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# A NEW SPECIES OF THE GENUS *COLOBODUS* AGASSIZ, 1844 (OSTEICHTHYES, ACTINOPTERYGII) FROM THE PELSONIAN (ANISIAN, MIDDLE TRIASSIC) OF GUIZHOU, SOUTH CHINA

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*Key words*: New taxon, actinopterygians, perleidiformes, *Colobodus*, Middle Triassic, Pelsonian, South China.

*Abstract*. Eight almost complete medium-large sized (about 33 cm in s.l.) fossil fishes, belonging to the family Colobodontidae, are described from the Pelsonian (Anisian, Middle Triassic) of South China. Their cranial and postcranial features fit those of the genus *Colobodus* Agassiz, 1844 from the western Tethys. However, they are older than the previously known *Colobodus* species and, furthermore, they come far from the western Tethys, where most colobodontids have been found so far. The significance of our new findings, beyond the erection of a new species, lies in the fact that they are the first definite record of *Colobodus* outside the western Tethyan faunal province, and represent the oldest unequivocal colobodontids worldwide, as well as suggest that they could have originated in the East rather than in the western Tethys, as previously thought.

*Riassunto*. Vengono descritti otto esemplari, pressoché completi, di pesci fossili di medie dimensioni appartenenti alla famiglia Colobodontidae, provenienti dal Pelsonico (Anisico, Triassico Medio) della Cina meridionale. I caratteri sia del cranio che dello scheletro postcraniale di questi esemplari corrispondono a quelli del genere *Colobodus,* noto dalla Tetide occidentale. L'importanza di questi nuovi ritrovamenti, al di là dell'istituzione di una nuova specie, risiede nel fatto che essi rappresentano la prima segnalazione di *Colobodus* al di fuori della provincia faunistica della Tetide occidentale e i più antichi colobodontidi attribuibili con certezza a questo gruppo; ne consegue inoltre che forse i colobodontidi hanno avuto origine nella Tetide orientale, piuttosto che in quella occidentale come ritenuto finora.

## Introduction

The Middle Triassic ichthyology has been experiencing a promising period since many fossiliferous layers were newly discovered in South China (Wang et al. 2001; Jiang et al. 2005; Jin 2006; Li 2006; Sun et al. 2006). Previously, only the western Tethyan sites were usually considered, as it was for the Monte San Giorgio area, the core of the marine vertebrate paleontology for the European Middle Triassic (Bürgin et al. 1989; Lombardo 2001; Tintori & Lombardo 1999). More recently, the Chinese Fossil-lagerstätten from Middle Anisian to Early Carnian yielded new findings of fossil fishes at both genus and/or species level (Jin 2001, 2006; Liu et al. 2002, 2003, 2006). Among these, probably the most important can be considered the so called Panxian Fauna from the Upper Member of the Guanling Formation, Xinmin District, Panxian County, Guizhou Province, South China (Fig. 1A). It is verified as Pelsonian (Anisian, Middle Triassic) in age, within the conodont *Nicoraella kockeli* zone (Fig. 1B) and it is providing several new genera, associated with many older representatives of genera previously recorded from the younger western Tethyan deposits, taken the Besano Formation near the Anisian/Ladinian boundary in the Monte San Giorgio area as an example. The Panxian Fauna therefore represents probably the beginning of the mid-Triassic radiation, one of the most important of the whole Mesozoic for the marine vertebrates (Jiang et al. 2005, 2006; Tintori et al. 2006).

The fossil-bearing layers of the Panxian Fauna can be subdivided into three horizons, namely Lower, Middle and Upper Reptile Horizons (LRH, MRH, and URH, respectively; Jiang et al. 2007). Marine verte-

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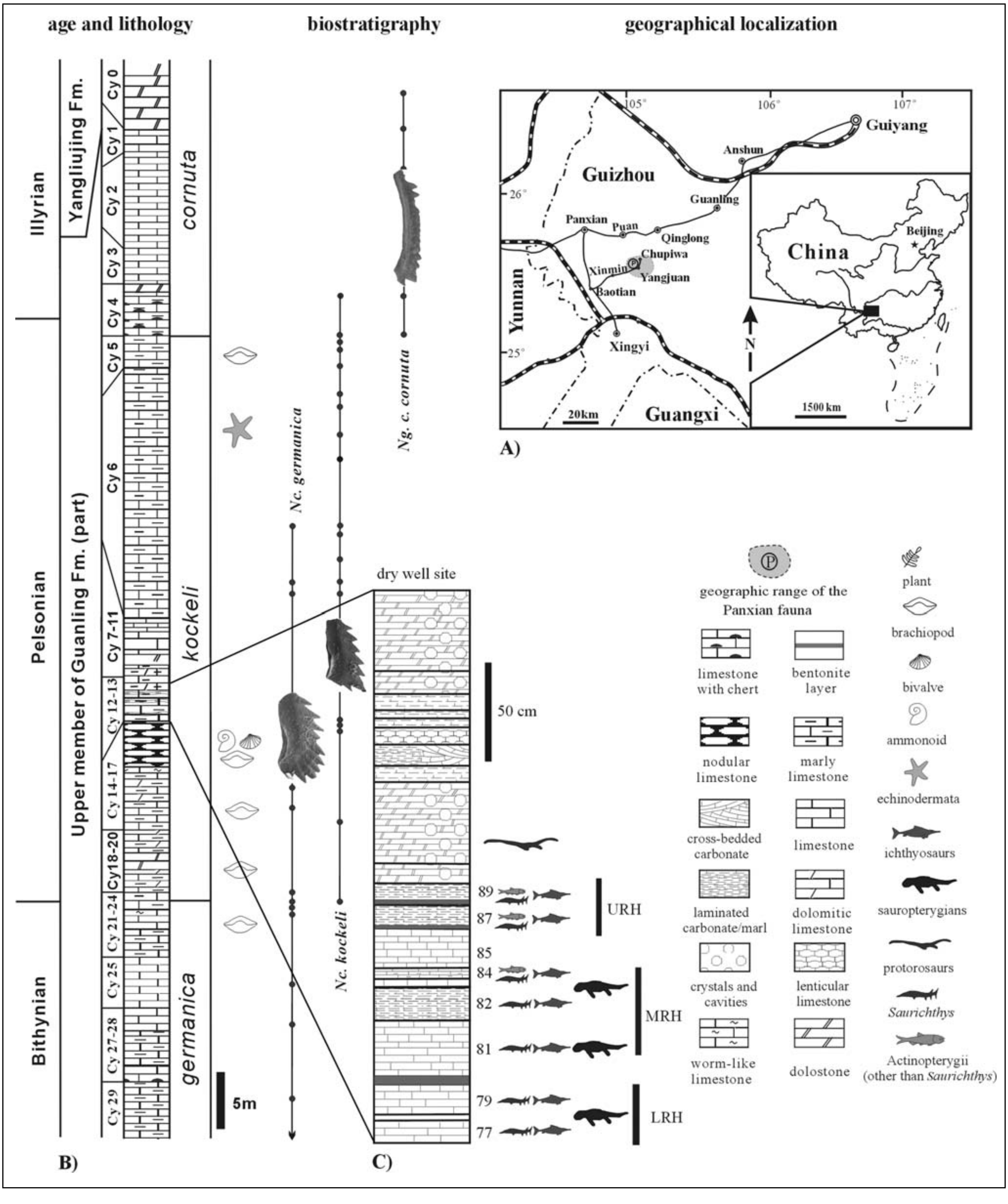


