Rivista Italiana di Paleontologia e Stratigrafia	volume 108	numero 3	tavole 2	pagine 399-414	Novembre 2002

CAELATICHTHYS GEN. N.: A NEW PALAEONISCIFORM FROM THE MIDDLE TRIASSIC OF NORTHERN ITALY AND CANTON TICINO (SWITZERLAND)

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Received March 3, 2002; accepted July 24, 2002

Key-words: post-paleozoic palaeonisciforms, late Ladinian, new taxa, ontogeny.

Riassunto. Sulla base di esemplari provenienti dalla Kalkschieferzone (Calcare di Meride, Ladinico superiore) di Ca' del Frate (Viggiù-Varese) e di Meride (Canton Ticino, Svizzera), viene descritto un nuovo genere appartenente ai 'palaeonisciformes', *Caelatichthys* gen. n. Questo piccolo pesce dal corpo allungato e fusiforme, è caratterizzato dal dermosfenotico a contatto con il margine ventrale del dermopterotico, dalla perdita del contatto tra dermosfenotico+dermopterotico ed il nasale, dalla mancanza di sopraorbitali, dalla presenza di 4-5 infraorbitali e da piccoli premascellari in contatto lungo la linea mediana. All'interno di questo genere sono state individuate due specie, *C. nitens* gen. n., sp. n. e *C. meridensis* gen. n., sp. n., ciascuna esclusiva di una singola località. Le due specie si differenziano, a parità di dimensioni, per il diverso sviluppo dell'ornamentazione delle ossa dermiche ma soprattutto a livello dei fulcri della pinna anale. Questo carattere non può essere attribuito a dimorfismo sessuale, in quanto le due forme con cui la pinna anale si presenta non si ritrovano mai contemporaneamente, ma ogni associazione mostra una sola tipologia. La presenza di due nuove specie del medesimo nuovo genere costituisce un'ulteriore conferma circa la grande variabilità della composizione faunistica dei diversi livelli fossiliferi della Kalkschieferzone, che ad oggi presenta otto specie descritte oltre a quelle in corso di studio. Il numero e la qualità della conservazione degli esemplari provenienti da Ca' del Frate hanno permesso inoltre di ricostruire gli stadi di crescita di *C. nitens* gen. n., sp. n., specie che caratterizza questa località.

Abstract. A new genus of 'palaeonisciformes', *Caelatichthys* gen. n., is described on the basis of well-preserved material from the Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù, Varese) and Meride (Canton Ticino, Switzerland). This small-sized fish, with elongate-fusiform body, is characterized by a dermosphenotic in contact with the ventral margin of the dermopterotic, the absence of contact between dermopterotic + dermosphenotic and the nasal bone, the lack of supraorbital bones, the presence of 4-5 infraorbital elements and small premaxillae meeting at the mid-line. Two species were recognized within this genus: *C. nitens* gen. n., sp. n. and *C. meridensis* gen. n., sp. n., each exclusive of a single locality. The two species differ in the development of dermal bone ornamentation, in specimens of the same size, and mainly in the pattern of the fulcra of the anal fin. This character cannot be ascribed to sexual dimorphism, as the two fishes showing the two kinds of anal fin were never found together in the same assemblage. The existence of two species of this new genus confirms the great variability of the faunal composition of the different fossiliferous levels of the Kalkschieferzone, with eight species described formally and others whose study is in progress. The good state of preservation of several specimens from Ca' del Frate also made it possible to reconstruct the growth stages of *C. nitens* gen. n., sp. n.

Introduction

Beginning about 20 years ago, systematic field work was started in the uppermost levels of Meride Limestone, the Kalkschieferzone (Tintori et al. 1985). This unit crops out between Valceresio (Varese-Italy) and Canton Ticino (Switzerland) and has been assigned to the uppermost Ladinian, based on palynological assemblages (Scheuring 1978) (Fig. 1). On the Italian side, studies started in locality of Ca' del Frate (now Besnasca, Viggiù, Varese) by the Dipartimento di Scienze della Terra of the Università degli Studi di Milano in conjunction with the Civico Museo Insubrico di Storia Naturale di Induno Olona (Tintori et al. 1985). Several hundred fishes, together with a few specimens of the nothosaur *Lariosaurus* and thousands of crustaceans have been collected during several seasons of field work and have been the subject of many studies (Tintori & Renesto 1983, 1990; Tintori 1990a, 1990b; Renesto 1993; Lombardo 1997, 1999, 2001).

Regarding the Swiss side, in 1994 the Museo Cantonale di Storia Naturale di Lugano and the Paläontologisches Institut und Museum der Universität in Zürich made an excavation in the upper part of the middle Kalkschieferzone of Val Mara (Furrer 1995; Bürgin 1995). Field work in the upper part of the lower Kalkschieferzone of Meride (Val Mara, CantonTicino) was started in 1997 by the Museo Cantonale di Storia Naturale di Lugano and the Dipartimento di Scienze della Terra of the Università degli Studi di Milano (Tintori et al. 1998; Lombardo et al. 1999; Tintori & Lombardo 2001). The fossiliferous levels of this site, intercalated with barren beds, are placed between layer 102 of Scheuring (1978) and layer 60 of Wirz (1945) and are

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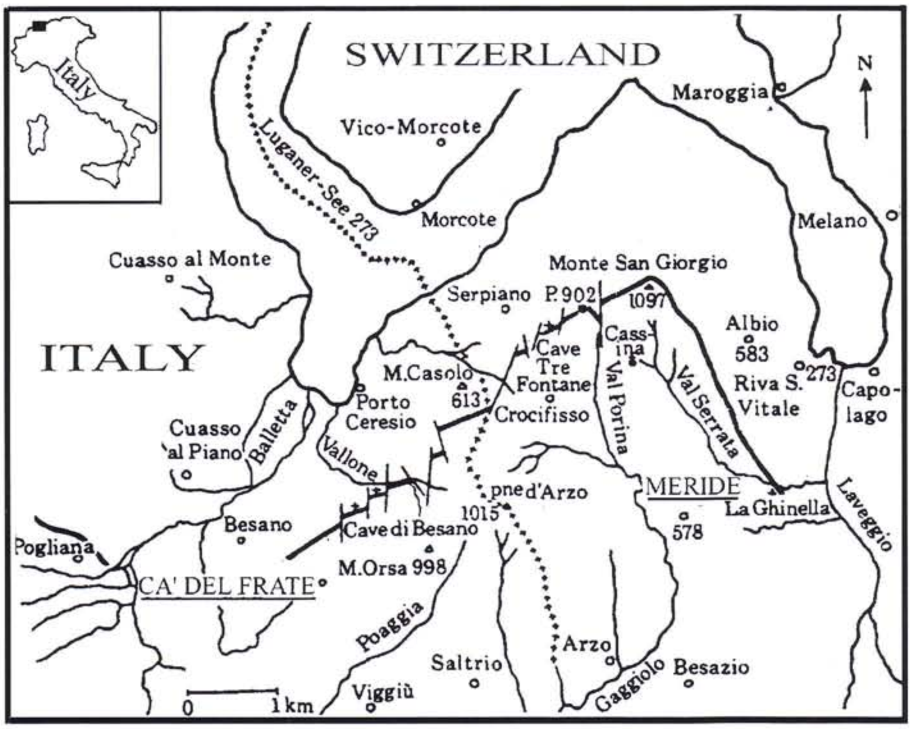


Fig. 1 - Geographic map of the Monte San Giorgio area, with the localities of Ca' del Frate and Meride.

somewhat older than those of Ca' del Frate. Besides fishes, crustaceans are common, sometimes concentrated in mass mortality layers; also terrestrial plants and a few insects were found (Krzeminski & Lombardo 2001).

Studies in progress are examining the fish faunas from these sites; they show a peculiar distribution of varied faunal assemblages, particularly as the fish species have a non-homogeneous stratigraphical distribution (Tintori et al. 1998; Lombardo et al. 1999; Lombardo 1999). Based on the data collected so far, these assemblages could be related both to age and to environmental variability (Tintori & Lombardo 1999; Lombardo 1999). The depositional environment for the Kalkschieferzone is interpreted as a shallow lagoon influenced by nearby land, with wide fluctuations in water temperature and salinity. Important periodic flow of fresh water from the adjoining land possibly lowered the water salinity of the basin (Tintori 1990a, 1990b, 1990c; Tintori & Renesto 1990), and deposited numerous plant remains, especially conifers, and conchostracan crustaceans, which currently are freshwater dwellers (Tintori 1990c).

Materials and methods

In this paper, the nomenclature adopted by Arratia & Cloutier (1996) was followed: in particular "parietal" and "postparietal" were used instead of "frontals" and "parietals" (Gardiner 1984). Most of the 70 specimens, both from the Ca' del Frate and Meride sites, were almost complete and were prepared only mechanically with sharp needles. Drawings were prepared with a camera lucida from the original specimens and used for reconstructions. Meristic and morphometric data were taken from the original material.

