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A Review of the Fossil Record of the Parrotfishes (Labroidei: Scaridae) with a Description of a New *Calotomus* Species from the Middle Miocene (Badenian) of Austria

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(With 5 figures and 4 plates)

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Summary

The status of 7 fossil species and 6 unidentified fossil fragments, currently placed in the family Scaridae are reviewed. Of these, two fragments are considered to be scarid material, both belonging to the genus *Bolbometopon* SMITH, 1956. The remainder include fragments of Diodontidae, Labridae and Oplegnathidae. Most are of uncertain affinity. A new species, *Calotomus preisli* n. sp., from the Upper Badenian (Middle Miocene) of the Bay of Eisenstadt, Austria, is described. This new species is the first unequivocal fossil representative of the Scaridae from Europe and provides new evidence for tropical conditions in the Central Paratethys during the Upper Badenian.

Zusammenfassung

Es erfolgt die Überprüfung der systematischen Zugehörigkeit von 7 fossilen Arten und weiteren 6 fossilen Fragmenten, die bisher der Familie Scaridae (Papageifische) zugeordnet wurden. Nur zwei der Fragmente sind aber eindeutige Belege für Scaridae; es handelt sich um Belege für die Gattung *Bolbometopon* SMITH, 1956. Einige der übrigen Fossilreste stammen von Diodontidae, Labridae und Oplegnathidae, aber die meisten lassen nicht einmal eine Zuordnung zu einer Familie zu. Ein Neufund aus der gebankten Fazies des Leithakalkes (Oberes Badenien, Mittel-Miozän) der Eisenstädter Bucht (St. Margarethen, Burgenland, Österreich) wird als neue Art beschrieben: *Calotomus preisli* n. sp. Diese neue Art ist der erste und einzige unzweifelhafte Beleg für fossile Scaridae in Europa und ein weiterer Beleg für tropische Verhältnisse in der Zentralen Paratethys zur Zeit des Oberen Badeniens.

Introduction

The Scaridae is a family of 79 species in 10 genera. They have a pantropical distribution and are a dominant group of reef associated herbivores. The fossil record of the Scaridae extends from the Eocene, with records from all major

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continents. However, the validity of many of these records may be questioned. The aim of this study is to 1) review the status of all existing scarid fossil records, 2) redescribe valid existing scarid material and 3) describe any new material.

The status of the family Scaridae

There are two main characters that have been traditionally used to identify parrotfishes: 1) the presence of coalesced teeth in the oral jaws forming beak-like dental plates and 2) the form of the pharyngeal apparatus which is characterized by an elongate dentigerous area on the lower pharyngeal bone and laterally compressed upper pharyngeal bones with rows of broad ovoid teeth.

Unfortunately neither of these characters, as defined above, are unique to the Scaridae. Coalesced teeth are present in several extant families including the Tetraodontidae, Diodontidae, Odacidae and Oplegnathidae, and in the extinct family Paleolabridae (ESTES, 1969). With the exception of the Odacidae, all are known from the fossil record. In addition, many scarid species do not posses coalesced teeth e. g. species in the genera *Cryptotomus, Nicholsina, Calotomus* and *Sparisoma.*

It must be noted, however, that although the form of the oral jaws of scarids and other families appears to be similar, the form of the coalesced teeth in scarids does differ from those of other groups. There are several types of coalesced teeth in the Scaridae with many forms being unique (BELLWOOD, in prep.).

In terms of the pharyngeal apparatus, a scarid-like structure is also found in the monotypic genus *Pseudodax* (f. Labridae) (figured in KNER 1860: Pl. 2, Fig. 18 [a–f] and BLEEKER 1862: Pl. 18, Fig. 5), and in the fossil labrids *Asima jugleri* (MÜNSTER, 1846) (figured by SCHULTZ 1978) and *Asima villaltai* (BAUZA, 1948) (as *Taurinichthys Villaltai;* additional descriptions in BAUZA 1950, BAUZA et al. 1963). *Asima* appears to be closely related to the extant genus *Pseudodax,* based on several unusual features of the pharyngeal apparatus which are shared by both genera.

Although there is a superficial similarity to the scarid condition, *Pseudodax* and *Asima* both differ significantly from the scarids in terms of the tooth development and tooth arrangement of the pharyngeal apparatus. *Pseudodax* and *Asima* both have a distinct raised tooth ridge around the margin of the dentigerous area of the lower pharyngeal bone, whereas there is no such ridge in scarids. In addition, the pattern of development of the teeth in scarids is unique. In the upper pharyngeal bones incisiform pharyngeal teeth erupt anteriorly and progress posteriorly forming distinct tooth rows, with numerous functional teeth in each row. There may be 1 to 3 such rows. In *Asima* and *Pseudodax* the upper pharyngeal teeth appear to erupt along the length of the upper pharyngeal bone. In scarids, the teeth of the lower pharyngeal bone erupt on the posterior edge and progress anteriorly wearing progressively. In this bone, a line of 5–6 broad incisiform teeth erupt adjacent to each other and maintain their relative positions as they progress forwards. This mode of tooth development is found only in the Scaridae. In *Asima* and *Pseudodax* the teeth appear to be produced basally, within the toothed ridge, erupting directly onto the dental plate as existing teeth are worn away.

There are numerous other morphological characters that unite the Scaridae (synapomorphies), many of which are unique (BELLWOOD, in prep). However, as the oral and pharyngeal tooth plates are the most frequently preserved structures one must rely on the morphological characteristics of these structures to define members of the Scaridae in this context. Fortunately the oral and pharyngeal tooth plates display many diagnostic features.

In this study, specimens were only included in the Scaridae if they displayed features which are unique to the family. Specimens were identified based on synapomorphies used to identify recent scarid taxa (following BELLWOOD, in prep.). Of the 7 fossil species and 6 fossil fragments placed in the Scaridae in published descriptions to date, only two are considered to belong in the Scaridae. In addition, a new species is described which represents the first unequivocal evidence of a fossil scarid from Europe.

Materials and methods

This work is based primarily on material held in the paleontology collections of the Naturhistorisches Museum Wien and British Museum (Natural History). Figures were traced from photographic enlargements or drawn from the original material using a dissecting microscope with a camera-lucida attachment.

Comparative material examined: BMNH – British Museum of Natural History, London; NMV Museum of Victoria, Melbourne; NMW – Naturhistorisches Museum, Wien, Fischsammlung; NHMW – Naturhistorisches Museum, Wien, Geolog.-Paläont. Abt.

Oplegnathidae:

Fossil – BMNH P. 38006: Miocene; Sharktooth Hill, Kern County, California, U.S.A.; left premaxilla. – BMNH P. 13933: Kalimnan; Beaumaris, Melbourne, Australia; dental plate fragments. – BMNH P. 13934: Kalimnan; Beaumaris, Melbourne, Victoria; dental plate fragment. – BMNH P. 9737: Kalimnan; Beaumaris, Melbourne, Victoria; dental plate fragment.

