

# A new basal actinopterygian fish from the Late Ladinian of Monte San Giorgio (Canton Ticino, Switzerland)

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**Abstract** A new taxon of Late Ladinian basal actinopterygian is described on the basis of a single specimen from the Meride Limestone (Kalkschieferzone) of Meride (Canton Ticino, Switzerland). The species is characterized by a single plate-like branchiostegal, a suboperculum larger than the operculum, a maxillary fixed and posteriorly expanded, a large and rectangular dermopterotic and a large triangular dermosphenotic; the scales are rectangular to rhomboidal, the lepidotrichia of median fins are segmented from their base and the caudal fin shows epaxial rays. These features resemble the condition of the Redfieldiiformes, a freshwater fish group, whose presence in Europe is still controversial, owing to poor preservation of specimens found so far.

**Keywords** Actinopterygians · Middle Triassic · Monte San Giorgio Lagerstätte · Taxonomy · Palaeobiogeography

## Abbreviations

MCSNL	Museo Cantonale di Storia Naturale di Lugano (Switzerland)
ant	Antorbital
b.f.	Basal fulcra
br	Branchiostegal ray
cl	Cleithrum
dpt	Dermopterotic
dsph	Dermosphenotic

d.s.	Dorsal scute
exsc	Extrascapular
f.f.	Fringing fulcra
fr	Frontal
gu	Gular
ifo	Infraorbital bone
lmd	Left mandibula
mx	Maxilla
na	Nasal
op	Operculum
pa	Parietal
pcl	Postcleithrum
pl	Pit line
pop	Preoperculum
pr	Post-rostral
pt	Posttemporal
rmd	Right mandibula
ro	Rostral bone
scl	Supracleithrum
sop	Suboperculum

## 1 Introduction

The Middle Triassic of the Monte San Giorgio area, located between Switzerland and Italy (Fig. 1), has been known for more than 150 years for its rich fossiliferous levels, which yielded among the most important marine vertebrate faunas of the Mesozoic (Kuhn-Schnyder 1974; Tintori et al. 1985; Bürgin et al. 1989; Tintori 1990a; Sander 1989; Lombardo and Tintori 2004; Tintori and Lombardo 2007). On the basis of these finds, the Swiss side of Monte San Giorgio has been included in the WHL UNESCO in 2003, followed in 2010 by the Italian part in

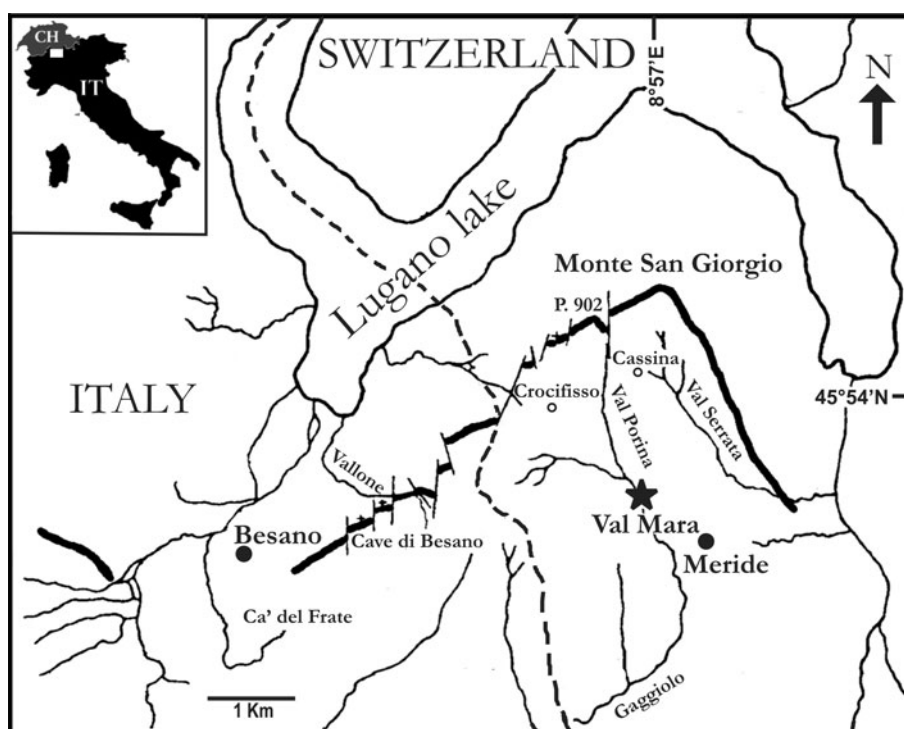
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**Fig. 1** Geographical and geological setting of the Monte San Giorgio area. The *stout black line* indicates the *Formazione di Besano* outcrops. The *star* indicates the position of the Meride site (Val Mara D: 45°53'32.17"N, 8°56'44.35"E). Modified after Lombardo (2002)



order to protect an outstanding and unique paleontological Lagerstätte.

In particular, the uppermost levels of Meride Limestone, the Kalkschieferzone (=KSZ), dating from the Late Ladinian, turned out to be very interesting for their faunal composition, and also for paleoenvironmental studies (Lombardo and Tintori 2002; Stockar 2010; Stockar and Renesto 2011; Stockar et al. 2012).

