Original article

A megalichthyid sarcopterygian fish from the Lower Permian (Autunian) of the Saar-Nahe Basin, Germany[☆]

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A R T I C L E   I N F O

A B S T R A C T

A nearly complete specimen of a sarcopterygian fish from the Lower Permian (Autunian) of the Saar-Nahe Basin, southwest Germany, is described as a new genus and species of megalichthyids, *Palatinichthys laticeps*. It is characterized by the following unique list of characters: (1) lacrimal forms lateral margin of external naris, (2) postparietal short with respect to parietal, (3) tabular broad and shorter than supratemporal, (4) anterior margin of median extrascapular very narrow, (5) supraorbitals short, thus parietal and intertemporal participating in formation of orbital margin, (6) distance between external naris and orbit very short, and (7) squamosal abbreviated and deep. A phylogenetic analysis finds a monophyletic Megalichthyidae consisting of two clades, (*Palatinichthys* nov. gen. + *Ectosteorhachis*) and [(*Megalichthys* + *Sengoerichthys*) + *Cladarosymblema*)]. The sister taxa *Palatinichthys* nov. gen. and *Ectosteorhachis* share a short posterior skull table as a derived character, whereas *Megalichthys*, *Sengoerichthys* and *Cladarosymblema* retain an elongate postorbital region of the skull, regarded as plesiomorphic for "osteolepiforms". After their nearly worldwide distribution in the Late Devonian and Carboniferous, megalichthyids had become rare in the Permian and have so far been reported only from North America (*Ectosteorhachis*) and Norway (?*Megalichthys*). *Palatinichthys* nov. gen. is a further representative within the European-North American equatorial distribution of megalichthyids during the Permian. It was probably not a common inhabitant of the large Saar-Nahe lakes. Rather, it might have lived in a different habitat within the same general area, such as deltaic streams or rivers.

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1. Introduction

Over the past 150 years, the Permo-Carboniferous sediments of the Saar-Nahe Basin in south-western Germany have yielded a rich fauna of aquatic vertebrates, including temnospondyl amphibians and other basal tetrapods (Boy and Sues, 2000; Witzmann, 2006; Boy, 2007; Schoch and Witzmann, 2009a, 2009b), xenacanth and hybodont sharks (Hampe, 1994, 1996), and osteichthyan fishes (Heidtke, 2007; Schindler, 2007a). Osteichthyans are represented by both actinopterygian and sarcopterygian fishes. A large number of actinopterygians have been described, most notably elonichthyids (Poschmann and Schindler, 2004), amblypterids (Boy, 1976; Dietze, 2000) and aeduellids (Boy, 1987; Uhl, 1997). In contrast to actinopterygians, sarcopterygian fishes are a very rare component of the vertebrate fauna in the Saar-Nahe Basin and comprise dipnoans, coelacanths and "osteolepiforms". The first dipnoan described in the Saar-Nahe Rotliegend was the conchopomid *Conchopoma* (Schultze, 1975); remains of a second dipnoan, the sagenodontid *Sagenodus*, were later reported by Schultze (1993) and

Boy and Schindler (2000). Scales of a coelacanth, probably *Rhabdoderma*, were found in Upper Carboniferous sediments (Waterlot, 1934). From "osteolepiforms", which are probably not a monophyletic group (Ahlberg and Johanson, 1998; Friedman et al., 2007), representatives of several forms are present.

An articulated specimen and isolated scales of the small-growing *Rhizodopsis* were described by Schultze and Heidtke (1986, 1993) and Boy and Schindler (2000). Isolated, large rhombic scales, probably attributable to cosmine-covered megalichthyids, can be found in Upper Carboniferous strata to the Meisenheim Formation (middle Autunian) (Schindler, 2007a), and a complete megalichthyid specimen was discovered in the Meisenheim Formation near Jeckenbach in Rhineland-Palatinate by Ingo and Rüdiger Meyer in 1982. Skull roof and dermal pectoral girdle elements were described from the specimen and referred to as *Megalichthys* sp. by Rüdiger Meyer (Meyer, 1989, unpublished diploma thesis). Baumbauer (1990) later referred the specimen as "Quastenflosser" (crossopterygian) and emphasized its scientific importance as a close relative of tetrapods, although it was neither described nor illustrated in this article. In their description of *Rhizodopsis*, Schultze and Heidtke (1993) mentioned this specimen and referred it to the megalichthyid genus *Ectosteorhachis*, but did not justify their assignment. Schindler (2007a: fig. 19) and

Krätschmer (2004: fig. 13) figured this material and followed Schultze and Heidtke (1993) in their generic assignment. In this study, we give a description of this complete specimen designated as *Ectosteorhachis* by Schultze and Heidtke (1993), and provide a phylogenetic analysis to ascertain its phylogenetic position.

2. Geographical and geological setting

The specimen was collected from the Jeckenbach Bank near the village of Jeckenbach in the federal state of Rhineland-Palatinate, southwestern Germany. The Jeckenbach Bank belongs to the Lower Autunian (Lower Permian) Meisenheim Formation, which is subdivided into the units M1 to M10 (replacing the former units L-O1 to L-O10) and comprises the lower Jeckenbach and upper Odernheim subformations (Schindler, 2007b). The Jeckenbach Bank belongs to M6 within the Jeckenbach subformation. It consists of a several metres thick, laminated mudstone with intercalated carbonate concretions and thin carbonate beds. Articulated specimens of paramblypterid fishes are abundant, whereas temnospondyls like *Apateon* and *Sclerocephalus* are rare components of the fauna (Boy et al., 1990).

