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Systematics of the mudskipper genus *Oxuderces* Eydoux & Souleyet 1848 (Teleostei: Gobiidae: Oxudercinae) with resurrection from synonymy of *O. nexipinnis* (Cantor 1849)

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The mudskipper (Gobiidae: Oxudercinae) genus *Oxuderces* Eydoux & Souleyet is re-diagnosed with five putative synapomorphies: (1) a fleshy, dorsal, interorbital trough or slit supported internally by expanded, curved medial margins of the frontal bones and lined with a thick epidermis and thin dermis (vs. no fleshy, interorbital trough, medial margins of the frontal bones expanded but not curved, and epidermis extremely thin and dermis thick); (2) highly thickened epidermis over the eye (vs. thickened dermis); (3) neural spine of the fourth vertebra broad and spatulate (vs. narrow and pointed); (4) anterior ceratohyal posterior to fourth branchiostegal ray insertion elongate and notched (vs. not elongate, or elongate and not notched); and (5) angle between the metapterygoid–symplectic–quadrate strut and the anguloarticular acute (vs. angle obtuse). The fleshy, dorsal, interorbital trough is a unique character for *Oxuderces* that is not observed in other oxudercine gobies or gobioid fishes. The extremely thick epidermis may help the skin remain moist when exposed to the air and facilitate cutaneous respiration. Two allopatric species are included in the genus *Oxuderces*: *Oxuderces dentatus* Eydoux & Souleyet, 1848, from the south-east coast of China, is the type species; *Oxuderces nexipinnis* (Cantor, 1849), from the Indo-West Pacific, is resurrected from synonymy of *O. dentatus* sensu Murdy (1989). *Apocryptodon wirzi* Koumans, 1937, a species classified in *Oxuderces* by Murdy (1989) is reassigned to *Apocryptodon* based on a posteriorly directed laminar process on the parapophyses of the fourth vertebra. *Oxuderces nexipinnis* uniquely has a dermal invagination of unknown function just posterior to the point of attachment of the pelvic-fin base.

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ADDITIONAL KEYWORDS: allopatry – histology – osteology – respiration – skin.

INTRODUCTION

Mudskippers (Teleostei: Gobiidae: Oxudercinae) live in mangrove forests, mudflats and tidally influenced lower reaches of rivers throughout the Indo-West Pacific. They spend nearly all their time submerged, occasionally within shallow, natural hypoxic pools (Murdy, 1989), yet may expose the entire or parts of the body to the air (Zhang *et al.*, 2000). Ten mudskipper genera are recognized (Murdy, 1989). Of these, four genera – *Boleophthalmus* Valenciennes, 1937, *Periophthalmodon* Bleeker, 1874, *Periophthalmus* Bloch & Schneider, 1801 and *Scartelaos* Swainson, 1839 – conspicuously emerge out of water to display, forage and defend territories during ebb tides. These fishes are thus relatively well known in popular culture. *Periophthalmodon* and *Periophthalmus*, in particular, have been the subject of numerous systematic and biological investigations (e.g. Murdy, 1989; Clayton, 1993; Ishimatsu *et al.*, 1998; Ishimatsu & Gonzales, 2011; Beon *et al.*, 2013). The

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remaining six genera – *Oxuderces* Eydoux & Souleyet, 1848, *Apocryptes* Valenciennes, 1937, *Apocryptodon* Bleeker, 1874, *Pseudapocryptes* Bleeker, 1874, *Parapocryptes* Bleeker, 1874 and *Zappa* Murdy, 1989 – are poorly known. Other than taxonomic treatments, distribution records, checklists and faunal studies, there is almost no scientific literature on these mudskipper taxa. The lack of information on the natural history of these mudskippers stems from inadequate sampling and documentation of the coastal and mangrove fish fauna throughout their range, coupled with a complex and confusing taxonomic history.

The type genus of the subfamily Oxudercinae is *Oxuderces*, described by Eydoux & Souleyet (1848) based on *Oxuderces dentatus* (Fig. 1). Springer (1978: 7) considered this genus monotypic, but in the most recent revision of the genus *Oxuderces*, Murdy (1989) recognized two species: *O. dentatus* and *O. wirzi* (Koumans, 1937), the latter described in the genus *Apocryptodon*. The sister group relationship of these congeners was supported by three putative synapomorphies: (1) presence of one fang-like canine tooth on each side of the premaxillary symphysis (Murdy, 1989: fig. 76); (2) anterior ceratohyal posterior to fourth branchiostegal ray insertion elongate (Murdy, 1989: fig. 77); and (3) anteriorly depressed head. Murdy (1989) did not include the restricted gill opening of *Oxuderces* as a synapomorphic character, a character Springer (1978) considered diagnostic for *Oxuderces*. Although not clarified in the treatment by Murdy (1989), the morphology of the restricted gill opening of *Oxuderces* is shared with one other oxudercine genus: *Scartelaos* Swainson, 1839. In both of these genera, the gill opening extends diagonally from a point just dorsal to the pelvic-fin origin, postero-dorsally, to a region just anterior to mid-height of the pectoral-fin base. In that same monograph, Murdy (1989: 9–10) diagnosed the genus *Apocryptodon* – which included two species, *A. madurensis* (Bleeker, 1849) and *A. punctatus* Tomiyama, 1934 – by a posteriorly directed laminar process on the parapophyses of the fourth vertebra and a supraorbital sensory pore (Murdy, 1989: fig. 74).

