

New semionotiform (Actinopterygii: Neopterygii) from the Late Jurassic of southern Germany

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We report on a new semionotiform taxon, *Scheenstia zappi* gen. et sp. nov., from Schamhaupten in the Late Jurassic limestones of the Franconian and Swabian Alb, southern Germany. Although the taxon is so far represented by a single specimen, excellent preservation allows a detailed description of its skeletal anatomy. *Scheenstia zappi* is distinguished by the presence of a sensory canal in the supraorbital bones and a saddle-like articular surface in the quadratojugal, both features so far unknown in other semionotiforms. The new taxon is further diagnosed by a unique combination of characters: more than three pairs of extrascapular bones; frontals less than three times longer than their maximal width; semitritorial dentition; four anterior infraorbitals; middle pit line contained in a groove in the dermopterotic and parietal; concave posterior border of the angular, robust bugle-like process of the posttemporal bone; large basal fulcra; eleven fin rays in the lower lobe of the caudal fin (below the lateral line); and a first, scale-like caudal fin ray reduced. Among semionotiforms it most closely resembles *Lepidotes*, in particular the large tritorial forms of the Late Jurassic and Early Cretaceous of Europe, such as *L. mantelli*, *L. maximus* and *L. laevis*. The peculiar shape of the quadratojugal in *Scheenstia zappi* resembles the condition in some basal teleosts in which a ventral articular surface of the quadrate probably served in the rotation of the lower jaw.

Keywords: Neopterygii; Semionotiformes; Jurassic; Kimmeridgian; Schamhaupten; Germany

Introduction

Semionotiformes are one of the basal groups of neopterygian fishes, an especially diverse and well represented group in the Jurassic and Early Cretaceous. According to the few available phylogenetic analyses (Olsen & McCune 1991; Brito 1997; Cavin & Suteethorn 2006; López-Arbarello 2006), Lepisosteidae and Macrosemiidae belong to the monophyletic Semionotiformes. All other semionotiforms have been classified in a single family, Semionotidae, probably a non-monophyletic assemblage (López-Arbarello 2008a, b; ongoing research). The history of Semionotiformes can be traced back to the Early Triassic (*Semionotus alsaticus* Deecke, 1889, from Elsass). They are well represented and already diverse in the marine Alpine Middle and Late Triassic (Deecke 1889; de Allessandri 1910; Stolley 1920; Tintori & Renesto 1983; Bürgin 1995; Tintori 1996; Tintori & Lombardo 2007; Lombardo & Tintori 2008). They are also represented in the continental Late Triassic of Germany (López-Arbarello 2008a) and North America (McCune 1987), and were quite common in the European epicontinental seas during the Early Jurassic (López-Arbarello 2008b). In the Late Jurassic and Early

Cretaceous, however, semionotiforms are especially well represented – with numerous and excellently preserved specimens – and highly diverse. The Late Jurassic limestones of the Franconian and Swabian Alb (Fig. 1) offer an excellent example of this high diversity of semionotiforms, with nine published species of ‘semionotids’ (Agassiz 1833, 1836; Münster 1842; Wagner 1863; Eastman 1914) and seven recognized species of macrosemiids (Bartram 1977). Although these ‘semionotids’ need revision, most of the species are probably valid, and several still poorly studied specimens – if they are studied at all – represent additional new taxa (López-Arbarello pers. obs.).

The Late Jurassic sediments of southern Germany are well known for their excellent fossils, the study of which has produced significant contributions to our understanding of the evolution of Mesozoic biotas. Most of these fossils come from the Solnhofen Plattenkalk, which formally constitutes the Lower Tithonian Solnhofen Formation (Fürsich *et al.* 2007; Fig. 2). Slightly older sediments of Kimmeridgian age (Rögling Formation; Fürsich *et al.* 2007; Fig. 2) in the vicinity of the city of Schamhaupten (Fig. 1) have also produced exceptionally preserved fossils, including among approximately 200 identified taxa (Viohl & Zapp

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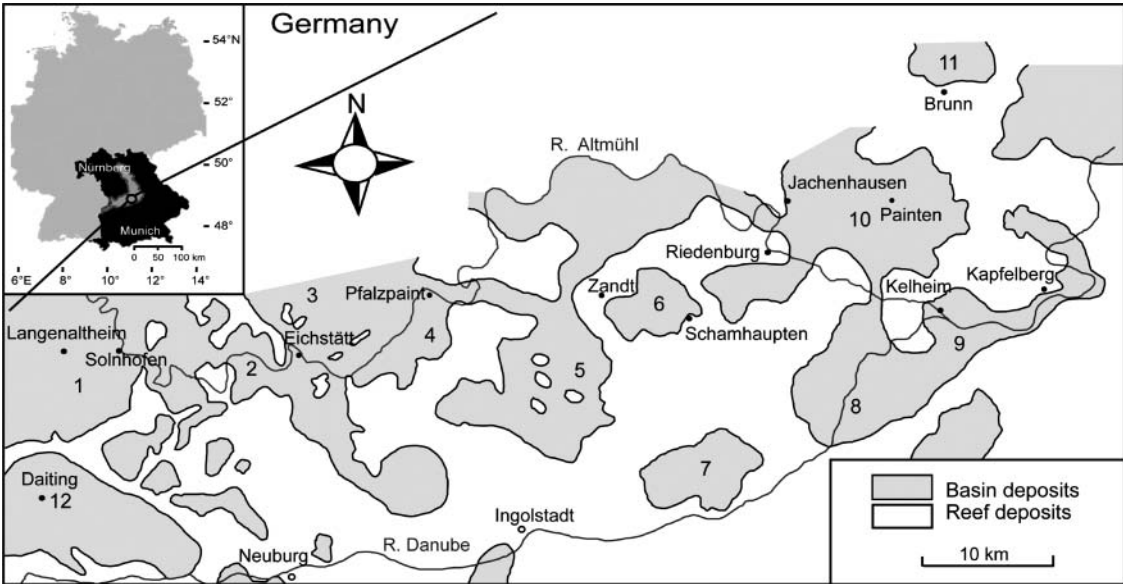


Figure 1. Geographic location of the main localities in the Late Jurassic limestones of the Franconian and Swabian Alb, Bavaria, Germany: Solnhofen/Langenaltheim Basin (1); Schernfeld Basin (2); Eichstätt Basin (3); Gungolding/Palzpainten Basin (4); Denkendorf/Böhmfelder Basin (5); Schamhaupten/Zandt Basin (6); Hartheim Basin (7); Hienheim Basin (8); Kelheim Basin (9); Painten Basin (10); Brunn Basin (11); and Daiting Basin (12). Modified from Meyer & Schmidt-Kaler (1989), Selden & Nudds (2004) and Burnham (2007).

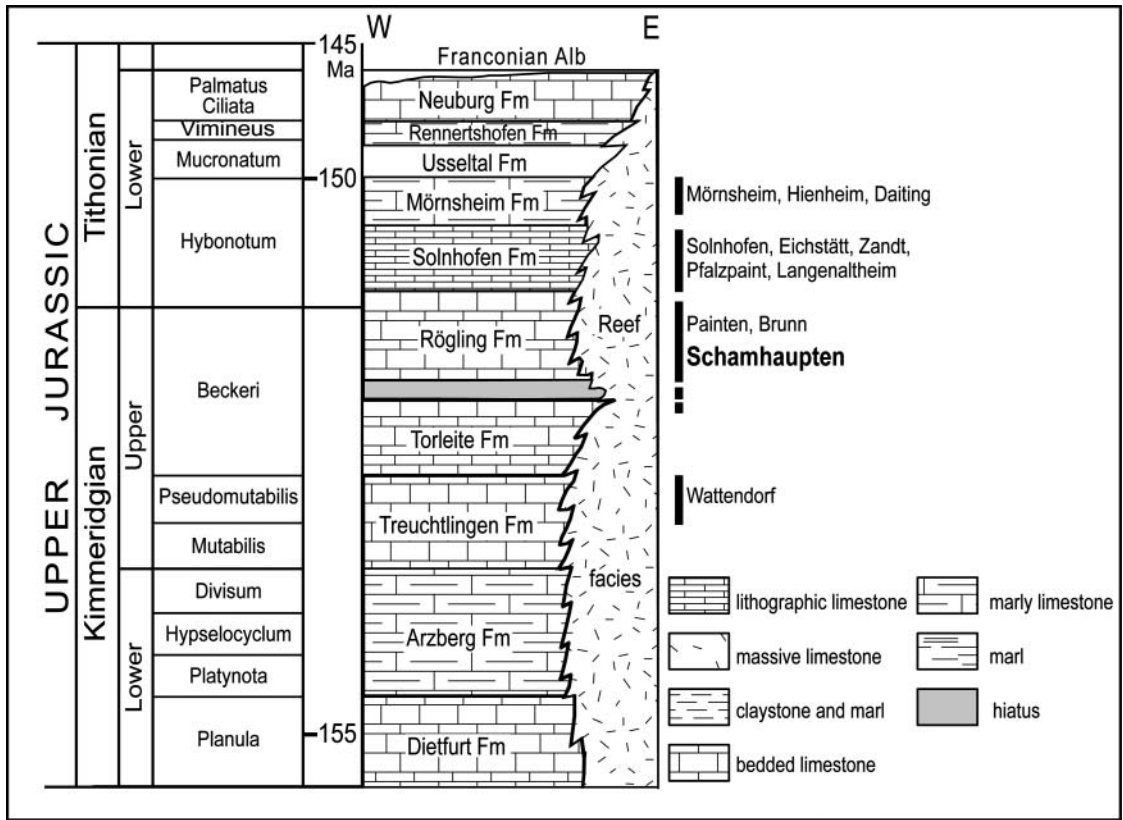


Figure 2. Stratigraphical chart of the Upper Jurassic sequence in the Franconian Alb showing the chronostratigraphical relationships of the Kimmeridgian sediments at Schamhaupten (Rögling Formation), Bavaria, Germany. Modified from Schmid *et al.* (2005) and Fürsich *et al.* (2007).

2007), remarkable vertebrates such as the teleost *Siemensichthys siemensii* Arratia, 2000, and the juvenile theropod *Juravenator starki* Göhlich & Chiappe, 2006. Another excellently preserved vertebrate from the same sequence is a fish already described and referred to as *Lepidotes* sp. (Semionotiformes) by Thies & Zapp (1997).