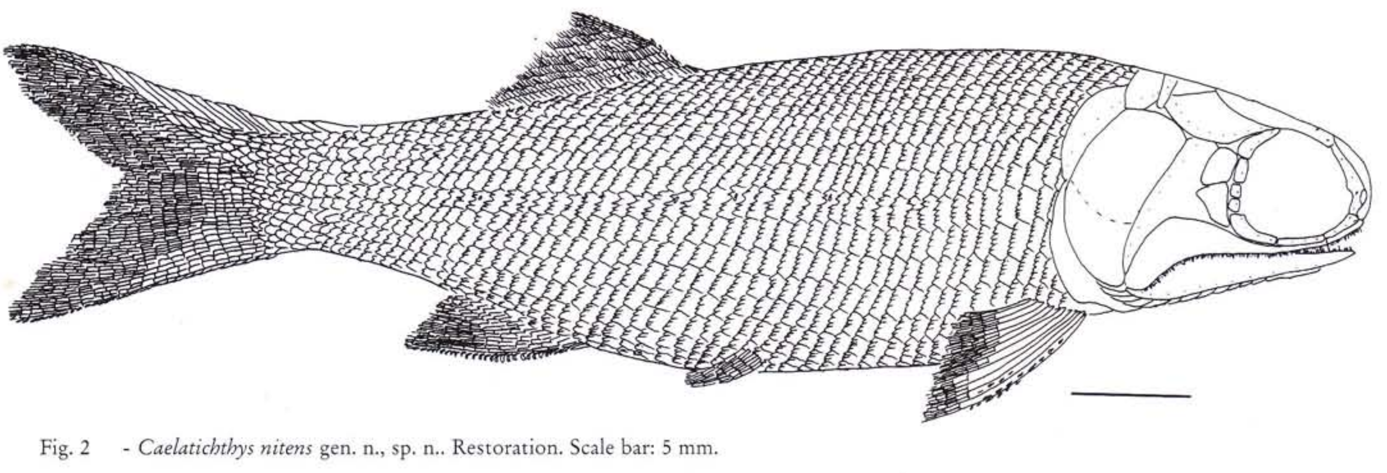


Fig. 2 - *Caelatichthys nitens* gen. n., sp. n.. Restoration. Scale bar: 5 mm.

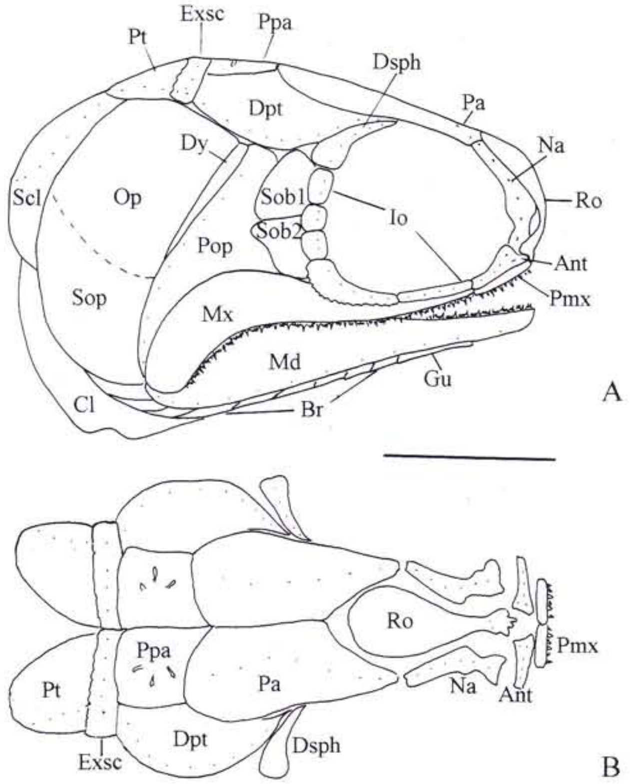


Fig. 3 - *Caelatichthys nitens* gen. n., sp. n.. Restoration of the skull in lateral (A) and dorsal (B) view. Scale bar: 5 mm.

Institution abbreviations: MCSNIO: Civico Museo Insubrico di Storia Naturale di Induno Olona (Varese, Northern Italy); MCSN: Museo Cantonale di Storia Naturale di Lugano (TI, CH).

Abbreviations.

Ant, antorbital; Br, branchiostegal rays; Cl, cleithrum; Dy, dermohyal; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; Gu, gular; Io, infraorbital bones; Md, lower jaw; Mx, maxilla; Na, nasal bone; Op, operculum; Pa, parietal bone (frontals auctorum); Ppa, postparietal bone (parietals auctorum); Pcl, postcleithrum; Pmx, premaxilla; Pop, preoperculum; Pt, posttemporal; Ro, rostral bone; S, spine; Sbo, suborbital bones; Sc, scute; Scl, supracleithrum; Sop, suboperculum.

Paleontological descriptions

Actinopterygii Cope, 1887

Palaeonisciformes Hay, 1929

Caelatichthys gen. n.

Diagnosis (as combination of characters): small-sized paleonisciform with fusiform body; large rostral with enlarged dorsal and a very narrow ventral region; nasal strongly notched for median and lateral narial openings; dermopterotic in contact with the dorsal margin of dermosphenotic: neither contact the nasal, and parietals form part of the orbital margin; supraorbitals absent; two suborbitals; 4-5 infraorbital bones; postorbital region of the maxilla not expanded dorsally and directed strongly downwards; dorso-ventrally narrow premaxillae meeting at the mid-line; skull bones strongly ornamented, with striae on lower jaws and tubercles and patches of ganoine on the skull roof; scales small, deeper than broad on the flanks, rhombic on the ventral and posterior region of the body, elongate at the base of the anal fin; all scales, except those of the caudal peduncle, posteriorly serrated; triangular, relatively long-based anal and dorsal fins; origin of dorsal fin well in front of the anal; small, short based pelvic fins; scaled lobe of caudal body axes extending to about half-length of dorsal fin lobe; progressive caudal scale inversion.

Type-species: *Caelatichthys nitens* gen. n., sp. n.

Etymology: from the latin word "caelatum" (chiselled), referred to the strongly sculptured skull.

Other species: *C. meridensis* n. sp.

Distribution: Upper Ladinian of Kalkschieferzone (Meride Limestone) of Ca' del Frate (Viggiù, Varese, Northern Italy) and Meride (Canton Ticino- Switzerland).

Remarks. At present *Caelatichthys* gen. n. is exclusive of the upper Ladinian of the Kalkschieferzone, both in its lower and middle levels at Meride and Ca' del Frate. Each site is characterized by a single species of the genus, *C. meridensis* gen. n., sp. n. and *C. nitens* gen. n., sp. n.: the species from Ca' del Frate is represented by individuals found in different levels and showing different ontogenetic stages, while those from Meride come mainly from the same bedding plane, with specimens of about the same size. Nevertheless, the differences between the specimens from the two sites cannot be ascribed to ontogeny, since they are evident even on individuals of the same size. Sexual dimorphism is excluded because the two anal fin morphotypes have not been found together in the same assemblage. Since the two species are very similar, they were at first diagnosed as a single species; for this reason, they were not cited separately in previous papers.

Caelatichthys nitens gen. n., sp. n..

Figs. 2-9, 12A; Pl. 1

1997 Gen. n A sp. n. Lombardo, pp.32-51, figs. 15-35.
1998 Gen. n A sp. n Tintori et al., pp. 13-14 (pro parte).
1999 Gen. n A sp. n Lombardo, p. 27 (pro parte).
1999 Gen. n A sp. n Tintori & Lombardo, pp. 497-507 (pro parte).
1999 Gen. n A sp. n Lombardo et al., pp. 102-103 (pro parte).

Diagnosis. *Caelatichthys* with SL up to 50 mm; skull length about ¼ of body length; two suborbitals; teeth small and acuminate, arranged in several rows; 11 branchiostegal rays; 50 transverse rows of scales posteriorly serrated; flank scales deeper than broad; pectoral fins with long proximal elements and fulcra-like ornamentation on the anterior margin of the first ray; anal fin triangular in shape, with hook-like fringing fulcra; origin of dorsal fin well in front of the anal; caudal fin made of about 40 lepidotrichia; most dermal bones heavily ornamented by tubercles and ridges of ganoine.

Etymology: from the latin word "nitens", meaning "rich in ornamentation".

Material: holotype: MCSNIO P 561 (complete specimen, without counterpart); paratypes: MCSNIO P 464, 465, 555, 556, 559, 562; other material (39 specimens): MCSNIO P554, 558, 560, 563-599 from the Kalkschieferzone of Ca' del Frate, stored at Civico Museo Insubrico di Storia Naturale di Induno Olona (Varese, Northern Italy).

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

Distribution: Kalkschieferzone (Upper Ladinian) of Ca' del Frate (Viggiù-Varese, Northern Italy).

