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ACTINOPTERYGIANS FROM THE MIDDLE TRIASSIC OF NORTHERN ITALY AND CANTON TICINO (SWITZERLAND): ANATOMICAL DESCRIPTIONS AND NOMENCLATURAL PROBLEMS

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Riassunto. Vengono descritti, sulla base di nuovi esemplari ben conservati provenienti dalla Kalkschieferzone (Calcare di Meride, Ladinico superiore) di Ca' del Frate (Viggiù, Varese) e di Meride (Canton Ticino, Svizzera), gli attinotterigi finora poco conosciuti *Allolepidotus bellottii* (Rüppell), *Furo trottii* (Balsamo Crivelli, 1839) e *Perleidus altolepis* (Deecke, 1889), specie istituite su materiale proveniente dagli Scisti di Perledo, parte sommitale della Formazione di Perledo-Varenna. I nuovi ritrovamenti hanno consentito di effettuare la prima dettagliata descrizione anatomica di *Allolepidotus bellottii* e la ricostruzione anatomica completa di *Perleidus altolepis*; la presenza del caturide *Furo* nel Triassico Medio, precedentemente messa in discussione, viene altresì confermata. Oltre alle descrizioni anatomiche vengono discussi alcuni dei numerosi problemi relativi alla nomenclatura adottata dagli autori precedenti, come pure la distribuzione stratigrafica del genere *Perleidus* che si riteneva esclusiva del Ladinico. Infine viene descritto un nuovo genere appartenente ai Perleidiformi.

Abstract. The actinopterygians *Allolepidotus bellottii* (Rüppell), *Furo trottii* (Balsamo Crivelli, 1839) and *Perleidus altolepis* (Deecke, 1889), so far known from the Perledo Member (upper member of the Perledo-Varenna Formation), are here redescribed on the basis of well-preserved material coming from the late Ladinian Kalkschieferzone of Ca' del Frate (Viggiù, Varese) and Meride (Canton Ticino, Switzerland). These new finds in the Kalkschieferzone are particularly important because they allow the first detailed anatomical description of *Allolepidotus bellottii* and the complete anatomical restoration of *Perleidus altolepis*; the presence of the caturid *Furo* in the Middle Triassic, which has previously been questioned, is confirmed. Besides the anatomical descriptions, the complicated and problematical nomenclature adopted by previous authors for the species of the Perledo Member is discussed. The stratigraphical distribution of the genus *Perleidus* is questioned, as the Triassic species previously ascribed to this genus are here considered as not related to it. Finally, a new genus of Perleiformes is erected.

Introduction and historical remarks

The locality of Ca' del Frate (Viggiù, Varese, Italy) belongs to the Kalkschieferzone, the upper member of Meride Limestone (Late Ladinian), which crops out between Valceresio (Italia) and the Meride area (Canton Ticino - Switzerland) (Fig. 1). This locality yielded a rich fauna made up of more than 3000 specimens of fishes, belonging to 15 species, and three specimens of the sauropterygian *Lariosaurus* (Tintori & Renesto 1983, 1990; Tintori et al. 1985; Tintori 1990a, 1990b; Renesto 1993). The fish fauna consists of five genera of basal actinopterygians and seven of primitive neopterygians (Lombardo 1997) but the former exceed the latter in number of specimens, with the exception of the neopterygian *Prohalecites porroi* (Bellotti, 1857) (Tintori 1990a), represented by thousands of specimens found also in mass mortality layers. Some of the fish species that constitute the Ca' del Frate fauna were already described on the basis of old material collected in the Perledo area, along the Eastern coast of Como Lake.

The Perledo-Varenna Formation has been known since the last century for its fossil finds, and in particular for its vertebrate fauna (Balsamo Crivelli 1839; Bellotti 1857; Bassani 1886; Deecke 1889; De Alessandri 1910). The study of the better-preserved material from Ca' del Frate provides a good correlation with the Perledo fauna (Tintori et al. 1985; Tintori & Renesto 1990; Lombardo 1997; Tintori & Lombardo 1999).

The comparison between the material from the two units has stressed that the so-called "Perledo fauna" actually consists of at least three different assemblages: the youngest one, coeval with Ca' del Frate, is most probably from the Perledo Member, the uppermost part of the Perledo-Varenna Formation (for discussion on stratigraphy, see Tintori 1998; Tintori & Lombardo 1999). The two sites share the best represented species in both: *Perleidus altolepis, Allolepidotus bellottii* and *Furo trottii*, which are to be described in this paper, together with *Prohalecites porroi* (Tintori 1990a) and *Peltopleurus nuptialis* (Lombardo 1999), as well as rarer species such as *Aneurolepis macroptera* (Lombardo 1997; Tintori & Lombardo 1999).

The comparison with the Perledo material is diffi-

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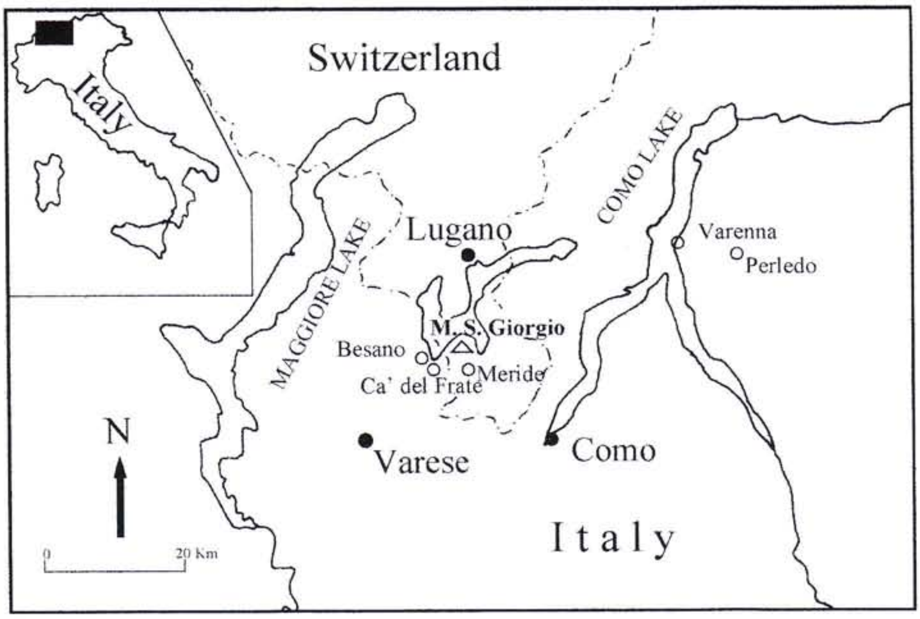

Fig. 1 - Geographic localization of the Monte San Giorgio and Perledo area.

cult, as most of the specimens and many of the holotypes, which were stored at Museo Civico di Storia Naturale di Milano, were destroyed during World War II. For many species the only means of comparison is given by the old literature (Deecke 1889; De Alessandri 1910).

The first note about the Perledo fauna dates from to 1839 with the work of Balsamo Crivelli, but the first paper on fossil fishes, without any illustrations, was that by Bellotti (Stoppani 1857) who simply described the different species. Later on, Bellotti (1873) wrote a manuscript catalogue of fossil fishes of the Museo di Storia Naturale di Milano; it was accompanied by drawings, but was not published till recently (Pinna 1991). Afterwards, Deecke (1889) made the first revision of the Perledo fauna, but he could not access the specimens described by Bellotti, so he worked only on Rüppell's collection stored at the Naturmuseum und Forschunginstitut Senckenberg in Frankfurt, and on a few specimens from Strasbourg and Wien. Using these new specimens Deecke gave new diagnoses for the forms described by Bellotti. Deecke erected new taxa also (*Allolepidotus nothosomoides, Archaeosemionotus connectens, Semionotus altolepis*), but again, since he could not compare his material with that of Bellotti, specimens that I now believe to be conspecific were often attributed even to different genera. As well, specimens belonging to different genera were attributed to the same species (pers. obs.).

This fact deeply influenced all further studies. De Alessandri (1910) made another revision of the Perledo fauna, comparing the material described by Bellotti with that stored at the Naturmuseum und Forschunginstitut Senckenberg in Frankfurt. However, De Alessandri did not realize the true relationships between the specimens from the two collections, adding new cases of synonymy and homonymy.

After the work of De Alessandri, studies on Perledo fishes were neglected, perhaps because of the very scarce new material that had been collected in the Perledo-Varenna Formation after the middle of the XIX century. For this reason, many Perledo species have been often cited but without any modern detailed anatomical descriptions.

The Ca' del Frate and Meride material, with its well preserved specimens, makes an important contribution in the form of a first comparison between the Kalkschieferzone fauna and that of Perledo Member. At the same time it allows finally to give detailed anatomical descriptions of species that were previously scarcely known.

Institutional abbreviations of the cited specimens: MCSNIO: Civico Museo Insubrico di Storia Naturale di Induno Olona (Varese, Northern Italy); MCSN: Museo Cantonale di Storia Naturale di Lugano; PIMUZ: Paläontologische Institut und Museum der Universität, Zurich; SM: Naturmuseum Senckenberg, Frankfurt am Main; MB: Museum für Naturkunde, Berlin.

Abbreviations

Af, anal fin; Ang, angular; Ant, antorbital; Br, branchiostegal rays; Cl, cleithrum; De, dentalo-splenial; Df, dorsal fin; Dhy, dermohyal; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; Fr, frontal bone; Gae, gill-arch elements; Gu, gular; Io, Io1, Io2, Io3, Io4, infraorbital bones; Iop, interoperculum; Md, lower jaw; Mpl, median pit line; Mx, maxilla; Na, nasal bone; Op, operculum; Pa, parietal bone; Pas, pre-anal scute; Pcl, postcleithrum(a); Pef, pelvic fin; Pf, pectoral fin; Pmx, premaxilla; Pop, preoperculum; Ppl, posterior pit line; Pt, posttemporal; Q, quadrate; Qj, quadratojugal; Ro, rostral bone; Sc, scales; Sbo, suborbital; Scl, supracleithrum; Smx, supramaxilla; So, supraorbital bones; Sop, suboperculum.

Remarks on anatomical terminology of the caudal skeleton

The morphology and evolution of the caudal skeleton of actinopterygian fishes has become an important tool in systematics (Nybelin 1973; Lauder 1989; Schultze & Arratia 1989); this is particularly important for primitive actinopterygians, as those here described, poorly known until recently. The study of the evolution of the caudal skeleton in fishes is very complicated and is beyond the aim of this paper: anyway some information about the anatomical terminology adopted here for the caudal region, is given.

One of the most important trend in actinopterygian phylogeny is the tendency to transform the heterocercal caudal fin into an at least externally and functionally symmetrical one (Nybelin 1973). One way to achieve this condition is through strong development of caudal fin rays dorsally inserted on the vertebral axis, which tend to straighten at the posterior end.

For these rays the term "epaxials" has been used in previous papers (Hutchinson 1973; Nybelin 1973; Gardiner 1988; Grande & Bemis 1998), to indicate the caudal fin rays dorsal to the notochord (or the upper caudal fin rays elongate beyond the termination of body axis, according to the definition of Gardiner & Schaeffer 1989). "Epaxial" caudal fin rays are present in many actinopterygian groups, such as perleidiforms, peltopleuriforms, pholidopleuriforms and saurichthyforms, even if in these two latter groups the tail is actually diphycercal, thus symmetrical both internally and externally.

The term "epaxial" is used also here for better explaining the differences with the caudal fin pattern of neopterygians, in which the caudal fin rays are all ventral to the vertebral axis. (Fig. 2). The caudal end of vertebral axis is, in most Triassic fishes, hidden by the squamation, made of thick, ganoine covered, scales. Anyway, Nybelin (1973), removing the scale covering from the axial body lobe in specimens of *Pholidopleurus* and *Australosomus*, which have "epaxial" caudal fin rays, showed the agreement between the shape of body lobe and the course of vertebral column. In this paper the expression "axial body lobe" refers to the region of caudal fin showing the scale covering, beginning from the transversal row of the last scale of the lateral line.

Since the caudal morphology is important in questions regarding phylogenetic relationships, deepened studies will be therefore necessary, as well as the use of new and more appropriate anatomical terminology, in order to avoid confusion.

Paleontological descriptions

Actinopterygii Cope, 1871

Neopterygii *incertae sedis*

Genus *Allolepidotus* Deecke, 1889

Diagnosis (emended from Deecke 1889): Small to medium-sized fusiform neopterygian; skull with elongate jaws; maxilla with posterior notch; four infraorbitals with large infraorbital 1 and infraorbital 3; one suborbital; preoperculum narrow and subvertical; nasal bones meeting on the midline; small triangular rostral bone; dorsal and anal fins triangular, with strong fringing fulcra; hemiheterocercal and forked caudal fin; scales thick, deeper than wide in lateral region of flank; ventral scales never wider than deep; all scales serrated at their

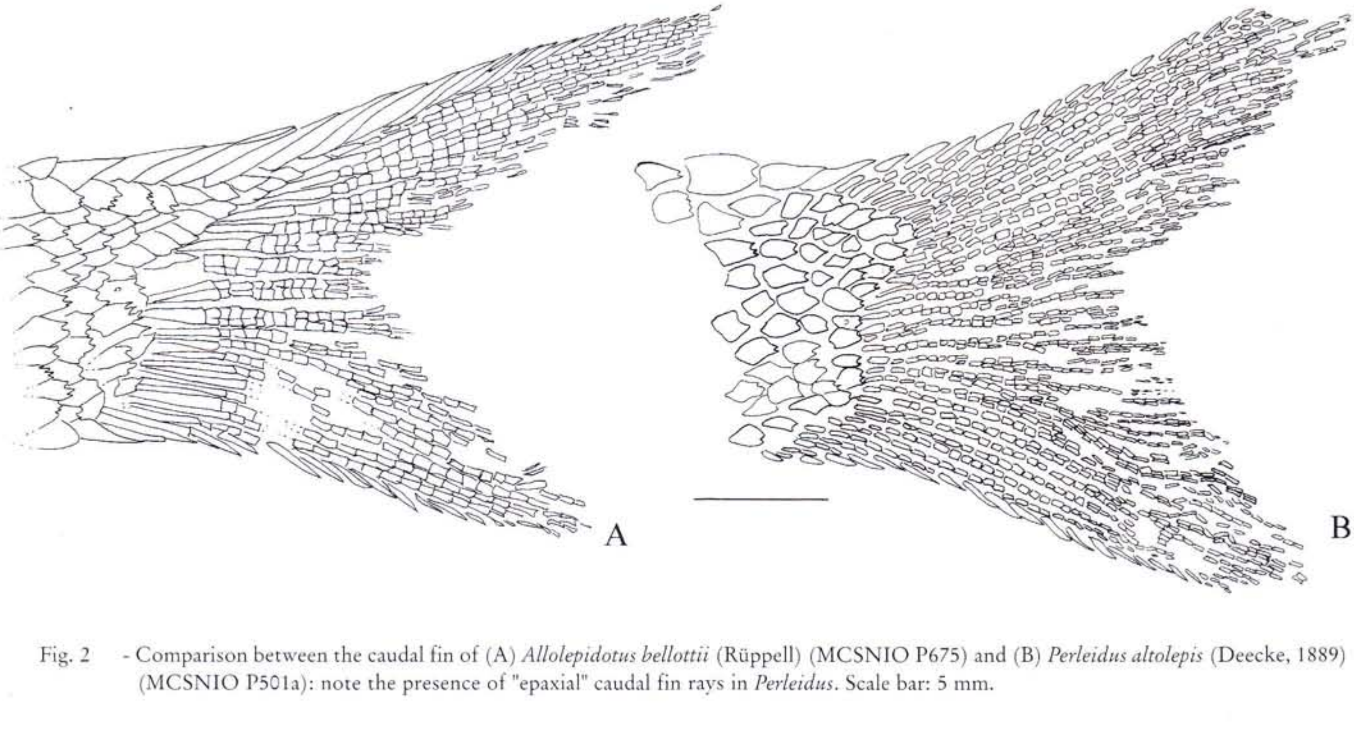

Fig. 2 - Comparison between the caudal fin of (A) *Allolepidotus bellottii* (Rüppell) (MCSNIO P675) and (B) *Perleidus altolepis* (Deecke, 1889) (MCSNIO P501a): note the presence of "epaxial" caudal fin rays in *Perleidus*. Scale bar: 5 mm.