Fig. 1 - Geographic localization (A) and biostratigraphic age (B) of the Panxian Fauna, and C) detailed stratigraphy of the vertebrate-bearing layers. Partly after Sun et al. (2006), simplified. *Ng.*, *Neogondolella*; *Nc.*, *Nicoraella*.

brates that go throughout these three horizons are the ichthyosaur *Mixosaurus panxianensis* and the actinopterygian *Saurichthys* (probably with more than one species) whereas the only known vertebrate taxon outside of these horizons is the protorosaur *Dinocephalosaurus orientalis*. URH is well laminated and yields shallow water marine reptiles that are not very large (less than 1 meter in total length, *M. panxianensis* being the largest), and small-sized fishes (generally less than 10 centimeters). In this horizon, one peculiar bed, layer 84, is usually called 'fish-layer' by local people and it yields also the new species of *Colobodus* described herein. The largest taxa in the area, including the archosaur *Qianosuchus* and nothosaurids, are known from MRH. The LRH is characterized by the occurrence of bivalves and three marine reptile species that are interpreted as shell-crushers.

So far, the fish genera found in the Panxian Fauna are *Saurichthys, Birgeria* and an undetermined paleoniscid among the basal palaeopterygians, *Colobodus* and '*Peltopleurus*' among the subholosteans, and *Placopleurus* and Semionotiformes among the neopterygians. *Colobodus* is the goal of this first paper regarding this new Pelsonian fish assemblage.

To date, *Colobodus* has been known, being also quite common, around the Anisian/Ladinian boundary of the Besano Formation in the western Tethys and the Ladinian of the Germanic Muschelkalk (Agassiz 1844; Dames 1888; De Alessandri 1910; Andersson 1916; Stolley 1920; Guttormsen 1937; Bürgin 1996; Mutter 2001, 2002, 2004). *Colobodus* or *Colobodus*-like remains from other ages and/or areas are highly questionable (Mutter 2001, 2004), except for those from the early Carnian of NE Italy (Rusconi et al. 2007) and the new Pelsonian material herein described. The importance of the latter, beyond the erection of a new taxon, lies in the fact that this is among the oldest Perleidiformes so far described and the first unequivocal representative of *Colobodus* outside the western Tethys. The further presence of Peltopleuriformes in the Panxian Fauna confirms the outset of the two groups in the Pelsonian, as previously supposed by Lombardo et al. (2006) for a small fish assemblage from the Braies Dolomites of North Italy (Tintori et al. 2001). This new finding furthermore confirms that these two orders had a very rapid dispersion across the Tethys, even if probably their major radiation took place later in the western part of it, as proved by the Monte San Giorgio faunas (Brough 1939; Tintori 1990; Bürgin 1992, 1996; Tintori & Lombardo 2007) as well as other Ladinian assemblages of northern Italy and southern Switzerland (Bürgin 1995; Lombardo 1995, 1997, 1999, 2001, 2002; Bürgin & Herzog 2002; Lombardo & Tintori 2004; Mutter & Herzog 2004).

## Material and methods

All specimens were collected around the Yangjuan village and are now stored in the collection of the Department of Geology and Geological Museum, Peking University, Beijing, China (GMPKU). They have been preliminary prepared by local people while the final detailed preparation has been made at the GMPKU laboratories by a combination of mechanical and chemical methods. The study has been done under a stereomicroscope Nikon SMZ645 and the drawings have been made from digital photographs. Bed by bed excavations, made in the last years by PKU team in cooperation with researchers from the University of California-Davis (UC-Davis) and from the Università degli Studi di Milano (UNIMI), point that *Colobodus* specimens, both complete or fragmentary, come mainly from layer 84 (the 'Fish layer' of local people).

## Abbreviations

Ant, antorbital; Br, branchiostegal rays; Dy, dermohyal; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; Ecpt, ectopterygoid; Fr, frontal; Hym, hyomandibular; Io$_{1, 2, 3}$, infraorbitas; Md, mandible; Mx, maxilla; Na, nasal; Op, operculum; Pa, parietal; Pmx, premaxilla; Pop, preoperculum; Pro, postrostral; Pt, posttemporal; Ro, rostral; Scl, supracleithrum; So, supraorbital; Sop, suboperculum; Sr, sclerotic ring; Ssc, supraorbital sensory canal.

## Systematic Paleontology

Class **Osteichthyes** Huxley, 1880
Subclass **Actinopterygii** Cope, 1887
Order **Perleidiformes** Berg, 1940
Family Colobodontidae Andersson, 1916
Genus C*olobodus* Agassiz, 1844
Type species: *Colobodus bassanii* De Alessandri, 1910
(ICZN 2005, opinion 2102, BZN)

**Diagnosis** (emended from Mutter 2004). Large sized fusiform perleidiform. Small rostral followed by a large median postrostral; large preoperculum slightly forward inclined; posterior region of maxilla well expanded dorsally and only slightly expanded downwards; suborbital absent; palatal bones mainly covered by small stout teeth; scales richly ornamented with longitudinal ridges; lepidotrichia of unpaired fins showing a short unsegmented proximal region; lepidotrichia branching asymmetrically at least in pectoral and dorsal fins; caudal fin almost externally symmetrical, with at least ten epaxial rays; ganoin patches covering leading fin rays.

**Remarks.** The Middle and Upper Triassic family Colobodontidae, originally erected by Andersson (1916) mainly based on cranial features of *Colobodus* from Bayreuth and Heidelberg in the German Muschelkalk, is now considered as a comparatively small array of large-sized advanced basal actinopterygians, which yield rather conservative skull osteology; this refers to characters such as a wedge-shaped preoperculum tightly fixed to the maxilla through its long infraorbital process and a snout composed of small medial rostral and large medial postrostral separating the nasals. This latter arrangement, proposed by Hutchinson (1973) for a possible colobodontid ancestor, is actually characteristic of this subholostean family, being distinctly different from that of other perleidiformes such as *Gabanellia* (Tintori & Lombardo 1996), *Perleidus* (Lombardo 2001) and *Dipteronotus* (Tintori 1990), which show a large, keyhole-like rostral and lack the postrostral.