In this unit, two main localities have been exploited by the UNIMI team: Ca' del Frate, on the Italian side (together with the Civico Museo Insubrico di Storia Naturale, then in Induno Olona), and Meride (in cooperation with the Museo Cantonale di Storia Naturale di Lugano) on the Swiss side, respectively belonging to the middle and lower part of the Kalkschieferzone. The single specimen belonging to the new taxon described herein has been found in the locality of Meride (Val Mara D) (Fig. 1). The fossiliferous layers of this site, intercalated with some barren beds, are placed between layer 102 of Scheuring (1978) and layer 60 of Wirz (1945). The vertebrate fossil fauna of the Kalkschieferzone consists mainly on fishes (both basal actinopterygians and neopterygians) possibly belonging to about 20 different species (Lombardo 1999, 2001, 2002; Tintori and Lombardo 1999, 2007), but also rare specimens of the sauropterygian *Lariosaurus* have been found (Tintori and Renesto 1990). Among invertebrates, crustaceans (ostracods, estherids and the mysidiacean *Schimperella*) are very common, often found in mass mortality layers.

Within the fossiliferous level of Meride D, at least six assemblages of fishes have been identified; some species are exclusive to this site, just considering the KSZ Member (as *Felberia excelsa*, *Saurichthys* sp., *Caelatichtys meridensis* and the new taxon described herein) while others show a wider distribution, also being found at other localities of the middle KSZ (Tintori and Renesto 1983, 1990; Tintori et al. 1985; Tintori 1990a, b; Renesto 1993; Lombardo 1999, 2001, 2002; Lombardo and Tintori 2004; Tintori and Lombardo 2007).

The often very good preservation of the material found at these layers has also allowed, in the last 20 years, redescription of several taxa erected at the end of the nineteenth and beginning of the twentieth centuries, on the basis of the material coming from the coeval layers of the Perledo-Varenna area, collections that have unfortunately been destroyed or scattered (see Lombardo 2001). New genera and new species have been erected as well, greatly improving the knowledge of the ichthyofaunas of the Triassic, a crucial time span in the evolutionary history of fishes.

## 2 Systematic palaeontology

Class	Osteichthyes Huxley 1880
Subclass	Actinopterygii Cope 1887 Actinopterygii <i>incertae sedis</i>
Genus	<i>Pacorichthys</i> gen. nov.

Type species *Pacorichthys sangiorgii* sp. nov.

*Etymology.* Dedicated to Enrico Pacor, who discovered the holotype

*Type-locality.* Val Mara D, near the village of Meride (TI-CH); late Ladinian

*Diagnosis.* As for the type and only known species

*Pacorichthys sangiorgii* gen. et sp. nov.

*Etymology.* From Monte San Giorgio palaeontological Lagerstätte at the frontier between Italy/Switzerland, where the holotype was found

*Type-locality.* Val Mara, near the village of Meride (TI-CH); Late Ladinian

*Distribution.* Upper Ladinian (Middle Triassic) Kalkschieferzone of Meride (TI-CH)

*Holotype.* MCSNL 5036a, b

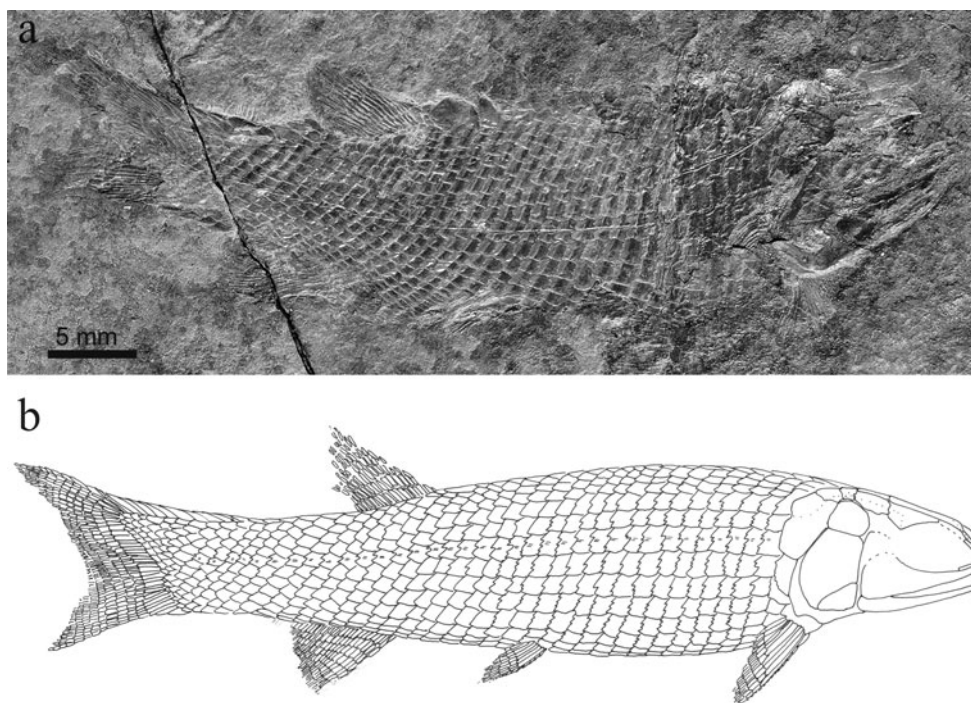
*Diagnosis.* (based on combination of characters) small, fusiform actinopterygian; frontals rectangular and broad with pores of the supraorbital canal arranged in a single row; parietals large and meeting medially in a short suture; wide opercular region with operculum much smaller than the suboperculum; preoperculum with a very narrow ventral region and an expanded dorsal one; small triangular rostral and large and rhombic post-rostral bones; deep and narrow antorbitals lining the anterior part of the orbit; large trapezoidal dermosphenotic; wide gape with elongated upper and lower jaws; maxilla with an expanded posterior region and a narrower anterior one; narrow dentary; bones smooth or slightly ornamented. Squamation made of rectangular scales, deeper than long, in the middle-lateral part of the body; scales rhomboidal or leaf-shaped on dorsal, ventral and posterior part of the body; denticulations present only on the antero-lateral region of the body; lepidotrichia of median fins completely segmented; paired fins with rays segmented from their bases. Caudal fin with short but not inconspicuous body lobe bearing epaxial rays.