## 3. Material and methods

3.1. Studied specimen

Specimen PW 1989/207-LS, stored in the Museum für Naturgeschichte in Mainz, Germany, was originally embedded within a calcareous geode and prepared in 1988 by Ingo and Rüdiger Meyer (Meyer, 1989). Preserved in articulation from the tip of the snout to the cloacal region including the pelvic fins, it measures approximately 38 cm in length and is dorsoventrally compressed (Figs. 1–3).
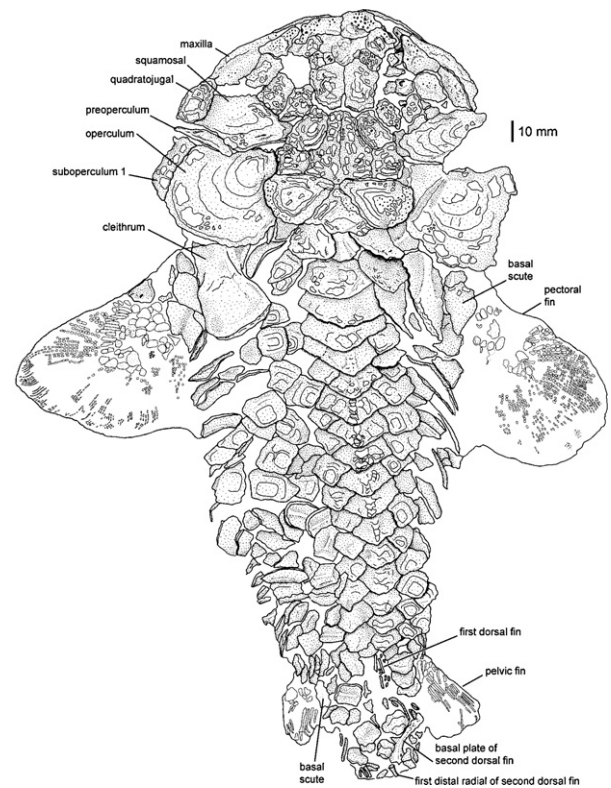
Fig. 2. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Drawing of the complete specimen in dorsal view.
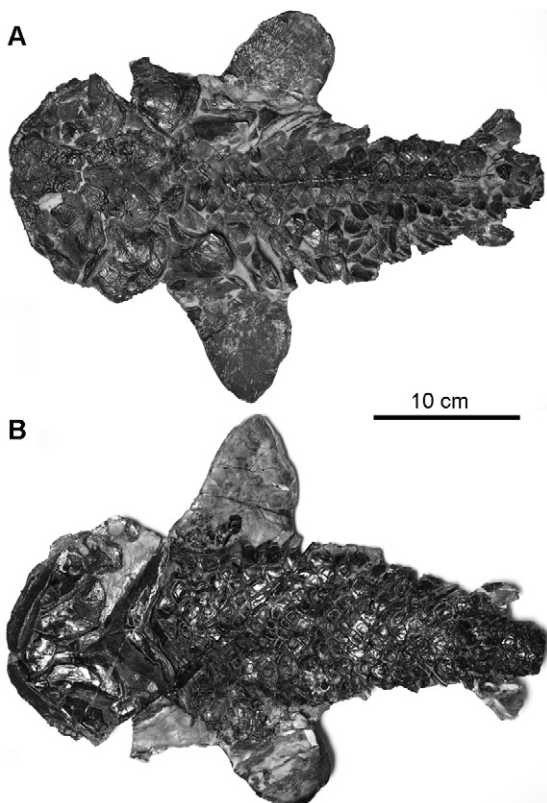
Fig. 1. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Photographs of complete specimen. **A**. Dorsal view. **B**. Ventral view.
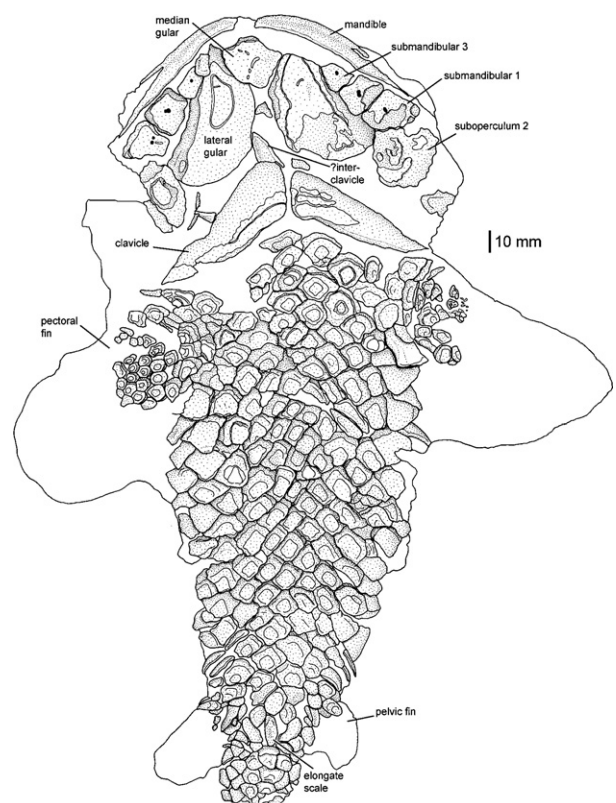
Fig. 3. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Drawing of the complete specimen in ventral view.

