



New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China)

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Abstract

We report on a new species of the neopterygian genus *Sangiorgioichthys* Tintori and Lombardo, 2007, from middle Anisian (Pelsonian) deposits in South China (Luoping County, Yunnan Province). *Sangiorgioichthys* was previously known from a single species, *S. aldae*, from the late Ladinian of the Monte San Giorgio (Italy and Switzerland). The recognition of the new species helped to improve the diagnosis of the genus, which is mainly characterized by the presence of broad posttemporal and supracleithral bones, one or two suborbital bones occupying a triangular area ventral to the infraorbital bones and lateral to the quadrate, and elongate supramaxilla fitting in an excavation of the dorsal border of the maxilla. *Sangiorgioichthys sui* n. sp. differs from the type species in having two pairs of extrascapular bones, the medial pair usually fused to the parietals, maxilla with a complete row of small conical teeth, long supramaxilla, more than half of the length of the maxilla, only two large suborbital bones posterior to the orbit, and flank scales with finely serrated posterior borders. With the discovery of *S. sui* n. sp., the number of fish genera shared by the Anisian/Ladinian deposits in the Alps and the Anisian deposits in South China increases, including not only the cosmopolitan *Birgeria* and *Saurichthys*, but also, among others, the subholosteans *Colobodus* (so far only in Panxian), *Luopingichthys* (so far only in Luoping), *Peltopleurus*, *Habroichthys*, and the very specialized neopterygians *Placopleurus* and *Marcopoloichthys* (only in Luoping). Therefore, although several fish taxa remain to be studied in the Chinese faunas, the so far available evidence indicates close biogeographic relationship between the Middle Triassic marine faunas of the Western Tethys region.

Key words: taxonomy, Actinopterygii, Middle Triassic

Introduction

Constrained between two of the biggest mass extinction events on Earth, around the Permo–Triassic and the Triassic–Jurassic boundaries, the Triassic period is one of the most important, though poorly studied times in the history of actinopterygian fishes. As is the case with other groups of organisms, the actinopterygians experienced profound faunal changes during this time. The typical actinopterygian faunas of the Palaeozoic, dominated by cheirolepidiforms, elonichthyiforms, amblypterids and palaeonisciforms, were rapidly replaced by the faunas of subholosteans and neopterygians (Tintori 1998). These fishes rapidly diversified during the Triassic and, although the subholosteans almost disappeared at the end of the Triassic, with only one taxon in the Early Jurassic lakes of the Newark Supergroup in eastern North America (Schaeffer & McDonald 1978, Olsen *et al.* 1982), the neopterygians went on diversifying and became dominant in our modern fish faunas.

The semionotiforms count among the earliest neopterygians and include the semionotids, macrosemiids and lepisosteids (Olsen & McCune 1991, Brito 1997, Cavin and Suteethorn 2006). The group is very well represented through the Mesozoic, but almost disappeared during the Late Cretaceous. Only the Recent lepisosteid genera (*Lepisosteus* and *Atractosteus*) are represented with a few fossil species after the middle Cretaceous. On the other hand, the Late Permian *Acentrophorus* Traquair, 1877 has been regarded as the oldest semionotiform. However,

this genus should be restudied to be certain about its systematic position. Similarly, Early Triassic taxa referred to the Semionotiformes need revision or have already been excluded from this group (Tintori & Lombardo 2007), and the oldest certain records of the group are so far from the Middle Triassic of the Monte San Giorgio (Italy and Switzerland). In this area, the semionotiforms are found in the Ladinian sediments of the Perledo Formation and Meride Limestone (Bellotti 1857, Deecke 1889, De Alessandri 1910, Tintori and Lombardo 2007). Among them, the late Ladinian genus *Sangiorgioichthys* Tintori and Lombardo, 2007 is a primitive semionotiform so far known from a single species, *S. aldae* Tintori and Lombardo, 2007, represented by a few specimens from the Meride Limestone and the Varena Formation (Ladinian, late Middle Triassic) stored at the Civico Museo Insubrico di Storia Naturale di Induno Olona (MCSNIO) in Varese, and Liceo « A. Volta » (LVC) in Como, Italy. The genus presents a very peculiar combination of morphological characters that allowed us to identify a second species of this genus in the middle Anisian (Pelsonian) of South China (Fig. 1). The present contribution includes a detail description of this new species, accompanied with a discussion of its systematic and biogeographic implications.

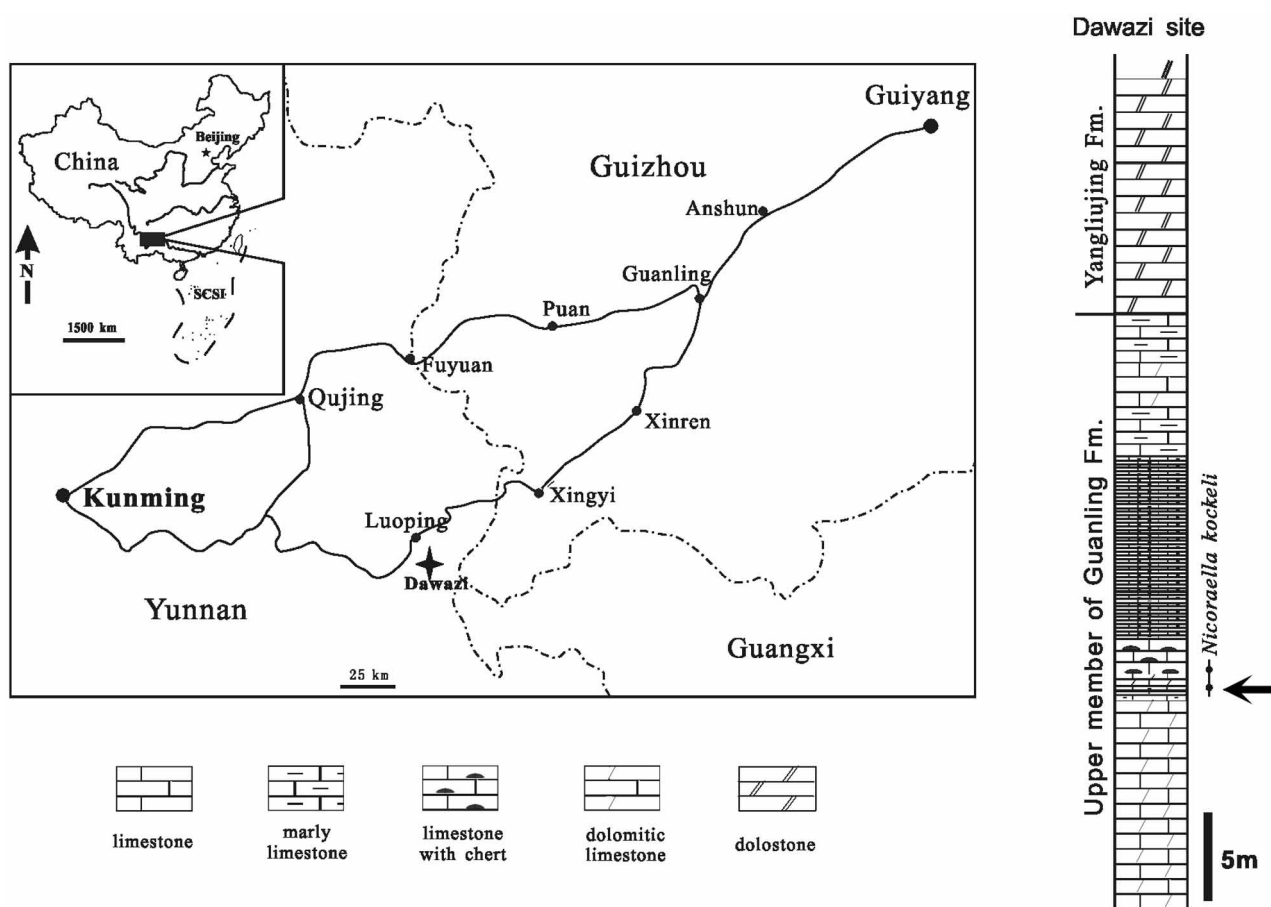


FIGURE 1. Geographic and stratigraphic location of the sediments with *Sangiorgioichthys sui* n. sp. The star in the map indicates the geographic position of the fossil locality. The arrow at the right of the stratigraphic column indicates the stratigraphic position of the levels with *S. sui* n. sp.