According to Viohl & Zapp (2007, pp. 138–139), in Schamhaupten: “the deposition of silicified plattenkalk occurred during a ‘transgressive systems tract’, which had started with the spongiolithic biostrome facies of the Treuchtlingen marble in the early late Kimmeridgian and reached the ‘maximum flooding surface’ probably during the deposition of the Solnhofen Plattenkalk in the early Tithonian (Keupp & Matyszkiewicz 1997)”. In Viohl & Zapp’s (2007) palaeoenvironmental reconstruction, as a consequence of a halocline in the Schamhaupten Basin, the bottom zone was dysaerobic and thus hostile to benthic life, with the exception of microbial mats, which were responsible for the high quality of fossil preservation. Unlike the bottom zone, the higher water column was rich in pelagic organisms, indicating good connections with the Tethys. Benthic, demersal and terrestrial organisms are allochthonous to the Schamhaupten Basin and were probably washed in during storm events.

This article includes a detailed description of a new semionotiform taxon represented by the fish previously referred to as *Lepidotes* sp. by Thies & Zapp (1997). We further discuss its systematic relations and the implications of several of its anatomical features for current ideas of homologies and character evolution in semionotiform and other neopterygian fishes. The specimen described herein was collected in Stark Quarry, north-west of Schamhaupten in the Southern Franconian Alb, Bavaria, Germany. The geological setting of the quarry is explained by Joyce (2000) and detailed geological information, including local profiles and description of the bearing sediments is provided by Röper (1992), Thies & Zapp (1997) and Viohl & Zapp (2007).

Material and methods

The specimen was chemically and mechanically prepared by M. Zapp. Detailed information on the preparation methodology is included in Thies & Zapp (1997). The specimen was studied under a Leica Wild M32 stereomicroscope equipped with a camera lucida Wild 308700. All drawings were made directly from the fossil.

Skull bones are named according to the use of most authors studying actinopterygians. The bones carrying the infraorbital sensory canal anterior to the orbit are referred to as ‘anterior infraorbitals’ following Wenz (1999, 2003) and López-Arbarello & Codorniu (2007). Fringing fulcra are named according to Patterson (1982). Scutes and unpaired and paired basal fulcra are identified according to López-

Arbarello & Codorniu (2007). It is possible to differentiate these structures because of their general shape and orientation, and particularly because of their position: the scutes lie on the caudal peduncle, but unpaired basal fulcra lie on the body lobe of the tail. The relative position of the fins and scale counts are expressed in a pterygial formula in which D, P, A and C indicate the number of scale rows between the first complete row behind the pectoral girdle and the insertion of the dorsal, pelvic, anal and caudal fins respectively, and T is the total number of scale rows between the pectoral girdle and the caudal inversion (Westoll 1944).

Institutional abbreviations

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **GSM:** British Geological Survey, Nottingham, UK; **JME:** Jura Museum, Naturwissenschaftliche Sammlungen Eichstätt, Germany; **MNHN:** Muséum National d’Histoire Naturelle, Paris, France.

Anatomical abbreviations

a.io: anterior infraorbital bone; **ag:** angular bone; **ao:** antorbital bone; **a.pl:** anterior pit line; **ap-dpt:** autodermopalatine ossification; **cl:** cleithrum; **co:** coronoid bone; **cor:** coracoid bone; **d:** dentary; **dpt:** dermopterotic bone; **dsph:** dermosphenotic bone; **enpt:** endopterygoid bone; **ex:** extrascapular bone; **io:** infraorbital bone; **io.c:** infraorbital sensory canal; **fr:** frontal bone; **fr.fu:** fringing fulcrum; **iop:** interoperculum; **let:** lateral ethmoid; **m.c:** mandibular sensory canal; **m.pl:** middle pit line; **mx:** maxilla; **na:** nasal bone; **o.c:** orbital sensory canal; **oc.c:** occipital sensory canal; **op:** operculum; **pa:** parietal bone; **p.b.fu:** paired basal fulcrum; **pcl:** postcleithrum; **p.d.c.fu:** paired dorsal caudal fulcrum; **pmx:** premaxilla; **pop:** preoperculum; **pop.c:** preopercular sensory canal; **ptt:** posttemporal bone; **q:** quadrate bone; **qj:** quadratojugal bone; **rar:** retroarticular bone; **ro:** rostral bone; **sag:** surangular bone; **s:** scale; **sc:** scapula; **scl:** supracleithrum; **sc.r:** scale-like fin ray; **sct:** scute; **so.c:** supraorbital sensory canal; **so:** supraorbital bone; **sop:** suboperculum; **su.o:** suborbital bone; **t.c:** temporal sensory canal; **u.b.fu:** unpaired basal fulcrum; **u.d.c.fu:** paired dorsal caudal fulcrum. An ‘l’ between brackets after the abbreviations indicates left elements.

Systematic description

Neopterygii Regan, 1923

Semionotiformes Arambourg & Bertin, 1958 sensu Olsen and McCune, 1991

Semionotiformes incertae family

Genus *Scheenstia* gen. nov.

Type species. *Scheenstia zappi* sp. nov.

Etymology. The name *Scheenstia* is a compound word in Bavarian dialect composed of 'schee' (= beautiful), which becomes 'scheens' after appropriate conjugation in genitive masculine, and 'Tia' (= animal).

Diagnosis. As for the type and only species.

Scheenstia zappi sp. nov.
(Figs 3–9)

1997 *Lepidotes* sp. Thies & Zapp: 18, pl. 4–7.

Holotype. JME-Sch 80, complete specimen preserved in right lateral view (Fig. 3).

Type locality. Stark Quarry, 0.5 km north-west of Schamhaupten in the Southern Franconian Alb, Bavaria, Germany. Gauss-Krüger Coordinates: R4469650/H5420160 (Thies & Zapp, 1997; Fig. 1).

Type horizon. Rögling Formation (Upper Kimmeridgian; Fürsich *et al.* 2007; Fig. 2). Malm Epsilon 2 Level 5 in the Profile of Thies & Zapp (1997).

Etymology. The species name *zappi* honours Mr Manfred Zapp, who not only discovered the specimen but also carried out excellent preparation and published the specimen for the first time.

Diagnosis. The following diagnosis is based on a unique combination of characters, among which possible autapomorphies are indicated with asterisks (*): more than three pairs of extrascapular bones; frontals less than three times longer than their maximal width; orbital sensory canal in the supraorbital bones*; saddle-like articular surface in the quadratojugal*; semitritorial dentition; four anterior infraorbitals; middle pit line contained in a groove in the dermopterotic and parietal; concave posterior border of the angular; robust bugle-like process of the posttemporal bone; large basal fulcra; 11 fin rays in the lower lobe of the caudal fin (below the lateral line); first, scale-like caudal fin ray reduced; anterior flank scales with serrated posterior borders. Pterygial formula:

$$\frac{\text{D26}}{\text{P8 A20 C32}} \text{T37}$$

Description

Scheenstia zappi is a medium size semionotiform with a relatively deep body (Fig. 3). As noted by Thies & Zapp (1997), the total length of the fossil is 34.5 cm. The fish has a standard length (SL: the length from the tip of the snout to the base of the caudal fin at the hinge line) of 30.2

cm, and the body depth is approximately 0.45 of the SL. The head is slightly longer than deep, head length being about 0.3 of total length. Although the bones in the most anterior region of the skull are generally disarticulated and slightly displaced, the antorbital portion of the skull is relatively short in comparison with other semionotiforms (Figs 4, 5). The preorbital length is only about 0.4 of the head length and approximately two times the longitudinal diameter of the eye. The depth of caudal peduncle is about 0.2 of the SL. The insertion of the pelvic fins is approximately midway between the pectoral and anal fins. The dorsal fin originates approximately midway between the pelvic and anal fins. Basal and fringing fulcra are preserved in all the fins, with the exception of the pectoral fins, which are more poorly preserved than the other ones. The body is completely covered with thick and unornamented rhomboid scales, among which most of the flank scales have serrated posterior borders. The dermal bones of the skull lack a ganoin cover, except for some ganoin patches and tubercles on the parietal, frontal, suborbitals, infraorbitals, dermopterotic, preoperculum and operculum. The pattern of ornamentation of the bones in the skull and pectoral girdle was described in detail by Thies & Zapp (1997).

Skull roof

Consistent with the observations of Thies & Zapp (1997), four small, approximately rectangular extrascapular bones are preserved on the right side of the fish (Figs 4–6). However, a fifth element is apparently missing medially. The preserved series of four extrascapulars does not reach the dorsal midline and there is no indication of the supraoccipital commissure in the parietal. Also, there is a slight thinness of the posterodorsal corner of the parietal, on which the putative fifth extrascapular would have been articulated. Therefore the complete extrascapular series probably included five paired elements. Preserved extrascapulars 1 to 4, from lateral to medial, articulate with the parietal and dermopterotic bones anteriorly, with the operculum ventrally, and with the posttemporal posteriorly. The first extrascapular articulates with the dermopterotic, the second extrascapular articulates with the dermopterotic and parietal, and the extrascapulars 3 and 4, the smallest in the series, articulate with the parietal only. Except for the extrascapular 4, which posteriorly contacts the dorsal-most scale of the first row, all extrascapulars articulate with the posttemporal posteriorly. The supraoccipital commissure is represented by relatively large pores in each of the extrascapular bones.

