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# The osteology of *Eucyclogobius newberryi* and *Quietula guaymasiae* (Teleostei: Gobiidae), two closely related Gobionellines from the East Pacific

G. Kindermann*, N. Miljković*, H. Ahnelt* & D.E. Stevenson**

## Abstract

*Eucyclogobius newberryi* and *Quietula guaymasiae* are two closely related Gobionellinae which are included within the 'bay gobies' of the *Chasmichthys* group. Both species occupy different ecological habitats. We present the osteology of these two related species, with *E. newberryi* representing the end of a phylogenetic line adapting to freshwaters and *Q. guaymasiae*, a representative of the basal assemblage occupying habitats of full marine condition.

**Key words**: Gobiidae, Gobionellinae, osteology, East Pacific

## Zusammenfassung

*Eucyclogobius newberryi* und *Quietula guaymasiae* sind zwei nahe verwandte Meergrundeln der Unterfamilie Gobionellinae. Innerhalb der monophyletischen *Chasmichthys*-Gruppe werden sie zu den ‚bay gobies' gezählt. *E. newberryi* und *Q. guaymasiae* besetzen unterschiedliche ökologische Nischen. Wir dokumentieren die Osteologie dieser beiden nah verwandten Arten, von denen *E. newberryi* das Ende einer phylogenetischen Entwicklung hin zu Süßwasserhabitaten repräsentiert, während *Q. guaymasiae*, ein Vertreter der basalen "bay gobies", küstennahe marine Habitate besiedelt.

## Introduction

*Eucyclogobius newberryi* (GIRARD 1856) and *Quietula guaymasiae* (JENKINS & EVERMANN 1889) are included in the *Chasmichthys* group of the Gobionellinae (BIRDSONG & al. 1988, PEZOLD 1993). This group is defined by one synapomorphy – the insertion of the anterior most pterygiophore of the first dorsal fin in the fourth or fifth interneural space. Genera are found on both sides of the North Pacific, two in the western North Pacific (*Chaenogobius* and *Gymnogobius*) and six along the Pacific coast of North America (*Clevelandia*, *Eucyclogobius*, *Gillichthys*, *Ilypnus*, *Lepidogobius*, and *Quietula*) (BIRDSONG & al. 1988). The North American gobies are usually lumped together as the 'bay gobies' (GINSBURG 1945, DAWSON & al. 2002).

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Recently STEVENSON (2002a, b) investigated the relationship of the *Chasmichthys* Group and found distinct morphological and molecular similarity. He concluded that morphology may not provide sufficient evidence to support a well-resolved phylogeny of this genus group. In addition STEVENSON (2002a) demonstrated that the *Chasmichthys* Group is not clearly separated into Asian and North American clades. He found two distinct lineages within this group: one represented by *Chaenogobius* and *Gillichthys*, the other by *Gymnogobius* and the five remaining genera of the 'bay gobies'.

Obviously morphological characters, as demonstrated for the lateral line system of members of the *Chasmichthy*s group, exhibit a great deal of potential for resolving relationships within the 'bay gobies' (STEVENSON 2002 b, AHNELT & GÖSCHL 2003, AHNELT & al. 2004). Nevertheless, a detailed knowledge of morphological characters is a prerequisite. Therefore we investigated the osteology of two 'bay goby' species in detail (MILJKOVIĆ 2004, KINDERMANN 2005). We focused on *E. newberryi* and *Q. guaymasiae* because both belong to the same phylogenetic lineage within the *Chasmichthys* group (STEVENSON 2002b), but occupy ecological different habitats: *E. newberryi* inhabits coastal lagoons, estuaries and low reaches of brooks and rivers in California (SWIFT et al. 1989), whereas *Q. guaymasiae* is a marine species which occurs inshore in the northern Gulf of California where it occupies silt and slick habitats (THOMSON & al. 2000). In addition, *E. newberryi* is most specialised among the 'bay gobies' and represents the 'end' of a phylogenetic line adapting toward freshwaters. On the contrary, *Q. guaymasiae* is a representative of the basal assemblage of this clade occupying habitats of full marine condition. It is very likely that in both species not only the lateral line system is differently developed but that also the osteology differs characteristically.

We present an osteological atlas of the two 'bay gobies' *E. newberryi* and *Q. guaymasiae*. Besides complexes like the neurocranium, jaws, suspensorium, caudal skeleton, and vertebrate column, we also figure the single bones of these complexes. This atlas is the first attempt for an extensive comparison of the osteology of the North American 'bay gobies' carried out as a part of the PhD thesis by N. Miljković. A detailed knowledge of the osteology will be helpful to identify characters important for the relationship of the members of the *Chasmichthys* group.

## Material and methods

Material examined: *Eucyclogobius newberryi*: 19 specimens from California (USA). CAS 31768, Los Angeles Co., at mouth of Malibu Creek; 2 spec., 18.1-19.3 mm SL. CAS 82445, San Luis Obispo Co., Little Pico Creek; 1 spec., 29.6 mm SL. CAS 86281, San Mateo Co., Pescadero Creek; 3 spec., 30.9-35.6 mm SL. LACM 36189-2, San Diego Co., San Mateo Creek, north of Camp Pendleton; 3 spec., 21.0.2-22.8 mm SL. LACM 37552-1, Humboldt Co., Stone Lagoon; 3 spec., 25.6-36.7 mm SL. SIO 7287, San Luis Obispo Co., San Simeon Creek; 1 spec., 32.2 mm SL. SIO 52-108A+B, Orange Co., near mouth of Aliso Creek; 2 spec., 28.8-31.8 mm SL. UMMZ 132897, San Diego Co., San Onofre Creek, near bridge over Hwy 101; 2 spec., 22.6-22.7 mm SL. UMMZ 133770, Santa Barbara Co., tributary of the St. Maria River; 2 spec., 36.9-37.3 mm SL.

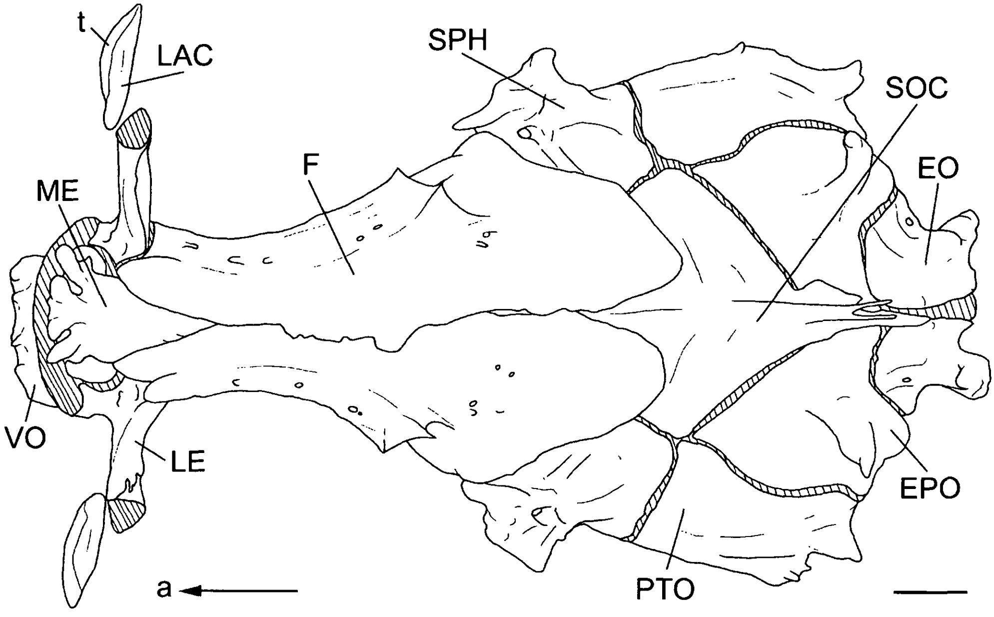


Fig. 1: Neurocranium and associated elements of *Eucyclogobius newberryi*, dorsal view; LACM 37552-1, 34.2 mm SL. Hatching represents cartilage. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

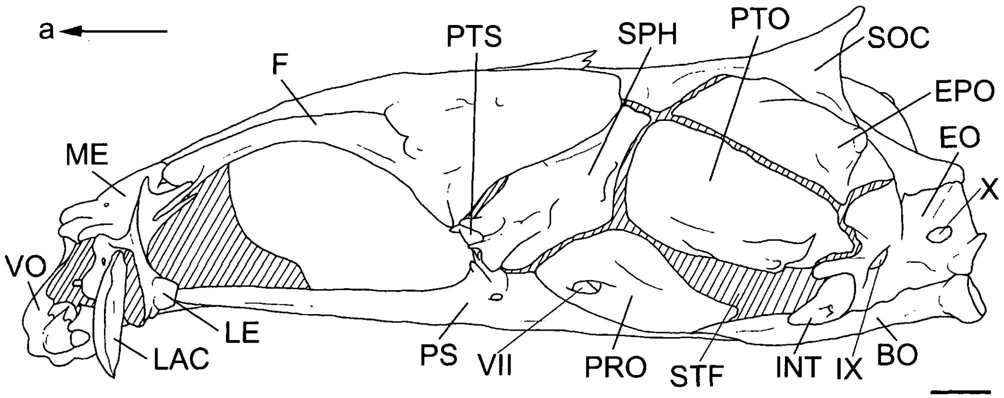


Fig. 2: Neurocranium and associated elements of *Eucyclogobius newberryi*, lateral view; LACM 37552-1, 34.2 mm SL. VII = foramen for facial nerve, IX = foramen for glossopharyngeal nerve, X = foramen for vagus nerve. Hatching represents cartilage. a = anterior, t = transparent. For additional abbreviations see Tab. 1. Scale = 1 mm.

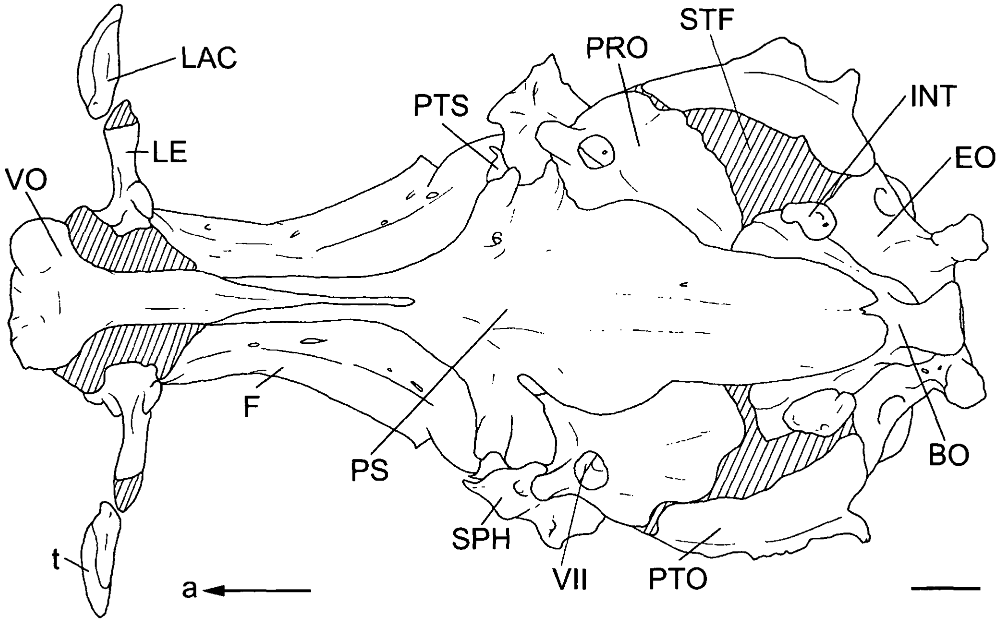


Fig. 3: Neurocranium and associated elements of *Eucyclogobius newberryi*, ventral view; LACM 37552-1, 34.2 mm SL. VII = foramen for facial nerve. Hatching represents cartilage. a = anterior, t = transparent. For additional abbreviations see Tab. 1. Scale = 1 mm.

*Quietula guaymasiae*: 8 specimens from Mexico. CAS 26056, Baja California Norte, San Felipe; 4 spec., 34.4-41.1 mm SL. LACM 35728-10, Sonora, Guaymas and surrounding areas; 2 spec., 40.2-43.9 mm SL. LACM 35733-11, Sonora, 2-3 km north of Guaymas at Miramar; 2 spec., 35.6-47.0 mm SL.

Specimens were cleared and stained (Dingerkus & Uhler 1977) and skeletons disarticulated (Mayden & Wiley 1984).

Institutions: CAS, California Academy of Sciences, San Francisco; LACM, Natural History Museum of Los Angeles County, Los Angeles; SIO, Scripps Institution of Oceanography, La Jolla.

## Tab. 1: Abbreviations used in figures:

A I = spine of anal fin, AC = anterior ceratohyal, ANG = retroarticular, ART = anguloarticular, BB = basibranchial, BH =basihyal, BO = basioccipital, BPT = basipterygium, BR = branchiostegal, CB = ceratobranchial, CL = cleithrum, COR = coracoid, D = dentary, D1 I = first spine of first dorsal fin, D2 I = spine of second dorsal fin, DH = dorsal hypohyal, DPC = dorsal procurrent cartilage, DPTG = distal pterygiophore, EB = epibranchial, EO = exoccipital, EPO = epiotic, EPR = epineural, EPT = ectopterygoid, EPU = epural, F = frontal, FIC = foramen for internal carotid artery, GR = gill raker, HB = hypobranchial, HS = haemal spine, HYO = hyomandibula, HYP = hypural, IAC = interarcual cartilage, IH = interhyal, INT = intercalary, IOP = interopercle, IPC = pelvic intercleithral cartilage, LAC = lacrimal, LE = lateral ethmoid, ME = median ethmoid,

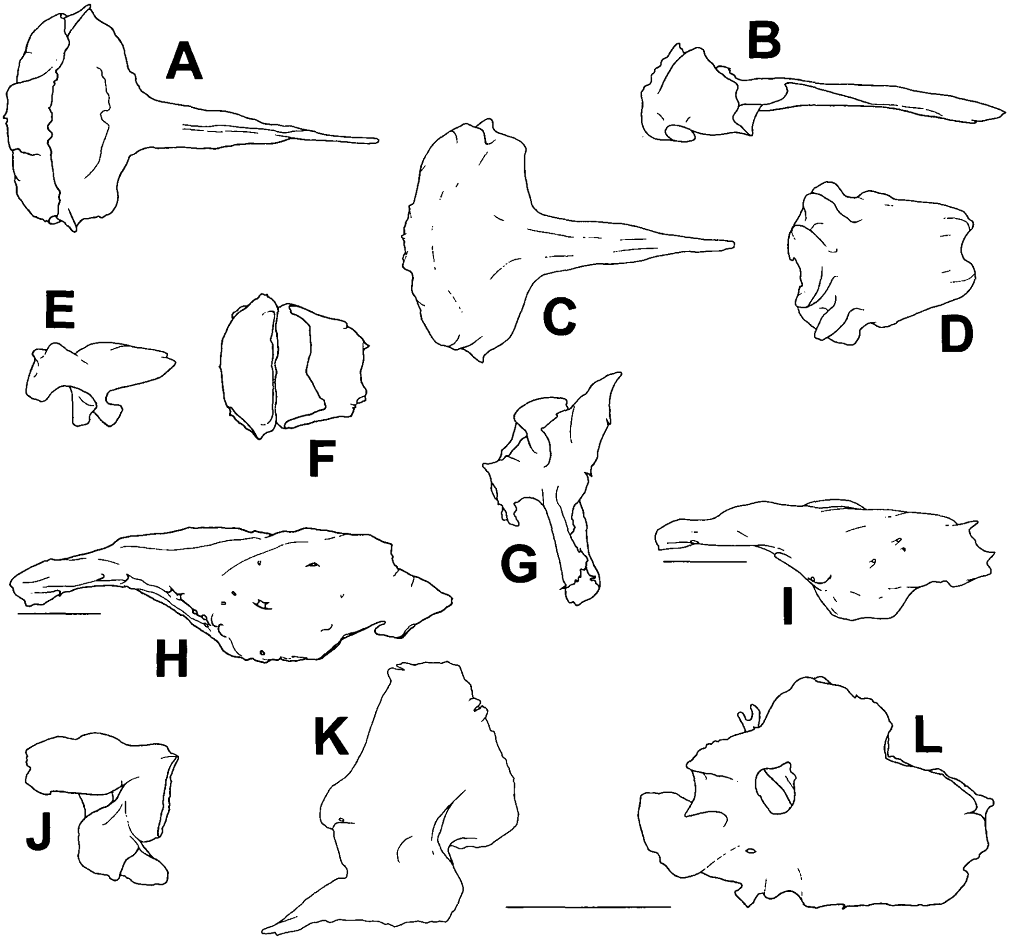


Fig. 4: Disarticulated cranial elements of *Eucyclogobius newberryi*; A-C, G-H, J-L: CAS 86281, 35.6 mm SL; D: CAS 86281, 30.9 mm SL; E-F, I: LACM 36189-2. A-C: vomer (dorsal, lateral, ventral view), D-F: median ethmoid (dorsal, lateral, ventral view), G: lateral ethmoid (lateral view), H-I: frontal (dorsal view), J: pterosphenoid (lateral view), K: sphenotic (lateral view), L: prootic (lateral view). Scale = 1 mm.

MEC = Meckel's cartilage, MPT = metapterygoid, MPTG = medial pterygiophore, MX = maxilla, NS = neural spine, OP = opercle, P1-20 = fin rays of pectoral fin, PAL = palatine, PAP = parapophysis, PB = pharyngobranchial, PC = posterior ceratohyal, PHYP = parhypural, PMX = premaxilla, POP = preopercle, PPTG = proximal pterygiophore, PR = pleural rib, PRO = prootic, PS = parasphenoid, PTG = pterygiophore, PTM = posttemporal, PTO = pterotic, PTS = pterosphenoid, QU = quadrate, RAD = pectoral radial, RC = rostral cartilage, SCA = scapula, SCL = supracleithrum, SES = sesamoid articular (coronomeckelian bone), SOC = supraoccipital, SOP = subopercle, SPH = sphenotic, STF = subtemporal fossa, SYM = symplectic, UH = urohyal, US = urostyle, V I = spine of pelvic fin, V1-5 = fin rays of pelvic fin, VH = ventral hypohyal, VIC = ventral intercleithral cartilage, VO = vomer, VPC = ventral procurrent cartilage, VT = vertebra.

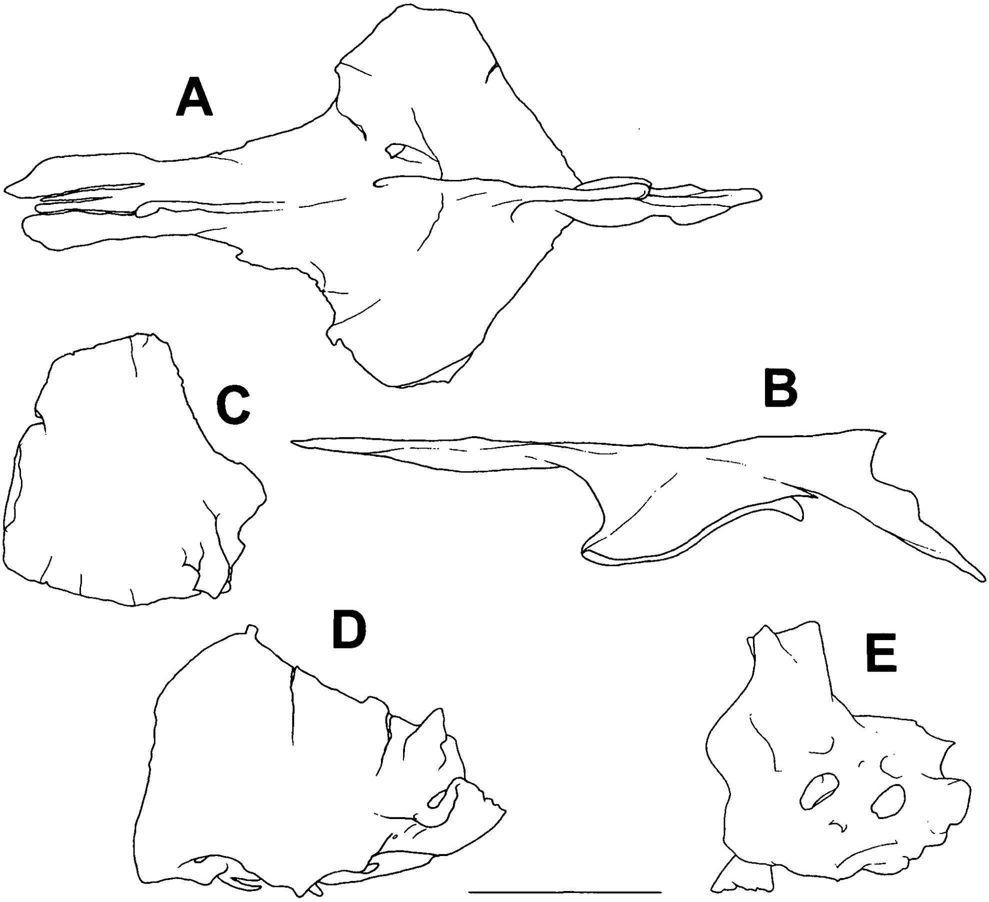


Fig. 5: Disarticulated cranial elements of *Eucyclogobius newberryi*; A, C-D: CAS 86281, 35.6 mm SL; B, E: CAS 86281, 30.9 mm SL. A-B: supraoccipital (dorsal, lateral view), C: epiotic (dorsal view), D: pterotic (lateral view), E: exoccipital (lateral view). Scale = 1 mm.