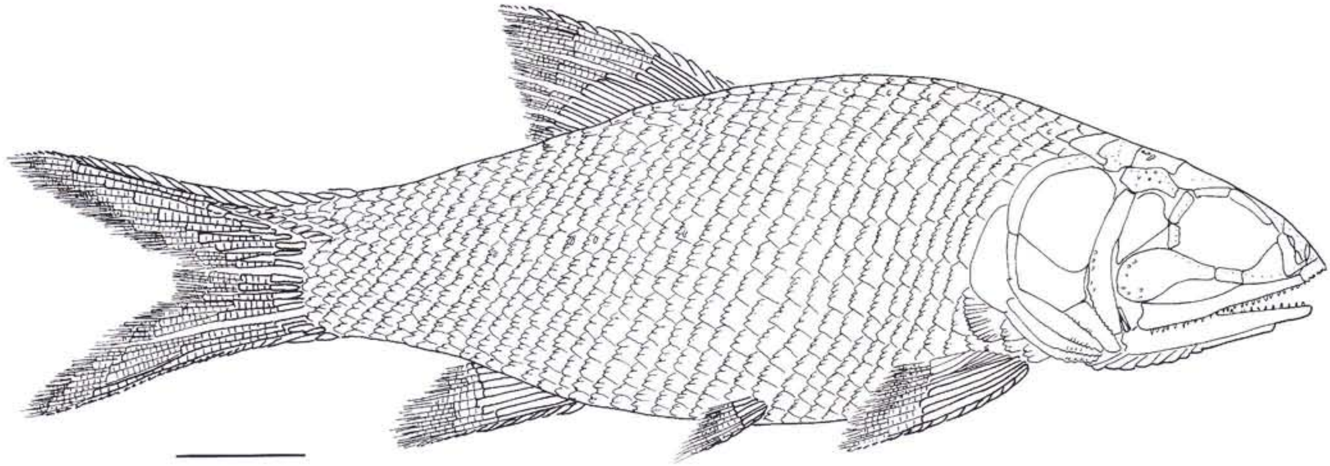

Fig. 3 - *Allolepidotus bellottii* (Rüppell). Restoration. Scale bar: 10 mm.

posterior margins.

Type-species: *Allolepidotus bellottii* (Rüppell).

Distribution: Middle Triassic; Late Ladinian of Perledo Member (Perledo-Varenna Formation) and of Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù-Varese) and Meride (TI-CH).

Remarks

The genus *Allolepidotus* was erected by Deecke (1889) on Perledo material of the species *A. nothosomoides*. With this name Deecke meant all those forms with deep flank scales and squarish ventral ones (Deecke 1889: 113) in order to distinguish them from *Heterolepidotus* and *Lepidotus*. He did not take into consideration the skull pattern.

Since the data relative to skull pattern were lacking, it was difficult to establish the systematic position of this form. It was usually attributed to Eugnathidae (Woodward 1895; Lehman 1966). Patterson (1973) disagreed on keeping *Allolepidotus* within this family together with other Triassic genera such as *Eoeugnathus* and *Sinoeugnathus*, though all were poorly known genera. All of them were relegated to the more primitive grade group, the Parasemionotidae, together with the families Tungusichthyidae, Promecosominidae and Paracentrophoridae (Patterson 1973: 283).

According to Patterson (1973) parasemionotids do not have an independent quadratojugal, but Olsen (1984) found a small and squarish quadratojugal in *Watsonolus*. In contrast, *Allolepidotus* has a splint-like quadratojugal, similar to that found in *Lepisosteus* (Wiley 1976; Arratia & Schultze 1991), *Semionotus* (Schaeffer & Dunkle 1950), *Dapedium (*Patterson 1973*)*, *Tetragonolepis* (Thies 1991), *Hulettia* (Schaeffer & Patterson 1984), *Prohalecites* and *Paralepidotus* (Tintori 1990a, 1996).

Allolepidotus has a narrow and subvertical preoperculum. Parasemionotids, such as *Watsonolus, Parasemionotus* and *Ospia*, show a wide preoperculum, even if in some genera, such as *Paracentrophorus, Promecosomina* and *Phaidrosoma*, the preoperculum is narrow. *Jacobulus, Thomasinotus, Stensionotus* have a preoperculum made of several elements: the posterior one is narrow and contained the preoperculum sensory canal. When in Parasemionotidae the preoperculum is fragmented into smaller elements, the antero-dorsal elements would correspond to suborbitals, according to Lehman (1952) and Lehman et al. (1959), and the preopercular sensory canal ran near the posterior margin of the bone.

As in all parasemionotids, the element corresponding to the suborbital in *Allolepidotus* does not overlap the preoperculum (Patterson 1973).

The number and arrangement of infraorbitals in *Allolepidotus* is similar to those shown by *Watsonolus* (Olsen 1984): there are four infraorbitals making the ventral and posterior margin of the orbit, with the Io1 and Io3 much bigger than Io2 and Io4. A well-expanded posterior region characterizes Io3. A posteriorly expanded infraorbital in the postero-ventral corner of the orbit, however, is present also in many halecomorphs and pholidophorids, but not in the parasemionotids *Watsonulus, Parasemionotus* and *Stensiönotus* (Lehman 1952; Olsen 1984).

The antorbital of *Allolepidotus* has a wide posterior region and a moderately long rostral process, as in parasemionotids (Lehman 1952; Patterson 1975; Olsen 1984), amiiforms and *Ophiopsis* (Bartram 1975). An antorbital with long rostral process is known also in *Acentrophorus* (Patterson 1975), macrosemiids (Bartram

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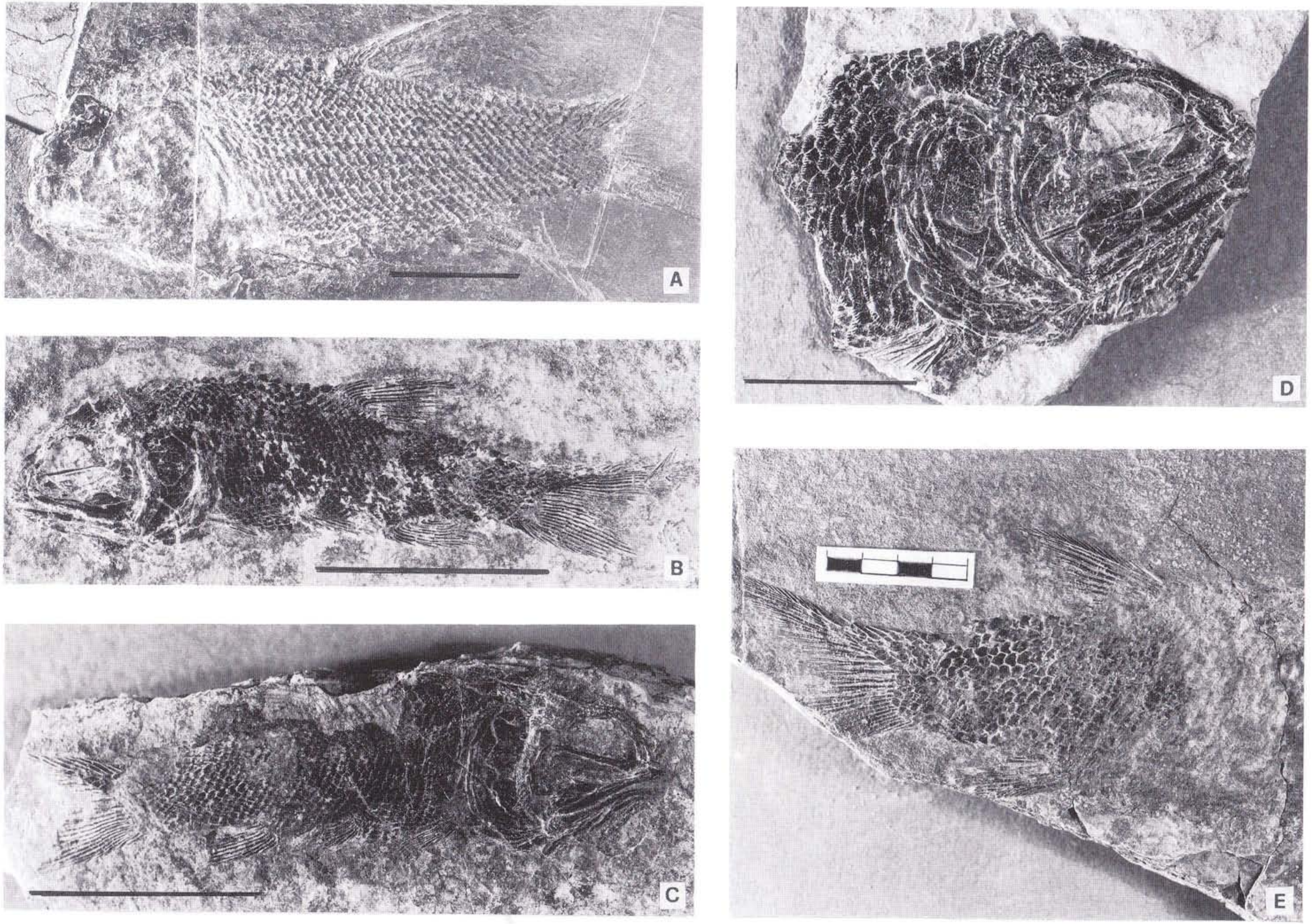
PLATE 1

A) *Allolepidotus bellottii* (Rüppell): the holotype 4431 P., before preparation. Scale bar: 20 mm; B) *Allolepidotus bellottii* (Rüppell): MCSNIO P669. Scale bar: 20 mm C) *Allolepidotus bellottii* (Rüppell): MCSNIO P655. Scale bar: 20 mm; D) *Allolepidotus bellottii* (Rüppell): MCSNIO P645a. Scale bar: 10 mm; E) *Allolepidotus bellottii* (Rüppell): MCSNIO P649. Scale bar: 20 mm.


A
B
C
D
E

1977), *Semionotus* (Olsen & McCune 1991), *Lepidotes* (Wenz 1967) and *Hulettia* (Schaeffer & Patterson 1984), though in these latter forms this bone is tube-like.

The rostral bone of *Allolepidotus* is triangular; in parasemionotids it is tube-like, a character considered primitive. A rostral bone similar to that of *Allolepidotus* is present in *Hulettia* (Schaeffer & Patterson 1984), *Caturus, Amblysemius* and amiiforms (Lambers 1992); many pholidophorids, too, have such a rostral bone (Nybelin 1966; Patterson 1975; Zambelli 1975, 1977, 1986).

The systematic position of this genus is uncertain: there are too few available data about basal neopterygians for a comparison. Moreover, they often concern such characters, as endocranial and endoskeleletal patterns, which are not available on Ca' del Frate specimens. For these reasons, I prefer to leave this genus as Neopterygii *incertae sedis*. The systematic position of this and other related genera can be cleared up only after study of the most primitive Triassic neopterygians.

Together with *Allolepidotus nothosomoides*, Deecke described also the species *Allolepidotus rueppelli*. The latter was previously described by Bellotti as *Pholidophorus rueppelli* (Bellotti in Stoppani 1857: 428) on the basis of a plaster mould that constitutes the holotype, the depository collection of the original specimen being unknown. Deecke attributed this species to the genus *Allolepidotus* on the shape of scales, deeper than wide on the lateral region of the trunk and rhombic on dorsal and ventral parts of the body (Deecke 1889: 117, pl. V, fig.5). Deecke did not describe the skull, that according to him is:" ..similar to that of *Lepidotus*" (Deecke 1889: 117). De Alessandri (1910) agreed with Deecke in attributing this species to the genus *Allolepidotus* according to the skull structure, fin and scale shape. He ascribed to the same species another specimen stored at the Museo Geologico dell'Università di Torino, that it is no longer available. The cast of the holotype of *Allolepidotus rueppelli*, stored at the Naturmuseum und Forschunginstitut Senckenberg in Frankfurt (SM P1266), and a specimen of this species stored at the Servizio Geologico d'Italia in Rome (1918 P), excludes this species from the genus, based on the different arrangment of the skull bones (pers. obs.).

Allolepidotus bellottii (Rüppell)

Figs. 2-6; Pl. 1

1849 *Palaeoniscus curionii* Haeckel, p.500.
1857 *Semionotus bellottii* Bellotti, Bellotti in Stoppani, p. 425.
1873 *Pholidophorus curionii* (Heckel), Bellotti, p.83 (manuscript) (in Pinna1991).
1889 *Allolepidotus nothosomoides* Deecke, p.118; pl. VI, fig.9.
1889 *Pholidophorus oblungus* Bellotti, Deecke, p. 124, pl. VI, fig.6.
1895 *Allolepidotus nothosomoides* Deecke, Woodward, part III, p.315.
1910 *Allolepidotus nothosomoides* Deecke, De Alessandri, pp. 116-118, pl. VIII, fig.7.
1910 *Allolepidotus bellotti* (Bellotti) (*pro parte*), De Alessandri, pp. 121-123, pl.VIII, fig. 1.
1910 *Pholidophorus curionii* De Alessandri, p. 127, pl. VIII, fig.8.
1910 *Pholidophorus oblungus* Bellotti (*pro parte*), De Alessandri, p. 129-131, pl. VIII, fig.10.
1997 *Allolepidotus nothosomoides* Deecke, Lombardo pp. 99-118, figs. 71-87.
1999 *Allolepidotus nothosomoides* Deecke Tintori & Lombardo, pp.495-504.

Diagnosis (emended from De Alessandri 1910): Small-sized neopterygian (up to 10 cm of standard length); spindle-shaped body with "hump" anterior to dorsal fin (juveniles slender); elongate upper and lower jaws with small conical teeth; narrow preorbital region of frontal bones; four infraorbitals with infraorbital 3 being larger than others; operculum rectangular and twice as deep as the suboperculum; elongate and triangular interoperculum; skull bones strongly ornamented by ganoine tubercles and ridges which follow course of sensory canals; dorsal and anal fins triangular with well-developed fringing fulcra; squamation of 35 transverse rows of thick scales, posteriorly serrated, deeper than wide only in anterior part of trunk.

Material: 4431 P (holotype) from Perledo-Varenna Formation, stored at Servizio Geologico d'Italia in Rome; MCSNIO P643-660; P669-677, P682ab, P683ab, P684ab, P685, P688, P689, P690 from the Kalkschieferzone of Ca' del Frate (Viggiù, Varese); SM 1237a/b, SM P1256, SM P1244 from the Perledo-Varenna Formation; MCSN 3126 from the Kalkschieferzone of Meride (TI-CH); MB 7597 (labelled as *Allolepidotus rueppelli*) from the Perledo-Varenna Formation.

Distribution: Middle Triassic: Upper Ladinian of the Perledo Member (Perledo-Varenna Formation) and of the Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù-Varese) and Meride (Canton Ticino, CH).

Description

Skull. The rostral bone is a small, triangular element, on which pores of the ethmoidal commissure are visible on the ventral part (Figs. 3, 4AB, 5ABD, Pl. 1BD). The nasal bones have an irregular shape and are dorso-ventrally elongated (Figs. 3, 4AB, 5ABCD, Pl. 1BCD). They meet medially. Length of nasal bones equal about 1/3 of frontal bones length.