Recent – *Oplegnathus woodwardii* WAITE, 1900, NMV A269; *Oplegnathus conwayi* RICHARDSON, 1840, NMV A712; both from Victoria, Australia.

Labridae:

Fossil – *Asima jugleri* (MÜNSTER, 1846). Upper Badenian, Middle Miocene; Devinska Nova Ves (= Neudorf a. d. March), Czechoslovakia: NHMW 1857/XIX/33/1–5, upper pharyngeal bone fragments (5); details in SCHULTZ 1978. – NHMW uncatalogued, lower pharyngeal dental plate fragments (3). – NHMW 1857/XIX/6, lower pharyngeal dental plate fragment. – NHMW 1979/2119/1–2, lower pharyngeal dental plate and lower pharyngeal dental plate fragment; details in SCHULTZ 1978. – NHMW 1990/169, lower pharyngeal dental plate fragment.

Asima villaltai (BAUZA, 1948): BMNH P. 44850, Miocene, Vindobonian, Muro, Mallorca; dental plate of lower pharyngeal bone.

Scaridae:

Numerous Recent scarid specimens were examined. A full list will be published in a phylogenetic study of the family (BELLWOOD, in prep).

Osteological terminology follows CLEMENTS & BELLWOOD 1988 and BELLWOOD & CHOAT 1990.

Otolith data. – In this study the otoliths of various Recent species from the Labridae and Scaridae were examined. Although variability was observed within the Labridae, no consistent character could be found to distinguish the two families based on the structure of the otoliths. Although some fish species may be identified by the form of their otoliths the task is nearly impossible in the Scaridae (NOLF 1985). This inherent degree of difficulty in the identification of scarids based on otoliths alone and the similarity between labrid and scarid otoliths make the identification of fossil scarid otoliths uncertain. In this study the identification of such fossils can not be regarded with any degree of confidence and precludes their inclusion in the Scaridae.

Results

The designation of the following species originally placed in the family Scaridae are reviewed. All are placed in other families or are considered as incertae sedis.

Otolithus (Pseudoscarus) crenulatus FROST, 1934: 431, Pl. 15, Fig. 17 (Otolith): Upper Eocene, Barton, Hampshire, U. K.; subsequently identified as *Lophius crenulatus* by NOLF 1985: 129.

Scaridé – CASIER 1946: 142, Pl. 3, Fig. 10 a, b, c (Oral dental plate fragment): incertae sedis – this may represent an oral plate fragment as suggested by CASIER but it does not resemble that of any scarid.

Scaridé – CASIER 1946: 142, Pl. 3, Fig. 11. Identified by CASIER as a pharyngeal plate: incertae sedis; this dental plate may be oral or pharyngeal but it does not resemble that of any scarid. Both this and the above specimen more closely resemble the dental plates of *Paleolabrus* (ESTES, 1969).

Scarus – PROBST 1874: 283–285, Pl. 3, Fig. 8, 9 (Isolated teeth of upper pharyngeal bone), Fig. 10, 11 (Isolated teeth): incertae sedis; the isolated teeth may be oral or pharyngeal.

Scarus baltringensis PROBST, 1874: 282–283, 298, Pl. 3, Fig. 7 (Dental plate fragment): incertae sedis, possibly Oplegnathidae.

Scarus baltringensis [PROBST, 1874] – WITTICH 1898: 44–47, Pl. 1, Fig. 6 (as *Scarus baltringensis* n. spec.; Dental plate fragments): incertae sedis; non-scarid, closely resembles oplegnathid oral jaws.

Scarus baltringensis PROBST, 1874 – PEYER 1928: 413–417, Fig. 1 a, b (Dental plate fragment): incertae sedis.

Scaroides gatunensis TOULA, 1909: 687–688, Fig. 3 a, b, c (Oral tooth plate): of Diodontidae.

Scaroides gatunensis TOULA [respectively] aff. *Scaroides gatunensis* TOULA [1909] – SURARU & SURARU 1966: 72–73, 77, Fig. 12–15. – *Scaroides gatunensis* TOULA – SURARU et al. 1980: 179–180, Fig. 4–11. – *Scaroides gatunensis* TOULA – SURARU & SURARU 1987: 129, Pl. 1, Fig. 2 a–c: Oral tooth plates: of Diodontidae.

Scarus miocenicus MICHELOTTI, 1861: 355, Pl. 10, Fig. 3, 3 a, 3 b (Lower pharyngeal bone fragment; Colline de Turin, Italy; Miocene): of *Asima jugleri* (MÜNSTER, 1846) [see p. 57 and SCHULTZ 1978].

Scarus miocenicus MICHELOTTI, 1861 – CAPPETTA 1969: 234–236, Pl. 21, Fig. 6 a, b (Oral dental plates?): incertae sedis.

Scarus miocenicus MICHELOTTI, 1861 – CAPETTA 1969: 234–236, Pl. 21, Fig. 4 a, b (Upper pharyngeal bone fragment): probably of *Asima jugleri* (MÜNSTER, 1846); SCHULTZ 1978 linked posible upper and lower pharyngeal jaw fragments of *Asima jugleri.*

Scarus priscus WITTICH, 1898: 44–47, Pl. 1, Fig. 7 a, b, c (as *Scarus priscus* PRST.; Dental plate fragment): not scarid, probably oplegnathid dentary.

Scarus suevicus PROBST, 1874: 281–282, 298, Pl. 3, Fig. 6 a, 6 b (Dental plate fragment): incertae sedis, possibly Oplegnathidae.

Scarus tetrodon POMEL, 1847: 586. – WOODWARD 1901: 553 already notes that nothing is known of the so-called *Scarus tetrodon:* nomen nudum respectively incertae sedis.

Sparisoma sp. – NOLF 1988: 94, 144, Pl. 13, Fig. 4 (Otolith): incertae sedis.

Family: Scaridae

Remarks: The following fossil forms are placed in the Scaridae, based on the criteria outlined above; see p. 57.

Genus: *Bolbometopon* SMITH, 1956

Bolbometopon sp.

(Fig. 1; Plate 1, Fig. 1 a, b)

1883–1887 *Balistes* und *Monacanthus* – MARTIN: 22–23, Pl. 1, Fig. 9, 9 a, 10. [description and figurs of two isolated pharyngeal teeth].

1928 *Pseudoscarus* – DE BEAUFORT: 5 [description only of jaw teeth and pharyngeal tooth-patches; refers to descriptions of MARTIN 1883–1887].

1937 *Callyodon* sp. – DERANIYAGALA: 364, Fig. 8 (description and figure of oral tooth plate).

Material: Single fragment of the oral dental plate, BMNH P. 21980, described and figured by DERANIYAGALA (1937). – Location: East shore, Dutch Bay, Aruakollu (Muringé, Malé), NW Province, Sri Lanka. – Formation: Mala beds. – Stratigraphy: Upper Miocene.

Discussion: There are two independent descriptions of material which may be placed in this genus, one based on an oral jaw fragment, the other on isolated pharyngeal teeth.