Description

Skull. The rostral is large, with an oval dorsal and a narrower ventral region. The ornamentation is made of ganoine ridges which follow the lateral margin of the bone; medially, the ridges are transversal; the ventral part, carrying the ethmoidal commissure and contacting the antorbital, has an irregular outline, due to ganoine tubercles (Figs. 3AB, 4ABC, 7, Pl.1A). The nasal bones are rectangular and narrow, elongated dorso-ventrally; the posterior margin of the elements lines the anterior margin of the orbit; the opening of the anterior nostril lies on the antero-ventral margin of the nasal bones; the posterior nostril lies on the postero-ventral corner of the element. Ridges and tubercles of ganoine are arranged along the lateral margin of the elements (Figs. 2, 3AB, 4ABCD, 7, Pl. 1AB). The parietal bones (frontals auctorum) are broad, subtrapezoidal in shape, with a broad, rounded postorbital region and a narrower anterior region ending with a tip. Pores of the supraorbital canals run through the medial region of the bones, reaching the postparietals bones. Ornamentation consists of ganoine ridges, arranged in parallel rows along the lateral margin of the elements, and of flat tubercles, often forming large patches on the postorbital region (Figs. 2, 3AB, 4ABCD, 7, Pl. 1AB). Postparietal bones (parietals auctorum) are small and quadrangular, with a straight medial suture; anterior, medial and posterior pit-lines are present and ornamentation is made of densely arranged flat tubercles (Figs. 2, 3AB, 4ABC, 7, Pl.1B). The extrascapular bones are triangular in shape, narrow and laterally elongate. They meet medially with a short suture. The ornamentation consists of short crests of ganoine transverse to the posterior margin of the bones (Figs. 2, 3AB, 4AC, 7, Pl.1B). The dermopterotic is broad; it has an enlarged posterior region and a narrower anterior one, embracing the postero-lateral corner of the parietal. The pores of the sensory canal are visible close to the lateral margin (Figs. 2, 3AB, 4ABC, Pl.1AB). There are two large suborbitals, trapezoidal in shape, overlapping the anterior margin of the preoperculum (Figs. 2, 3A, 4ABD, Pl.1A). The dermosphenotic is triangular and elongate dorso-ventrally. The antero-dorsal end contacts the tip of the dermopterotic, and the anterior margin forms the postero-dorsal margin of the orbit (Figs. 2, 3AB, 4ABC, Pl.1AB). The first infraorbital is a narrow element, elongate antero-posteriorly while the second consists of a large crescent bone placed on the postero-ventral margin of the orbit, dorsal to the maxillary. Two or three small and square infraorbitals line the posterior orbital margin. The ornamentation is visible on the larger element and it is made of short ridges of ganoine arranged perpendicularly to the lower margin of the bone. (Figs. 2, 3A, 4ABCD, 7, Pl. 1AB). A triangular bone placed anteriorly to the first infraorbital is interpreted as the antorbital, due to the triradiate arrangement of the pores of the sensory canals (the confluence of ethmoidal commissure, infraorbital and supraorbital canals) (Figs. 3AB, 4ABC, 7, Pl.1AB). The maxilla is slender, with a postorbital region not expanded dorsally and strongly bent downwards, and a very low anterior one. Several rows of minute conical teeth are present on the oral margin; they are different in size, large teeth alternating with smaller ones; ornamentation is made of parallel rows of ganoine striae, arranged at a slant (Figs. 2, 3A, 4ABC, 7, 8C). There is a rectangular premaxilla bearing a series of small teeth, similar to those borne by the maxilla (Figs. 2 3AB, 4BD, Pl.1A). The wedge-like lower jaw shows an oral margin bearing teeth similar in shape and size to those of the maxilla (Figs. 2, 3A, 4ABC, 7, 8C, Pl.1A); pores of the mandibular canal are visible on the ventral part of the element. The ornamentation is very strong, consisting of longitudinal rows of striae and ridges of ganoine. The preoperculum shows a slender ventral part and a wider dorsal region, sloping anteriorly; the pores of the preopercular sensory canal are visible on the posterior margin of the bone (Figs. 2, 3AB, 4ABCD, 8BC, Pl.1A). The ornamentation is made of sparse ganoine tubercles. The exact shape and relative proportions between operculum and suboperculum are difficult to detect in almost all the specimens, due to the delicacy of the bones: the rectangular operculum is higher than broad and, apparently, somewhat larger than the suboperculum. The postero-dorsal margin is rounded and ventrally contacts the suboperculum with a slightly convex suture. The suboperculum is subrectangular, slightly broader than deep (Figs. 2, 3A, 4ABCD, 8BC, Pl.1A). The ornamentation is similar to that of the preoperculum: the number and density of tubercles increase with the size of the specimens. A narrow, triangular dermohyal is placed between the anterior margin of the operculum and preoperculum (Figs. 2, 3A, 4ABCD, 8BC, Pl.1A). The post-temporals are large, rounded triangular elements, separated by the mid-dorsal scale rows. Pores of the main lateral line are visible on the lateral region (Figs. 2, 3AB, 4ABCD, 7, 8BC, Pl.1AB). The ornamentation is made of flat tubercles, elongated antero-posteriorly. The oval supracleithrum is large, elongated dorso-ventrally and partially covered by the operculum (Figs. 2, 3A, 4ABCD, 7, 8BC, Pl. 1AB). Longitudinal ridges of ganoine form the ornamentation. The cleithrum is strong and prominent ven-

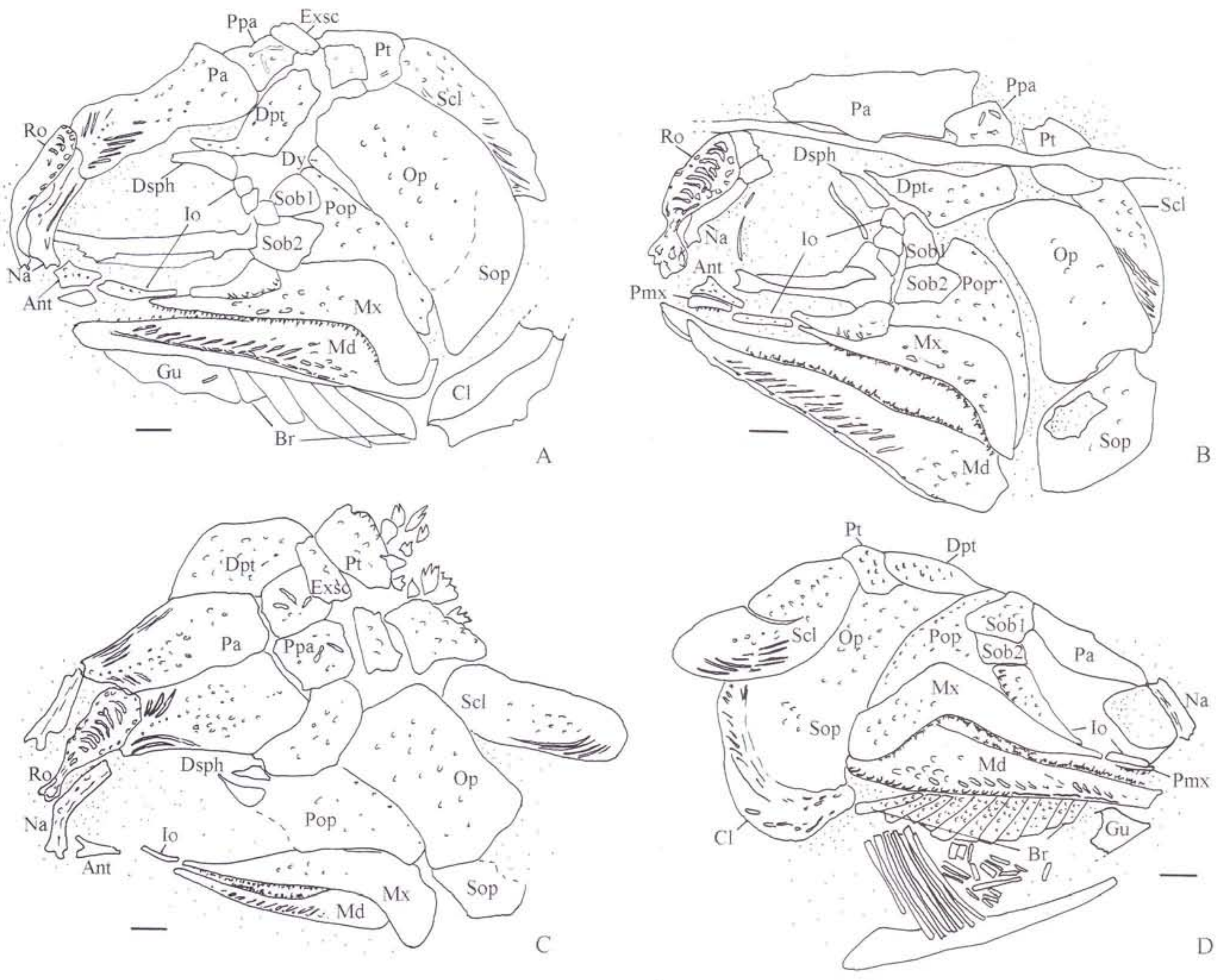


Fig. 4 - *Caelatichthys nitens* gen. n., sp. n.. Skull bones as preserved in the specimens: A) MCSNIO P464; B) MCSNIO P465; C) MCSNIO P562; D) MCSNIO P559. Scale bars: 1 mm.

trally; the ornamentation is heavy and consists of ganoine crests densely arranged (Figs. 2, 3A, 4AD, 7, 8BC, Pl. 1AB). Up to 11 branchiostegal rays were counted. A single oval gular is visible, but always only partially (Figs. 2, 3A, 4AD).

Fins. The pectoral fins are preserved only partially in most of the specimens: up to 17 rays were counted. The lepidotrichia are made of long proximal segments and shorter, but always longer than broad, distal ones; they branch at least twice (Figs. 2, 5A, 7, 8C, Pl. 1AB). The first ray is preceded by a long spine: it bears on its anterior margin a series of ganoine ridges similar in arrangement to fringing fulcra (Figs. 2, 5A, 8C, Pl.1A); small tubercles are present on the inner surface of the fin (P 559) (Fig. 5A). The pelvic fins are short and consist of at least eight segmented rays (Figs. 2, 5B, 7, 8C, Pl. 1AB); it is not possible to state if they branch or not. Fringing fulcra are not visible. The base of each fin is covered by an elongate scute, with an irregular posterior margin (Figs. 5B, Pl. 1B). The dorsal fin is triangular in shape, with a broad base; it lies at the level of the 30th scale row and consists of at least 30 lepidotrichia; each ray is segmented and branches at least once: its distal end is very thin and delicate. The anterior margin of the fin bears minute fringing fulcra (Figs. 2, 6A, 7, 8C, Pl. 1B). The anal fin lies at the level of the 25th scale row and is similar in size to the dorsal fin. It is made up of about 30 lepidotrichia, all segmented from the very base. The anterior margin of the fin, with a curved outline, shows a series of characteristic hooked fringing fulcra, with a drop-like rounded end (Figs. 2, 8C, 12A, Pl. 1AC). On smaller specimens (about 35 mm of SL) this kind of fulcra is missing and presumably their presence is related to ontogeny (Fig. 8ABC).

The caudal fin is heterocercal and consists of about 40 lepidotrichia, branching at least three times. The dorsal body lobe shows a series of about 20 strong basal fulcra, preceded by two or three basal scutes and followed by minute fringing fulcra. Fringing fulcra are present also along the margin of the ventral lobe of the fin (Figs. 2, 6B, 7, 8C, Pl. 1AB).