## Results

### The osteology of *Eucyclogobius newberryi* (Figs. 1 – 22)

### The osteology of *Quietula guaymasiae* (Figs. 23 – 51)

## Comparative osteology and discussion

**Neurocranium** (Figs. 1-6, 23-31). The neurocrania of both species are elongated and depressed, more distinctly in *Q. guaymasiae*. The skull is about twice as long as wide in *Q. guaymasiae* and shorter and wider in *E. newberryi*. This is especially obvious in the interorbital region of both species. In general, several bones of the neurocranium (e.g.,

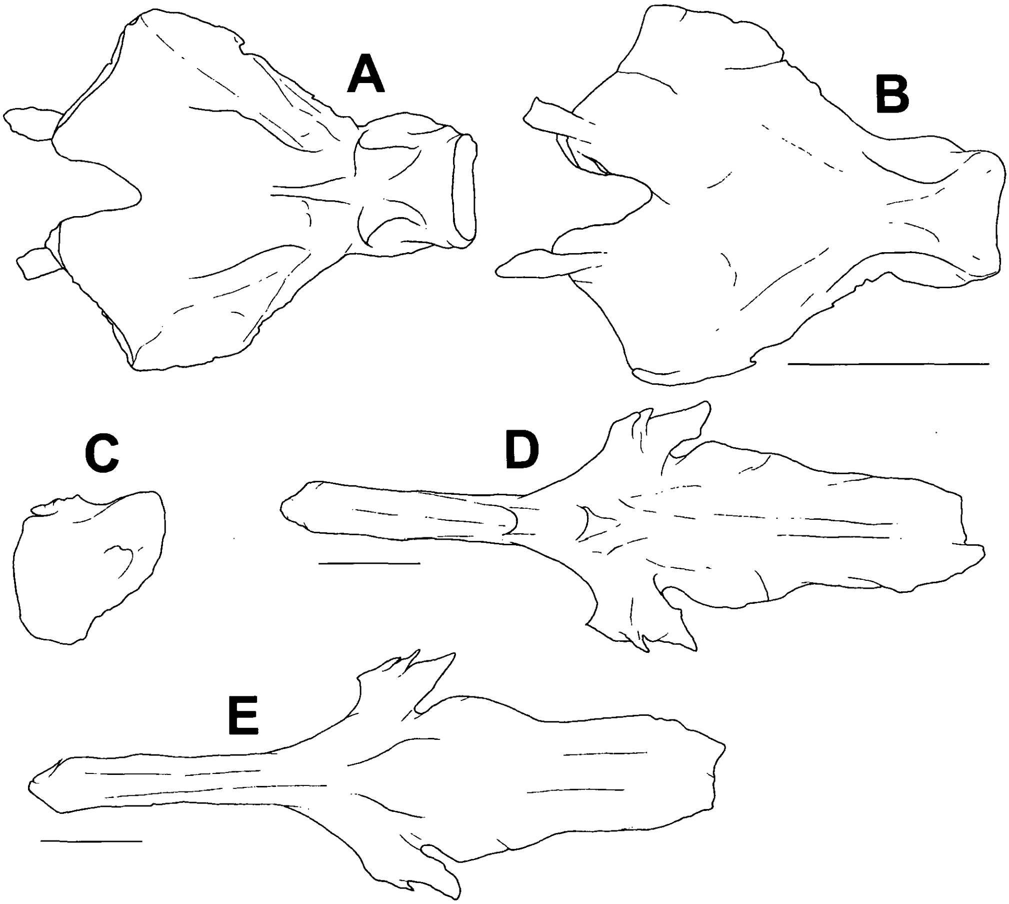


Fig. 6: Disarticulated cranial elements of *Eucyclogobius newberryi*; CAS 86281, 35.6 mm SL. A-B: basioccipital (dorsal, ventral view), C: intercalar (lateral view), D-E: parasphenoid (dorsal, ventral view). Scale = 1 mm.

the vomer, median ethmoid, pterotic, and basioccipital) are more elongate in *Q. guaymasiae*. The orbits are large but the anterior and the posterior border are more distinct in *Q. guaymasiae*. The lateral process of the lateral ethmoid, which forms the anterior border of the orbit, is much wider in *Q. guaymasiae* and its lateral rim, which forms the posterior border of the orbit, is more pronounced. Its posterior surface is flat and plate-like in *E. newberryi* but cup-shaped in *Q. guaymasiae*. The median ethmoid is primarily flat in both species but with a distinct bony ventral extension in *Q. guaymasiae*. This ventral extension (interocular septum of BIRDSONG (1975)) separates the anterior region of the orbits medially. It is cartilaginous in *E. newberryi*. The frontal bones are broad and flat posteriorly and narrow anteriorly between the orbits, successively in *E. newberryi* and abruptly in *Q. guaymasiae*. STEVENSON (2002a) found a wide gap between the anterior extensions of the frontals in the specimens of *E. newberryi* he examined, but this gap was absent in the specimens examined for this study. The lateral margin of the

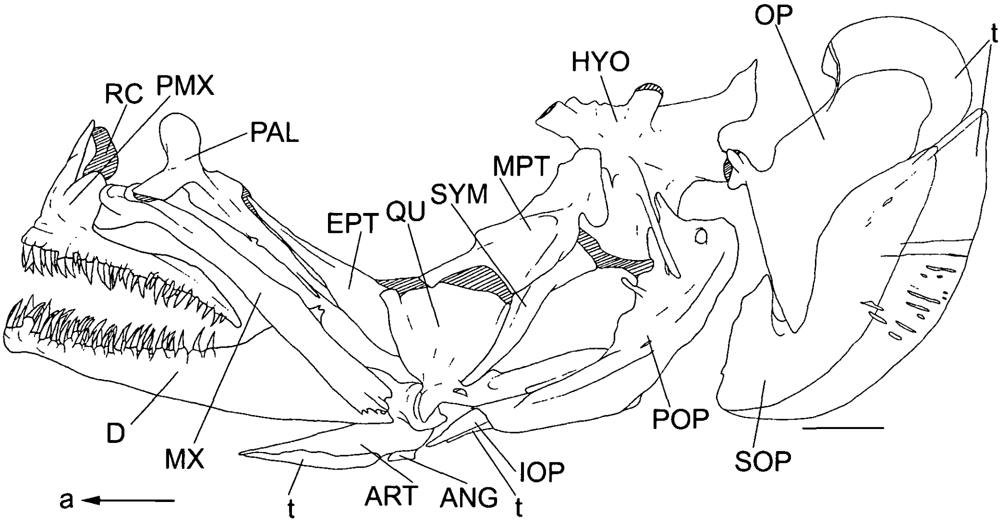


Fig. 7: Jaws, suspensorium and opercular bones of *Eucyclogobius newberryi*, lateral view; LACM 37552-1, 34.2 mm SL. Hatching represents cartilage. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

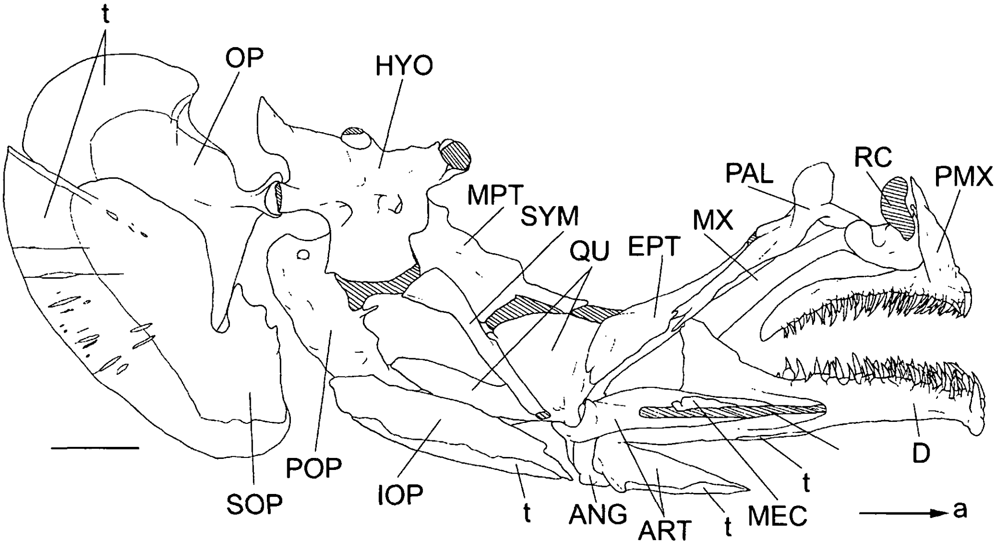


Fig. 8: Jaws, suspensorium and opercular bones of *Eucyclogobius newberryi*, medial view; LACM 37552-1, 34.2 mm SL. Hatching represents cartilage. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

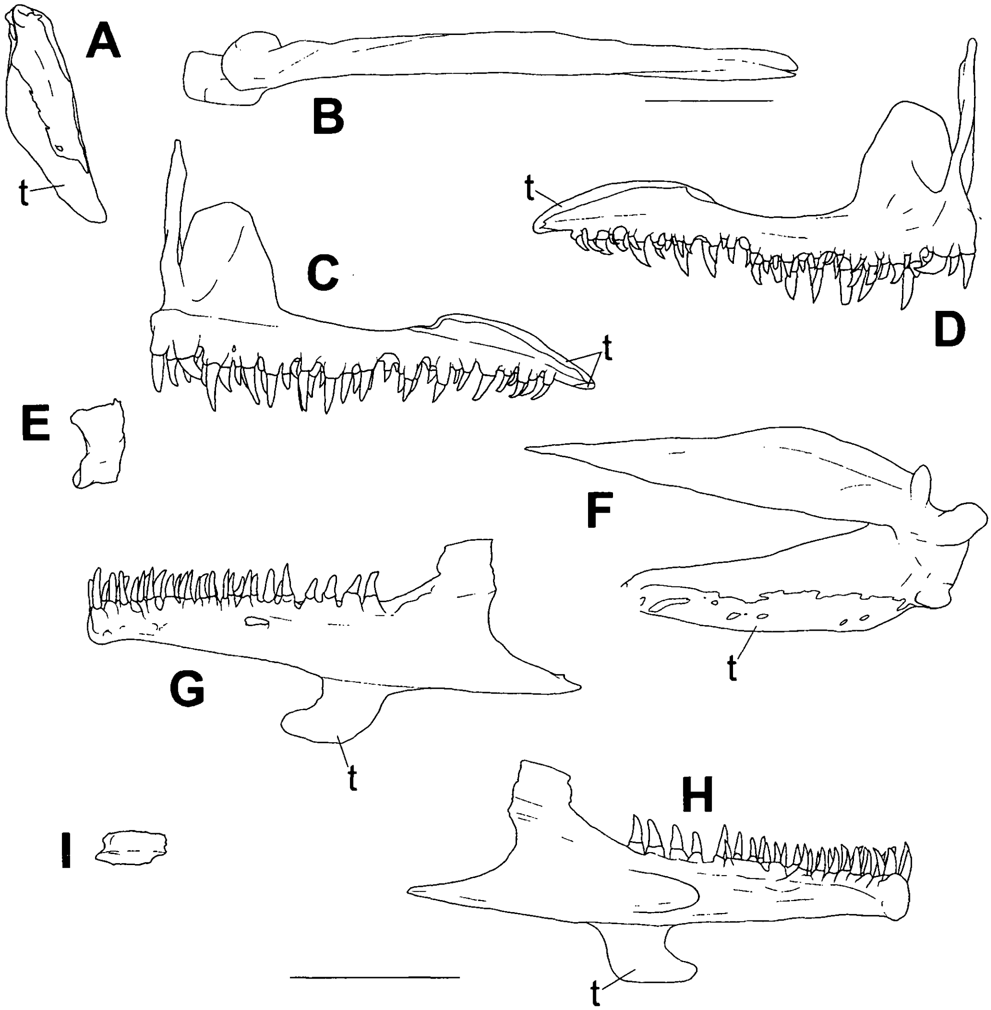


Fig. 9: Disarticulated elements of the suspensorium, opercular bones and lacrimal of *Eucyclogobius newberryi*; A: LACM 36189-2, 22.2 mm SL; B, E: CAS 86281, 35.6 mm SL; C-D, F, I: CAS 86281, 30.9 mm SL; G-H: LACM 36189-2, 22.8 mm SL. A: lacrimal (lateral view), B: maxilla (lateral view), C-D: premaxilla (lateral, medial view), E: retroarticular (lateral view), F: anguloarticular (lateral view), G-H: dentary (lateral, medial view), I: sesamoid articular (lateral view). t = transparent. Scale = 1 mm.

frontal, posterodorsal to the orbit, carries a shallow trough in *E. newberryi.* This trough is distinctly developed in *Q. guaymasiae* and carries the supraorbital canal of the lateral line system. The posterior part of the frontal bone bears a small foramen. A small branch of the supraorbital trunc passes through this foramen to innervate a transversal row of free neuromasts posterior to the supraorbital canal (AHNELT & GÖSCHL 2003, AHNELT & BOHACEK 2004). Such a foramen in the flat portion of the frontal bone is known from several gobiid species (e.g. MURDY 1985, GILL 1993) including 'bay gobies'

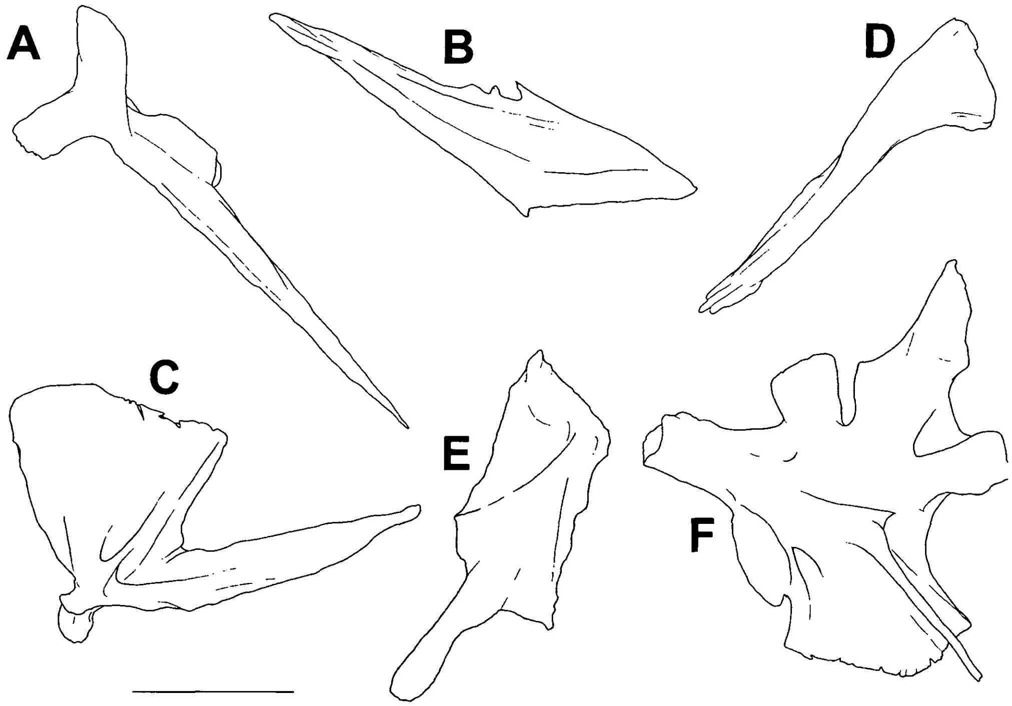


Fig. 10: Disarticulated elements of the suspensorium of *Eucyclogobius newberryi*, lateral view; A-D, F: CAS 86281, 35.6 mm SL; E: CAS 86281, 30.9 mm SL. A: palatine, B: ectopterygoid, C: quadrate, D: symplectic, E: metapterygoid, F: hyomandibular. Scale = 1 mm.

(Miljković 2004, Kindermann 2005), but seemingly does not occur in all gobiids (e.g. Birdsong 1975, Mestermann & Zander 1984, Economidis & Miller 1990, Gill 1993). The sphenotic and the pterotic of *Q. guaymasiae* display distinct bony ridges ventrolaterally. These ridges are remnants of the bony support of the otic and postotic canals of the lateral line system, present in many Gobionellinae but absent in *E. newberryi* and *Q. guaymasiae*. The intercalar bones, generally reduced in size in the Gobioidei, are somewhat larger in *Q. guaymasiae* compared with those of *E. newberryi*. A small lateral process marks the position of insertion of the ligament which connects the ventrolateral process of the posttemporal with the neurocranium in both species. The lacrimal bones of both species, last remnants of the infraorbital series, are small and flat. The lacrimal of E. *newberryi* is straight and most of it is ossified, while the lacrimal of *Q. guaymasiae* has the shape of a sickle and is only ossified in its dorsal part. The largest part does not stain for calcium and is transparent in enzymatic cleared and stained specimens. A nasal bone is absent in both species, as in all other members of the *Chasmichthys* group and several other Gobionellines (Stevenson 2002a).

**Jaws, Suspensorium and Opercular series** (Figs. 7-11, 32-37). The suspensorium of gobioid fishes differs considerably from the typical perciform type. Most notably, there is a large suspensorial interspace between the preopercle and the symplectic in all but the most basic gobioids, the Rhyacichthyidae (Miller 1973, Harrison 1989). Like the

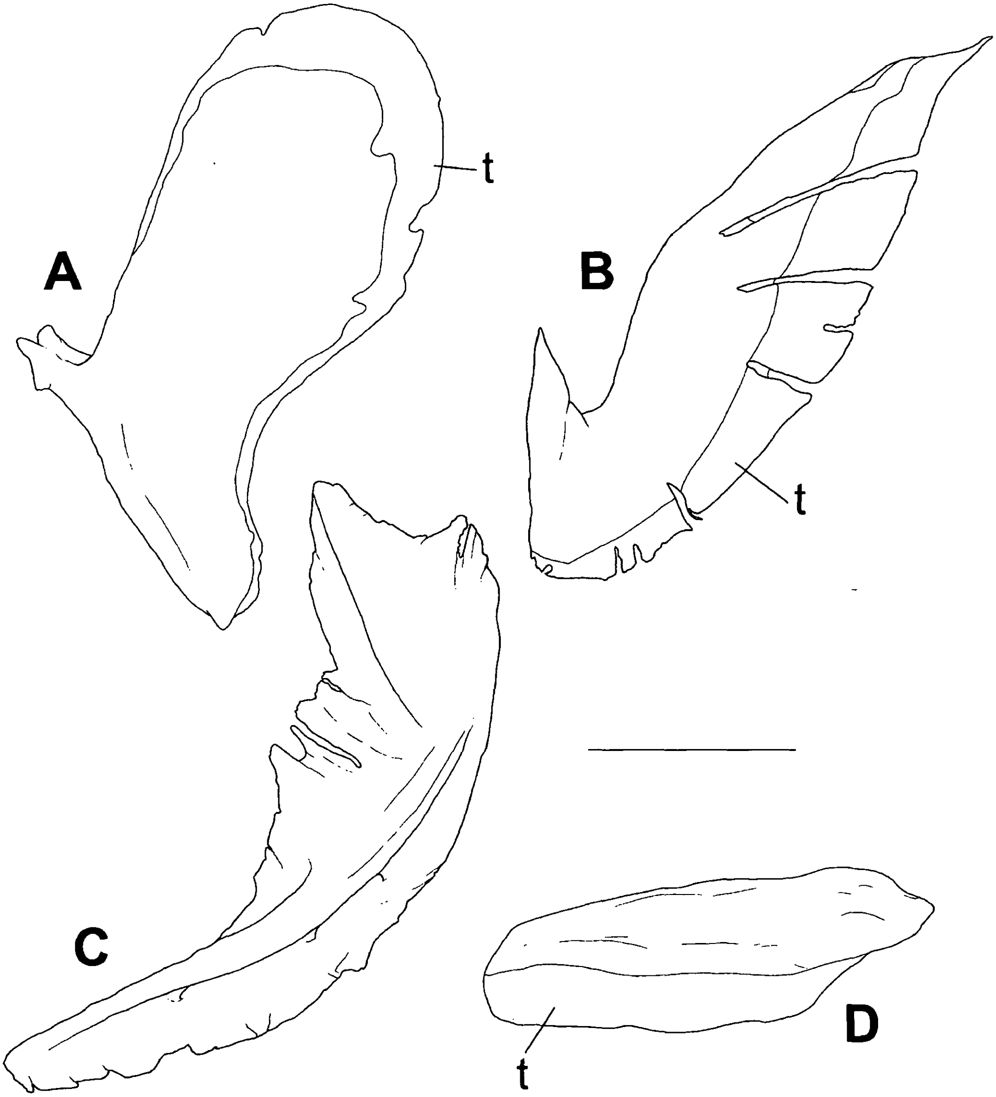


Fig. 11: Disarticulated opercular bones of *Eucyclogobius newberryi*, lateral view; A-B: LACM 36189-2, 22.8 mm SL; C: CAS 86281, 35.6 mm SL; D: LACM 36189-2, 22.2 mm SL. A: opercle, B: subopercle, C: preopercle, D: interopercle. t = transparent. Scale = 1 mm.

neurocranium, the suspensorium of many gobiids exhibits character simplification, for example in the reduction or absence of the endopterygoid (also referred to as mesopterygoid by several authors) (SPRINGER 1983, HARRISON 1989). The palatoquadrate complex of *E. newberryi* and *Q. guaymasiae*, formed by the palatine, ectopterygoid, and quadrate, is unspecialised *sensu* HARRISON (1989): the palatine extends about half the length of the ectopterygoid, the ectopterygoid joins with the vertical anterior edge of the quadrate and the dorsal lamina of the quadrate is long.