Materials and methods

The fossil fishes were mechanically prepared at the GMPKU (Geological Museum of Peking University, Beijing, China) laboratories. The specimens were studied under binocular microscopes and drawings were made with camera lucida and later digitalized with illustration software.

Skull bones are named according to the use of most authors in 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). The cephalic sensory canals are named after Nelson (1972). Fringing fulcra are named according to Patterson (1982). Scutes, unpaired and paired basal fulcra are identified accord-

ing to López-Arbarello & Codorniu (2007). The relative position of the fins and the scale counts is expressed in a pterygial formula where 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).

Systematic Palaeontology

Infraclass Neopterygii Regan, 1923

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

Genus *Sangiorgioichthys* Tintori and Lombardo, 2007

Type species. *Sangiorgioichthys aldae* Tintori and Lombardo, 2007

Other species. *Sangiorgioichthys sui* n. sp.

Diagnosis (emended from Tintori and Lombardo 2007; unique characters are indicated with an asterisk). Small semionotiforms of up to 124 mm DSL; dermal bones covered with ganoine; broad posttemporal and supracleithral bones; elongate anterior supraorbital; large infraorbital at the posteroventral corner of the orbit; single anterior infraorbital; one or two suborbital bones occupying a triangular area ventral to the infraorbital bones and lateral to the quadrate*; elongate supramaxilla fitting in a an excavation of the dorsal border of the maxilla*; small dorsal fin, limited to the area between the origin of the pelvic and anal fins; complete row of scales in the body lobe above the last scale of the lateral line; dorsal ridge of scales conspicuous, but with only a small spine.

Geographic distribution. Rio Vallone and Ca'del Frate (Viggiù, Varese, Italy), Perledo (Italy), Val Mara D (Meride, Canton Ticino, Switzerland), and village of Dawazi (Luoping County, Yunnan Province, South China).

Stratigraphic distribution. Kalkschieferzone of the Meride Limestone and Perledo Member of the Varenna Formation (both Ladinian, late Middle Triassic), and Vertebrate Level of the Upper Member of Guanling Formation (Pelsonian, middle Anisian, early Middle Triassic).

***Sangiorgioichthys aldae* Tintori and Lombardo, 2007**

Holotype. MCSNIO P457

Paratypes. MCSNIO P458, P665

Referred material. LVC 3878-6-10579

Diagnosis (emended from Tintori and Lombardo 2007). Species of *Sangiorgioichthys* distinguished by the following combination of features: a single pair of extrascapular bones; edentulous maxilla; dentition concentrated in the anterior region of the mouth; supramaxilla short, less than half of the length of the maxilla; several small suborbital bones posterior to the orbit, the most dorsal elements arranged in two rows; flank scales with straight posterior margins, except for a few denticles randomly arranged on the different part of the body; 30 transversal rows of scales along the lateral line.

Type locality. The Kalkschieferzone of Rio Vallone (Viggiù, Varese, Italy), just above the aqueduct track.

Type horizon. Uppermost Ladinian of the Kalkschieferzone of the Meride Limestone (Ladinian, late Middle Triassic; Furrer 1995).

Geographic distribution. Rio Vallone and Ca'del Frate (Viggiù, Varese, Italy), Perledo (Italy), and Val Mara D (Meride, Canton Ticino, Switzerland).

Stratigraphic distribution. Kalkschieferzone of the Meride Limestone and Perledo Member of the Varenna Formation (both Ladinian, late Middle Triassic).

***Sangiorgioichthys sui* n. sp.**

(Figs 2–7)

2007 *Archaeosemionotus* in Tintori *et al.*, pp. 13, fig. 1.

2009 *Archaeosemionotus* in Sun *et al.*, pp. 461, fig. 1.

2009 *Peltopleurid* in Wang *et al.*, pp. 519, fig. 10C

Etymology. The species is named after Prof. Su Dezao, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, honouring his important contribution to the knowledge of Triassic fishes from South China.

Holotype. GMPKU-P-1568 (Figs 2A, 3–7). Almost complete specimen preserved in left lateral view, SL = 81 mm.

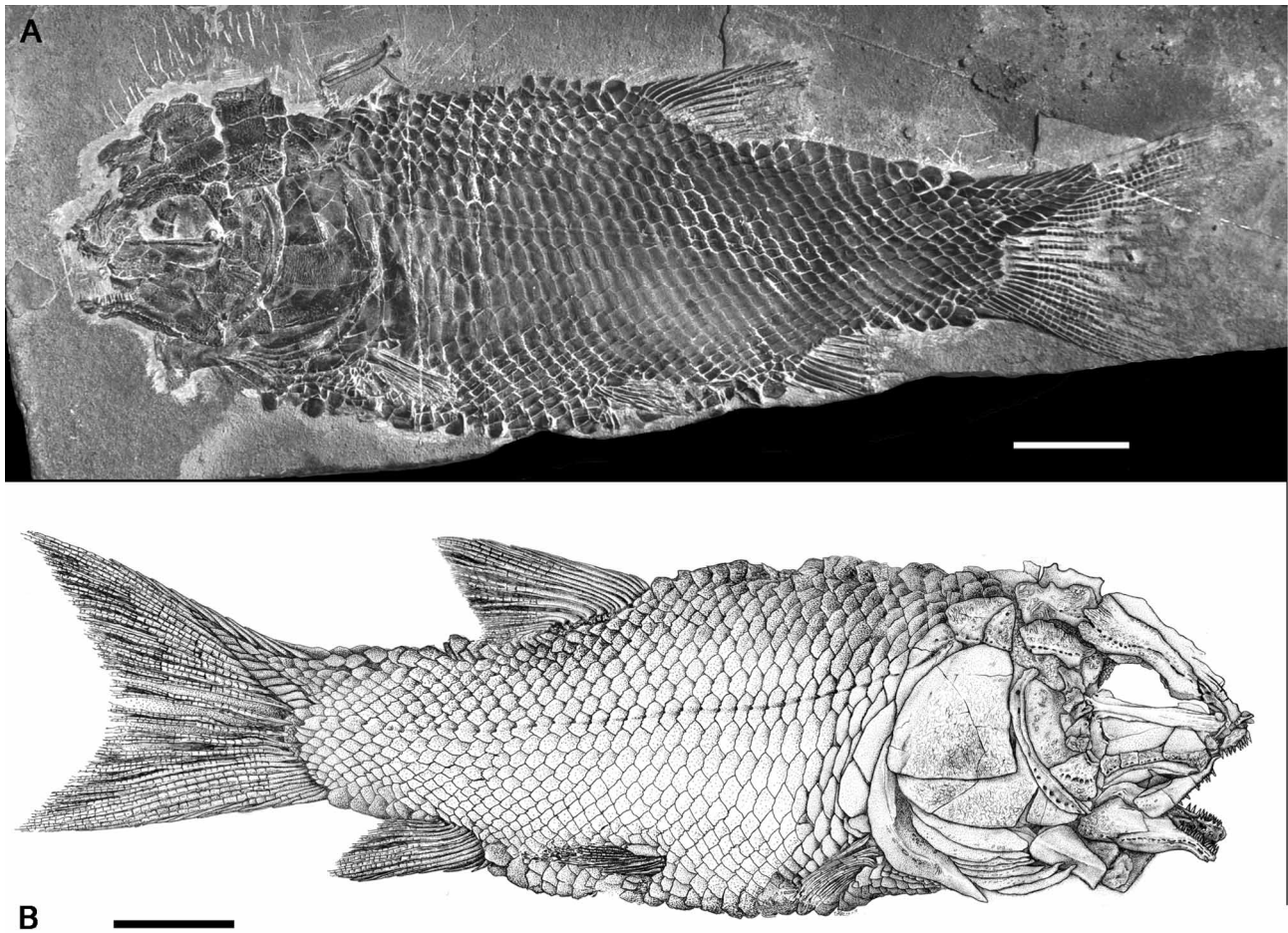


FIGURE 2. *Sangiorgioichthys sui* n. sp. A, Holotype (GMPKU-P-1568), SL = 81 mm. B, Reconstruction of the species based on GMPKU-P-1995. Scale bars = 10 mm.

Paratypes. GMPKU-P-1357–9, 1472, 1558, 1567, 1609, 1636, 1642, 1656, 1661, 1695, 1707, 1973, 1995.