Squamation. The scale covering is made of about

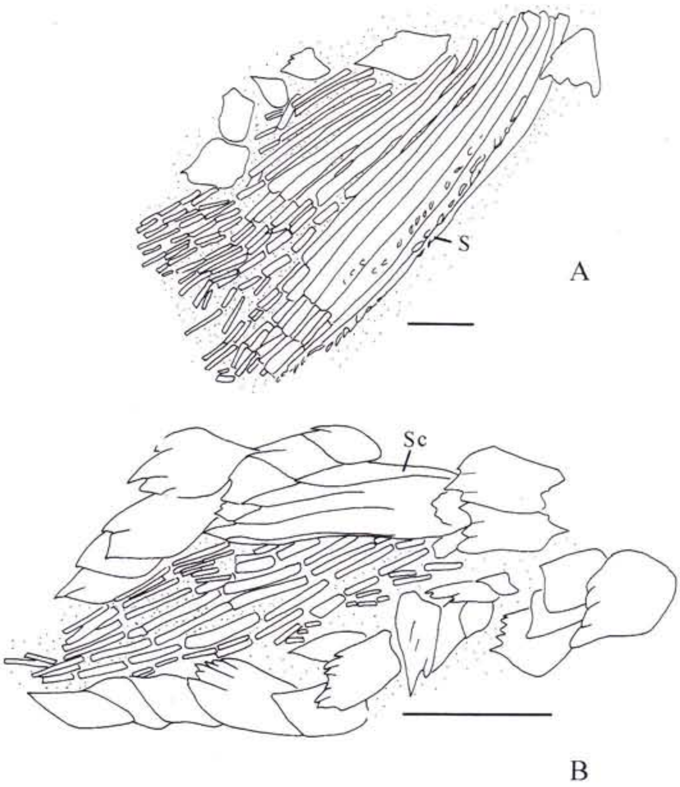


Fig. 5 - *Caelatichthys nitens* gen. n., sp. n.. A) MCSNIO P561: pectoral fin; B) MCSNIO P556: pelvic fin. Scale bars: 1 mm.

50 transverse scale rows. Single scales are deeper than broad on the middle region of the flanks; they gradually decrease posteriorly and towards the dorsal and ventral regions of the trunk (Figs. 2, 7, 8C, Pl. 1AB). Their surface is smooth, except for the scales of the first transverse rows behind the cleithrum, which show minute ridges and tubercles. The lateral line scales are all characterized by a small notch on their posterior margin; few of them show pores on the free surface. All scales have serrated posterior margins, except for those covering the caudal peduncle. Small rhombic scales cover the mid-dorsal region of the body: they are ornamented by 2-3 longitudinal ridges and show a couple of denticles on the posterior margin (Figs. 2, 7, 8C, Pl. 1AB). Antero-ventrally scales tend to become as deep as broad, but larger than those of the dorsal region; the region between the pelvic and anal fins is covered by lower scales and the base of the anal fin is covered with scales much longer than deep (Figs. 2, 7, 8C, Pl. 1AB). On the caudal pedicle all the scales are of equal size, slightly longer than deep. The scaled body lobe is covered by antero-posteriorly elongated , diamond-shaped scales and it extends to about half-length of the dorsal lobe of the fin. The scales between the two lobes of the caudal fin are very small, with a rounded posterior margin (Figs. 2, 6B, 7, 8C, Pl. 1AB).

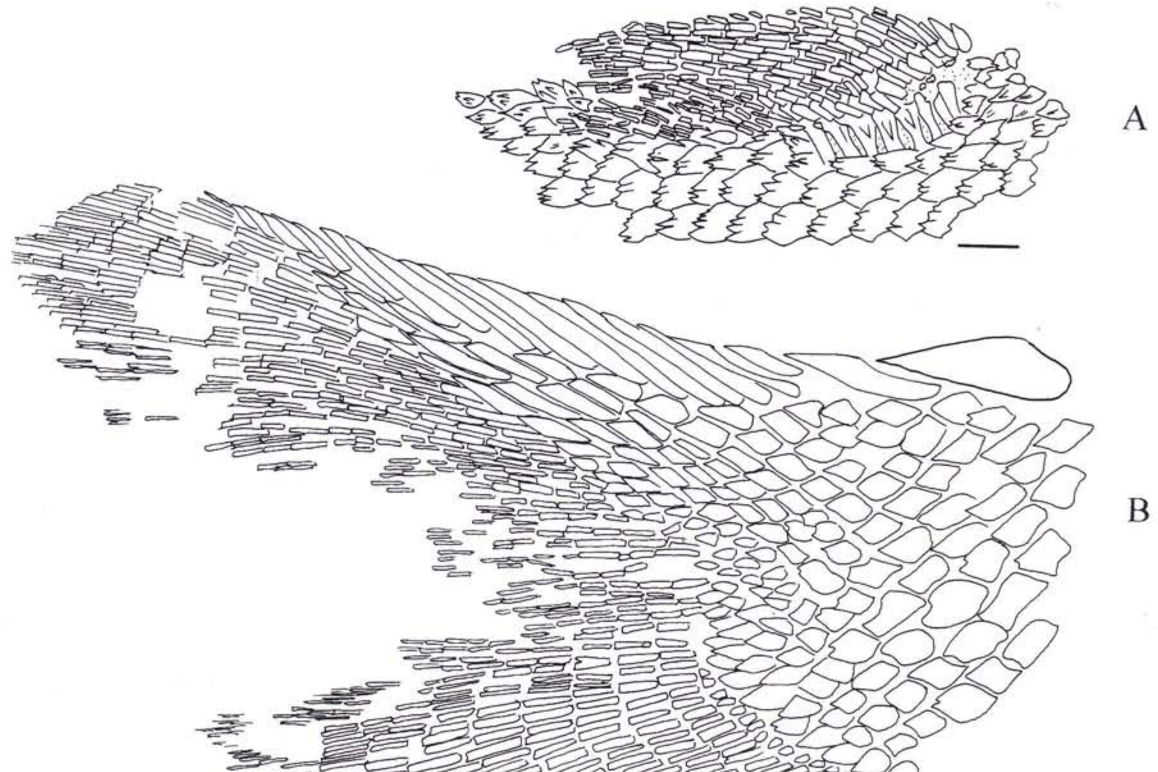


Fig. 6 - *Caelatichthys nitens* gen. n., sp. n.. A) dorsal fin and B) caudal fin of specimen MCSNIO P555. Scale bars: 1 mm.

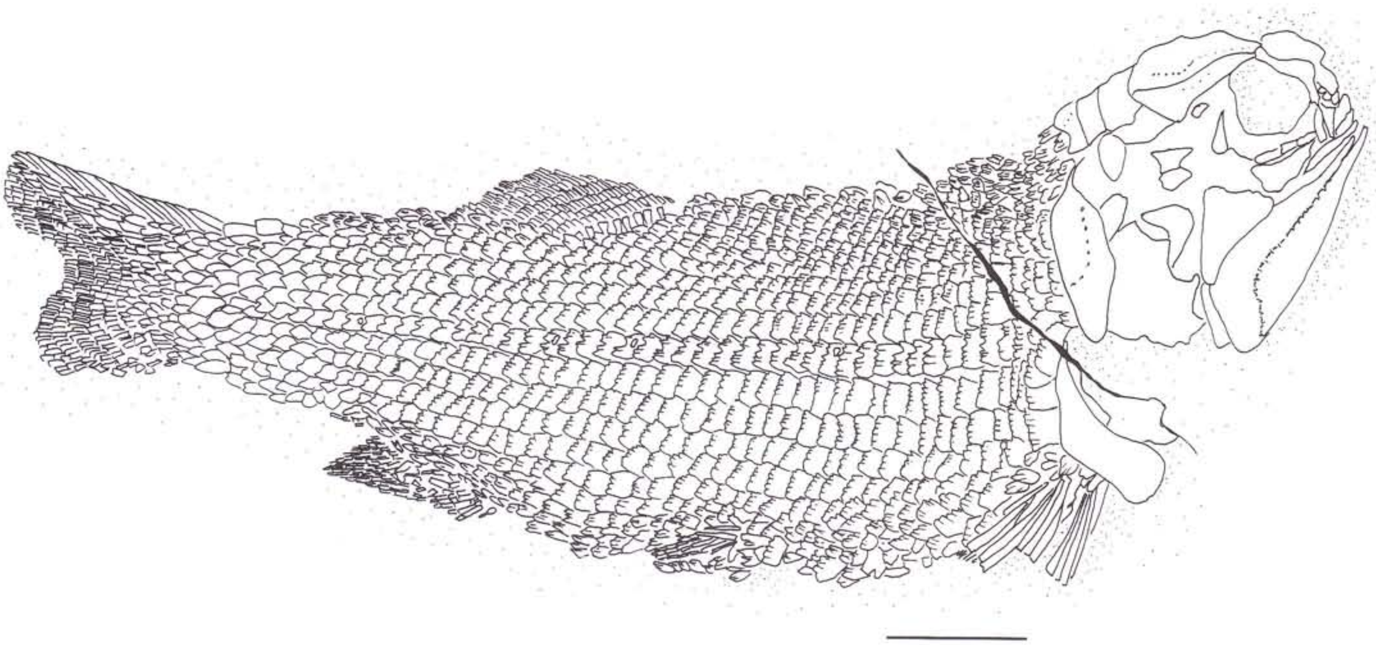


Fig. 7 - *Caelatichthys nitens* gen. n., sp. n.. Specimen MCSNIO P556. Scale bar: 5 mm.

Paleobiological remarks.