The frontal bones are broad, with an expanded posterior region and a narrower anterior one (Figs. 3, 4AB, 5ABCD, Pl. 1BCD). The interfrontal suture shows interdigitations at about half-length. There is an embayment at the level of the orbit, where the frontal bones contact the supraorbital bones. The supraorbital sensory canal ran close to the lateral margin in the frontal bones and extends into parietal bones (Figs. 4AB, 5ABCD).

The parietal bones are squarish, with irregular margins. Interparietal suture is not clearly detectable, but it seems slightly wavy. Median and posterior pit lines are visible (Figs. 4AB, 5BCD, Pl. 1BCD).

The dermopterotics are trapezoidal, with an irregular dorsal margin. The surface of the bones is strongly irregular for the presence of many circular openings. The infraorbital sensory canal ran along the ventral margin, entering the extrascaspular (Figs. 3, 4AB, 5ABCD).

The extrascapulars are large, trapezoidal elements, deeper than the parietals. The supratemporal commissure is paralleled by a series of small spines (Figs. 5ABCD, Pl. 1CD).

Two elongate, rectangular supraorbital bones are present; they form the dorsal margin of the orbit (Figs. 3, 4AB, 5ABC, Pl. 1BD).

The dermosphenotics are small elements whose margins are not clearly detectable, owing to the state of preservation of all specimens (Figs. 3, 4AB, 5AB). The infraorbital bones are four elements of different sizes. They border the postero-ventral margin of the orbit (Figs. 3, 4A, 5ABCD, Pl. 1BD): Io1 is large, with a thin bony lamella dorsal to the infraorbital sensory canal tube. Infraorbital 2 is smaller than Io1. The bone is rectangular and ventrally meets the supramaxilla. The third infraorbital bone is the biggest element of the series; it is posteriorly expanded and it forms the postero-ventral corner of the orbit. Many spines, following the course of the posterior ends of the infraorbital sensory canal branches, characterize the surface of this bone. The fourth element is the smallest and is deeper than wide. Along the dorsal edge of all elements of the series are detectable pores of the infraorbital canal. The antorbital shows a moderately long anterior process and a broad posterior region (Figs. 3, 4AB, 5ABCD, Pl. 1BD).

The preoperculum is subvertical and narrow. The surface of the bone is irregular, with small spines that follow the course of preopercular sensory canal. Pores are scattered along the longitudinal axis of the bone (Figs. 5ABCD, Pl. 1CD). The operculum is higher than broad and twice as deep as the suboperculum (Figs. 3, 4A, 5ABCD, Pl. 1BCD). The dorsal margin is curved while the ventral one contacts the suboperculum through a convex suture. The suboperculum is rectangular and about twice as broad as high. At the anteroventral corner of the suboperculum there is a long and narrow triangular interoperculum. It shows well-developed ganoine ridges on its posterior margin (Figs. 4A, 5ABC, 6, Pl.1D).

The maxilla is rather long and narrow, with a peg-like internal head that articulates with the premaxilla and slightly wavy oral and dorsal margins (Figs. 5ABCD). The maxillary posterior border shows a notch (Figs. 3, 5ACD, Pl. 1C). The oral border of the maxilla is almost straight and bears about thirty small, conical teeth. There is a large supramaxilla (Figs. 3, 4A, 5ABCD, Pl. 1BCD), extending from the postero-dorsal corner of the maxilla for almost the 2/3 of its length. There is a strong, triangular premaxilla; it bears 8-9 conical teeth, somewhat larger of those borne by the maxilla (Figs. 3, 4A, 5ABD, Pl. 1BCD).

On most of the specimens the quadrate, few elements of gill arches and the splint-like quadratojugal are visible (Figs. 3, 5ABCD, Pl. 1D).

The lower jaw is a strong element, slightly longer than the maxilla (Figs. 5ABCD, Pl. 1C). The oral margin bears a series of conical teeth similar to those borne by the maxilla. The precise number of teeth is unclear since the oral border of the maxilla always covers them. Pores of the sensory mandibular canal are visible on ventral margin of lower jaws (Figs. 5ABCD, Pl. 1BCD).

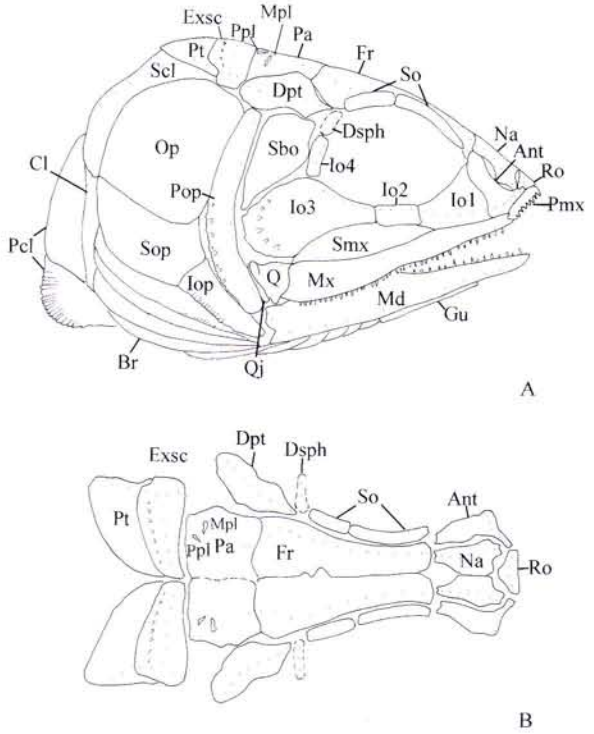


Fig. 4 - *Allolepidotus bellottii* (Rüppell). Restoration of the skull in lateral (A) and in dorsal (B) views.

Up to 10 branchiostegal rays were counted (Figs. 3, 4A, 5ABD, Pl. 1CD). There is a median, rectangular gular, with a V-shaped pit-line visible on the middle of the bone (Figs. 5AD, Pl. 1D).

The posttemporal is a large element posteriorly placed to the extrascapular. The two posttemporals meet along a short suture. Pores of the main lateral line are visible on the ventral margin of the bone (Figs. 4AB, 5ABCD, Pl. 1D). The supracleithrum is quite large, dorso-ventrally elongated and partially covered by the operculum (Figs. 3, 4A, 5ABCD, Pl. 1D). There are two postcleithra; the uppermost one is the biggest, rectangular, and dorso-ventrally elongated. Below this is a second squarish element, characterized by many ganoine ridges arranged perpendicularly to the posterior margin of the bone (Figs. 3, 4A, 5ABC, Pl. 1CD). The cleithrum is only partially visible, since it is covered by the opercular region (Figs. 3, 4A, 5B, 6).

Fins. In all specimens the pectoral fins are only partially preserved, showing their proximal bases (Fig. 6, Pl. 1BCD). Up to 14 lepidotrichia were counted. The lepidotrichia are narrow, and well-developed fringing fulcra border the anterior margin of the fins. Pelvic fins are made up at least of 10 lepidotrichia. They are placed anteriorly to the dorsal fin. On the anterior border of

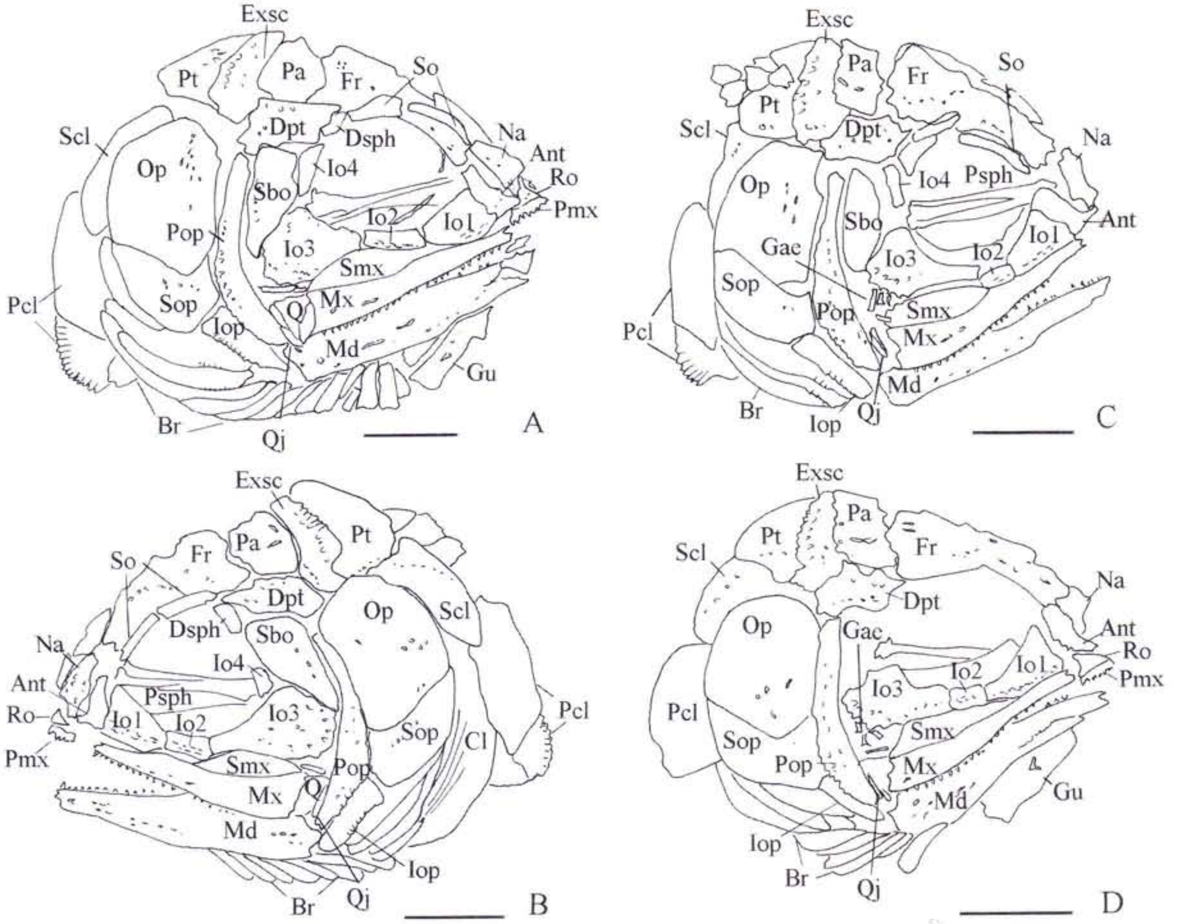


Fig. 5 - *Allolepidotus bellottii* (Rüppell). Skull bones as preserved in specimens: A) MCSNIO P645a; B) MCSNIO P660; C) MCSNIO P657; D) MCSNIO P655. Scale bars: 5 mm.

these fins there is a series of fringing-fulcra (Fig. 3, Pl. 1BC).

The dorsal fin is triangular and placed at the middle of the body (Figs. 3, 6, Pl. 1ABE). It is made up of at least 16 strong lepidotrichia, with long proximal bases and short distal segments. Each ray branches at least three times, becoming very thin at the distal end. There are two to three basal fulcra and a series of well-developed fringing fulcra along the anterior margin of the fin.

The anal fin is similar in shape and structure to the dorsal one, but it is smaller (Figs. 3, 6, Pl. 1BCE). Two to three basal fulcra precede the fin that is made up of at least 11 lepidotrichia, which branch three times.

The caudal fin is hemiheterocercal with a short body lobe. It is deeply forked and it is made up of 21 rays, which branch at least four times. The axial body lobe shows six-seven large basal fulcra and the first dorsal ray is bordered by fringing fulcra. The ventral lobe is preceded by a couple of basal fulcra and shows a series of fringing fulcra less developed than those borne by the dorsal lobe (Figs. 3, 6, Pl. 1BCE).

Squamation. Scale covering is made up of 35 transverse rows of thick scales with serrated posterior margins (Figs. 3, 6, Pl. 1ABCE). Scales are deeper than wide on the lateral region of the trunk; their depth decreases gradually towards the posterior part of the body. The scales of the first two rows behind the cleithrum are much deeper than wide; their posterior margin is serrated. The sizes of scales decrease towards the dorsal and ventral part of the body, though they never become wider than deep. The scales bearing the lateral line are slightly deeper than are the others. The dorsal scales are as deep as wide; a dorsal scale row between the posttemporal and the dorsal fin shows the pores for the passage of the dorsal lateral line (Pl. 1D). Posterior to the dorsal fin, scales are smaller and rhombic, with two or three serrations on posterior margin. The scales of ventral region between pectoral and pelvic fins of the body are very small. Posteriorly to the anal fin the ventral scales are equal in size to the others. The axial body lobe is covered by small rhombic scales (Figs. 3, 6, Pl. 1BCE).

Taxonomic history

The taxonomic history of *Allolepidotus bellottii* is very complicated. Heckel (1849) quoted this species as *Palaeoniscus curionii* on the basis of a specimen coming from Perledo; however, he gave neither an illustration

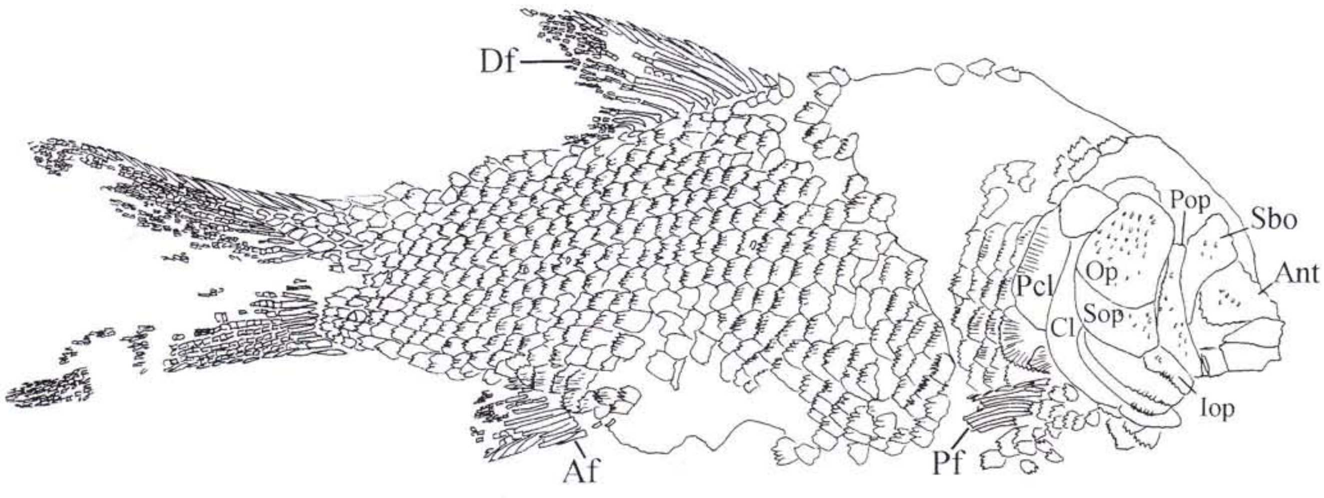


Fig. 6 - *Allolepidotus bellottii* (Rüppell). Specimen MCSNIO P647. Scale bar: 10 mm.

nor a picture of it. Afterwards, on the basis of a plaster cast of Heckel's specimen (once stored at Museo Civico di Storia Naturale di Milano), Bellotti (1873) gave a description of the species, in his *Catalogo manoscritto dei pesci fossili del Museo Civico di Milano* (which was never published), but he ascribed it to the genus *Pholidophorus*.