Referred material. GMPKU-P-1353, 1356, 1554, 1557, 1569, 1570–2, 1574–9, 1624, 1630, 1637, 1646–7, 1658–9, 1713, 1717, 1721, 1728, 1739, 1742, 1969, 1970–1.

Diagnosis. Species of *Sangiorgioichthys* Tintori and Lombardo, 2007, distinguished by the following combination of features: two pairs of extrascapular bones, the medial paired usually fused to the parietals; maxilla with a complete row of small conical teeth; supramaxilla long, more than half of the length of the maxilla; only two large suborbital bones posterior to the orbit, a dorsal smaller and a ventral much larger elements; flank scales with finely serrated posterior borders.

Pterygial formula: $\frac{18-20}{7-9 \quad 15-18 \quad 27-30} \quad 32-36$

Type locality. near the village of Dawazi, Luoping County, Yunnan Province, South China (Fig. 1).

Type horizon. Vertebrate Level of the Upper Member of the Guanling Formation (Fig. 1), Pelsonian (middle Anisian; Sun *et al.* 2009, Zhang *et al.* 2009, Wu *et al.* 2009).

Description. Resembling the other species of this genus, *Sangiorgioichthys sui* n. sp. is a rather small and fusi-form fish (Fig. 2). The standard length (SL) of the holotype is 81 mm, the total length being >105 mm and the maximum body-depth 30 mm: the ratio of body-length vs. body-depth is 3.5. The orbit is about 9 mm, 32% of the head length. The studied specimens vary between 42 mm and 124 mm SL. The length of the head ranges between 29–43 % of the SL, showing a nice negative correlation with the size of the specimens, i.e. the smaller individuals have larger heads and vice versa (Fig. 3: HL/SL). The opposite trend is observed in the depth of the body, which ranges between 34–49% of the SL from smaller to larger individuals (Fig. 3:BD/SL).

Specimen	LS (mm)	HL/SL	BD/SL
GMPKU-P-1658	42	0,43	0,43
GMPKU-P-1659	58	0,34	0,34
GMPKU-P-1356	72	0,33	0,35
GMPKU-P-1637	72	0,36	0,35
GMPKU-P-1610	72	0,39	0,39
GMPKU-P-1578	76	0,37	0,38
GMPKU-P-1973	77	0,35	0,39
GMPKU-P-1360	78	0,40	0,42
GMPKU-P-1636	80	0,41	0,39
GMPKU-P-1558	80	0,39	0,39
GMPKU-P-1568	81	0,38	0,40
GMPKU-P-1359	81	0,33	0,35
GMPKU-P-1357	82	0,38	0,41
GMPKU-P-1661	85	0,40	0,42
GMPKU-P-1567	91	0,31	0,42
GMPKU-P-1609	91	0,37	0,37
GMPKU-P-1358	103	0,36	0,49
GMPKU-P-1695	115	0,29	0,48
GMPKU-P-1472	119	0,32	0,46
GMPKU-P-1630	124	0,29	0,48

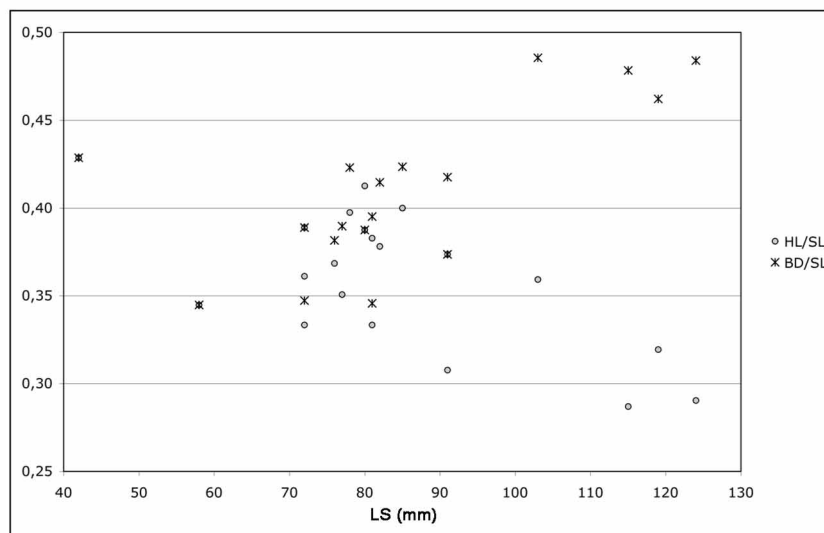


FIGURE 3. Size related variation in the proportions of the head and body depth in 20 specimens of *Sangiorgioichthys sui* n. sp. Specimen, collection number of each measured specimen; LS(mm), standard length in millimeters; HL/SL, ratio between the length of the head (HL, measured from the tip of the snout to the posterior border of the operculum along the longitudinal axis) and the standard length; BD/SL, ratio between the maximal body depth (BD) and the standard length.

Ornamentation. All dermal bones are covered with ganoin, mostly on tubercles, ridges and flat patches (Fig. 4). In the holotype, the shoulder girdle is smooth on the surface, except for several rows of toothed ridges on the cleithrum. There are very sparse (6-7 in number) ganoin tubercles on the anterodorsal portion of the operculum, the rest of which is covered by strongly radiated ganoin ridges. The snout region, the anterior third of the frontal, the anterior third and the ventral part of the maxilla, the anteroventral half of the interopercular, the anterior half of the subopercular, the dorsal half of the first and second infraorbitals are ganoin-covered, with smooth surface. In smaller, most probably younger specimens, the ornamentation is curiously stronger than in the holotype and larger specimens.

Skull roof. There are two pairs of extrascapular bones. The lateral extrascapulars are subtriangular, wider ventrally, and larger than the medial extrascapulars. The medial extrascapulars are approximately quadrangular, though they are partially or totally fused to the parietals in most of the specimens (Fig. 3). In GMPKU-P-1357 (82 mm SL), GMPKU-P-1558 (80 mm SL), and GMPKU-P-1661 (85 mm SL) however, both medial extrascapulars are separate bones. The fusion of the medial extrascapular with the parietal does not correlate with the size of the specimens and does not seem to be age-related. The dermopterotics are rectangular, about 1.8 times longer than deep. The parieto-extrascapular complex also forms a subrectangular bone, which is about 2 times longer than broad. In GMPKU-P-1568 the left parietal is slightly broader, though equal in length, than the right parietal. The frontals are 2.5 times longer than wide, a little wider (1.3) posteriorly than anteriorly, and with a well noticeable interorbital constriction. The nasals are very long and narrow, and laterally curved anteriorly.

The sensory canals are not observable directly, but their trajectories can be at least partially inferred by the presence of series of pores in many of the bones of the skull (Fig. 4). The extrascapulars are pierced by the supraoc-

cipital commissure, which is complete and the medial portion of which is thus contained in the probably compound parietal, except in those few specimens with an independent pair of extrascapulars (GMPKU-P-1357, 1558 and 1661). The temporal canal runs close to the ventral margins of the lateral extrascapulars and dermopterotics, and through the dorsal margin of the dermosphenotic. Anteriorly, the series of pores representing the temporal canal continues in the most posterior supraorbital.

The supraorbital canal traverses the frontal, approximately following its lateral border, describing a sinuous line, and enters the parietal close to its lateral margin reaching the middle of the bone. There are no other canals or pit lines additional to the supraorbital canal in the frontal. A groove margined by a ridge running in anteroventral to posteroventral direction in the posterior region of the dermopterotic and parietal might represent the middle pit line. Similarly, a short groove and ridge placed anterior to this possible middle pit line in the parietals of GMPKU-P-1636 and GMPKU-P-1357 might represent the anterior pit line.

