

## A NEW EARLY SEMIONOTIDAE (SEMIONOTIFORMES, ACTINOPTERYGII) FROM THE UPPER LADINIAN OF MONTE SAN GIORGIO AREA (SOUTHERN SWITZERLAND AND NORTHERN ITALY)

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**Key words:** Actinopterygii, Early Semionotidae, Ladinian, Monte San Giorgio.

**Abstract.** The early history of the Semionotiformes is still scarcely known as, apart from the Permian *Acentrophorus*, most of the Early and Middle Triassic taxa traditionally ascribed to this order are often poorly known and/or they actually belong to other groups. *Sangiorgioichthys aldae* gen. n. sp. n. is described from the Upper Ladinian Kalkschieferzone (Upper Meride Limestone) of the Monte San Giorgio area on specimens coming from both Italy and Switzerland. The new genus is ascribed to the family Semionotidae as it shows several of the characters usually considered as diagnostic of the family itself, even if no real synapomorphies have been so far proposed for it. As a Semionotidae, *Sangiorgioichthys* gen. n. has an almost complete circumorbital series, large ascending process of the premaxilla, rostral and nasals almost tube-like, short maxilla, several suborbital bones posterior and ventral to the infraorbitals, long antero-dorsal process of the suboperculum, sensory canal system very rich in pores, mid dorsal ridge scales with an incipient spine. Peculiar characters of the new genus are dermal skull bones completely covered by ganoine, a very large ventral infraorbital almost attaining the anterior edge of the preoperculum, two 'ventral' suborbitals, very elongate anterior supraorbital bone, dentition made of a number of tiny pencil-like teeth, anterior and posterior lateral line scales differentiated.

**Riassunto.** La storia dei primi Semionotiformes è ancora scarsamente conosciuta: a parte *Acentrophorus* del Permiano, la maggior parte dei taxa del Triassico Inferiore e Medio tradizionalmente attribuiti a questo ordine sono spesso scarsamente conosciuti e/o appartengono in realtà ad altri gruppi. *Sangiorgioichthys aldae* gen. n. sp. n. viene descritto sulla base di esemplari trovati in località sia sul lato italiano che svizzero dell'area del Monte San Giorgio, riferite al Ladinico Superiore della Kalkschieferzone (Calcere di Meride Superiore). Il nuovo genere viene attribuito alla famiglia Semionotidae in quanto mostra diversi caratteri generalmente considerati diagnostici per la famiglia, anche se per questa finora non è stata proposta alcuna vera sinapomorfia. Come Semionotidae, *Sangiorgioichthys* gen. n. presenta una serie circumorbitale quasi completa, un processo ascendente del premaxel-

lare ben sviluppato, rostrale e nasali tubolari, mascellare corto, numerosi suborbitali posteriori e ventrali agli infraorbitali, un lungo processo antero-dorsale del subopercolare, il canale del sistema sensoriale ricco di pori, una fila di scaglie medio-dorsali con una spina posteriore. Caratteri peculiari del genere sono le ossa dermiche del cranio completamente ricoperte da ganoine, un infraorbitale ventrale molto grande quasi a contatto con il margine anteriore del preopercolare, due suborbitali "ventrali", un supraorbitale anteriore molto allungato; la dentatura è costituita da denti a matita numerosi e sottili e le scaglie della linea laterale sono differenziate in anteriori e posteriori.

### Introduction

A widely accepted definition of the Semionotiformes is still far from being settled (Cavin & Suteethorn 2006) and so is also the origin of the group. Regarding the systematic content of the order Semionotiformes, there are two main interpretations: the traditional one by Arambourg & Bertin (1958) and the more recent one by Olsen & McCune (1991), the latter including also macrosemiids and lepisosteids. At the moment, waiting for a broad revision of most of its representatives, a possible solution could consider an order Semionotiformes which include only the semionotid families Acentrophoridae, Semionotidae, Dapedidae (but see also Gardiner et al. 1996) and possibly a new family for the genus *Sargodon*, based on the absence of ganoine on all scales and on the peculiar histology of its chisel-like teeth (Tintori 1983; Lombardo & Tintori in press).

Regarding the early history of the order, the Permian *Acentrophorus* has long been considered the oldest neopterygian and the first representative of this family

(Woodward 1895). Indeed, so far no real semionotids have been convincingly described from rocks dating from Late Permian to the Norian (Late Triassic), when *Semionotus* and *Paralepidotus* were very common. Several Middle Triassic genera have been named recalling Semionotidae, and often they have been considered as belonging to this family. In the XIX century also a few species have been ascribed to *Semionotus* and *Lepidotes*, but for most of them a close revision would change their classification. As a starting point for a future revision of the family Semionotidae, in the next paragraphs we list a series of these putative Middle Triassic semionotids, in many cases described or cited only in the Italian literature, therefore nearly unknown to most paleontologists.

*Serrolepis* (Dames, 1888), known only for a few isolated scales and a dentary with teeth, has been considered a semionotiform (Lehman 1966) until it was demonstrated that the fish is a perleidiform, possibly related to *Felberia* (Lombardo & Tintori 2004).

*Eosemionotus*, originally from the German Muschelkalk, was erected by Stolley (1920) on a single specimen after being previously ascribed to *Allolepidotus vogelii* (Fritsch, 1906). New species have been added by Schultze & Moeller (1986) and Bürgin (2004); however, its features seem to place it far from semionotids. In fact, nothing is known about the circumorbital series, the preoperculum is L-shaped (only gently bent in semionotids), the suboperculum is large and without the antero-dorsal process, there is no supramaxilla, sensory pores are very few, there are no conspicuous mid dorsal ridge scales, the anterior flank scales are much higher than long, and the body lobe is very reduced. Only the rather large ascending process of the premaxilla is a sure semionotiform character, but it should be associated with at least some of the other features (see above).

Deecke (1889) erected *Archaeosemionotus* on a single specimen from the Ladinian of the Perledo area. The specimen is badly preserved and is lacking in diagnostic characters (C.L. pers. obs.). Actually, De Alessandri (1910, p. 71) considered *Archaeosemionotus connectens* a junior synonym of *Semionotus balsami* (Bellotti, 1857), also from the Perledo area. De Alessandri (1910) ascribed to this latter species a few specimens then in the collections of the Civico Museo di Storia Naturale di Milano, besides *Archaeosemionotus connectens* and *Semionotus dubius* material. Unfortunately, De Alessandri's description of *S. balsami* is poor as the specimens were not prepared: therefore, pictures are also quite useless. However, the three specimens (one is Bellotti's type) figured by De Alessandri (1910, Pl. I, figs. 13-14; Pl. II, fig. 3) are clearly different from one another. At least two of them are not semionotiforms, as they show scales much longer than deep at least on the abdomen; this feature has never been recorded in semionotids while it often occurs in many early amiiforms

(Lombardo 2001 and pers. obs. on undescribed material). Furthermore, most of the material was destroyed after the heavy bombardments on Milano during the II World War.

Bürgin (1995) considered some specimens from the Kalkschieferzone of Meride as belonging to this genus but we think they are likely closer to '*Legnonotus obtusus*' Tintori & Renesto (1983). Bürgin et al. (1991) and Bürgin (1999) used again the name *Archaeosemionotus* for several fishes from the Prosanto Formation, considering valid the species *S. balsami* (whom apparently the Swiss material resembles) but ascribing it to the genus *Archaeosemionotus* as clearly they are not *Semionotus*. The main character considered by Bürgin et al. (1991) is that the numerous suborbitals are arranged in a mosaic pattern. As already pointed out, the type of *Archaeosemionotus connectens* (= *S. balsami* – but see above, thus *Archaeosemionotus balsami*) does not show this character as do the specimens figured by De Alessandri (1910). Furthermore, the original description of this region by De Alessandri (1910, p. 69) is: "Il preopercolo è ben distinto, sottile e falcato ed è preceduto nella regione superiore da un postorbitale largo ed in quella inferiore da un suborbitale pure sviluppato e di forma triangolare. Anteriormente a questo suborbitale se ne osserva un altro che ha dimensioni minori, forma rettangolare e che si appoggia al mascellare" ("The preoperculum is clearly distinct, crescent shaped, and there is a large 'postorbital' in front of its dorsal region, while a similarly large, triangular suborbital is in front of the ventral part of the preoperculum. A third smaller element reaches the maxilla being ventral to the orbit"), thus nothing recalling a mosaic of bones. While it is possible that the specimens described by Bürgin et al. (1991) are semionotiforms, we prefer not to use the genus name *Archaeosemionotus* as all the original material is lost or uninformative.

*Archaeolepidotus leonardii* (Accordi, 1955, but see also Accordi 1956), has been erected on a single specimen from the Triassic basal beds in the Dolomites (N. Italy) and considered as belonging to Semionotidae. Preservation of the specimen is quite poor, but on the basis of the shape of marginal teeth and opercular bones, it is possibly that *Archaeolepidotus* could be a junior synonym of *Acentrophorus*. In this case, *Acentrophorus* went across the Permo-Triassic boundary. Lehman (1966) wrote that *Archaeolepidotus* could be a parasemionotiform as suggested also by Patterson (1973).