Caelatichthys nitens gen. n., sp. n. is represented by individuals of different size. This can be ascribed to the presence of different ontogenetic stages as some growth patterns can be recognized: specimens with otherwise similar species characteristics show changes in scale covering with increasing body size; smaller individuals are assumed to be juveniles. The growth changes involve also body proportion and shape, development of fin fulcra and skull bone ornamentation (Lombardo 1997; Tintori & Lombardo 1999) (Figs. 8ABC, 9). Size changes were described in a few palaeonisciforms and redfieldiiforms (Wade 1935; Hutchinson 1973; Wang 1979; Lowney 1980; Schultze & Bardack 1987). Some pattern of changes involve the decrease of head length relative to the increase of body length; the increase of the depth of the anterior body relative to the increasing length; the gradual appearance of the scales, first along the lateral line and on the upper caudal lobe and finally covering the base of dorsal and anal fins; the increase of fin rays segmentation and the appearance of branching lepidotrichia in larger forms; the gradual appearance of dermal bone ornamentation (Wade 1935; Heyler 1969; Wang 1979; Lowney 1980; Schultze & Bardack 1987). In *Caelatichthys nitens* gen. n., sp. n. the standard length ranges from 21 to 50 mm; the body shape changes from elongate fusiform to anteriorly deep and scales develop from the caudal region forward. The smallest specimen (MCSNIO P593) shows the scale covering only on the middle- posterior part of the body, beginning from the level of the anal fin to the axial body lobe (Figs. 8ABC, 9). Ganoine growth rings are visible on the preopercular and opercular bones of specimens of *Caelatichthys nitens* gen. n., sp. n. with a standard length of 35 mm. At this stage fins lack fringing fulcra and the basal fulcra on the axial body lobe are narrow and delicate; the squamation is incomplete at the base of both dorsal and anal fins. In specimens reaching 50 mm, only the most anterior radials of the dorsal fin are uncovered; the skull bones are fully ornamented and basal and fringing fulcra are completely developed. The body is deeper, and the skull is proportionately shorter than in smaller specimens. Concerning body proportions, in specimens up to about 30 mm of standard length the skull length is larger than the body depth; from 30 mm on, this ratio tends to reverse (Fig. 9). Even larger specimens of *Caelatichthys nitens* gen. n., sp. n. are likely to represent juvenile individuals because they show the dorsal fin base still uncovered. This was already observed in some species of *Elonichthys* from the Middle Pennsylvanian of the Mazon Creek fauna (Schultze & Bardack 1987).

Most of the 15 fish species found at Ca' del Frate show different growth series; in fact, ontogenetic changes were described for *Prohalecites porroi* (Tintori 1990a), *Aneurolepis macroptera, Perleidus altolepis, Allolepidotus bellottii*, gen. n. *B obtusus* (Lombardo 1997), suggesting for the Ca' del Frate area a depositional environment made of a shallow protected lagoon, used for reproduction and nursery (Tintori & Lombardo 1999).

Caelatichthys meridensis gen. n. sp. n.

Figs. 10-11, 12B; Pl. 2

1998 Gen. n A sp. n Tintori et al., pp. 13-14 (pro parte).
1999 Gen. n A sp. n Lombardo, p. 27 (pro parte).
1999 Gen. n A sp. n Tintori & Lombardo, pp. 497-504 (pro parte).
1999 Gen. n A sp. n Lombardo et al., pp. 102-103 (pro parte).

Diagnosis: a species of *Caelatichthys* with SL over 50 mm; teeth smaller than those of *C. nitens*; anal fin with minute lanceolate fringing fulcra; strong ornamentation mainly on upper and lower jaws.

Etymology: from the village of Meride, near the type locality.

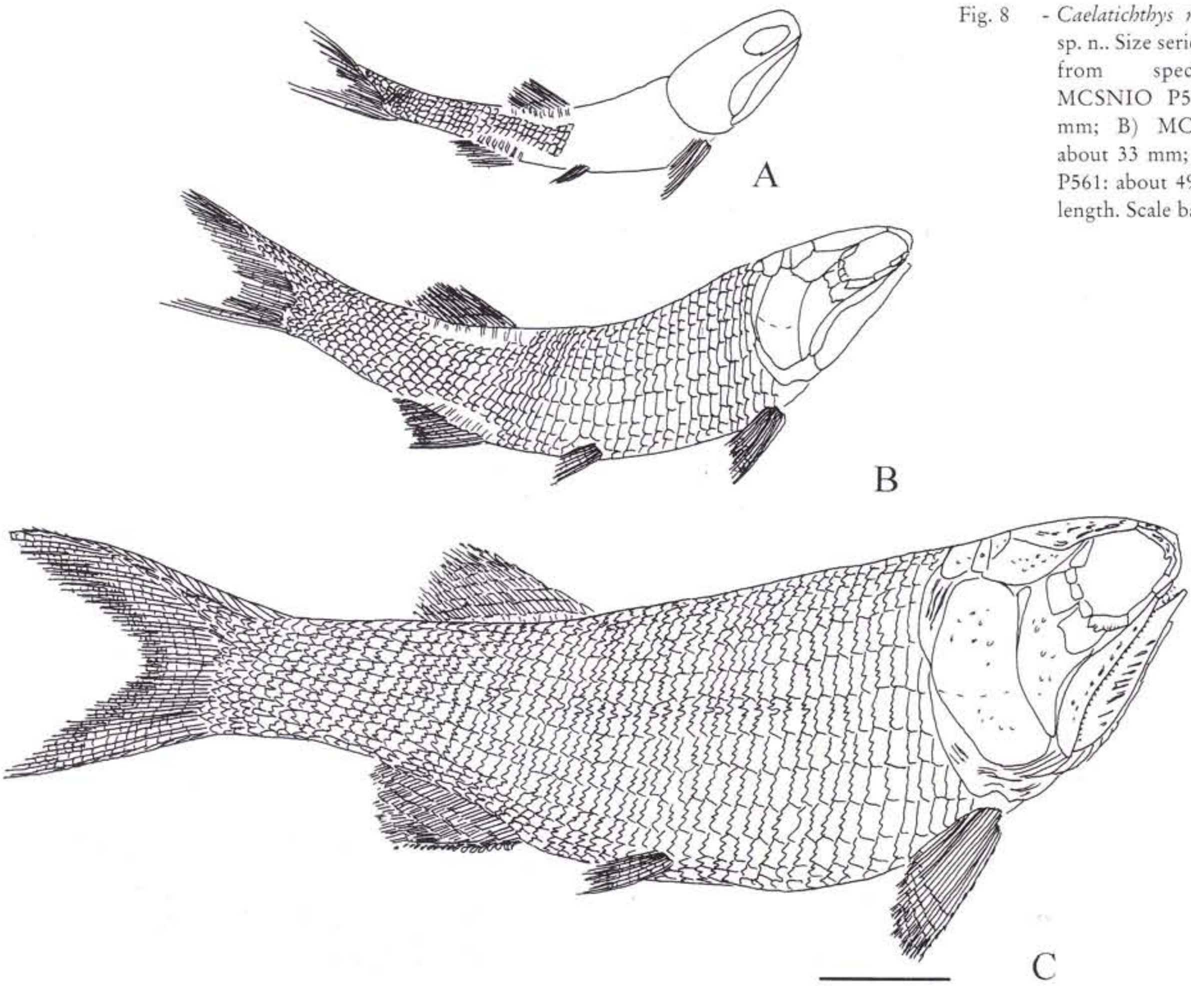


Fig. 8 - *Caelatichthys nitens* gen. n., sp. n.. Size series schematized from specimens A) MCSNIO P594: about 22 mm; B) MCSNIO P578: about 33 mm; C) MCSNIO P561: about 49 mm standard length. Scale bar: 5 mm.

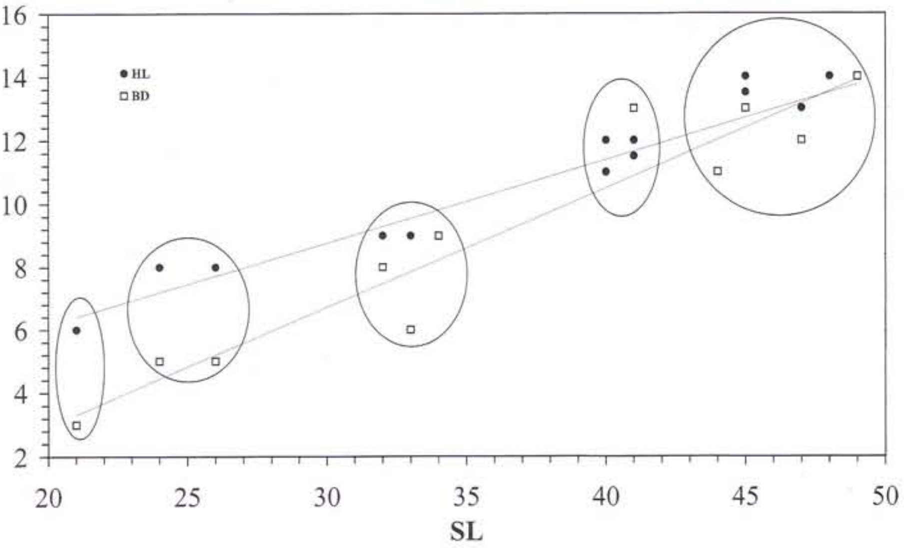
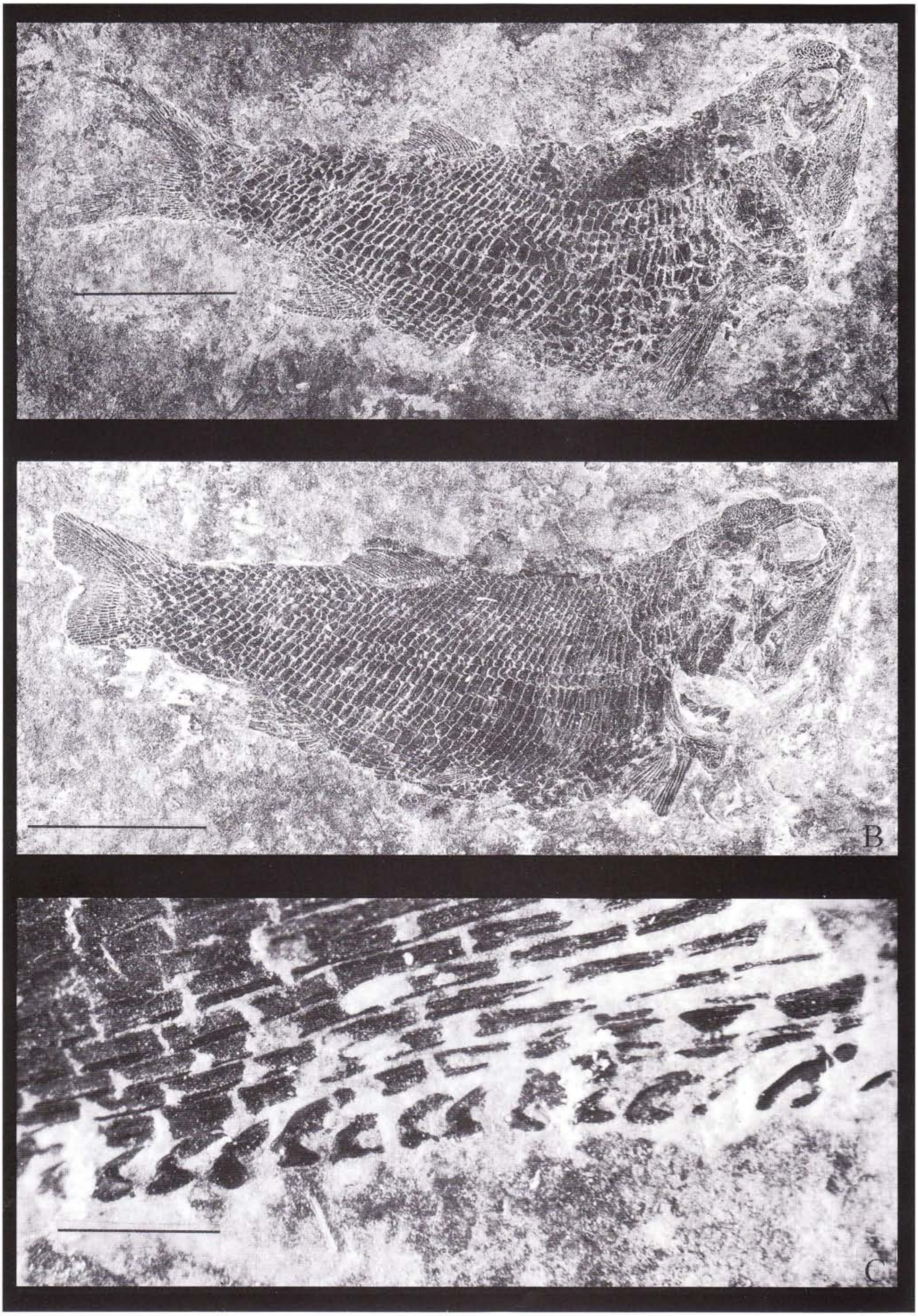