Both ventral and dorsal sides of the specimen have been fully prepared, with the skull roof, the complete operculo-gular series, the dermal pectoral girdle with pectoral fins, parts of the two dorsal fins, pelvic fins and scales preserved. No ossified endoskeletal elements can be discerned with the exception of the basal plate of the second dorsal fin. The material was photographed with a Nikon D700, Macro Lens 60 mm Nikkor, at the Museum für Naturkunde, and radiographed and CT-scanned at the Department of Radiology at Charité Hospital, Berlin.

3.2. Phylogenetic analysis

In order to elucidate the phylogenetic affinities of *Palatinichthys* nov. gen., we ran a cladistic analysis using the data set from Johanson and Ahlberg (2001), which is based on the matrix of Ahlberg and Johanson (1998) (Appendix A, Table S1). In the present analysis, we have deleted all dipnomorph taxa (*Porolepis*, *Glyptolepis, Powichthys, Youngolepis, Diabolepis, Dipterus*) and a number of tetrapodomorph taxa (*Mandageria, Eusthenodon, Platycephalichthys, Jarvikina, Tristichopterus, Canowindra, Beelarongia, Gyroptychius, Medoevia, Ichthyostega, Kenichthys, Notorhizodon*) since our aim is not a comprehensive analysis of dipnomorph and tetrapodomorph relationships, but rather to elucidate the phylogenetic position of *Palatinichthys* nov. gen. within the Megalichthyidae. We have thus reduced the number of taxa accordingly. We follow Fox et al. (1995) and Janvier et al. (2007) in that *Lohsania* (Thomson and Vaughn, 1968), *Megapomus, Megistolepis* (Vorobyeva, 1977) and *Mahalalepis* (Young et al., 1992) do not show the most diagnostic features of the Megalichthyidae or are too poorly known. Therefore, these taxa are not included in the present analysis. We added *Palatinichthys* nov. gen. (this study) and the megalichthyid *Sengoerichthys* (Janvier et al., 2007).

One new character (#100) was added: ratio length of parietal to length of postparietal (p/pp): less than 0.7 (0); 0.7 or more (1). The problem with this character is discussed below in the discussion Section. The state for this new character is listed in the following for each taxon, with the reference given in each case: *Cabonnichthys* (1; Ahlberg and Johanson, 1997: fig. 5), *Eusthenopteron* (1; Jarvik, 1944: fig. 18), *Koharalepis* (1; Young et al., 1992: figs. 7, 10), *Gogonasus* (0; Holland and Long, 2009: fig. 2b), *Osteolepis* (0; Jarvik, 1948: fig. 32a), *Megalichthys* (0; Thomson, 1964: fig. 5), *Ectosteorhachis* (1; Thomson, 1964: fig. 1), *Cladarosymblema* (0; Fox et al., 1995: fig. 14a), *Barameda* (0; Long, 1989: fig. 5a), *Gooloogongia* (0; Johanson and Ahlberg, 2001: fig. 17), *Panderichthys* (1; Vorobyeva and Schultze, 1991: fig. 4), *Acanthostega* (1; Clack, 2003: fig. 1a), *Palatinichthys* nov. gen. (1, this study), and *Sengoerichthys* (0, Janvier et al., 2007).

The analysis was run with PAUP* 4.0 (Swofford, 2002) using the heuristic search option with all characters unordered except for characters 15, 20, 23, 25, 32, 70 and 80 (Johanson and Ahlberg, 2001). The rhizodontids *Barameda* and *Gooloogongia* served as the outgroup in the present analysis. ACCTRAN character-state optimization (accelerated transformation) was used, giving one most parsimonious tree.

4. Systematic palaeontology

OSTEICHTHYES Huxley, 1880
SARCOPTERYGII Romer, 1955
TETRAPODOMORPHA Ahlberg, 1991
MEGALICHTHYIDAE Hay, 1902
Diagnosis: A family of Tetrapodomorpha showing the following derived characters: external naris elongate or slit-like; external naris partly enclosed by posterior tectal bone; interpremaxillary process with teeth on premaxilla; vomer is short and broad, sometimes with a strong medial process; pineal foramen closed;

parietal anterolaterally concave to receive the posterior nasal; lacrimal notch is well developed; skull low and wide; maxilla high, with its highest point posterior; outline of squamosal approximately equidimensional; preoperculum short and standing vertically; operculum large, subquadrate in outline, with a height/length ratio of approximately 1; scales rhombic but lacking peg and socket articulation; pectoral fins large and fan-shaped (also present in *Gyroptychius*).