Bolbometopon is a monotypic genus represented by the Recent widespread Indo-Pacific species *Bolbometopon muricatum* (VALENCIENNES, 1840 in CUVIER &

VALENCIENNES, 1840). It is the largest species in the Scaridae, with individuals attaining sizes of up to 1000 mm standard length (SL). This is an unusual species and is easily recognised, one of the most distinctive features being the unique form of the oral teeth. In *Bolbometopon,* each tooth is elongate with only the distal face showing on the dental surface, forming a regular mosaic pattern (Fig. 1; Plate 1, Fig. 1–2). The exposed surface of each tooth is roughly square, with a distinct nodule or tubercle at the proximal apex (Fig. 1; Plate 1, Fig. 1–2).

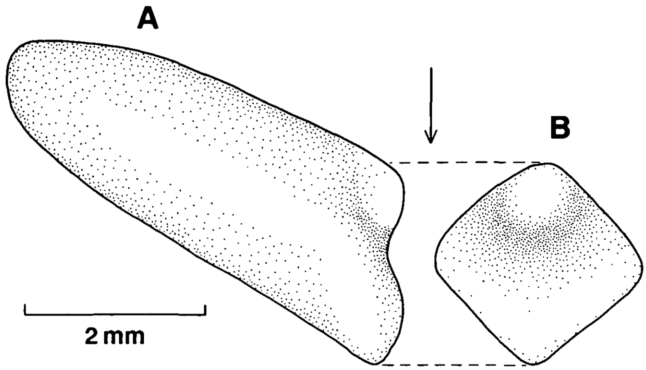

Fig. 1: *Bolbometopon* sp.; East shore, Dutch Bay, Aruakollu (Muringé, Malé), NW Province, Sri Lanka; Mala Beds, Upper Miocene; BMNH P. 21980. A single tooth from the serrated margin: A) lateral view, B) anterior view (surface exposed on outer face of dental plate). Arrow indicates direction of cutting edge.

The combination of an elongate tooth, a roughly square exposed face, a basal nodule and the lack of a thick cement covering over the dental plates is a unique combination found only in *B. muricatum.* Each character alone is shared by very few other scarid species, whilst BELLWOOD (in prep.) regards the nodule on the teeth as an autapomorphy of *Bolbometopon.* This tooth structure of *Bolbometopon* differs markedly from that in the Oplegnathidae, where each tooth has a distinctly rounded exposed surface, and no nodule.

The dental plate described by DERANIYAGALA 1937 is identical in almost every respect to a comparable region of the oral jaws of *B. muricatum,* including the autapomorphic basal nodules. This specimen is therefore placed in the genus *Bolbometopon.* It can not be distinguished from *B. muricatum* but the lack of sufficient material precludes a specific identification.

A comparison of the curvature of the fragment and the size of individual teeth with those of the Recent species *B. muricatum,* suggest that the specimen was approximately 780 mm standard length and 930 mm total length. This is significantly smaller then the 1166 mm SL estimate of DERANIYAGALA 1937.

The second description of material which may be provisionally placed in this genus is by MARTIN (1883–1887: 22–23, Pl. 1, Fig. 9, 9 a, 10), who described and figured two isolated teeth from Ngembak, Java. MARTIN compared them with the oral teeth of *Balistes* and *Monacanthus.* DE BEAUFORT 1928 examined similar teeth in collections from Kleripan, Central Java. He described them as the pharyngeal teeth of *Pseudoscarus* or an allied genus, and upon examining MARTINS descriptions, stated that "There is no doubt [. . .] that these [the teeth described by MARTIN] too are pharyngeal teeth of *Pseudoscarus* or an allied genus."

As part of a generic revision of the family Scaridae (by BELLWOOD, in prep.) the pharnygeal teeth of numerous species of Recent scarids have been examined, with representatives from all Recent genera. Considerable variation between species was observed. The teeth figured by MARTIN 1883–1887 are indistinguishable from isolated teeth of the lower pharyngeal jaw of *Bolbometopon muricatum.* The most characteristic aspects being the truncate basal margin, the thin, slightly inflected profile and the overall length of the tooth. This tooth form is found only in the Scaridae, and such large deep teeth are characteristic of the larger species (> 350 mm standard length). The unusually thin profile of the teeth suggests that these teeth came from an exceptionally large individual. The teeth described by MARTIN were almost certainly from a large scarid. The only recent genus with teeth of a comparable form is *Bolbometopon.* This material is therefore provisionally referred to this genus.

Fossil distribution: Miocene.

MARTIN 1883–1887 estimated the age of his material to be young-Miocene, whilst DE BEAUFORT 1928 estimated the age of his material to be old-Miocene. However, in both studies, there is some degree of uncertainty with regards to these age estimates.

Genus: *Calotomus* GILBERT, 1890

The following description is based on a single specimen. In this specimen both the oral and pharyngeal jaws are clearly preserved. This enabled the specimen to be readily identified to a generic level based on criteria presently used to define genera within the Scaridae. It provides the first unequivocal evidence of the presence of the Scaridae in the Middle Miocene of Europe.

Calotomus preisli n. sp.

(Figs 2–5; Plate 2, Figs 3–4; Plate 3, Figs 5–6)

Material = Holotype: Head region of a single specimen preserved as part, NHMW 1989/90 a (with premaxillae, dentaries, etc.), and counterpart, NHMW 1989/90 b (with upper pharyngeal bones, operculae, etc.).

Type locality: 47°48′N, 16°38′E: Leitha limestone quarry (KUMMER, operating company), St. Margarethen, Ruster Bergland, Burgenland, Austria.

Formation: Laminated facies of Leitha limestone (Gebankte Fazies des Leithakalkes).

Stratigraphy: Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene.

Etymology: The name *preisli* refers to Mr. Herbert PREISL, who collected the specimen and donated it to the Natural History Museum Vienna.

Description of the specimen

A comparison of the size of the operculae and upper pharyngeal bones of the specimen with those of Recent species suggest that the specimen was approximately 150 mm standard length, 190 mm total length.

Superficial dermal bones (Fig. 4): Four circumorbitals are visible, a series of three and an isolated element. The bones are relatively deep and are comparable to those of recent *Calotomus* species.

Oral jaws (Figs 2, 4; Plate 2, Figs 3, 4): Both premaxillae are preserved. The dentition of the left premaxilla is clearly visible, as are the medial and posterior aspects of the dentition of the right premaxilla. Anteriorly, the left premaxilla bears 5 slightly recurved conical teeth. The teeth alternate in their prominence, a pattern which may be interpreted as representing three oblique rows of 1–2 teeth. The premaxilla has a relatively short ascending process and a large alveolar process. At the base of the alveolar process, immediately beneath the maxillary fossa, the fractured remains of the bone form a round fossa. This probably represents the socket of a large lateral canine.

A bony ridge runs along the posterior portion of the alveolar process and bears two slightly oblique rows of 2–4 small laterally compressed conical teeth. Anterior to these teeth, and medial to the bony ridge, are two small conical teeth. A single small conical tooth is visible on the internal face of the right premaxilla near to the symphysis (Fig. 2; Plate 2, Fig. 4).