Among the other features typical of Colobodontidae, there are: hemidurophagous dentition, richly ornamented dermal skull bones and flank scales, ganoin patches covering leading fin rays, and almost symmetrical caudal fin due to the presence of epaxial rays (Andersson 1916; Stolley 1920; Guttormsen 1937; Bürgin 1996; Mutter 2001, 2002, 2004; Rusconi et al. 2007). The generic composition of this family has been controversial since it was established (Gardiner 1967; Hutchinson 1973). More recently Mutter (2001, 2002, 2004), on the basis of material from bituminous shales and laminated dolomites in the latest Anisian/earliest Ladinian of Besano Formation at Monte San Giorgio (Italy and Switzerland), reconsidered this family including the type genus *Colobodus* Agassiz, 1844, the poorly known genus *Crenilepis* Dames, 1888 and a new genus not been formalized as yet. *Colobodus* was first described on the bases of several dentition and scale fragments from the German Muschelkalk (Agassiz 1844; Dames 1888; Stolley 1920; Oertle 1927), but it is now better known from the western and eastern Tethys sites (this paper). *Colobodus bassanii* De Alessandri, 1910 from the Anisian/Ladinian boundary of the Besano Formation, has been accepted as the type species by the International Commission on Zoological Nomenclature (Mutter 2003; ICZN 2005) even if from a different paleogeographical area and from older beds, considering that the type specimen of *Colobodus hogardi* Agassiz, 1844 is not available. Mutter (2001, 2004) also considered *Crenilepis* as a valid genus and placed it into the family, and he accepted the validity of at least two species of *Crenilepis* in the Monte San Giorgio faunas. However, the type specimen of *Crenilepis sandbergeri* Dames, 1888 from the upper Muschelkalk (=Late Ladinian) of Germany is lost and, anyway, the specimen was an undiagnostic fragment of body. Mutter (2004) made a totally new diagnosis of the genus and species, based on Monte San Giorgio material. However, it should be pointed out that the type specimen of *Crenilepis sandbergeri* was from a much younger (at least 7-8 Ma) level than the specimens from Monte San Giorgio. The inner sea represented in the Muschelkalk is furthermore a different environment than the coastal area represented in the Monte San Giorgio. This case seems to be unique among the Triassic fishes, especially if we consider the group (subholosteans) to which *Crenilepis* belongs. The very closely related (following Mutter's idea) genus *Colobodus* is highly variable. Mutter himself (2002) proposed several new species just from a few beds in the middle part of the Besano Formation. Therefore, it would be a very special case to have a species (*C. sandbergeri*) lasting for such a long time (7-8 Ma), as well as to have species and even genera differing only for the number and shape of the ganoin ridges on the scales. Furthermore, nobody knows the shape of the body of the original *Crenilepis sandbergeri*: as we already mentioned, the type specimen was just a small body fragment. The same is for the new genus Mutter (2002) considered in his thesis: it consists of a single incomplete specimen and the major differences are again in the scale ornamentation.

Thus, in our opinion, the differences detected by Mutter (2002) among *Colobodus* spp., '*Crenilepis*' spp. and the supposed new genus can be considered as simply intrageneric, at least until there will be new material from the original sites of *Crenilepis sandbergeri* and better, not so scattered, material from the Besano Formation. Thus, our comparison for the new material has been done mainly with *Colobodus bassanii*.

### **Colobodus baii** sp. n.

Figs 2-9

**Diagnosis.** Medium- (up to 33 cm standard length) sized *Colobodus* with 56 vertical scale rows along the l.l., each consisting of about 33 scales; postrostral narrower in front of nostrils and well convex in the posterior margin to insert between the frontals; infraorbital sensory canal running along the anterior margin of the posterior elements; hyomandibular with a large dorsal head; caudal fin consisting of 48 lepidotrichia (ten epaxial); single ganoin patch arranged on each segment of the leading rays of the median fins; scale ornamentation visible also in the caudal pedicle.

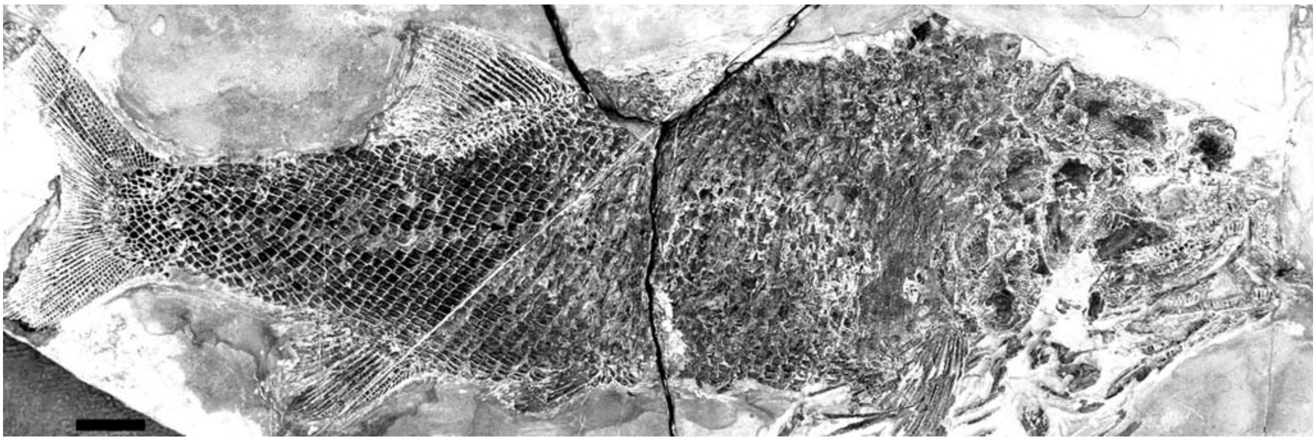


Fig. 2 - *Colobodus baii* sp. n. The holotype GMPKU-P-1207 in lateral view. Scale bar equals 20 mm.

Tab. 1 - Measurements (in mm) of *Colobodus baii* sp. n.

| Specimen number | 1084 | 1085 | 1207 | 1217 | 1218 |
|---|---|---|---|---|---|
| Standard length | 310 | ? | 330 | 235 | 170 |
| Distance head-dorsal fin | 205 | 215 | 210 | 145 | 109 |
| Distance head-anal fin | ? | 260 | 255 | 175 | ? |
| Distance head-pelvic fin | 190 | 210 | 201 | 139 | ? |
| Depth at dorsal fin | ? | 90 | 86 | 70 | 61 |
| Depth at caudal fin | ? | ? | 30 | 28 | 21 |
| Head length | 97 | 105 | 100 | 75 | 52 |
| Orbital length | 22 | ? | 25 | ? | 12 |

**Etymology.** Dedicated to Prof. Bai Shunliang, a senior and respectable professor of Peking University, for his constant contributions to geology.

**Holotype.** GMPKU-P-1207 (Fig. 2), a fairly complete and articulated specimen.

**Paratypes.** GMPKU-P-1083, 1084, 1205, 1217, 1218, 1489 all of them mostly well articulated.

**Other material.** GMPKU-P-1085 (a possibly assembled specimen).

**Type-locality.** Neighborhood of the village of Yangjuan, Xinmin District, Panxian County, Guizhou Province, South China.

**Stratotype.** Layer 84 of the Upper Member of the Guanling Formation, Pelsonian, Middle Anisian, Middle Triassic, within the conodont *Nicoraella kockeli* zone (Sun et al. 2006).

## Description

*Shape and size.* Medium sized fossil fishes (Tab. 1). The standard-length of the largest specimen GMPKU-P-1207 is 330 mm and that of the smallest one, GMPKU-P-1218, is 170 mm. The ratio of skull- to standard-length is approximately 31%. The body shape is slender fusiform with a body length vs body depth (at the beginning of the dorsal fin) ratio being about 5 (Fig. 2).

*Snout region.* The snout is typically convex and obtuse, composed of the unpaired rostral and postrostral, and the paired antorbitals and nasals (Fig. 3).

The medial rostral is roughly rectangular in outline, being about twice as wide as long; it shows a regularly arched ethmoidal commissure of the sensory canal system. Its slightly convex posterior margin fits the concave anterior outline of the medial postrostral.