Remarks: The above given diagnosis is based on Young et al. (1992: p. 20) and Fox et al. (1995: p. 107). Fox et al. (1995) doubted the significance of character "parietal anterolaterally concave to receive the posterior nasal" since it is too variable. These authors included the following taxa in the Megalichthyidae: *Megalichthys* Agassiz, 1835 (Carboniferous of Nova Scotia, Illinois, Kansas, Ohio, Morocco, Great Britain, Ireland, Belgium and possibly Lower Permian of Norway), *Ectosteorhachis* Cope, 1880 (Lower Permian of Texas and Oklahoma), *Cladarosymblema* Fox, Campbell, Barwick and Long, 1995 (Lower Carboniferous of Queensland), an undescribed specimen from the Permian of Norway and a form from the Frasnian of Turkey, subsequently described by Janvier et al. (2007) as *Sengoerichthys ottoman* Janvier, Clément and Cloutier, 2007 and considered as the earliest and most basal megalichthyid. *Mahalalepis* Young, Long and Ritchie, 1992 (Middle Devonian of Antarctica) and *Megistolepis* Obruchev, 1955 (Upper Devonian of Russia) were excluded from the Megalichthyidae by Fox et al. (1995) for being poorly known.

The specimen from the Saar-Nahe Basin shares the above-listed characters of the Megalichthyidae, with the exception of the interpremaxillary process and the short, broad vomer, for which preservation precludes an assessment, and the outline of squamosal being approximately equidimensional, since the squamosal is deeper than long (ratio 1.4:1). However, the squamosal seems to be equidimensional only in *Cladarosymblema*; in *Megalichthys* (Moy-Thomas, 1935: fig. 1; Jarvik, 1966: fig. 15c) and *Ectosteorhachis* (Thomson, 1964: fig. 2a; Thomson, 1975: fig. 2b) it is longer than deep, and the ratio is unknown in *Sengoerichthys*. Considering the listed characters, the Saar-Nahe specimen can be firmly assigned to the Megalichthyidae.

Genus **Palatinichthys** nov. gen.
Derivation of name: After Palatinatus, the Latin word for Palatinate (Pfalz) in southwestern Germany.
Type species: *Palatinichthys laticeps* nov. gen., nov. sp.
Diagnosis: Same as for the type species, by monotypy.

Palatinichthys laticeps nov. gen., nov. sp.
Figs. 1–7 and Figs. S1–S7
1989. *Megalichthys* sp. - Meyer, figs. 1, 5–7, 9, 10, 14–28, 32–34.
1990. Quastenflosser - Baumbauer, p. 13–14.
1993. *Ectosteorhachis* sp. - Schultze and Heidtke, p. 141.
2004. *Ectosteorhachis* sp. - Krätschmer, p. 71, fig. 13.
2007a. *Ectosteorhachis* sp. - Schindler, p. 252, fig. 19.
Derivation of name: From the Latin word "latus", meaning wide, and "ceps", meaning head, due to the proportionally broad skull of this new species.
Holotype and only specimen: PW 1989/207-LS, complete skull roof, operculo-gular series, dermal pectoral girdle, pectoral and pelvic fins.
**Type locality and horizon:** "Heinzköpfchen" locality near Jeckenbach, Rhineland-Palatinate, southwestern Germany (Meyer, 1989). Lower Autunian (Lower Permian, Unter-Rotliegend), Meisenheim Formation, Jeckenbach subformation, Jeckenbach Bank, unit M6 (Schindler, 2007b).
Diagnosis: Derived characters of *Palatinichthys laticeps* relative to other megalichthyids are as follows: lacrimal forms lateral margin of external naris; postparietal short with respect to parietal, ratio parietal length/postparietal length is 0.8; tabular
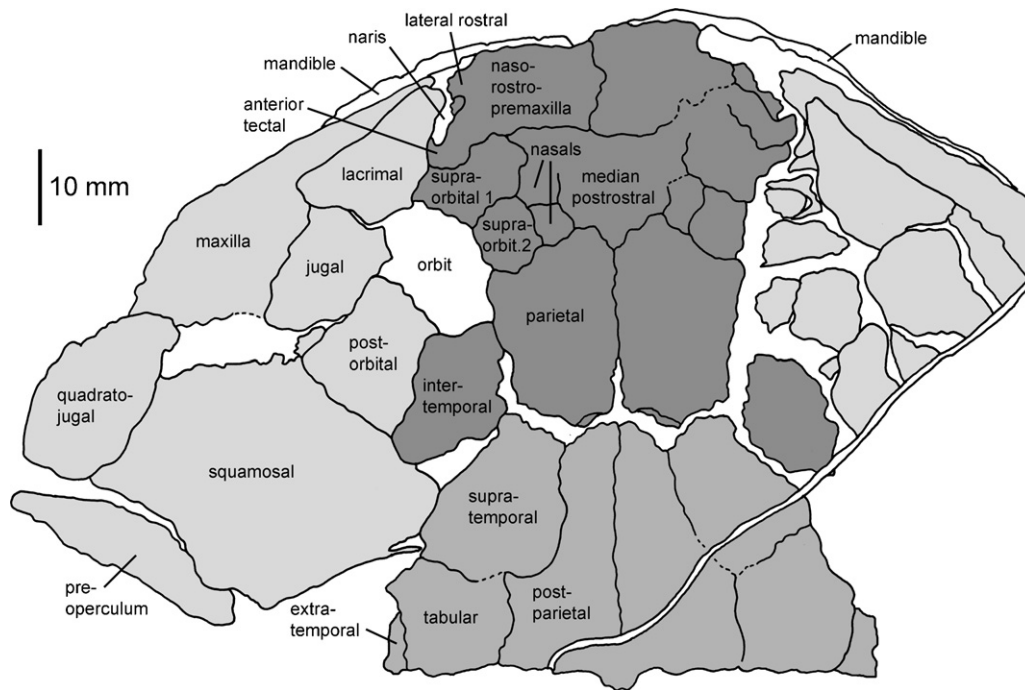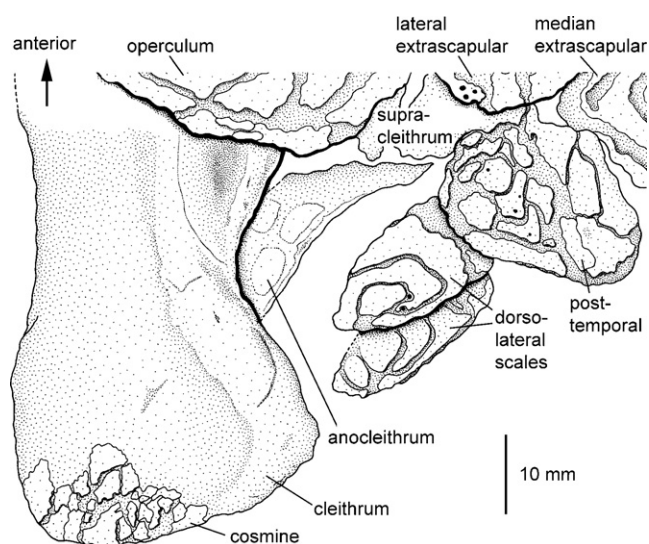
Fig. 4. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Schematic drawing of dermal skull in dorsal view. The three portions of the dermal skull are marked in different shades of grey: parieto-ethmoidal plate in dark grey, postparietal plate in medium grey, and cheek plate in light grey.
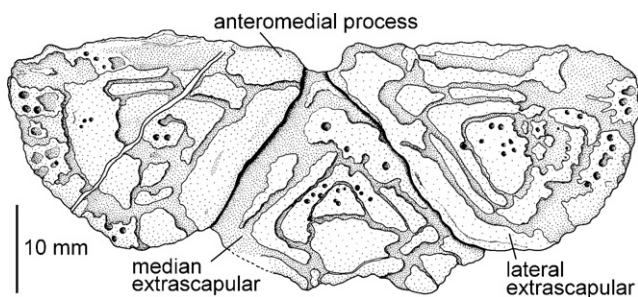
Fig. 5. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Extrascapulars in dorsal view.