Fig. 9 - Standard length versus head length (HL) and maximum body depth (BD) in *Caelatichthys nitens* gen. n., sp. n.: specimens are grouped in size classes.

PLATE 1

Caelatichthys nitens gen. n., sp. n: A) MCSNIO P561, the holotype; B) MCSNIO P556; C) MCSNIO P561: detail of the fringing fulcra on the anal fin. Scale bars: 10 mm on A) and B); 1 mm on C).


A
B
C

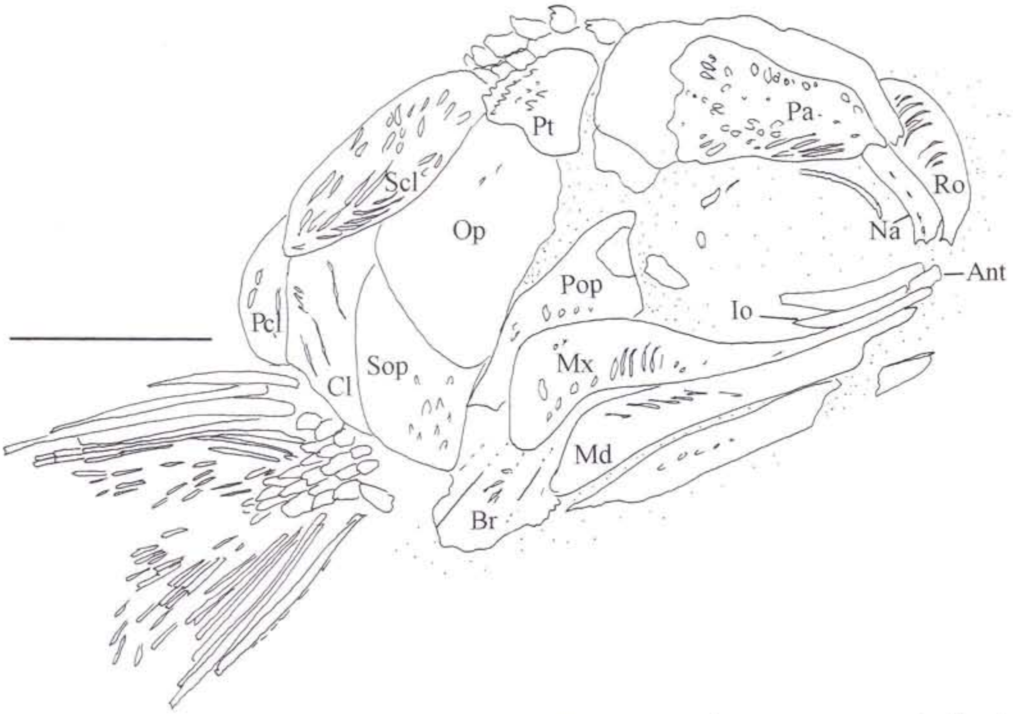


Fig. 10 - *Caelatichthys meridensis* gen. n., sp. n.. Skull as preserved on specimen MCSN 5004. Scale bar: 5 mm.

Type locality: Site D in Val Mara (Tintori et al. 1998) near Meride (TI-CH); late Ladinian.

Material: holotype: MCSN 5003 (complete specimen, without counterpart); paratypes: MCSN 3150, 3152, 3153, 5004-5011, all from the Kalkschieferzone of Meride (TI-CH), stored at Museo Cantonale di Storia Naturale di Lugano.

Distribution: Kalkschieferzone (Upper Ladinian) of Meride (Canton Ticino- Switzerland).

Remarks

This species is very similar to *C. nitens* gen. n., sp .n.: both share meristic characters, including the number of lepidotrichia of all fins and the number of transverse scale rows; also the shape and disposition of the skull elements are very similar. In spite of the strong resemblance between the two species, there are some differences related to the kind of ornamentation on both dermal bones and fins. All specimens from Meride are larger than those from Ca' del Frate, and show a much less developed ornamentation of the skull bones and a more delicate structure of the fins. In both species the ornamentation of the dermal bones consists of ganoine tubercles and crests, but in *C. nitens* gen. n., sp n. these elements are densely arranged almost on all skull bones, while in *C. meridensis* gen. n., sp. n. they are much more sparse, except on the maxilla and lower jaw (Fig. 10; Pl. 2BC). In general, fin rays of the species of Meride are made of longer and more slender elements than those of

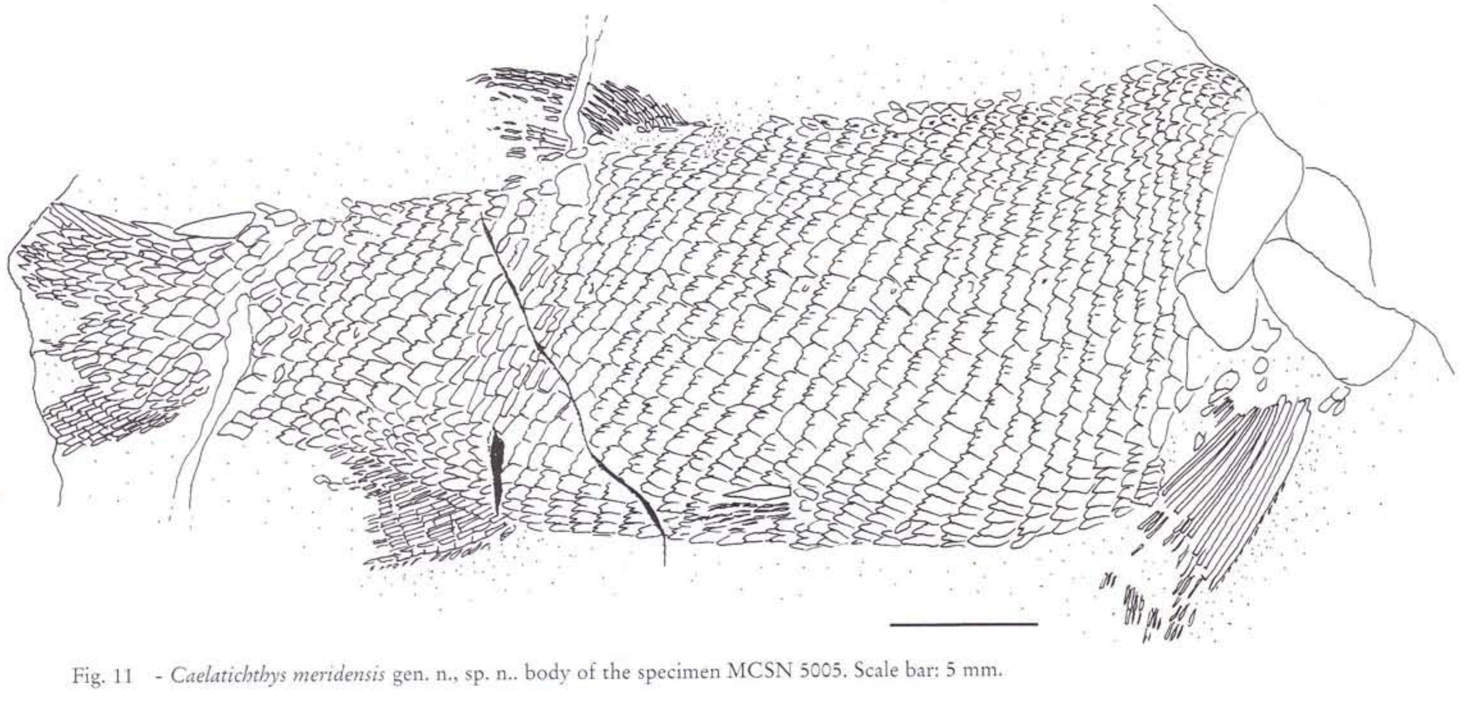


Fig. 11 - *Caelatichthys meridensis* gen. n., sp. n.. body of the specimen MCSN 5005. Scale bar: 5 mm.