The same species has been named by Rüppell *Semionotus bellottii*, without giving any published description, on the basis of a single specimen. *Semionotus bellottii* has not been even cited, before the formal description given by Bellotti both on Rüppell's specimen and another specimen from the Curioni collection. In a footnote, Bellotti wrote that this description was made together with Rüppell during a visit to Milano (1857: 425). According to the International Code of Zoological Nomenclature Rüppell has to be considered the author of the species, even if he did not formally describe it (Art. 50.1.1).

Deecke (1889), in his revision of the Perledo fauna, based only on specimens of the Rüppell collection (see above), erected another species, *Allolepidotus nothosomoides*, without realising the conspecificity of the specimens he ascribed to his new species and those described as *Pholidophorus curionii* and *Semionotus bellottii.* In a successive study, De Alessandri (1910) again did not notice the similarity between the different species erected on the basis of the two collections, even though he had the possibility to access to the material from Milano and Frankfurt. As a consequence, he redescribed all these species as separate taxa: *Pholidophorus curionii, Semionotus bellottii* and *Allolepidotus nothosomoides.* Concerning *Pholidophorus curionii,* De Alessandri confirmed the taxonomic assessment of Bellotti, providing a new description and a picture of the cast that constituted the holotype of the species (but which was lost during the World War II). However, judging from the drawing in the Bellotti's manuscript and from the picture in De Alessandri's paper (1910, tav. VIII, fig. 5), it can be confidently excluded from the genus *Pholidophorus* and at the same time confirmed as belonging to the species currently under study.

In his revision of the Perledo material, De Alessandri (1910) redescribed the species *Semionotus bellottii,* attributing it to the genus *Allolepidotus* because of the skull pattern and shape. The specimen on which De Alessandri based his description and revision of *Allolepidotus bellottii* belongs to the Curioni collection. De Alessandri considered it to be the specimen described by Bellotti (1857) (this specimen is still available, being stored at Servizio Geologico d'Italia in Rome (4431 P)). Finally, De Alessandri cited and described *Allolepidotus nothosomoides* but he believed this species was lacking in the collection of the Museo Civico di Milano, being clearly different from the others.

The descriptions and the pictures of the holotypes of *Pholidophorus curionii* (De Alessandri 1910: 127 pl. VIII, fig. 5) and the comparison with the holotypes of *Allolepidotus nothosomoides* (SM 1237 a, b, pers. obs.) and *Allolepidotus bellottii* (4431 P, pers. obs.) confirm the correspondence between these three nominal species. To the same species seems to belong also the specimen that had been described and figured by Deecke as *Pholidophorus oblungus* (Deecke 1889: 124, pl. VI, fig. 6) and stored at the Naturmuseum und Forschunginstitut Senckenberg in Frankfurt (SM 1256; pers. obs.).

Without a doubt, the Ca' del Frate specimens correspond both to the holotype of *Allolepidotus nothosomoides* and that of *Allolepidotus bellottii.* In previous studies of the Ca' del Frate material (Lombardo 1997; Tintori & Lombardo 1999) this species was cited as *Allolepidotus nothosomoides*, for the comparison had been possible only with the holotype of that species. The presence of the holotype of *Allolepidotus bellottii* in the Curioni collection at Servizio Geologico in Rome was discovered later. Moreover, this specimen was not prepared and the skull pattern was hidden (Pl. 1A): only after preparation has it been possible to confirm the determination and to verify the correspondence with the Ca' del Frate specimens. *Allolepidotus bellottii* is therefore to be considered the valid name of the species.

Halecomorphi

Family Caturidae, Owen (1860)

Genus *Furo* Gistl, 1848

Diagnosis (from Woodward 1895: 286-290): "Trunk elongate-fusiform. External bones feebly ornamented with tuberculations or rugae; teeth relatively large and speced on the dentary, smaller and more closely arranged on the margin of the upper jaw, minute and almost granular on the inner bones, in more than one series over the whole of the splenial; preoperculum smooth and narrow; suboperculum of moderate size, about half as large as the nearly rectangular operculum, and with a short ascending process at its antero-superior angle. Ossification in the sheath of the notochord observed only in the largest species; ossified ribs slender. Fulcra biserial, well developed on all the fins except the pectorals, on which they are feeble. Pectoral much exceeding the pelvic fins in size, but the latter well developed; dorsal and anal fins triangular , the former arising opposite or immediately behind the pelvic fins; caudal fin forked. Scales thick, with a narrow overlapped border, an inner rib, and a feeble peg-and-socket articulation; superficial ganoine smooth on the anterior half of each scale, passing on part of the body into transverse rugae and crenulations posteriorly; principal flank scales rarely, and then only in part, deeper than broad, several series of ventral scales much broader than deep; post-clavicular scales large; no enlarged scales on the dorsal ridge or in the region of the anus. Lateral line inconspicuous."

Type-species: *Furo orthostomus* (Agassiz, 1833-44)

Distribution: Middle Triassic of Italy (Ca' del Frate, Perledo); Lower Jurassic of England (Dorsetshire: Lyme Regis; Leicestershire; Warwickshire; Whitby; Yorkshire) and France (Valz; Lozère; Normandie: La Caine); Upper Jurassic of France (Ain: Cerin) and Germany (Bavaria: Eichstätt and Solnhofen).

Remarks

The genus *Furo* was erected by Agassiz (1833-44) as *Eugnathus* for material the Lower Lias of Lyme Regis and Kimmeridgian of Bavaria. Since the name *Eugnathus* had been used to designate a different animal in 1833 (White & Moy-Thomas 1940), the generic name *Furo*, proposed by Gistl in 1848, has been reconsidered. Agassiz included in the genus *Eugnathus* fishes with an elongate body, strong dentition and scales more or less ornamented and pectinated. Woodward (1895) distinguished six species from the English Lower Lias (*Eugnathus orthostomus, E. philpotae, E. minor, E. serratus, Eugnathus altus* and *Eugnathus hastingsiae*) and three from the Kimmeridgian of Bavaria (*Eugnathus longiserratus, Eugnathus microlepidotus, Eugnathus latimanus*). The genus was reported by De Alessandri (1910) in the Late Ladinian of Scisti di Perledo; according to De Alessandri, the genus is represented in this unit by two species: *Eugnathus hermesi* and *Eugnathus trottii* (De Alessandri 1910: 93-99).

Later on, *Furo* has been reported in the Upper Lias with the species *Eugnathus broussolavali* (Arambourg 1935) and in the Kimmeridgian of Cerin (*Eugnathus praelongus*, Thollière 1873; Saint-Saine 1949). Wenz (1965) successively erected the species *Furo normandica*, from the Upper Lias of Normandy.

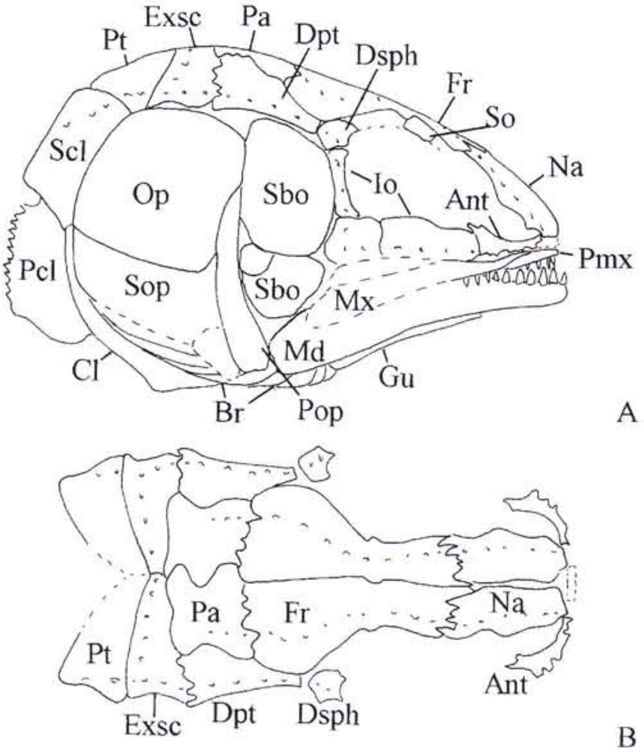


Fig. 7 - *Furo trottii* (Balsamo Crivelli, 1839). Restoration of the skull in lateral (A) and dorsal (B) views.

The specimen of Ca' del Frate corresponds in the general shape of the body and in the skull pattern to one of the two species described by De Alessandri on Perledo material (1910: 97-99): *Furo trottii*. Though incompletely preserved, this specimen shows some skull features that are typical of the genus *Furo* and generally of caturids. There are asymmetrical parietal bones (which are also present in *Furo orthostomus, Furo minor* and *Furo elongatus* (Saint-Seine 1949: fig. 69)) showing an interparietal suture strongly interdigitated, visible also in *Furo normandica* (Wenz 1967: fig.71). The suture between parietal and frontal bones is irregular, with a lateral process anterior to the suture with the frontal bones, which is also visible in *Caturus* and *Amblysemius* (Lambers 1992: 150). The presence of irregular parietal bones is reported also for *Watsonulus* (Olsen 1984; fig.2) so that this character is considered primitive for the halecomorphs (Lambers 1992: 151). Two large suborbitals are typical for Caturidae (Wenz 1967: 165); they are present, for instance, in *Furo orthostomus* (Woodward 1895) and *Caturus porteri* (Rayner 1941). The preoperculum is straight and subvertical and is separated from the skull roof by the upper suborbital, as in *Furo normandica* (Wenz 1967: 166).

These features, together with a squamation similar

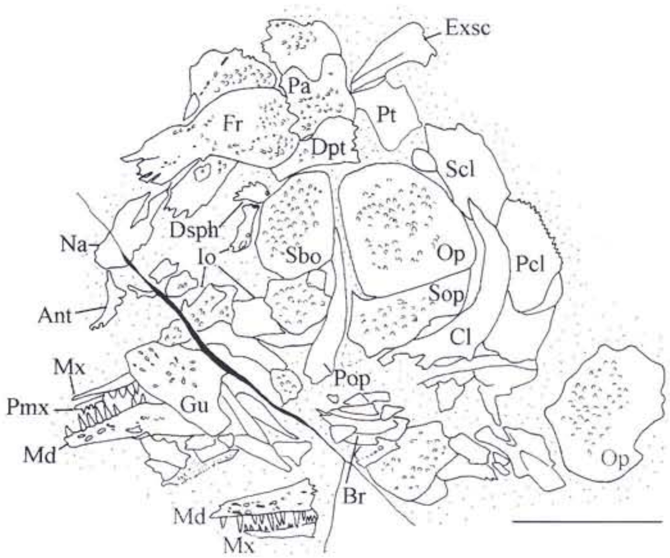


Fig. 8 - *Furo trottii* (Balsamo Crivelli, 1839). Skull of specimen MCSNIO P456. Scale bar: 10 mm.

to that described by Woodward in the diagnosis of the genus, makes possible the attribution of the Ca' del Frate specimen to the genus *Furo*.

Furo trottii (Balsamo Crivelli, 1839)

Figs. 7-9, Pl. 2A

1839 *Lepidotus trottii* Balsamo Crivelli, p. 7
1857 *Semionotus trottii* (Balsamo Crivelli), Bellotti in Stoppani, p. 289
1895 *Lepidotus trottii* Balsamo Crivelli, Woodward, part III, p. 64
1910 *Eugnathus trottii* (Balsamo Crivelli), De Alessandri, pp. 97-99, tav. V, fig. 3
1997 *Furo trottii* (Balsamo Crivelli), Lombardo, pp. 120-130, figs. 89-91.
1999 *Furo trottii* (Balsamo Crivelli), Tintori & Lombardo, pp. 495-504.

Material: MCSNIO P456 from the Kalkschieferzone (Meride Limestone, Upper Ladinian) of Ca' del Frate (Viggiù, Varese). The holotype, stored at Museo Civico di Storia Naturale di Milano, had been lost, during World War II.

Distribution: Upper Ladinian of the Scisti di Perledo (Perledo-Varenna Formation) and of the Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù, Varese).

Diagnosis (emended from De Alessandri 1910): Body elongate-fusiform; frontal bones anteriorly constricted and enlarged posteriorly; nasal bones long and broad; antorbital narrow; long jaws with strong conical teeth; two large suborbitals with smaller one between them; skull bones ornamented by densely spaced tubercles; scales deeper than broad behind cleithrum, broader than deep in mid-posterior region of trunk, narrow ventrally; deep axial body lobe; well-developed fringing fulcra on anterior margin of all fins.

Description

This species is represented by a single incomplete specimen with a SL of 10.4 cm. Its skull lacks part of the dermal bones and shows displacement of others.

Skull. A large bone rectangular, dorso-ventrally elongated, and visible from the inside, is interpreted as nasal (Figs. 7AB, 8, Pl. 2A). The frontal bones are rather short with a narrow anterior region and a broader posterior one. Their anterior margin is irregular and the interfrontal suture is almost straight (Figs. 7AB, 8, Pl. 2A). The supraorbital sensory canal runs along the lateral margin of the bones, entering the parietal bones.

The parietal bones are quadrangular, with irregular margins and interparietal suture slighlty interdigitating. There is a short antero-lateral process on the anterior part of the bones; on their surface the pores of the supraorbital sensory canal are visible (Figs. 7AB, 8, Pl. 2A).

The trapezoidal dermopterotics are elongate antero-posteriorly. At the level of the contact between the parietal and the frontal the dermopterotics produce a short anterior process. The pores of the supratemporal canal are placed along the inferior margin of the bones (Figs. 7AB, 8, Pl. 2A). The extrascapulars are triangular and large (Figs. 7AB, 8, Pl. 2A).

There are two large suborbital bones and a third, much smaller, placed between the first two. The dorsal element, the larger one, lies below the dermopterotic: it is slightly quadrangular, with round margins. The shape of the second one is more irregular and it contacts the preoperculum at its posterior margin (Figs. 7A, 8, Pl. 2A).

The dermosphenotics are small (Figs. 7AB, 8, Pl. 2A); the pores of the infraorbital sensory canal are visible along their posterior and posteroventral margins. The infraorbital series is badly preserved: there is a dorso-ventrally elongate element bordering the posterior part of the orbit and two to three larger elements making the ventral orbital region. A narrow, slightly curved element with traces of the pores of the infraorbital sensory canal, is interpreted as the antorbital (Figs. 7AB, 8, Pl. 2A).

The preoperculum is subvertical, with a narrower dorsal region and a ventral one slightly expanded and forwardly directed. The surface is smooth (Figs. 7A, 8, Pl. 2A). The opercular region is large, with a semicircular outline. The operculum is quadrangular. The suboperculum is about 1/3 of the depth of the operculum and shows a short antero-dorsal process (Figs. 7A, 8, Pl. 2A). The triangolar interoperculum should have been short, being represented only as impression on the slab.

Of the maxilla is visible only the narrow anterior region because in the only available specimen it is partially covered by gular bone and branchiostegal rays; its oral margin bears a series of strong conical teeth (Figs. 7A, 8, Pl. 2A). Ventral to the anterior process of the maxilla, a small premaxilla is visible, bearing teeth smaller than those borne by maxilla (Figs. 7A, 8, Pl. 2A).