From the same Dolomitic area, Accordi (1955) described two teeth-plates from the uppermost Permian beds and one from the lower Triassic ones. Accordi (1955) erected for each specimen a new species and ascribed them tentatively to *Paralepidotus*. Similar teeth-plates are known from the Muschelkalk (Guttormsen 1937) and have been also ascribed to cf. *Paralepidotus*.

In our opinion these plates may be confidently ascribed to *Bobasatrania*. Complete specimens of *Bobasatrania* are common in the Early Triassic from British Columbia, Greenland, Madagascar, but recently it has been described from the Middle Triassic Formazione di Besano (Grenzbitumenzone) of Monte San Giorgio (Bürgin 1992) and from the Middle Anisian of the Braies Dolomites (Tintori et al. 2001). On the other hand, so far, *Paralepidotus* has been known only from the Norian (Late Triassic) (Tintori 1996).

*Pericentrophorus* (Jörg, 1969) has been usually related to semionotids (Patterson 1973; Gall et al. 1974) but Bürgin (2004) proposed to consider it as *Halecostomi incertae sedis*. Actually, *Pericentrophorus* shows none of the peculiar semionotiform characters reported above.

Several other Middle Triassic nominal genera are known from uninformative material and, so far, cannot be used (e.g., *Plesiolepidotus*, *Asiatolepidotus*, *Sinosemionotus*) in tracing the early semionotid history. At present several new specimens from the Middle Triassic of Guizhou Province (Southern China), possibly related to this genera, are becoming available to study (Jin Fan, pers. comm. 2006).

The beautifully preserved material from the Ladinian of Monte San Giorgio area allows to add some new information about this topic. Anyway, it appears more and more clear, as studies proceed, that the definition of Semionotidae is far to be established, as this problem arises whenever new forms are found.

### Stratigraphical remarks

The specimens used for the description of this new taxon have been recovered from the Ladinian of the Meride Limestone. Another incomplete specimen (LVC 3878-6-10579) found in the historical collection of Liceo A. Volta (Como, Italy) comes from the Perledo-Varenna Formation. Within Meride Limestone two main localities have been exploited: Ca' del Frate, on the Italian side, and Meride on the Swiss one, respectively belonging to the middle and lower part of the Kalkschieferzone. This unit crops out between Valceresio (Italy) and the Meride area (Canton Ticino, Switzerland) and includes the uppermost of five vertebrate levels of the Monte San Giorgio area (for a summary, see, e.g., Bürgin 1995, 1999; Lombardo 1999, 2001; Tintori & Lombardo 1999; Lombardo & Tintori 2004).

The fish fauna comprises also genera (e.g. *Perleidus*, *Furo*, *Allolepidotus*) found in the levels of the Perledo Member (uppermost part of the Perledo-Varenna Formation). This latter is considered of Ladinian age on the basis of conodonts (Gaetani et al. 1992) and we confidently assume that the Kalkschieferzone is coeval with the Perledo Member, similarly characterized both

lithologically and for the identification of similar faunal assemblages (Tintori & Lombardo 1999).

If the Monte San Giorgio is the heart of these fossiliferous sequences, both West and East of it we have new rich sites within a few dozen kilometers (Tintori & Lombardo 1999; Lombardo et al. 2006). To the West the Formazione di Cunardo yields a fish fauna of Early Ladinian age: however, the geological setting of the area is very complicated and the paleogeography is not yet well understood. Actually, a late Ladinian *Peltopleurus nuptialis* has been described from an isolate outcrop near the eastern Maggiore Lake shores (Bassani 1914; Lombardo 1999). Fragments of fishes apparently close to the new taxon described in this paper come from the Early Ladinian Formazione di Cunardo of Valtravaglia (Lombardo et al. 2006), but we need better preserved material for an appropriate description. To the East, the classical fauna from Perledo encompasses most of the Ladinian (Tintori & Lombardo 1999). At least one of the specimens collected in the first half of the XIX century can be ascribed to the new taxon (see above), proving once more the relationships between the Kalkschieferzone of Monte San Giorgio and the upper part of the Formazione di Perledo-Varenna. So far, no semionotid specimens have been recorded from the new excavation in the lower Ladinian Formazione di Buchenstein (Tintori et al. 2004; Lombardo et al. 2006).

**Abbreviations used in figures:** *acer*, anterior ceratoyal; *ang*, angular; *ant*, antorbital; *br*, branchiostegal rays; *c.eha.*, canal for efferent hyoidean artery; *cl*, cleithrum; *de*, dentary; *dpt*, dermopterotic; *dspb*, dermosphenotic; *exsc*, extrascapulars; *fr*, frontal bone (following the traditional terminology); *hb*, hypoyal; *hy*, hyomandibula; *io*, infraorbital bones; *iop*, interoperculum; *mx*, maxilla; *na*, nasal; *op*, operculum; *pa*, parietal bone (following the traditional terminology); *pcer*, posterior ceratoyal; *pcl*, postcleithra; *pmx*, premaxilla; *pop*, preoperculum; *pspb*, parasphenoid; *pt*, posttemporal; *ro*, rostral bone; *sbo*, suborbital bone; *scl*, supracleithrum; *smx*: supramaxilla; *so*, supraorbital bones; *sop*, suboperculum; *smg*, surangular.

**Institutional abbreviations:** MCSNIO: Civico Museo Insubrico di Storia Naturale di Induno Olona (Varese - Italy); MCSNL: Museo Cantonale di Storia Naturale di Lugano (Switzerland); LVC: Liceo "A. Volta" (Como - Italy).

### Systematic Palaeontology

Subclass **Actinopterygii** Cope, 1887

Infraclass **Neopterygii** Regan, 1925

Order **Semionotiformes** Arambourg & Bertin, 1958

Family Semionotidae Woodward, 1890 *pro parte*

*Sangiorgioichthys* gen. n.

Type species: *Sangiorgioichthys aldae* gen. n. sp. n.

**Diagnosis:** as for the only known species.

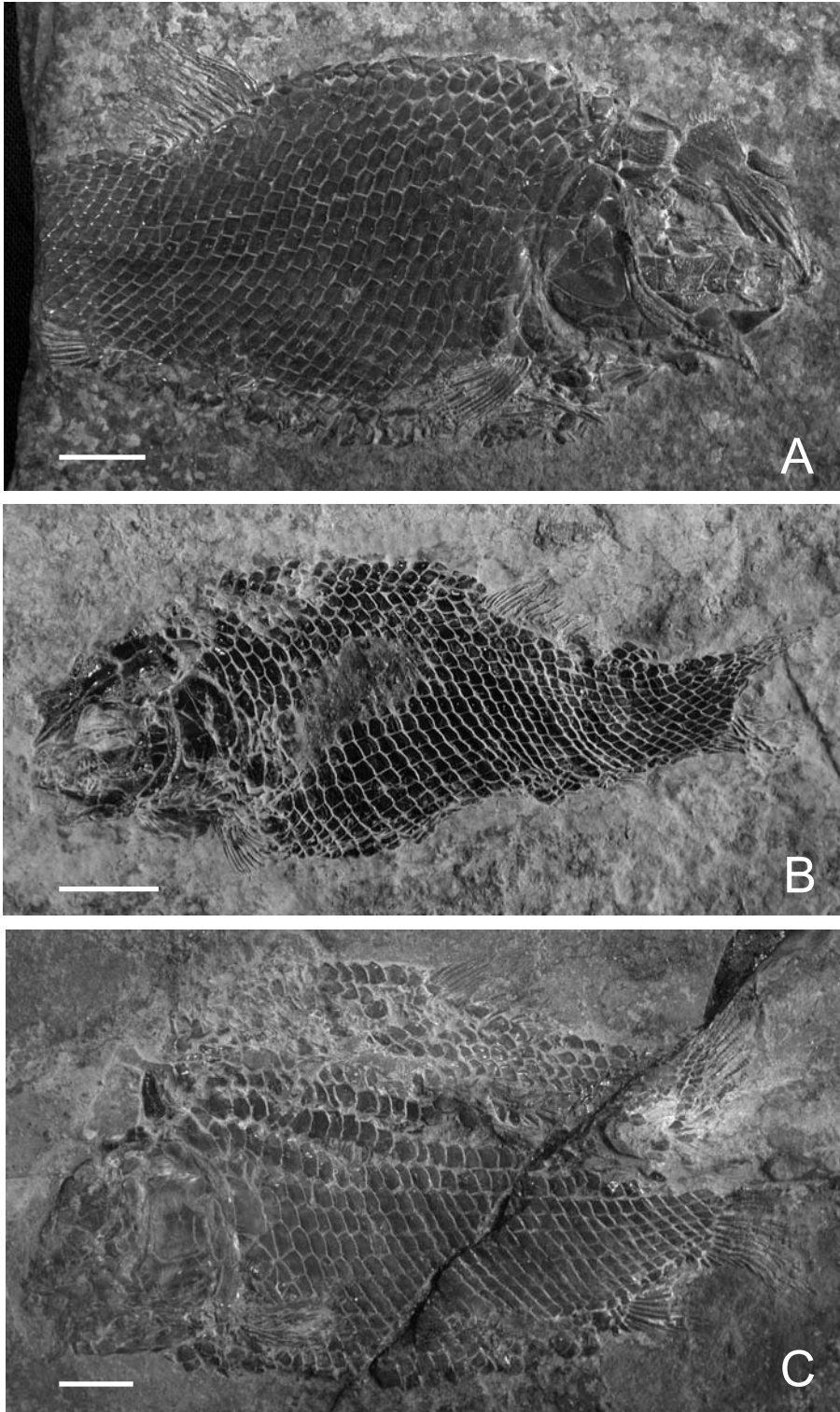


Fig. 1 - *Sangiorgioichthys aldae* gen. n. sp. n. in lateral view. A) the holotype MCSNIO P457; B) specimen MCSNL 5050; C) MCSNIO P458. Scale bars: 10 mm.