In the lower jaw, both dentaries are preserved although the dentition of only the anterior part of the left dentary is visible. Anteriorly, the dentary bears three oblique imbricate rows of 2–4 slightly recurved flattened conical teeth. The coranoid process of the right dentary is clearly visible and is relatively narrow. Both left and right angulo-articulars are preserved. These display a deep ventral flange and a raised posterior ascending process.

The right maxilla and part of the left maxilla are preserved. The maxilla has a typical scarid form and, as in Recent *Calotomus* species, has an anteriorly projecting medial process bearing a distinct ventral process on the anteroventral margin.

Palatine arch (Figs 2, 4 and 5): The palatine arch is largely fragmented. Nevertheless several structures can be identified. Parts of the hyomandibula, pterygoid, quadrate, entopterygoid and palatine are preserved. The palatine dorsal process is grooved along the dorsolateral margin (a characteristic of Recent *Calotomus* species) whilst the anterior margin is truncate and has a slight ventral projection (a condyle?).

Opercular series (Figs 4, 5; Plate 2, Fig. 3; Plate 3, Fig. 5): The left preoperculum and the two operculae are preserved. The preoperculum is broad, with a short horizontal limb. The posterior margin is entire with no evidence of serrations (Fig. 4; Plate 2, Figs 3, 4).

Hyoid arch (Fig. 4; Plate 2, Fig. 3): Seven branchiostegal rays are preserved whole or in part. All are laterally flattened. The outline of the urohyal is

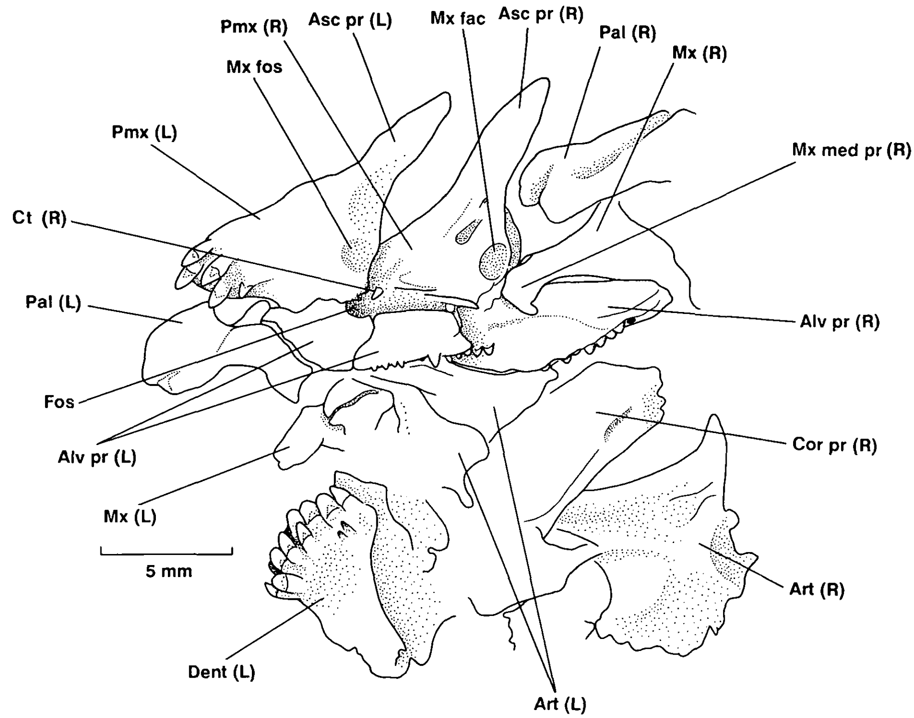

Fig. 2: *Calotomus preisli* n. sp.; holotype, NHMW 1989/90 a. Details of the oral jaw region. Abbreviations: Art, articular; Alv pr, alveolar process of the premaxilla; Asc pr, ascending process of the premaxilla; Cor pr, coranoid process of the dentary; Ct, conical tooth on the internal face of the right premaxilla near to the symphysis; Dent, dentary; Fos, fossa of lateral canine; Mx, maxilla; Mx fac, maxillary facet of the premaxilla; Mx fos, maxillary fossa of premaxilla; Mx med pr, medial process of the maxilla; Pal, palatine; Pmx, premaxilla; (L), left hand element; (R), right hand element.

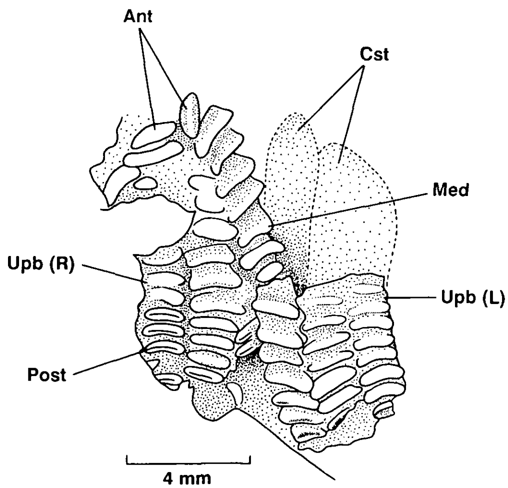

Fig. 3: *Calotomus preisli* n. sp.; holotype, NHMW 1989/90 b. Details of the pharyngeal bones. Abbreviations: Ant, anterior developing and newly erupted teeth; Cst, cast of the anterodorsal region of the left upper pharyngeal bone; Med, medial tooth row; Post, posterior teeth showing wear; Upb, upper pharyngeal bone; (L), left hand element; (R), right hand element.