The postrostral is a large squarish bone, capping the most of the snout and separating the nasals, like in the palaeoniscoids (Schaeffer 1955). It abuts against the frontal with its angled posterior border. A half-circle notch, located at the level of the anterior 1/3 height of the postrostral in specimen GMPKU-P-1489, is interpreted as the anterior narial opening.

The paired nasals are irregularly rhomboidal, wider dorsally than ventrally, and form the anterior borders of the orbits. The antorbitals are triangular-shaped and possibly were sutured with the lateral borders of the rostrals and nasals, and the antero-dorsal embayment of the maxillaries, which partially exclude the nasals from the orbital rim (Fig. 3). The sensory canal passes through the rostral transversely, then it enters the antorbital, where it branches in two parts: one continues along the anterior margins of the infraorbitals and the other goes into the nasals.

*Skull-roof.* The frontal seems to form a large shield-like bone, about two times longer than wide and three times longer than parietal. It reaches its maximum width near its mid-length and then becomes narrower anteriorly and posteriorly, showing a '^'-shape in lateral view. Postero-laterally it is partially overlapped by the rostro-mesial side of the dermopterotic and posteriorly it is overlaid by the anterior border of the parietal. The posterior margin of the frontal appears convex, a little broader than the anterior, while the latter looks wavy and prominently concave. The interfrontal suture is likely wavy, as observed on specimen GMPKU-P-1489. The lateral margins of the frontals are covered by ganoin tubercles, whereas the remaining parts are ornamented by elongate ganoin ridges.

The parietal is roughly square and laterally overlapped by the dermopterotic.

The extrascapular is a trapezoid-like element, expanded antero-medially and slightly concave on both anterior and posterior margins. Parietal and extrascapular are ornamented by longitudinally-arranged ganoin ridges. Supraorbital sensory canal is sinuous: the parietal branch is straight and visible only in the anterior half of the parietal; the frontal branch enters the frontal at the antero-lateral corner and converges medially, where it is curved and diverges thereafter, running straight to the parietal.

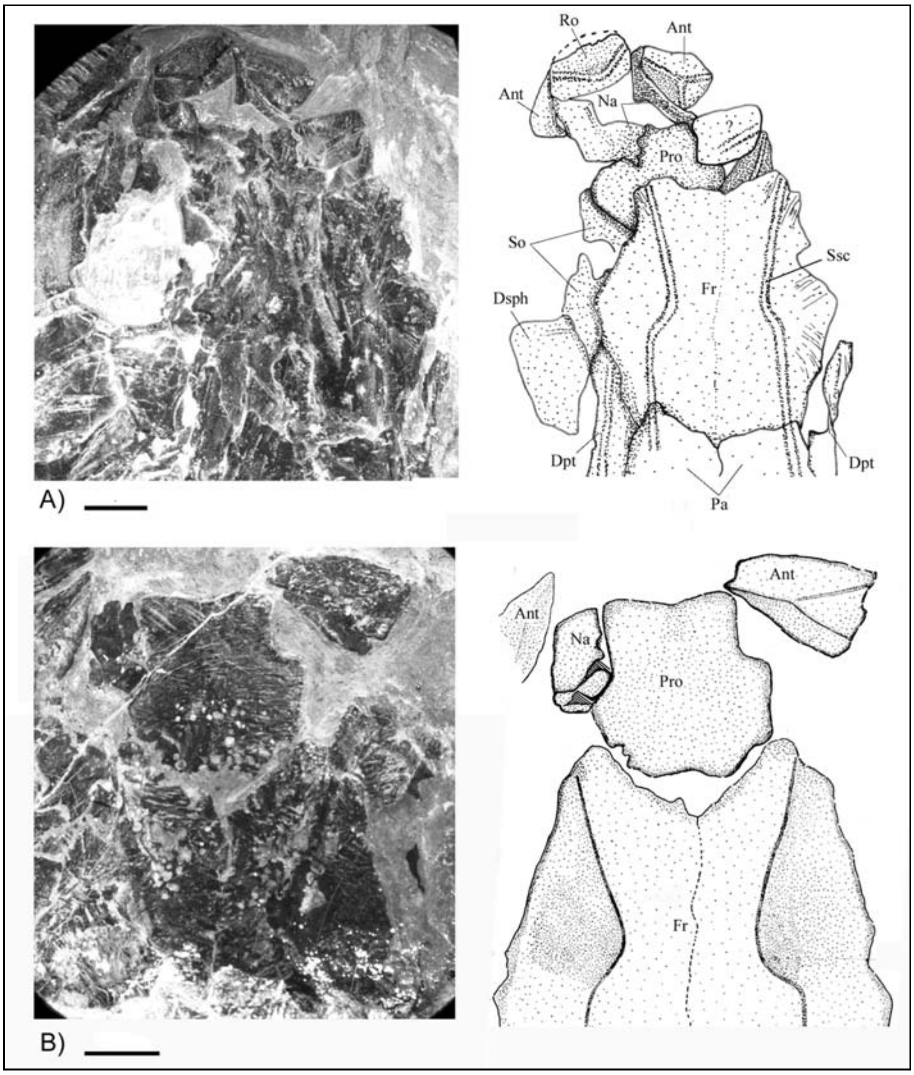


Fig. 3 - *Colobodus baii* sp. n. Drawings of the dermal skull roof in mesial view. A) Specimen GMPKU-P-1218 and B) specimen GMPKU-P-1489. Scale bar equals 5 mm.

*Cheek region*. The condition of the cheek is typically perleidid, having a large wedge-shaped preoperculum. The preoperculum is slightly forward inclined and yields a dirk-like infraorbital process (a situation present also in *Colobodus bassanii;* Mutter 2002) through which the preoperculum is tightly fixed with the posterior margin of the maxilla. The sensory canal runs along its posterior and dorso-posterior borders. The element is covered by ganoin tubercles and short ridges. Its postero-dorsal edge meets the dermohyal, a small triangular bone.

*Gill cover*. The gill cover, composed of the operculum and suboperculum, is broad, with a rounded posterior margin (Fig. 4). The operculum is a rectangle with round posterior and dorso-posterior borders, and a straight, thickened anterior margin. It is slightly larger than the suboperculum and overlaps the latter ventrally with its convex ventral margin. The suboperculum is trapezoidal in outline, with a relatively far forward projection at its antero-ventral corner, similar to that of *Colobodus bassanii* (Mutter 2002, Fig. 71). The exposed surface of the opercular bones shows elongated ganoin tubercles.

*Suspensorium*. Specimen GMPKU-P-1084 preserves a complete hyomandibular bone. It is a triradiate element comprising a dorsal head, a ventral shaft and a prominent opercular process (Fig. 5). The dorsal head is triangular in outline with flat and smooth surface. The ventral shaft is deeply furrowed and bears a distinct, obliquely running crest. The opercular process is located at about one third of the total hyomandibular length, and protrudes caudally. In front of the opercular process lies a small circular foramen, that we interpret as for the passage of the facial nerve.