**Diagnosis** (based on a combination of plesiomorphic characters): small Semionotidae up to 100 mm of SL; dermal bones totally covered by ganoine; a very large postero-ventral infraorbital (io3) almost attaining the anterior edge of the preoperculum, several suborbitals two of which are ventral to the infraorbital 3; very elongate anterior supraorbital; edentulous maxilla; dentition with crowded thin pencil-like teeth concentrated in the anterior region of the mouth, mouth-gape small; sensorial pores very widespread on both canal-bearing and anastomose bones; dorsal fin very small; lateral line scales with one or more round pores on each scale (posterior l.l. scales may be without pores but with posterior margin deeply indented). Complete last scale-row on the body-lobe above the last scale of the lateral line. Squamation consisting of 30 transversal rows of scales with straight posterior margin except for few denticles randomly arranged on the different part of the body. Sub-hexagonal scales on the anterior part of the trunk, rectangular to rhombic on the dorsal and ventral region of the body. Dorsal ridge scales with small posterior spine.

**Etymology.** Dedicated to Prof. Alda Nicora who found the first specimen in the Rio Vallone.

**Holotype.** MCSNIO P457 from the Kalkschieferzone of Rio Vallone (Viggiù, Varese, Italy) just above the aqueduct track.

**Paratypes.** MCSNIO P458, P665 from the middle Kalkschieferzone of Ca' del Frate (Viggiù-Va); MCSNL 5050 from the lower Kalkschieferzone of Val Mara D (Meride, Canton Ticino, CH).

**Other material.** LVC 3878-6-10579 from the Perledo Member.

**Age and stratigraphical distribution.** Middle Triassic: Uppermost Ladinian of Kalkschieferzone (Meride Limestone) and of Perledo Member (Perledo-Varenna Formation).

**Remarks.** Bellotti (1857) erected the species *Lepidotus serratus* from Perledo. De Alessandri (1910), following Deecke (1889), ascribed this species to *Heterolepidotus*. Actually, the type of the species is *Perlepidus altolepis* (De Alessandri 1910, pl. VI, fig. 3; see

**Etymology.** From Monte San Giorgio, the paleontological area at the boundary Italy/Switzerland, where the holotype and the paratypes were found.

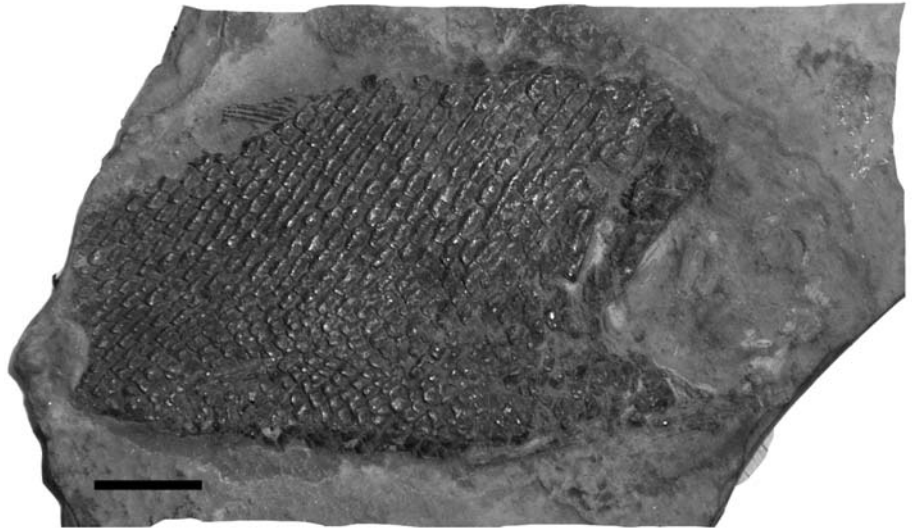
**Age.** As for the only known species.

**Stratigraphical distribution.** As for the only known species.

***Sangiorgioichthys aldae* sp. n.**

Figs 1-8

Fig. 2 - *Sangiorgioichthys aldae* gen. n.  
sp. n. Specimen LVC 3878-6-  
10579 from Perledo. Scale bar:  
10 mm.



Lombardo 2001): the counterpart of the type is still existing in the Liceo 'Volta' collection in Como (n. 3890-107-10623). In the same collection is deposited the second specimen (n. 3878-6-10579) cited by De Alessandri (1910, p. 104) for this species. It is clearly not *Perleidus* and it is here ascribed to the new taxon (Fig. 2).

### Description

**Skull.** The rostral bone is a small trapezoidal element carrying the ethmoidal commissure along its ventral part (Figs. 3B, 4B, 5AB). The nasal bone is narrow and tube-like, fitting into the deep anterior notches of the frontals (Figs. 1AB, 3AB, 4AB, 5AB).

The frontals are about three times longer than the parietals: they are characterized by a remarkable orbital constriction and by an irregular anterior margin, tapering anteriorly. Their maximum width is about 1/5 of their length. There is a deep anterior notch to slot the nasals. The supraorbital canal enters this notch and ran near to the orbital margin, ending in the parietals. The interfrontal suture is slightly wavy (Figs. 1AB, 3AB, 4AB, 5AB). The parietals are broad and rectangular, joined to the frontals by an irregular suture; on the antero-lateral corner of the element is present a small projection, anteriorly directed. Few pores of the supraorbital sensory canal are visible on the anterior region of this element, while a single pit line is detectable on the posterior one (Figs. 1AB, 3AB, 4AB, 5AB). There is a single pair of triangular extrascapulars, which meet in midline; the supratemporal commissure is well detectable by large pores, especially on the lateral margin of each bone (Figs. 1AB, 3AB, 4AB, 5AB). The dermopterotic has an irregular shape, with wavy margins; its surface shows pores of the sensory canal along the ventral part (Figs. 1AB, 3AB, 4AB, 5AB).

The circumorbital ring was most likely complete, with the long anteriormost supraorbital bone reaching the dorsal margin of the deep infraorbitals. The infra-

orbital series is made of six elements. The antorbital is reduced to a tube around the sensory canal and joined posteriorly to the first of the three deep elements bordering the ventral margin of the orbit. The first and second infraorbitals are triangular, with their apices contacting each other; the third element is very large and rectangular, with a convex anterior margin and the dorso-lateral corner projecting forward, leaning against the second infraorbital. Along the ventral margin there are large openings corresponding to the exits of the branches of the infraorbital canal, which ran in the middle of the bone. Dorsally to the third infraorbital there are further two small, squarish elements, forming the posterior part of the orbit; the last infraorbital contacts the small dermosphenotic (Figs. 1AB, 3AB, 4AB, 5A).

The region between the preoperculum and the infraorbitals is covered by 9 suborbitals. The four dorsal ones, below the dermopterotic, are arranged in a double series, followed ventrally by a single row of three elements; other two triangular suborbitals lie ventrally to the third large infraorbital. The shape and arrangement of the four suborbitals around the third infraorbital seems to be a steady feature of this taxon, being very similar in all specimens; it is not possible to state if also the other elements keep the same arrangement at the level of the dorsal region, as it is well preserved in a single specimen (Figs. 1AB, 3AB, 4AB, 5A). On specimen MCSNL 5050 each couple of suborbitals behind and below the third infraorbital is made of only partly separated elements (Figs. 3B, 4B).

The preoperculum is narrow with a ventral limb slightly larger than the dorsal one and it bends slightly forward. The posterior part of the element shows a row of large openings corresponding to the passage of the preopercular canal. Other much smaller pores are detectable on the dorsal part of the bone, randomly arranged (Figs. 3AB, 4AB, 5A).