The parietal bone is rectangular, approximately 1.5 times longer than wide (Figs 4–6). The length of the parietal is about 0.3 of the length of the frontal. The parietal sutures with the frontal anteriorly, laterally with the dermopterotic and posteriorly with the three last extrascapular bones. The most dorsal scale of the first vertical series has a strong, broad anterodorsal articular process, which contacts the

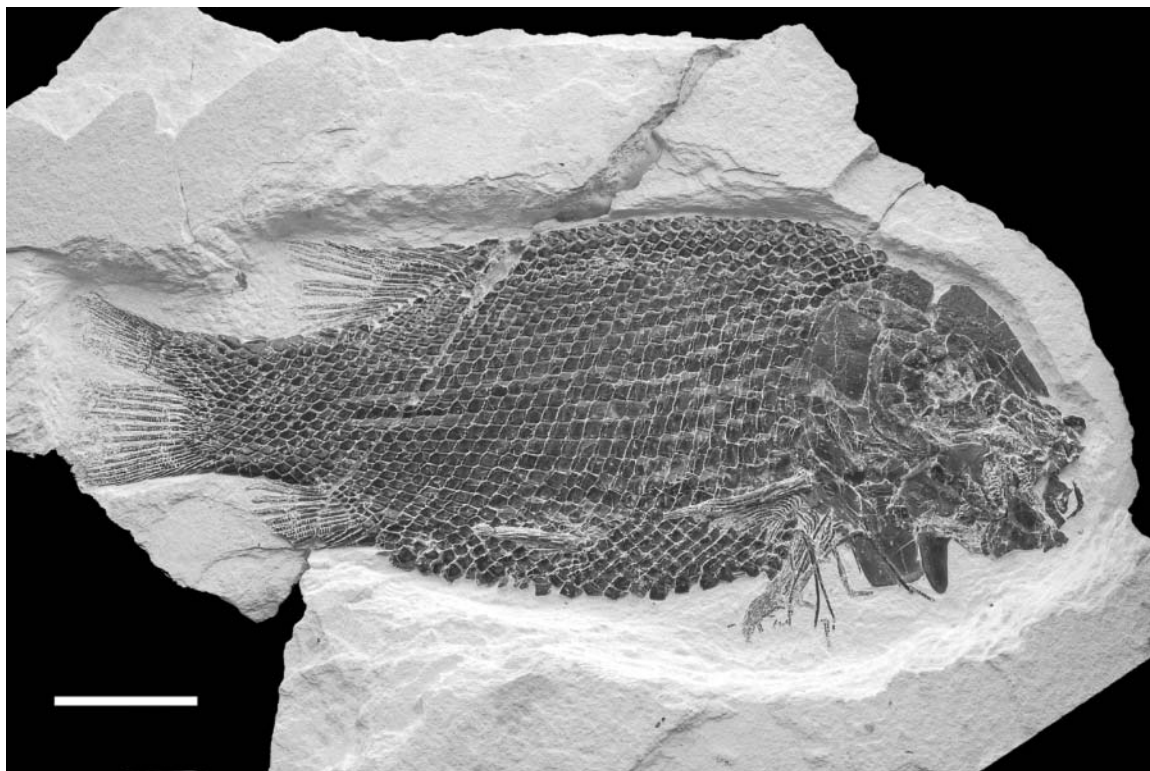


Figure 3. *Scheenstia zappi* gen. et sp. nov. Photograph of the holotype and only known specimen, JME-Sch 80, preserved in right lateral view. Scale bar = 5 cm.

posterior border of the parietal (Fig. 6). The medial border of the parietal is smooth with a single excavation posteriorly, indicating a mostly smooth inter-parietal suture and a posterior medial expansion of the left parietal. The supraorbital sensory canal enters the parietal very close to its lateral margin and bends posteriorly towards the midline. A dorsoventral groove in the posterior half of the parietal, which is pierced by three pores, is interpreted, in agreement with Thies & Zapp (1997), as the middle pit line. Similarly a series of three pores aligned in an antero-posterior direction immediately in front of the middle pit line and medial to the supraorbital canal is interpreted as the anterior pit line. A posterior pit line is absent. Additionally, several very small pores intercalate between the supraorbital sensory canal and the anterior and middle pit lines. These additional pores might represent ramifications or even connections between these sensory lines. The parietal is ornamented with tubercles of variable size, most of which are covered with ganoin.

The frontal is disarticulated, a little displaced anterodorsally and slightly rotated in clockwise direction. It is a long, approximately rectangular bone (Figs 4, 7). Anteriorly smoothly narrowed, it presents a supraorbital constriction and slightly widens posteriorly. The frontal is approximately 2.6 times longer than its maximal width. As noted by Thies & Zapp (1997), the inter-frontal suture is smooth, as evidenced by the smooth medial border of the preserved

right frontal. The posterior border of the frontal is also smooth, excepting a strong triangular posterior expansion close to its lateral border which articulates between the parietal and dermopterotic (Figs 7–8). Additionally, the frontal presents a medioventrally directed process, overlapped by the dermosphenotic. Therefore, the frontal articulates with the dermopterotic posterolaterally, and with the dermosphenotic and supraorbitals laterally. The supraorbital sensory canal is represented by a main line of pores, contained in a groove which is especially deep in the anterior third of the bone (Fig. 7). The canal runs at about one third from the lateral margin of the frontal in the anterior two thirds of the bone, before curving laterally to closely approximate the lateral margin of the frontal. Medial to the area where the main supraorbital canal curves laterally, there is an accumulation of numerous pores, which might represent branches of this main canal or pit lines. Except for the most anterior portion, which is smooth, the frontal is ornamented with scattered tubercles, most of which are covered with ganoin.

Both nasal bones are preserved, though it should be noted that the right element was misinterpreted by Thies & Zapp (1997, fig. 6; cf. Figs 4–5, 9 herein). The right nasal is preserved more or less in place, in external view. The left nasal is displaced anteriorly and dorsally, lying anterior to the right nasal and showing its internal view. The bones are small and approximately crescent-shaped. The sensory

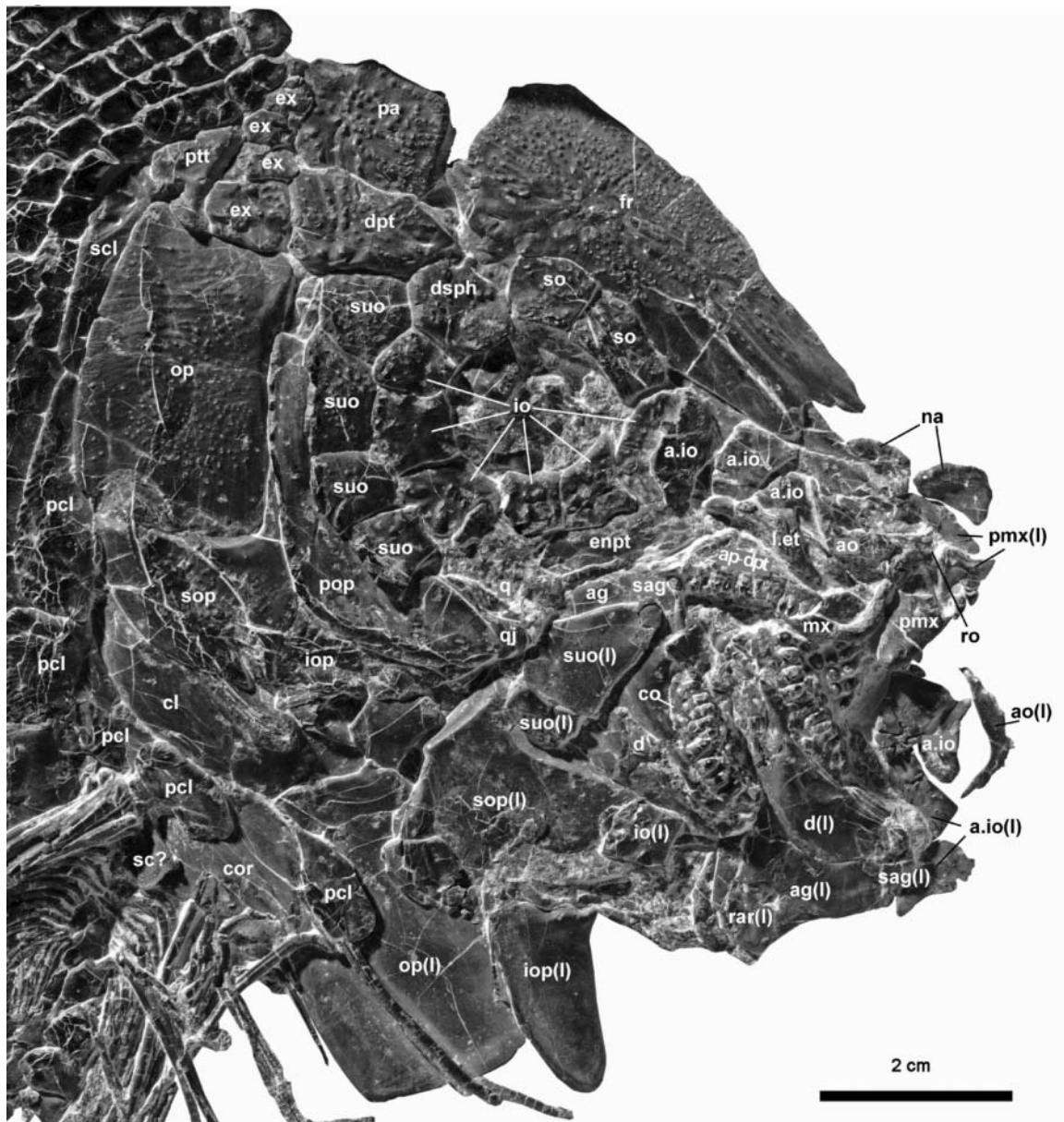


Figure 4. *Scheenstia zappi* gen. et sp. nov. Photograph of the skull of the holotype, JME-Sch 80. Scale bar = 2 cm.

canal runs into a groove close to the medial margin and bends laterally in the anterior portion towards the connection with the infraorbital canal in the antorbital bone, though such a connection is not directly observable. Lateral to the canal, the bone turns into a very thin, laminar membrane.

The dermopterotic bone is subrectangular in shape and smoothly narrowed in its anterior part (Figs 4–6). It is 1.4 times longer than deep and 1.2 times longer than the parietal. The dermopterotic contacts posteriorly with the anterodorsal corner of the operculum and with the two lateral-most extrascapular bones, and sutures with the parietal medially, with the frontal anteromedially, with

the dermosphenotic anterolaterally, and laterally with the dorsal-most suborbital and the preoperculum. The temporal canal is represented by relatively large pores aligned very close to the ventral margins of the dermopterotic and lateral-most extrascapular bones (Fig. 6). A dorsoventral groove in the posterior portion of the dermopterotic, which is pierced by four pores and is in continuity with a dorsoventral groove in the parietal, is interpreted as the ventral portion of the middle pit line. Additional pores, which may represent isolated pits, are placed anterior (three) and posterior (one) to the middle pit line. The ornamentation of the dermopterotic is very similar of that of the parietal.