Fig. 6. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, PW 1989/207-LS. Left dermal pectoral girdle in dorsal view.

broad and shorter than supratemporal; bone surface of cleithrum roughened, but without ornament of ridges, pits and grooves; posterior median process of the postparietals overlapping anterior margin of median extrascapular; anterior margin of median extrascapular very narrow; supraorbitals short and confined to the anteromedial margin of the orbit, thus parietal and intertemporal participating in formation of orbital margin; distance between external naris and orbit very short.

Description: A detailed comparative description of the specimen is available in Appendix B, incl. Figs. S1–S7. The dermal bones including the scales of *Palatinichthys* nov. gen. are covered by a sheet of cosmine in different states of resorption.

Parieto-ethmoidal shield: The parietal (Fig. 4; Fig. S1) is elongate and forms a part of the medial orbital margin. No trace of a pineal plate or parietal foramen can be discerned, as in other megalichthyids. A bone of rhombic outline is located posterolateral to the parietal and is interpreted here as intertemporal (dermosphenotic sensu Thomson, 1964; Jarvik, 1980; Young et al., 1992), although the intertemporal in tetrapodomorph fishes normally neither participates in the orbital margin nor contacts the squamosal (see below). The anterior and posterior supraorbitals are small, roughly quadrangular bones located anterodorsal and dorsal to the orbit (Fig. 4; Fig. S1). Sensory pores of the supraorbital canal are present on the surface of the bones, what can only be seen in the presumed megalichthyid *Megapomus* (Vorobyeva, 1977: fig. 33b). The bones of the nasal series are located medial to the supraorbitals, the cosmine cover making it difficult to ascertain how many nasals are actually present. The unpaired, large median postrostral is located anterior to the parietals and medial to the nasal series (Fig. 4). Anterior to this bone are two broad rectangular elements, the naso-rostro-premaxillae. The naris is medially and posteriorly bounded by a posterolateral process of the naso-rostro-premaxilla that probably represents the fused anterior tectal (Fig. 4; Fig. S1). In contrast to all other known megalichthyids, the naris is delimited laterally by the lacrimal. Since no sutures of the lateral rostral (or prenarial) are discernable in the specimen, one might speculate if this bone was fused with the naso-rostro-premaxilla (Fig. 4). With respect to the

rather small orbit, the slit-like naris is comparatively large and elongate in *Palatinichthys* nov. gen. (Fig. 4), similar to that of *Megalichthys* (Jarvik, 1966; Schultze, 1974), but unlike the short, rather round narial opening of *Ectosteorhachis* (Schultze, 1974) and *Sengoerichthys* (Janvier et al., 2007), which probably represents the plesiomorphic condition in "osteolepiforms" (Jarvik, 1948).

