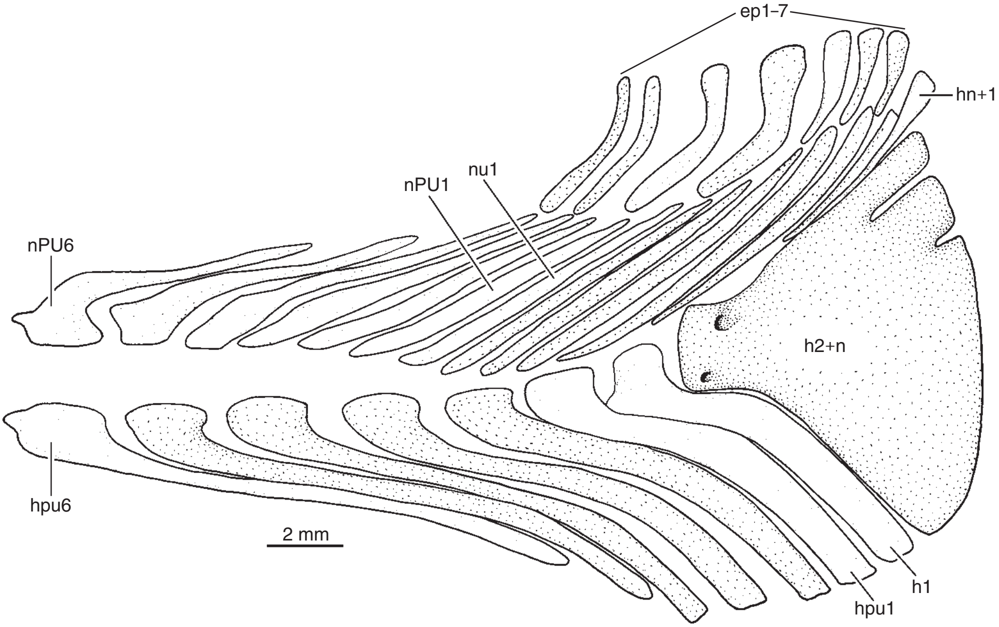

Fig. 17.
Diagrammatic illustration of the caudal endoskeleton of †*Pachycormus curtus* redrawn from PATTERSON (1973: fig. 19). Abbreviations: **ep1–7**, epurals 1–7; **h1**, first hypural; **h2+n**, hypural plate, comprising second and an unknown number of succeeding hypurals; **hn+1**, probably a free hypural; **hpu1,6**, haemal arches and spines of first and sixth preural vertebrae; **nPU1,6**, neural arches and spines of first and sixth preural vertebrae; **nu1**, ural neural arch 1 (however, these are preural neural arches).

Final comments

A re-analysis of the phylogenetic position of Pachycormiformes among Actinopterygii or of the relationships within Pachycormiformes is outside the scope of this paper. Throughout this work we became aware that we are still missing significant morphological information for many pachycormiforms after studying specimens with relatively good or very good preservation, in contrast to most poorly preserved members of the group. It also became clear that it is a mistake to assume that a feature observed in one pachycormiform must be present in others. The present state of knowledge of pachycormiforms is clearly illustrated by FRIEDMAN et al. (2010, Suppl. materialonline: 20–30 and 40–46, taxon-by-character matrix) where the data matrix shows pachycormiforms with almost 50 % of characters coded as "?" for 93 characters. The morphological information is higly incomplete (e.g., characters 10, 11, 14, 15, 16, 21, 22, 39) for many taxa with 10 or 11 taxa marked with question marks among the 13 taxa, or the information is only known in one taxon (e.g., character 8), or the information is even lacking completely (e.g., characters 6 and 16 with questions marks for the 13 taxa). †*Pachycormus* spp., only 3 % of question marks, appears to be better known than other pachycormiforms. Additionally, the matrix reveals that knowledge is very incomplete on features concerning the head, especially the braincase, and that the postcranial region is better known.

Furthermore, many characters and information on species are often gathered from the available literature. For instance, the phylogenetic hypothesis in KEAR (2007) is based on characters from LAMBERS (1988) that were taken from MAINWARING (1978). FRIEDMAN et al. (2010, Suppl. materialonline: 20) based their phylogenetic analysis on a character set derived from PATTERSON (1973, 1977, 1982), PATTERSON & ROSEN (1977), MAINWARING (1978), GARDINER & SCHAEFFER (1989), OLSEN & McCUNE (1991), LAMBERS (1992), GARDINER et al. (1996), COATES (1999), LUND (2000), CAVIN & SUTEETHORN (2006), HURLEY et al. (2007), LISTON (2007), and from "A", who is not listed in FRIEDMAN et al., but corresponds to ARRATIA (1999). "The placement of pachycormids as crown neopterygians is uncontroversial (e.g., Patterson 1973, 1977a; Gardiner et al. 1996; Brito 1997; Hurley et al. 2007) so the matrix found in Hurley et al. (2007) has been pared accordingly" (as stated in FRIEDMAN et al. 2010, Suppl. materialonline: 20). However, the position of pachycormiforms as crown actinopterygians, especially their interpretation as teleosts, becomes uncertain when the cited literature is revised. BRITO (1997: figs. 56, 57) did not show that the pachycormiforms are crown neopterygians or teleosts because all the ingroup taxa in his phylogenetic analysis are neopterygians and among those, the pachycormiforms are in an unresolved polytomy with other neopterygians. The goal of GARDINER et al. (1996) and HURLEY et al. (2007) was not the placement of pachycormiforms, with only one pachycormiform included in the analysis. Additionally, the selection of taxa as well of characters is often not the best choice to answer questions about the phylogenetic position of pachycormiforms, because that question was not a goal of those studies.