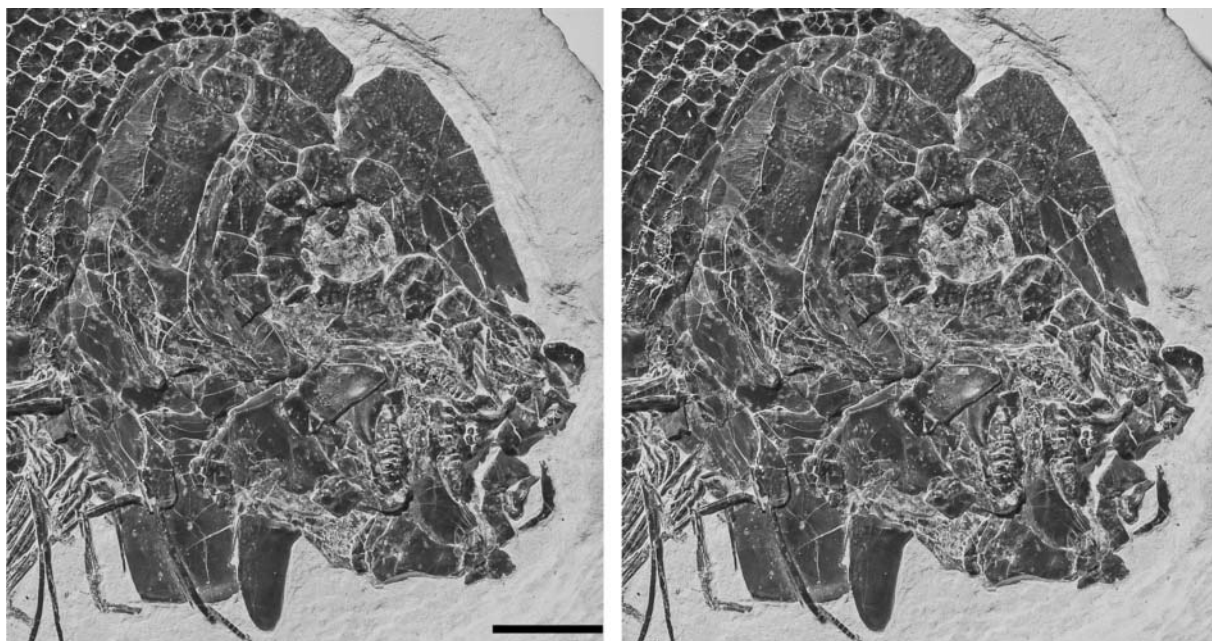


Figure 5. *Scheenstia zappi* gen. et sp. nov. Stereo photographs of the skull of the holotype, JME-Sch 80. Scale bar = 2 cm.

Braincase

The braincase is almost completely hidden, but a well-ossified lateral ethmoid protrudes at the level of the second anterior infraorbital (Figs 4–5, 9). The lateral ethmoid has a large, longitudinally elongated lateral process which is ventrally concave, forming a trough. This ventral trough resembles the condition in *Amia* (Grande & Bemis 1998) and *Pholidophorus germanicus* (Patterson 1975) in which such a trough forms an articular surface for the large autopalatine. Lateral ethmoids are rarely known in fossil basal neopterygians (Patterson 1975). Among semionotiforms, right lateral ethmoids are only known in one specimen of *Araripelepidotes temnurus* (MNHN MSE 635) where they are also well ossified, but in this specimen the lateral process is incompletely preserved and cannot be compared (Wenz & Brito 1996). Lateral ethmoids were doubtfully identified, but not described and only roughly illustrated in *Lepidotes semiserratus* (Stensiö 1932; Holmgren & Stensiö 1936; Rayner 1948).

Orbital series

The circumorbital series is complete and comprises two supraorbitals, a dermosphenotic, six infraorbitals, four anterior infraorbitals, and an antorbital (Figs 4–5, 8). All bones in this series are ornamented with scattered tubercles, which are covered with ganoin only in the supraorbitals, dermosphenotic and infraorbitals at the posterior border of the orbit. The supraorbital bones are rectangular and relatively large. The anterior supraorbital is the largest, as deep as the posterior supraorbital but about 1.2 times longer. It is

approximately two times longer than deep, and articulates with the first infraorbital anteriorly closing the circumorbital ring. The posterior supraorbital is about 1.3 times longer than deep. Both supraorbital bones are longitudinally traversed by a smooth groove perforated by small pores. This groove and pores are interpreted as a sensory canal, here named the orbital canal (Fig. 8).

The dermosphenotic is irregularly hexagonal, located at the posterodorsal corner of the orbit (Figs 4–6). It constitutes the largest bone located around the orbit. The bone overlaps the medioventrally directed process of the frontal and articulates with the dermopterotic dorsoposteriorly, with the dorsal-most suborbital posteriorly, with the last infraorbital ventrally, and the posterior supraorbital anteriorly. The sensory canals are shown by several pores (Fig. 6). In the anterodorsal portion, the dermosphenotic makes an anterodorsally-directed step where two relatively large pores face two large pores of the supraorbital canal close to the posteroventral margin of the frontal. Posterior to this step, two other pores open very close to the dorsal margin of the dermosphenotic and probably represent the connection with the temporal sensory canal. Close to the posteroventral margin of the dermosphenotic, a wide groove indicates the initial path of the infraorbital canal in the dermosphenotic. Additionally, a series of five smaller pores in a groove in the central portion of the bone represents the infraorbital canal. Close to the centre of the bone, this groove bifurcates several times, indicating intense branching of the infraorbital canal. However, two larger branches indicate a connection with the temporal canal on the one hand, and a connection with the

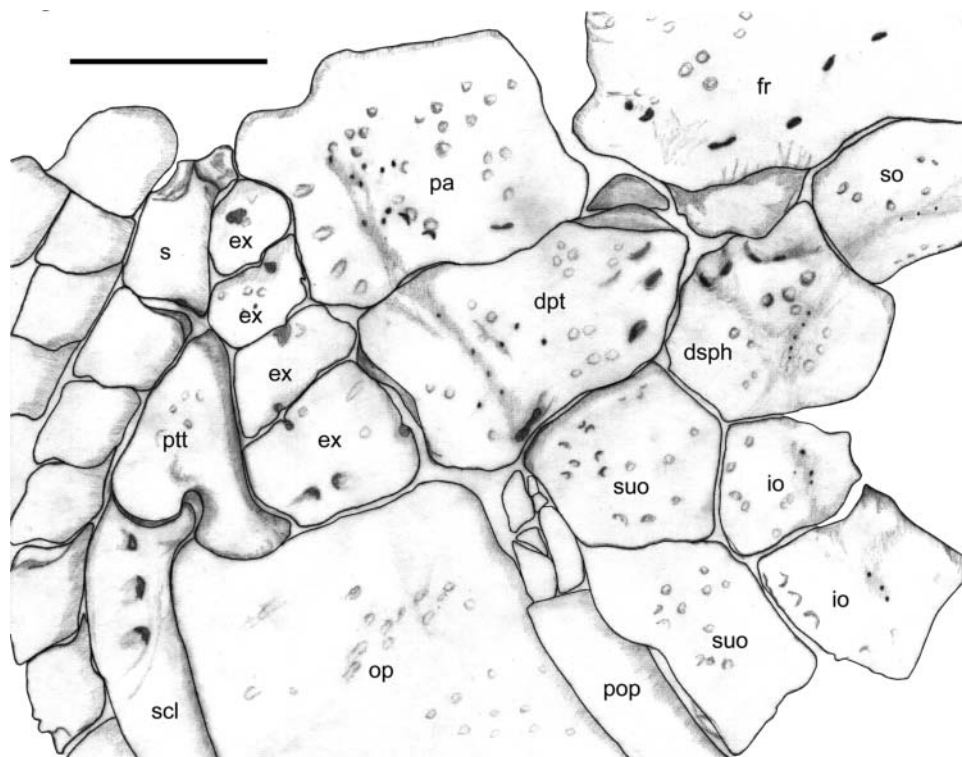


Figure 6. *Scheenstia zappi* gen. et sp. nov. Line drawing of the temporal and occipital regions of the skull of the holotype, JME-Sch 80. Scale bar = 1 cm.

orbital canal in the supraorbital bones on the other hand (Fig. 8).

There are six infraorbital bones (io1–io6 in anterior to posterior direction) and four anterior infraorbital bones (a.io1–a.io4 in anterior to posterior direction) (Figs 4–5, 8). Thies & Zapp (1997) did not distinguish between infraorbitals and anterior infraorbitals and reported nine infraorbitals in total, including a fragment of the third infraorbital as a separate element: “Das kleinste Infraorbitale befindet sich innerhalb des Ringes in einer ventrocaudalen Position und scheint durch Fragmentation aus einem der beiden benachbarten, größeren Infraorbitalia entstanden zu sein” (Thies & Zapp 1997, p. 19). The first and second anterior infraorbitals were also omitted in their count, but it should be noted that the first anterior infraorbital is completely disarticulated and displaced, while the second anterior infraorbital is approximately in place, but broken and badly preserved (see below). The last three infraorbitals (io4–io6) are quite similar in size and shape, all approximately quadrangular, narrowing smoothly towards the orbit. The posterior margins of these infraorbitals, io4–io6, are partially covered with patches of ganoin; io5 and io6 form the posterior margin of the orbit, and io4 is located at the posteroventral corner of the orbit. The trajectory of the infraorbital sensory canal in these three bones is indicated by a smooth groove running almost parallel to the margin

of the orbit, perforated by several small pores. Branches of the canal are not evident in infraorbitals 5 and 6. Instead, in io4, branching is indicated by four superficial grooves radiating from the centre of the main groove. The following two infraorbitals (io3–io2) are a little smaller than the preceding ones and slightly dorsally displaced. They form the ventral border of the orbit. The posteroventral portion of io3 is broken, still in articulation with io4; as mentioned above the rest of the bone is slightly displaced. Infraorbitals io3 and io2 are somewhat trapezoidal in shape, io2 being deepest anteriorly and only slightly larger than io3. In infraorbitals 2 and 3 the trajectory of the infraorbital canal is indicated by a groove, pierced by several small pores, running in the dorsal halves of these bones. Several larger ventrally directed openings indicate branches of the main sensory canal. The first infraorbital closes the circumorbital ring. It is a rectangular bone, approximately 2.2 times deeper than long, and articulates dorsally with the anterior-most supraorbital. There are four anterior infraorbitals (a.io4–a.io1) between the first infraorbital bone and the antorbital bone. The anterior infraorbitals are disarticulated and a little displaced, except for a.io1, which is completely displaced, and preserved isolated anterior to the skull (Figs 4–5, 9). However, their natural topographic relationships can be reconstructed (Fig. 8). All of the anterior infraorbitals have free dorsal margins, i.e. do not contact

other bones dorsally; a.io4–a.io2 are lateroventral to the anterior portion of the frontal and a.io1 is placed anterior to the frontal. The third and fourth anterior infraorbitals (a.io3–a.io4) are approximately rectangular; a.io4 is about 1.8 times deeper than long and a.io3 is 1.4 times deeper than long. The anterior infraorbital a.io3 forms a triangular anterodorsal expansion; the a.io2 is preserved in place, though broken, lying on the massive lateral ethmoid (Fig. 9). However, its shape can be reconstructed, also considering the shape of the disarticulated left anterior infraorbitals. The first two anterior infraorbitals (a.io1–a.io2) are approximately triangular, tapering dorsally. The infraorbital sensory canal runs through the centre of the first infraorbital (io1) and last anterior infraorbital (a.io4), and bends ventrally to approximate the ventral border of the other three anterior infraorbitals (a.io3–a.io1) (Fig. 8).