Postparietal plate: The postparietal is distinctly longer than wide and forms a posterior median process (Fig. S2). The supratemporal is a stout bone in which an anterolateral process as described in *Megalichthys* (Bjerring, 1972), *Cladarosymblema* (Fox et al., 1995) and *Sengoerichthys* (Janvier et al., 2007) cannot be discerned. The lateral margin of the small, quadrangular to rhombic tabular is separated from the anteromedial margin of the operculum by a small bony element, the extratemporal (Fig. 4). The lateral portion of the postparietal plate, at the height of the supratemporal-tabular suture, is embayed for the spiracular notch. The three extrascapulars are preserved in articulated, with the median element being overlapped by the two lateral counterparts (Figs. 2 and 5).

Cheek plate: This portion of the skull consists of the lacrimal, jugal and postorbital (all participating in the orbital margin), maxilla, quadratojugal, squamosal and preoperculum (Figs. S1 and S3). The anterior portion of the maxilla and the posterodorsal lamina of this bone bear several sensory pores which might be derived from branches of the infraorbital canal running through lacrimal and jugal. Sensory pores on the maxilla are rarely found in tetrapodomorph fishes; they have been illustrated in *Megalichthys hibberti* (Moy-Thomas, 1935: fig. 1), *Koharalepis jarviki* (Young et al., 1992: fig. 9a), and *Gogonasus andrewsae* (Long et al., 1997: fig. 19c; Holland and Long, 2009: fig. 2c). The squamosal is the largest bone of the head (Fig. 4) and is much deeper than long. The preoperculum is a slender, bar-like bone that is steeply oriented.

Operculo-gular series: The operculum is a large bone that is only slightly deeper than long (Fig. 2); its ventral margin overlaps suboperculum 1. On the ventral side of the head, two large lateral gulars, the median gular, the submandibulars and suboperculum 2 are preserved (Fig. 3).

Pectoral girdle: The dermal elements of the pectoral girdle comprise the elongate, triangular clavicle, a possible small interclavicle, the large, massive cleithrum, poorly preserved anocleithrum and supracleithrum, and the ovate posttemporal (Figs. 3 and 6). The endoskeletal scapulocoracoid cannot be observed externally.

Fins: The length of the scale-covered, roughly semicircular proximal lobe of the pectoral fin accounts for slightly less than half the fin's length. At the base of the lobe, a large elongate basal scale or scute is visible (Fig. 2; Fig. S4). The proximal segments of the dermal fin rays are elongate and rod-like, with successive segments becoming shorter and thinner distally (Fig. S4). Distal to the short lobate portion of the pelvic fins, a number of fin rays with a long, unsegmented proximal part are visible. Of the unpaired fins, only a number of dermal fin rays that derive from the first dorsal fin are present, and the basal plate of the second dorsal fin with the first distal radial is preserved (Fig. 2).

Scales: On the dorsal side and ventral side of the body, a median row of scales is well preserved (Figs. 1–3; Fig. S6). From each median scale, one posterolaterally directed scale row extends on the left and on the right side. Scales are rhombic to rectangular in shape and some of them show a peg-like outgrowth on their dorsal margin.

Remarks: In *Palatinichthys* nov. gen., the posterior supraorbital terminates posteriorly approximately at the level of the middle of the orbit, so that a small portion of the parietal and the anterior margin of the intertemporal participate in formation of the orbital margin. This feature is exceptional in tetrapodomorph fishes because the posterior supraorbital extends posteriorly and contacts the intertemporal and postorbital (e.g., Thomson, 1964; Fox et al., 1995; Ahlberg and Johanson, 1997; Holland et al., 2010).

The unusual extent of the intertemporal, which not only forms part of the orbital margin but also contacts the squamosal, appears to be an autapomorphy of *Palatinichthys* nov. gen. An alternative interpretation might be that the bone in question represents the postorbital (or a broken part of it), and the intertemporal proper is fused with the parietal. However, there are no indications of a compound nature of the parietal in *Palatinichthys* nov. gen., and the actual postorbital can be clearly identified on the basis of its location dorsal to the jugal and anterior to the squamosal. Its margins are well defined, so that the bone in question cannot be a broken part of another one.
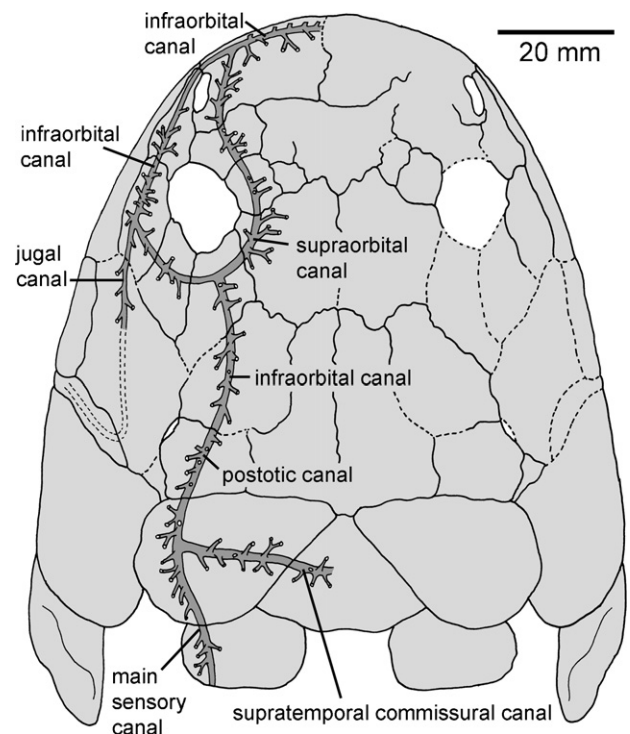
5. Results