The lower jaw is a strong element, whose ventral margin is slightly concave (Figs. 7A, 8, Pl. 2A). The antero-ventral region is characterized by the presence of oval openings and along the ventral margin the pores of

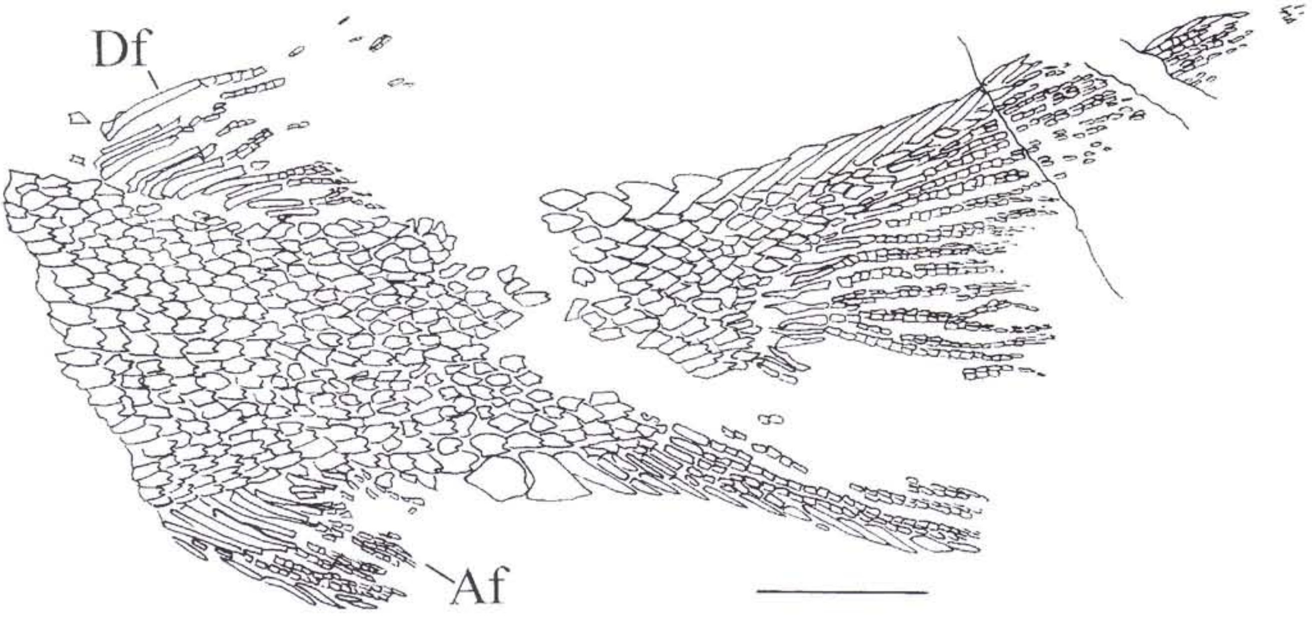


Fig. 9 - *Furo trottii* (Balsamo Crivelli, 1839). Posterior part of the body of specimen MCSNIO P456. Scale bar: 10 mm.

the mandibular canal are visible. The oral border of the bone bears conical teeth bigger than those of the maxilla.

There is a large shield-like gular, with a smooth surface (Figs. 8, Pl. 2A). Up to nine elongate branchiostegal rays have been counted. Their surface is smooth (Figs. 7A, 8, Pl. 2A).

All the skull bones, if not otherwise specified, are ornamented by strong and rounded densely arranged ganoine tubercles (Figs. 8, Pl. 2A).

The posttemporals are rectangular; these elements are incomplete, so that their precise size and shape are unclear (Figs. 7AB, 8, Pl. 2A). The supracleithrum is a large, subrectangular element with smooth surface (Figs. 7A, 8, Pl. 2A). The postcleithrum is also a large rectangular element, with a gently pectinated posterior margin. The cleithrum is well-developed and sickle-shaped (Figs. 7A, 8, Pl. 2A).

Fins. The fins are preserved only in part, as the specimen is lacking the antero-ventral region of the trunk; the pectoral and pelvic fins are therefore not preserved.

The dorsal fin lacks the most anterior lepidotrichia; it has at least 15 rays, with long proximal bases and short distal segments (Figs. 9, Pl. 2A). Fringing fulcra are not preserved, but their presence is deducible from the impression left on the rock. The anal fin is opposite the dorsal one. It is smaller than the dorsal fin and it has at least 11 rays; the distal end of the fin is made of delicate and short elements (Figs. 8, Pl. 2A).

A large dorsal lobe characterizes the caudal fin (Figs. 9, Pl. 2A). It is not possible to state the exact number of the lepidotrichia because of a fold that divides the dorsal region of the fin from the ventral one. However, about 22 lepidotrichia have been counted; each branches at least three times. The anterior margin of the body lobe is bordered by a series of long and well-developed basal fulcra; three basal fulcra precede the ventral lobe. There are elongate and narrow fringing fulcra on the margins of both dorsal and ventral lobes.

Squamation. The single specimen of this species shows only the scale covering of the posterior and caudal region of the trunk. For this reason it is impossible to state the number of transverse scale rows. On the anterior region of the trunk only few scales are visible; they are deeper than broad immediately behind the supracleithrum and postcleithrum but they decrease in size posteriorly (Figs. 9, Pl. 2A). The scales of the lateral region of the flank, at the level of the dorsal and anal fins, are broader than deep. The depth of the scales decreases on the dorsal and ventral regions. At the base of the anal fin, scales are narrow. All scales have serrated posterior margins, except those covering the body lobe. The latter is covered by rhombic scales, with longer longitudinal axes; they cover the dorsal lobe of the caudal fin for half of its length (Figs. 9, Pl. 2A).

Taxonomic history

Balsamo Crivelli (1839) erected the species *Furo trottii* on Perledo material. The author ascribed this species to the genus *Lepidotus* but he provided neither detailed description nor an illustration of the specimen. Bellotti (1857) studied again the specimen of Balsamo Crivelli but he considered it more similar to the genus *Semionotus* because of the shape of the body and the position of the fins (Bellotti in Stoppani 1857: 11). De

Alessandri (1910) made another revision of this species: he included it into the genus *Eugnathus* based on the ornamentation of the skull bones, the serration on the posterior margins of the scales and the narrow ventral scales (De Alessandri 1910: 99). He also produced the first picture of the holotype.

The comparison between the specimen from Ca' del Frate and the holotype of *Furo trottii* is possible only by means of the description of De Alessandri and the picture of the specimen, for this latter has been lost during the World War II. Nevertheless the two specimens seems to correspond in body shape, skull pattern and ornamentation of the bones, scales shape, position of the fins and shape of the caudal fin.

The other species of Perledo attributed to this genus, *Furo hermesi*, is represented by a single incomplete specimen, with a crashed skull; the inclusion of the Ca' del Frate specimen in this species can be excluded on the basis of the caudal fin, well visible on the photograph of the holotype (De Alessandri 1910, tav. V, fig. 2), and the conclusively less developed fulcra on the anterior margin of the anal fin and on both lobes of the caudal one.

Order Perleidiformes Berg ,1940

Family Perleididae Brough, 1931

Genus *Perleidus* De Alessandri ,1910

Diagnosis (emended from De Alessandri 1910): Small to medium-sized perleidiform fishes with fusiform body; maxilla with narrow anterior region and expanded posterior one; peg-like teeth on oral jaws and larger ones on palatal bones; preoperculum with wide dorsal region; wide opercular region with operculum slightly smaller than the suboperculum; caudal fin with 6 or 7 "epaxial" rays; lepidotrichia of all fins with long proximal bases. Lateral trunk scales moderately high and deeper than wide; all scales serrated.

Type-species: *Perleidus altolepis* (Deecke, 1889)

Distribution: Middle Triassic: Upper Ladinian of Perledo Member (Perledo-Varenna Formation) and of Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù-Varese) and Meride (Canton Ticino-CH).

Remarks

The genus *Perleidus* was erected by De Alessandri (1910) on material coming from Perledo, previously described as *Semionotus altolepis* by Deecke (1889). The new finds in the Kalkschieferzone of Ca' del Frate allowed to a certain attribution to the type species and the first complete anatomical restoration of it. This reaveals the incompatibility of many species so far ascribed to the genus *Perleidus*. Several authors have erected species of *Perleidus* from Early Triassic of Spitzbergen (*Perleidus woodwardi* Stensiö, 1921), Madagascar (*Perleidus madascariensis* Piveteau, 1934; *Perleidus piveteaui* Lehman, 1952), Greenland (*Perleidus stoschiensis* Stensiö, 1932), Angola (*Perleidus lutoensis* Teixeira, 1947), China (*Perleidus yangtzensis* Su, 1981) and Canada (cf. *Perleidus* Schaeffer & Mangus, 1976); from Middle Triassic of Spain (*Perleidus giganteus, Perleidus viai* Beltan, 1972), South-western Turkey (*Perleidus* sp., Beltan et al., 1979), of France (*Perleidus* sp., Mazin & Martin, 1983) and the Upper Triassic of Morocco (cf. *Perleidus* Martin, 1982).

The attribution of all these species to the genus has been made only on the skull pattern, of primitive type, and often on very poorly preserved material. Nevertheless, the revision, mostly bibliographical, of each species revealed a different structure of the caudal fin, a diagnostic feature for the family Perleididae. The representatives of this family possess "epaxial" fin rays sensu Hutchinson (Hutchinson 1973) and Gardiner (Gardiner 1988; Gardiner & Schaeffer 1989; Tintori 1990b). Since none of the cited species other than the type species has "epaxial" rays, the attribution of these species to the genus *Perleidus* is questioned as is the presence of the genus in the Early Triassic.

This misinterpretation started when Stensiö studied this genus, erecting the species *Perleidus woodwardi* on material from the Early Triassic of Spitzbergen. *Perleidus woodwardi* is a species of remarkable size (up to 30 cm of SL); its skull presents a long and narrow rostral bone and large triangular nasal bones (Stensiö 1921: 259, fig. 81). The pattern of the ethmoidal region is clearly different from that found in *Perleidus altolepis* and in perleidiforms (*Cleithrolepis* Gardiner 1988; *Dipteronotus* Tintori 1990; *Thoracopterus* Tintori & Sassi 1990; *Peltoperleidus* Bürgin 1992; *Gabanellia* Tintori & Lombardo 1996), which show a large pentagonal rostral bone and dorso-ventrally elongated or T-shaped nasal bones. In Stensiö's paper the ethmoidal elements are cited with different names: nasal bones as antorbitals, the rostral bone as nasal-postrostral bone and the antorbital as rostral bone. The course of sensory canals, well visible on the skull restoration of *Perleidus woodwardi* (Stensiö 1921: 259, fig.81) proves the wrong interpretation of these elements, as has already been stressed by Patterson (1975: 507). The antorbital is recognizable by the infraorbital sensory canal, which in this element bifurcates to join the supraorbital one, and the ethmoidal commissure. In the restoration of *Perleidus woodwardi* the element interpreted as the antorbital is crossed by the supraorbital canal, being obviously the nasal bone. *Perleidus woodwardi* has ventral scales longer than deep, in contrast with the typical rhombic shape of the ventral scales of *Perleidus*; the scales of the lateral region of the trunk are rhombic, as high as deep (Stensiö 1921: pl. 33). The caudal fin is defined as "abbreviate heterocercal" and it is clear that the axial body lobe makes the dorsal margin of the fin (Stensiö 1921: pl. 33).

Subsequent authors kept consideration the work of Stensiö, owing to his authority, and they ignored the descriptions of Deecke and De Alessandri: the attribution of the different species to the genus *Perleidus* was made on the basis of the skull pattern and by compari-

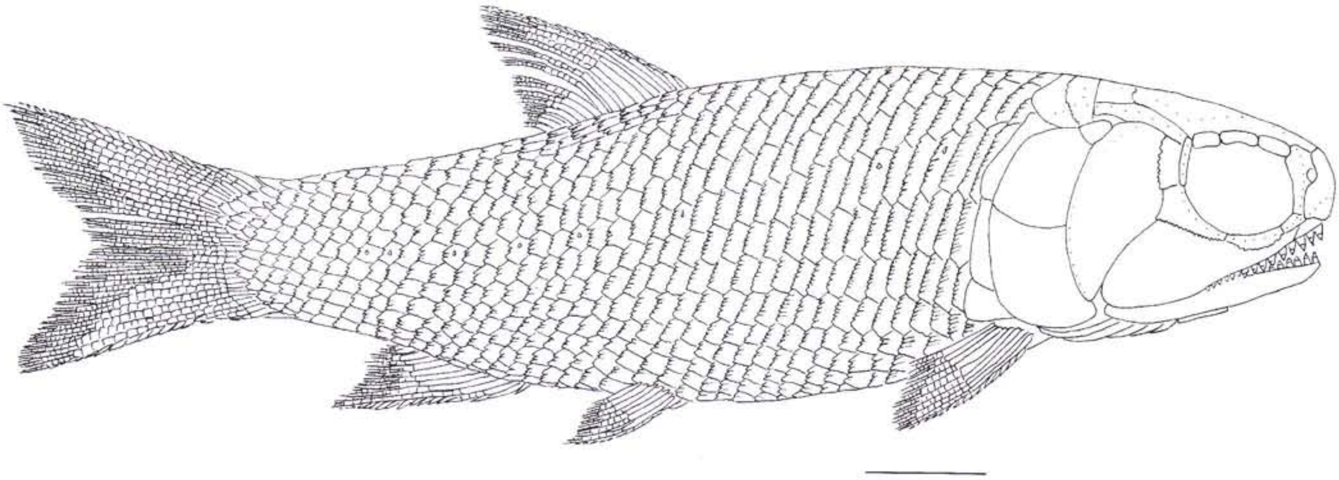


Fig. 10 - *Perleidus altolepis* (Deecke, 1889). Restoration. Scale bar: 10 mm.

son with the species coming from the Spitzbergen, rather than with the type species of Perledo.

For example, *Perleidus madagascariensis* (Piveteau 1934) shows a hemiheterocercal tail, visible in the paper of Pivetaeu (1934: 48, fig. 32, pl. VI, fig. 4) and on the original material stored at Muséum National d'Histoire Naturelle de Paris (MAE 652a; MAE 1371ab; MAE 364ab; MAE 1104b; MAE 1023b; MAE 1100; MAE 125); it also shows an ethmoid region similar to that of *Perleidus woodwardi* (Stensiö 1921: 259, fig. 81) and of *Perleidus stoschiensis* (Piveteau 1934: 46, fig. 30-31). The other species from Madagascar, *Perleidus piveteaui* (Lehman 1952), is represented by few specimens, often incomplete, so that the description of the caudal region is not given. The skull shows elements different from those of the other species, e.g., spiracular plates of variable shapes and the presence of a posterior parietal (Lehman 1952).

Perleidus yangtzensis (Su 1981) is represented by a single specimen, lacking the posterior part of the body. The skull is characterized by a maxilla with a very short postorbital region and a weakly convex oral border; teeth are different from those typical of Perleididae: they are conical on the anterior part of maxilla and blunt with a small acrodine cap on the posterior part of the oral margin.

Perleidus lutoensis Teixeira, 1947 and *Perleidus lehmani* Schaeffer, 1990 from the Lower Triassic of Angola, clearly do not belong to this genus: "....the uppermost principal caudal ray meets the longest scale row in the axial lobe and there are no "epaxial" fin rays...: both species have been identified as perleidids on the basis of dermal skull pattern and the squamation" (Antunes et al. 1990: 25).

The species from Lower Triassic of Canada, cf. *Perleidus* (Schaeffer & Mangus, 1976) was already questioned by Bürgin (1992) for its resemblance with *Platysiagum minus* Brough, 1939 in the skull pattern, the shape of upper and lower jaws, the preoperculum, and the caudal fin, clearly hemiheterocercal. This species was attributed to the genus *Perleidus* only on the basis of the pattern of dermal bones of the cheek and the posterior serration of the scales.

The species coming from the Spanish Middle Triassic, *Perleidus giganteus* and *Perleidus viai* (Beltan, 1972) were already attributed by Bürgin (1992) to different genera, *Colobodus* and *Ptycholepis*, respectively. A recent revision of the Alcover fauna confirms the attribution of *Perleidus giganteus* to *Colobodus*, while *Perleidus viai* is more likely to belong to the Neopterygii, owing to the shape of the preoperculum and the presence of an interoperculum bone (Lombardo, pers. obs.).