The right antorbital is preserved in approximately its natural position and the left antorbital is completely displaced, preserved anterior to the skull (Figs 4, 5). Thies & Zapp (1997) misinterpreted the left antorbital as the right element and did not recognize the other antorbital. The bone is slender and typically boomerang-shaped, with tapering ends. The horizontal arm is 1.35 (right element) to 1.4 (left element) times longer than the vertical arm. Little evidence of the trajectory of the sensory canal is preserved with the exception of two small openings on the most anterior portion of the lateral surface of the horizontal arm of the right antorbital (this surface is completely broken posteriorly) (Fig. 9). A small rostral bone is preserved almost in place, anterior to the antorbital (Fig. 9). The rostral has a right-angled triangle shape with its opposite side oriented to the midline, indicating that there were two paired rostrals, of which the right element is preserved. The ethmoidal commissure is revealed by a pore in the central part of the rostral.

Four suborbital bones are preserved articulated on the right side of the skull (Figs 4, 5) but this series is certainly incomplete. Two semiarticulated additional suborbital bones are separately preserved lateral to the right lower jaw (Figs 4, 5). They are preserved in lateral view and, considering their shape and bringing them back to their natural position (Fig. 8), we conclude that they correspond to the left side of the skull (in contrast to Thies & Zapp 1997). Consequently, the complete series of six suborbital bones in *Scheenstia zappi* is arranged in one row between the preoperculum and the circumborbital bones (Fig. 8). We thus disagree with Thies & Zapp (1997) who concluded that additional suborbital bones might have been present but not preserved. The dorsal-most suborbital is approximately trapezoidal, acuminate ventrally, and articulates with the last infraorbital and the dermosphenotic anteriorly, the dermopterotic dorsally and the dorsal tip of the preoperculum posteriorly (Figs 4–6). The following suborbital is the largest of the series, approximately rectangular, with an anterior narrowed portion, posterodorsally acuminate and

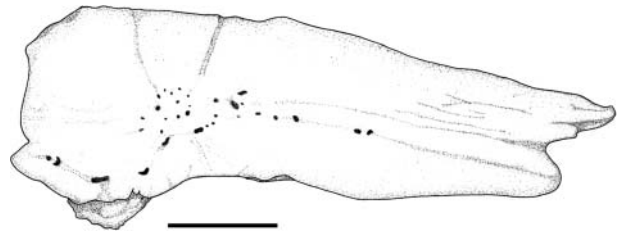


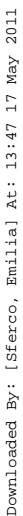
Figure 7. *Scheenstia zappi* gen. et sp. nov. Line drawing of the frontal bone in the holotype, JME-Sch 80. Scale bar = 1 cm.

about 1.5 times deeper than wide (Figs 4–6). The following two suborbitals are quadrangular, approximately the same width as the second (Figs 4, 5). As mentioned above, the second suborbital bone (numbering the bones in anterior to posterior direction) is disarticulated and displaced, and corresponds to the left side of the skull. It is the smallest in the series and approximately rectangular. The most anterior suborbital, which is also disarticulated and displaced from the left side of the skull, is subtriangular and completes the dermal cover of the cheek, which completely hides the ossifications of the palatoquadrate. Reconstructing the suborbital series in its natural position, suborbital 1 is placed ventral to the orbit, suborbitals 2 and 3 articulate following the posteroventral corner of the orbit, and suborbitals 4–6 are placed posterior to the orbit.

Hyopalatine bones

The quadratojugal is well exposed at the anterior end of the preoperculum (Figs 4, 5, 9, 10). The exact shape of the bone is unknown because it is partially covered by the preoperculum and dorsally broken. The exposed portion forms a strongly sinuous anterodorsal border and an expanded, anteroventrally rounded anterior portion. The quadratojugal is an independent bone articulating with the quadrate medially and with the preoperculum laterally. The ventrolateral surface of the expanded anterior portion is free and forms a saddle-shaped surface directed anteriorly, which probably articulated with the lower jaw (Fig. 10). The quadrate is incomplete and rather poorly preserved. The dorsal and posterior borders of the bone are broken, but the ventral and articular portions are relatively well preserved. The articular portion is relatively large and strongly ossified (Fig. 10). The posteroventral margin of the quadrate is laterally expanded forming a flat surface, slightly concave anteriorly, which articulates with the anterior expanded portion of the quadratojugal anteromedially. The quadratomandibular articulation is not preserved. However, considering the location of the quadrate, it probably took place halfway between the centre and the anterior border of the orbit.

The metapterygoid lamina is only partially exposed and poorly preserved dorsal and posterior to the quadrate. The pterygoid bones are very difficult to interpret. The



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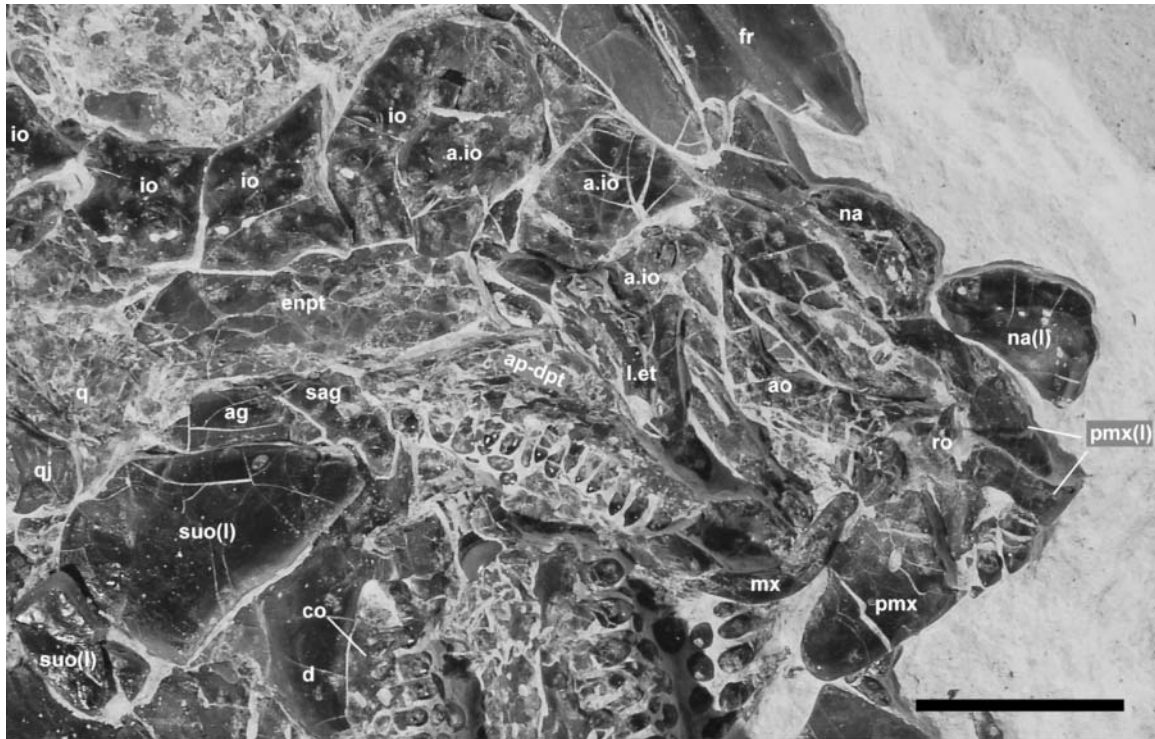


Figure 9. *Scheenstia zappi* gen. et sp. nov. Detailed photograph of the ossifications of the palatoquadrate and snout in the holotype, JME-Sch 80. Scale bar = 1 cm.

0.5 of the depth of the operculum. The suboperculum has a well developed anterodorsal process, which is about half the length of the suboperculum and reaches up to approximately 0.25 of the total depth of the operculum. The free borders are smooth and it shows a similarly rugose and tuberculous surface to that of the operculum, though the tubercles are less abundant. The suboperculum is pierced by several small pores. Both interoperculae are also preserved. The right interoperculum is articulated and, thus, partially hidden by the preoperculum. The left interoperculum is disarticulated, displaced ventrally and preserved in medial view. It is two times longer than its maximal depth and does not reach the anterior end of the preoperculum. It is also pierced by numerous small pores. As noticed by Thies & Zapp (1997), branchiostegal rays are very badly, if at all, preserved.

The strongly ossified preoperculum is crescent-shaped, concave anteriorly, forming an angle of about 110° . It reaches the dermopterotic dorsally and articulates with the suborbital series anteriorly. The preopercular sensory canal runs enclosed in the thickened anterior and anterodorsal margin of the preoperculum and exits the bone through six large openings. The most anterior three openings are anteroventrally directed, while the posterior three openings are posteroventrally directed. The preopercular sensory canal enters the dermopterotic close to its posterior border and is in continuity with the median pit line (Fig. 6). Small

pores are also present in the preoperculum. The posterior and ventral borders of the preoperculum are straight, and the surface is smooth, with only a thin layer of ganoin covering the posterior margin of the bone (Figs 4, 5).

Jaws

The upper jaw is completely disarticulated (Figs 4, 5, 9). Both premaxillae are only partially preserved. As noted by Thies & Zapp (1997), the nasal processes of the premaxillae are large, though badly preserved. A relatively small foramen for the olfactory nerve is placed at the base of the nasal process of the right premaxilla (Fig. 9). Some premaxillary teeth are shown, but their exact number and arrangement is unknown. The premaxillary teeth are strong and styliiform. Thies & Zapp (1997) noticed that the maxilla is broken and poorly preserved between the bones of the palatoquadrate and the displaced left lower jaw. It has a long, cylindrical, anteromedially directed articular process. The main body of the maxilla is badly broken, thus it is not possible to reconstruct its shape and extent. A supramaxilla is not preserved or absent.