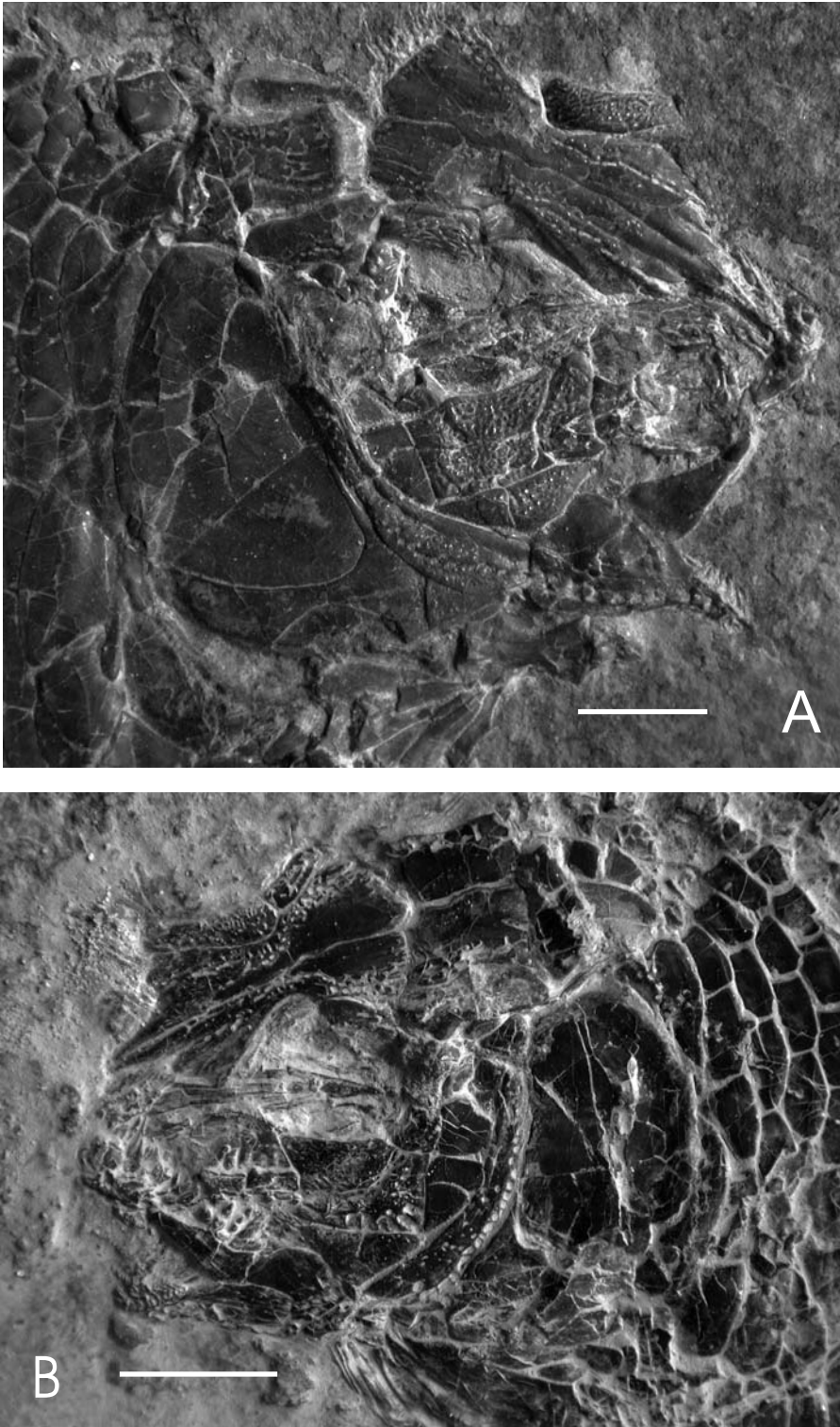


Fig. 3 - *Sangiorgioichthys aldae* gen. n. sp. n. A) skull of the holotype MCSNIO P457 and B) of specimen MCSNL 5050. Scale bar: 5 mm.

backwardly. On the ventral margin of the dentary large openings of the mandibular canal are visible (Figs. 3AB, 4AB, 5A).

The edentulous maxilla is small and triangular, with a long narrow anterior end bending upward. A narrow supramaxilla is clearly detectable on specimen MCSNIO P457 and MCSNIO P665; in the other specimens it has been most likely fused with the maxilla (Figs. 3AB, 4AB). The premaxilla is T-shaped, with a long ascending process, and bears conical teeth whose number is not determinable (Figs. 3AB, 4AB, 5AB).

**Pectoral girdle.** The large posttemporal has a rounded posterior margin and the two lateral elements are separated by the dorsal ridge scales; the rounded pores on the latero-ventral region shows the course of the sensory canal which passes into the supracleithrum (Figs. 3AB, 4AB, 5AB). The supracleithrum is a large element dorso-ventrally elongated and tapering ventrally. Pores of the lateral line are visible in the dorsal region (Figs. 3AB, 4AB). There are three postcleithra, decreasing in size from the most dorsal to the ventral one. The cleithrum is broad and sickle-shaped (Figs. 3AB, 4AB, 5A).

**Palatal bones.** The palatal bones bear numerous conical teeth of different size in specimens MCSNIO P457 and MCSNIO P458; on the small specimen MCSNIO P665 palatal teeth are stronger than those borne by the maxilla. In none of the specimens it is possible to distinguish the single bones of this complex, being always fragmented or incomplete.

The opercular region is broad with a semicircular posterior outline: the series is made by a deep operculum, a suboperculum with a well-developed antero-dorsal process and a small triangular interoperculum (Figs. 3AB, 4AB, 5A).

**Jaws.** The lower jaw is deep and short and it is made of large angular and surangular bones and a dentary tapering anteriorly, whose anterior oral margin bears several rows of conical and pointed teeth, turned

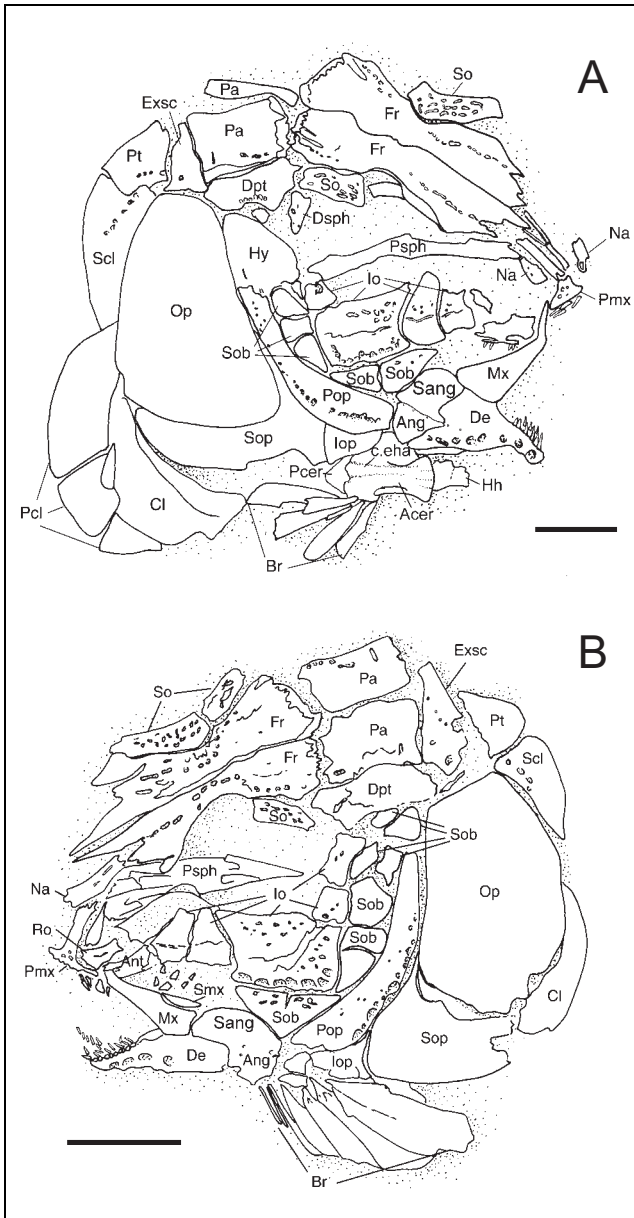


Fig. 4 - *Sangiorgioichthys aldae* gen. n. sp. n. Drawing of the skulls illustrated in Fig. 3: A) MCSNIO P457 and B) MCSNL 5050. Scale bar: 5 mm.

**Hyoid arch.** On the holotype MCSNIO P457 some elements of the hyoid arch are exposed. The anterior ceratohyal is elongated and subrectangular, with an anterior border lower than the posterior one. The groove for the hyoidean artery ran on the median region of the lateral surface of the bone. A triangular element, partly covered by the anterior ceratohyal, is interpreted as the posterior ceratohyal (Fig. 4A). The hypohyal is visible in front of the anterior ceratohyal, but the state of preservation does not allow to state if there was a single element (Fig. 4). Up to nine branchiostegal rays have been counted (Figs. 3AB, 4AB, 5A).