*Infraorbital series*. Four canal-bearing bones border postero-ventrally the orbit. The uppermost infraorbital bone is considered as the dermosphenotic or $Io_4$. It is sub-rectangular and located directly behind the orbit. $Io_3$ is a rather large and crescent element, which outlines the postero-ventral corner of the orbit. $Io_1$ and $Io_2$, located below the orbit, are slender rectangular bones. The infraorbital sensory canal runs along the anterior

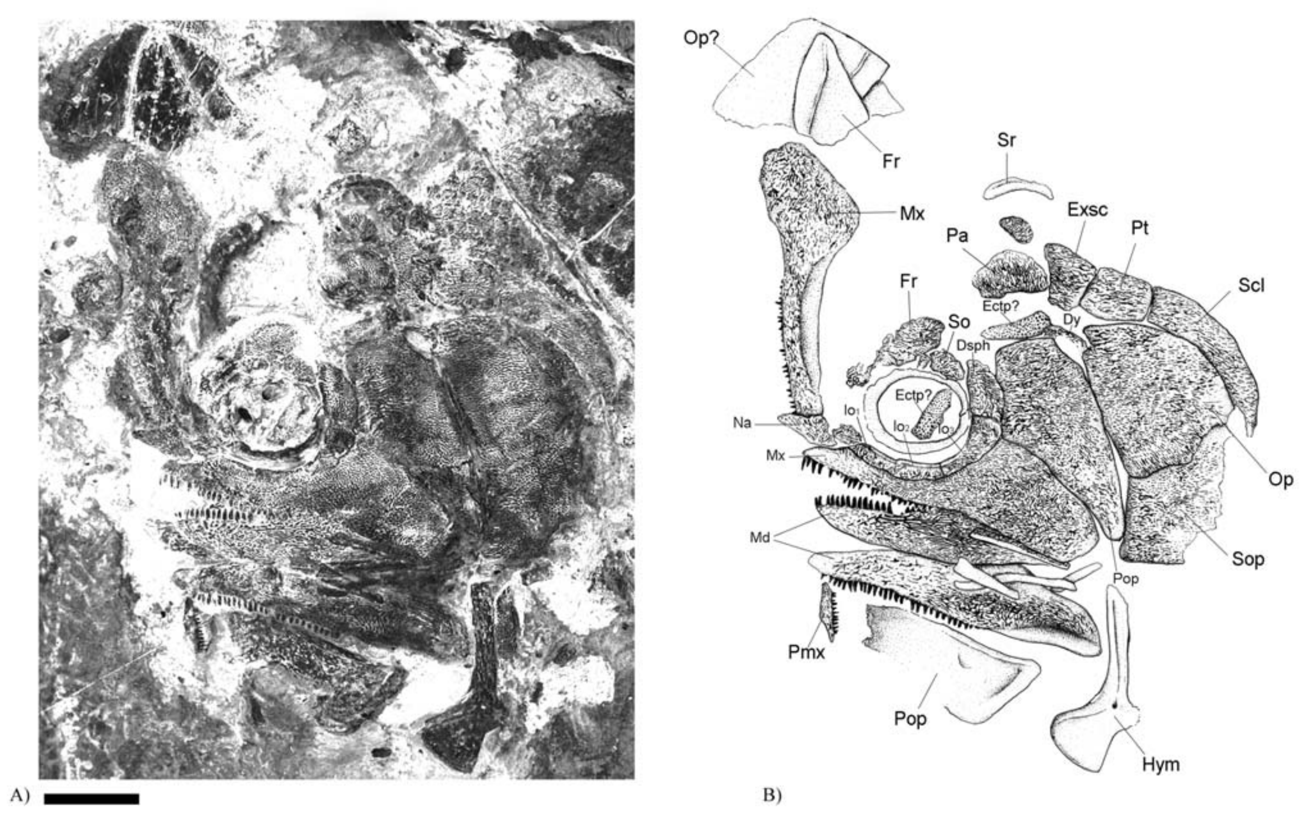


Fig. 4 - *Colobodus baii* sp. n. Specimen GMPKU-P-1084 in lateral view. A) Photograph of the skull; B) drawing of the dermal bones. Scale bar equals 20 mm.

margin of the posterior infraorbitals as clearly shown in the specimens GMPKU-P-1207 (Fig. 6) and GMPKU-P-1084.

*Upper jaw.* The maxilla is perleidid-like, with a narrow anterior region and a typically deep, expanded posterior plate, which partially overlaps the antero-ventral margin of the preoperculum. Short ganoin ridges and tubercles cover most of the maxilla, but close to the oral margin they become elongated and fused to each other. A thickened ridge hems the jaw border, mesially (Fig. 7A). There are about 35 teeth hemming the upper jaw border: anteriorly, they are typically slender-conical, striated and slightly curved on their upper part, and posteriorly they diminish in size. The hindmost teeth are smaller, rather stout and broadly-hemispherical, showing a tendency towards crushing adaptation (Fig. 7B, C). In the specimen GMPKU-P-1084 several small hemispherical, finely striated crushing teeth with wart-like acrodine caps on their tips, are found (Fig. 7D) on an unidentified palatal bone.

*Lower jaw.* The lower jaw is wedge-shaped and has both blunt anterior and posterior extremities. Thick ganoin ridges cover most part of the lower jaw; however near the oral margin separate ganoin tubercles are present. The dentition of the lower jaw consists of a single row of teeth that are long, slender conical anteriorly, becoming small and stout posteriorly. The oral margin is straight and there is no coronoid process at all.

*Parasphenoid and vomer.* They are partially three-dimensionally preserved in the specimen GMPKU-P-1085. The parasphenoid has an elongate anterior portion, a well developed ascending process and a broadened posterior plate. The anterior region is slender and partially dentigerous, and makes over 2/3 of the length of parasphenoid. The ascending process is very slender and rostro-laterally projecting. The posterior plate is massive, with a posterior margin bearing a posteriorly projecting knob. The vomer yields very tiny teeth, but its precise shape and size cannot be discerned.

*Ectopterygoid.* Its precise shape is difficult to distinguish. It bears numerous small stout and striated teeth which have distinct acrodin caps. They are slightly larger and sparser than those of *Colobodus* cf. *bassanii* (Guttormsen 1937; Mutter 2004).

*Shoulder girdle.* The shoulder girdle is well developed. It consists of a couple of crescent posttemporals usually separated from each other by scales, of an elongate, plate-like supracleithrum, and of a prominently sickle-shaped cleithrum which is associated with the

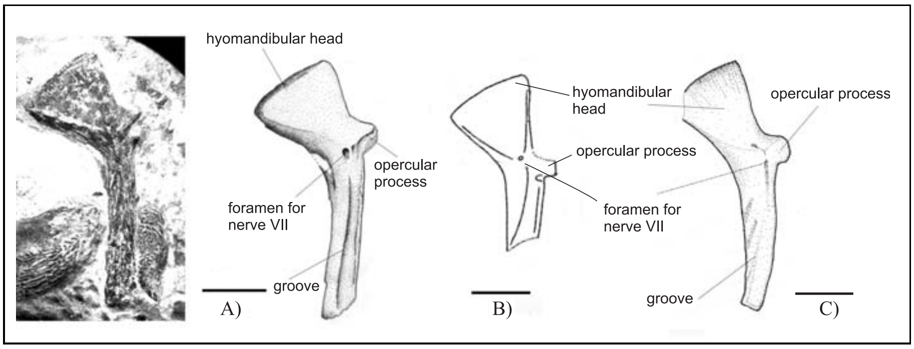


Fig. 5 - Hyomandibular bones in: A) *Colobodus baii* sp. n., specimen GMPKU-P-1084; B) *Colobodus bassanii*, (after Mutter 2002, Fig. 65); C) *Crenilepis* sp. n. (After Mutter 2002, Fig. 18). Scale bar equals 10 mm.