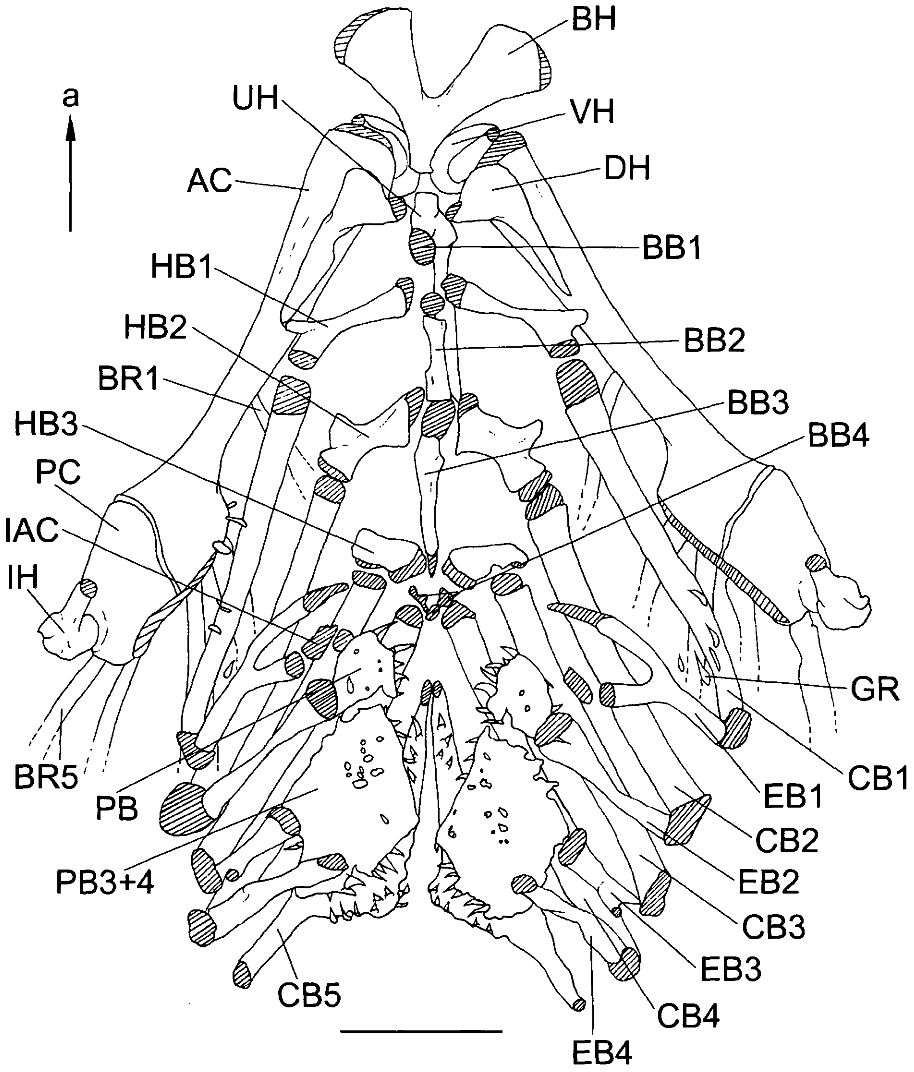
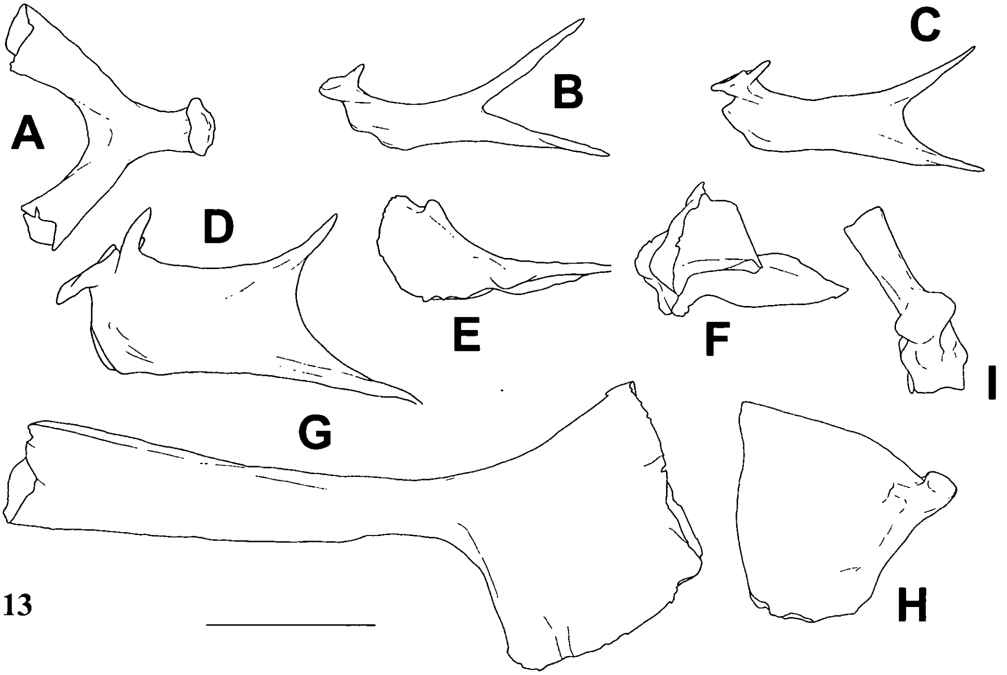


Fig. 12: Branchial apparatus and hyoid arch of *Eucyclogobius newberryi*, dorsal view; LACM 37552-1, 34.2 mm SL. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

Fig. 13: Disarticulated branchial and hyal bones of *Eucyclogobius newberryi*; A, E-I: CAS 86281, 35.6 mm SL; B: LACM 36189-2, 22.8 mm SL; C: LACM 36189-2, 21.0 mm SL. A: basihyal (dorsal view), B: urohyal (lateral view), C-D: variations of urohyal (lateral view), E: dorsal hypohyal (lateral view), F: ventral hypohyal (lateral view), G: anterior ceratohyal (lateral view), H: posterior ceratohyal (lateral view), I: interhyal (lateral view). Scale = 1 mm.

Fig. 14: Branchiostegals of *Eucyclogobius newberryi*, lateral view; LACM 36189-2, 22.8 mm SL. A: branchiostegal 1, B: branchiostegal 2, C: branchiostegal 3, D: branchiostegal 4, E: branchiostegal 5. t = transparent. Scale = 1 mm.



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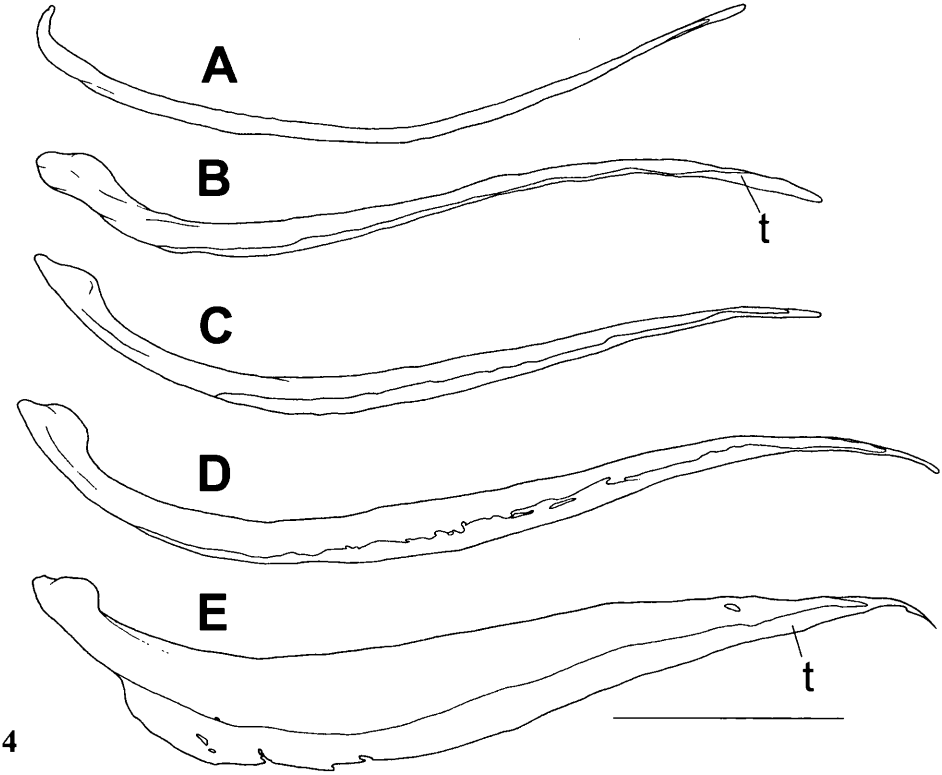

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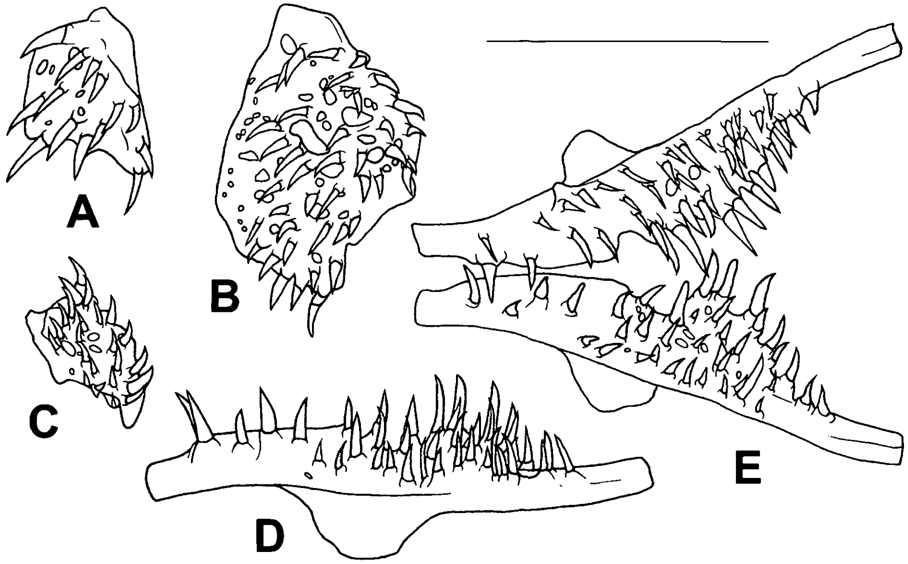
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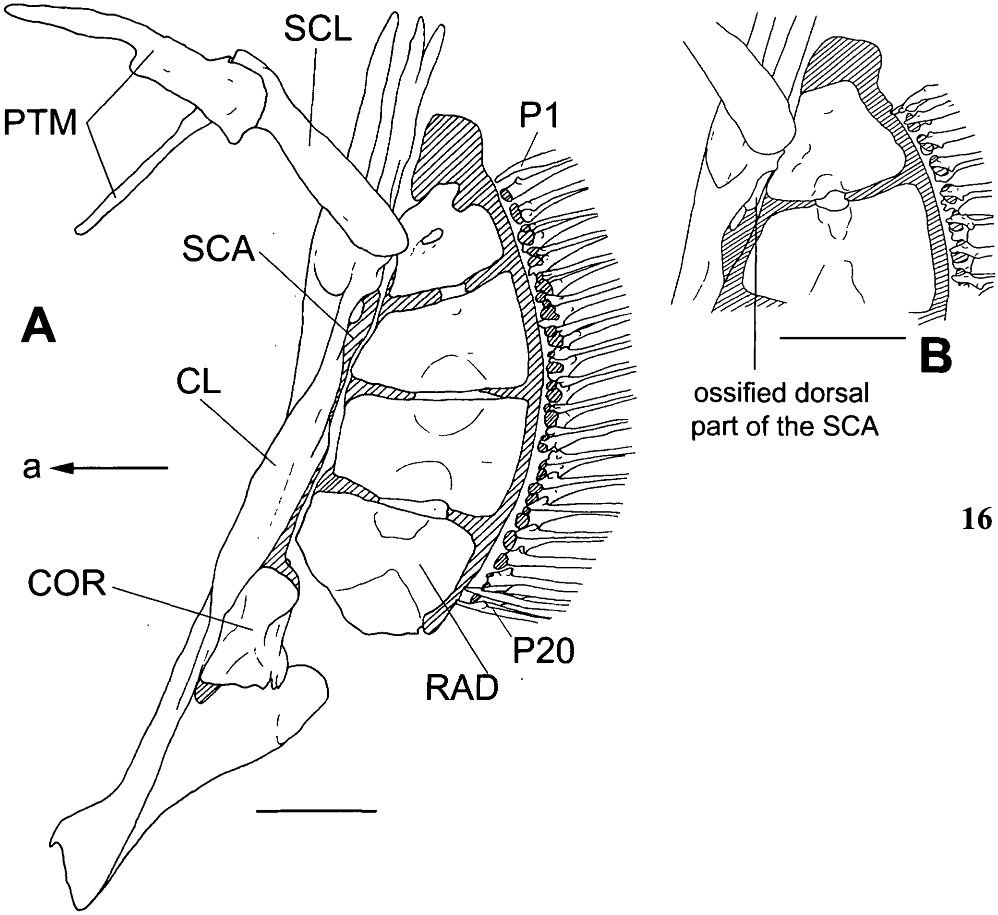
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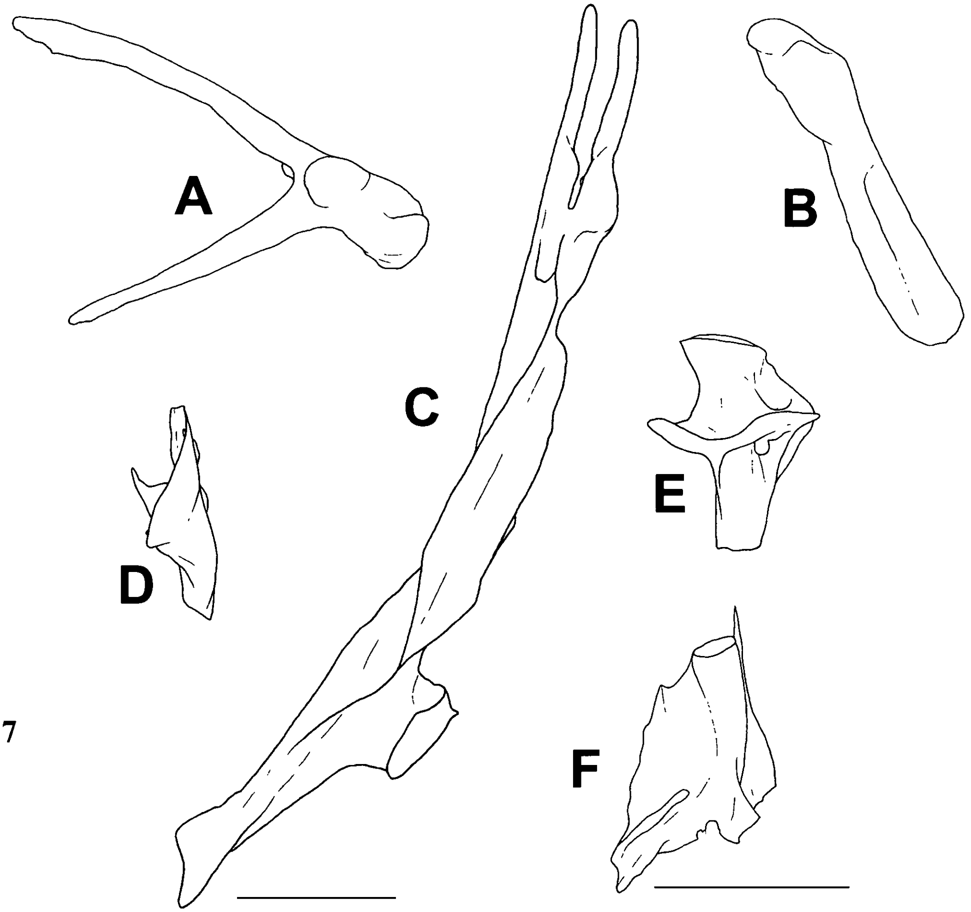


Fig. 17: Disarticulated elements of the pectoral and pelvic girdle of *Eucyclogobius newberryi*; A-C: CAS 86281, 35.8 mm SL; D-E: CAS 86281, 30.9 mm SL; F: LACM 36189-2, 22.8 mm SL. A: posttemporal (lateral view), B: supracleithrum (lateral view), C: cleithrum (lateral view), D-E: coracoid (lateral, medial view), F: basipterygium (ventral view). Scale = 1 mm.

Fig. 15: Disarticulated pharyngeal tooth plates of *Eucyclogobius newberryi*; A-C: LACM 36189-2, 22.8 mm SL; D-E: LACM 36189-2, 22.2 mm SL. A: pharyngobranchial 2 (ventral view), B: pharyngobranchial 3 (ventral view), C: pharyngobranchial 4 (ventral view), D: left ceratobranchial 5 (lateral view), E: left and right ceratobranchial 5 (dorsal view). Scale = 1 mm.