**Ornamentation.** The dermal bones are almost smooth, except for the posterior region of the skull

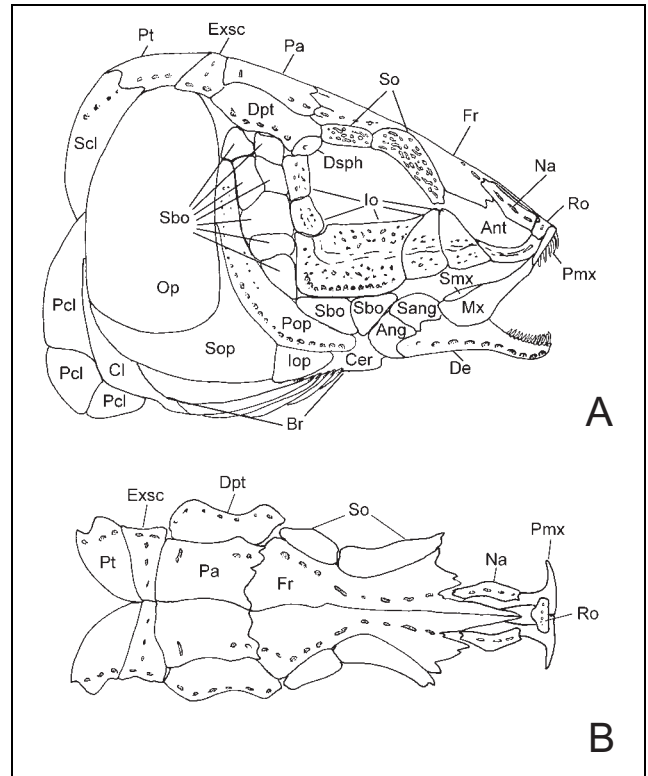


Fig. 5 - *Sangiorgioichthys aldae* gen. n. sp. n. Restoration of the skull in A) lateral, and B) dorsal views.

roof, the supraorbitals, the preoperculum, the infraorbitals and the ventral elements of the suborbitals, which are ornamented by tubercles and short ridges of ganoine. On frontals, the ornamentation is made of flat tubercles that become longer and coalescent on the posterior region of the bones (Figs. 3AB, 4AB).

**Squamation.** The squamation is made by 30 transverse and 16-17 horizontal scale rows, which show a smooth free surface. The shape of the scales varies according to their position: the scales of the lateral region of the body, deeper than broad, are sub-hexagonal up to the level of the insertion of the dorsal fin; from the dorsal fin backwards they become rectangular to rhombic, gradually decreasing in size. Scales of the belly region between the pectoral and the pelvic fins are rhombic, as long as deep, while the ones at the base of the anal fin are lower, longer than deep (Figs. 1ABC, 2, 6AB, 7ABC). The depth of the scales decrease also on the caudal peduncle, where they become diamond-shaped (Figs. 1B, 8AB). A dorsal ridge scale row is present; each scale is rhombic in shape, with a small posterior spine. The shape of the scales and the length of the spines are constant throughout the dorsal ridge; the ganoine covering is homogeneous (Figs. 1AB, 6AB, 7AB).

All scales of the lateral line show both pores and slits on their surface, which alternate until the level of

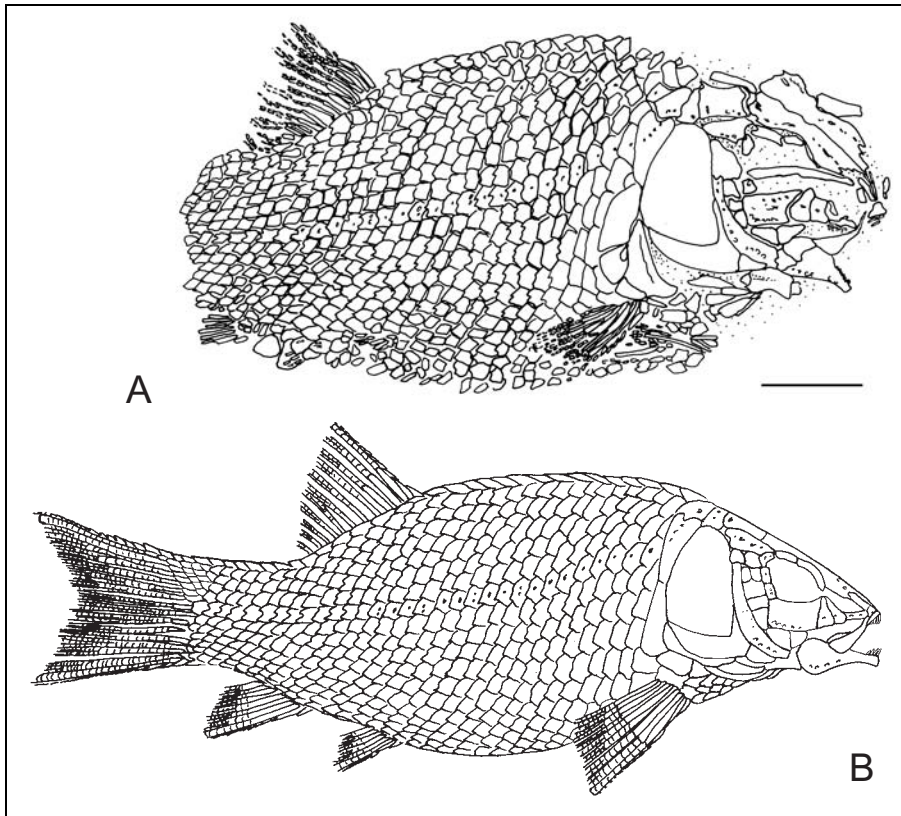


Fig. 6 - *Sangiorgioichthys aldae* gen. n. sp. n. A) drawing of the holotype MCSNIO P457 and B) restoration in lateral view. Scale bar: 10 mm.

the dorsal fin; in some of them pores are coupled or a pore and a slit are found together. In the posterior region of the body these openings are not more visible and the passage of the sensory canal is marked by a notch on posterior margin of the scales (Figs. 1AB, 6AB, 7D). Unfortunately, the preservation of the caudal fin on all specimen is not good enough to give a precise description of the scale arrangement. In specimen MCSNIO P458, in which the dorsal lobe of the caudal fin is not disturbed, the scales that constitute the posterior margin of the axial body lobe seems to be arranged on a single row beginning from the last scale of the lateral line (Fig. 8AB).

The posterior margin of some scales is characterized by few denticles with no precise topographical distribution (1ABC, 2, 6AB).

*Fins.* In the pectoral fin, up to 10 lepidotrichia have been counted; the rays are unsegmented for about half of their length. They branch at least twice, with their distal ends very delicate. There are a couple of long basal fulcra and a series of small fringing fulcra along the anterior margin of the fins. The pelvic fins are not completely preserved in any specimen: they are inserted at about the 11<sup>th</sup> vertical scale row (Fig. 6AB).

The dorsal fin is placed at the level of 20<sup>th</sup> vertical scale row: it is made up of 16-17 lepidotrichia quite spaced from each others, each showing long proximal and very short distal segments. The rays branch at least twice, becoming very thin at their distal end. There are

two-three long basal fulcra and thin fringing fulcra (Fig. 6AB).

The small triangular anal fin is placed at the level of the 18<sup>th</sup> scale row; about ten rays, branching at least twice, have been counted, with 2-3 basal fulcra in front of them. Also in this case, a series of thin fringing fulcra is present (Figs. 1ABC).

The tail is hemiheterocercal with the axial body lobe rather short. It is impossible to state the exact number of the caudal fin rays: specimen MCSNIO P458 and P665 lack the caudal region, while in P457 the dorsal part of the body is separated from the ventral one by a slump, so that the caudal fin is partly disarticulated in its median part; also specimen MCSNL 5050 shows only part of the lepidotrichia. The caudal fin is made of at least 17 rays, with short stout proximal elements and small and squarish distal ones which branch at least three times. There are three-four dorsal caudal scutes and at least one basal fulcrum on the dorsal lobe of the fin (Fig. 8 AB); a series of thin fringing fulcra is present both along the dorsal and ventral edge of the fin.

#### Comparison and discussion

Following different authors (Olsen & McCune 1991; Wenz 1999; Arratia & Schultze 1999) the presence of all or several of the following characters allows to put a genus within the family Semionotidae: dorsal ridge scales with a more or less prominent spine; more than



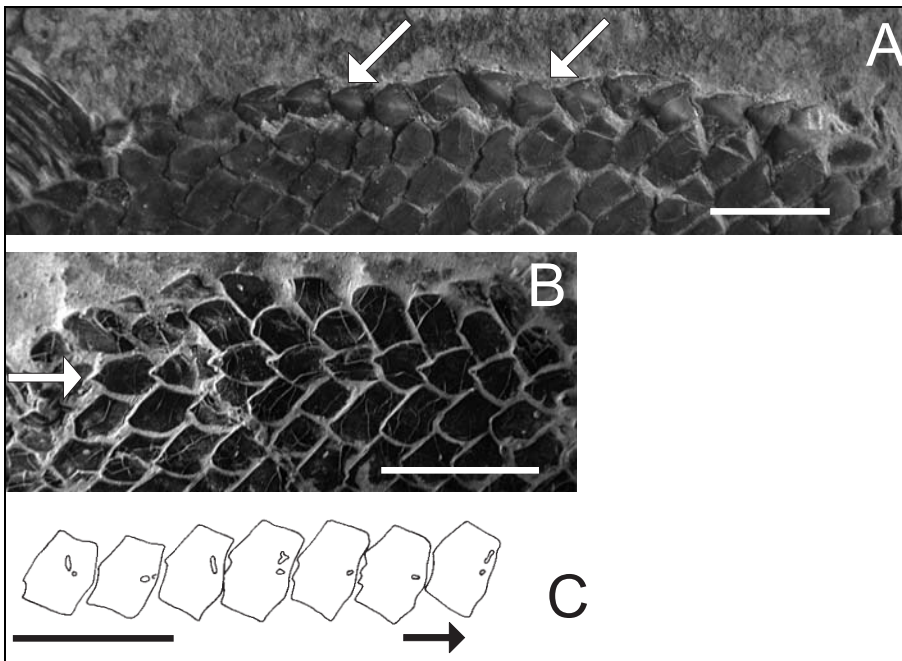


Fig. 7 - *Sangiorgioichthys aldae* gen. n. sp. n. A) dorsal ridge scales in the holotype MCSNIO P457 and B) MCSNL 5050; C) drawing of some lateral line scales of the holotype MCSNIO P457, showing the arrangement of the pores of the sensory canal. White arrows point to the dorsal ridge scales, the black arrow points to the anterior region of the specimens. Scale bar: 5 mm.