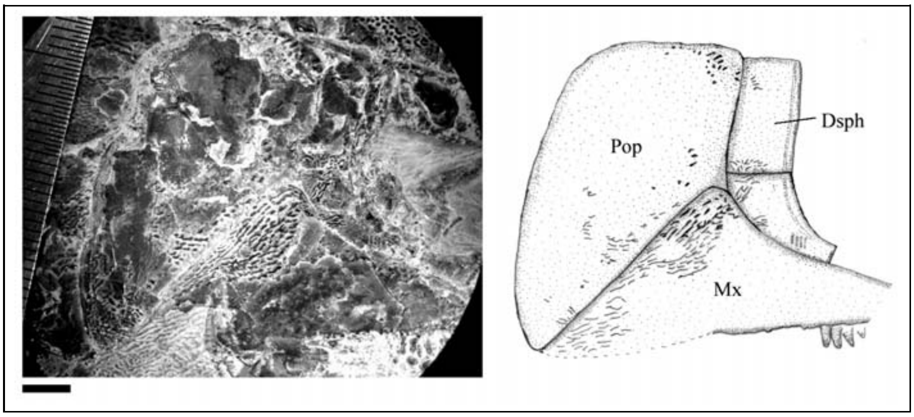


Fig. 6 - *Colobodus baii* sp. n. Specimen GMPKU-P-1084 in lateral view. Note the wedge-shaped preoperculum tightly fixed with the maxilla and the infraorbital canal running along the anterior margin of the infraorbital series. Scale bar equals 5 mm.

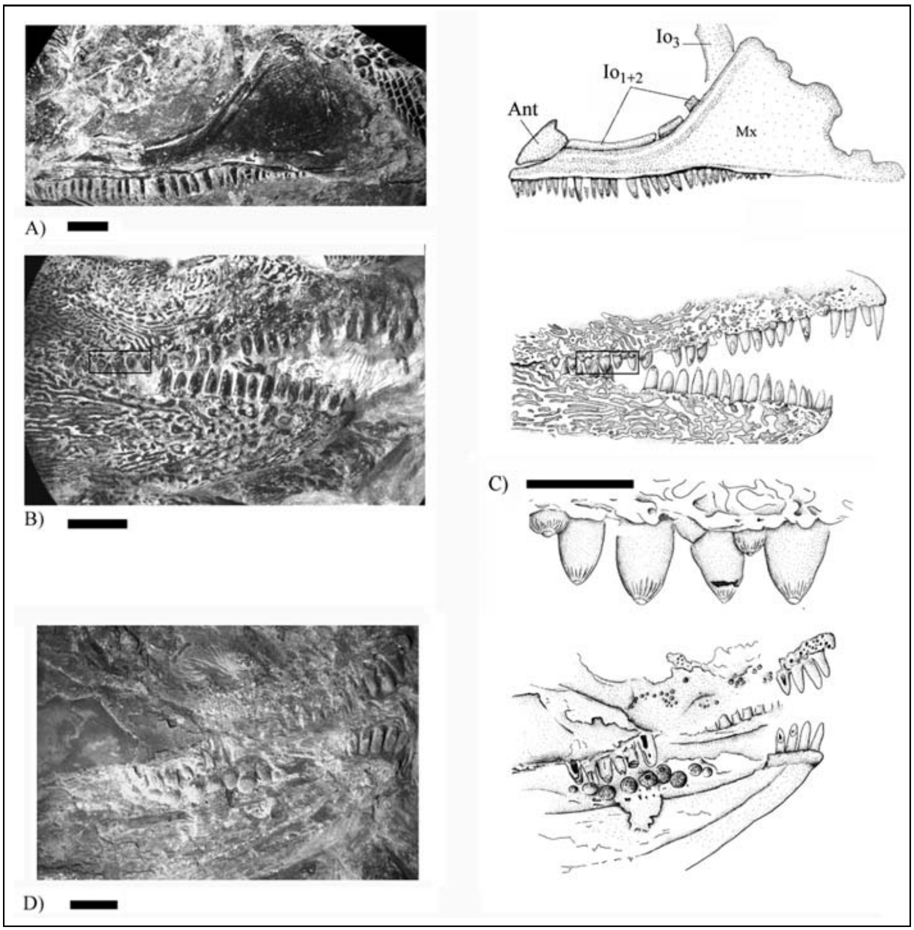


Fig. 7 - *Colobodus baii* sp. n. Maxilla and tooth morphology. A) Maxilla of specimen GMPKU-P-1489 in mesial view; B) teeth of specimen GMPKU-P-1084 in lateral view; C) enlargement of hindmost teeth of maxilla in specimen GMPKU-P-1084; D) crushing teeth covering the possible ectopterygoids of specimen GMPKU-P-1207. Scale bars equal 5 mm.

pectoral fin, three-dimensionally preserved on the specimen GMPKU-P-1085.

*Paired fins*. Only the proximal part of the pectoral and pelvic fins are visible in all material. The fin rays have long proximal bases and much shorter distal segments which are rather shorter than broad. The pectoral fins are the largest of all fins and have approximately 16 lepidotrichia. A row of fringing fulcra lies on the anteriormost rays. Ganoin ornamentation of the leading fin rays consists of small elements irregularly arranged, usually one segment being covered by two or three small ganoin patches. The first ray is not branched; the others branch asymmetrically at least twice, occasionally three times (Fig. 8A). No detail of the pelvic fins, except for the presence of fringing fulcra and the proximal long bases of lepidotrichia, can be distinguished unequivocally. They are inserted at the level of the 18th-21st scale row.

*Unpaired fins*. All unpaired fins bear well-developed fringing fulcra and strongly reduced basal fulcra. Most of their lepidotrichia have quite short proximal elements, however well distinct from the distal ones. Oval ganoin patches regularly cover at least the proximal segments of the leading rays.