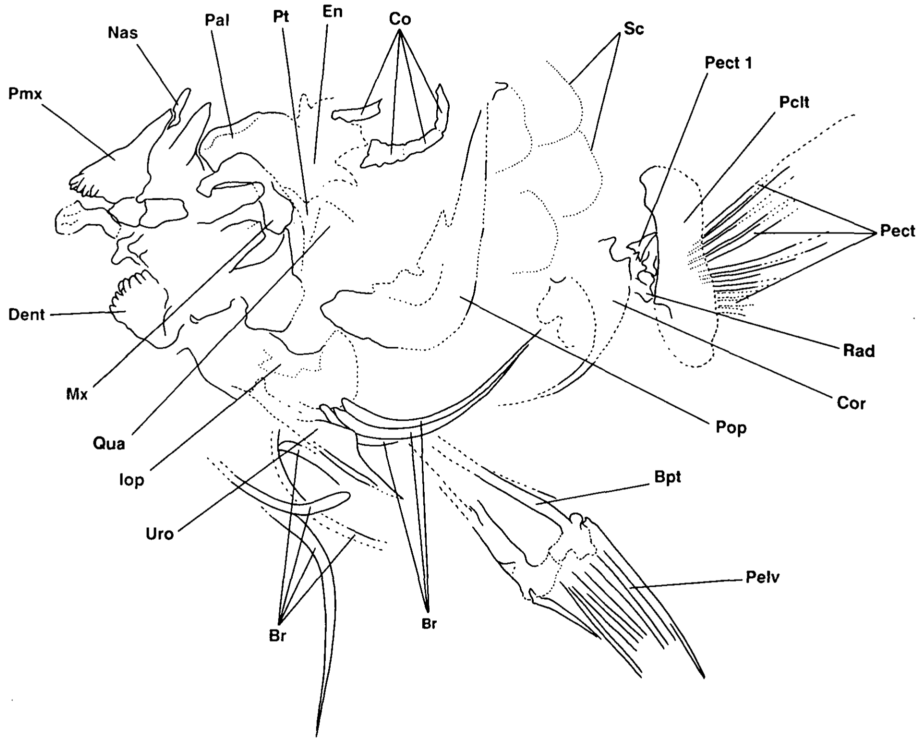

Fig. 4: *Calotomus preisli* n. sp.; NHMW 1989/90 a. Holotype, showing oral and pectoral structures. Abbreviations as Fig. 2 except: Bpt, basipterygium; Br, branchiostegal rays; Co, circumorbitals; Cor, coracoid region of pectoral girdle; En, entopterygoid; Hyo, hyomandibula; Iop, interoperculum; Nas, nasal; Pclt, postcleithrum; Pect, pectoral fin rays; Pect 1, first rudimentary ray of the pectoral fin; Pelv, pelvic fin rays; Pop, preoperculum; Pt, pterygoid; Qua, quadrate, Rad, radials of pectoral fin; Sc, scales in opercular region; Uro, urohyal.

visible (NHMW 1989/90 a; Fig. 4). It is elongate with a short dorsal process anteriorly and a low dorsal ridge.

Branchial arches: The branchial arches are represented by the paired upper pharyngeal bones (preserved in the counterpart specimen, NHMW 1989/90 b). The teeth of both elements are clearly visible (Figs 3 and 5; Plate 3, Figs 5, 6). The outline of the left bone is indicated by a deep cast. The orientation of the bones was determined by comparison with osteological preparations of Recent *Calotomus* species. Each bone bears three rows of teeth, with up to 13 teeth in each row (based on the most complete row = second row of right bone). The teeth in the outer two rows are approximately in line. The medial row is at an acute angle to these rows, projecting anteriorly. Each tooth is approximately 4.5 times as wide as long. The relative widths of the teeth from the medial to outer row are approximately 1.15 : 1.19 : 1.00. Developing and newly erupted teeth are visible anteriorly. Posteriorly, the teeth show clear signs of wear with the outer enamel layer remaining as a narrow ovoid ridge with a central depression. The estimated total length of the upper pharyngeal bone is 10.6 mm.

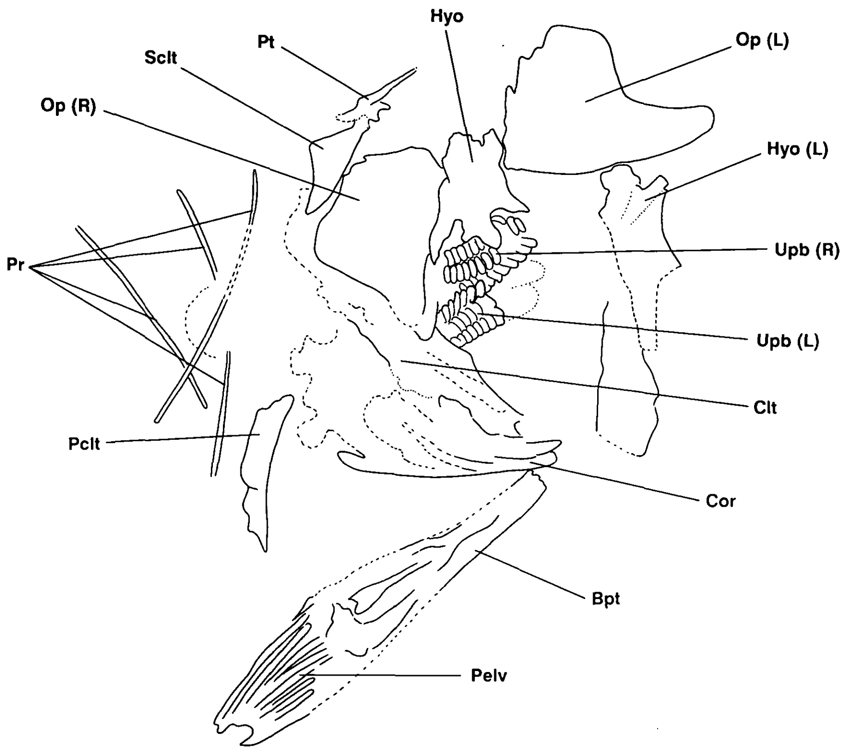

Fig. 5: *Calotomus preisli* n. sp.; NHMW 1989/90 b. Holotype, counterpart specimen showing upper pharyngeal bones. Abbreviations as Figs 2 and 4 except: Clt, cleithrum; Op, operculum; Pr, pleural ribs; Pt, posttemporal; Hyo, hyomandibular; Sclt, supracleithrum; Upb, upper pharyngeal bone.

Pectoral girdle (Fig. 4; Plate 3, Fig. 5): There are 13 pectoral rays, the first rudimentary and unbranched, the second unbranched, the remainder branched. The pectoral girdle comprising the post-temporal, supracleithrum, cleithrum, coracoid, radials and post-cleithra are all preserved. All have a typical scarid/labrid form (cf. RUSSELL 1988).

Pelvic girdle: The basipterygium and pelvic fin rays are both preserved. Each pelvic fin comprises one spine and five branched rays (Figs 4, 5; Plate 2, Fig. 3; Plate 3, Fig. 5).

Squamation (Fig. 4; Plate 2, Fig. 3): The scales are large and cycloid.

Systematic position

The possession of upper pharyngeal bones with 1–3 rows of teeth, is a unique character found only in the Scaridae, and clearly place this specimen in this family (Fig. 3; Plate 3, Fig. 6; cf. Plate 4, Figs 9, 12). This character is a unique, non-reversed synapomorphy of the Scaridae (BELLWOOD, in prep.). The inclusion of this specimen in the Scaridae is supported by the possession of a lateral canine (a synapomorphy of the family) (Fig. 2).

Of the 10 Recent scarid genera recognised by BELLWOOD (in prep.), only four have non-coalesced teeth in the oral jaws, namely *Cryptotomus, Nicholsina, Calotomus* and *Sparisoma.* Of these, the oral jaw teeth of *Sparisoma* are invariably flattened and numerous (occasionally coalesced), whilst the premaxillae of *Cryptotomus* and *Nicholsina* lack conical teeth on the medial face near the symphysis. In *Sparisoma* the teeth on the upper pharyngeal bones are more robust than in *Calotomus* whilst in *Cryptotomus* and *Nicholsina* they are of a shorter, lighter form. The overall form of the specimen most closely resembles that of Recent *Calotomus* species.