*Description.* The specimen, about 4.5 cm in total length, is almost complete, but it shows delicate and thin bones and some elements of the skull and part of the squamation lie on the two different parts of the slab. For this reason, the bones of the skull roof and the orbital region appear partly disarticulated, shifted and overlapping each other.

*Skull.* The rostral is a small triangular element originally placed between the ventral regions of antorbitals and contacting the post-rostral with its dorsal end; the post-rostral is a large, smooth rhombic shield whose ventral margins are lined by the nasals. These are long, S-shaped

elements, which do not take part to the anterior orbital margin, being flanked by antorbitals; pores of the infraorbital canal are visible along the length of each bone allowing to recognize the misplaced element (the left?), moved to the anterior part of the skull (Figs. 2, 3, 4). The wide frontals are trapezoidal in shape, with a straight medial suture. The anterior region of each bone ends with a lateral tip, while the posterior outline is rounded. The lateral margin, flanked for almost its entire length by the dermosphenotic, is straight. The supraorbital sensory canal enters the antero-ventral corner and runs straight for 2/3 of the length of the bone, ending with a rounded pit-line. The surface of the bone is ornamented with feeble patches of ganoine. Only the left element of the parietals is visible: it shows a triangular shape, with a medial margin shorter than the lateral one and a pit-line visible on the median part of the bone. The anterior margin is straight while the posterior one seems slightly concave and it possibly received an accessory element. However, it is not possible to give a precise description of the elements making this region of the skull roof, because they partly overlap. The dermosphenotic is only partially visible, being in its posterior region disturbed. The detectable part of the element is subrectangular in shape, with the sensory canal running along its medial part; the straight ventral margin contacts the operculum, while posteriorly it reaches the extrascapular and anteriorly the dermosphenotic bones. The extrascapulars are narrow and triangular elements, with a rounded posterior margin and a straight ventral one, carrying the horizontal branch of the intertemporal commissure; these bones contact posteriorly the large post-temporals (Figs. 3, 4). The large triangular dermosphenotic has probably moved with respect to its original position, following the displacement of the bones of the skull roof. Its straight dorsal margin touches the lateral one of the frontal bone for almost its entire length, while ventrally it is slightly concave, forming the dorsal part of the orbit. Part of the infraorbital sensory canal is visible on the expanded posterior region of the element; the canal, coming from the dermosphenotic, turns downwards toward the infraorbital elements (Figs. 3, 4). Owing to the delicacy of the bones and the bad preservation of the orbital region, infraorbitals are not detectable except the first, placed on the anterior end of maxillary, in correspondence to the ventral margin of the left antorbital; it is narrow, elongate antero-posteriorly, and it bears a series of the small pores corresponding to the passage of the infraorbital sensory canal. Only the left antorbital is detectable, posteriorly to the rostral bone; it is a long, narrow element, with an irregular shape: it shows an anteroventral concavity for the suture with lateral margin of the rostral, and a median notch, presumably the anterior margin of the narial opening. Its posterior margin is part to the anterior orbital region (Figs. 3, 4). The

**Fig. 2** *Pacorichthys sangiorgii* gen. et sp. nov. **a** Holotype MCSNL 5036a. **b** Restoration



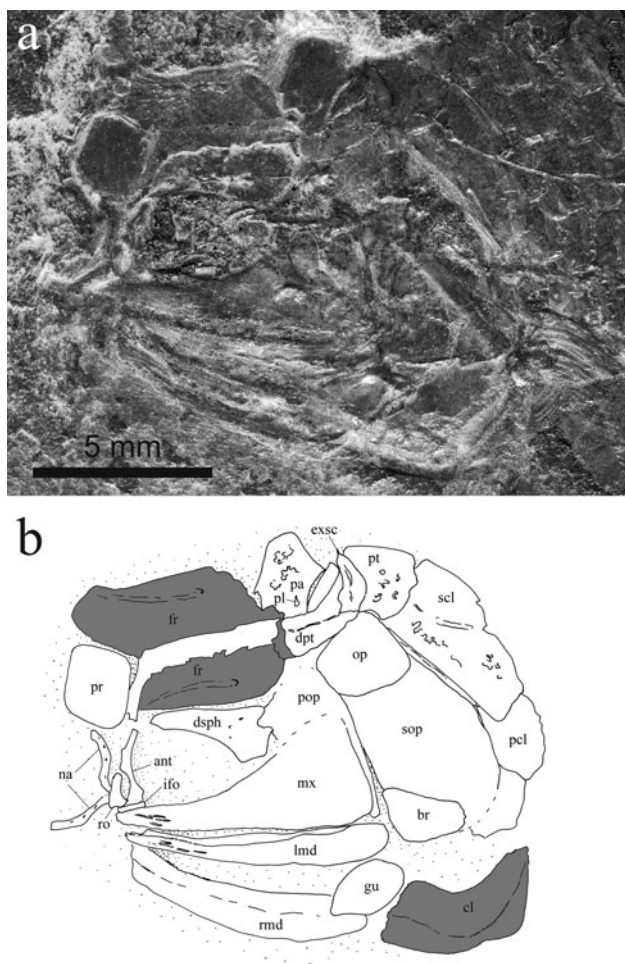
opercular region has a subtriangular shape with the dorsal region narrower than the ventral one, being made of a small operculum and a much larger suboperculum. The squarish operculum is about 1/3 as deep as the suboperculum and it is delimited by preoperculum, dermopterotic, posttemporal and supracleithrum proceeding cranio-caudally. The suture with the suboperculum is slightly concave. The suboperculum has an irregular shape, with the straight anterior margin much shorter than the rounded posterior one. The antero-ventral margin of the suboperculum contacts, by an oblique suture, the single branchiostegal ray; this is a triangular element, broader than deep, contacting both the posterior end of the lower jaw and the ventral tip of the preoperculum. The surface of the elements of the opercular region is smooth. The almost vertical preoperculum is “r”-shaped and is characterized by a very narrow ventral branch and a dorsal one horizontally expanded; owing to the state of preservation of the posterior orbital region, it is not possible to clearly detect the anterior outline of the element (Figs. 3, 4). The maxilla is long, with a narrower anterior margin and a dorsally-expanded posterior one, even if the postero-dorsal margin is not entirely visible. The straight oral margin bears very minute teeth, visible only at high magnification, especially on the posterior part of the element. Feeble ridges of ganoine are visible on the anterior end of the bone. The two disjointed branches of the lower jaw are visible, the right one in an inner view; it is a quite narrow element, bearing a series of very minute teeth, as for the maxilla. An ovoid plate, interpreted as a median gular, is placed posteriorly between the two branches of the