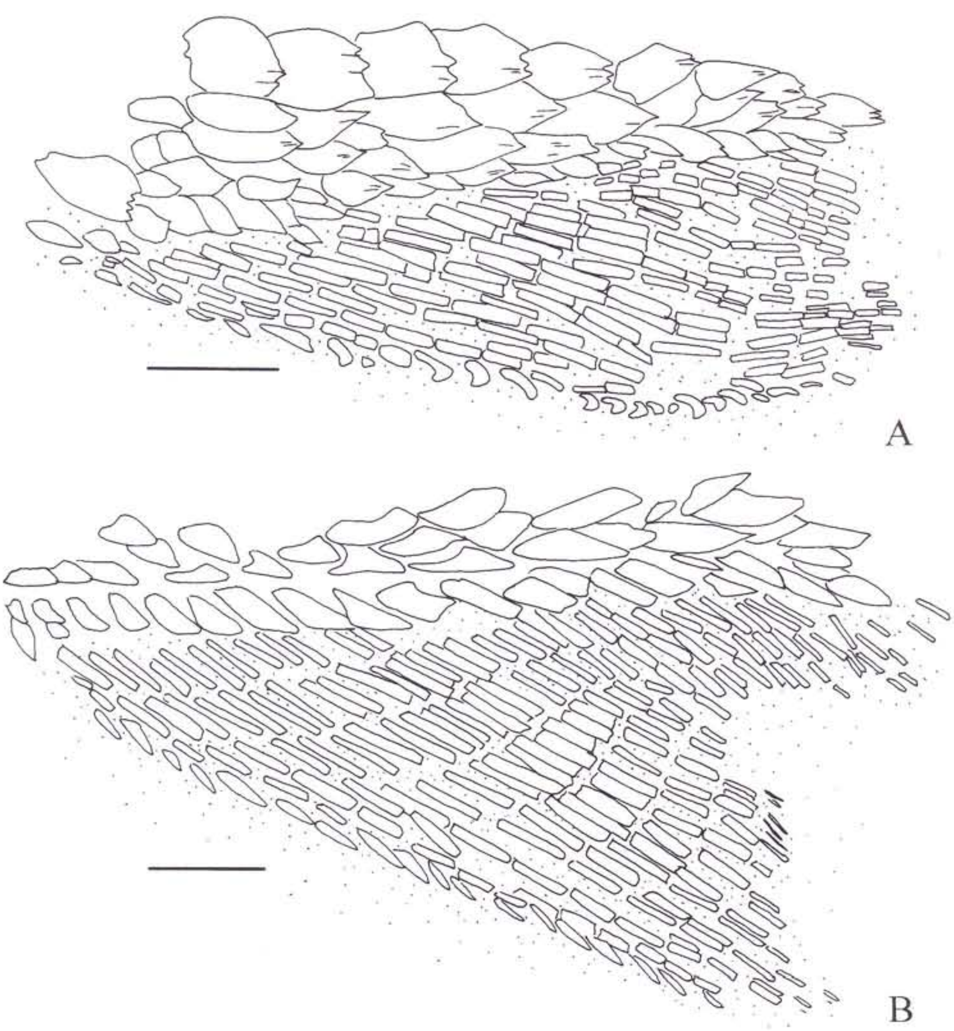


Fig. 12 - Anal fins in A) *Caelatichthys nitens* gen. n., sp. n. (MCSNIO P 555) and B) *Caelatichthys meridensis* gen. n., sp. n. (MCSN 5003), showing the different shapes of the fringing fulcra. Scale bars: 1 mm.

the other species, but above all there are some differences in the structure of the fringing fulcra. In *C. nitens* gen. n., sp .n. the fringing fulcra are different on the dorsal and anal fins: the dorsal fin shows a series of small lanceolate elements, while the anal fin has peculiar hook-like and thick ones, visible on all specimens on which the anal fin is well preserved. On the contrary, in *C. meridensis* gen. n., sp. n. the anal fin of all specimens shows a series of lanceolate fringing fulcra, similar to those borne by the dorsal fin (Figs. 11, 12B, Pl. 2ABC). In addition, the outline of the anal fin of *C. nitens* gen. n., sp .n. is different from that of *C. meridensis* gen. n., sp. n., probably due to the structure of modified fringing fulcra. On the former, the anterior margin of the fin is curved, in contrast to the straight margin of the fin of the species from Meride (Fig. 12AB). In both species the pectoral fins are preceded by a long spine with a fringing fulcra-like ornamentation on its anterior margin (Figs. 10, 11; Pl. 2AB) but the small tubercles on the inner face of the fin visible on specimen P559 of *C. nitens* gen. n., sp. n., are lacking in *C. meridentis.*

Some problems could be related to the presence of different ontogenetic stages in *C. nitens* gen. n., sp. n., while almost all specimens of *C. meridensis* gen. n., sp. n. come from the same bedding plane, suggesting their belonging to the same growth stage. The larger size of *C. meridensis* gen. n., sp. n. in comparison with that of *C. nitens* gen. n., sp. n., can be in fact ascribed to the adult stage of the specimen of the former species. Nevertheless, the different development of skull bone ornamentation cannot be related to ontogeny because *C. meridensis* gen. n., sp. n., which is represented by larger specimens, shows less developed ornamentation. Equally, teeth are apparently smaller than in specimens of *C. nitens* gen. n., sp. n. Regarding the different structure of the anal fin, it should not be related to sexual dimorphism, as the two kinds of fin were never found together in the same assemblage.

Discussion

Early actinopterygians, mainly Palaeozoic forms, have been long included in the taxon Palaeonisciformes, ranked in the chondrostean grade, together with extant sturgeons and paddlefishes. As new taxa were discovered, in particular in the Late Palaeozoic and Triassic, and with the works of Gardiner (1967), Schaeffer (1973) and Patterson (1982), it became clear that chondrosteans, when including the 'palaeonisciformes', are paraphyletic (Janvier 1996). Gardiner & Schaeffer (1989) defined 27 monophyletic non-neopterygian actinopterygian taxa with the cladistic method, analyzing a large number of characteristics, taken from the dermal bones, fin structure, or endoskeleton in a large number of taxa.

The general morphology of 'paleonisciforms' is very conservative and the differences that can be observed in the dermal skull patterns of the skull roof are quite difficult to interpret and use in reconstructing a phylogeny (Janvier 1996). Exoskeletal characteristics, such as the naso-temporal bone series, have been used for reconstructing the relationships and systematics of this group (Gardiner & Schaeffer 1989). According to Stensiö (1921) and Watson (1928) also some endocranial features, and particularly the braincase, have proved to be helpful. Recently, Coates (1999) revised the hypothesis of Gardiner & Schaeffer (1989) about primitive actinopterygian interrelationships, by adding new data on endocranial morphologies of 'palaeonisciforms'. Anyway, the kind of preservation of Italian and Swiss Middle Triassic fishes does not allow the use of endocranial characters considered in phylogeny.

Caelatichthys gen. n. is one of the most recent forms of the paleoniscoid group, before its dramatic decline at the end of the Triassic and, apparently, it shows a unique combination of primitive and derived characters. In *Caelatichthys* gen. n. the contact between both dermosphenotic+dermopterotic and nasal has been lost, with the parietals making the dorsal margin of the orbit: the primitive character is represented when the dermosphenotic and /or the dermopterotic reach the nasal (Gardiner & Schaeffer 1989). Among the few exceptions is *Strepheoschema* (included in the '*Watsonichthys group*' of the cladogram of Gardiner & Schaeffer (1989)), in which the parietal (=frontal) bone takes part of the dorsal margin of the orbit, as in *Caelatichthys* gen. n. Nevertheless, this genus, from the Late Carboniferous of Scotland, is quite different from *Caelatichthys* gen. n., in having large mid-dorsal and mid-ventral ridge scales, scales with posterior rounded margin, large fins and a strongly heterocercal caudal fin (Gardiner 1985). The new genus shows also additional infraorbital bones between the "jugal" and the dermosphenotic, contrary to the generalized lower actinopterygians that show an infraorbital series consisting only of a large jugal and a smaller lachrymal (Gardiner & Schaeffer 1989). More than three infraorbitals are found also in *Wendyichthys dicksoni*, a rhadinichthyid from the Carboniferous Bear Gulch Limestone of Montana (Lund & Poplin 1997; Poplin & Lund 2000). However, the Rhadinichthyidae are characterized by the absence of premaxillae, resulting in a rostral notch below the rostro-postrostral and between the antorbitals, and by a scaled lobe of the caudal fin whose tip projects beyond the first rays (Lund & Poplin 1997). In more general terms, the extremely elongated scaly lobe of the caudal fin is a primitive feature and is typical of all Paleozoic forms. In contrast, the shortening of the scaly lobe, shown by *Caelatichthys* gen. n., is present in some other Triassic paleonisciforms, such as *Boreosomus* from the Early Triassic of Madagascar and Greenland (Stensiö 1921, Nielsen 1942, Lehman 1952) and the Triassic species of *Ptycholepis* and *Platysiagum* from the Besano Formation (Brough 1939; Bürgin 1992). However, all these genera differ from *Caelatichthys* gen. n. in retaining some primitive characters in the skull pattern, such as the dermopterotic still separated in supratemporal and intertemporal with the latter contacting the nasal. Compared to *Caelatichthys* gen. n., *Boreosomus* shows relatively short jaws and a series of five antero-posteriorly elongated suborbitals; the infraorbitals are reduced to narrow tubular elements surrounding the infraorbital canal and medial extrascapulars are present (Stensiö 1921; Nielsen 1942; Lehman 1952). *Ptycholepis* is represented in the Besano Formation with four species (*P. barboi*, *P. magnus*, *P. schaefferi* and *P. priscus*), different in body size and ornamentation of skull bones and scales (Bürgin 1992). *Ptycholepis* has a skull pattern quite similar to that of *Boreosomus* (it is in fact comprised in the '*Boreosomus* group' of Gardiner & Schaeffer 1989) and is different from *Caelatichthys* gen. n. in the number and shape of the postorbital bones, ornamentation of skull bones and shape and ornamentation of scales (Bürgin 1992). *Platysiagum* is clearly different from the genera mentioned above in having a large preoperculum, expanded dorsally, a wide skull roof and the absence of suborbitals. The elements of the snout are not preserved in the specimens studied by Bürgin making it impossible to describe the shape of nasal and rostral bones (Bürgin 1992).