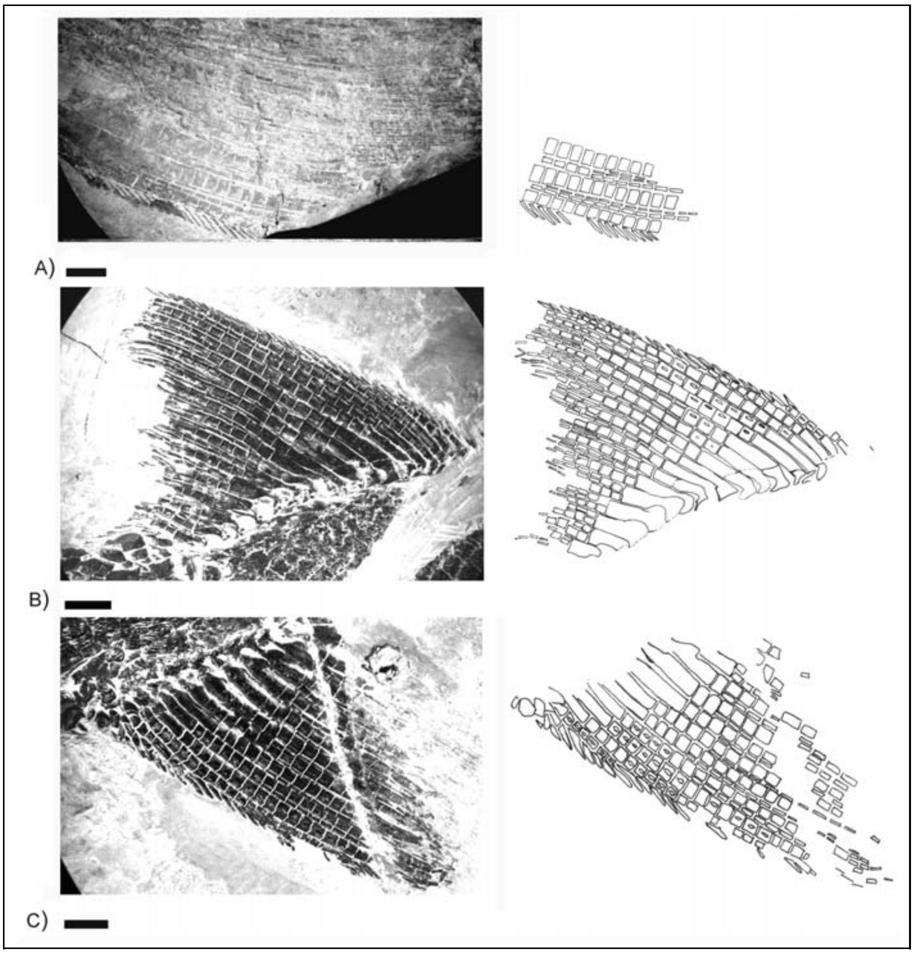
The dorsal fin is triangular-shaped with a rather wide base. It is placed between the 30th to 36th scale row and consists of about 20 lepidotrichia with long basal segments: the 6th or 7th is the longest lepidotrichium. The lepidotrichia other than the leading rays branch off at least twice, starting at about half way of their length and the second branching occurs after about three segments from the first one (Fig. 8B). The segments of fin rays are much longer than broad, differing totally from those of the anal fin.

The anal fin is also triangular and characterized by stout segments that are broader than long (Fig. 8C). It is placed between the 27th to 31st scale row and it consists of about 16 lepidotrichia, branching with the same pattern of the dorsal fin.

The caudal fin is almost symmetrical externally and moderately forked: the body lobe is greatly reduced and there are about ten epaxial rays (Fig. 9). It is composed of about 48 lepidotrichia with somewhat elongated proximal elements. The distal segments are short but always much longer than broad. Ganoin patches are present on each proximal segment of the leading fin rays.

The pattern of branching fits that of colobodontids, described by Mutter (2002): following the first branching, the second and third ones take place in an

Fig. 8 - *Colobodus baii* sp. n. A) Partially preserved pectoral fin of specimen GMPKU-P-1083; B) the dorsal fin of specimen GMPKU-P-1217; C) the anal fin of specimen GMPKU-P-1217. Scale bars equal 5 mm.



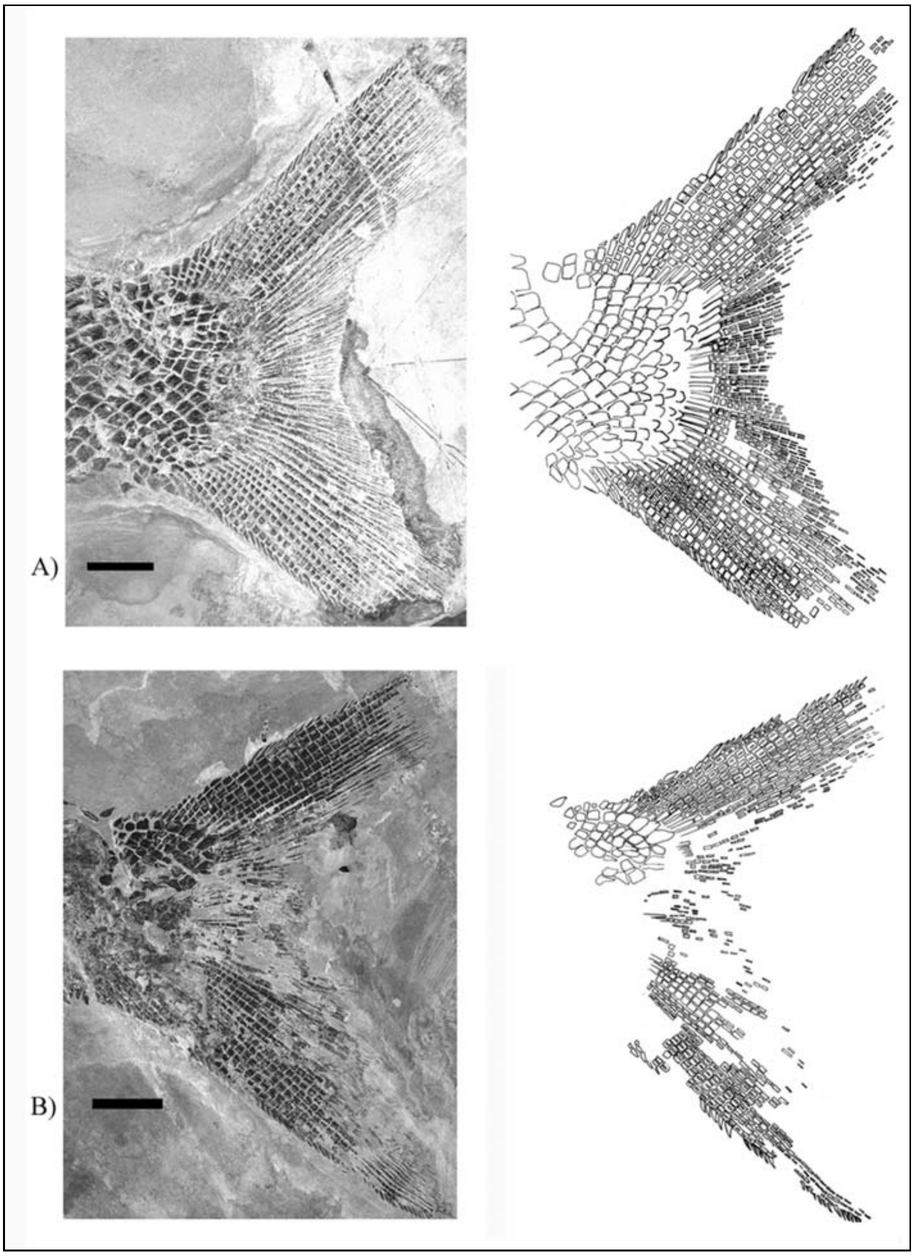


Fig. 9 - *Colobodus baii* sp. n. A) caudal fin of specimen GMPKU-P-1207 and B) of specimen GMPKU-P-1217. Scale bars equal 10 mm.

asymmetrical way, the innermost rays branching earlier than the outer ones. Due to poor preservation, only three branches are observed in each lepidotrichium. There are four or five small basal fulcra.

The fin/scale formula and fin formula are as follow:

Fin/scale formula=D30/Pe18A27C56

Fin formula=D20/P16Pe?A16C48.