5.1. Reconstruction of skull, opercular region and pectoral girdle

Fig. 7 shows a reconstruction of the skull and opercular region of *Palatinichthys laticeps* nov. gen., nov. sp. in dorsal view, including the presumed course of the lateral line canals on the left side of the skull. To assess outline and approximate width of the three-dimensional skull in dorsal view, gular plates, submandibulars and mandibles were drawn and put together in articulation. The three-dimensionally reconstructed skull is broader than the reconstructed skulls of other megalichthyids like *Sengoerichthys* (Janvier et al., 2007: fig. 6), *Cladarosymblema* (Fox et al., 1995: fig. 14), *Megalichthys* (Bjerring, 1972: fig. 7) and *Ectosteorhachis* (Thomson, 1975: fig. 8a). This can mainly be attributed to the proportionally short postparietal compared to the parietal, the abbreviated squamosal (that is deeper than long) and the short distance from anterior orbital margin to the posterior narial rim.

5.2. Phylogenetic analysis

In the present phylogenetic analysis, the Megalichthyidae come out as a monophyletic group, comprising two clades, one

Fig. 7. *Palatinichthys laticeps* nov. gen., nov. sp., Lower Permian, Saar-Nahe Basin, reconstruction of skull, opercular region and dermal pectoral girdle in dorsal view. Ano- and supracleithrum are omitted due to their poor preservation. The presumed course of the lateral line canal system is shown on the left side of the skull.
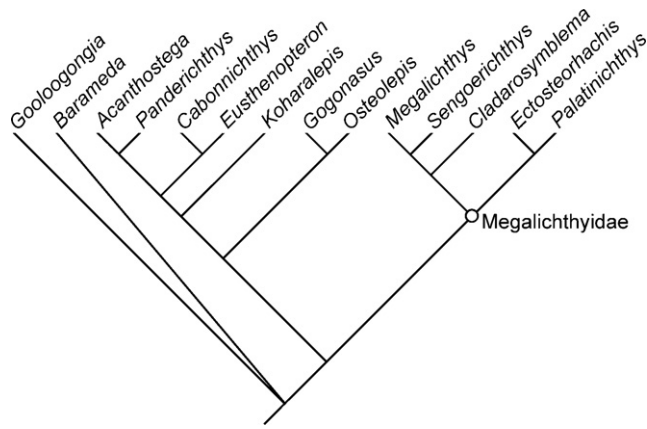
Fig. 8. Phylogeny of *Palatinichthys* nov. gen. nesting within Megalichthyidae. Data matrix based on Johanson and Ahlberg (2001); see text for the modifications of data set. Tree metrics: length = 73, Consistency Index (CI) = 0.685, Retention Index (RI) = 0.763, Rescaled Consistency Index (RC) = 0.523.

consisting of [(*Megalichthys* + *Sengoerichthys*) + *Cladarosymblema*], the other of (*Ectosteorhachis* + *Palatinichthys* nov. gen.) (Fig. 8). At this point, it is necessary to address the problem and significance of the new character #100 for this result. We have chosen this character to distinguish between taxa with proportionally long postparietal shields from those with proportionally shorter ones. However, the ratio of parietal length/postparietal length is close from each other in the megalichthyids under consideration: 0.8 in *Palatinichthys* nov. gen., 0.5 in *Megalichthys* (Thomson, 1964), 0.7 in *Ectosteorhachis* (Thomson, 1964), approximately 0.6 in *Sengoerichthys* (cannot be determined with certainty; Janvier et al., 2007: fig. 6), and 0.6 in *Cladarosymblema* (Fox et al., 1995). We must therefore admit that this character is somewhat arbitrary and that ontogenetic development of the skull table might also affect these proportions in each taxon. Without this character, the Megalichthyidae remain unresolved in the resulting cladogram. We therefore decided to retain this character in spite of these problems, and we regard this analysis of megalichthyid intra-relationships as a first step. A comprehensive phylogenetic analysis of megalichthyids requires thorough redescriptions of both *Megalichthys* and *Ectosteorhachis*, since the existing anatomical descriptions of these taxa are not exhaustive and often contradictory.