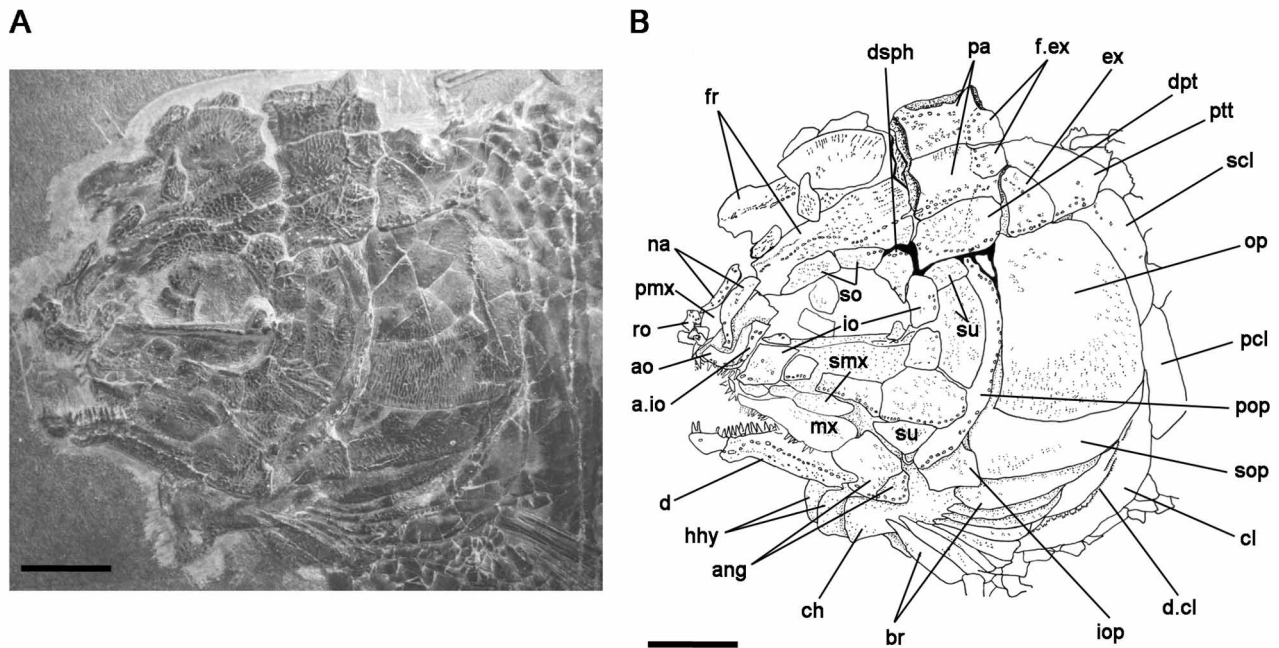


FIGURE 4. Skull of the holotype of *Sangiorgioichthys sui* n. sp. (GMPKU-P-1568). A, photograph. B, line drawing. Scale bars = 5 mm. Anatomical abbreviations: a.io, anterior infraorbital bone; ao, antorbital bone; ang, angular bone; br, branchiostegal ray; ch, anterior ceratohyal; cl, cleithrum; d, dentary; d.cl, series of denticles on the cleithrum; dpt, dermopterotic bone; ex, extrascapular bone; f.ex, extrascapulars partially or totally fused to the parietals; fr, frontal bone; hhy, hypohyal; io, infraorbital bones; iop, interoperculum; mx, maxilla; na, nasal bone; op, operculum; pa, parietal bone; pmx, premaxilla; pop, preoperculum; ptt, posttemporal bone; ro, rostral; scl, supracleithrum; smx, supramaxilla; so, supraorbital bone; sop, suboperculum; su, suborbital bones.

Orbital series. The circumborbial series of bones in the holotype (GMPKU-P-1568) consists of two supraorbitals, a dermosphenotic, six infraorbitals plus one anterior infraorbital, and the antorbital (Fig. 4). The supraorbital bones are longer than deep and form the whole dorsal border of the orbit. There are usually two supraorbital bones, but several specimens show a different number: three supraorbitals in GMPKU-P-1359 and GMPKU-P-1636, or four supraorbitals in GMPKU-P-1357. The first, most anterior supraorbital is the largest, about 1.5 times larger than the second supraorbital. The second or most posterior supraorbital is pierced by the most anterior portion of the temporal sensory canal. As usual in actinopterygians, the dermosphenotic occupies the posterodorsal corner of the orbit and receives the temporal sensory canal. However, in the case of *Sangiorgioichthys sui* n. sp. the temporal canal traverses the dorsal margin of the dermosphenotic and goes on into the posterior supraorbital, instead of turning ventrally into the infraorbital canal. Although pores of the infraorbital sensory canal are present along the orbital margin of the dermosphenotic, there is no evidence for a connection between the infraorbital and temporal canals.

The six infraorbital bones vary largely in shape when compared to one another (Fig. 4). In anterior to posterior direction, the first infraorbital is large, but it is not the largest bone in the series. It is approximately trapezoidal,

with convex ventral border, generally deeper than long and slightly deeper anteriorly than posteriorly. The second infraorbital is comparatively small and approximately quadrangular. The third infraorbital places ventral to the centre of the orbit and is longitudinally elongated, about 3.5 times longer than deep. The ventral border of this infraorbital bone is concave, following the shape of the supramaxilla. This bone is apparently the result of the fusion of at least two elements, which are separate in GMPKU-P-1357. The fourth infraorbital is the largest circumborbital bone. It is placed at the posteroventral corner of the orbit and reaches the preoperculum in all the specimens, except in GMPKU-P-1359 and GMPKU-P-1973 (Fig. 5). The last two infraorbitals are relatively small, a little deeper than long, and form the posterior border of the orbit.

There is only one anterior infraorbital in *Sangiorgioichthys sui* n. sp. and it is small and slender (Fig. 4). It is triangular in shape, with the base dorsal and the apex pointing ventrally. The bone is tightly bound to the antorbital in most of the specimens in which it is preserved. The antorbital is L shape, with the horizontal portion approximately as long as the depth of the vertical portion.

There are three or four suborbital bones in most of the specimens representing *S. sui* n. sp. (Fig. 4). The first and second suborbitals overlap the preoperculum posteriorly and are overlapped by the infraorbitals five and six anteriorly. The dorsal element is much smaller than the ventral one. It is subrectangular, about two times longer than deep, and articulates with the dermopterotic dorsally, but it generally does not reach the dermosphenotic; the dermosphenotic and first suborbital being separated by an anteroventral extension of the dermopterotic in most of the specimens. The second suborbital is large, more than four times deeper than the dorsal suborbital, with concave anterior border and convex posterior border. A very peculiar feature of *Sangiorgioichthys* is the presence of one or two suborbital bones (suborbitals 3 and 4) covering the quadrate and quadratojugal laterally and contacting the ventral region of the preoperculum.

As mentioned above, the fourth infraorbital bone does not reach the preoperculum in GMPKU-P-1359 and GMPKU-P-1973 (Fig. 5). In these specimens, the area between the fourth infraorbital and the preoperculum is occupied with two small additional suborbitals in GMPKU-P-1359 (Fig. 5A). In GMPKU-P-1973 however, the same area is occupied with the second and third suborbital bones, which are ventrally and dorsally expanded respectively (Fig. 5B).