Perleidus sp. from Amélie-Les-Bains (Eastern Pyrenees, Mazin & Martin 1983) is represented only by few massive teeth, with a pointed translucent cusp. The attribution to the genus *Perleidus* was made only by comparison with teeth of *Perleidus stoschiensis*, being clearly insufficient for determination. *Perleidus* sp. from the Ladinian of Turkey (Beltan et al. 1979) and cf. *Perleidus* from the Upper Triassic of Morocco (Martin 1982) are represented by disarticulated skulls and few scale rows, inadequate for a proper determination.

Therefore, *Perleidus altolepis* seems to be the only valid species of the genus *Perleidus*; this implies a remarkable change in the geographic and stratigraphic distribution of the genus, till now considered cosmopolitan and present throughout the Triassic (Battail et al. 1987; Beltan 1988). Its presence should be restricted to the Late Ladinian of the Southern Alps (Lombardo 1995).

The diagnosis of the genus has been emended since it was formerly made on the basis of Lower Triassic material that cannot be ascribed to this genus for the mentioned reasons.

Perleidus altolepis (Deecke, 1889)

Figs. 2, 10-13, Pl. 2BC

1857 *Lepidotus serratus* Bellotti, Bellotti in Stoppani, pag. 419.
1857 *Pholidophorus oblungus* Bellotti, Bellotti in Stoppani, pp. 428-9.
1889 *Semionotus altolepis* Deecke, Deecke pp. 120-121; tav. VI, fig. 10.
1895 *Semionotus altolepis* Deecke, Woodward, part III, p. 57.
1901 *Semionotus altolepis* Deecke, Schellwien, pp. 24-25.
1910 *Perleidus altolepis* (Deecke), De Alessandri, pp. 49-51, tav. II, fig.2.
1910 *Heterolepidotus serratus* (Bellotti), De Alessandri, pp. 103-105, tav. VI, fig. 3.
1910 *Pholidophorus oblungus* (Pro parte) Bellotti, De Alessandri, pp. 129-131, pl. VIII, fig. 9.
1920 *Perleidus altolepis* (Deecke), Stolley, pag. 65.
1921 *Perleidus altolepis* (Deecke), Stensiö, pp. 256-257, figs. 78-79.
1921 *Heterolepidotus pectoralis* (Bellotti), Stensiö, pp. 256-257, figs. 78a,b.
1934 *Perleidus altolepis* (Deecke), Piveteau, p. 131.
1952 *Perleidus altolepis* (Deecke), Lehman, p. 137.
1966 *Perleidus altolepis* (Deecke), Lehman in Piveteau, pp. 114-115, fig. 103.
1990 *Perleidus altolepis* (Deecke), Tintori, p. 193, tav.1.
1992 *Perleidus sp*., Bürgin, pp. 60-61, fig. 59.
1995 *Perleidus altolepis* (Deecke), Bürgin, pp. 806-813, figs. 2-6.
1997 *Perleidus altolepis* (Deecke), Lombardo, pp. 51-75, figs. 36-55.
1999 *Perleidus altolepis* (Deecke), Tintori & Lombardo, pp. 495-504.

Material: MCSNIO P461-463, P501, P599-616, P676-681, P686, P687, P691ab, P692ab, MCSN 3007, 3008, 5004ab, 5005, 5006ab, 5007abcd, PIMUZ T 4960, T 4961, T 4798.

Distribution: Late Ladinian of Scisti di Perledo (Perledo-Varenna Formation) and of Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù-VA) and Meride (Canton Ticino-CH).

Diagnosis (emended from De Alessandri 1910): Medium-sized species of 120 mm of maximum length; operculum slighty smaller than suboperculum; single suborbital; dentition made of peg-like teeth on oral margin of maxilla and dentary and blunt teeth on palatal bones; squamation of 37 transverse scale rows, lateral trunk scales deeper than wide, caudal fin of 28 lepidotrichia with 6 "epaxial" rays; bone ornamentation represented by ganoine tubercles and short ridges.

Description

. *Skull.* The rostral bone is large and subpentagonal; the lateral border presents a narial notch. Its surface is ornamented by ganoine ridges (Figs. 10, 11AB, 12BC, Pl. 2B). The ornamentation is different on specimens at different ontogenetic stages, being stronger on larger specimens. The nasal bones are irregular and elongated dorso-ventrally. They present an anterior expansion, with the opening for the narial notch below. The posterior border is slightly convex and outlines the anterior margin of the orbit. The supraorbital sensory canal ran along the length of the bone (Figs. 10, 11AB, 12ABC, Pl. 2B).

The frontal bones are broad and rectangular; the border in contact with the supraorbital bones is slightly convex. The interfrontal suture is straight, except for an indentation in the posterior half. The supraorbital sensory canal entered at the antero-lateral corner and reached the posterior margin of the bones, ending in the parietal bones (Figs. 10, 11AB, 12ABC, Pl. 2BC).

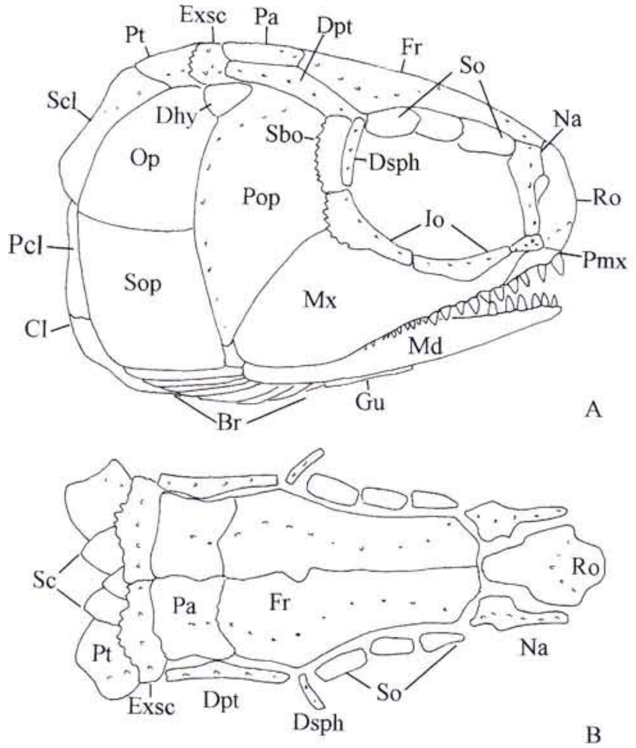


Fig. 11 - *Perleidus altolepis* (Deecke, 1889). Restoration of the skull in lateral (A) and dorsal (B) views.

The parietal bones are large and squarish; the interparietal suture is wavy, as is the anterior and lateral margin of the bones, where they contact the frontal bones and the dermopterotics. Pores of the supraorbital sensory canal are visible in the anterior half of the bones (Figs. 10, 11AB, 12ABC, Pl. 2B). The dermopterotics are trapezoidal, elongate elements. The supratemporal sensory canal ran along the median part of the bones, where pores are detectable (Figs. 10, 11AB, 12ABC, Pl. 2BC).

The extrascapulars are rectangular with rounded posterior edge. The median suture is short and straight. Pores of the supratemporal commissure are visible on the whole length of the bones. The supratemporal sensory canal entered the dermopterotic anteriorly and the post-temporal posteriorly (Figs. 10, 11AB, 12ABC, Pl. 2BC).

The dorsal margin of the orbit is bordered by three supraorbital bones; the first two are rectangular, the last one is bigger and triangular (Figs. 10, 11AB, 12A, Pl. 2C). The dermosphenotics are very thin and elongate elements placed on the postero-dorsal margin of the orbit and posteriorly in contact with suborbital. Pores of the infraorbital sensory canal are visible on the length of the bones (Figs. 10, 11AB, 12A, Pl. 2BC). The infraorbital series is made of two large crescentic elements, which outline the latero-ventral edge of orbital

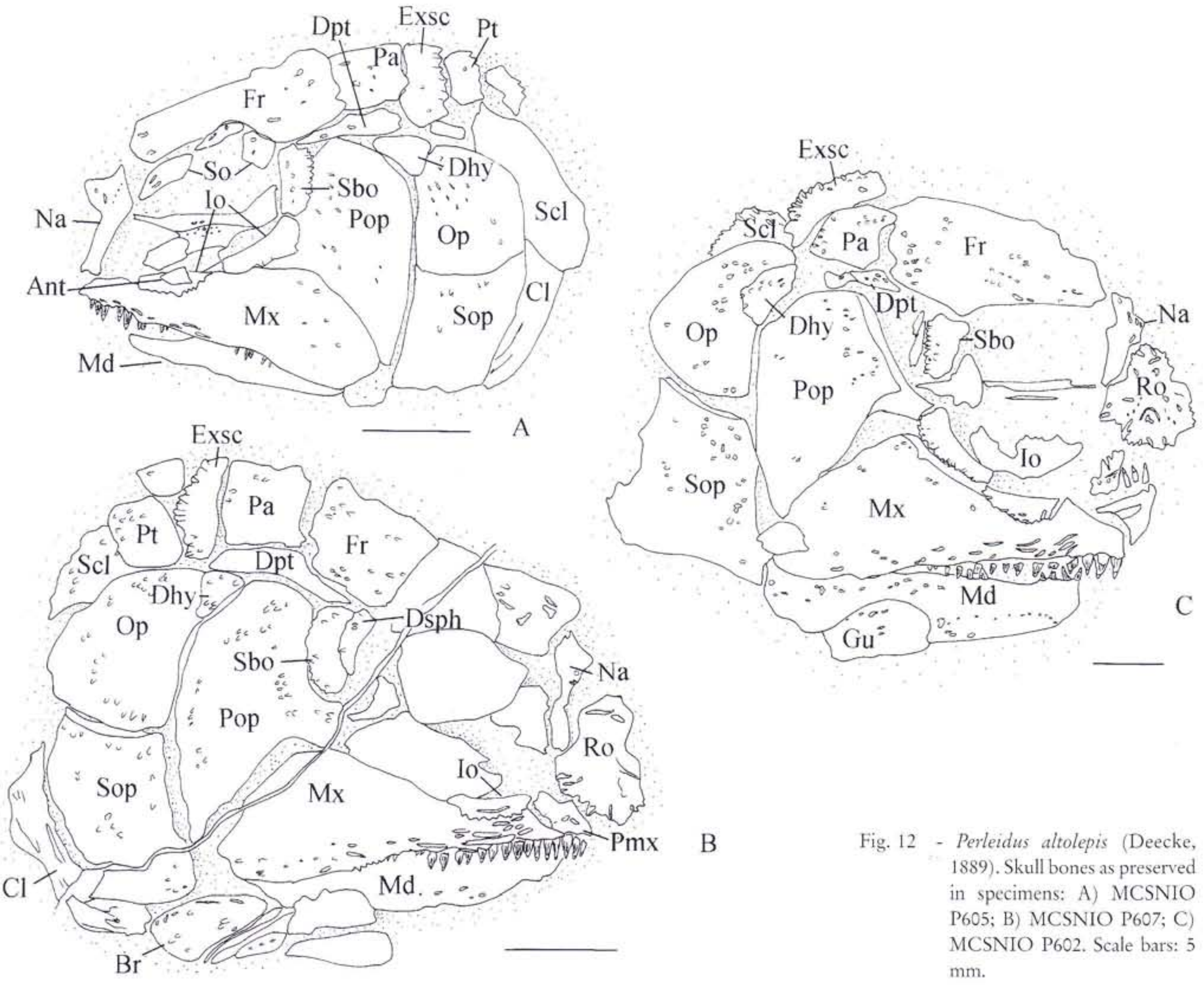


Fig. 12 - *Perleidus altolepis* (Deecke, 1889). Skull bones as preserved in specimens: A) MCSNIO P605; B) MCSNIO P607; C) MCSNIO P602. Scale bars: 5 mm.

opening. The element in contact with the dermosphenotic is larger than the second one; both have serrated ventral borders. A small antorbital reached the rostral bone (Figs. 10, 11A, 12ABC, Pl. 2B). There is a single suborbital: it is quite large and rectangular and contacts the dermosphenotic anteriorly. The posterior border is serrated (Figs. 10, 11A, 12ABC, Pl. 2BC).

The preoperculum is very large, with an expanded dorsal region and a narrow ventral one. The posterior edge contacts the dermohyal; the pores of preopercular sensory canal are arranged in a line along the posterior border of the bone. A well-developed infraorbital process is present (Figs. 10, 11A, 12ABC, Pl. 2BC). The operculum is deeper than wide; it contacts the suboperculum with a slightly convex suture. The rectangular suboperculum is bigger than the operculum (Figs. 10, 11A, 12ABC, 13A, Pl. 2BC).

The upper jaw is formed by a strong maxilla and a small premaxilla, bearing 4 or 5 teeth similar in shape and size to those borne by the maxilla. This latter has a narrow anterior region and an expanded postorbital one (Figs. 10, 11A, 12ABC, Pl. 2BC). The oral margin is straight; teeth are absent in the posterior part of the bone. The dentition is made of 20-25 strong teeth, with the typical peg-like shape; the first 10 are similar in size; teeth become smaller in the posterior part of the maxilla (Figs. 10, 11A, 12ABC, Pl. 2B). The palate is dentigerous, bearing teeth of different size. Large and stout teeth predominate. The lower jaw is elongate, with straight oral and ventral margin. Anterior teeth are similar in shape and size to those of the anterior part of the maxilla; posteriorly they become larger. Pores of the mandibular sensory canal are visible on the ventral part of the dentary (Figs. 10, 11A, 12ABC, Pl. 2B).

Up to 6 triangular branchiostegal rays were counted (Fig. 12C). There is a single median oval gular (Figs. 12C, Pl. 2B).

The posttemporals are two large and trapezoidal elements, separated from each other by a couple of scales (Figs. 10, 11AB, 12AB, Pl. 2BC). The posterior edge is rounded and laterally are detectable the pores of the supratemporal sensory canal coming from the extrascapular. The supracleithrum is elongated dorsoventrally and contacts the cleithrum at the level of the suture between operculum and suboperculum (Figs. 10, 11A, 12ABC, 13A, Pl. 2BC). The anterior margin is

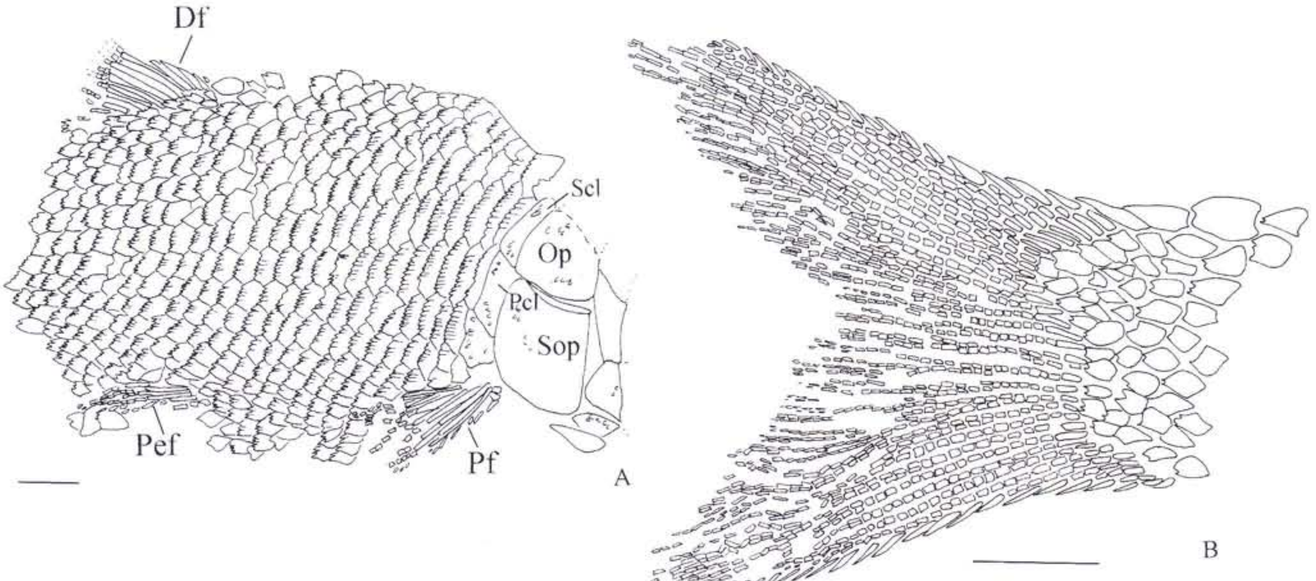


Fig. 13 - *Perleidus altolepis* (Deecke, 1889). A) MCSNIO P604b; B) Caudal fin of MCSNIO P501a. Scale bar: 5 mm.

always hidden by the operculum. Postcleithrum is a large element ornamented by tubercles and short ridges of ganoine (Figs. 10, 11A, 13A, Pl. 2BC). The cleithrum is partially visible, being covered by the suboperculum. The posterior part is convex with ornamentation made of short ridges of ganoine (Figs. 10, 11A, 12AB, Pl. 2B).