Fig. 16: Left pectoral girdle of *Eucyclogobius newberryi*, lateral view; A: LACM 37552-1, 34.2 mm SL; B: LACM 37552-1, 36.7 mm SL. A: pectoral girdle, B: detail with partly ossified scapula. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

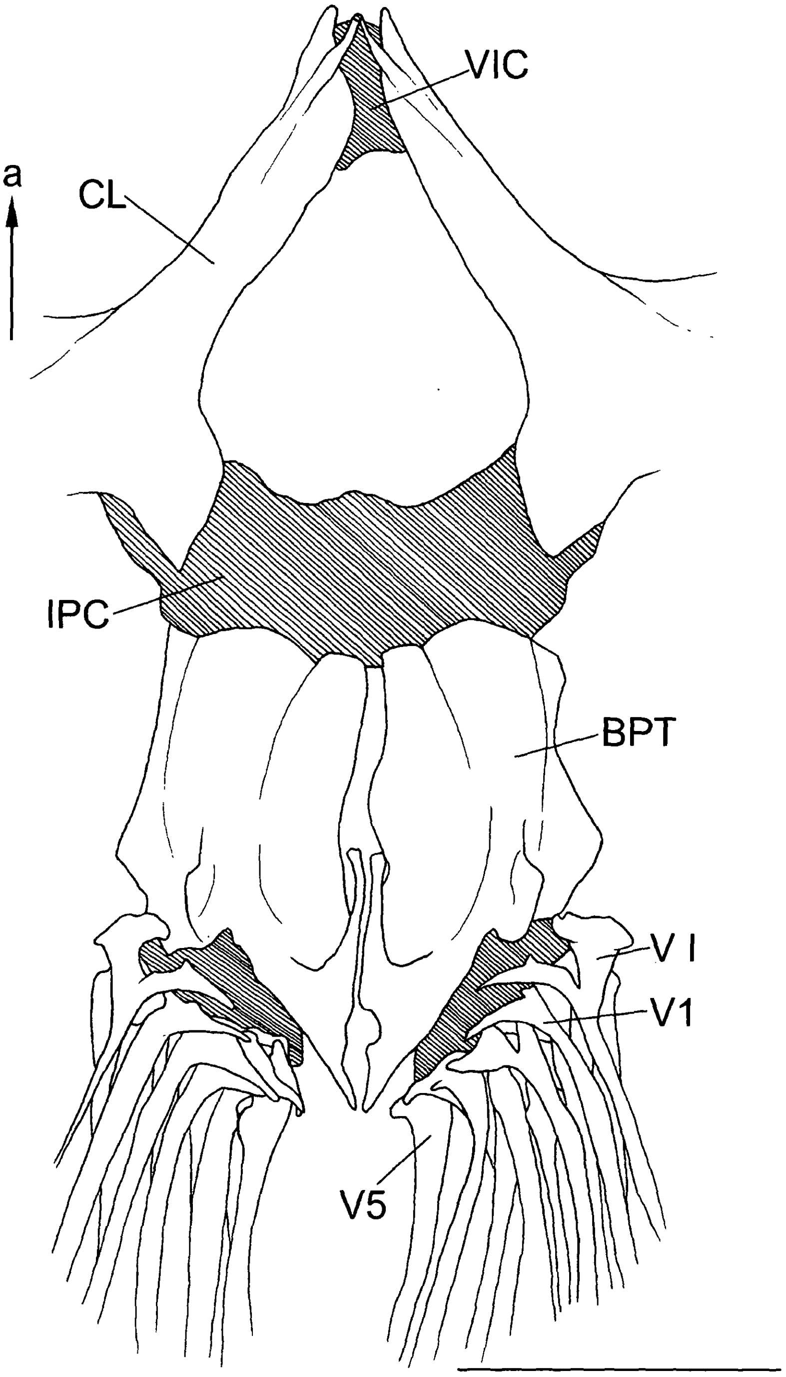


Fig. 18: Pelvic girdle of *Eucyclogobius newberryi*, ventral view; UMMZ 132897, 22.7 mm SL. Hatching represents cartilage. a = anterior. Scale = 1 mm.

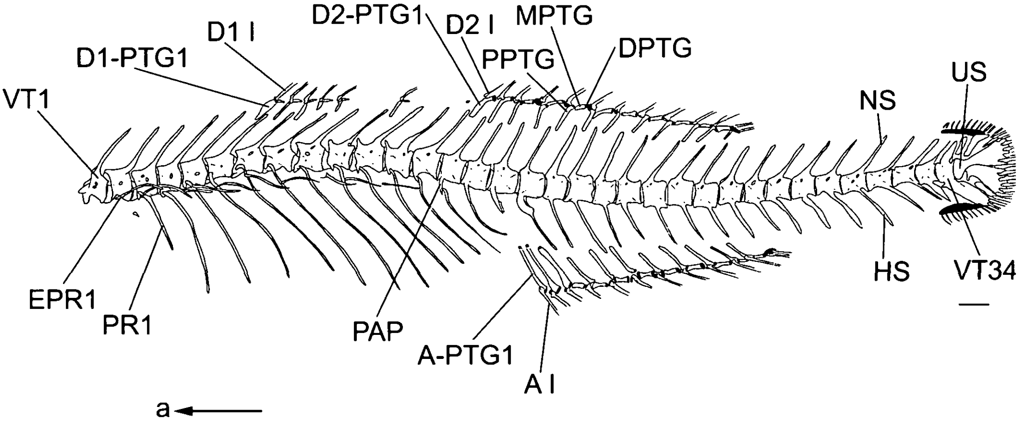


Fig. 19: Vertebral column and median fin elements of *Eucyclogobius newberryi*, lateral view; LACM 37552-1, 34.2 mm SL. Black areas represent cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

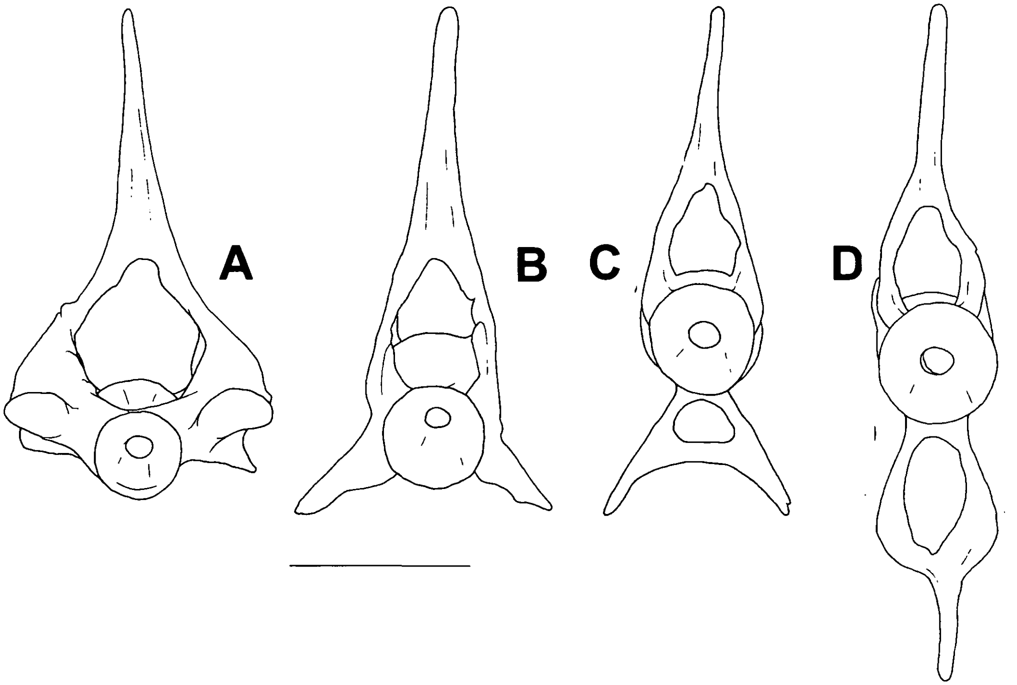


Fig. 20: Disarticulated vertebrae of *Eucyclogobius newberryi*, anterior view; A: CAS 86281, 30.9 mm SL. B-D: CAS 86281:6, 35.6 mm SL; A: first vertebra, B: penultimate precaudal vertebra, C: last precaudal vertebra (intermediate vertebra), D: first caudal vertebra. Scale = 1 mm.

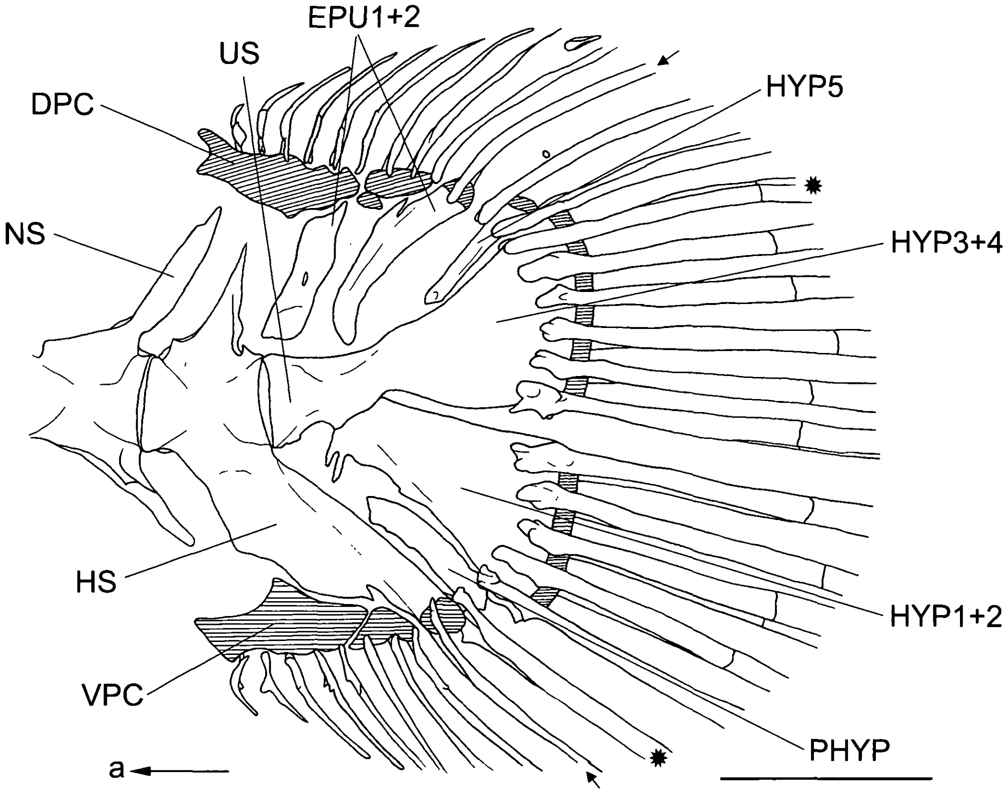


Fig. 21: Caudal skeleton of *Eucyclogobius newberryi*, lateral view; LACM 37552-1, 25.6 mm SL. Arrows mark most dorsal and ventral segmented fin rays, stars represent most dorsal and ventral segmented and branched fin rays. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

In general the jaws and the anterior bones of the suspensorium are more elongate in *Q. guaymasiae*. The maxilla is especially long and slender in this species, extending posteriorly distinctly behind the jaw articulation. The premaxilla is similarly shaped in both species, but the postmaxillary process is more distinct in *Q. guaymasiae*. The dentary and the anguloarticular are longer and more slender in *Q. guaymasiae* and are more robust in *E. newberryi*. A ventral process originates in approximately the middle of the dentary in both species. It is not ossified and its tip extends anteriorly. This process is distinctly longer in *Q. guaymasiae*. The teeth in the premaxilla and the dentary of both species are conical and similarly arranged. Probably because of elongation of these bones the teeth are more numerous in *Q. guaymasiae*.

The palatine is T-shaped and similar in both species, whereas the ectopterygoid differs in length. It is somewhat shorter than the palatine in *E. newberryi*, but it is more slen-

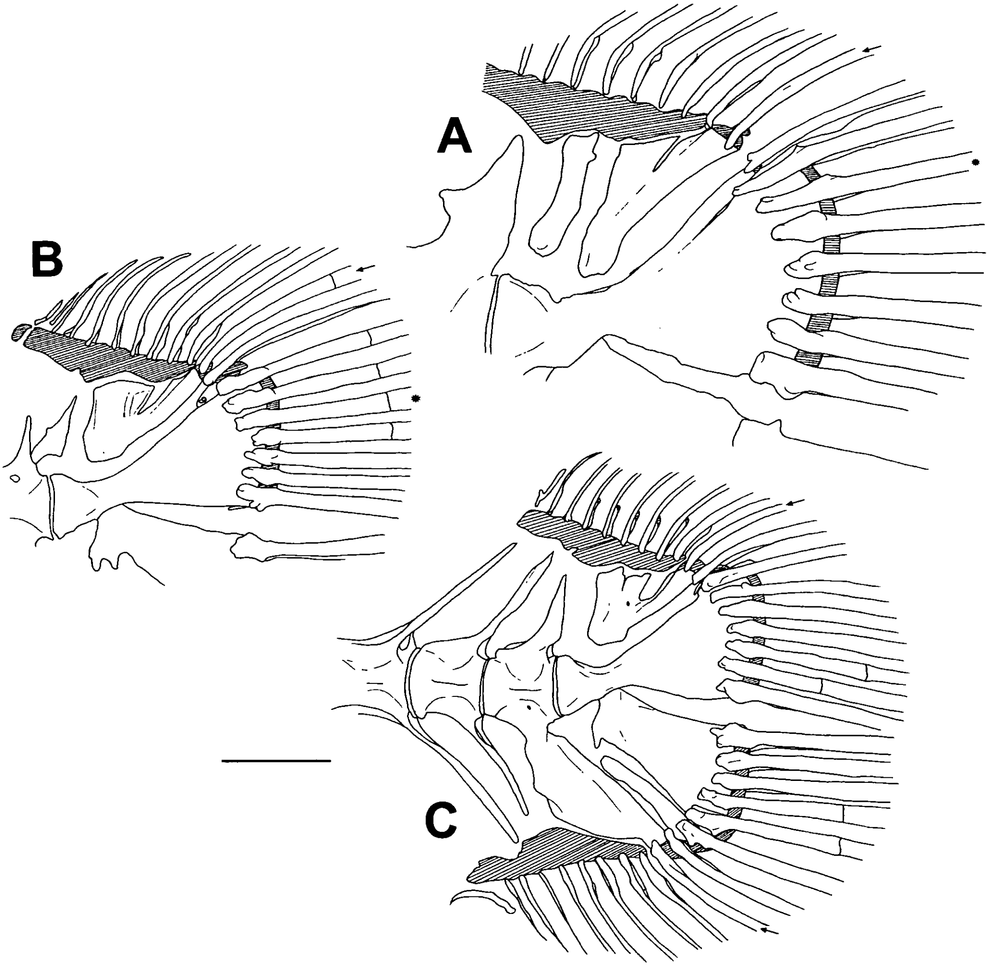


Fig. 22: Variations of the caudal skeleton of *Eucyclogobius newberryi*, lateral view; A: LACM 37552-1, 36.7 mm SL; B: UMMZ 132897:1, 22.6 mm SL; C: UMMZ 132897:2, 22.7 mm SL. A: HYP5 fused with HYP3+4, B: one single EPU, HYP reduced, C: HYP5 reduced, no segmented and branched fin rays. Arrows mark most dorsal and ventral segmented fin rays, stars represent most dorsal segmented and branched fin rays. Hatching represents cartilage. Scale = 1 mm.

der and longer in *Q. guaymasiae*. The shape of the metapterygoid differs distinctly between the two species. This bone is elongate and slender in *E. newberryi*, but wide and triangular in *Q. guaymasiae*. This difference is mostly based on the divergent development of the bony 'bridge' which extends anteriorly from the metapterygoid to the dorsal lamina of the quadrate. This bony 'bridge' is narrow and short in *E. newberryi* and broad and long in *Q. guaymasiae*. In the latter species it reaches anteriorly to the ectopterygoid. In addition, the metapterygoid of *Q. guaymasiae* is pierced by a foramen, through which the ramus mandibularis internus of the facial nerve passes. This is seem-

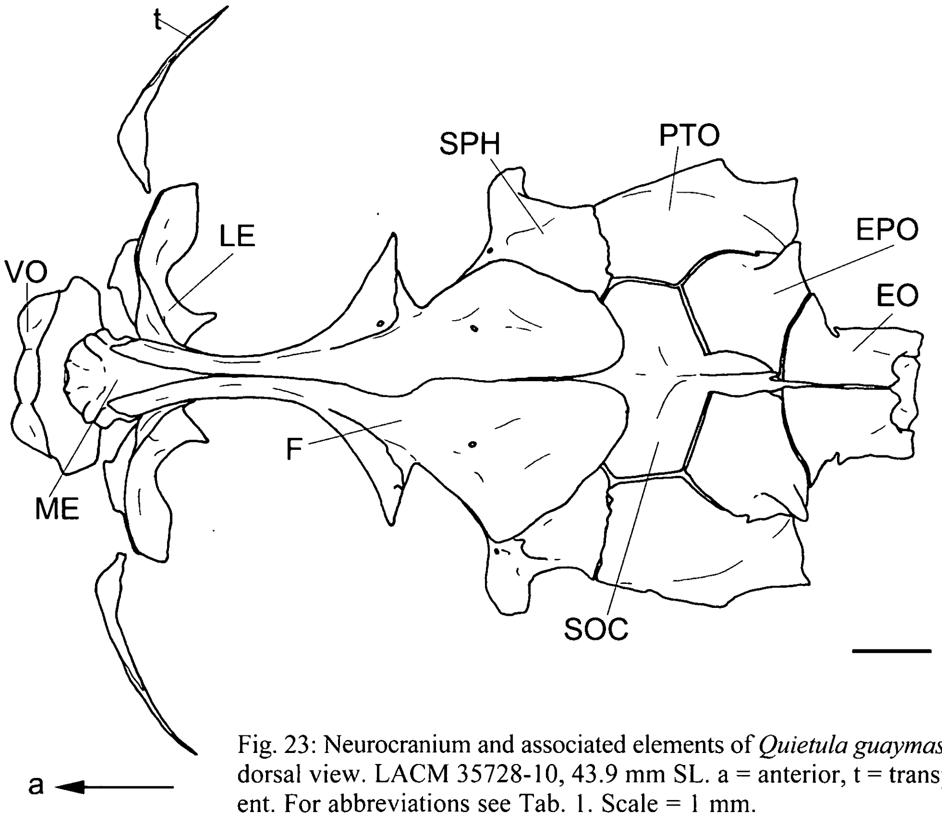


Fig. 23: Neurocranium and associated elements of *Quietula guaymasiae*, dorsal view. LACM 35728-10, 43.9 mm SL. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

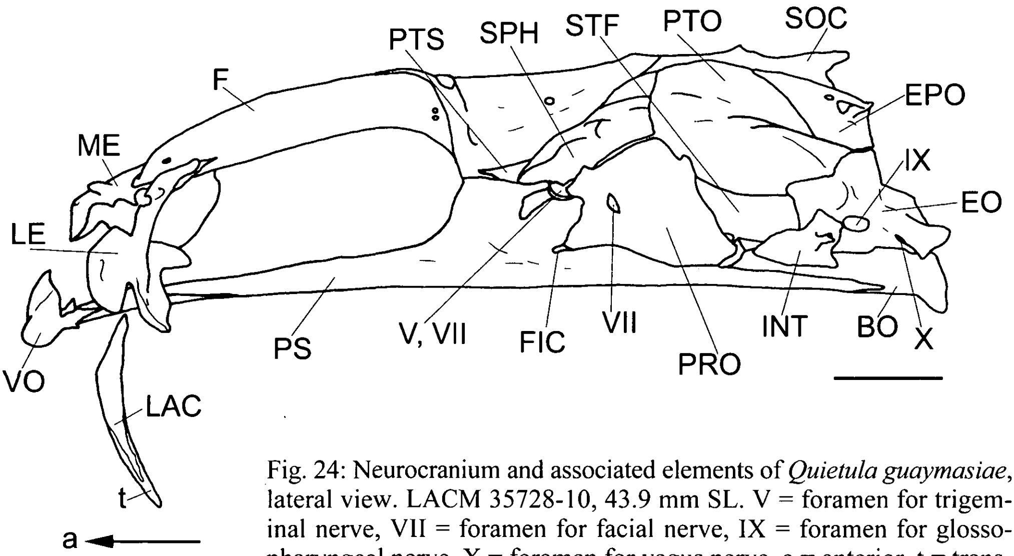


Fig. 24: Neurocranium and associated elements of *Quietula guaymasiae*, lateral view. LACM 35728-10, 43.9 mm SL. V = foramen for trigeminal nerve, VII = foramen for facial nerve, IX = foramen for glossopharyngeal nerve, X = foramen for vagus nerve. a = anterior, t = transparent. For additional abbreviations see Tab. 1. Scale = 1 mm.