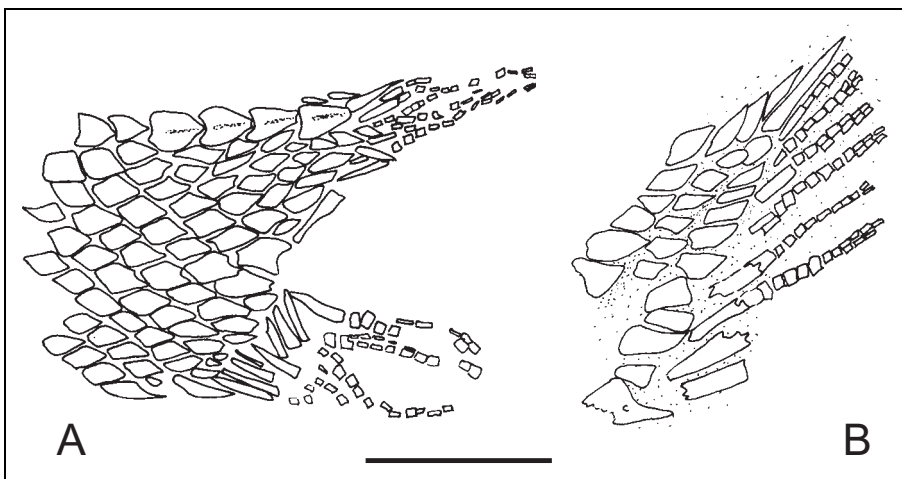


Fig. 8 - *Sangiorgioichthys aldae* gen. n. sp. n. Pattern of squamation of the axial body lobe in A) MCSNL 5050 and B) MCSNIO P458. Scale bar: 10 mm.

one lacrimal, large anterodorsal process on the suboperculum, large dorsal process on the premaxilla, single supramaxilla, preoperculum narrow and gently bent, dentition usually powerful, high coronoid process, dentary going back ventrally to the angular, snout not completely covered by dermal bones (rostral and nasals more or less tube like). As a consequence, *Semionotus*, *Lepidotes* s.l., *Paralepidotus*, *Pliodetes*, *Araripelepidotus*, *Semiolepis* are currently considered part of the Semionotidae.

One of the more widely accepted criterion for separating the different representatives of Semionotidae is the number of suborbitals (single or more than 1). Wenz (1999) divided the family in three groups: 1) a group including *Semionotus* and *Paralepidotus* (single suborbital); 2) a group including *Araripelepidotes* and some species of *Lepidotes* (2-10 suborbitals in a single row); 3) a group forming by *Pliodetes* and other *Lepidotes* species (mosaic of suborbitals).

Following the distinction based on number of suborbitals, the discussion about the new taxon is focused mainly on the comparison among the genera with more than one suborbital (*Araripelepidotes*, *Pliodetes* and *Lepidotes*); nevertheless, concerning some features, *Sangiorgioichthys* gen. n. will be compared also with taxa belonging to the other groups identified by Wenz, stressing once more the presence in semionotids of crossing combinations of characters.

*Sangiorgioichthys* gen. n. is clearly different from *Araripelepidotes* both in skull (e.g. jaws arrangement, shape of preoperculum, circumorbital region) and body pattern (squamation, caudal fin structure); also *Pliodetes* shows very different characteristics, mainly for the pattern of skull roof and cheek. Moreover the new taxon shows three ossifications on the lateral face of the lower jaw, as *Lepidotes*. This latter seems to be the closest to *Sangiorgioichthys* gen. n., in the general skull pattern and body morphology, although this genus is in need

of a deep revision and it may be considered, at present, as a “basket-genus”. With respect to *Lepidotes*, *Sangiorgioichthys* gen. n. shows a combination of characters which may be found isolated in some of its species: among these, some not common features such as the very large postero-ventral infraorbital, separating the posterior and ventral suborbitals, the preorbital gap between the anterior region of the frontals, the first infraorbital and the nasal and the edentulous maxilla. *Sangiorgioichthys* gen. n. is characterized by a very large infraorbital (the third) that constitutes the entire ventral margin of the orbit, almost reaching the preoperculum with its postero-ventral corner. This character is present in some species of *Lepidotes* (e.g. *L. tendaguruensis*, *L. microrhis*, *L. buddhabutrensis*; Arratia & Schultze 1999; Wenz 2003; Cavin et al. 2003) and in *Araripelepidotes* (Maisey 1991): in these species of *Lepidotes* there are enlarged infraorbitals at the postero-ventral corner of the orbit, but the difference in size with the other elements of the series is not very pronounced; on the contrary, in *Araripelepidotes*, the fifth infraorbital extends from the orbit to the preoperculum (Maisey 1991). In *Araripelepidotes*, anyway, the ventral elements of the infraorbital series do not leave any space for suborbitals, which are represented by three elements aligned in a vertical series. The enlarged infraorbital occupying the postero-ventral corner of the orbital region is seen also in semionotids with a single suborbital, such as *Paralepidotus ornatus* (Tintori 1996), and *Semionotus kanabensis* (Schaeffer & Dunkle 1950).

In *Sangiorgioichthys* gen. n. nine suborbitals have been counted, unfortunately entirely visible in only one specimen (MCSNL 5050); the number and disposition of five elements, the three most ventral of the vertical series and the two below the third infraorbital, is identical in all specimens, with the exception of MCSNL 5050, in which the couples of suborbitals behind and below the third infraorbital are not completely separated and in one of the specimens (MISNIO P458) there are two separated bones instead of one, as clearly detectable on the other material. Suborbitals arranged around the postero-ventral infraorbitals is a typical feature of *Lepidotes*, and many attempts to find a criterion for grouping the different situations found in the *Lepidotes* species have been made. Suborbitals may vary in number within the same species or even on different sides of the same specimen (Jain 1983), so that this character should be used with caution. According to Jain (1983) the different species of *Lepidotes* forms three groups: 1) with 2-7 suborbitals arranged in a single row; 2) with more than 7 suborbitals in a single row; 3) with more than 7 suborbitals which form a mosaic of bones. Moreover, Jain recognizes a trend to increase the number of these elements during the history of the genus, from Lower Jurassic to the Upper Cretaceous

(Jain 1983). Wenz simplifies this scheme, recognizing for *Lepidotes* (and the other semionotids with more than one suborbital) two groups: 1) 2-10 suborbitals in a single rows; 2) many suborbitals forming a mosaic of bones (Wenz 1999). Arratia & Schultze separated the species of *Lepidotes* in two groups: 1) 3-6 plates distributed in a single row; 2) 7 or more plates in one or more rows (Arratia & Schultze 1999), emphasizing the number of suborbitals rather than their arrangement. In *Sangiorgioichthys* gen. n. the arrangement of suborbitals is peculiar, being the plates below the dermopterotic arranged in a double series followed ventrally by a single row of 3 elements, representing a somehow “intermediate” situation between the single row and the mosaic of bones.

In most of the species of *Lepidotes* the anterior region of the snout, when preserved, is covered by the deep first infraorbitals and/or the enlarged anteriormost suborbital (e.g. Jain 1983, p. 33, fig. 9); there are few exceptions, such as *L. lennieri* (Wenz 1967) and *L. notopterus* (de Saint Seine 1949). A similar pre-orbital gap is visible also in *Sangiorgioichthys* gen. n., showing a gap just anterior to the first infraorbital, which comes into contact to the elongated anteriormost suborbital.

The new taxon has an edentulous maxilla, a character which is considered as exceptional in *Lepidotes*, being reported only in *L. alagoensis* (Gallo 2000), *L. microrhis* and *L. tanyrhis* (Wenz 2003), but which is present, among semionotids devoid of crushing teeth, also in *Araripelepidotes temnurus* (Maisey 1991) and *Pliodetes nigeriensis* (Wenz 1999). Among semionotids with a single suborbital, the edentulous maxilla is present in *Semionotus kanabensis* (Schaeffer & Dunkle 1950).