element. The post-temporals, placed between the small extrascapulars and the very large supracleithrum, are triangular-shaped with rounded posterior margin: the sensory canal of the lateral line is well visible along the ventral margin of the bone, passing into the supracleithrum. On the surface of the element very feeble patches of ganoine are detectable.

The supracleithrum is a very large rectangular element, dorso-ventrally elongated. Its posterior margin shows a notch at the level of half-length of the bone, where the sensory canal of the lateral line reaches the first scale of the mid-lateral scales row. This element is ornamented by small and flat patches of ganoine. Ventral to the supracleithrum there is a much smaller sub-rectangular postcleithrum, about 1/3 as deep as the supracleithrum. The posterior margin of this bone is slightly serrated. The cleithrum is very strong and sickle-like, as suggested by the broad ventral region of this element, visible on the counterpart of the specimen (5036b). On its medial surface a serrated ridge is detectable (Figs. 3, 4).

*Squamation.* All scales are very thin, so that dark bands of organic matter, most likely corresponding to the muscular tissues, are visible by transparency (Figs. 2, 5). The scale covering is made of 36 transversal scale rows; the individual scales are rectangular, deeper than broad, in the middle-lateral part of the body. The scales of the dorsal region are as deep as broad up to the dorsal fin; posteriorly they become much broader than deep. On the ventral region, particularly between pelvic and anal fins, the scales

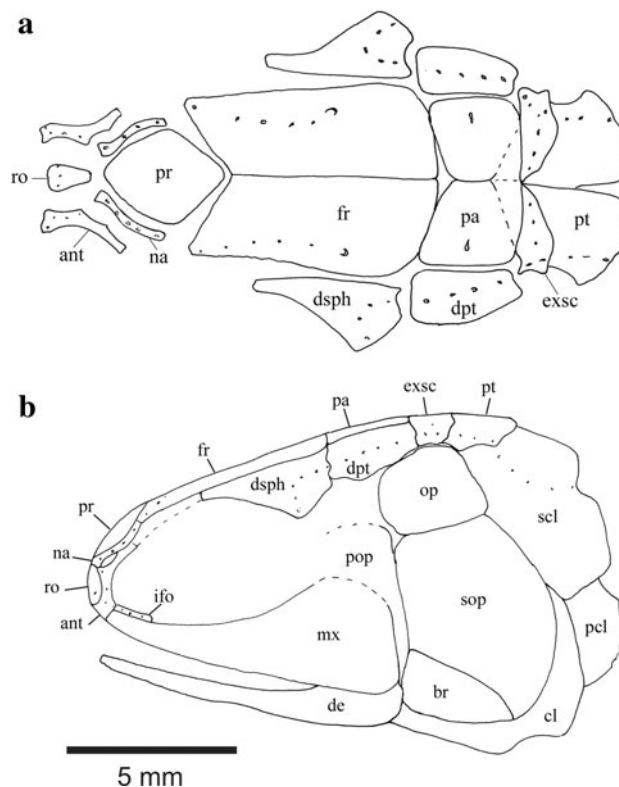




**Fig. 3** *Pacorichthys sangiorgii* gen. et sp. n. MCSNL 5036b. **a** Skull **b** camera lucida drawing of the skull. The shaded areas indicate the elements preserved on the counterpart (MCSNL 5036a) of the specimen. These were drawn, reversed and reported on this drawing

are very narrow, much broader than deep. On the posterior part of the body the morphology of the scales become more homogeneous, with the elements covering the flank being rhomboidal or leaf-shaped. The scales show a marked denticulation only on the antero-lateral region of the body. Each scale of the lateral line is characterized by the presence of a notch on its posterior margin and, on the anteriormost part of the trunk, by small rounded openings on surface. The abbreviate, but not inconspicuous, axial body lobe shows a covering made of small diamond-shape scales, more elongate than the flank ones (Figs. 2a, b, 5a, b, 6c, d).