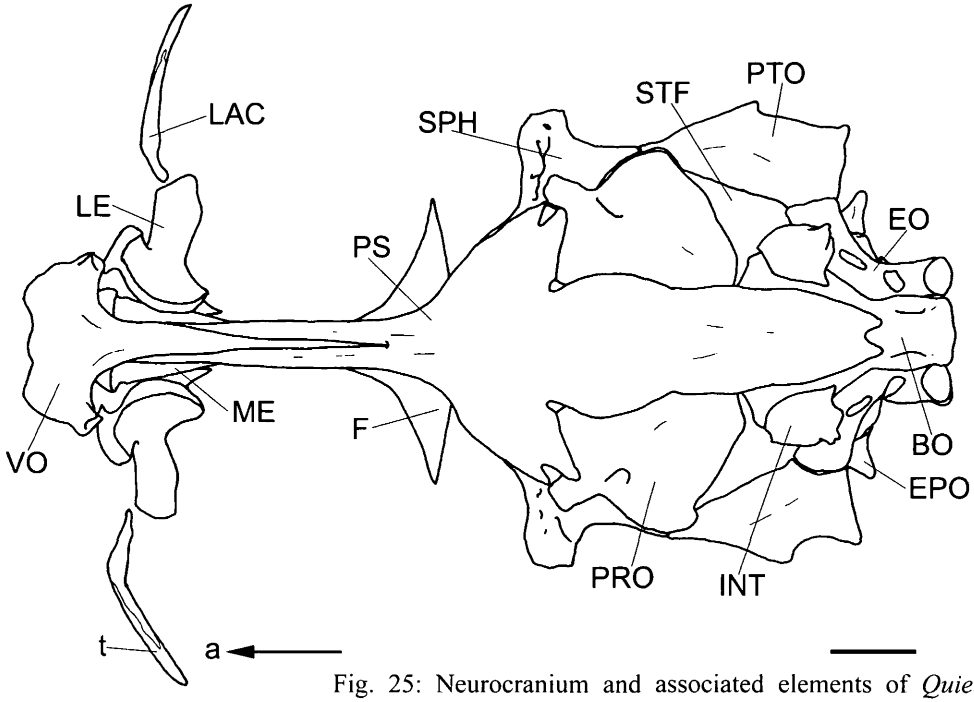


Fig. 25: Neurocranium and associated elements of *Quietula guaymasiae*, ventral view. LACM 35728-10, 43.9 mm SL. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

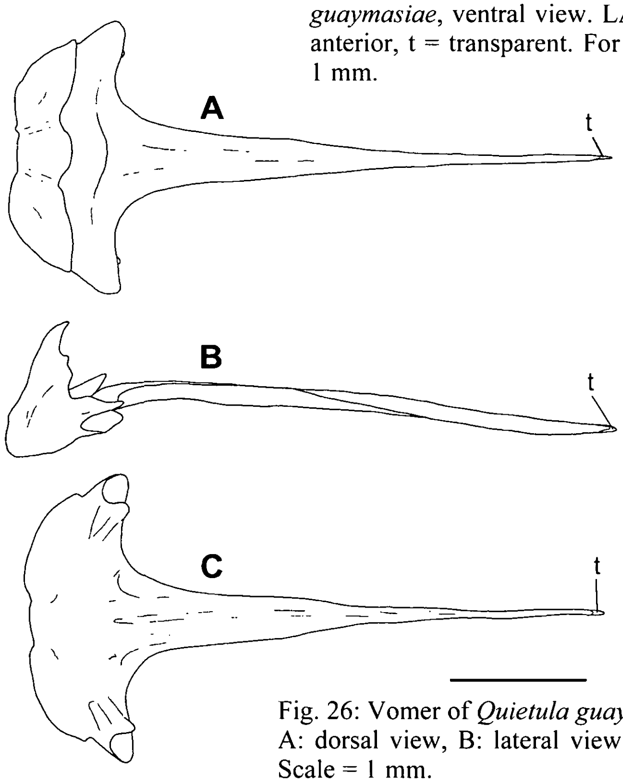


Fig. 26: Vomer of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A: dorsal view, B: lateral view, C: ventral view. t = transparent. Scale = 1 mm.

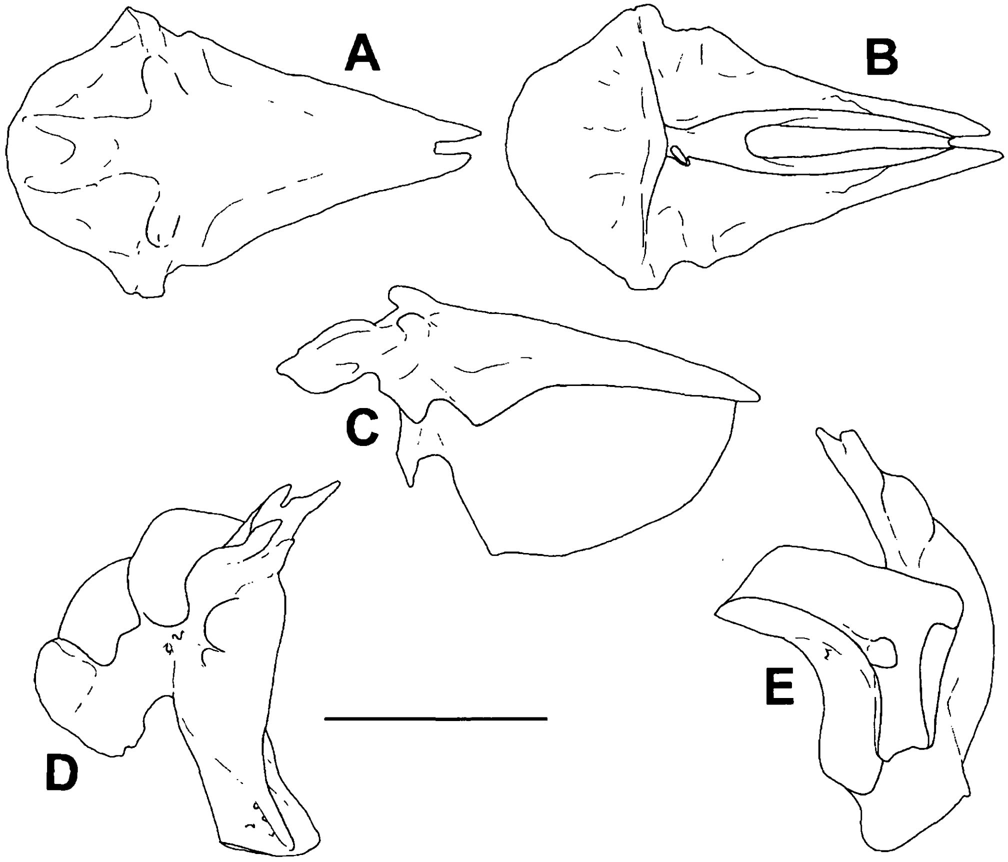


Fig. 27: Disarticulated cranial elements of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-C: median ethmoid (dorsal, ventral, lateral view), D-E: lateral ethmoid (lateral, medial view). Scale = 1 mm.

**Figs. 29 - 32 see next pages**

Fig. 29: Disarticulated cranial elements of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: pterosphenoid (lateral, medial view), C-D: sphenotic (lateral, medial view), E-F: pterotic (lateral, medial view). Scale = 1 mm.

Fig. 30: Disarticulated cranial elements of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: prootic (lateral, medial view), C-D: epiotic (lateral, medial view), E: intercalar (lateral view), F-G: exoccipital (lateral, medial view). Scale = 1 mm.

Fig. 31: Disarticulated cranial elements of *Quietula guaymasiae*; A-B: parasphenoid (dorsal, ventral view), CAS 26056, 41.1 mm SL. C-D: basioccipital (dorsal, ventral view), CAS 26056:4, 34.4 mm SL. Scale = 1 mm.

Fig. 32: Jaws, suspensorium and opercular bones of *Quietula guaymasiae*, lateral view; LACM 35728-10, 43.9 mm SL. Hatching represents cartilage. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

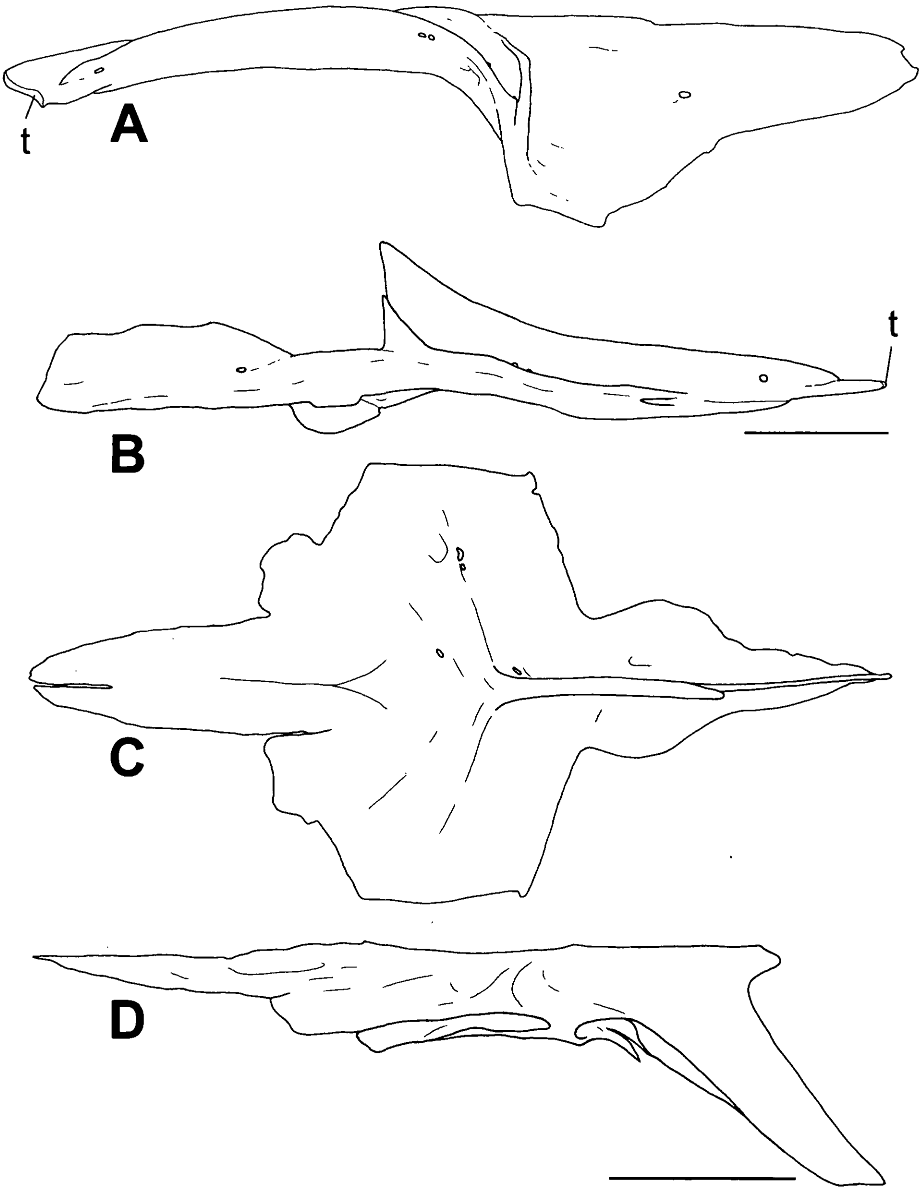
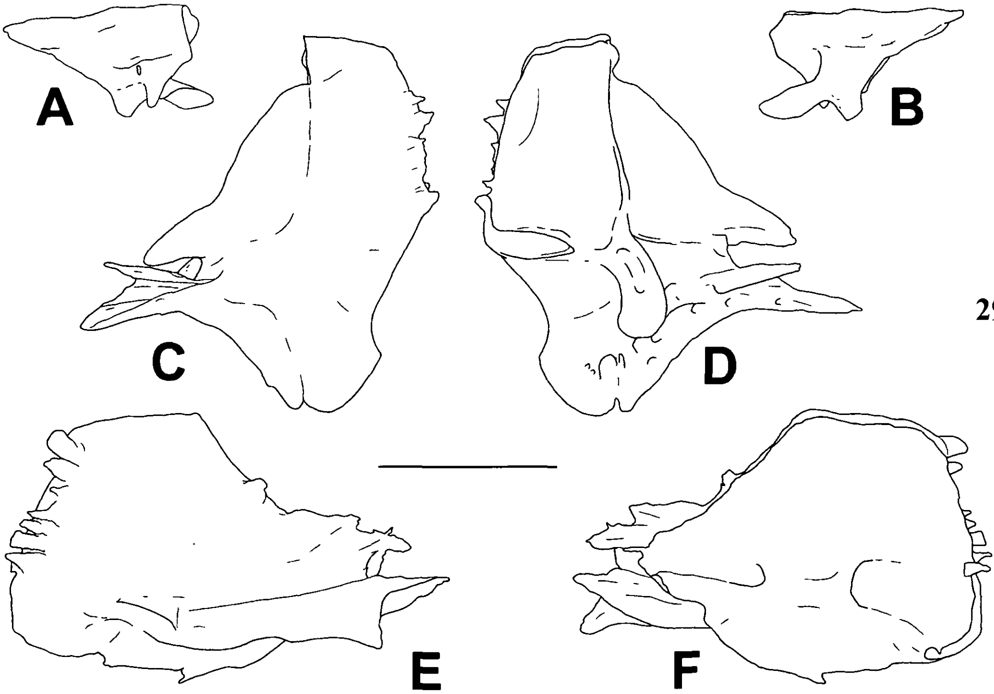


Fig. 28: Disarticulated cranial elements of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: frontal (lateral, medial view), C-D: supraoccipital (dorsal, lateral view). t = transparent. Scale = 1 mm.



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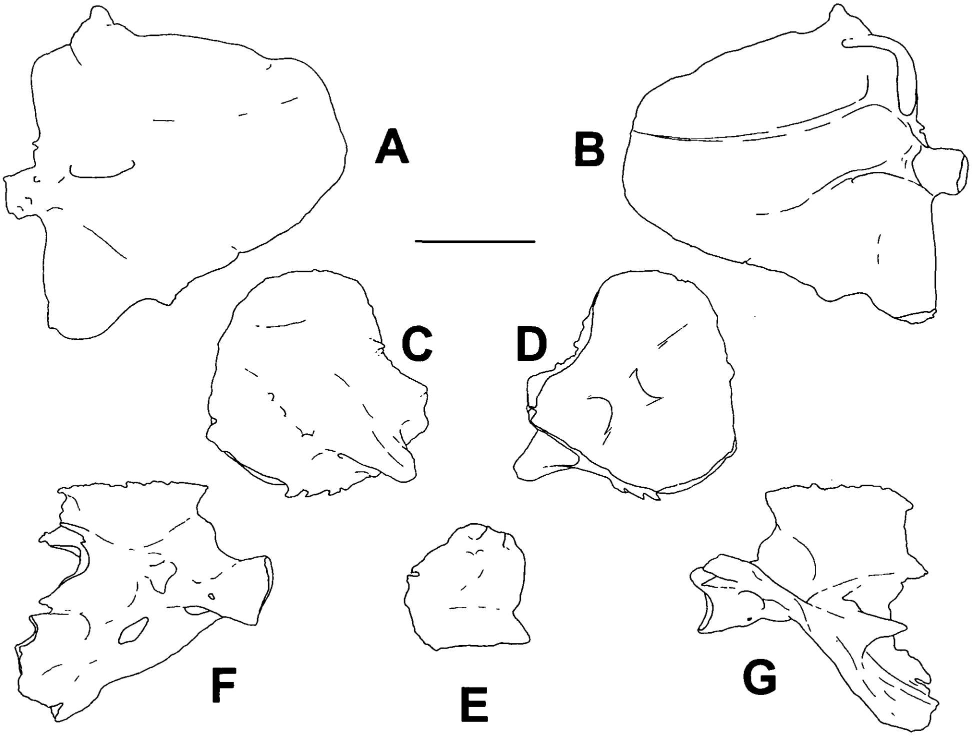

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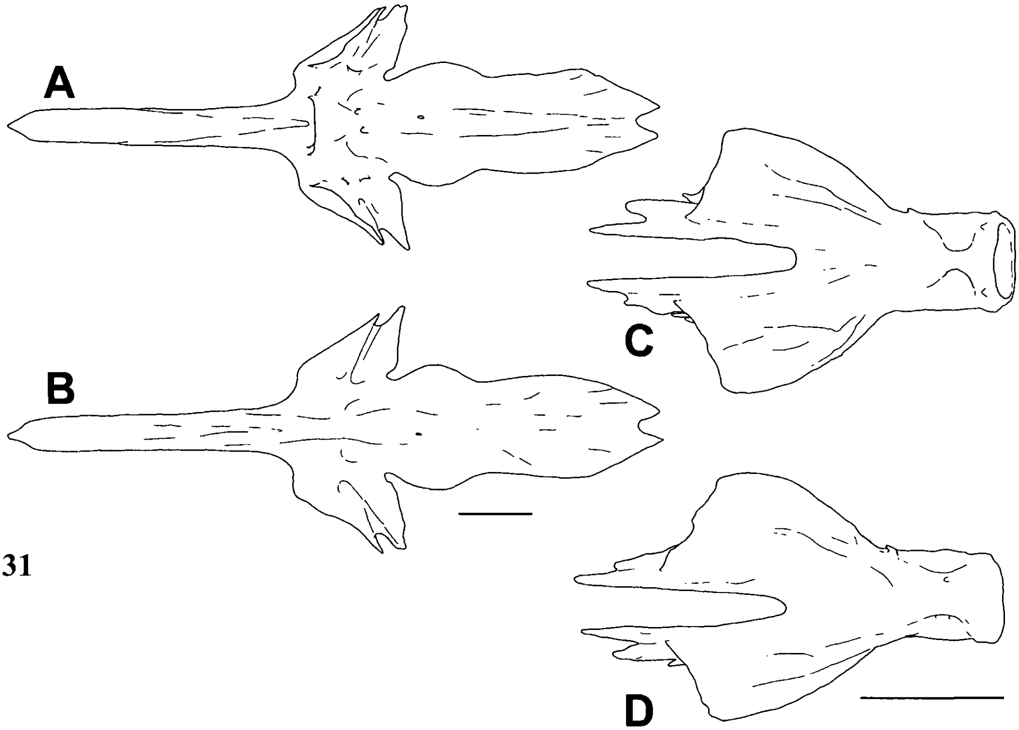

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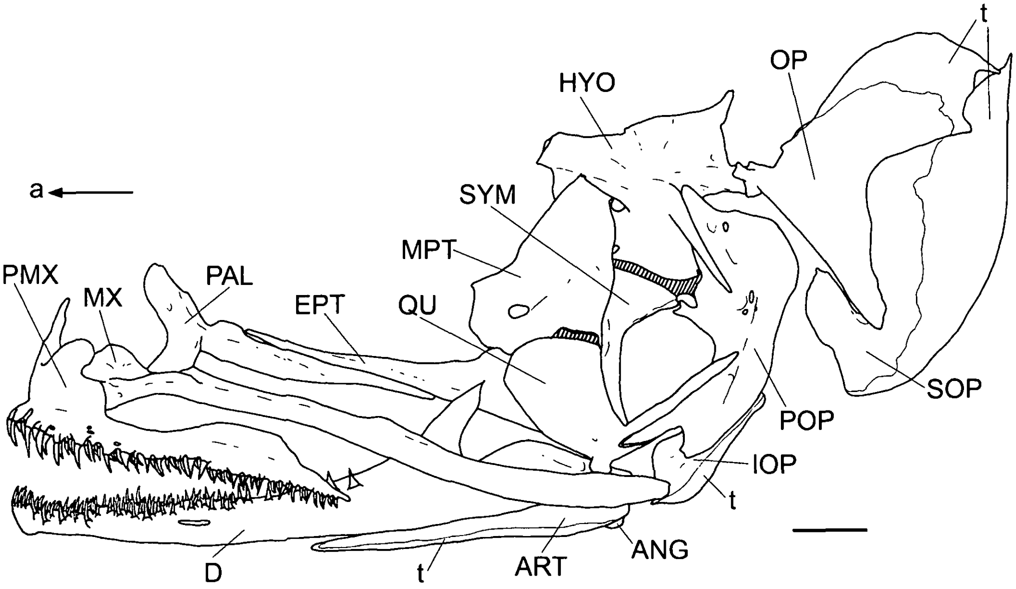