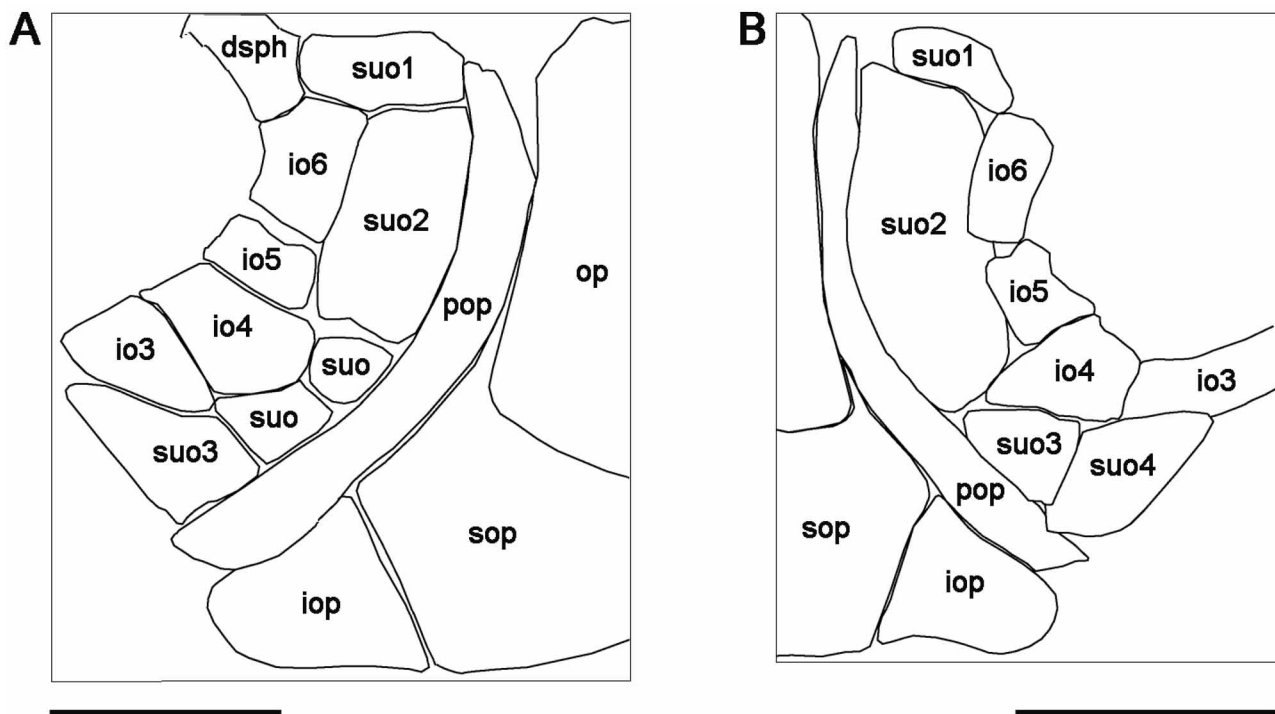


FIGURE 5. Abnormal pattern of circumborbital bones in *Sangiorgioichthys sui* n. sp. A, line drawing of the condition in GMPKU-P-1359; B, line drawing of the condition in GMPKU-P-1973. Scale bars = 5 mm. Anatomical abbreviations as in Figure 4 and: io3–io6, infraorbital bones one to six; suo1–suo4, suborbital bones one to four.

Hyoid arch and palatoquadrate. Of the hyoid arch, only the anterior ceratohyals and hypohyals are well exposed (Fig. 4). The anterior ceratohyals are more or less rectangular, without a median constriction. There is a single hypohyal articulating with the whole anterior border of the anterior ceratohyal.

The palatoquadrate is well ossified and exposed in GMPKU-P-1695 and GMPKU-P-1707 (Fig. 6). The quadrate has the usual sub-triangular shape, with an anteroventral articular process and a laterally expanded posteroventral margin. The articular process is directed ventrally. A quadratojugal is exposed, tightly bound to the posteroventral margin of the quadrate in GMPKU-P-1568 and GMPKU-P-1695, but this bone is usually hidden by the most ventral suborbitals. The quadratojugal has a rounded anterior portion, which does not reach the ventral articular border of the quadrate and, thus, the quadratojugal does not participate in the jaw articulation. Anteriorly, the quadrate articulates with a broad and laminar entopterygoid and a slender ectopterygoid. The ectopterygoid bears only three teeth, which are attached to its most anterior portion. The entopterygoid extends beyond the ectopterygoid anteriorly. Vomers are not clearly exposed in any of the studied specimens, but they are indicated by several rows of teeth medial to the anterior end of the maxilla in several specimens.

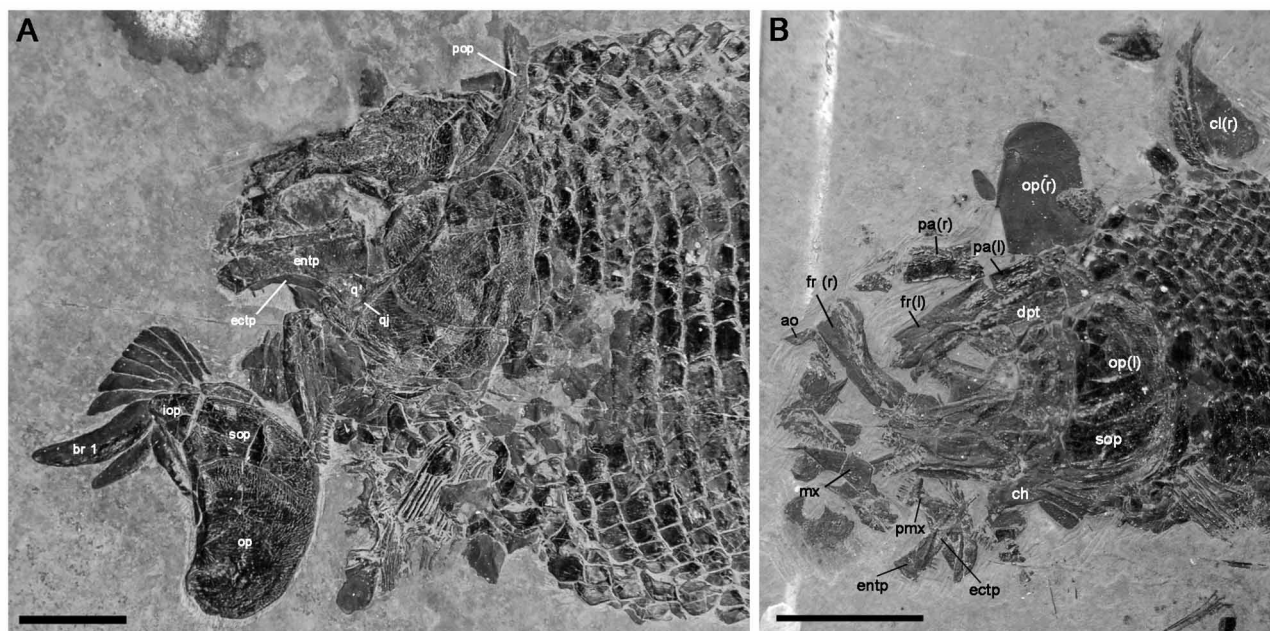


FIGURE 6. Partially disarticulated skulls of *Sangiorgioichthys sui* n. sp. A, GMPKU-P-1695; B, GMPKU-P-1707. Scale bars = 10 mm. Anatomical abbreviations as in Figure 4 and: br 1, first branchiostegal ray; ectp, ectopterygoid bone; entp, entopterygoid bone; q, quadrate; qj, quadratojugal. Left and right elements are indicated with “(l)” and “(r)” respectively.

Opercular series and branchiostegal rays. The preoperculum of *Sangiorgioichthys sui* n. sp. is narrow and almost vertical (Figs 4–6). A series of numerous pores following and very close to the posterior border of the preoperculum represent the preopercular sensory canal. The operculum is sub-rectangular, a little broader ventrally than dorsally and deeper than long in all the studied specimens, though the proportions of this bone are highly variable. The ratio between the maximal depth and the maximal width of the operculum varies between 1.03–1.51 independently of the size of the specimens. The anterior border of the operculum is slightly concave and the dorsal and posterior borders are slightly convex, while the ventral border of the operculum is more deeply convex. The suboperculum has straight anterodorsal and anteroventral borders articulating with the preoperculum and interoperculum respectively. The maximal depth of the suboperculum, at the level of the ascending process is 30–40 % of the depth of the operculum and the ascending process stands up to approximately one third of the depth of the anterior border of the operculum. Posterior to the ascending process, the suboperculum narrows posterodorsally, so that the dorsal border of the bone is concave while the ventral border is convex. The posterior border of the suboperculum follows the slight convexity of the posterior border of the operculum. The interoperculum is short and robust, with rounded borders, but still approximately triangular shape.

There are eight (e.g., GMPKU-P-1568, GMPKU-P-1609, GMPKU-P-1661) to nine (e.g., GMPKU-P-1359, GMPKU-P-1695) branchiostegal rays (Figs 4, 6). The first, most dorsal branchiostegal ray is notably larger and more strongly ornamented than the other ones, resembling the so-called branchiopercle of *Amia* (Grande and

Bemis, 1998: 97) and other halecomorphs. The remaining branchiostegal rays have the usual acuminate shape and all of them articulate with the anterior ceratohyal.