**Fins.** The pectoral fins are incomplete: they are made by ten lepidotrichia, made of long proximal bases and short distal elements; the first ray is preceded by a series of small fringing fulcra. The pelvic fins are only partly visible (Figs. 2, 5a). The dorsal fin consists of about 12 lepidotrichia, all segmented from their base. The fin is preceded by a large scute and it is followed by a series of small



**Fig. 4** *Pacorichthys sangiorgii* gen. et sp. n. Restoration of the skull in **a** dorsal view and **b** lateral view

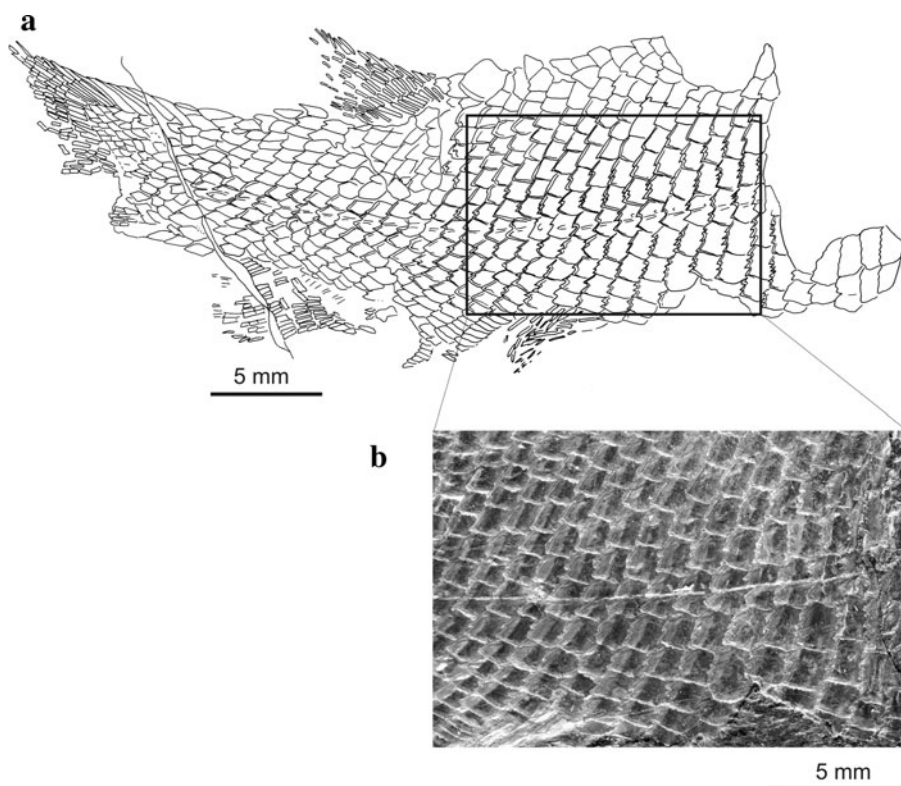
fringing fulcra. The rays bifurcate at least once, but the distal end of the fin is very delicate, so it is not possible to detect their posterior margin. The anal fin consists of about 20 lepidotrichia, with the same structure shown by those of the dorsal one. The fin has a broad base and its anterior margin shows a series of fringing fulcra (Figs. 2, 5a, 6a, b). The caudal fin consists of about 30 lepidotrichia, 5 being epaxial in position. Each one is characterized by a proximal base, slightly longer than the distal elements, and branches at least twice. There are about 6 strong basal fulcra bordering the axial body lobe, and a series of fringing fulcra along the first rays of the caudal fin (Figs. 2, 5a, 6c, d).

### 3 Discussion

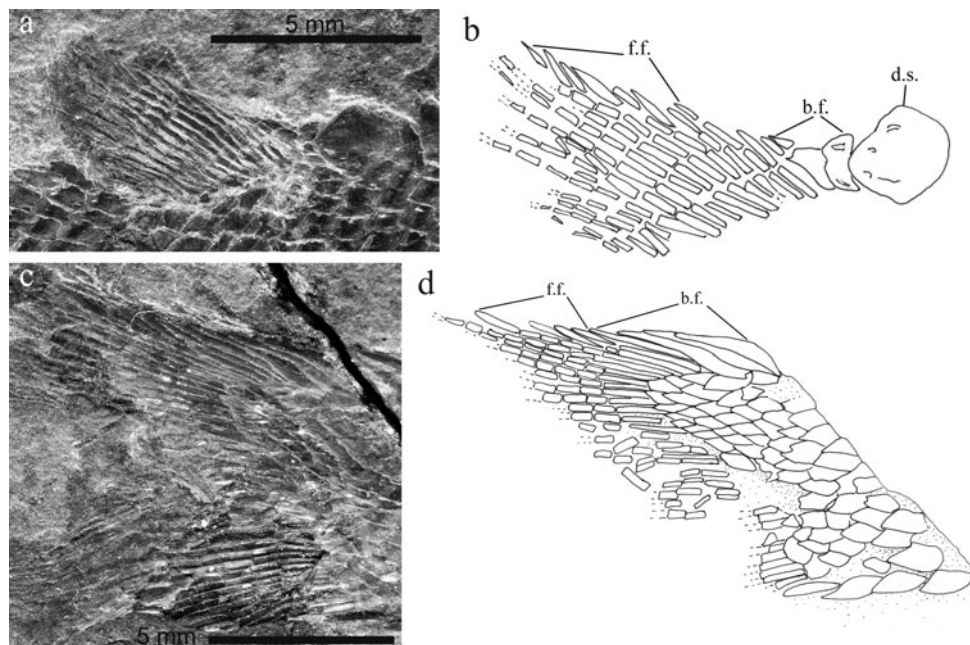
#### 3.1 Systematic assessment

*Pacorichthys sangiorgii* gen. et sp. n. is characterized by a skull pattern with a single plate-like branchiostegial ray, separate rostral and post-rostral bones, a narial opening surrounded by antorbital (or premaxillo-antorbital), rostral and nasals, an operculum much smaller than suboperculum, a maxillary fixed to preopercular and expanded posteriorly, large rectangular dermopterotic and triangular

**Fig. 5** *Pacorichthys sangiorgii* gen. et sp. n. MCSNL 5036a. **a** Squamation. **b** Close-up of the scales of the lateral region of the flank



**Fig. 6** *Pacorichthys sangiorgii* gen. et sp. n. MCSNL 5036a. **a–b** Dorsal fin. **c–d** Caudal fin



dermosphenotic. Concerning the structure of the fins, the rays of the remote opposite median fins of *P. sangiorgii* gen. et sp. n. are completely segmented, fringing fulcra are present on all fins and basal fulcra border the unpaired ones. The caudal fin shows an abbreviated axial body lobe with upper caudal fin rays dorsally inserted (epaxial fin

rays sensu Gardiner 1988). Scales are rhomboidal to leaf-shaped, with peg-and socket articulation.