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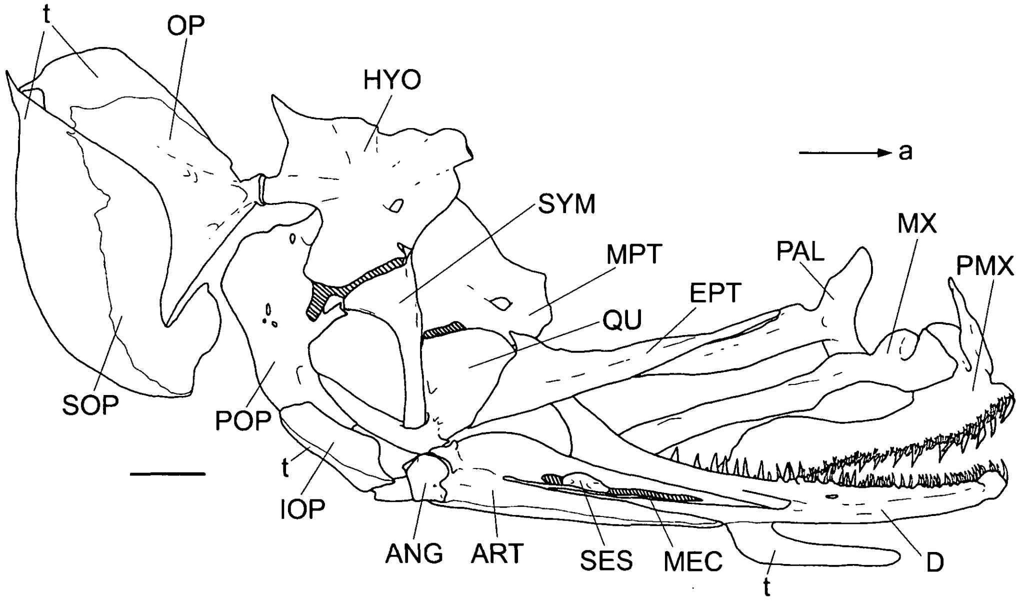


Fig. 33: Jaws, suspensorium and opercular bones of *Quietula guaymasiae*, medial view; LACM 35728-10, 43.9 mm SL. Hatching represents cartilage. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

ingly a unique feature for *Q. guaymasiae* and otherwise not reported for other species of the *Chasmichthys* Group. The symplectic, similarly shaped in both species, has a small preopercular process extending from the posterordorsal margin. In *Q. guaymasiae* this process meets a similar symplectic process on the anterodorsal margin of the preopercle. This symplectic process is absent or only weakly developed in *E. newberryi*. Therefore the suspensorial interspace is dorsally partly bordered by the ventral margin of the hyomandibular in *E. newberryi* but by the processes of the symplectic and the preopercle in *Q. guaymasiae*. The hyomandibular of both species articulates with the neurocranium via two cylindrical processes. These two processes, especially the anterior one for articulation with the sphenotic, are more distinctly developed in *E. newberryi*. In both species the hyomandibular has a distinct bony flange, which posteriorly receives the anterodorsal margin of the preopercle. Medially the hyomandibular bears the large hyomandibular foramen, the entrance of the short hyomandibular canal which branches laterally and exits in two foramina, a large one anterior to the lateral bony flange and a smaller one posterior to it. The hyomandibular trunc of the facial nerve and the anterior lateral line nerve pass through this canal. The hyomandibular trunc splits into two branches, one passing through the anterior the other through the posterior foramen. A branched hyomandibular canal terminating in two foramina laterally on the hyomandibular is seemingly unusual for gobiid fishes. There is not much information in the literature concerning this feature, but seemingly in many gobies this short canal is unbranched and opens laterally with a single foramen immediately anterior to the dorsal origin of the lateral flange (BIRDSONG 1975, MESTERMANN & ZANDER 1984, MURDY

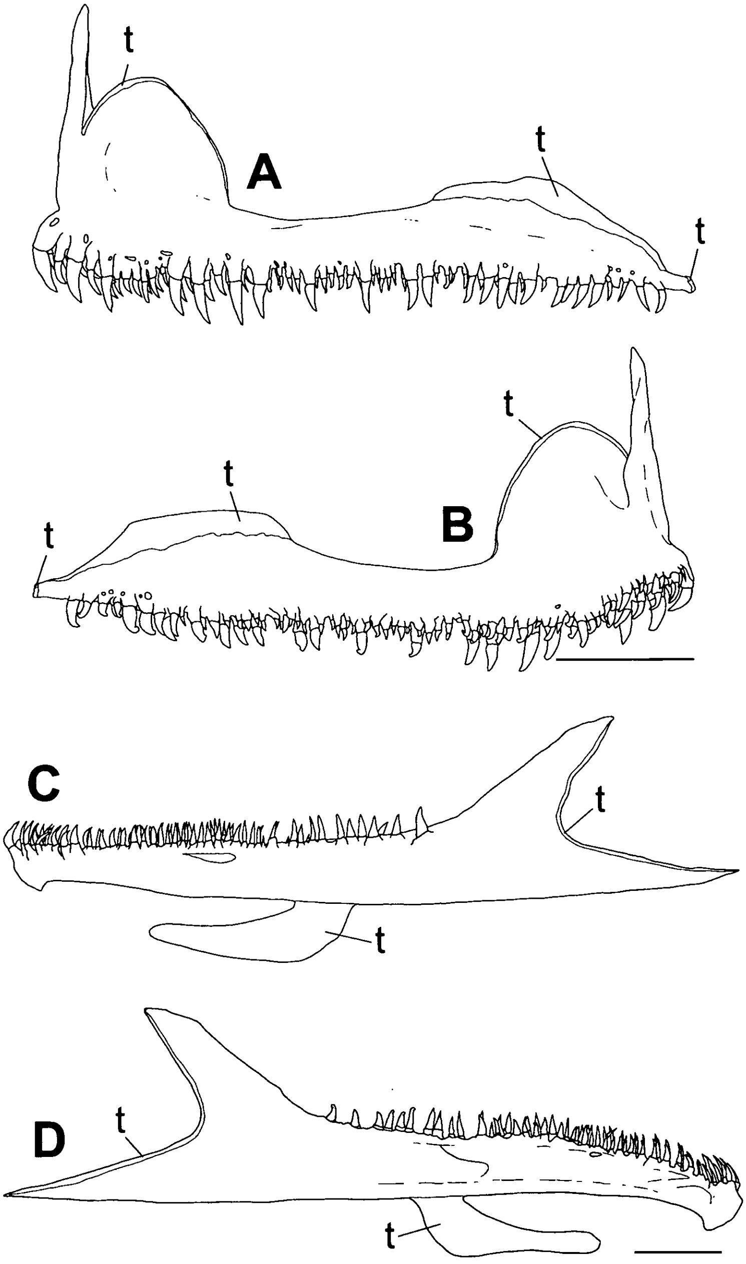


Fig. 34: Disarticulated jaw elements of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: premaxilla (lateral, medial view), C-D: dentary (lateral, medial view). t = transparent. Scale = 1 mm.

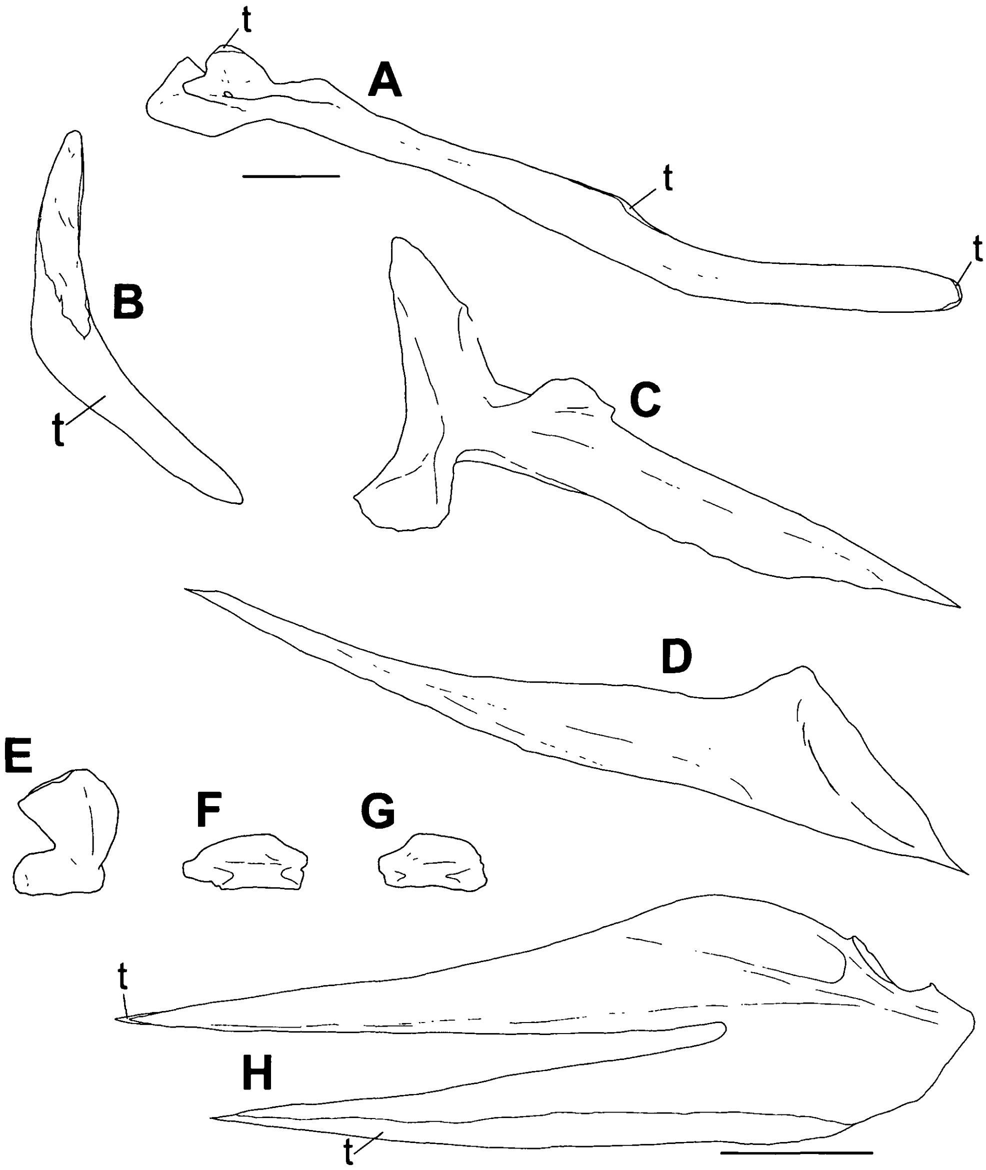
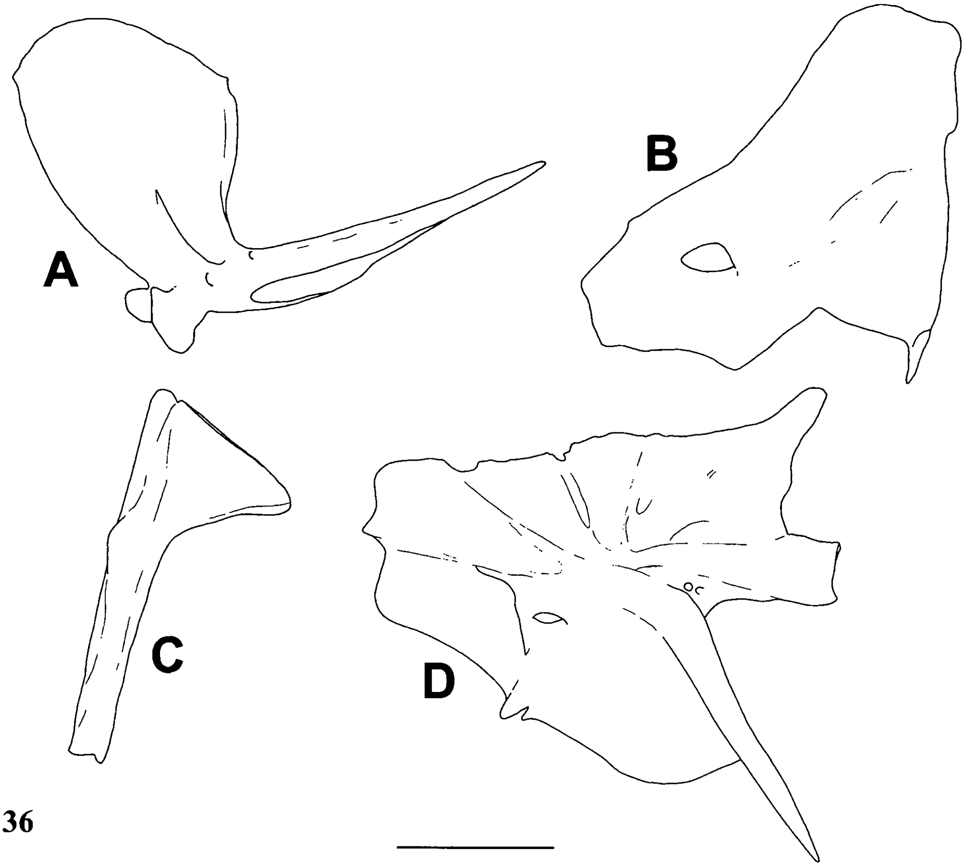


Fig. 35: Disarticulated elements of the suspensorium and lacrimal of *Quietula guaymasiae*, lateral view; CAS 26056, 41.1 mm SL. A: maxilla, B: lacrimal, C: palatine, D: ectopterygoid, E: retroarticular, F: left sesamoid articular, G: right sesamoid articular, H: anguloarticular. t = transparent. Scale = 1 mm.

Fig. 36: Disarticulated elements of the suspensorium of *Quietula guaymasiae*, lateral view; CAS 26056, 41.1 mm SL. A: quadrate, B: metapterygoid, C: symplectic, D: hyomandibular. Scale = 1 mm.



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1985, AHNELT unpublished). An unbranched hyomandibular canal with a single lateral foramen is possibly the plesiomorphic character state for Gobioidei. A branched hyomandibular canal with one foramen medially, two foramina laterally, and subsequently a branched hyomandibular trunc are characteristic for the 'bay gobies' and possibly represent a synapomorphy for the *Chasmichthys* group. Nevertheless, if apomorphic this condition is not an autapomorphy for this group as a branched hyomandibular canal occurs in some Gobiinae (GILL 1993 Fig. 10A, AHNELT unpublished).

The preopercle is wider in *Q. guaymasiae* with a distinct symplectic process projecting from its anterodorsal margin (compare suspensorial interspace). It bears some vestige of a preopercular canal still recognisable by a shallow bony trough posterolaterally. Several foramina are developed for branches of the ramus opercularis superficialis and the ramus hyoideus, which innervate free neuromasts in the trough. These are the last remnants of the absent preopercular canal of the lateral line system.

**Hyoid arch and Branchial apparatus** (Figs. 12-15, 38-42). The hyoid arch is essentially similarly developed in both species. However, there are differences in the basihyal bone. The basihyal is in both species Y-shaped with its anterior margin deeply notched.

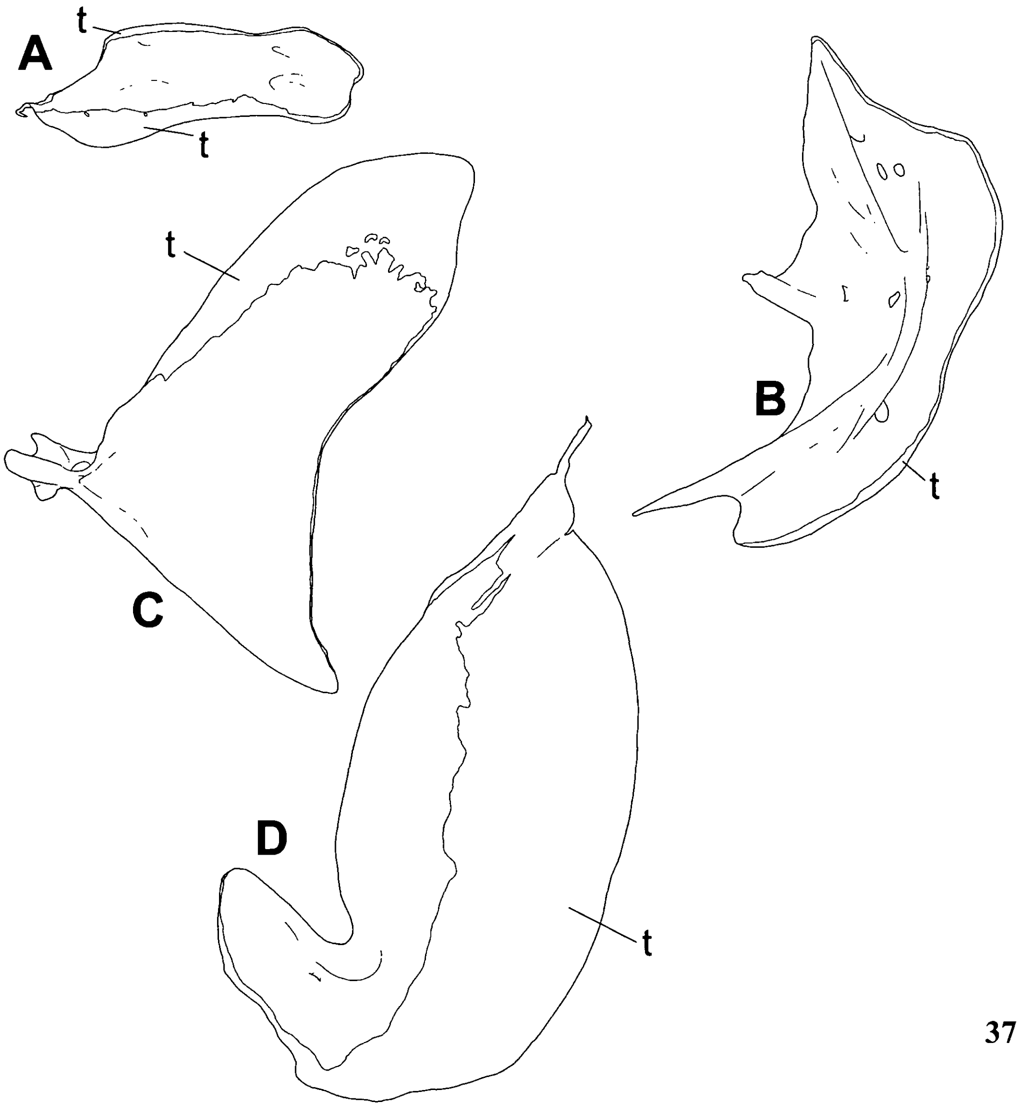

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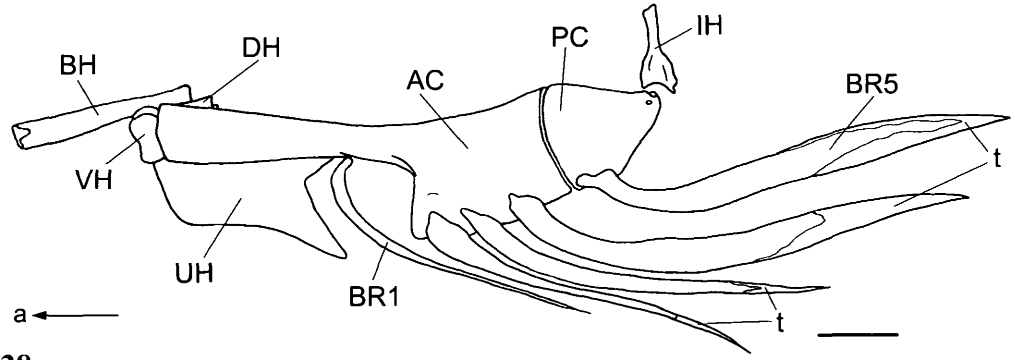
Fig. 37: Disarticulated opercular bones of *Quietula guaymasiae*, lateral view; CAS 26056, 41.1 mm SL; A: interopercle, B: preopercle, C: opercle, D: subopercle. t = transparent. Scale = 1 mm.

Fig. 38: Left hyoid arch of *Quietula guaymasiae*, lateral view; LACM 35728-10, 43.9 mm SL. a = anterior, t = transparent. For abbreviations see Tab. 1. Scale = 1 mm.

Fig. 39: Disarticulated branchial and hyal bones of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A: basihyal (dorsal view), B: urohyal (lateral view), C: dorsal hypohyal (dorsal view), D: ventral hypohyal (lateral view), E: anterior ceratohyal (lateral view), F: posterior ceratohyal (lateral view), G: interhyal (lateral view). Scale = 1 mm.