Both lower jaws are displaced and preserved in lateral view (Figs 4, 5). The dentary is a large, robust bone which deepens posteriorly in the coronoid process. As usual in semionotiforms, the dentary has a well developed posteroventral process, which in this case does not reach the posterior border of the lower jaw. The dentaries

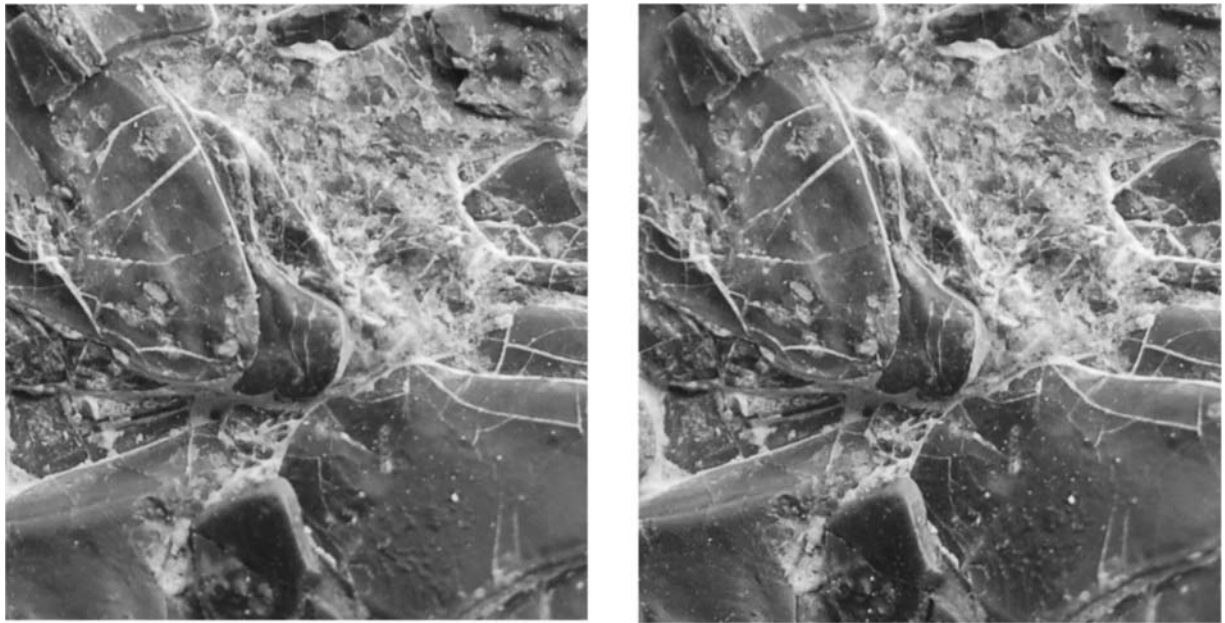


Figure 10. *Scheenstia zappi* gen. et sp. nov. Detailed stereo photographs of the holotype (JME-Sch 80) showing the peculiar shape of the quadratojugal. Scale bar = 0.5 cm.

have a row of five marginal, robust styliform teeth. As described by Thies & Zapp (1997), one coronoid bone is preserved in place, articulating with the dentary posterior to its toothed portion. This coronoid has a marginal row of at least five styliform teeth, which are only slightly smaller than the teeth on the dentary. Additional rows (at least four additional rows are evident in the right mandible) of gradually more tritorial teeth are preserved medially. The most internal teeth are button-like and as large as the observed palatopterygoid teeth. Two completely disarticulated button-like teeth are even larger than the largest teeth observed in the lower jaw or the palatopterygoid region. The coronoid process is very high, representing approximately 0.55 of the total length of the lower jaw. The angular bone is large, with a slightly concave posterior border. The posteroventral corner of the angular is well preserved and forms a triangular projection beyond the retroarticular. The surangular bone crowns the coronoid process, articulating with the most dorsal borders of the dentary and angular bones. The retroarticular bone was not recognized by Thies & Zapp (1997), but is partially preserved ventral to the angular and posterior to the posteroventral process of the dentary. The passage of the mandibular sensory canal is revealed by a series of pores close to the ventral margin of the angular bone. It continues in the dentary dorsal to the posteroventral process and follows forwards through the centre of the bone. Additional smaller pores are distributed dorsal and ventral to the mandibular canal in the dentary and only dorsally in the angular. Thies & Zapp (1997) interpreted some of these pores as an additional canal, but we

find no evidence to confirm that the pores would have been related to a series of additional neuromasts.

Pectoral girdle

The cleithrum, supracleithrum, posttemporal, five postcleithra and two coracoids are preserved (Figs 4, 5). With the exception of the two most dorsal postcleithra, all the dermal bones in the pectoral girdle are smooth and with smooth posterior borders. The cleithrum is a large crescent-shaped bone with narrowing anterior and posterior ends. The dorsal portion of the cleithrum is hidden by the operculum and suboperculum. After reconstructing its natural position, the ventral portion of the cleithrum reaches the level of the posterior border of the orbit anteriorly (Fig. 8). The edge between the branchial and lateral surfaces of the cleithrum forms a robust ridge, along which rest at least three series of tiny denticles, also noted by Thies & Zapp (1997) (Figs 4, 5).

The supracleithrum is almost completely exposed, deep and narrow, about four or five times deeper than wide, with thickened anterior border and laminar posterior portion. Anterodorsally, the supracleithrum is laterally expanded forming an approximately circular concave articular surface for the posttemporal (Fig. 6). The supracleithrum is not covered with ganoin. Three large pores indicate that the lateral line traverses the central portion in the dorsal third of the supracleithrum in anterodorsal to posteroventral direction. The posttemporal is relatively small, but robust, and triangular, tapering dorsally, reaching the level of the articulation between the second and third extrascapulars

(Figs 6, 8). The posterior portion of the posttemporal is ornamented with scarce tubercles, some of which are covered with ganoin. The posttemporal has a very robust cylindrical anteroventral process with a slender shaft and an expanded distal end (Fig. 6). The distal surface of this bugle-like process (only the edge of which is exposed) is slightly convex and oriented ventro-medially. Despite the orientation of the bugle-like process, it does not seem to have reached the braincase. The posteroventral portion of the posttemporal is deeply convex and articulates with the expanded concave surface of the supracleithrum. It is not possible to recognize a trajectory of the sensory canal in the posttemporal with certainty. A single pore is placed at the base of the bugle-like process, in the deep concavity between this process and the posterior rounded portion of the bone.

There are five postcleithra aligned along the distal margin of the cleithrum (Figs 4, 5). Unlike Thies & Zapp (1997), we find no evidence for additional elements in this series. All postcleithra have ganoin on their distal margins. Close to the distal border of the dorsal-most postcleithra (postcleithra 5 and 4 if the bones are numbered in anterior to posterior direction) the ganoin cover forms posteroventral to posteriorly directed ridges. The dorsal-most postcleithrum is the largest, about two times deeper than the following postcleithrum, which is approximately as deep as long, with the anterior border slightly sinuous. On the dorsal portion of the distal margin of the most dorsal postcleithrum, the ganoin ridges end before reaching the distal border of the bone, which is smooth. Ventrally, the ganoin ridges on the fifth and fourth postcleithra gradually approximate the distal border of these bones. The ventral portion of the distal border of the fifth postcleithrum and the distal border of the fourth postcleithrum are broken, but according to the extension of the ganoin ridges these borders were probably serrated, as is the case of the adjacent scales. The third postcleithrum is the smallest in the series and is approximately quadrangular in shape. The second postcleithrum is oblong and the first postcleithrum, displaced anteroventrally, is petal-like. According to the extension of the ganoin cover and presence of small tubercles, the three anterior-most postcleithra partially overlapped each other (Fig. 8).

The endochondral elements of the pectoral girdle are partially exposed. There is a very large and laminar coracoid ossification, exposed ventral to the cleithrum (Figs 4, 5). A fragment of bone preserved at the base of the pectoral fin might represent the scapula. The propterygium is poorly exposed anterior to the basis of the right pectoral fin rays. Two elongate radials are poorly preserved below the scapular ossification.

Paired fins

Both pectoral fins are partially preserved (Fig. 3). Although the right pectoral fin is partially disarticulated and the fin rays are distally broken, it is clear that only one pair of

basal fulcra was present. The presence of fringing fulcra is doubtful. Although no fringing fulcrum is preserved, the quality of preservation is not good enough to be certain about their absence. The first fin ray is broken, but was probably not segmented or branched. The next few rays only branched very distally, if at all. The exact number of pectoral rays is dubious, but the bases of 13 lepidotrichia are articulated in the right pectoral fin; this is probably the total number. When the bases of the pectoral rays are well preserved a small spinous process is evident. In the few articulated rays this process is directed dorsally.

Only the right pelvic fin is preserved (Fig. 3). This pelvic fin is placed at about 0.5 of the standard length, approximately midway between the pectoral and anal fins, immediately behind the eighth vertical row of scales. The pelvic fin inserts at about 87.5% of the body depth, where a well developed unpaired basal fulcrum is followed by one pair of basal fulcra and at least four long and slender paired fringing fulcra. The two most distal fringing fulcra are segmented. The number of pelvic fin rays is unknown because the fin is completely folded.

Unpaired fins

The dorsal fin inserts about midway between the pelvic and anal fins, approximately 0.7 of the standard length, immediately behind the 26th vertical row of scales (Fig. 3). The dorsal fin is preceded by a large scute and has one small, unpaired basal fulcrum and three paired basal fulcra (Fig. 11A). Six long and slender fringing fulcra are preserved lying on the first ray. There are 12 lepidotrichia (versus 11 lepidotrichia reported by Thies & Zapp 1997). All the dorsal fin rays are segmented, with the basal segment notably longer than the following ones. In all the rays, excepting the first, the segments are fused together in the basal portion before the first branching. The number of segments fused in this basal, more rigid portion of the ray increases from the anterior part to the centre of the fin and decreases posteriorly. Excepting the first ray, which is unbranched, all other rays branch distally at least twice. The basal and fringing fulcra and the basal portion of the first dorsal fin ray are covered with a thin layer of ganoin.