Concerning the skull pattern, the most peculiar feature is the single plate-like branchiostegal ray. Enlarged branchiostegal elements reduced to one or two plate-like bones are considered to be a synapomorphy of the Redfieldiiformes (Schaeffer 1984).

Hutchinson (1973), following his study on the Triassic ichthyofaunas from South Africa and Australia, recognized three families of redfieldiiforms: Brookvaliidae, Redfieldiidae and Schizurichthyidae, later leaving the genus *Helichthys* in an indeterminate status (Hutchinson 1978). According to Hutchinson, Brookvaliidae are characterized by large orbits, narrow crescentic-shaped dermosphenotics, a snout in which the antorbital is excluded from the upper jaw margin by a toothed element and by a long and slender lower jaw; Redfieldiidae have small orbits, deep rectangular dermosphenotics, a snout lacking premaxilla and with the antorbital bordering the margin of upper jaw; the lower jaw is short and robust (Hutchinson 1973). The family Schizurichthyidae was erected to contain the single genus *Schizurichthys* which is unique in having a caudal fin with a separate “epaxial lobe”, bordered dorsally and ventrally by fringing fulcra. In his survey on the relationships of Triassic and Jurassic redfieldiiforms, Schaeffer (1984), although questioning the usefulness in recognizing the Hutchinson’s families except in a vernacular sense, supported with a cladistic analysis the subdivision of the Redfieldiiformes into the Brookvaliidae and Redfieldiidae; at the same time he considered it was unjustified to assign *Schizurichthys* to a separate family only on the basis of a specialization in the caudal fin, as this character is an autapomorphy for this genus, which is otherwise a generalized redfieldiiform (Schaeffer 1984).

Following the character states used by Schaeffer for his cladogram, the representatives of Brookvaliidae sensu Hutchinson 1978 (Schaeffer 1984, Fig. 6, node 2–8: *Atopecephala*, *Schizurichthys*, *Ischnolepis*, *Brookvalia*, *Phlyctaenichthys*) are considered the more plesiomorphic for the long jaws and the wide gape; for this character and the presence of the antopercular they show a condition different from that of *P. sangiorgii* gen. et sp. n. Concerning the other redfieldiiforms recognized by Schaeffer (1984) in his analysis, the new taxon differs also from *Helichthys*, which shows two pairs of parietals, antoperculars but has shortened maxillae; as noted by Hutchinson (1978) and confirmed by Schaeffer (1984), the phylogenetic position of *Helichthys* is uncertain, (Schaeffer 1984, Fig. 6, node 11–12), but it is probably more related to redfieldiids than to brookvaliids. Succeeding taxa (*Geitonichthys* and *Molybdichthys*; nodes 11–13) have skull roofs of the redfieldiid type and no antoperculars, but broad premaxillae; with respect to *P. sangiorgii* gen. et sp. n. they show a narrower opercular and posttemporal region. Also the genus *Daedalichthys* (Node 15) shows a redfieldiid dermal skull, but two branchiostegal rays and the long scaly lobe of the caudal fin make it distinct from the other forms. Among redfieldiids *P. sangiorgii* gen. et sp. n. resembles the American taxa *Cionichthys*, *Redfieldius* and *Dictyopyge*, (representing a trichotomy which Schaeffer

considered unresolved, Schaeffer 1984) for the absence of antopercular, narrow premaxillae and maxillae shortened with a snout profile lowered (node 16 of the cladogram, Schaeffer 1984: 12, Fig. 6). In particular, the pattern of skull roof and cheek region shown by *Dictyopyge* is the closest, for the relative proportion of the elements, to that of *P. sangiorgii* gen. et sp. n. Nevertheless, the American forms differ from the new taxon for the multiple extrascapulars and for the ornamentation of the snout, strongly tuberculated.

The last taxa taken into consideration by Schaeffer (1984) in his cladogram are *Mauritanichthys* (node 18) *Lasalichthys* and *Synorichthys* (19–20), characterized by reduced to absent postrostral; *Lasalichthys* and *Synorichthys* have double rows of sensory canal pores. These characters clearly do not fit *P. sangiorgii* gen. et sp. n. The difficulty of verifying the relationships of new supposed redfieldiiform taxa must be stressed, however, since the genera recognized (with few exception, as the taxa from Eastern and Western USA) are often represented by scanty specimens, or by incomplete or poor preserved ones. State of preservation is crucial especially for the region of the snout, whose pattern represents one of the synapomorphies of the group, as stressed by descriptions, drawings and restorations given by several authors (Wade 1935; Brough 1931; Hutchinson 1973, 1978; Schaeffer 1984).