Concerning the morphology of marginal teeth of the lower jaw, in both tritorial or non-tritorial forms, *Lepidotes* is generally characterized by styliform teeth, with a narrowing at the basis of the acrodine cap (e.g., *L. elevensis*, *L. microrhis*; Wenz 1967, 2003). In some species (e.g. *L. mantelli*) these are set on long pedicles with moderately swollen crowns, in others (*L. affinis*) teeth are more slender, with obtusely conical tips (Jain 1983). *Sangiorgioichthys* gen. n. is characterized by slender and conical teeth, slightly bending backwards and no distinctive pedicles are detectable. Moreover, all teeth have similar shape and are arranged on several rows on the lower jaw, as well as on premaxilla. *Sangiorgioichthys* gen. n. is therefore devoid of specialized crushing teeth, as *L. tendaguruensis* (Arratia & Schultze 1999), *L. elevensis*, *L. deccanensis* (Wenz 1967; Jain 1983), *L. microrhis* (Wenz 2003).

A character which is seemingly unique for *Sangiorgioichthys* gen. n. is represented by the scales of the lateral line, with the peculiar shape and arrangement of the external traces of the sensory canal. The presence of

small slits and rounded pores both alternating and together on all scales has never been reported in any other taxon of this family. Concerning the last scales of the lateral line, they do not show the openings of the sensory canal, but they are notched in some specimens of *Sangiorgioichthys* gen. n. Jain (1983) reports the presence of a double spur on the posterior margin of some lateral line scales on a number of specimens of *Lepidotes* sp. (previously described as *L. deccanensis* by Egerton (1878)) from the Lower Jurassic Kota Formation, as well as in *Lepidotes minor*, *L. mantelli* and *L. notopterus* (Woodward 1916), but nothing is said about the morphology of the pores corresponding to the openings of the canals of the lateral line.

Concerning the caudal fin, the only known tails of *Sangiorgioichthys* gen. n. (MCSNL 5050 and MCSNIO P458) are not completely preserved: the posterior margin of the axial body lobe shows a single row of scales beginning from the last scale of the lateral line; therefore, it seemingly lacks the additional scale row that seems to be typical, with different number and arrangement of its elements, of the other semionotids (Lombardo & Tintori in press).

Owing to all these combination of characters, it was necessary to erect a new genus for this semionotid; moreover, this new taxon is particularly important because it adds new information to the early history of Semionotidae, and therefore it could help in establishing the apomorphic characters polarity.

The overall richness of the fish faunas from the Middle Triassic marine units in western Tethys, as well as the probable similar situation for the Guizhou Province in S. China ones (Liu et al. 2003; Chang et al. 2004) allows to hope in a better understanding of this group before its Norian radiation when *Semionotus*, *Paralepidotus*, *Semiolepis* and other taxa from the Calcareo di Zorzino became very common (Tintori 1998; Lombardo & Tintori in press). After the Triassic/Jurassic boundary, Semionotidae remains an important group in the fish faunas of fresh water lakes (Olsen & McCune 1991; Arratia & Schultze 1999; Wenz 2003; Cavin et al. 2003; Gallo 2000, 2005; Gallo & Brito 2004) or in marine environments mainly related to coastal lagoons or intra-carbonatic platform basins (Wenz 1967, 1999; Jain 1983, 1986; Maisey 1991; Arratia & Schultze 1999) at least until the end of the Early Cretaceous.

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## REFERENCES

- Arambourg C. & Bertin L. (1958) - Super-Ordres des Holostéens et des Halécostomes (Holostei et Halecostomi). In: Grassé, P. (Ed.) - *Traité de Zoologie* 13(3): 2173-2203, Masson et Cie., Paris.
- Accordi B. (1955) - *Archaeolepidotus leonardii* n. gen. n. sp. e altri pesci permo-werfeniani delle Dolomiti. *Mem. Ist. Geol. Miner. Univ. Padova*, 19: 1-28, Padova.
- Accordi B. (1956) - A new genus of Lower Triassic Holostean fish from the Dolomite Alps. *J. Paleontol.*, 30: 345-351, Lancaster.
- Arratia G. & Schultze H.-P. (1999a) - Semionotiform Fish from the Upper Jurassic of Tendaguru (Tanzania). *Mitt. Mus. Naturkd. Berlin.*, Geowiss. Reihe 2: 135-153, Berlin.
- Arratia G. & Schultze H.-P. (1999b) - Mesozoic fishes from Chile. In: Arratia, G. & Schultze, H.-P. (Eds) - *Mesozoic Fishes II - Systematic and Fossil Record*: 565-593, Verlag Dr. F. Pfeil, München.
- Bassani F. (1914) - Sopra un pesce fossile degli scisti calcareo marnosi triassici del Galletto presso Laveno sul lago maggiore (*Peltopleurus humilis* Kner). *Boll. R. Comitato Geol. Italia*, XLIV(2): 101-105, Roma.
- Bellotti C. (1857) - Descrizione di alcune nuove specie di pesci fossili di Perledo e di altre località lombarde. In: Stoppani A. - *Studii geologici e paleontologici sulla Lombardia*. Biblioteca Politecnica: 419-438, C. Turati Editore, Milano.
- Bürgin T. (1992) - Basal Ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (C. Tessin, Switzerland). *Schweiz. Paläontol. Abh.*, 114: 1-164, Basel.
- Bürgin T. (1995) - Actinopterygian fishes (Osteichthyes, Actinopterygii) from the Kalkschieferzone (uppermost Ladinian) near Meride (Canton Ticino, Southern Switzerland). *Eclogae geol. Helv.*, 88(3): 803-826, Basel.
- Bürgin T. (1999) - Middle Triassic marine fish faunas from Switzerland. In: Arratia, G. & Schultze, H.-P. (Eds) - *Mesozoic Fishes II - Systematic and Fossil Record*: 481-494, Verlag Dr. F. Pfeil, München.
- Bürgin T. (2004) - *Eosemionotus ceresiensis* sp. nov., a new semionotiform fish (Actinopterygii, Halecostomi) from the Middle Triassic of Monte San Giorgio (Southern Switzerland). In: Arratia, G. & Tintori, A.