The anal fin inserts at about 0.78 of the standard length, immediately behind the 20th vertical row of scales (Fig. 3). It is smaller than the dorsal fin and has one unpaired and two paired basal fulcra followed by a series of fringing fulcra, the number of which is unknown because the distal portion of the fin is not preserved (Fig. 11B). There are 10 lepidotrichia (versus eight lepidotrichia reported by Thies & Zapp 1997). The first lepidotrichium is more robust than the following ones. All lepidotrichia are segmented, with a notably longer basal segment. Resembling the case of the dorsal fin, the rays have a more rigid proximal portion, including the basal segment and a few fused segments; however, in the more anterior rays the branching starts more distally. The preserved portion of the first leading ray is not

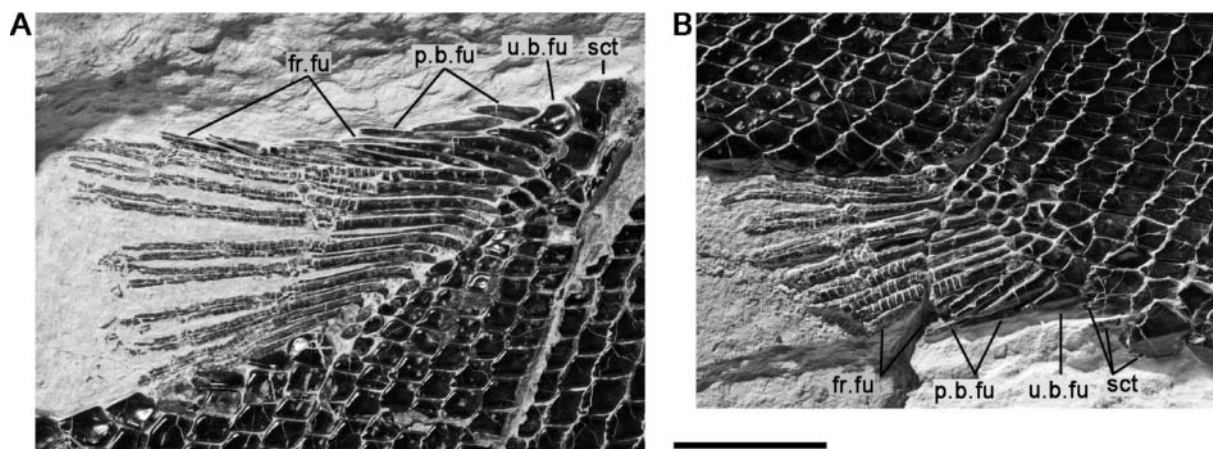


Figure 11. *Scheenstia zappi* gen. et sp. nov., holotype, JME-Sch 80. **A**, photograph of the dorsal fin; **B**, photograph of the anal fin. Scale bar = 2 cm.

branched and the following ray branches at least once. The basal and fringing fulcra and the basal segment of the first ray are covered with ganoin. Tiny patches of ganoin lie on the centre of several segments in the first ray.

The caudal fin is very well preserved and the fin web is concave (Fig. 3). There are three ventral paired basal fulcra followed by at least six long and slender fringing fulcra (Fig. 12). The first pair of basal fulcra insert at the 32nd vertical row of scales. Eight dorsal caudal fulcra lie on the body lobe of the tail. Only the last two dorsal caudal fulcra are paired. They are followed by at least five long and slender fringing fulcra. The first caudal ray is largely reduced, only represented by two scale-like segments between the dorsal fringing fulcra and the first principal caudal fin ray, aligned with the inverted row of scales immediately ventral to the major axis of the body lobe. There are 23 principal caudal fin rays in total, 11 and 12 lepidotrichia ventral and dorsal to the lateral line, respectively. The central lepidotrichia are the thickest, becoming thinner both dorsally and ventrally. However, the most dorsal rays are thinner than the most ventral rays. In the central rays, segments are shorter than in more marginal ones. Along a single ray, all segments, except the proximal-most, are of about the same length. The proximal segment is always longer, but only by up to about 20% of the total length of the ray, measured on the marginal rays. In both dorsal and ventral margins of the caudal fin there is a single unbranched marginal principal ray. The second ventral principal ray is also unbranched, and all other lepidotrichia branch at least two times. All the caudal fulcra (ventral basal fulcra, dorsal caudal fulcra, and ventral and dorsal fringing fulcra) are covered with ganoin, and there are patches of ganoin on the segments of all the principal caudal fin rays.

Squamation

There are 37 vertical rows of scales between the pectoral girdle and the hinge line, with a maximum of 26 scales at

the seventh vertical row (Fig. 3), and 10 inverted rows of scales forming the body lobe of the tail (Fig. 12). Three additional vertical rows of a few scales (5, 4 and 3 from anterior to posterior, respectively) are placed posterior to the 37th vertical row and ventral to the inverted rows of the body lobe. The scales of the lateral line are aligned with the most dorsal scales of these additional vertical rows. However, no pores are observed beyond the 37th vertical row. The posterodorsal to anteroventral axis (major axis) of the body lobe is 0.7 of the depth of the caudal peduncle, and approximately equivalent (1.1) to the depth below the lateral line (measured including the scales of the lateral line). At this major axis, the two longest inverted rows of scales include 10 and 12 scales, the last of which are largest and tapering posterodorsally (Fig. 12). Four inverted scale rows participate on the posterior margin of the body lobe, including 12, 12, 9 and 2 scales from dorsal to ventral, respectively.

The ganoid scales on the flanks are rectangular, approximately 1.5 times deeper than long (Fig. 3). The scales become quadrangular both dorsally and ventrally, and rhomboidal on the caudal peduncle. The surface of all the scales is smooth, but their posterior border is variably serrated or smooth: completely serrated in scales of the anterior portion of the flank, but serrations decrease gradually in dorsal, ventral and posterior directions. Thus the scales close to the dorsal and ventral midlines and on the caudal peduncle have smooth borders. There is a complete series of 24 dorsal ridge scales between the skull and the dorsal fin, only slightly larger than adjacent scales and covered with ganoin. Each dorsal ridge scale presents a pronounced spine directed posteriorly. These spines are gradually larger posteriorly. The exposed area of the more anterior dorsal ridge scales (about 10) is remarkably circular and flat. Immediately following the series of dorsal ridge scales and preceding the dorsal fin is a large median scute, which is broad and flat and has a low posterior spine

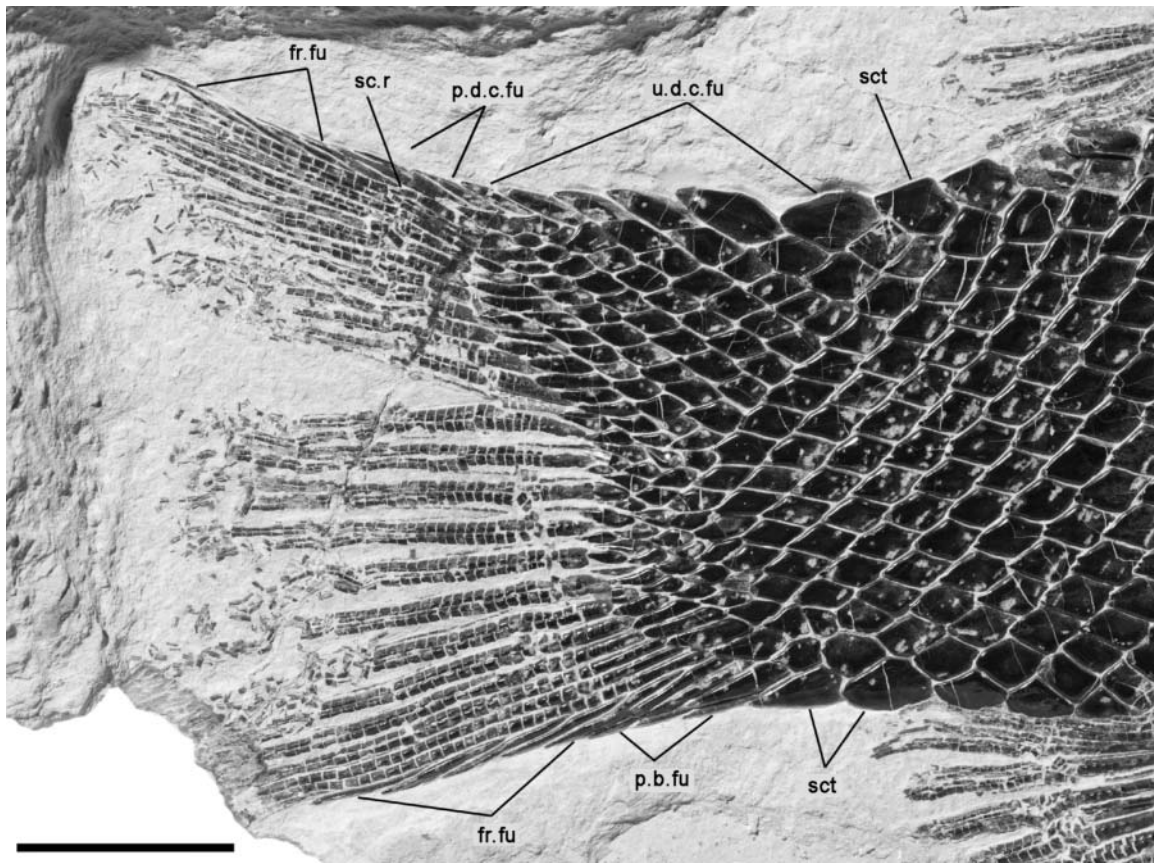


Figure 12. *Scheenstia zappi* gen. et sp. nov. Photograph of caudal fin in the holotype, JME-Sch 80. Scale bar = 2 cm.

(Fig. 11A). This large scute is aligned with a series of four additional rhomboid scales, which are distinct, not aligned with the vertical rows of scales, but surrounding the bases of the dorsal basal fulcra and first and second dorsal fin rays. Otherwise the scales at the base of the dorsal fin are well aligned with vertical rows of scales, but notably smaller. About six hexagonal, unornamented median scales, which increase in size posteriorly, garnish the dorsal midline between the dorsal fin and the hinge line (Fig. 12). Only the most posterior of these dorsal scales is notably larger than the adjacent scales and can be distinguished as a scute. A series of five median scales also lie on the ventral midline between the anal and caudal fins (Fig. 12). As the dorsal equivalents, these ventral median scales are distinct in shape, but only the two most posterior are larger than adjacent scales and thus distinguished as scutes. There are three large scutes preceding the anal fin, a median element followed by a pair of lateroventral scutes (Fig. 11B). These scutes probably surrounded the vent. The left lateroventral scute is preserved in sagittal view, but the other two scutes are well exposed and show smooth surfaces and strongly serrated posterior borders.

Discussion

As mentioned in the Introduction, although ‘semionotids’ from the Late Jurassic limestones of the Franconian and Swabian Alb are in need of revision, not only do most of the species seem to be valid but additional new taxa are being discovered (López-Arbarello pers. obs.). Among these the specimen described in this article, previously published by Thies & Zapp (1997) as *Lepidotes* sp., is shown to represent a new taxon, *Scheenstia zappi* gen. et sp. nov. The presence of a series of anterior infraorbital bones and the absence of gular plates in *S. zappi* support its referral to the Semionotiformes (Olsen & McCune 1991, Cavin & Suteethorn 2006, López-Arbarello 2009). Among semionotiforms, *S. zappi* lacks the synapomorphies of Lepisosteidae (Wiley 1976) or Macrosemiidae (Bartram 1977). As mentioned in the Introduction, all semionotiforms that are not lepisosteids or macrosemiids are currently grouped in a single Family Semionotidae, but since such an assemblage is probably polyphyletic (López-Arbarello 2008b) and no other family is properly defined within this order, we leave *Scheenstia* as Semionotiformes

incertae family, pending the completion of an ongoing analysis of semionotiform phylogenetic relationships (López-Arbarello in press.).