PATTERSON (1973) introduced radical changes to previous concepts of Actinopterygii by discarding the Holostei and proposing a new classification for neopterygian fishes: Division Ginglymodi (e. g., lepisosteids), Division Halecostomi including Halecomorphi (e. g., amiids) and Teleostei (including pachycormids and pholidophorids with crown teleosts), and †Pycnodontiformes and †Luganoiidae as Neopterygii incertae sedis. Recent studies based on both morphological and molecular evidence have resurrected the Holostei (e. g., GRANDE 2005, 2010, HURLEY et al. 2007) and additionally have proposed the lepisosteiforms as sister group of amiiforms (e. g., NORMARK et al. 1991, GRANDE 2010). Thus the division Halecostomi has been abandoned in these works, and Ginglymodi and Halecomorphi, together with others such as the †Semionotidae, have been reunited as Holostei.

The placement of †Pachycormidae and †Aspidorhynchidae in the Subdivision Teleostei, with †Pachycormidae as "the sister-group of all other teleosts," (PATTERSON 1973: 299) is based on misinterpretation of certain characters, e. g., in the caudal skeleton (ARRATIA & LAMBERS 1996 and see above). Five characters support the inclusion of †Pachycormiformes within the Teleostei after PATTERSON (1977: 628, fig. 19). However, most of these features are misinterpretations of the condition present in pachycormiforms. They include paired ural neural arches modified as uroneurals in all extant teleosts versus the specialized condition present in pachycormiforms where modified neural spines of preural vertebrae have been confused with "true" uroneurals and coded as the same structure (see page 106 for discussion). Another example is the movable premaxilla; however, the premaxilla is sutured to the rostrodermethmoid in pachycormiforms where the condition has been studied (e. g., KEAR 2007, herein and Figs. 4B, 5A). An internal carotid foramen enclosed in the parasphenoid is another proposed teleostean synapomorphy scarcely known in pachycormiforms (e. g., 3 taxa among 13 in FRIEDMAN et al. 2010, Suppl. materialonline: 22, character 21). A pectoral propterygium fused with the first pectoral ray is another problematic character proposed by PATTERSON (1977) and used by FRIEDMAN et al. (2010, Suppl. materialonline: p. 29, 44, character 83) as a teleostean synapomorphy present in pachycormiforms. From the 13 pachycormiform taxa studied, only †*Orthocormus*, †*Pachycormus* and †*Protosphyraena* are coded with this character state. We suggest that this character should be re-studied because, to the best of our knowledge, the propterygium is not fused with the first pectoral ray in these fishes (see for instance, WOODWARD 1908: fig. 44, pl. 32, figs. 5, 5a for †*Protosphyraen*a; pers. observ.; WOODWARD 1895: pl. 11, fig. 6 for †*Hypsocormus tenuirostris*). Among extant teleosts *Elops hawaiensis* is coded with a question mark (FRIEDMAN et al. 2010, Suppl. materialonline: 44), but a propterygium fused with the pectoral ray is present in *Elops*, including *Elops hawaiensis* (ARRATIA 1999, 2000, 2008: figs. 38A,B, 39). Additional synapomorphies justifying the inclusion of pachycormiforms in the total-group Teleostei are given in FRIEDMAN et al. (2010, Suppl. materialonline: 52, characters 15, 20, 56, and 79). However, information for characters 15 (large posttemporal fossa and discrete fossa Bridgei), 56 (symplectic articulation on medial surface of quadrate), and 79 (clavicle absent) is incompletely known for most pachycormiforms. Character 20 (state 1: basipterygoid process absent) is also unknown for most pachycormiforms.

PINNA (1996: 150–157) compiled 27 synapomorphies of Teleostei available in the literature at that time and briefly analyzed each. However, with few exceptions (ARRATIA 1999, 2000, and others) researchers have largely ignored most of these synapomorphies. It is notable that most of these synapomorphies seem to be absent in pachycormiforms where the information is available. For instance, pachycormiforms have coronoid bones in the lower jaw, but they are absent in teleosts; pachycormiforms have more than four pectoral proximal radials versus four bones present in teleosts; pachycormiforms do not have an unpaired tendon-bone urohyal as teleosts do; and adult pachycormiforms do not have a diural caudal skeleton.

Pachycormiforms were interpreted as possible stem-group teleosts by ARRATIA (2004) based on phylogenetic analyses performed by ARRATIA (1999). However, as ARRATIA (2004: 295) noted: "if the pachycormiforms are stem-group teleosts, then we are missing a significant part of the early evolutionary history of the group because the oldest pachycormiforms are reported from the Early Jurassic, but the supposedly oldest teleosts are older (Late Triassic). While pachycormiforms remain poorly known, any comment concerning their phylogenetic position or phylogenetic relationships among their members is inappropriate."

We are aware that pachycormiforms are a highly autapomorphic group, like aspidorhynchiforms and pycnodontiforms, and while they are easy to identify, their uniqueness make them difficult to place among actinopterygians. It complicates matters that the preservation of numerous species is poor or highly incomplete, and the number of specimens available for study of numerous species is few. There are many reasons for our incomplete knowledge about pachycormiforms, but in addition to all the problems derived from incomplete preservation, a further complication is the shortage of active researchers on pachycormiforms; at the present time we can identify only one (Jeff LISTON) who is dedicated to this fascinating group of fishes.

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