Jaws and dentition. The upper jaw consists of a premaxilla, maxilla and one supramaxilla (Fig. 4). As in other semionotiforms, the premaxilla has a broad and very high nasal process and bears large conical teeth (six in GMPKU-P-1707, Fig. 6B; the complete number is uncertain in other specimens). The maxilla is elongate and slender, with approximately straight posterior and ventral borders (Figs 4, 6B). The bone has a short rod-like articular process followed by a very shallow anterior portion. At the level of the second infraorbital, the maxilla deepens rapidly and forms a subrectangular plate, which is deepest at the posterior margin of the bone. The dorsal border is concave in the posterior half of the bone, where it articulates the supramaxilla, and makes a second concavity in the anterior half of the bone before turning downwards in the anterior end, towards a well-developed articular process. The anterior concavity probably articulates the convex ventral border of the first infraorbital, though these two bones are not preserved in articulation in any of the studied specimens. There is a complete row of small conical and pointed teeth all along the ventral border of the maxilla. Eighteen maxillary teeth are preserved in GMPKU-P-1357, but the total number might be a little larger, probably 20 teeth in total. These maxillary teeth are the smallest marginal teeth on the jaws, and gradually decrease in size posteriorly. The single supramaxilla is oval and elongate, fitting in the posterior concavity of the dorsal edge of the maxilla, and in the concave ventral border of the third infraorbital dorsally.

Dentary, angular, surangular, articular, and prearticular bones are distinguished in the lower jaw (best exposed in GMPKU-P-1567, GMPKU-P-1661, and GMPKU-P-1695; Fig. 7). The dentary is generally slender, with a relatively short posteroventral process and low symphysis. It bears a series of approximately 12 marginal teeth, which resemble the premaxillary teeth in size and shape. Medial to the dentary, the prearticular also bears teeth (7 in GMPKU-P-1695), which have the same size and shape as the dentary teeth. The quadrate fossa is formed by the angular (laterally) and the articular (medially), but the articular facet is restricted to the articular.

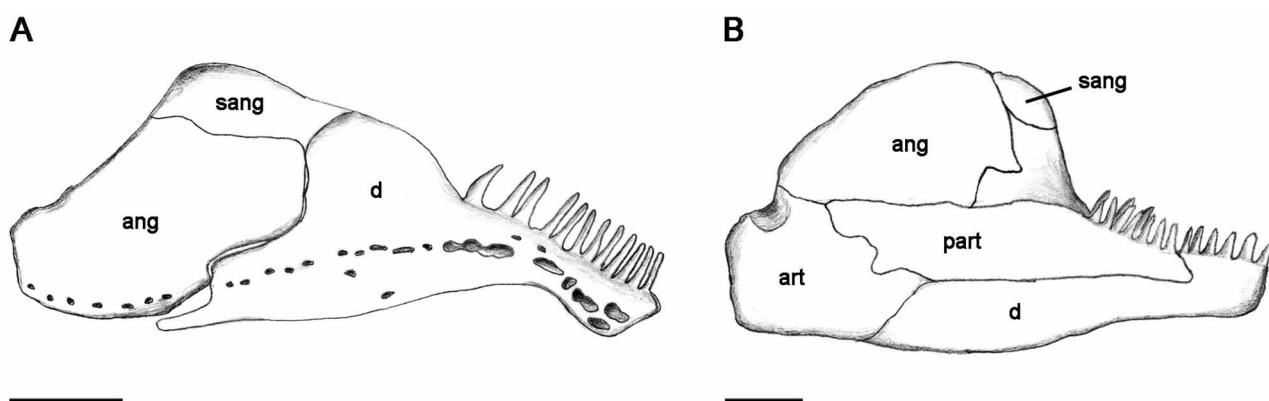


FIGURE 7. Lower jaw in *Sangiorgioichthys sui* n. sp. A, line drawing of the lower jaw preserved in lateral view in GMPKU-P-1567, the dorsal border of the surangular and dentary are hidden in the specimen and were thus reconstructed in this figure; B, line drawing of the lower jaw preserved in medial view in GMPKU-P-1695. Scale bars = 2 mm. Anatomical abbreviations as in Figure 4 and: art, articular bone; part, prearticular bone; sang, surangular bone.

Paired girdles and fins. As usual in semionotiforms, the dermal components of the pectoral girdle of *Sangiorgioichthys sui* n. sp. are the posttemporal bone, supracleithrum, a large cleithrum and several postcleithra (Fig. 4). Like in the other species of *Sangiorgioichthys* the posttemporal and supracleithrum are notably large. The main body of the posttemporal is broadest ventrally, tapering anterodorsally reaching the dorsal midline. The ventral border of the posttemporal is convex and articulates on a facet of the supracleithrum. Anteroventrally, the posttemporal forms a broad anteroventral process, which is traversed by the temporal canal. The supracleithrum is very broad dorsally and narrows ventrally. The trajectory of the lateral line in this bone is shown by a line of pores starting at the dorsal border and following a posteriorly concave curve towards the middle of the lateral border of the bone. The cleithrum has a relatively narrow lateral wing and broad medial wing. Several rows of toothed ridges are aligned along the edge between the lateral and medial wings. The number and arrangement of these ridges varies between individuals. Similarly, the number and arrangement of postcleithra is somewhat variable between the specimens. However, three large postcleithra are normally present.

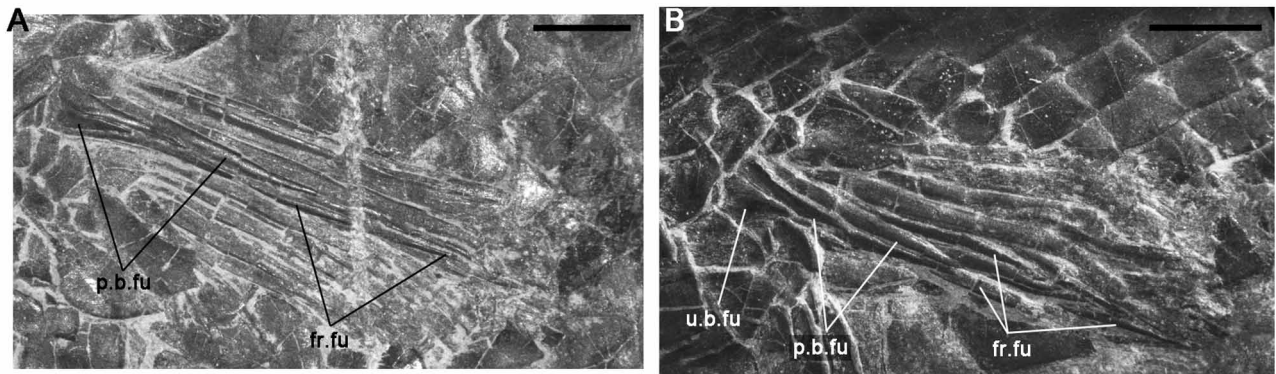


FIGURE 8. Paired fins in *Sangiorgioichthys sui* n. sp. (holotype, GMPKU-P-1568). A, pectoral fin. B, pelvic fin. Scale bars = 2 mm. Abbreviations: fr.fu, fringing fulcra; p.b.fu, paired basal fulcra; u.b.fu, unpaired basal fulcra.

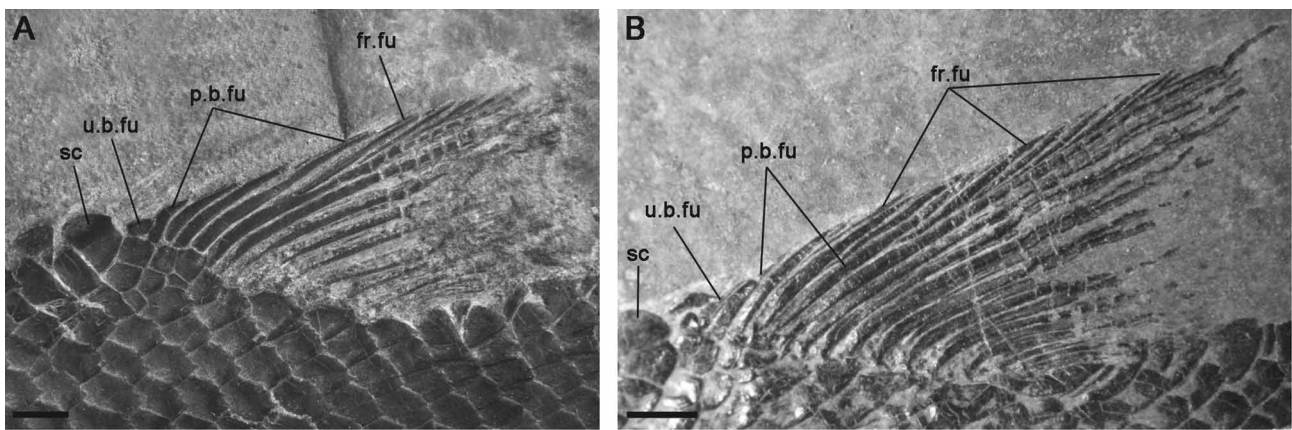


FIGURE 9. Dorsal fin in *Sangiorgioichthys sui* n. sp. A, Holotype GMPKU-P-1568. B, GMPKU-P-1359. Scale bars = 2 mm. Abbreviations: fr.fu, fringing fulcra; p.b.fu, paired basal fulcra; sc, scute; u.b.fu, unpaired basal fulcra.