In a phylogenetic study of the Scaridae, the osteology and myology of all scarid genera have been examined (BELLWOOD, in prep.). In this study, *Calotomus* was defined by a number of synapomorphies three of which were autapomorphic, the remainder were found in a number of other genera. Of the three autapomorphies defining *Calotomus,* two are based on the structure of the neurocranium and one on the oral jaw dentition. The lack of a clear neurocranium in the specimen examined precludes the use of neurocranial characters in the identification of this specimen. The oral jaw character, however, is particularly useful i. e. the presence of a conical tooth on the medial face of the premaxilla immediately adjacent to the symphysis (Fig. 2). This feature has only been recorded in adult *Calotomus* species.

The specimen is therefore placed in the genus *Calotomus,* based on the structure of the oral jaws. This decision is supported by the close similarity between this specimen and Recent *Calotomus* species in terms of all the other observed structures, including the upper pharyngeal bones.

In their revision of the genus *Calotomus* BRUCE & RANDALL 1985 recognised five species: *Calotomus carolinus* (VALENCIENNES) (Plate 4, Figs 10–12), *C. spinidens* (QUOY & GAIMARD) (Plate 4, Figs 7–9), *C. japonicus* (VALENCIENNES), *C. viridescens* (RÜPPELL) and *C. zonarchus* (GILBERT). The first two species have widerspread distributions throughout the Indo-Pacific. The latter three species are regional endemics restricted to Japan, the Red Sea and Hawaii, respectively.

Recent *Calotomus* species are distinguished primarily on the basis of colour patterns and body proportions, features which are of no comparative value in this study. However, the descriptions of each species given by BRUCE & RANDALL 1985 include descriptions of the oral dentition. Some species differ in this respect and may be distinguished based on dental patterns. It is these differences that enable *C. preisli* to be differentiated from all extant species.

The premaxillary tooth pattern of *C. preisli* most closely resembles that of *C. spinidens* (Plate 4, Fig. 7) which, like *C. preisli,* has relatively few teeth (usually 5, rarely up to 8) which do not form discrete rows. All other species have numerous flattened teeth in distinct imbricate rows (Plate 4, Fig. 10). In *C. spinidens* some flattening of the teeth is apparent, *C. preisli* differs in this respect, in that the teeth are recurved but show little if any indication of flattening.

In the lower jaw, *C. preisli* has relatively few teeth. The dentary, although damaged, appears to bear only three imbricate rows with 2, 3, and 4+ teeth respectively. Of the five Recent *Calotomus* species only *C. spinidens* is reported to have three imbricate rows in the lower jaw (Plate 4, Fig. 8). In this species, however, the three rows barely overlap and the third row extends along the dorsal edge of the coranoid process. In species with more rows (Plate 4, Fig. 11), the teeth are closely applied and the rows slope at a more oblique angle than in *C. preisli*. Overall, the form of the oral dentition in *C. preisli* differs from that in all Recent *Calotomus* species.

In summary, *C. preisli* may be separated from Recent *Calotomus* species by: 1) the stout conical nature of the teeth on the anterior face of the premaxilla and 2) the presence of three broadly overlapping rows of teeth on the dentary (Fig. 2).

Biological notes

C. preisli most closely resembles *C. spinidens,* a species with a broad distribution from the east coast of Africa, throughout the Indo-Malay Archipelago and into the Western Pacific. *C. spinidens* is the smallest member of the genus reaching a maximum of only 154 mm SL, only slightly larger than the estimated size of the *C. preisli* specimen (150 mm SL). In Recent species, the presence of a conical tooth on the medial surface of the premaxilla near to the symphysis is a characteristic of adult specimens. The presence of such a tooth in the specimen examined (Fig. 2) suggests that it was an adult and that *C. preisli* only grew to relatively small size.

Like most other *Calotomus* species, *C. spinidens* is a tropical species. The habitats occupied by Recent species vary from exclusively in seagrasses *(C. spinidens),* in seagrass beds and on reefs *(C. viridescens),* on shallow reefs *(C. carolinus)* or in deep reef areas (approximately 160–180 m; *C. zonarchus*) (Bruce & Randall 1985).

In comparison, *C. preisli* appears to have been a relatively typical *Calotomus* species, living in shallow tropical waters in or in the immediate vicinity of seagrass beds.

Description of the sediment and biotope

The specimen is preserved in a laminated facies of Leitha limestone. Leitha limestone usually occurs as a white to yellowish massive or a light brown porous limestone which is typically composed of crustose coralline algae. Different types of Leitha limestones, including a reef limestone (with corals), can be distinguished in the Leithagebirge and in the Ruster Bergland, situated a little to the east. The Leitha limestone is a typical sediment of the Vienna Basin area during Middle Miocene and commonly crops out along the borders of the basin, overlying Mesozoic sediments or crystalline rocks (Fuchs 1965: 167–169; Dullo 1983: 38–40).

Today the laminated facies is only preserved in a small area covering several 100 m^2, with a thickness of approximately 10 m, and is partially surrounded by unlaminated Leitha limestone. The laminated facies is characterized by a cyclic sedimentation which begins basally with a white porous chalky phase 2–5 cm thick, and ends with a blue-green marl up to 1 cm thick on the top. The sediment is composed primarily of reworked biogenic material, although some intact material is present: red algal nodules, bryozoans, shells of oysters, scallops and regular echinoids are common. The lamination indicates lagoonal conditions, whilst the foraminiferal fauna is indicative of a biotop with seagrasses (cf. RÖGL in BACHMAYER 1980: 30–31).

Numerous fish have been found in these deposits during the last 150 years although only a small proportion have been described: Clupeidae – *Clupea haidingeri* HECKEL, 1850; Myctophidae – *Palimphemus anceps* KNER, 1862; Syngnathidae – *Nerophis zapfei* BACHMAYER, 1980; Scorpaenidae – *Scorpaena prior* HECKEL, 1861 (in HECKEL & KNER), *Jemelkia jemelka* (HECKEL, 1856); Triglidae – *Trigla infausta* HECKEL, 1861 (in HECKEL & KNER); Serranidae – *Serranus pentacanthus* HECKEL, 1861 (in HECKEL & KNER); Sparidae – *Pagrus priscus* KNER, 1862; Carangidae – *Caranx boeckhi* GORJANOVIC-KRAMBERGER, 1902; Labridae – *Labrus agassizi* (MÜNSTER, 1846), *L. parvulus* HECKEL, 1856, *Julis sigismundi* KNER, 1862. New excavations in the last twenty years have revealed specimens from the Cetorhinidae *(Cetorhinus)*, Muraenidae, Lophiidae, Centriscidae, Scorpaenidae *(Sebastes?)*, and Sparidae. The above lists include lagoonal and offshore species, the latter presumably drifting in from these areas.