As pointed by López-Albarello et al. (2006), a single or an enlarged first branchiostegal ray occurs also in other actinopterygians, such as haplolepidids, aeduellids and polyodontids (Westoll 1944; Poplin 1997, 2001), but they all greatly differ from *P. sangiorgii* gen. et sp. n. both in the pattern of the other dermal bones and in the strongly heterocercal tail. In particular, haplolepidids, represented by several genera and species from the Carboniferous, are different for the pattern of skull roof and snout, the squamation made of deep lateral flank scales and for the structure of the fins with few, not bifurcated, lepidotrichia (Westoll 1944; Poplin 1997). Among other features, the Carboniferous/Permian aeduellids differ from *P. sangiorgii* gen. et sp. n. in the vertical preopercular made of a single ventral element and a mosaic-like small dorsal ones, the opercular region with the large opercular, similar in size to subopercular and the heterocercal tail (Heyler 1969; Poplin 2001). The differences from the extant Polyodontidae, both for skull pattern, heterocercal tail and very reduced squamation, are so evident as to make detailed comparison unnecessary (Grande and Bemis 1996).

Regarding the structure of the fins, the complete segmentation of the lepidotrichia of the median fins, shown by *P. sangiorgii* gen. et sp. n., is typical of the basal actinopterygians traditionally included in the order Paleonisciformes (Gardiner 1967; Schaeffer 1973; Patterson 1982; Carroll 1988). Although lower actinopterygian



interrelationships are still controversial (Gardiner and Schaeffer 1989; Janvier 1996; Coates 1999) in all the representatives of this group this pattern is usually associated to a strong heterocercal caudal fin and a primitive skull pattern, including a series of several branchiostegal rays, an oblique suspensorium and a long gape.

A hemiheterocercal caudal fin is on the contrary a typical feature of both “subholosteans” (Perleidiformes and Peltopleuriformes: Brough 1939; Schaeffer 1955, 1973; Gardiner 1988; Bürgin 1992, 1996; Lombardo 1999, 2001; Tintori and Lombardo 2005; Sun et al. 2009, among others) and, again, Redfieldiiformes (Schaeffer 1967, 1984; Hutchinson 1973). Concerning “subholosteans”, a primitive skull-pattern, with the maxilla strictly jointed to the preopercular bone, is always associated both to the hemiheterocercal caudal fin nearly reaching an external symmetry—owing to the presence of rays inserted dorsal to the axial body lobe (the epaxial fin rays sensu Gardiner and Schaeffer 1989; but see also Grande and Bemis 1996; Lombardo 2001; Lombardo and Tintori 2005; López-Arbarello and Zavattieri 2008)—and to an advanced dorsal and anal fin structure, with lepidotrichia equaling in number the endoskeletal supports and made of long proximal elements and much shorter distal ones (as for the neopterygians). Therefore, besides the general morphology of the dermal bones (a different arrangement of ethmoidal region with large rostral and nasals bones, small dermosphenotic, numerous branchiostegal rays; see Bürgin 1992, 1996; Lombardo 1999, 2001; Tintori 1990b; Tintori and Sassi 1992), *P. sangiorgii* gen. et sp. n. can not fit this group of advanced chondrosteian actinopterygians, also for the median fin patterns. The complete segmentation of the rays of the median fins is shared by Redfieldiiformes and *P. sangiorgii* gen. et sp. n., but this character has never been taken into account in papers after Schaeffer (1967) and the other redfieldiiform synapomorphy concerning the fins structure, i.e., the lepidotrichia exceeding the number of radials, is not verifiable on the only specimen available of *P. sangiorgii* gen. et sp. n., owing to the complete scale covering. As regards the structure of the caudal fin, within redfieldiiforms there are differences in the relative length of the caudal axis with various degrees of reduction, as Brough first noted (1931, 1936): the maximum reduction is attained in the Late Triassic forms (Schaeffer 1967). *Dadalicthys* has the longest axis, extending almost to the tip of the dorsal lobe of caudal fin, which all the same does not reach the complete heterocercy (Brough 1931); in the other redfieldiiform genera the axis is considerably shorter, with the dorsal lobe of the caudal fin showing the presence of epaxial rays.

Summarizing, *P. sangiorgii* gen. et sp. n. resembles the condition of Redfieldiiformes in the combination of features unique to the group (see Schaeffer 1967) but

unfortunately, the only available specimen does not allow to confidently established a relationship with them. For this reason it is preferable at present considering it as an *Actinopterygii incertae sedis*.

### 3.2 Palaeobiogeographic remarks

The description of a new basal actinopterygian resembling the condition of Redfieldiiformes calls once more into question, in a more general sense, the problem about the systematic attribution of taxa when the kind of preservation places restrictions to the identification of some of the synapomorphies. Although the skull pattern is basic in determination, new finds and new studies are more and more suggesting the fact that the post-cranial characters have often been underestimated in systematic studies. Structure of the median and caudal fins and squamation pattern could in fact turned to be crucial in understanding the relationships between seemingly related taxa and consequently the palaeobiogeographic distribution of the group they belong to.

The main papers concerning Redfieldiiformes are based on complete, often exceptionally well-preserved specimens (i.e. the fish fauna of the Late Triassic/Early Jurassic of the Newark Supergroup, Western USA; Schaeffer and McDonald 1978; Schaeffer 1984), but preservational bias has often strongly conditioned the determinations of specimens belonging to other ichthyofaunas, coming mostly from Europe. This fact affected our documentation on the evolutionary history of the group and consequently its palaeobiogeographic distribution. Concerning the distribution of Redfieldiiformes, Schaeffer (1967, 1984) pointed out that the record is a discontinuous one, both temporally and geographically and that occurrence of redfieldiids is restricted to a different continent for each major subdivision of the Triassic. It is generally assumed that they were common in fresh-water habitats of certain parts of Pangaea: the earliest and most generalized forms have been found in Australia and South Africa and the most specialized in North America and Morocco, but this is not decisive in stating a distributional pattern; Schaeffer himself did not exclude that Redfieldiiformes could be unknown, but not absent, from other Triassic continental deposits (Schaeffer 1984).