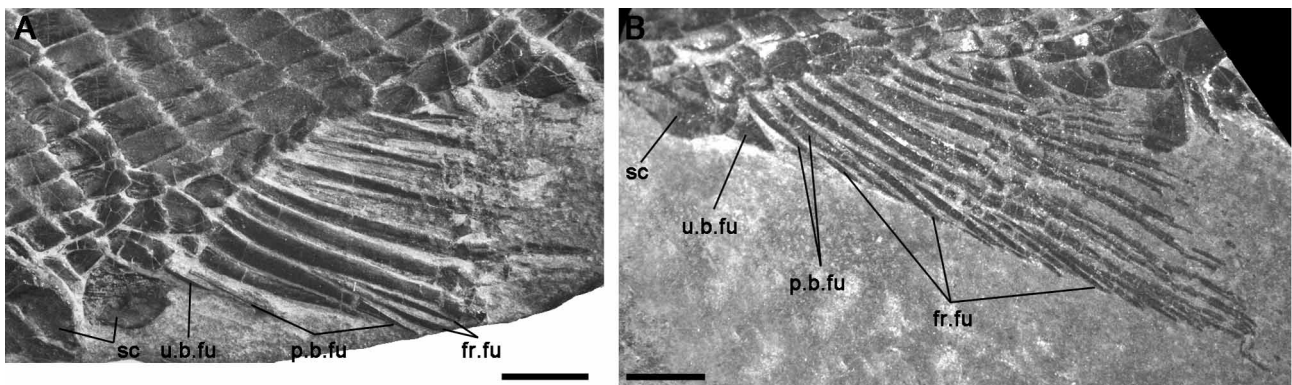


FIGURE 10. Anal fin in *Sangiorgioichthys sui* n. sp. A, Holotype GMPKU-P-1568. B, GMPKU-P-1359. Scale bars = 2 mm. Abbreviations: fr.fu, fringing fulcra; p.b.fu, paired basal fulcra; sc, scute; u.b.fu, unpaired basal fulcra.

Of the chondral components of the pectoral girdle, only a few poorly preserved radials are exposed in GMPKU-P-1656, and the pelvic girdle is not exposed in any of the studied specimens.

The paired fins are best preserved in GMPKU-P-1472. The pectoral consists of 2 basal fulcra, 10 lepidotrichia and several slender fringing fulcra (Fig. 8A). The pelvic fin has one basal fulcrum, at least 5 lepidotrichia and several fringing fulcra (Fig. 8B).

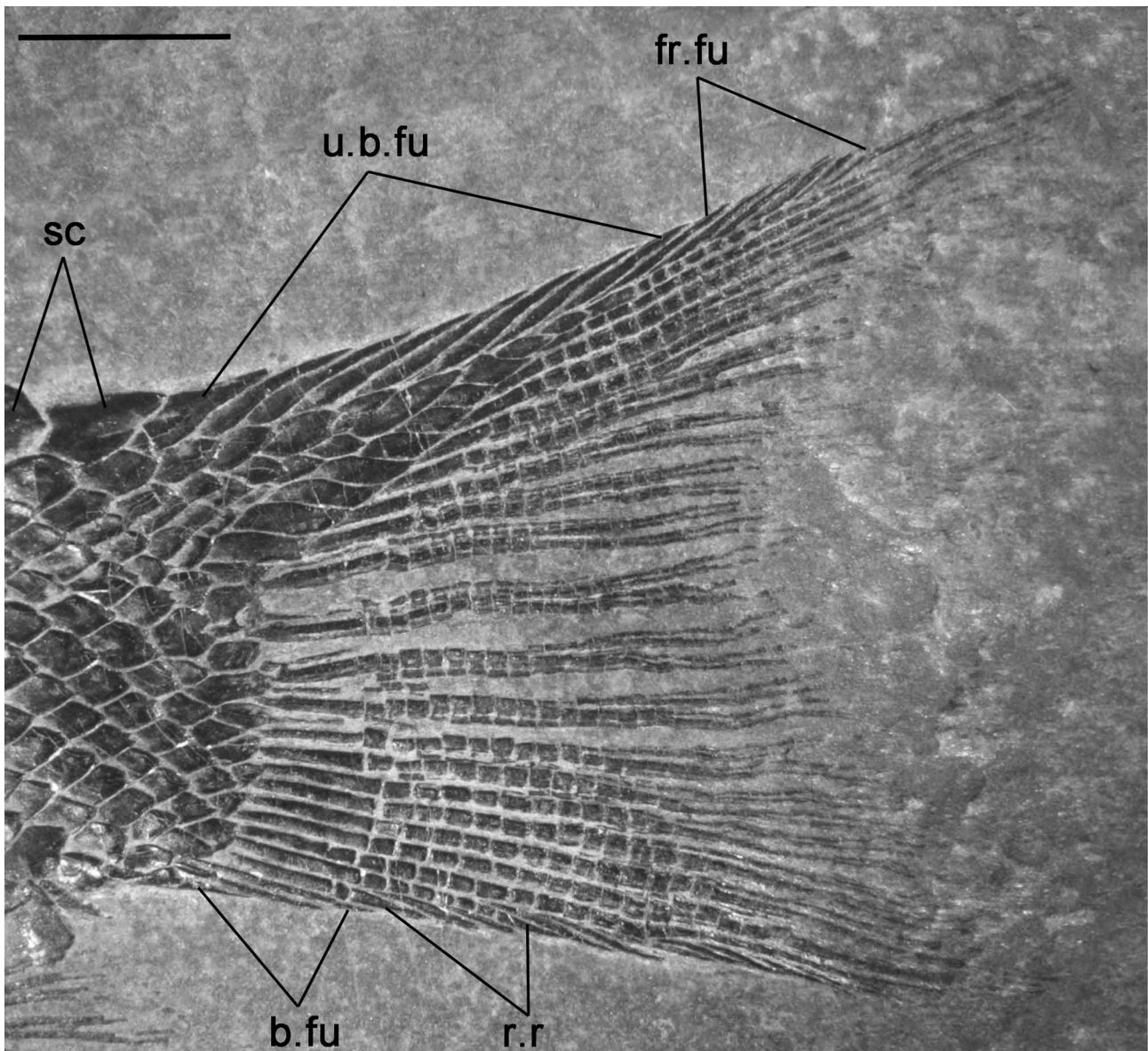


FIGURE 11. Caudal fin in *Sangiorgioichthys sui* n. sp. (GMPKU-P-1359). Scale bar = 5 mm. Abbreviations: b.fu, basal fulcra; fr.fu, fringing fulcra; r.r, rudimentary rays; sc, scute; u.b.fu, unpaired basal fulcra.

Unpaired fins. The dorsal and anal fins are relatively small (Fig. 2). The dorsal fin is placed at the middle of the trunk, originating at approximately 0,6 of the SL, slightly behind the level of insertion of the pelvic fins and ending well anteriorly to the level of origin of the anal fin. There is usually one unpaired basal fulcrum preceding the dorsal fin, and the number of basal fulcra varies normally between 4–5 (Fig. 9), a few specimens having 3 (GMPKU-P-1357, GMPKU-P-1358, GMPKU-P-1558) or 6 (GMPKU-P-1636) basal fulcra. The most posterior basal fulcra usually, though not always, bear one or two fringing fulcra (Fig. 9B); otherwise the fringing fulcra are lying on the first, marginal ray. There are 11–12 lepidotrichia in the dorsal fin, including a single, highest marginal unbranched ray, and the following only distally branched rays, the height of which decrease rapidly posteriorly.