Fins. Pectoral fins have 8-13 lepidotrichia. Each ray consists of a long proximal base and shorter distal segments. Each branches at least twice. The anterior margin of the fin bears a series of strong fringing fulcra (Figs. 10, 13A, Pl. 2BC). The pelvic fins are smaller than the pectorals; they have 7-13 lepidotrichia, similar in structure to those of the pectorals (Figs. 10, 13A, Pl. 2C).

The dorsal fin is in the posterior half of the body. It is triangular and consists of 12-17 lepidotrichia. Distal segments branch at least twice. Two or three basal fulcra are present, and there is a series of fringing fulcra along the anterior margin of the fin (Figs. 10, 13A, Pl. 2BC). The anal fin is small and triangular and is made of 7-10 lepidotrichia. A couple of basal fulcra and a series of fringing fulcra on the anterior margin of the fin are present (Figs. 10, Pl. 2C). On specimen P 605 there are two large preanal scutes, with serrated posterior edge.

The caudal fin is almost symmetrical, with a short axial body lobe. There are about 28 lepidotrichia; 6-7 of them are "epaxial". The rays are segmented and they branch at least three times. Both the dorsal and ventral margins bear fringing fulcra (Figs. 2, 10, 13B, Pl. 2C).

Squamation. The scale covering consists of 37 vertical scale rows. The scales of the anterior region of the trunk are deeper than wide; they become gradually smaller towards the posterior part of the body. The scales of the antero-lateral flank region are rectangular; their depth decreases towards both the dorsal and ventral region where they become rhomboidal (Figs. 10, 13A, Pl. 2BC). A mid-dorsal ridge scale is present. At the base of the dorsal fin, scales are small and wider than deep (Figs. 10, 13A, Pl. 2BC). Scales of the posterior part of the body are rhombic, only slightly wider than deep. All scales are serrated.

Taxonomic history

Perleidus altolepis was erected by Deecke in 1889 as *Semionotus altolepis* on material coming from Perledo. Schellwein questioned the assignment of this species to the genus *Semionotus*, stressing the primitive pattern of the skull (Schellwein 1901: 24-25) and De Alessandri erected the new genus *Perleidus* for it. The species had actually been described, but not figured in 1857 by Bellotti as *Lepidotus serratus* (Bellotti 1857: 419) and *Pholidophorus oblungus* (Bellotti 1857: 428). Comparisons with the counterpart (the only available part) of the holotype of *Lepidotus serratus* and with the drawing of the holotype of *Pholidophorus oblungus* made for Bellotti's paper confirm the attribution of these specimens to *Perleidus altolepis*.

For *Perleidus altolepis*, as well as for many species coming from Perledo, there exists considerable taxonomic confusion. Deecke (1889), revising the Perledo material, erected the species *Perleidus altolepis* without comparing his material with that of Bellotti. Deecke considered the paper of Bellotti not valid, being without drawings (Deecke 1889: 110-111). Later on, De Alessandri (1910) re-studied the original material of Bellotti, but he did not understand that *P. altolepis*, *L. serratus* and *P. oblungus* were the same species: he just erected a new genus for the Deecke's species. I think that *Perleidus serratus*, as well as *Perleidus oblungus*, could be considered a *nomen oblitum*. It has never been used after De Alessandri, while subsequent authors always mentioned

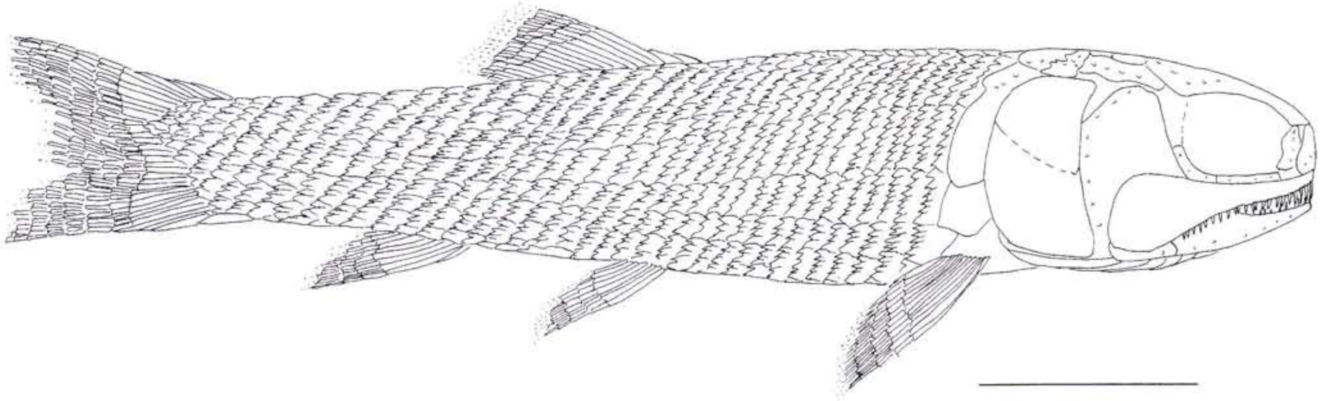


Fig. 14 - *Daninia spinosa* gen. n. sp. n. Restoration. Scale bar: 5 mm.

only *Perleidus altolepis*, except for Bürgin (1995) who first noted the nomenclatorial problems. Since more than 50 years has passed without mentioning *Perleidus serratus* or *Perleidus oblungus*, one can consider *Perleidus altolepis* (although "junior synonymous") to be the only valid name.

Daninia gen. n.

Diagnosis: as for species.

Type-species: *Daninia spinosa* gen. n. sp. n.

Etymology: dedicated to Gianluca Danini, curator of Civico Museo Insubrico di Storia Naturale di Induno Olona, for his basic and constant contribution to the study of the locality of Ca'del Frate.

Type-locality: Ca' del Frate (Viggiù-Va), Italy; late Ladinian.

Remarks

This species is attributed to Perleidiformes on the skull pattern, with the large rostral bone separating the nasal bones, the maxilla showing an enlarged postorbital region, and the preoperculum dorsally expanded (Bürgin 1992; Tintori & Lombardo 1996). Also, the structure of caudal fin, with the presence of "epaxial" fin rays, and the lateral scales deeper than wide on the anterior region of the body are typical of this group (Gardiner 1988; Gardiner & Schaeffer 1989; Bürgin 1992; Tintori & Lombardo 1996). Basically, some peculiar characters do not allow attributing it to any known genus: this genus is in fact different from any other perleidiform taxon in the strongly serrated scales and in the structure of the fins. These are characterized by long proximal bases and by distal segments that are shorter but always much longer than broad. In addition, the caudal fin rays, in other genera usually segmented beginning from the base of the fin, show very long proximal bases.

Daninia spinosa gen. n. sp. n.

Figs. 14-17, Pl. 2D-F

1995 *Ophiopsis* cf. *lepturus* Bürgin, pp. 818-820, fig.12-14.

1997 *Perleidus* sp. Lombardo, pp. 76-78, fig. 56.

Etymology: from the Latin word *spinosus*, referred to the thorny appearance of the scale covering.

Material: MCSNIO P668ab (holotype), from the Kalkschieferzone of Ca' del Frate (Viggiù-VA); MCSNIO P618ab, P666ab, P667, P669, P670, P671ab, P672ab, P673ab, P674, P675ab from the Kalkschieferzone of Ca' del Frate (Viggiù-VA) (stored in the Civico Museo Insubrico di Storia Naturale di Induno Olona) and MCSN P5008 from the Kalkschieferzone of Meride (Canton Ticino-CH) (stored in the Museo Cantonale di Storia Naturale di Lugano).

Type-locality: Ca' del Frate (Viggiù-Va), Italy; late Ladinian.

Distribution: Upper Ladinian (Middle Triassic) of Kalkschieferzone (Meride Kalk) of Ca' del Frate (Viggiù-VA) and of Meride (Canton Ticino-CH).

Diagnosis: Small perleidiform with elongate fusiform body; opercular region wide; properculum with narrow ventral region and

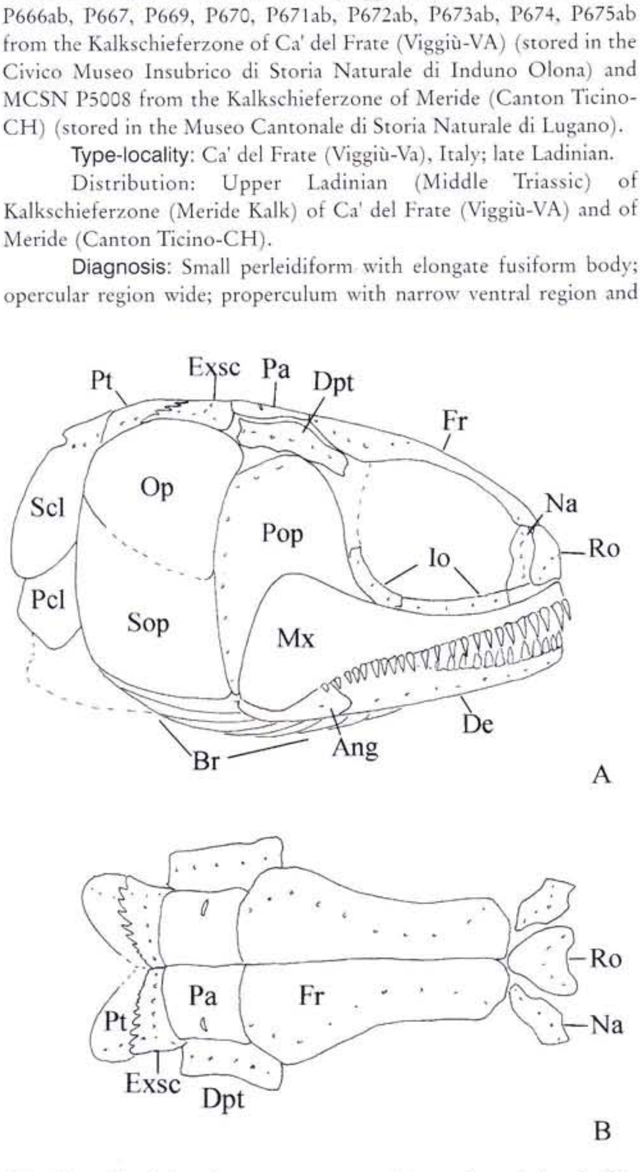


Fig. 15 - *Daninia spinosa* gen. n. sp. n. Restoration of the skull in lateral (A) and in dorsal (B) views.

expanded dorsal one with developed infraorbital process; long and pointed teeth on both upper and lower jaws; squamation of 36 or 37 transverse scale rows; scales deeper than wide in antero-lateral region of trunk; all scales deeply serrated; anal and dorsal fins with broad base; caudal fin of about 27 lepidotrichia; seven "epaxial" caudal fin rays.

Description

Skull. The rostral bone is large and pentagonal, with the typical perleidiform outline. The ethmoidal commissure is well visible on the ventral margin of the element and is lined by short ganoine crests (Figs. 14, 15AB, 16AC, Pl. 2F). The nasal bones consist of large sub-rectangular elements: the supraorbital sensory canal enters the postero-dorsal corner, where the nasal bones meet the frontal bones. The surface is smooth (Figs. 14, 15AB, 16AC, Pl. 2F). The frontal bones are wide, with an expanded posterior region and a narrower anterior one. The posterior margin is rounded. The supraorbital sensory canal has an S-shaped course; it enters the antero-ventral corner of the bones and reaches the parietal bones. The interfrontal suture is straight. The surface of these elements is only feebly ornamented by rugae in a few specimens (Figs. 14, 15AB, 16ABCD, Pl. 2DF). The parietal bones are large and squarish; they receive the sensory canal from the frontal bones and a median pit line is present. The interparietal suture is straight (Figs. 14, 15AB, 16BD).

The dermopterotics have a sub-rectangular shape and their surface is irregular owing to the presence of small openings and pores of the sensory canal, well detectable on the ventral margin of the elements (Figs. 14, 15AB, 16ABD, Pl. 2F).

Extrascapulars are triangular and narrow, with an irregular outline due to the presence of tubercles and short ganoine ridges perpendicularly arranged to the posterior margin of the elements. The two elements are in contact by means of a short suture (Figs. 14, 15AB, 16ABD, Pl. 2F). It is impossible to locate a dermosphenotic.

The series of infraorbitals is made up of one or two slender and elongate elements bordering the dorsal margin of the maxilla, followed by a larger crescentic bone on the postero-ventral corner of the orbit. Pores are detectable on all elements (Figs. 14, 15AB, 16AD, Pl. 2F).