Palaeogeographical remarks

The Bay of Eisenstadt extends east of the Leithagebirge, which was an island between the Vienna Basin in the west and the Pannonian Basin in the east. The Vienna Basin represented the western end of the tropical marine Paratethys during the Upper Badenian (Middle Miocene, approximately 14 m. yrs. B. P.). During this period, the Vienna Basin was connected to the Persian Gulf area and to the Indian Ocean via the Black Sea (see RÖGL & STEININGER 1983: Pl. 10; STEININGER & RÖGL 1984: 663, Fig. 6).

Concluding Discussion

Despite the relatively large number of fossil records of species and specimens which have been placed in the family Scaridae, only one previously described species and one new species are recognised herein. This result raises two points. Firstly, it appears that a large proportion of the fossil material placed in the Scaridae should be placed in the Oplegnathidae. These families show an unusual degree of homoplasy in the form of the oral jaws. Recent members of the Oplegnathidae are restricted primarily to relatively deep waters, on the fringe of the tropics, in South Africa, Australia, Japan and the North Pacific. The presence of fossil oplegnathid material in North America is interesting as this family appears to be absent today from the coastal waters of North America and the Atlantic Ocean.

Secondly, given 1) the unusual and easily recognised structure of scarid oral and pharyngeal teeth and tooth plates, and 2) the good state of preservation of these structures in the fossil scarids examined and in fossils of the closely related Labridae, it is strange that so few scarid specimens have been recorded. It is not known whether this reflects a recent origin, chance, patchy collections or a strong association with exposed coral reefs or other areas where fossilization is not likely. However, it is interesting to note that on modern reefs, two herbivorous reef fish families predominate, the Acanthuridae and the Scaridae, with comparable species numbers. Today, these families have comparable distributions, both geographically and within reefs. In contrast, in the Eocene deposits of Monte Bolca, the Acanthuridae are well represented but no scarids have been reported to date (BLOT 1980; BELLWOOD unpublished data). This suggests that the Scaridae may be a relatively Recent group.

One can conclude from the present study that the Scaridae were represented in the Middle Miocene (approximately 14 m. yrs. B. P.) and that their form at this time bore a strong resemblance to that of Recent species. The specific location of the specimens and their general location within the Paratethys region indicates that this family had tropical representatives at this time, that probably lived on, or in the immediate vicinity of, seagrasses and coral reefs.

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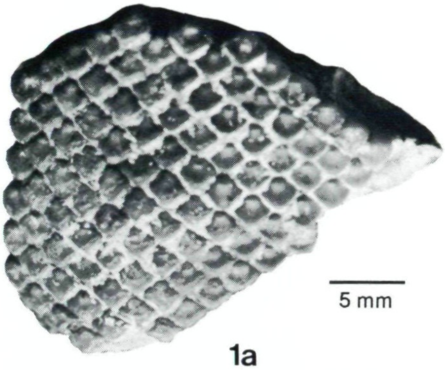
Plate 1

Fig. 1: *Bolbometopon* sp., East shore, Dutch Bay, Aruakollu (Muringé, Malé), NW Province, Sri Lanka; Mala Beds, Upper Miocene; oral tooth plate; BMNH P. 21980; 2× natural size. a) oral surface; b) profile.

Fig. 2: *Bolbometopon muricatum* (VALENCIENNES, 1840 in CUVIER & VALENCIENNES, 1840); 860 mm TL; Philippines; right premaxilla, outer view; 2× natural size.



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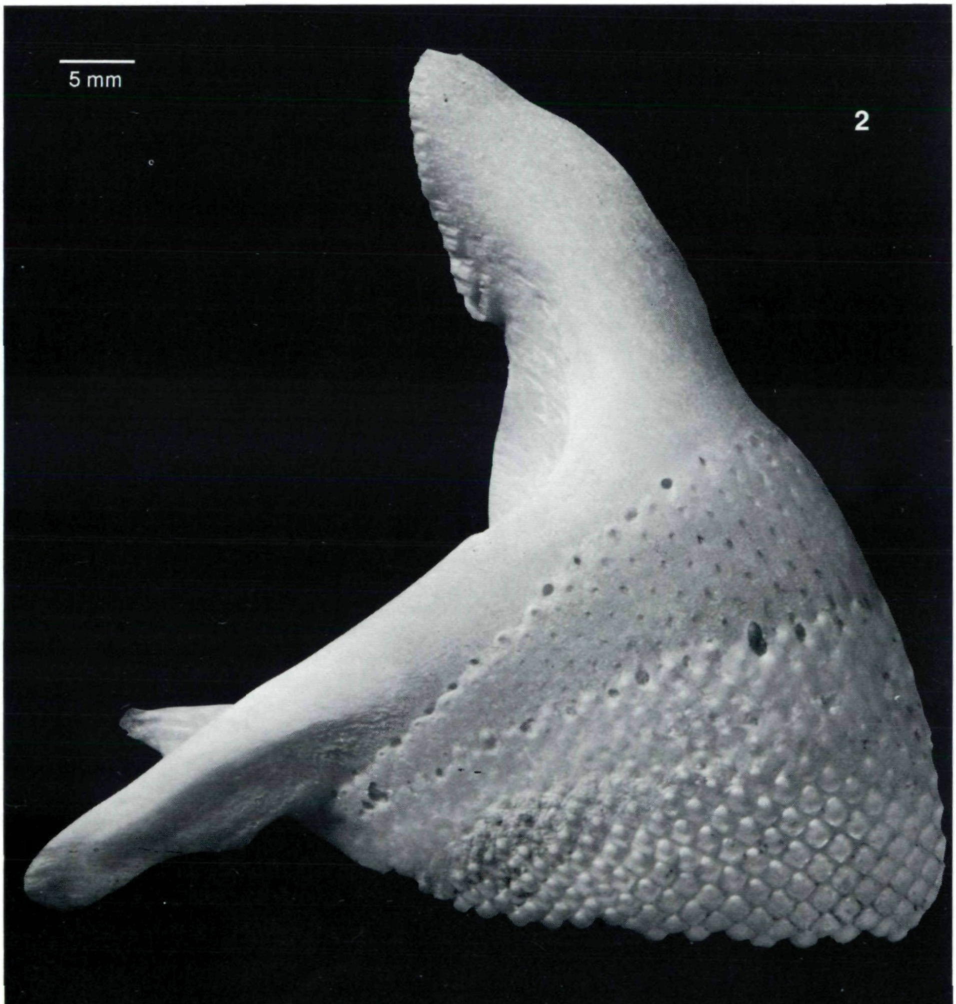


Plate 2

Fig. 3: *Calotomus preisli* n. sp.; holotype, NHMW 1989/90 a; see Fig. 4 and Plate 2, Fig. 4 for details. Natural size.

Fig. 4: *Calotomus preisli* n. sp.; holotype, NHMW 1989/90 a, 3,5× enlargement of the oral jaw region; see Fig. 2 for details.