Due to the lack of phylogenetic analyses of interrelationships between species currently grouped in Semionotidae, autapomorphic features in *S. zappi* cannot be properly established. However, *Scheenstia* differs from all other semionotiforms represented by comparable material, in the presence of a sensory canal in the supraorbital bone, here called the orbital canal, and a saddle-like articular surface in the quadratojugal. This saddle shape in the ventrolateral surface of the expanded anterior portion of the quadratojugal probably articulated with the lower jaw, posterior to the articulation of the quadrate. The right lower jaw in the single specimen of *S. zappi* is disarticulated, and the displaced left lower jaw is preserved in lateral view. Therefore, no direct evidence for such articulation is observed. However, we have observed a comparable condition in the quadrato-mandibular articulation of some Jurassic basal teleosts. In teleosts the lower jaw articulates only with the quadrate, but in several taxa this bone has a ventrally directed articular surface additional to the larger anteriorly directed articular prong (Fig. 13). Such a condition is present at least in the Jurassic *Tharsis dubius* (specimens BSPG 1960-XVIII-98 in Fig. 13A, BSPG 1964-XXIII-280, BSPG 1961-III-23, and BSPG 1964-XXIII-160 among others; also Nybelin 1974, pl. 14, fig. 2) (see Nybelin 1974, *Leptolepis normandica*, pl. 3, fig. 3, pl. 4, fig. 2, and *Leptolepides sprattiformis*, pl. 25, fig. 3), *Anaethalion knorri* (specimens BSPG 1991-I-122 in Fig. 13B; BSPG 1960-XVIII-93, BSPG 1969-XVI-39, BSPG 1969-XVI-31, BSPG 1964-XXIII-394, BSPG 1953-I-97 among others; see also Nybelin 1967, pl. 2, fig. 1 (*Anaethalion knorri*) and fig. 2 of (*Anaethalion angustus*)) and *Orthogonikleithrus leichi* (JME-SOS 2632; Fig. 13C). In these fishes, the ventral articular surface is placed at the level at which it would be the ossification centre of the quadrate (Arratia & Schultze 1991, Arratia 1999), and apparently enables the vertical rotation of the lower jaw. The saddle-shaped surface in the quadratojugal of *Scheenstia* takes a similar position to that of the ventral articular surface of the teleost quadrate, and might have played a similar role (see discussion below).

Apart from two possible autapomorphic features, the combination of characters in the diagnosis is uniquely found in *Scheenstia zappi*. Among semionotiforms outside Lepisosteidae and Macrosemiidae, this new taxon most closely resembles the species of *Lepidotes* Agassiz, 1832 and, unsurprisingly, the new fish from Schamhaupten was initially identified as a species of this genus (Thies & Zapp 1997). *Scheenstia* resembles *Lepidotes* in several morphological features, such as the series of suborbital bones arranged in one row and extending anteriorly, ventral to the orbit, and the presence of a reduced scale-like first caudal fin ray. The first of these features represents a

condition otherwise only present in *Isanichthys* among semionotiforms. The second feature is only found in fishes within Semionotiformes, but might represent a plesiomorphic condition because a reduced, scale-like first caudal fin ray is also present in *Dapedium* (Wenz 1968) and some basal teleosts like *Pholidophorus bechei* (Patterson 1968). Among semionotiforms the most common – though probably derived – condition is the presence of a fully developed, scale-like first caudal fin ray. Such a feature is observed in the lepisosteids *Lepisosteus* and *Atractosteus* (Wiley 1976), macrosemiids *Macrosemius* (Bartram 1977), *Propterus* (Bartram 1977; BSPG 1986-XV-121, BSPG 1964-XXIII-145b) and also in *Paralepidotus* (BPG 2003-XXIX-632, BSPG 2007-I-62), *Semiolepis* (Lombardo & Tintori 2008) and *Semionotus minor* (lectotype GSM 27975).

The large tritorial forms of the Late Jurassic and Early Cretaceous of Europe, currently referred to *Lepidotes* (i.e. *L. mantelli* Agassiz, 1833, *L. fittoni* Agassiz, 1833, *L. laevis* Agassiz, 1837, *L. maximus* Wagner, 1863, *L. decoratus* Wagner, 1863, *L. degenhardti* Branco, 1885) differ from the new taxon in the presence of an extremely tritorial dentition (see Jain 1983 for a definition of this kind of dentition) and a very deep mandibular symphysis, features that are absent in *Scheenstia*. Furthermore, *Scheenstia* can be distinguished by the shape of the infraorbital bones placed at the posterior border of the orbit, which are expanded posteriorly (thus being longer than deep) in those tritorial species of *Lepidotes*. The latter feature is also present in the primitive gar *Masillosteus* Micklich & Klappert, 2001, *Araripelepidotes* Santos, 1990, *Pliodetes* Wenz, 1999, and *Isanichthys* Cavin & Suteethorn, 2006. *Scheenstia* further has high basal fulcra, a condition that resembles the case in *Semionotus* Agassiz, 1832, but is very different from that in *Lepidotes*, in which the basal fulcra are low and small (López-Arbarello 2008a).

In addition to the taxonomically significant morphological features discussed above, other anatomical characters in *Scheenstia* deserve discussion due to their importance concerning character evolution of in neopterygian fishes. The saddle-like articular surface of the quadratojugal is a very interesting feature of *Scheenstia*. As mentioned above, the additional ventral articular surface observed in the quadrate of some basal teleosts (see species indicated above), might enable the rotation of the lower jaw. In these fishes, when the mouth is closed, the ventral articular surface of the quadrate is free (Fig. 13), but when the mouth is open it articulates with the postarticular process of the lower jaw (*Tharsis dubius*, BSPG 1964-XXIII-280). Due to the development of the postarticular process of the lower jaw in teleosts (Nelson 1973), such a ventral articular surface might have developed in the quadrate of these basal teleosts to allow the rotation of the lower jaw. Simultaneously, the articular surface of the quadrate might have served as a stop, preventing an extreme downward rotation of the lower jaw. Although the saddle-like articular surface

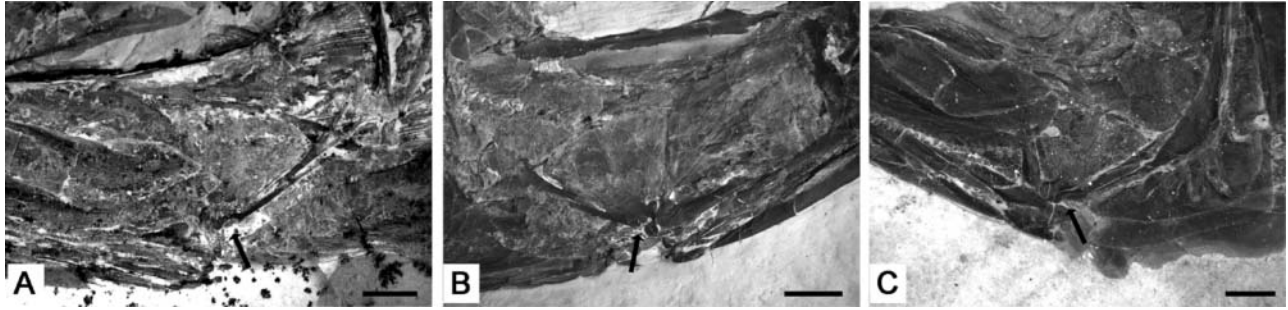


Figure 13. Detailed photographs of the quadrate bone in three Jurassic teleosts showing a ventrally directed articular surface (indicated with black arrows) additional to the larger anteriorly directed articular prong. **A**, *Tharsis dubius* (BSPG 1960-XVIII-98); **B**, *Anaethalion knorri* (BSPG 1991-I-122); **C**, *Orthogonikleithrus leichi* (JME-SOS 2632). Scale bars = 0.2 cm.

in the quadratojugal of *Scheenstia* differs in shape (saddle versus concave) and orientation (anteroventral versus ventral) from the ventral articular surface in the quadrate of basal teleosts, it might also have served in the rotation of the lower jaw, though in a way that we cannot yet understand due to inadequate evidence. Although the area forming this ventral articular surface, as well as the whole posteroventral margin and posterodorsal process of the teleost quadrate, might be homologous with the quadratojugal (Allis 1909; Holmgren & Stensiö 1936; Patterson 1973, 1977; Jollie 1975, 1984, 1986; Wiley 1976; Bartram 1977; Sanford 2000), the condition in *Scheenstia* and basal teleosts is probably not homologous. The evolutionary trend in teleosts is towards the complete fusion and reduction of the quadratojugal, which might be limited to the postero-dorsal process of the compound quadrate in advanced teleosts (Patterson 1977; López-Arbarello & Sferco pers. obs.). Among semionotiforms, a similar trend is observed in macrosemiids (Bartram 1977) and closely related forms (López-Arbarello unpublished data). However, in lepisosteids, *Lepidotes* and *Scheenstia* the quadratojugal is very well developed, and in *Scheenstia* and the gars it takes an important role in quadrato-mandibular articulation (Wiley 1976).

Another interesting feature in the anatomy of *Scheenstia zappi* is the presence of numerous small pores on the dermal bones forming the skull roof, circumborbital series, suborbitals and preopercular bones and opercular series. Thies & Zapp (1997, p. 22) judged these pores to be related to superficial neuromasts. Thies & Zapp (1997) further noticed the similarity between the pores in *S. zappi* and those described by Malzahn (1963) in the operculum of a specimen of *Lepidotes elvensis* from the Toarcian of Mecklenburg, Germany. Based on the histological analysis of these structures, Malzahn (1963) concluded that the pores were associated with the nutritional system of the epidermis. This hypothesis was rejected by Thies & Zapp (1997) who argued that, in that case, similar pores would also be present and regularly spread in the other skull bones, includ-

ing the jaws. We find this argument unfounded. Nutritional pores are not necessarily regularly distributed and, for both nutrition and irrigation, such pores are not expected where the musculature separates the bones from the epidermis. Thus we find both hypotheses equally plausible and it is not possible to distinguish between them on the basis of fossil evidence alone.

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