Redfieldiiformes have been controversial since the establishment of the family Catopteridae (=Redfieldiidae Berg 1940) by Woodward in 1890, until the end of the 80's of 1900. Discussions on Redfieldiiform relationships can be find beginning from Stensiö (1921) and afterwards in Brough (1931, 1936), Schaeffer (1955, 1967), Hutchinson (1973, 1978) then again by Schaeffer (1984) and Gardiner and Schaeffer (1989). Most of the taxa positively recognized have been described or re-described on the basis of American, South African and Australian ichthyofaunas,



even if there are many reports from other countries (Wade 1935; Brough 1931; Hutchinson 1973; Schaeffer 1967).

The Redfieldiiform remains, often locally abundant, have been found in continental sediments in Australia (Wade 1933, 1935, 1940, 1942; Woodward 1890, 1908; Hutchinson 1973), South Africa (Brough 1931; Haughton 1934; Hutchinson 1973, 1978), Zambia and Morocco (Martin 1982) (for a general review of the Mesozoic fishes from Gondwana see López-Arbarello 2004); Eastern and Western United States (Schaeffer 1967, 1984; Schaeffer and McDonald 1978; Olsen et al. 1982; Wilson and Bruner 2004), China (Liu 1958; Chang and Miao 2004) and questionably in Madagascar (Lehman et al. 1959). Recently, a genus (*Rastrolepis* López-Arbarello et al., 2006) resembling the condition in the Redfieldiiformes, has been reported from the Triassic of Argentina (López-Arbarello et al. 2006).

Concerning European localities, various specimens, some of which previously assigned to other genera (e.g., *Semionotus socialis* Berger, 1843, *Paleoniscus catoptera* Egerton, 1858, *Paleoniscus superstes* Egerton, 1858) were referred to the genus *Dictyopyge* Lyell, 1847: *D. socialis*, from the Late Keuper of Germany; *D. catoptera*, from the Keuper of Ireland; *Dictyopyge superstes* from the Late Keuper of England; *Dictyopyge rhenana* from the Bunter Sandstone of Switzerland (Deecke 1889). Brough (1931) had already noted that the Old World forms assigned to *Dictyopyge* should have been removed from this genus, lacking unequivocal diagnostic evidence, but this opinion has never been formalized: still in Lehman (1966) Lehman included the European species in the distribution of *Dictyopyge*. This genus has been revised, together with *Redfieldius*, by Schaeffer and McDonald (Schaeffer and McDonald 1978), which confirmed the opinion of Brough, on the basis of the examination of the original figures. Moreover, they affirmed that most of the specimens were probably indeterminate. Personal observation of some of the specimens of these taxa stored in the British Museum (Natural History) (*Dictyopyge catoptera* BMNH P. 3491 and 1033; *D. socialis* BMNH P. 3488; *D. superstes* BMNH P. 7614) and the type of *D. rhenana* stored in the Naturhistorisches Museum Basel (NMB 1641) confirms the opinion of Schaeffer and McDonald (1978) concerning the poor state of preservation of European material and the difficulty to demonstrate a certain redfieldiiform affinity. Nevertheless, concerning at least the holotype of *D. rhenana*, but especially the holotype of *D. superstes* (incomplete but well preserved), the belonging of these specimens to the redfieldiiform group cannot be excluded, as the structure of the median fins and scales suggests (pers. obs.). More recently, Dzik and Sulej (2007) reported the find of specimens probably related to Redfieldiiformes also from the Late Triassic Krasiejów biota from Silesia

(Poland), but also in this case, the fragmentary preservation of the specimens did not allow a firm attribution. According to these authors these specimens resemble "*Dictyopyge*" *socialis* (Berger 1843), but the published data did not provide enough diagnostic characters for comparison with the Krasiejów material.

### 3.3 Palaeoenvironmental remarks

If the attribution of *P. sangiorgii* gen. et sp. n. to redfieldiiforms, which are considered mainly fresh water dwellers, should be eventually confirmed, it would not be in contrast with the palaeoenvironmental restoration for the Kalkschieferzone depositional environment. The data collected so far point to a lagoon whose waters were subject to variations in chemical or physical parameters, probably due to periodic inflow of freshwater from the nearby land, consequently affecting the fauna living in the basin (Tintori 1990c; Stockar 2010; Stockar and Kustatscher 2010; Stockar et al. 2012). The proximity of emerged land is deduced from the presence of abundant freshwater crustaceans (estherids), terrestrial plants and several insects, mostly at present under study (Tintori 1990c; Krzeminski and Lombardo 2001; Stockar and Kustatscher 2010; Becchly and Stockar 2011). These organisms could have been transported into the basin, from at least temporary fresh water ponds, if not small permanent lakes and rivers, under a monsoonal climate. Thus, it is possible that the fossiliferous levels in the Kalkschieferzone, deposited in coastal marine environments, sometimes contain also organisms from brackish or fresh waters habitats as a consequence of seasonal floods (Tintori and Brambilla 1991; Tintori 1990b, c; Lombardo and Tintori 2002). Moreover, it must be pointed out that most of the fishes known from the KSZ levels are considered as strictly marine (e.g. the genera *Prohalecites*, *Perleidus*, *Furo*, *Allolepidotus*, which have been found also in the coeval levels of the uppermost part of the Perledo-Varenna Limestone, whose origin is considered marine; Tintori 1990a; Lombardo 2001), but at least one genus, the perleidiiform *Dipteronotus*, is on the contrary always been found in paralic environments (Gall et al. 1974; Tintori 1990b).

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