*Squamation*. The squamation consists of about 56 transverse rows (from the first row to the line of inversion), each with about 33 scales. The anterior flank scales are high-rectangular in outline, about twice deeper than broad. They partially overlap each other and exhibit a well-developed peg-and-socket articulation. The scales decrease in height posteriorly: medial flank scales are fairly squarish; scales close to or within the caudal region are roughly rhombic. Dorsalmost scales behind the dorsal fin and ventralmost ones behind the pectoral fin become very low, the length being nearly twice as their height. All scales are serrated posteriorly, and richly ornamented by ganoin ridges that are strongly variable relative to their positions (Fig. 10). They are ornamented by densely-spaced, straight and nearly parallel ganoin ridges, about 18-20 ridges each scale. Close to or within the caudal peduncle the ganoin ridges are strongly reduced, but still evident.

## Discussion

The actinopterygian genus *Colobodus* has been used as a wastebasket-genus: almost all Triassic striated molariform teeth and ornament-rich ganoin scales were determined as *Colobodus* or *Colobodus*-like remains.

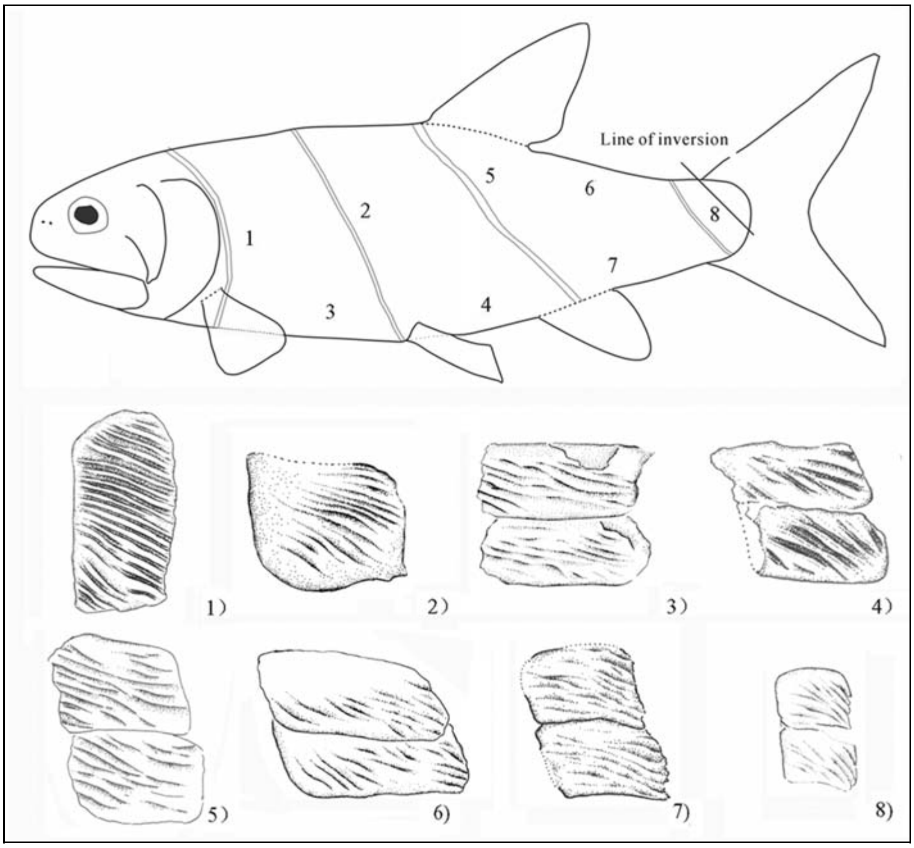


Fig. 10 - Variation of the pattern of ganoin ornamentation and scale shape in *Colobodus baii* sp. n., following the pattern given by Mutter (2002).

Recently, Mutter (2004) reevaluated the diagnosis of the genus and considered that at least three relatively well-known species of *Colobodus* are valid. These are *Colobodus bassanii* De Alessandri, 1910, which is now accepted as the type species of the genus (Mutter 2003), *Colobodus maximus* (Quensted, 1867) and *Colobodus koenigi* Stolley, 1920. Moreover, Mutter himself (2002) proposed several other new species from a single fossiliferous level just a few meters thick (middle part of the Besano Formation). This fact confirms once more the problems of the remarkable morphological variability within subholosteans and the subsequent difficulty in finding features useful to characterize and distinguish the different taxa belonging to this group.

Moreover, we must keep in mind that several of subholostean taxa, such as *Colobodus* and *Peltopleurus* (and peltopleuriforms in general), show a very high intrageneric variability even in short time and in the same basin (Mutter 2002; Lombardo 1999; Lombardo and Tintori pers. obs.). Concerning *Colobodus*, unfortunately, the tentative diagnosis of the genus proposed by Mutter (2004) is highly equivocal. Our comparison is therefore made only with *Colobodus bassanii*, as it is considered the type species of the genus. Mutter (2002) made already a comparison between *C. bassanii* and *C. maximus*: the two species show differences in the infraorbital bones, *C. maximus* having very large elements. Thus, even if the size of this latter species is comparable to *C. baii* sp. n., the infraorbital bones are again a sound difference; furthermore, the age of *C. maximus* is late Ladinian. *C. koenigi* is another species that Mutter (2002) considered as valid, even if on poor preserved specimens: actually only slight differences in the scale ornamentation seems to differentiate this species from *C. bassanii*.

Though the skull bones of the *C. bassanii* and *C. baii* sp. n. show the same general pattern, there are some differences in morphology of some elements, such as the anterior outline of the frontals, the shape of postrostral and the infraorbital series for the dermal skull, and the hyomandibular bone for the suspensorium. In *Colobodus baii* sp. n., the frontals show a deep embayment at their anterior end for housing the postrostral, while in *C. bassanii* the anterior margin of the same elements are more aligned; the postrostral itself of the new taxon is different for the outline of its ventral and dorsal margin. The infraorbital canal of *Colobodus baii* sp. n. runs along the anterior edge of the dermosphenotic instead of the posterior one (Fig. 83 in Mutter 2002)

The hyomandibular bone, well visible on specimen GMPKU-P-1084 (fig. 6A), is characterized by a shorter and larger dorsal head, respect to that of *Colobodus bassanii*; moreover, the angle between the dorsal head and the ventral shaft is more obtuse in the latter species.

The scales of *C. baii* sp. n. are ornamented by densely-spaced, straight and nearly parallel ganoin ridges (about 18-20 ridges each scale): this pattern is similar to that of *Colobodus bassanii* (Mutter 2004), however in the former the ridges are much finer and sometimes anastomosing anteriorly. Moreover, contrary to what happens in *Colobodus bassanii*, in our specimens the ornamentation of the scales remains somewhat stronger in the caudal peduncle. Concerning the ornamentation on the rays of the median fins, *C. baii* sp. n. shows a single ganoin patch for each segment, being much more irregular on *C. bassanii*.

Differences in body size, as specimens of *Colobodus bassanii* can be much larger than the new species, could be due only to the scarcity of specimens from the Panxian area, even if at least 7 almost complete and articulated specimens are available for study so far. Furthermore, it must be pointed out that *Colobodus baii* sp. n. is middle Pelsonian (Anisian, Middle Triassic) in age, while *Colobodus bassanii* is late Anisian/early Ladinian, and that the two sites are, and were, several thousand kilometers far apart. Age and distance are not sufficient to justify the erection of new species, but therefore, the observed morphological differences may be considered sufficient to allow the institution of a new taxon within the genus *Colobodus*.

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