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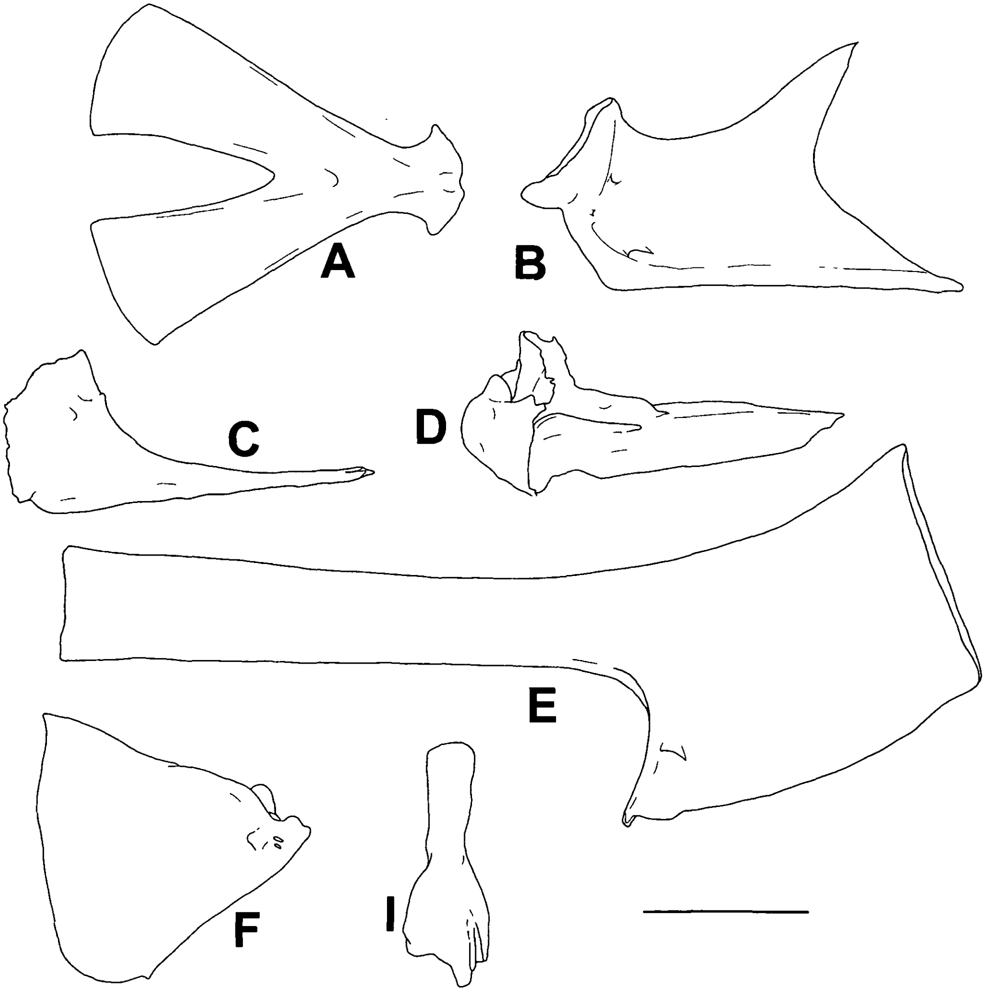

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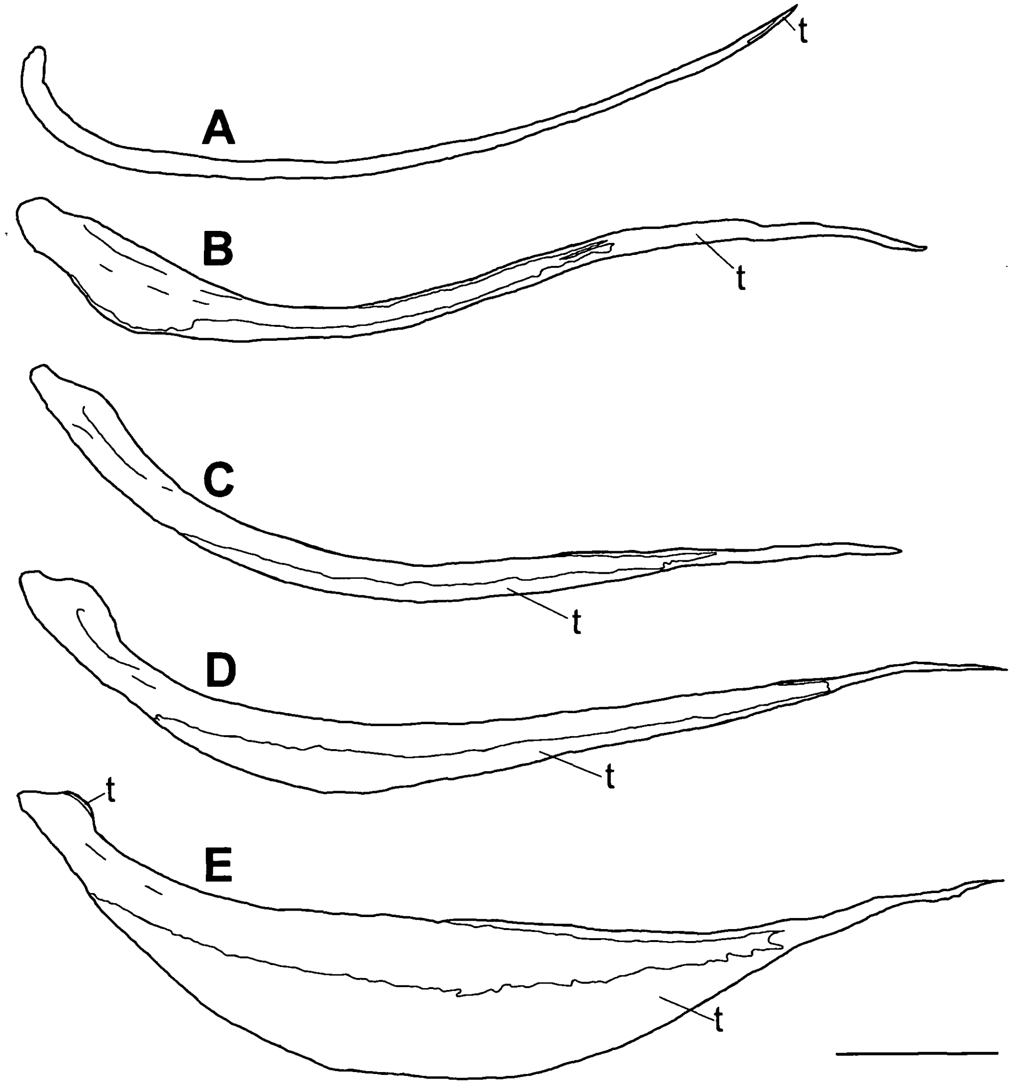
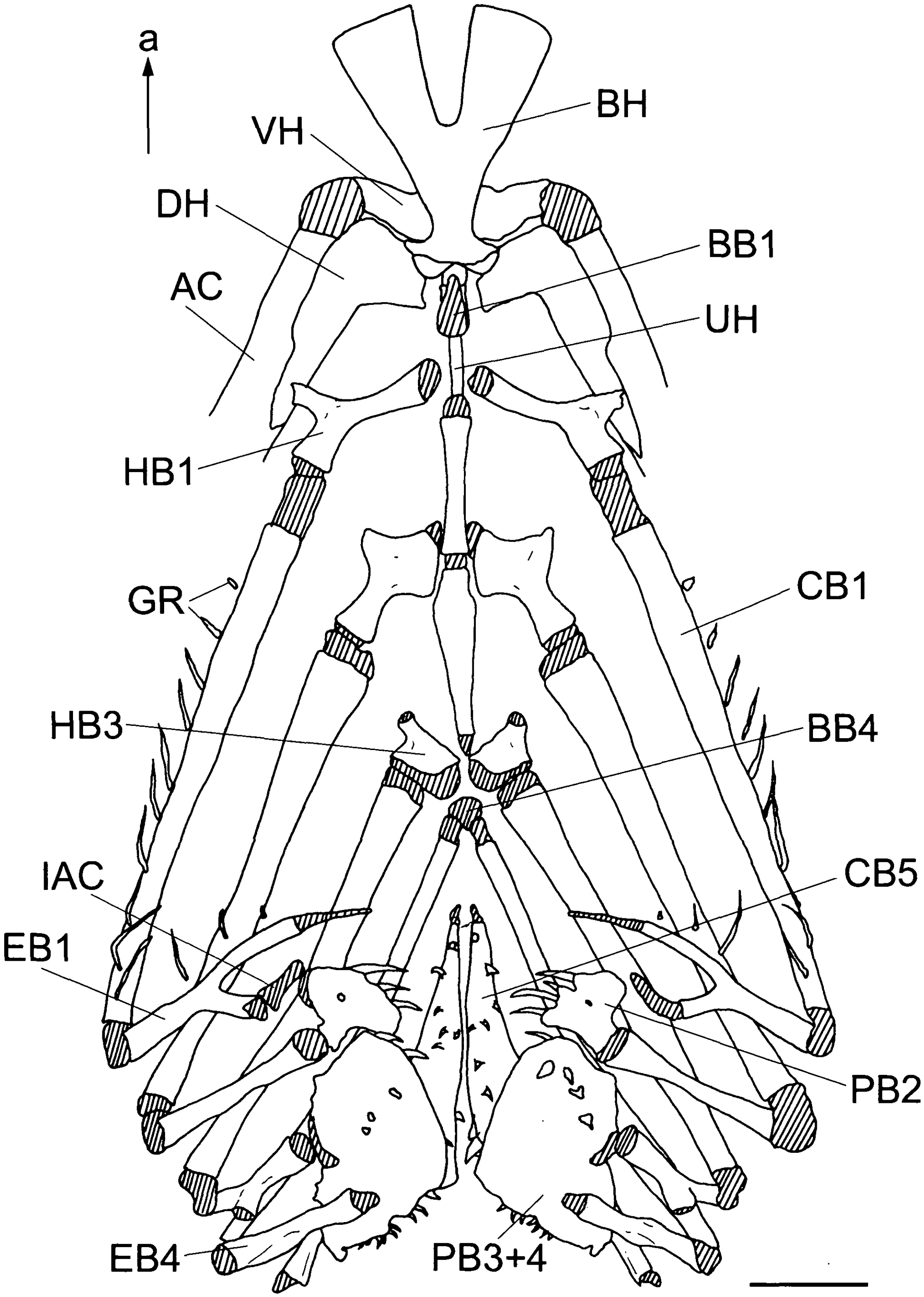


Fig. 40: Branchiostegals of *Quietula guaymasiae*, lateral view; CAS 26056, 41.1 mm SL. A: branchiostegal 1, B: branchiostegal 2, C: branchiostegal 3, D: branchiostegal 4, E: branchiostegal 5. t = transparent. Scale = 1 mm.

Fig. 41: Branchial apparatus of *Quietula guaymasiae*, dorsal view; LACM 35728-10, 43.9 mm SL. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.



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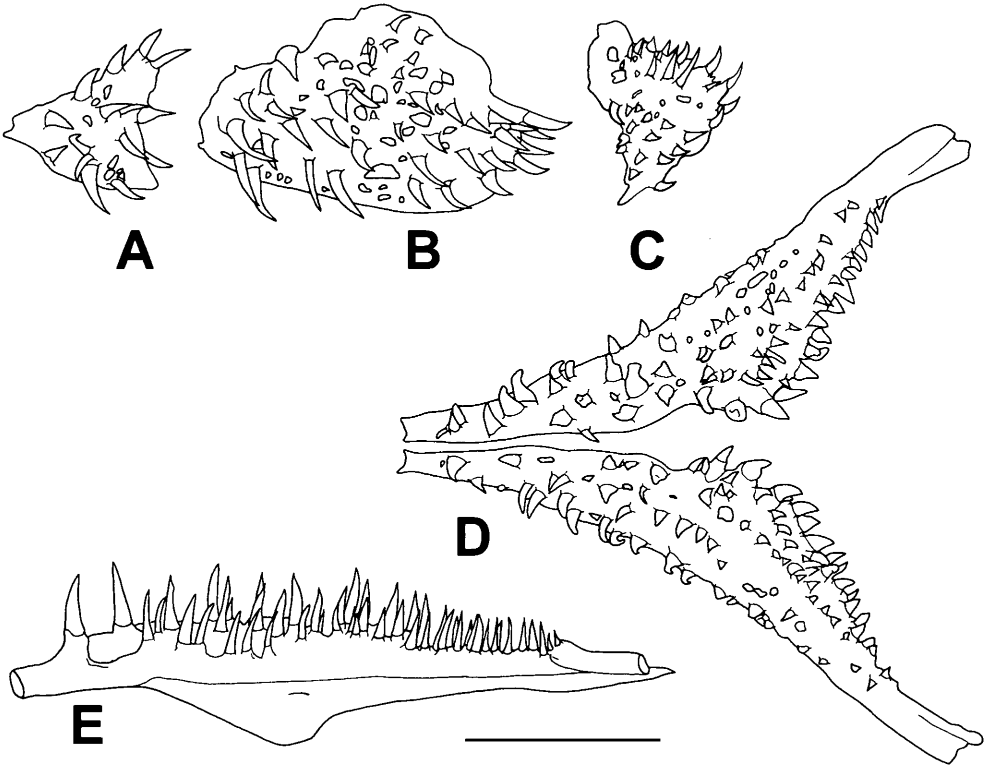

Fig. 42: Disarticulated pharyngeal tooth plates of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A: pharyngobranchial 2 (ventral view), B: pharyngobranchial 3 (ventral view), C: pharyngobranchial 4 (ventral view), D: left and right ceratobranchial 5 (dorsal view), E: left ceratobranchial 5 (lateral view). Scale = 1 mm.

Nevertheless, the two struts are distinctly more diverging in *E. newberryi*. According to TAKAGI (1950) and BIRDSONG (1975) the basihyal (his glossohyal) of both species must be regarded as specialised.

The branchial apparatus of *E. newberryi* and *Q. guaymasiae* differs only in a few features. Most notably, the hypobranchial 3 of *Q. guaymasiae* bears a conspicuous anterolateral extension with a cartilaginous tip, a character found in most members of the *Chasmichthys* Group (STEVENSON 2002a). Such an extension is absent in *E. newberryi*. The reduction and the loss of this anterolateral extension of the hypobranchial 3 is interpreted as a derived condition by STEVENSON (2002a). Gill rakers are developed on the first ceratobranchial and epibranchial. They are well separated in both species but less numerous and shorter in *E. newberryi*. Gill rakers extend nearly along the entire length of the ceratobranchial 1 in *Q. guaymasiae* but are absent in the anterior half of this bone in *E. newberryi*. The teeth of the lower (ceratobranchial 5) and upper (pharyngobranchials 2 – 4) pharyngeal jaws are conical in both species, but more numerous in *Q. guaymasiae*.

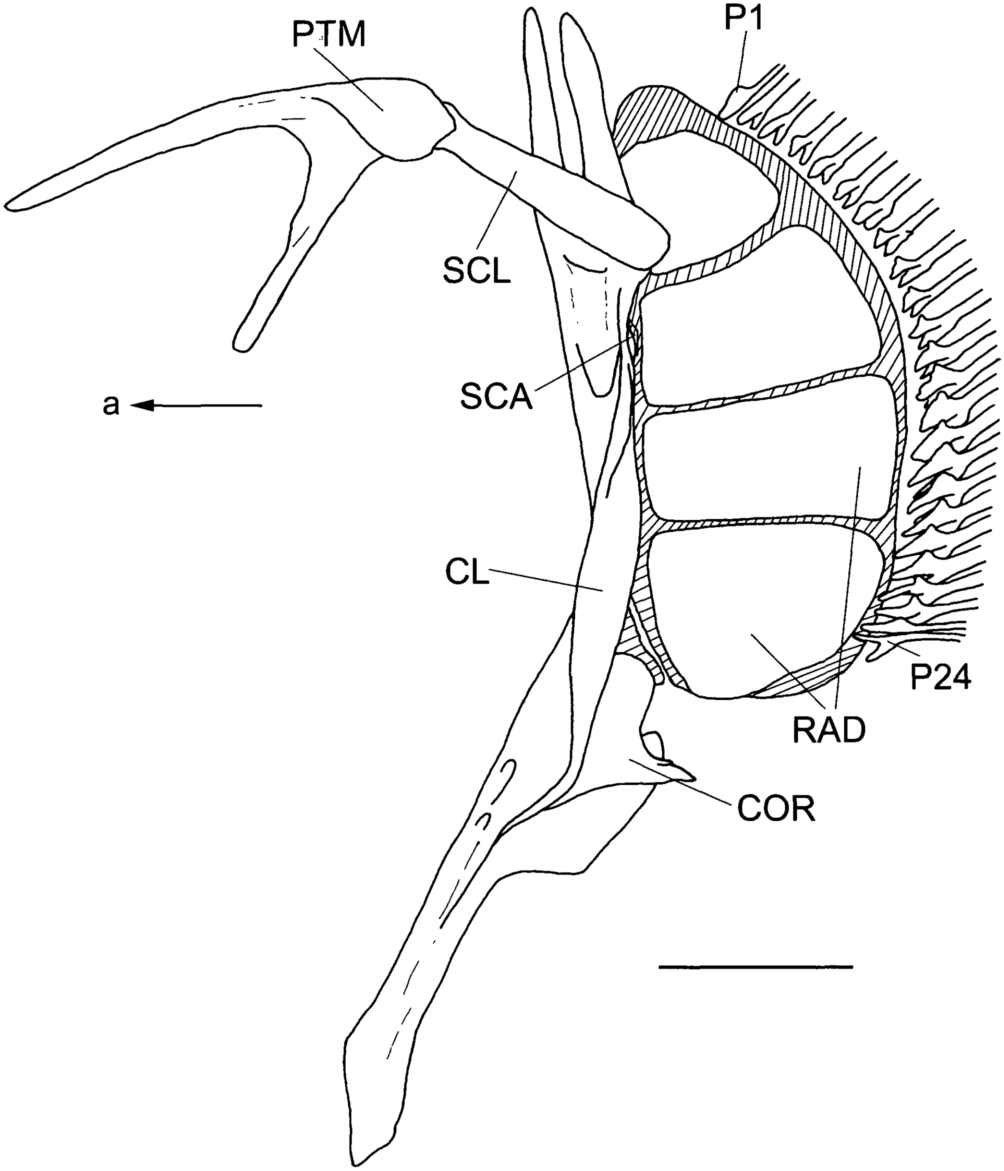

Fig. 43: Left pectoral girdle of *Quietula guaymasiae*, lateral view; LACM 35728-10, 43.9 mm SL. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

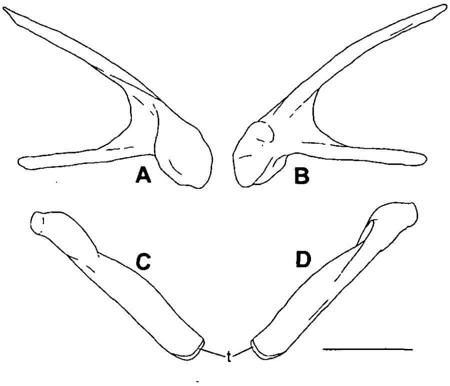

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Fig. 44: Disarticulated elements of the pectoral girdle of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: posttemporal (lateral, medial view), C-D: supracleitrum (lateral, medial view). t = transparent. Scale = 1 mm.

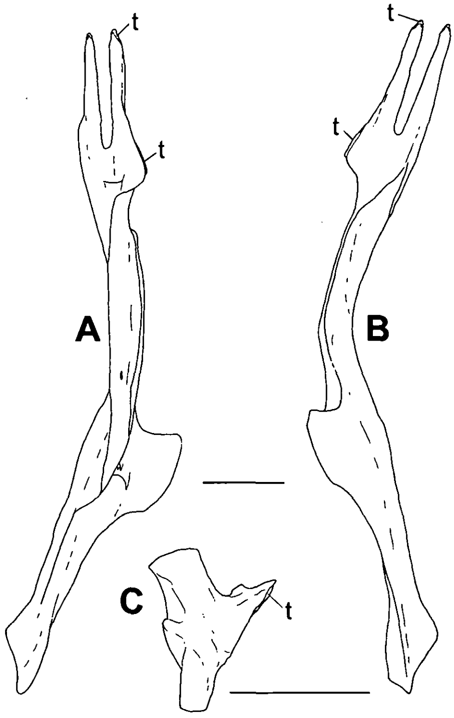

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Fig. 45: Disarticulated elements of the pectoral girdle of *Quietula guaymasiae*; CAS 26056, 41.1 mm SL. A-B: cleithrum (lateral, medial view), C: coracoid (anterolateral view). t = transparent. Scale = 1 mm.

**Paired fins** (Figs. 16-18, 43-47). Both species lack dorsal and ventral postcleithra in the secondary pectoral girdle. The broad lateral surface of the posttemporal is flat and has no remnants of a posterior oculoscapular canal of the lateral line system. In all species of the American 'bay gobies' (AHNELT unpublished) and of the Asian species of the *Chasmichthys* group (STEVENSON 2002b) the posterior oculoscapular canal is absent. This is a derived condition but not an autapomorphy for the *Chasmichthys* group.