Among the characters of primitive actinopterygians fishes discussed by Lehman (1966), Kazantseva-Selezneva (1981), Patterson (1982), Gardiner (1984), Long (1988), Gardiner & Schaeffer (1989), Coates (1993), Lund et al. (1995), Arratia & Cloutier (1996), Lund & Poplin (1997), the following are shared by *Caelatichthys* gen. n.:

fusiform body more or less elongated; presence of ganoine; posterior narial opening little or not visible on the edge of the nasal; one pair of parietals (=frontals); dermosphenotic and dermopterotic; dermopterotic contacting parietal (=frontal) and post-parietal (=parietal); one series of two to three suborbitals; very oblique suspensorium; one elongate triangular dermohyal; numerous branchiostegal rays and one medial gular; single dorsal fin; pelvic fins short based; fulcra along the dorsal edge of all fins; rhombic scales.

Caelatichthys gen. n. shares the following characters with 'paleonisciforms':

parietals (=frontals) much longer than post-parietals (=parietals); large orbit, placed anteriorly; preop-

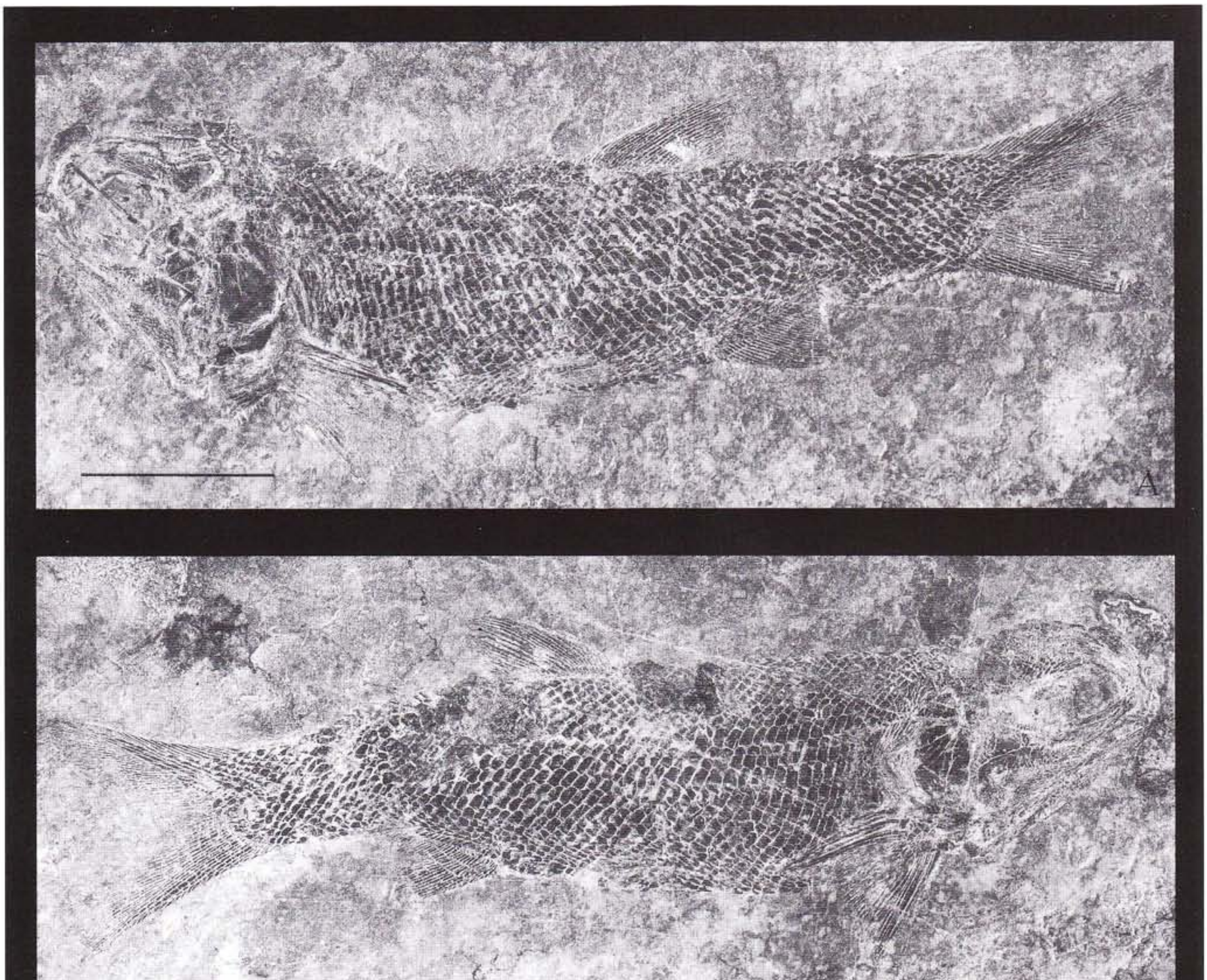


PLATE 2

Caelatichthys meridensis gen. n., sp. n:. A) MCSN 5003, the holotype; B) MCSN 5004; C) MCSN 5004: detail of the fringing fulcra on anal fin. Scale bars: 10 mm on A) and B); 1 mm on C).

erculum with two branches, the horizontal longer than the vertical; maxillary with postorbital plate and pronounced postero-inferior angle; heterocercal caudal fin; scaly lobe of the caudal fin slim; pectoral fin rays articulated only distally.

The following combination of characters distinguishes *Caelatichthys* gen. n. from the other 'paleonisciforms': loss of the contact between nasal and both dermosphenotic and dermopterotic, with the parietals forming the dorsal margin of the orbit; additional 2-3 infraorbital bones between the "jugal" and the dermosphenotic; small premaxillae, meeting in the mid-line and contacting the antorbitals and the rostral bone; scaly lobe of caudal fin extending only to about half-length of dorsal lobe.

At present, inferring precise relationships between *Caelatichthys* gen. n. and other primitive actinopterygians is difficult but this genus can be tentatively placed near to the Node H of the cladogram of Gardiner & Schaeffer (1989), for the presence of a dermopterotic derived from the fusion of intertemporal and supratemporal. The relationship between the taxa sharing this character is not clear, and some subgroups were made mainly on the basis of the relationships of the dermal bones in naso-temporal series: H1 (*'Watsonichthys group'*), H2 (*'Australichthys group'*), H3 (*'Belichthys group'*) and H4 (*'Amblypterus group'*) (Gardiner & Schaeffer 1989). In most of the taxa included in the Node H of the cladogram, the dermosphenotic is in contact with the nasal along with the dermopterotic (*Watsonichtys*, *Rhabdolepis*, Gardiner 1963); in a few taxa (*Cosmoptychius*, Gardiner 1963) the dermosphenotic has receded from the nasal, and in one taxon (*Strepheoschema*, Gardiner 1985) the dermopterotic has receded as well. In more advanced lower actinopterygians, including the chondrosteans, the dermopterotic does not reach the nasal (Gardiner & Schaeffer 1989) and a series of supraorbital bones is found above the orbit. In the more generalized condition, when separated from the nasals, the dermopterotic is in contact with the posterodorsal border of the dermosphenotic, as in *Australichthys* and *Mentzichthys* (Gardiner 1969, Gardiner & Schaeffer 1989).

Caelatichthys gen. n. shows a dermosphenotic which does not reach the nasal: this character is shared with some genera included in the Node H1 of the cladogram. The genera included in the *'Watsonichthys group'* share the more generalized condition for the relationships of the dermal bones of the nasal-temporal series: the dermopterotic contacting the postero-dorsal margin of the dermosphenotic (Gardiner & Schaeffer 1989). In some representatives of this group there is the loss of the contact nasal-dermosphenotic, but the dermopterotic still reaches the nasal bone (e. g. *Willomorichthys* Gardiner 1969 and *Cosmoptychius* Gardiner 1963). The only genus without nasal-dermopterotic contact, assigned (with doubt) to this group, is *Strepheoschema* (Gardiner 1985).

Concerning the other subgroups comprised in the node H of the cladogram, in the *'Australichthys group'* (Node H2) the dermopterotic is well behind the nasal and there is a large dermohyal; in the *'Belichthys group'* (Node H3) and *'Amblypterus group'* (Node H4) the dermopterotic is placed posteriorly, rather than dorsally to dermosphenotic. For these reasons, the inclusion of *Caelatichthys* gen. n. in these subgroups can be excluded.

Therefore, *Caelatichthys* gen. n. is a palaeoniscoid-grade actinopterygian displaying a mixture of primitive and advanced characters. Consequently, I prefer to leave this new genus as 'paleonisciform' *incertae sedis*: its features do not allow an attribution to any known family of this group, since most genera and species, especially from the Triassic, are too poorly known for useful comparisons.

Acknowledgements. Thanks are due to Cécile Poplin and Michael Coates who reviewed an early version of this paper. Financial support for field work in Ca' del Frate and Meride was given by the Civico Museo Insubrico di Storia Naturale di Induno Olona, the Dipartimento del Territorio del Canton Ticino and the Museo Cantonale di Storia Naturale di Lugano. Special thanks go to G. Danini and M. Felber for their help during all these years of excavations in the Kalkschieferzone and to R. Stockar for the 2001 field work in Meride. My sincere gratitude to all the people who helped in collecting the specimens and to the Museo dei Fossili di Meride for the logistic support. My warm thanks go to A. Tintori for his continuous help and precious advice and to S. Renesto for the nice photographs.

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