The shape of the preoperculum is typical of perleidiforms, with an enlarged dorsal region and a narrower ventral one. Its ventral margin embraces the dorsal margin of the maxilla. The preopercular sensory canal ran along the posterior margin of the bone (Figs. 14,

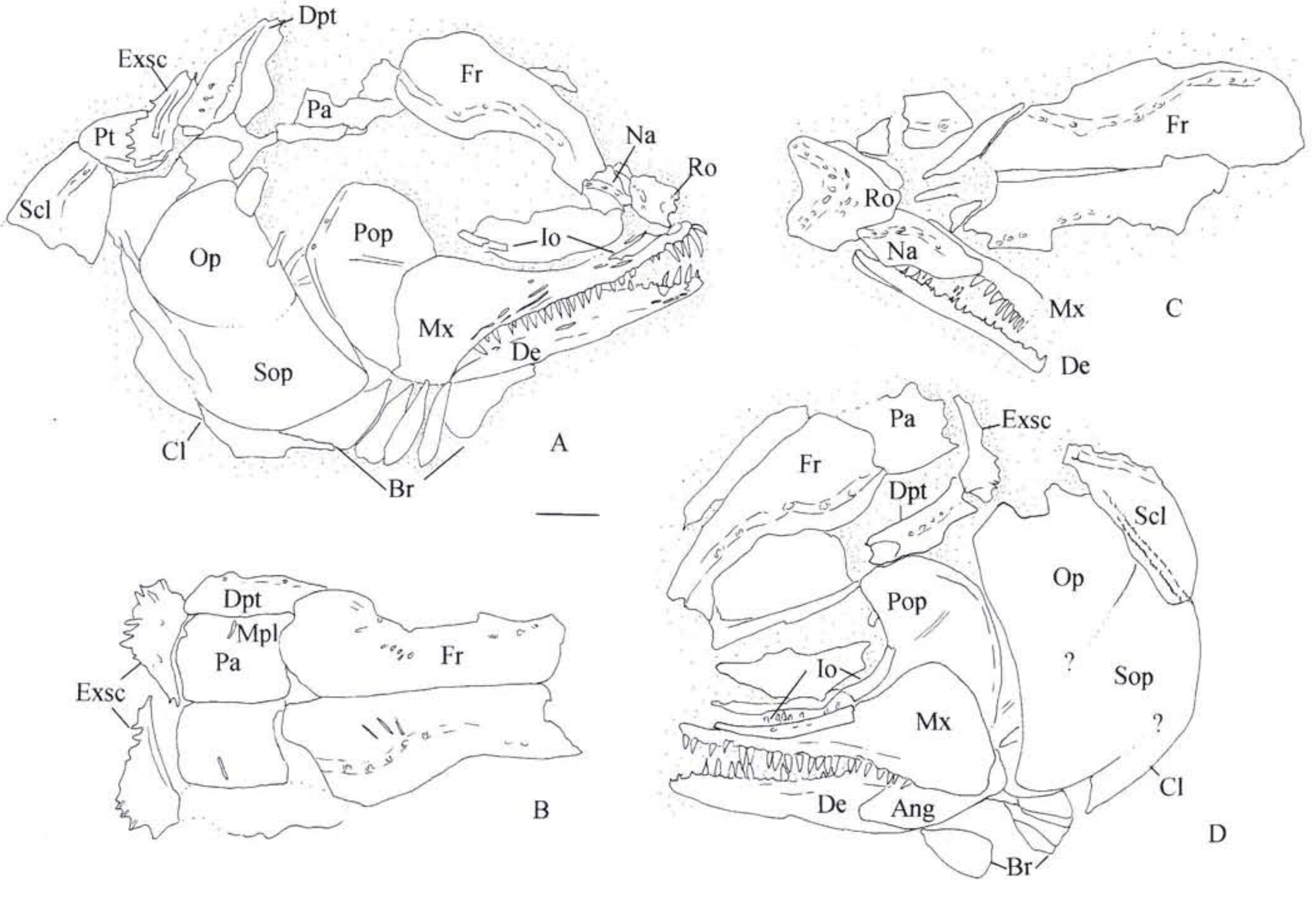


Fig. 16 - *Daninia spinosa* gen. n. sp. n. Skull bones as preserved in specimens: A) MCSNIO P667; B) MCSNIO P669; C) MCSNIO P670; D) MCSNIO P672b. Scale bar: 1 mm.

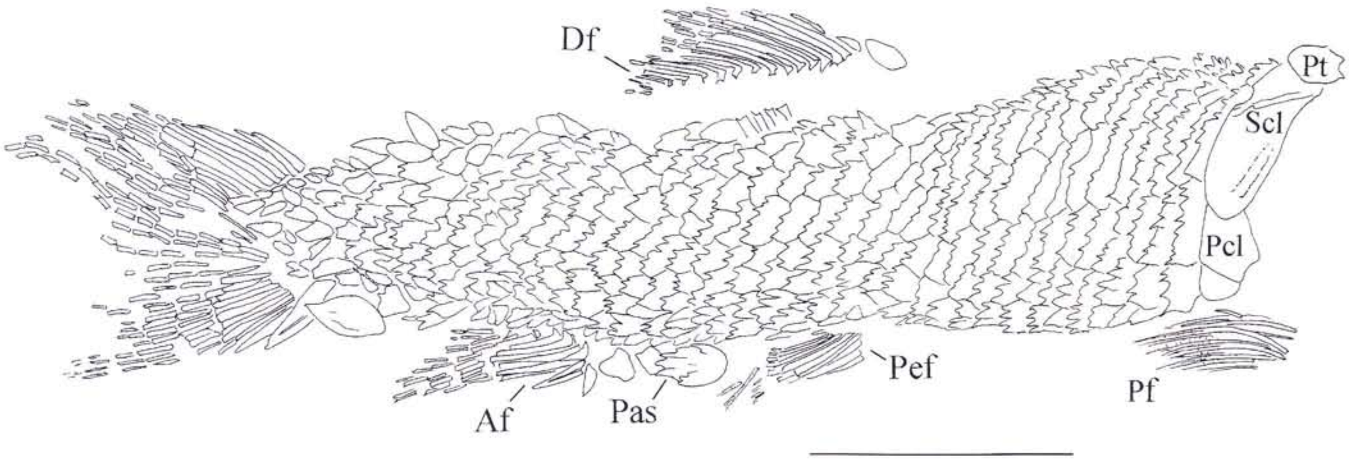


Fig. 17 - *Daninia spinosa* gen. n. sp. n. Part of pectoral girdle and body of MCSNIO P673a. Scale bar: 5 mm.

15A, 16AD, Pl. 2DF). The opercular region is wide and rectangular, with a rounded posterior margin. The suture between operculum and suboperculum is always difficult to detect, owing to the thinness of the bones, so that the shape and size of each element remains uncertain. On specimen MCSNIO P667 a small antero-dorsal process of the suboperculum gives the position of boundary between the two bones (Figs. 16A, Pl. 2F). The surface of the opercular region is ornamented by concentric striae at least on the dorsal margin.

The maxilla shows the typical perleidiform outline, with an expanded postorbital region and a slender anterior one. The oral margin bears several rows of long and pointed teeth; on the anterior tip of the maxillary (premaxillary?) teeth are slightly longer (Figs. 14, 15A, 16AD, Pl. 2DF). The mandible is a strong wedge-like element bearing teeth similar in shape and size to those of the maxilla. On its posterior part a large angular is present, and the ventral region shows the course of the mandibular sensory canal (Figs. 14, 15A, 16AD, Pl. 2DF).

The palatal region bears conical teeth larger than those borne by maxilla and lower jaws, arranged in several rows.

At least five triangular branchiostegal rays have been counted; their surface is smooth.

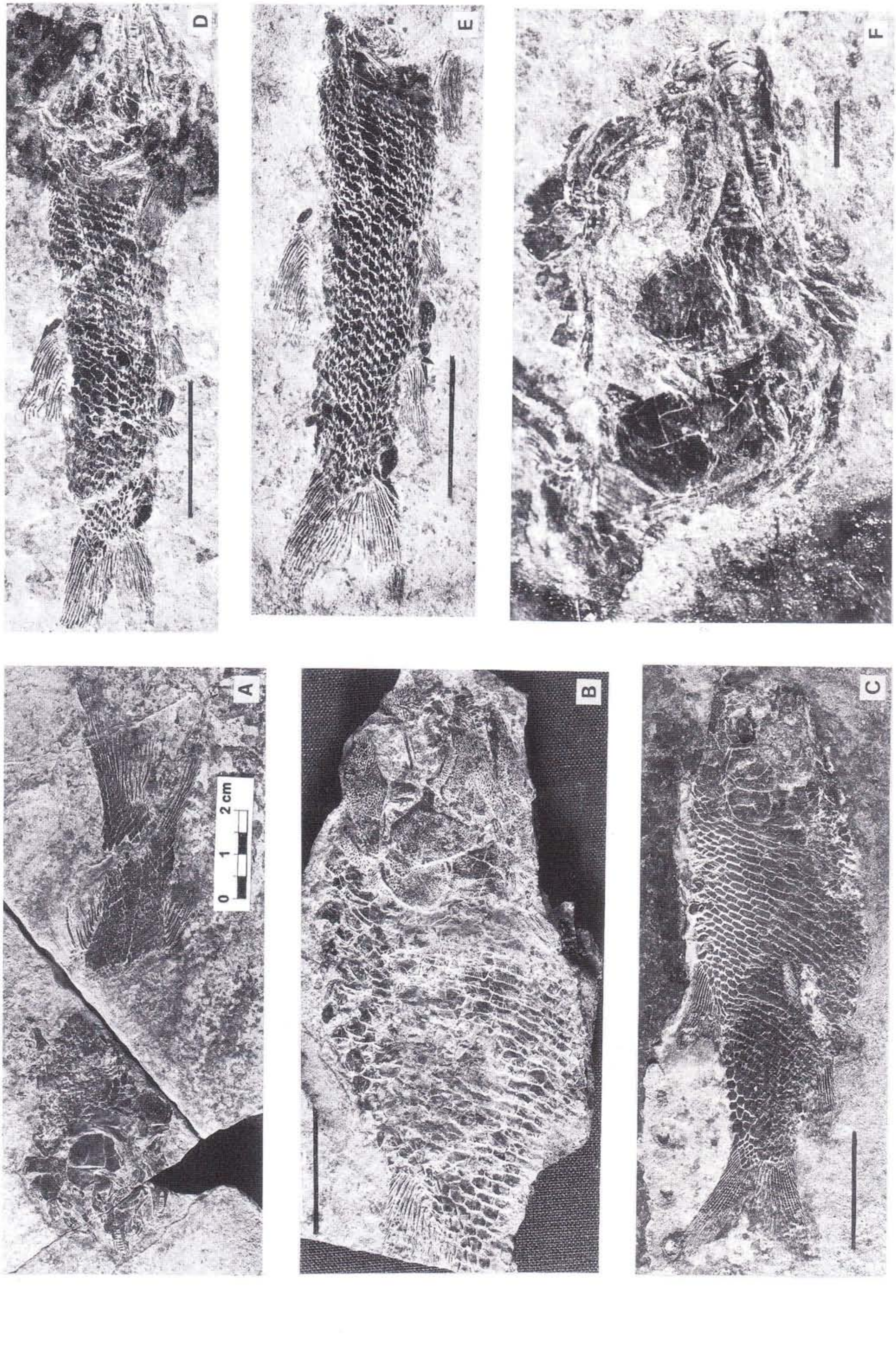
Behind the extrascapulars there are two posttemporals with a rounded posterior margin; the supraorbital sensory canal ran on the ventral region of each element and reaches the supracleithrum behind (Figs. 14, 15AB, 16A, 17, Pl. 2EF). There is a large oval supracleithrum with ornamentation that consists of delicate concentric striae (Figs. 14, 15A, 16AC, 17, Pl. 2EF); on a few specimens there are two rows of minute denticles arranged along the antero-ventral margin of the element. On the dorsal area the course of the lateral line sensory canal is visible. The postcleithrum is subtriangular, with a rounded posterior margin and a straight ventral one; the ornamentation is similar to that shown by the supracleithrum. The cleithrum is wide and sickle-like, but its outline is not clear, owing to the state of preservation.

Fins. All fins are characterized by a remarkable development: paired fins are long, while median fins show a broad base. Owing to the delicacy of all fins, their distal ends are poorly preserved. The pectoral fins have about ten lepidotrichia, with long proximal bases and short distal segments. They branch at least twice and there are strong fringing fulcra along the anterior margin. Pelvic fins are made of long and slender rays; they are placed at the 12th scale row and opposite the dorsal fin. Fringing and basal fulcra are not visible (Figs. 14, 17, Pl. 2DE).

The dorsal fin is placed at about the 18-20th scale row and shows a broad base; it has at least 15 lepidotrichia, with very long proximal bases. An oval scute and 2-3 strong basal fulcra precede the fin. The anal fin is located at about the 20th scale row and it shows the same structure as the dorsal one; it has at least 15 rays and two or three basal fulcra. In front of the fin there are two or more pre-anal scutes: on specimen MCSNIO 673a the larger one shows a sub-oval outline, with a rounded anterior margin and an irregular posterior one. Ganoine ridges ending with a tip ornament the surface (Figs. 14, 17, Pl. 2DE). The caudal fin has 25-27 rays,

PLATE 2

A) *Furo trottii* (Balsamo Crivelli, 1839): MCSNIO P456; B) *Perleidus altolepis* (Deecke, 1889): MCSNIO P602; C) *Perleidus altolepis* (Deecke, 1889): MCSNIO P501a; D) *Daninia spinosa* gen. n. sp. n.: the holotype MCSNIO P668a; E) *Daninia spinosa* gen. n. sp. n.: MCSNIO P673a; E) *Daninia spinosa* gen. n. sp. n.: MCSNIO P667.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with seven "epaxial" rays; lepidotrichia are segmented and even distal elements are elongate. Both the dorsal and ventral lobes show strong and long basal fulcra; fringing fulcra are not visible (Figs. 13, 16, Pl. 2DE).

Squamation. Squamation consists of about 37 transverse scale rows; all scales are characterized by a distinctively serrated posterior margin. Scales are deeper than broad on the antero-lateral region of the flank, while scales of the ventral and dorsal region are lower but, owing to the deep serration, it is impossible to identify their precise outline. Beginning from the dorsal fin and towards the posterior part of the body, scales decrease in depth, becoming lanceolate on the axial body lobe. There are large basal scutes in front of both the dorsal and ventral lobe of the caudal fin and one or two pre-anal scutes with large denticles on their posterior margin. The surface of the scales is smooth; the lateral scales behind the cleithrum show 6-7 long denticles whose number decreases towards the posterior, dorsal and ventral region of the body (Figs. 14, 17, Pl. 2DE).

Discussion

The size of most specimens belonging to this species is very small; they reach about 35 mm of total length. Almost all specimens show the same size and come from the same bedding plane. As for other taxa coming from Ca'del Frate, which are clustered in size-classes, (Lombardo 1997; Tintori 1990a; Tintori & Lombardo 1999), they probably represent the same ontogenetic stage, most likely juvenile: this is supported by the presence in the collection of a single specimen of larger size (MCSNIO P618ab). This kind of sampling may be related to the seasonality of the Ca' del Frate depositional environment (Tintori & Lombardo 1999).

Some specimens coming from the Middle Kalkschieferzone of Meride, stored at Museo Cantonale di Storia Naturale of Lugano and at Paläontologische Institut und Museum der Universität in Zürich, are attributed to that same species. The state of preservation of these specimens allowed comparison them with the Ca' del Frate specimens and, at the same time, questioning the determination made by Bürgin (1995). Bürgin described these specimens as *Ophiopsis* cf. *lepturus*, but the observation of some skull elements (especially on specimens T 4964 and MCSN 3014) such as the opercular region, shape and size of preoperculum, rostral bone, and maxilla, excludes these specimens from the genus *Ophiopsis*, and more generally, from a neopterygian group (pers. obs.). The preoperculum is not narrow, as in neopterygians, but it shows a wide dorsal region and along the posterior margin pores of the preopercular sensory canal are detectable; consequently, this area is not occupied by the large suborbitals mentioned by Bürgin (1995: 819). The element interpreted as the premaxillary is, on the contrary, a large rostral bone well recognisable on specimen T 4964 for its pentagonal shape and the ethmoidal commissure that runs through it. The maxilla is not narrow and elongate, but is made of a postorbital enlarged region and a narrower anterior one. The interoperculum is absent. The axial body lobe, according to Bürgin, extends about half way along the length of the dorsal lobe of the caudal fin (Bürgin 1995, pg. 819); the specimens from Ca' del Frate and Meride show "epaxial" fin rays, excluding this genus from neopterygians. The attribution of these specimens to the genus *Ophiopsis* and in particular to the Perledo species seems to have been made by Bürgin on the basis of the general shape of the body and the fins, though the author himself stresses some differences in most meristic characters (Bürgin 1995: 819). The holotype of *Ophiopsis lepturus* (figured by De Alessandri 1910, tav. III, fig. 4) has been lost, but a cast of it, stored at the Naturmuseum und Forschunginstitut Senckenberg in Frankfurt (P 1243), shows clearly some of the typical neopterygian features, such as a narrow and vertical preoperculum and the interoperculum (pers. obs.).

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