The anal fin consists of 3–4 basal fulcra, the first of which is usually unpaired and 9–10 lepidotrichia (Fig. 10). Resembling the case of the dorsal fin, there is a single unbranched marginal ray, which is the deepest and bears the series of fringing fulcra. The remaining lepidotrichia are gradually shallower in posterior direction and branch two times. Fringing fulcra might also be intercalated between paired basal fulcra (Fig. 10B).

The caudal fin is usually very well preserved. Although the distinction between median scutes and dorsal caudal basal fulcra is difficult because the caudal endoskeleton is hidden by the thick scales, based on their morphology, two scutes and 8–9 unpaired basal fulcra are distinguished on the body lobe of the tail (Fig. 11). There is a

total of 21 to 22 lepidotrichia in the caudal fin. There are 10 principal caudal rays placed dorsal to the lateral line and 9–10 principal caudal rays below the lateral line. The dorsal and ventral marginal principal rays are unbranched and the other rays branch up to two times. In the ventral margin of the fin there are two short, rudimentary marginal rays bearing fringing fulcra, which are preceded by a variable number (2–5) of unpaired and paired basal fulcra.

Squamation. The body is completely covered with thick rhomboid scales (Fig. 2A). There are 32–36, though mostly 34–35, vertical rows of scales along the lateral line. The anterior flank scales are rectangular, up to two times deeper than long, with smooth surface and serrated posterior borders. The degree of these serrations varies during ontogeny, the serration being much stronger in small individuals becoming gradually more delicate in larger specimens. They have a well-developed peg-and-socket articulation, but no anterior articular processes like in the genus *Lepidotes*. As usual in actinopterygians, more posteriorly the scales become gradually rhomboidal and with smooth posterior borders. There are three pre anal scutes, one median scute followed by a paired of lateral scutes. Two dorsal and two ventral scutes precede the series of dorsal and ventral caudal basal fulcra respectively. In the heterocercal tail, the body lobe is covered with 6–7 inverted rows of scales, the longest of which usually includes 11 scales. The scales forming the posteroventral margin of the body lobe are not rhombic, but parallelogram in shape. They are notably larger than the other scales in the body lobe, and up to four times longer than deep.

Discussion

The presence of anterior infraorbital bones, premaxilla with long nasal process, several suborbital bones, conspicuous dorsal ridge scales (with posterior spine) and the lack of gular plates support the referral of *Sangiorgioichthys* to the Semionotiformes sensu Olsen and McCune 1991. The phylogenetic relationships within Semionotiformes have not been explored so far and such a study is beyond the scope of the present contribution. However, *Sangiorgioichthys* most probably represents a rather primitive form among semionotiforms and at present cannot be placed in a particular family within this group. Tintori and Lombardo (2007) referred *Sangiorgioichthys* to the family Semionotidae, but López-Arbarello (2008) noted the poor definition of this group, which, including a variety of genera ranging from the Middle Triassic to the Early Cretaceous, most probably represents a non-monophyletic assemblage.

Strongly suggesting a basal position for *Sangiorgioichthys* among semionotiforms are the lacks of the specialized dentition or scale articulation present in other semionotiform taxa. Most semionotiforms developed semitritoral to extremely tritotal dentitions, ranging from the pencil-like teeth typical of *Lepidotes elvensis* to the button-like teeth of *Paralepidotus ornatus* (Tintori 1996) and *Lepidotes maximus* (Jain 1983). Many semionotiforms, including the gars, also developed a peculiar mode of articulation between adjacent scales in antero-posterior direction. In this mode of articulation, there are additional articular processes developed from the anterodorsal and sometimes also the anteroventral corners of the rhomboid scales, which articulate with the scale immediately anterior. Also, the short snout and low number of anterior infraorbitals are primitive conditions among semionotiforms, which have a general tendency to develop elongate snouts (particularly very elongate in the gars) with numerous anterior infraorbital bones (Cavin & Suteethorn 2006, López-Arbarello 2008, 2009, ongoing research, López-Arbarello & Sferco in press). Additionally, the presence of numerous suborbital bones is the most generalized condition among semionotiforms, with a highly homoplastic distribution and, thus, probably representing a primitive condition (López-Arbarello 2006).

Besides these primitive features *Sangiorgioichthys* presents some features that are so far only known in this fish among semionotiforms. Very peculiar is the presence and disposition of one or two suborbital bones laterally covering the quadrate and quadratojugal. These bones do not show any signal of bearing sensory canals or pit lines and correspond to the suborbital series in other semionotiforms (e.g. several species of *Lepidotes* in Jain 1983 and Forey *et al.* in press, a new Late Jurassic genus from Germany López-Arbarello & Sferco in press), which is here interrupted by a large infraorbital. The other unique feature in *Sangiorgioichthys* is an excavation of the dorsal border of the maxilla housing the supramaxilla. Similarly excavated maxillae are known in halecomorphs (see supra-maxillary notch in Grande & Bemis 1998), but such a feature is unknown in other semionotiforms.

Sangiorgioichthys sui furthermore presents several very interesting features, which are not unique of this taxon. The potential fusion of medial extrascapular and parietal bones has been discussed by Bartram (1977) in macrosemiids and is probably also de case in *Lepidotes microrhis* (Wenz 2003). The presence of a sensory canal

entering the most posterior supraorbital has recently been reported in a new semionotiform taxon from the Late Jurassic of Germany (López-Arbarello & Sferco in press). Since the distribution of these features among semionotiforms is largely unknown, it is not possible to evaluate their meaning and implications for semionotiform systematics.

Not less important than the new anatomical information provided by the abundant and well-preserved material of *Sangiorgioichthys sui*, the numerous specimens representing this new taxon reveal a significant intraspecific variation. Besides the expected size-related variation in body proportions (Fig. 3), this variability includes the occasional appearance of separate bones, which are normally fused (the parietals and medial extrascapulars, the infraorbitals at the ventral margin of the orbit), a variable number of supraorbital and suborbitals, and variable shape and relative size of certain bones of the skull (the infraorbital placed at the posteroventral corner of the orbit and the operculum). This evidence of such variation is very important and should be watched carefully when considering similar features as diagnostic of phylogenetically significant characters.

Although the phylogenetic relationships and, thus, the role of *Sangiorgioichthys* in the history of semionotiforms are still poorly understood, the discovery of *S. sui* in the Luoping Fauna provides further significant evidence for the close biogeographic relationship between the Middle Triassic marine faunas of South China and the Swiss and Italian Alps. The Triassic sequences of the Swiss and Italian Alps have been the main source of information for the vertebrate faunas of the Palaeotethys at that time. The discovery of two Middle Triassic Lagerstätte in South China, Panxian and Luoping (both of Pelsonian age), have dramatically changed this picture. The Middle Triassic Panxian and Luoping faunas, have yielded numerous and excellently preserved fishes including a large diversity of taxa, mainly subholosteans and neopterygians, but also new species of saurichthyds (Wu *et al.* 2009). These faunas therefore represent a new and valuable window into the Triassic fish faunas of the Palaeotethys. The Panxian and Luoping faunas have shown several taxa in common with the slightly younger Ladinian faunas of the Alps. Advances in the study of the fish faunas in the middle Anisian of South China and the late Anisian-early Ladinian of the Alps indicate that a first major radiation of the neopterygian fishes (Neopterygii) already took place during the early Middle Triassic (Sun *et al.* 2008, 2009) rather than the previously suggested radiation in the Norian (Late Triassic, about 20 Ma later; Tintori, 1998). During the Early Triassic, the Indosinian orogeny started affecting South China, producing an east-west palaeogeographic differentiation: western South China stayed in Tethyan domain while eastern South China was subjected to uplift and water regression with progressive influence of the Palaeo-Pacific (Zhou *et al.* 2008). In western South China, the areas of Panxian and Luoping were subjected to marine transgression at the eastern margin of the Palaeotethys during the Early Triassic, but later uplifted and emerged towards the end of the Triassic (Zhou *et al.* 2008). On the other side, the area of the Monte San Giorgio submerged and was flooded by the waters of the Palaeotethys from the East during the Early Triassic. Therefore, both areas, at two opposite extremes of the closing Palaeotethys (Stampfli and Borel 2002), were subjected to strong palaeoenvironmental changes due to intense tectonic activity during the Middle Triassic. Such changes probably resulted in the opening of new ecological niches and, thus, largely favored the rapid evolution and diversification of subholosteans and basal neopterygians in the Eurasian coasts of the Palaeotethys.

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