6. Discussion

6.1. Taxonomic assignment and phylogeny

Several synapomorphies linking *Palatinichthys* nov. gen. to members of the Megalichthyidae are listed in the Systematic Palaeontology section above. Within this family, the specimen cannot be assigned to an existing taxon. *Palatinichthys* nov. gen. differs from the other megalichthyids in the proportionally shorter postparietals with respect to the parietals, and supratemporals that are longer than the tabulars. A further difference is that the lacrimal forms the lateral border of the external (i.e., anterior) naris. Further autapomorphies of the Saar-Nahe megalichthyid are the bone surface of the cleithrum being devoid of dermal ornament, the posterior process of the postparietals slightly overlaps the median extrascapular, a very narrow anterior margin of the median extrascapular, an abbreviated, deep squamosal and an absence of contact between the posterior supraorbital and intertemporal. These autapomorphic features justify the erection of a new genus and species, *Palatinichthys laticeps*.

In the phylogenetic analysis, *Palatinichthys* nov. gen. is placed as the sister group of the North American genus *Ectosteorhachis*. Both taxa share one unambiguous synapomorphy: ratio between length

of parietal to length of postparietal is 0.7 or more (character #100). This high ratio is reflected by the comparatively shorter skulls of both taxa compared to other megalichthyids. A long postorbital region as in *Sengoerichthys*, *Megalichthys* and *Cladarosymblema* certainly represents the plesiomorphic state for "osteolepiforms". Surprisingly, *Sengoerichthys*, assumed to be the most basal known megalichthyid by Janvier et al. (2007), turns out to be the sister taxon of *Megalichthys*, with *Cladarosymblema* as successive outgroup. This clade forms the sister group of *Ectosteorhachis* and *Palatinichthys* nov. gen. and is supported by one synapomorphy (shared with *Cabonnichthys*), the kite-shaped pineal series with distinct posterior corner (character 39; Johanson and Ahlberg, 2001), although the character state is unknown in *Sengoerichthys*. *Megalichthys* and *Sengoerichthys* are united by the long parasymphysial plate that is sutured to the coronoid, and is denticulate or with tooth row (character 1; Johanson and Ahlberg, 2001); this character is also present in *Panderichthys*. If this grouping is correct, it would indicate an early separation of longer-skulled and shorter-skulled megalichthyids already in the Late Devonian. However, this should be clarified in the future in a broader analysis with additional characters.

6.2. Palaeogeographic and palaeoecological remarks

Janvier et al. (1979, 2007) and Young et al. (1992) suggested a Gondwanan origin of megalichthyids, with worldwide distribution of the group in the Late Devonian and Carboniferous. The earliest known megalichthyid is *Sengoerichthys* from the Frasnian of Turkey, indicating that megalichthyids did not disperse into other areas, including Europe and North America before the Famennian (Janvier et al., 2007). Remains of a megalichthyid were reported by Daeschler et al. (2003) from the Famennian Red Hill locality in North America, and possible megalichthyid remains might be present in the Famennian of Russia (Vorobyeva, 1977; Lebedev, 1995). *Cladarosymblema* is a megalichthyid from the Early Carboniferous of Queensland, Australia (Fox et al., 1995), while several species of *Megalichthys* are known from the Carboniferous of North America (Nova Scotia, Illinois, Kansas, Ohio) and Europe (Great Britain, Ireland, Belgium) (Demanet, 1941; Andrews and Westoll, 1970; Schultze, 1974; Schultze and Heidtke, 1993). Scales and vertebrae described from the Early Carboniferous of Morocco probably also belong to this genus (Janvier et al., 1979). Permian megalichthyids are rare; with material (?*Megalichthys*) being reported from Norway (Heintz, 1934), and *Ectosteorhachis* described from the Permian Redbeds of Texas (Romer, 1958) and Oklahoma (Olson, 1967). Thus, the occurrence of *Palatinichthys* nov. gen. in the Saar-Nahe Basin represents a further megalichthyid within the Permian equatorial distribution of Europe.

Megalichthyids are commonly interpreted as freshwater fishes, but at least some representatives lived in deltaic and brackish environments (Schultze, 1974; Janvier et al., 1979). The presumed sister-taxon of *Palatinichthys* nov. gen., *Ectosteorhachis*, is quite common in the Wichita Group of the Permian Redbeds, generally regarded as deltaic freshwater sediments (Romer, 1958; Thomson, 1975). Swamps as well as open sand flats and shallow pools were abundant in this environment and seasonal flooding and drying was present. The complete specimens of *Ectosteorhachis* show a similar preservation as *Palatinichthys* nov. gen.; Thomson (1975) suggested that these specimens probably died from desiccation and were mummified, either on a bank or in a drying pool. There is no direct evidence that *Ectosteorhachis* lived in the nearby marine environments (Romer, 1958; Thomson, 1975).

The Jeckenbach Bank, in which the specimen of *Palatinichthys* nov. gen. was found, is interpreted as being deposited in a large-area lake (Boy, 1987; Schindler, 2007b; for a different view of the palaeoecology of the Saar-Nahe Basin, see Schultze and Soler-Gijón,

2004). The fact that *Palatinichthys* nov. gen. is represented by only one specimen in these sediments might indicate that it is allochthonous and could have lived in a different habitat within the same general area, possibly deltaic streams.

Acknowledgements

Appendix A. Supplementary data

Supplementary text and data (Table S1 and Figs. S1–S7) with this article can be found, in the online version, at doi:10.1016/j.geobios.2011.03.002.

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