- (Eds) - Mesozoic Fishes III - Systematics, Paleoenvironments and biodiversity: 239-251, Verlag Dr. F. Pfeil, München.
- Bürgin T., Eichenberger U., Furrer H. & Tschanz K. (1991) - Die Prosanto Formation - eine fischreiche Fossil-Lagerstätte in der Mitteltrias der Silvretta-Decke (Kanton Graubünden, Schweiz). *Eclogae geol. Helv.*, 84(3): 921-990, Basel.
- Cavin L., Suteethorn V., Khansubha S., Buffeteaut E. & Tong H. (2003) - A new semionotid (Actinopterygii, Neopterygii) from the Late Jurassic-Early Cretaceous of Thailand. *C. R. Palevol*, 2: 291-297, Paris.
- Cavin, L. & Suteethorn V. (2006) - A new semionotiform (Actinopterygii, Neopterygii) from the Upper Jurassic - Lower Cretaceous deposits of north-east Thailand, with comments on the relationships of semionotiforms. *Palaeontology*, 49(2): 339-353, London.
- Chang Mee-Man & Miao Desui (2004) - An overview of Mesozoic fishes in Asia. In: Arratia, G. & Tintori, A. (Eds) - Mesozoic Fishes III - Systematics, Paleoenvironments and biodiversity: 535-563, Verlag Dr. F. Pfeil, München.
- Cope E. D. (1887) - Zittel's manual of palaeontology. *Am. nat.*, 21: 1014-1019, Chicago.
- Dames W. (1888) - Die Ganoiden des deutschen Muschelkalks. *Paläontol. Abh.*, 4(2): 133-179, Berlin.
- De Alessandri G. (1910) - Studi sui pesci triasici della Lombardia. *Mem. Soc. Ital. Sci. Natur.*, 7: 1-147, Milano.
- Deecke W. (1889) - Ueber Fische aus verschiedenen Horizonten der Trias. *Palaeontographica*, 35: 97-138, Stuttgart.
- Egerton P.M.G. (1878) - On some remains of ganoid fishes from the Deccan. *Palaeontol. Indica*, 1(2): 1-8, Calcutta.
- Fritsch K. v. (1906) - Beitrag zur Kenntnis der Tierwelt der deutschen Trias. *Abh. Naturforsch. Ges. Halle*, 24: 2017-285, Berlin.
- Gaetani M., Gnaccolini M., Poliani G., Grignani D., Gorza M. & Martellini L. (1992) - An anoxic intraplateau basin in the Middle Triassic of Lombardy (Southern Alps, Italy): anatomy of a hydrocarbon source. *Riv. It. Paleontol. Strat.*, 97: 329-354, Milano.
- Gall J. C., Grauvogel L. & Lehman J. P. (1974) - Faune du Buntsandstein. V. Les poissons fossiles de la Collection Grauvogel-Gall. *Ann. Paléontol.*, 60(2): 129-147, Paris.
- Gallo V. (2000) - First occurrence of *Lepidotes* (Actinopterygii: Semionotiformes: Semionotidae) in the Coqueiro Sec Formation, early Aptian of the Sergipe-Alagoas Basin, Northeastern Brazil. *Boll. Mus. Nac. n.s. Geol.*, 51: 1-14, Rio de Janeiro.
- Gallo V. (2005) - Redescription of *Lepidotes pianhyensis* Roxo and Löfgren, 1936 (Neopterygii, Semionotiformes, Semionotidae) from the ?Late Jurassic-Early Cretaceous of Brazil. *J. Vert. Palaeontol.*, 25(4): 757-769, Lawrence.
- Gallo V. & Brito P.M. (2004) - An overview of Brazilian semionotids. In: Arratia, G. & Tintori, A. (Eds) - Mesozoic Fishes III - Systematics, Paleoenvironments and biodiversity: 253-264, Verlag Dr. F. Pfeil, München.
- Gardiner B.G., Maisey J.G. & Littlewood D.T.J. (1996) - Interrelationships of Basal Neopterygians. In: Stiassny, M.L.J., Parenti, L.R. & Johnson, G.D. (Eds) - Interrelationships of Fishes: 117-146, Academic Press, San Diego.
- Guttormsen S. E. (1937) - Die Triasfauna der Tessiner Kalkalpen. XIII. Beiträge zur Kenntnis des Ganoidengebisses, insbesondere des Gebisses von *Colobodus*. *Abh. Schweiz. paläontol. Ges.*, 60: 1-42, Zürich.
- Jain S. L. (1983) - A revision of the genus *Lepidotes* (Actinopterygii: Semionotiformes) with special reference to the species of the Kota Formation (Lower Jurassic), India. *J. Palaeontol. Soc. India*, 28: 7-42, Calcutta.
- Jain S. L. (1986) - Reflections on some Mesozoic fish faunas of the world. *Quart. J. Geol. Miner. Soc. India*, 58: 1-28, Bangalore.
- Jörg E. (1969) - Eine Fischfauna aus dem Oberen Buntsandstein (Unter-Trias) von Karlsruhe-Durlach (Nordbaden). *Beitr. Naturkd. Forsch. Südwestdtschl.*, 28(2): 87-102, Karlsruhe.
- Lehman J.P. (1966) - Actinopterygii. In: Piveteau J. (Ed.) - *Traité de Paléontologie* 4(3): 1-242, Masson Cie, Paris.
- Liu Guan-Bang, Yin Gong-Zheng, Wang Xue-Hua, Luo Yong-Ming & Wang Shang-Yan (2003) - New discovered fishes from *Keichousaurus* bearing horizon of Late Triassic in Xingyi of Guizhou. *Acta Paleontol. Sinica*, 43(3): 355-359, Beijing.
- Lombardo C. (1999) - Sexual dimorphism in a new species of the actinopterygian *Peltopterus* from the Triassic of Northern Italy. *Palaeontology*, 42(4): 741-760, London.
- Lombardo C. (2001) - Actinopterygians from the Middle Triassic of Northern Italy and Canton Ticino (Switzerland): anatomical descriptions and nomenclatural problems. *Riv. It. Paleontol. Strat.*, 107(3): 345-369, Milano.
- Lombardo C., Renesto S. & Tintori A. (2006) - Primi vertebrati fossili dalla Formazione di Cunardo (Ladinico Inferiore, Triassico Medio) della Valtravaglia (Varese). *Geol. Insubrica*, 8(2): 5-9, Morbio inferiore.
- Lombardo C. & Tintori A. (2004) - New perleidiforms from the Triassic of the Southern Alps and the revision of *Serrolepis* from the Triassic of Württemberg (Germany). In: Arratia, G. & Tintori, A. (Eds) - Mesozoic Fishes III - Systematics, Paleoenvironments and biodiversity: 179-196, Verlag Dr. F. Pfeil, München.
- Lombardo C. & Tintori A. (in press): A new semionotid fish (Actinopterygii, Osteichthyes) from the Late Triassic of the Northern Italy. In: Arratia, G., Schultze, H.P. & Wilson, M. (Eds) - Mesozoic Fishes IV - Systematics, Homology, And Character Definition, Verlag Dr. F. Pfeil, München.
- Maisey J. (1991) - *Araripelepidotus* Silva Santos, 1958. In: Maisey, J. (Ed.) - Santana fossils. An illustrated atlas: 118-123, T. F. H. Publications, Inc., Neptune, New Jersey.
- Olsen E. O. & McCune A. R. (1991) - Morphology of the *Semionotus elegans* species group from the Early Jur-

- assic part of the Newark Supergroup of Eastern North America with comments on the family Semionotidae (Neopterygii). *J. Vert. Palaeontol.*, 11(3): 269-292, Lawrence.
- Patterson C. (1973) - Interrelationships of holosteans. In: Greenwood, P.H., Miles, R.S & Patterson, C. (Eds) - Interrelationships of Fishes. *Zool. J. Linn. Soc., London* 53, suppl. 1: 233-305, Academic Press, London.
- Piveteau J. (1934) - Contribution à l'étude des Actinopterygiens, Paléontologie du Madagascar XXI. Les Poissons du Trias Inférieur. *Ann. Paleontol.*, 23: 81-181, Paris.
- Regan C. T. (1925) - The skeleton of *Lepisosteus*, with remarks on the origin and evolution of the lower Neopterygian fishes. *Proc. Zool. Soc. London*, 1923: 445-461, London.
- Saint-Seine, P. de (1949) - Les poissons des calcaires lithographiques de Cerin (Ain). *Nouv. Arch. Mus. Hist. Natur. Lyon*, 2: 1-357, Lyon.
- Schaeffer B. & Dunkle D. H. (1950) - A semionotid from the Chinle Formation, with consideration of its relationships. *Am. Mus. Nov.*, 1457: 1-29, New York.
- Schultze H.-P. & Möller H. (1986) - Wirbeltierreste aus dem Mittleren Muschelkalk (Trias) von Göttingen, West-Deutschland. *Paläontol. Z.*, 60: 109-129, Stuttgart.
- Silva Santos R. da (1985) - Nova Conceituação Taxonômica do *Lepidotes temnurus* Agassiz, do Cretáceo Inferior da Formação Santana, Nordeste do Brasil. IX Congr. Brasil. Paleontol., Res. Comun. 16, Fortaleza.
- Stolley E. (1920) - Beiträge zur Kenntnis der Ganoiden des deutschen Muschelkalk. *Palaeontographica*, 63: 25-86, Stuttgart.
- Tintori A. (1983) - Hypsomatic Semionotidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Riv. Ital. Paleontol. Strat.*, 88(3): 417-442, Milano.
- Tintori A. (1990) - *Dipteronotus olgiatii* sp. n. (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' del Frate (N. Italy). Preliminary note. *Atti Ticin. Sci. Terra*, 33: 191-197, Pavia.
- Tintori A. (1996) - *Paralepidotus ornatus* (Agassiz, 1833-43): A semionotid from the Norian (Late Triassic) of Europe. In: Arratia, G. & Viohl, G. (Eds) - Mesozoic Fishes - Systematic and Paleocology: 167-179, Verlag Dr. F. Pfeil, München.
- Tintori A. (1998) - Fish biodiversity in the marine Norian (Late Triassic) of Northern Italy: the first Neopterygian radiation. *Ital. J. Zool.*, 65, Suppl.: 193-198, Roma.
- Tintori A. & Lombardo C. (1999) - Late Ladinian fish faunas from Lombardy (North Italy): stratigraphy and paleobiology. In: Arratia, G. & Schultze, H. -P. (Eds) - Mesozoic Fishes II - Systematics and Fossil Record: 495-504, Verlag Dr. F. Pfeil, München.
- Tintori A., Lombardo C., Gozzi E. & Brunetti M. (2004) - I pesci del Triassico Medio della Grigna Settentrionale (Lecco). Giornate di Paleontologia 2004, Soc. Paleontol. Ital. Bolzano, 21-23 Aprile 2004.
- Tintori A., Posenato R., Kustatscher E. & Wachtler M. (2001) - New Triassic fish remains from paralic environments in the Alps. Abstract of III Internatl. Meeting on Mesozoic Fishes: 66, Serpiano, August 2001.
- Tintori A. & Renesto S. (1983) - The Macrosemiidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Riv. It. Paleont. Strat.*, 89(2): 209-222, Milano.
- Wenz S. (1967) - Compléments à l'étude des poissons actinoptérygiens du Jurassique français. *Cahiers Paléontol.*, 1-276, Paris (Centre Nat. Rech. Scient.).
- Wenz S. (1999) - *Pliodetes nigeriensis*, gen. nov., sp. nov., a new semionotid fish from the Lower Cretaceous of Gadoufaoua (Niger Republic): phylogenetic comments. In: Arratia, G. & Schultze, H. -P. (Eds) - Mesozoic Fishes II - Systematics and Fossil Record: 107-120, Verlag Dr. F. Pfeil, München.
- Wenz S. (2003) - Les *Lepidotes* (Actinopterygii, Semionotiformes) du Crétacé inférieur (Barrémien) de Las Hoyas (Province de Cuenca, Espagne). *Geodiversitas*, 25(3): 481-489, Paris.
- Woodward A. S. (1890) - The fossil fishes of the Hawkesbury series of Gosford, New South Wales. *Mem. Geol. Surv. New South Wales, Palaeontol.*, 4: 1-55, Sydney.
- Woodward A. S. (1895) - Catalogue of the Fossil Fishes in the British Museum (Natural History). Part III: 544 pp., British Museum (Natur. Hist.), London.
- Woodward A. S. (1916) - The fossil fishes of the English Wealdan and Purbeck formations. *Palaeontogr. Soc. Monogr.*, 1916: 1- 48, London.