AKIHITO (1969) showed that there is a tendency for a reduced ossification in the primary pectoral girdle, affecting especially the scapula. He characterised the scapular development in a long list of gobiid species, dividing them by degree of ossification. Several members of the *Chasmichthys* group were characterised as having the 'forked scapula' type, in which the dorsal margin of the scapular foramen is ossified, but the ventral margin of the foramen and the main shaft of the scapula are composed of cartilage. STEVENSON (2002a) found this 'forked scapula' type in all the species of the *Chasmichthys* group which he investigated. Nevertheless, the scapula of *Q. guaymasiae*, a 'bay goby' not included in STEVENSON's (2002a) study, is completely cartilaginous and therefore does not represent the forked type. A 'forked scapula' type is seemingly typical for *E. newberryi*, but we also found some specimens with the entire scapula cartilaginous. This character may be variable in other species as well.

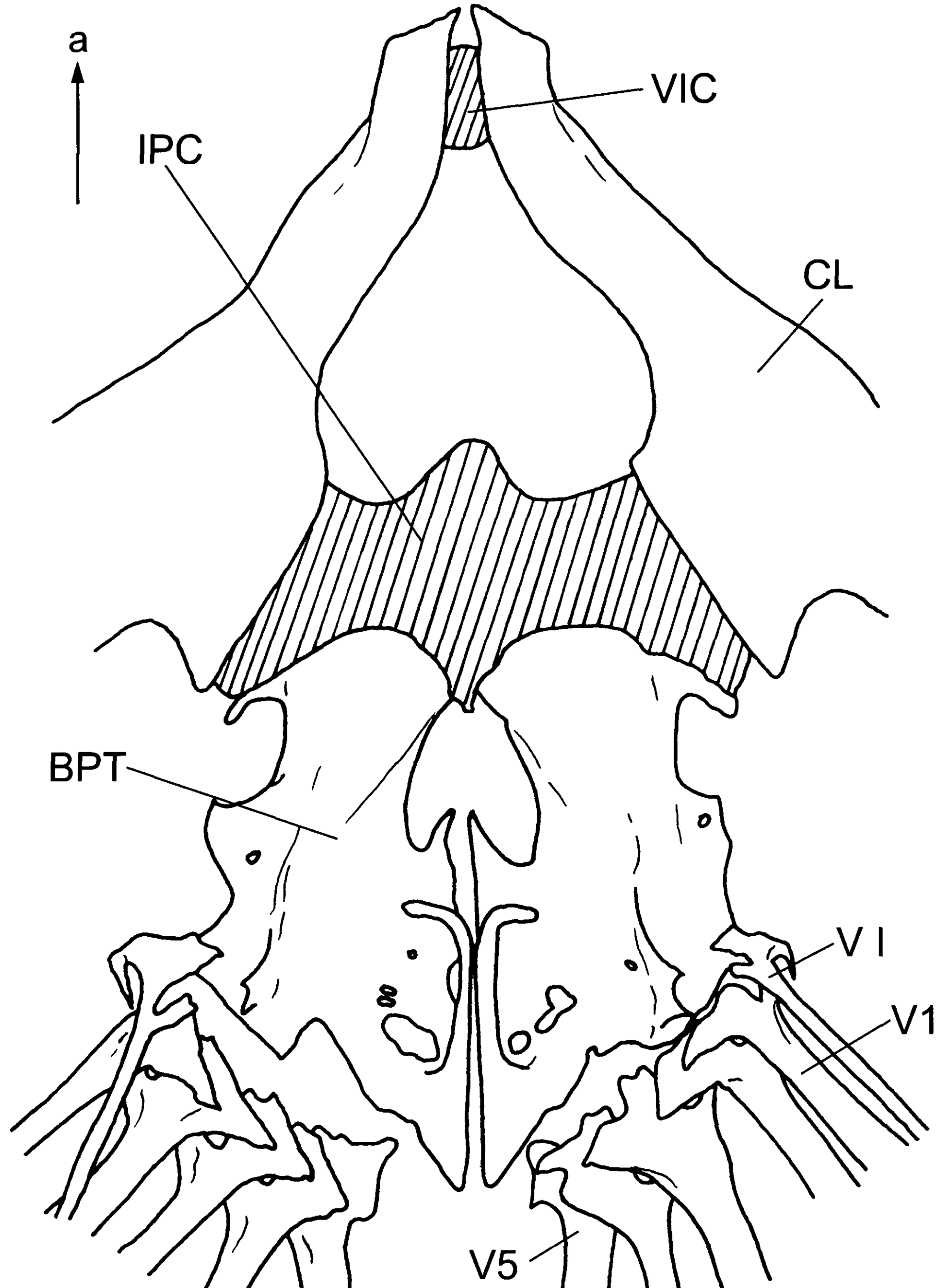

Fig. 46: Pelvic girdle of *Quietula guaymasiae*, ventral view; CAS 26056, 36.0 mm SL. Hatching represents cartilage. a = anterior. Scale = 1 mm.

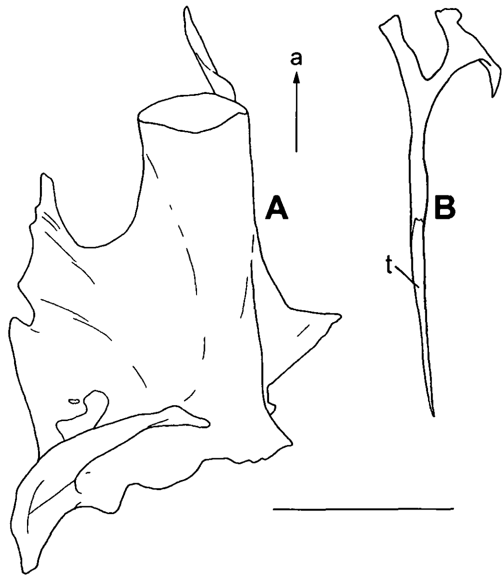

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Fig. 47: Disarticulated elements of the pelvic girdle of *Quietula guaymasiae*, ventral view; CAS 26056, 41.1 mm SL. A: basipterygium, B: spine of pelvic fin. a = anterior, t = transparent. Scale = 1 mm.

Fig. 48: Vertebral column and median fin elements of *Quietula guaymasiae*, lateral view; LACM 35728-10, 43.9 mm SL. Hatching represents cartilage. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

Fig. 49: Disarticulated vertebrae of *Quietula guaymasiae*, anterior view; CAS 26056, 41.1 mm SL. A: first vertebra, B: second to last precaudal vertebra, C: penultimate precaudal vertebra, D: last precaudal vertebra (intermediate vertebra), E: first caudal vertebra. Scale = 1 mm.

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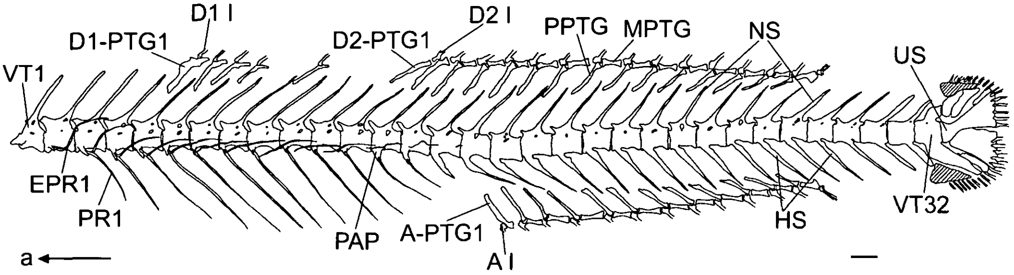

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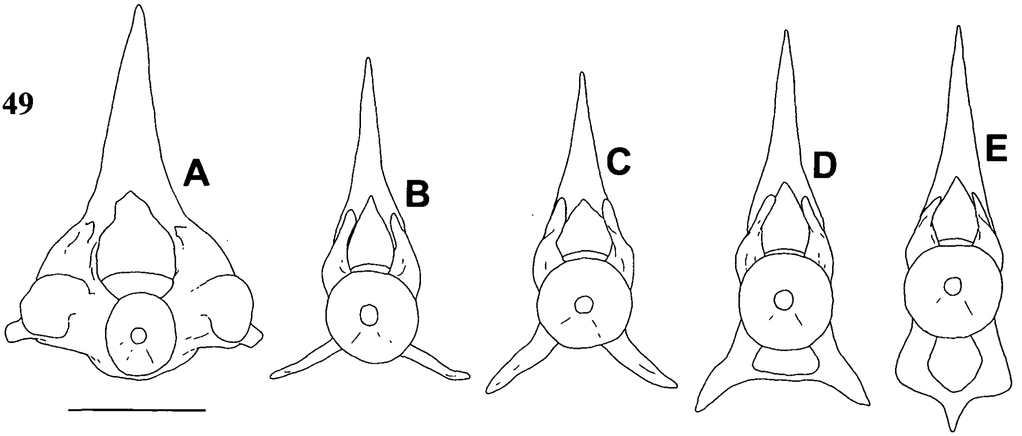

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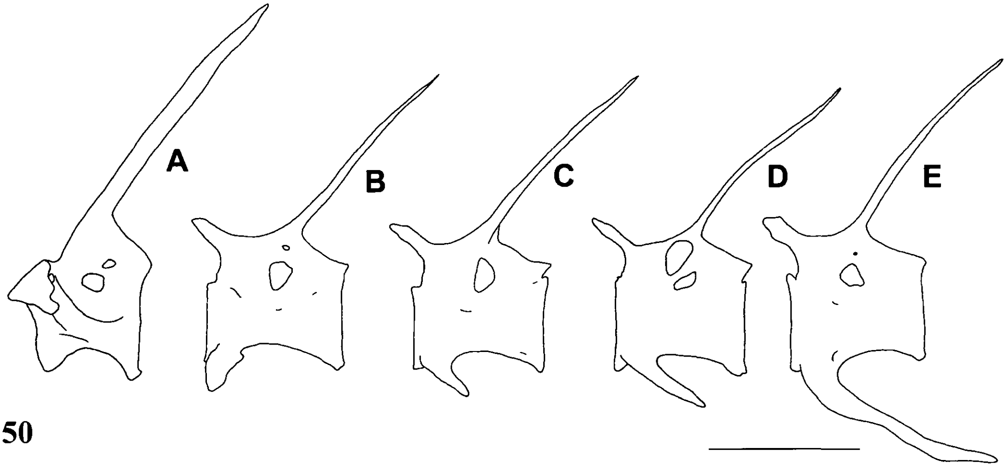

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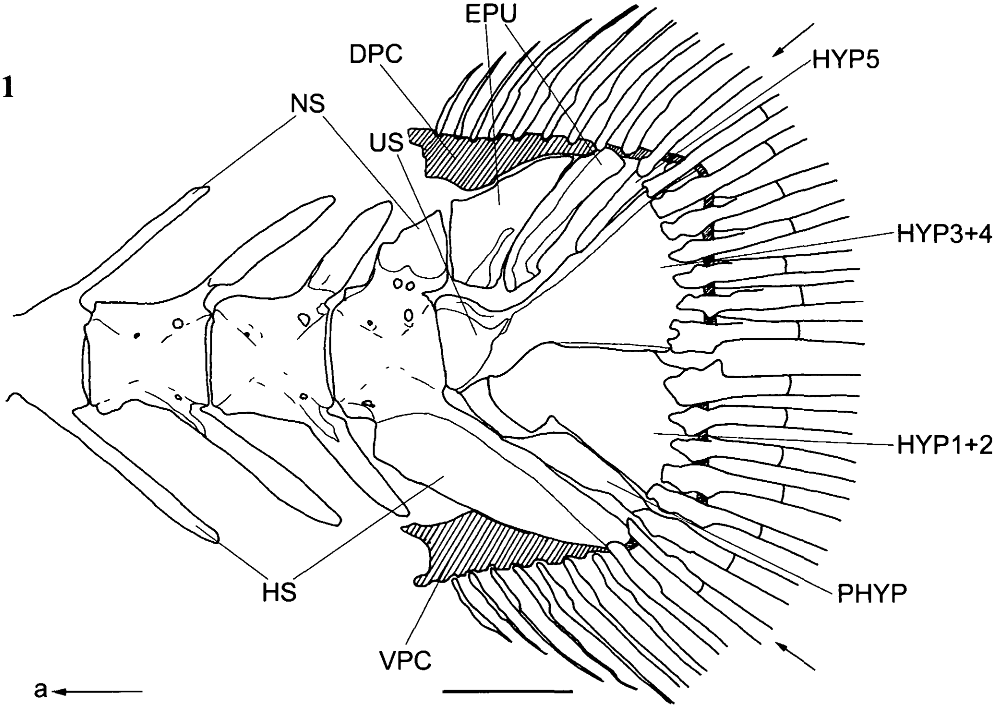

Fig. 50: Disarticulated vertebrae of *Quietula guaymasiae*, lateral view; CAS 26056, 34.4 mm SL. A: first vertebra, B: second to last precaudal vertebra, C: penultimate precaudal vertebra, D: last precaudal vertebra (intermediate vertebra), E: first caudal vertebra. Scale = 1 mm.

Fig. 51: Caudal skeleton of *Quietula guaymasiae*, lateral view; LACM 35733-11, 42.2 mm SL. Hatching represent cartilage. Arrows mark most dorsal and ventral segmented fin rays. a = anterior. For abbreviations see Tab. 1. Scale = 1 mm.

**Vertebral column, Median Fins and Caudal skeleton** (Figs. 19-22, 48-51). The plesiomorphic vertebral count including the urostyl for Gobiidae is 26 - 27 (Akihito & al. 1984, Birdsong & al. 1988, McKay & Miller 1997, Ahnelt & Duchkowitsch 2004). *Eucyclogobius newberryi* (33 – 35 vertebrae) and *Q. guaymasiae* (33 – 34 vertebrae) both have an elevated vertebral count. This is high for Gobiidae but not strikingly for Gobionellinae (Birdsong & al. 1988, Stevenson 2002a). The last abdominal (precaudal) vertebra of *E. newberryi* and *Q. guaymasiae* represents an 'intermediate' type. The parapophyses of the ultimate abdominal vertebra are joined by a bony bridge, forming a narrow haemal arch, but with their tips not fused (Figs. 20C, 49D). This narrow arch surrounds the caudal aorta but not the caudal vein. From the first caudal vertebra posteriorly both blood vessels are enclosed by haemal arches formed by the parapophyses (haemapophyses), which are completely fused at their tips. 'Intermediate' vertebrae are also known from Gobiinae (Ahnelt & Duchkowitsch 2004).

Within the *Chasmichthys* group most species have a pair of epineurals associated with the first vertebra and a pair associated with each subsequent abdominal vertebra. Nevertheless, several 'bay gobies' (*Clevelandia ios*, *E. newberryi*, *Ilypnus gilberti*, *Lepidogobius lepidus*, and *Quietula y-cauda*) lack the anteriormost pair of epineurals. In these species, the first pair of epineurals is associated with the second vertebra (Stevenson 2002a). This is also the case in *Q. guaymasiae*. The absence of epineurals on the first vertebral centrum in Gobioidei has otherwise only been reported for the two Xenisthimidae (*Tyson belos*, *Rotuma lewisi*) (Springer 1988). Therefore, this character is interpreted as a synapomorphy uniting these six species of the 'bay gobies'.

Typically in gobioids the first pterygiophore of the first dorsal fin is inserted in the third interneural space, between the neural spines of the third and the fourth abdominal vertebrae (Birdsong & al 1988). In both *E. newberryi* and *Q. guaymasiae* this anteriormost pterygiophore is displaced posteriorly. It inserts in the fourth interneural space in *Q. guaymasiae* and in the fifth in *E. newberryi*. This character, posterior displacement of the first pterygiophore of the first dorsal fin in the fourth or fifth interneural space, was the justification for creating the *Chasmichthys* Group in the first place (Birdsong & al. 1988) and it is possibly a derived condition (Pezold 1993, Ahnelt 2003). Both species have two interneural gaps between the posteriormost pterygiophore of the first dorsal fin and the anteriormost pterygiophore of the second dorsal fin, and both species generally have two anal fin pterygiophores preceding the haemal spine of the first caudal vertebra. The first pterygiophore of the anal fin is positioned opposite to the fourth or fifth pterygiophore of the second dorsal fin.

Members of the *Chasmichthys* group also appear to have a posterior displacement of the second dorsal fin (Stevenson 2002a) and of the anal fin. Although Birdsong & al. (1988) did not explicitly report the posterior displacement of the second dorsal fin in their extensive survey, it can be derived from their first dorsal fin pterygiophore formulae that the overwhelming majority of Gobioidei have the first pterygiophore of the second dorsal fin inserted in the eighth or ninth interneural space. However, the second dorsal fin also appears to be posteriorly displaced relative to the first dorsal fin. The majority of gobiid genera have a single interneural space without a pterygiophore between the posteriormost pterygiophore of the first dorsal fin and the anteriormost pterygiophore of the second dorsal fin (Birdsong & al. 1988, Hoese & Gill 1993, Ahnelt 2003), but those of the *Chasmichthys* group have two such interneural spaces (STEVENSON 2002a, MILJKOVIĆ unpublished). The posterior shift of the second dorsal fin in this genus-group may be correlated with the displacement of the first dorsal fin. The position of the first pterygiophore of the anal fin opposite to the fourth or fifth pterygiophore of the second dorsal fin is seemingly an apomorphic character state compared with the insertion below the third pterygiophore of the second dorsal fin of species with the plesiomorphic ten precaudal vertebrae (AHNELT 2003, AHNELT & DUCHKOWITSCH 2004).

There is little variation in the caudal skeleton of *E. newberryi* and *Q. guaymasiae*. PEZOLD (1993) used the presence of one epural as a diagnostic character for the Gobiinae, thereby excluding the *Chasmichthys* group and the rest of the Gobionellinae which are characterised by two epurals. This character is seemingly variable within the Gobionellinae (AHNELT unpublished). Nevertheless, all members of the *Chasmichthy*s group except *E. newberryi* have two epurals (STEVENSON 2002a, MILJKOVIĆ unpublished). With the absence of the anteriormost of the typical two epurals sometimes only one epural occurs in the caudal fin skeleton of *E. newberryi*.

**Scales**. Only the trunk of *E. newberryi* and *Q. guaymasiae* is scaled. Posteriorly from a line between the dorsal origin of the pectoral fin and about the middle of the base of the first dorsal fin rearwards to the base of the caudal fin the body of both species is covered by small cycloid scales. The head, nape, predorsal area, breast, and the lobe of the pectoral fin are naked. There is some variability in this character in *E. newberryi*. In several specimens the abdomen is partly unscaled (MILJKOVIĆ 2004). Generally gobioid fishes are covered by ctenoid scales. The loss of ctenii is regarded as a derived character (MILLER 1971, SCSEPKA et al. 1999) and unites all North American members but not all Asian members of the *Chasmichthys* Group (STEVENSON 2002a).

This detailed osteological examination confirms the close relationship of *Eucyclogobius newberryi* and *Quietula guaymasiae*. Both share the following combination of diagnostic osteological characters (i) branched hyomandibular canal opening laterally through two foramina, (ii) premaxilla with postmaxillary process, (iii) basihyal Y-shaped, (iv) head canals of lateral line system reduced to supraorbital canals, (v) posterior displacement of first dorsal fin, (vi) insertion of first pterygiophore of first dorsal fin posterior to third interneural space, (vii) two interneural spaces between last pterygiophore of first dorsal fin and first pterygiophore of second dorsal fin, (viii) first pterygiophore of anal fin posterior to third pterygiophore of second dorsal fin, (ix) elevated number of abdominal and caudal vertebrae, (x) intermediate vertebrae and, (xi) cycloid scales.

Although both species are similar in their osteology, they are nevertheless distinguishable by the following characters (condition for *E. newberryi* in parentheses): (i) median ethmoid with distinct bony ventral extension (ventral extension cartilaginous), (ii) frontal with distinct trough for the supraorbital canal of the lateral line system (shallow trough), (iii) jaws and anterior bones of the suspensorium more elongate, especially the dentary, maxilla, anguloarticular and ectopterygoid (jaws and anterior bones of the suspensorium relatively short), (iv) bony 'bridge' of metapterygoid reaches anteriorly to posterior margin of ectopterygoid (metapterygoid does not reach ectopterygoid), (v) bony 'bridge' of metapterygoid broad with a foramen (bony 'bridge' slender, without foramen), (vi) preopercle with distinct anterodorsal process (anterodorsal process reduced or absent), (vii) hypobranchial 3 with anterolateral extension (anterolateral extension absent), (viii) first pterygiophore of first dorsal fin inserts in fourth interneural space (inserts in fifth interneural space), (ix) first pterygiophore of anal fin opposite fourth pterygiophore of second dorsal fin (opposite fifth pterygiophore) and, (x) two epurals (one or two epurals).

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