1 cm
3

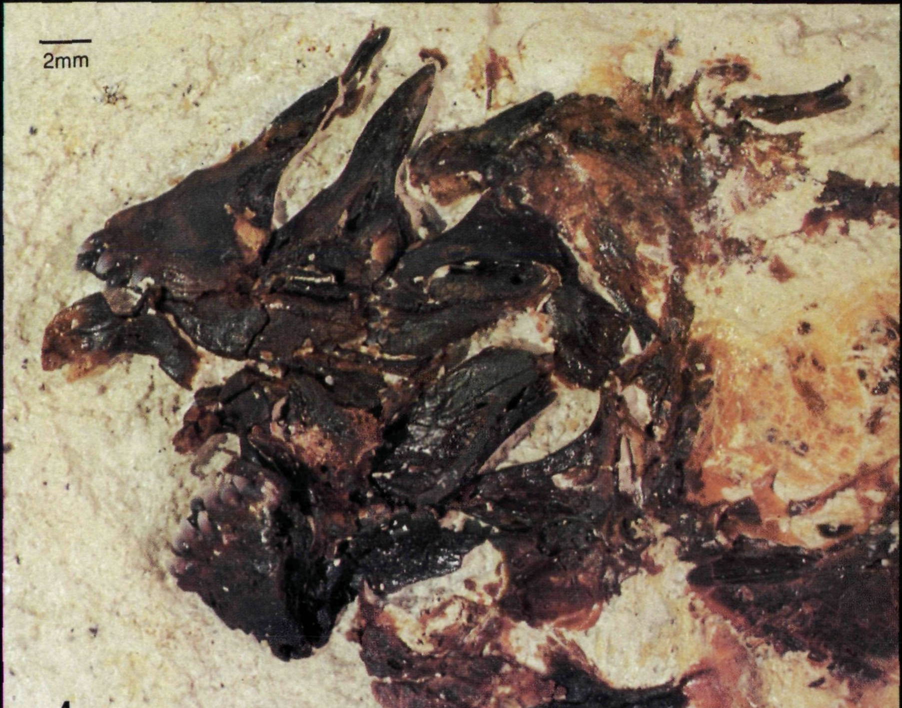

2mm
4

Plate 3

Fig. 5: *Calotomus preisli* n. sp.; holotype, counterpart, NHMW 1989/90 b; see Fig. 5 and Plate 3, Fig. 6 for details. Natural size.

Fig. 6: *Calotomus preisli* n. sp.; holotype, counterpart, NHMW 1989/90 b: 7× enlargement of the upper pharyngeal bones; see Fig. 3 and 5 for details.

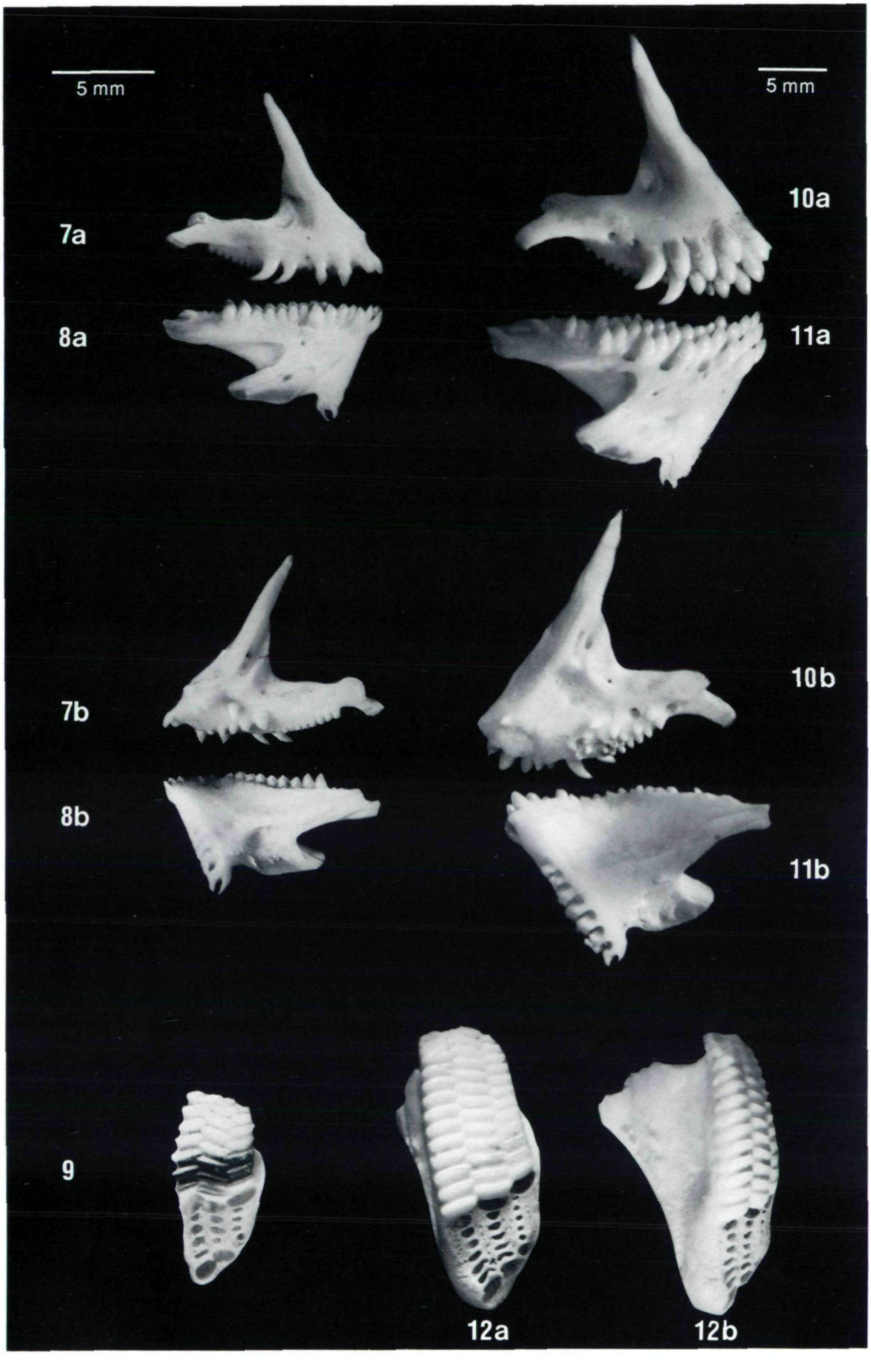

1 cm
5


1mm
6

Plate 4

Fig. 7–9: *Calotomus spinidens* (QUOY & GAIMARD, 1824), 129 mm SL, Philippines; NMW 90305; 3× natural size. – 7. right premaxilla, a) outer view, b) interior view. – 8. right dentary, a) outer view, b) interior view. – 9. right upper pharyngeal bone, natural state showing normal dentition, ventral view.

Fig. 10–12: *Calotomus carolinus* (VALENCIENNES, 1840 in CUVIER & VALENCIENNES, 1840), ♂, 220 mm SL, Apo Island, Philippines; NMW 90306; 2× natural size. – 10. right premaxilla, a) outer view, b) interior view. – 11. right dentary, a) outer view, b) interior view. – 12. right upper pharyngeal bone, natural state showing normal dentition, a) ventral view, b) medial view.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