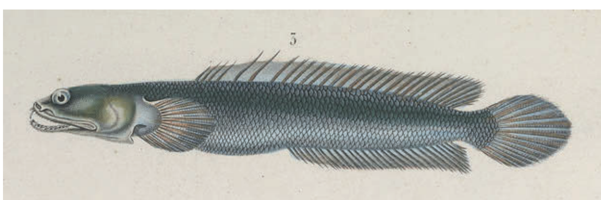


Figure 1. Illustration of the holotype of *Oxuderces dentatus* Eydoux & Souleyet (1848: pl. 8, fig. 3) from the original description. Image courtesy of the Smithsonian Institution Libraries.

While examining cleared and stained specimens of oxudercine fishes as part of a phylogenetic analysis of the subfamily, we discovered that *O. wirzi* has a posteriorly directed laminar process on the parapophyses of the fourth vertebra, one of the diagnostic characters of *Apocryptodon* sensu Murdy (1989; see below). Consequently, we classify *O. wirzi* in the genus *Apocryptodon*, and treat this taxon as distinct from *Oxuderces*. Examination of more and recent material, including histological preparations, of species of *Oxuderces* and putative close relatives revealed another valid species, *Apocryptes nexipinnis* Cantor, 1849 (Fig. 2), which Murdy (1989) treated as a synonym of *O. dentatus*, and Springer (1978: 3) considered the closest relative of *O. dentatus*. *Apocryptes nexipinnis* and *O. dentatus* share a unique, fleshy, interorbital trough lined externally with a thick epidermis in which sits the anteriorly located supraorbital pore C (Fig. 3A, B), a new gobioid character which we describe in more detail below. Both species also have an extremely thick epidermis over the eye (Figs 4A, 5A). These and the other characters mentioned above prompted us to re-examine available specimens of *Oxuderces* and *Apocryptodon*, as well as specimens of the closely related *Parapocryptes* (see cladogram in Murdy, 1989: fig. 55) to better understand character distributions and clarify generic limits. Of equal importance, we describe the newly discovered skin characters of the head and interpret them relative to what is known about the form and function of the skin of the mudskippers. This study has three major aims: (1) to re-diagnose *Oxuderces*; (2) to resurrect *Apocryptes nexipinnis* from synonymy (sensu Murdy, 1989) and re-describe two valid species of *Oxuderces*; and (3) to describe a new mudskipper character: the fleshy, interorbital trough and discuss its possible role in the life history of mudskippers.

MATERIAL AND METHODS

Measurements and counts

Measurements and counts follow Murdy (1989) with these exceptions: (1) body depth was measured as the vertical distance from the anus to the base of the second dorsal fin; (2) the elements of the dorsal and anal

Figure 2. *Oxuderces nexipinnis* (Cantor, 1849), ZRC 53919, 53.2 mm SL, West Bengal, India. Scale bar = 1 cm.

fins were differentiated between spines and segmented rays; and (3) the length of the base of the first and second dorsal fins (D1 and D2) as well as of the anal fin (A) were not measured because the degree of unification of paired and medial fins among *Oxuderces*, *Apocryptodon* and *Parapocryptes* differed, and therefore homologous points could not be identified with confidence. Measurements were made with vernier calipers to the nearest 0.1 mm. The following measurements are reported as a percentage of standard length (%SL): head length, predorsal length, pelvic-fin length, caudal-fin length, pectoral-fin length, body depth at anus and body width at anus. The following measurements are expressed as a percentage of head length (%HL): head width, head depth, snout length, eye diameter, interorbital distance and jaw length, following Murdy (1989). Results are presented in Table 1. Although we report counts and percentage measurements for the holotype of *Oxuderces dentatus*, MNHN A-1822, we did not consider these values when making congeneric comparisons because the specimen is in poor condition.

Osteological preparations

Representative specimens of each species were cleared in trypsin and counterstained with alcian blue for cartilage and alizarin red for bones following the method of Dingerkus & Uhler (1977). Gill arches were dissected in accordance with Weitzman (1974). Specimens were examined under a Zeiss SV8 or Wild M5 dissecting microscope and photographed with a Nikon Digital camera (DXM 1200) mounted on a Nikon SMZ1500 dissecting microscope.

Histological preparations

Heads were excised from four adult specimens taken from these catalogued lots: *Oxuderces nexipinnis* (USNM 427099), *Apocryptodon wirzi* (ZRC 52259), *Pseudapocryptes elongatus* (USNM 343560) and *Hemigobius hoevenii* (USNM 432507). The specimens had been fixed in 10% formalin and preserved in 75% ethanol. The heads were decalcified, cleared and embedded in Paraplast Xtra and sectioned at 8 μm using a Leica 2255 automated microtome. Sections were stained with Masson's Trichrome Stain. Slides were examined with a Leitz light microscope and photographed using an Olympus VS120 Virtual Slide System. All histological slides are maintained in the Division of Fishes, USNM.

Comparative material

Apocryptes batoides BMNH 1889.2.1.3472, male (131.0 mm), Madras, India; lectotype of *Apocryptes cantoris* BMNH 1870.5.18.23, male (65.6 mm), Andaman Islands, India; syntypes of *Apocryptes madurensis* RMNH 4520, 3 females (50.8–73.8 mm), male (59.3 mm), Madura Straits near Surabaya and Bangcallang, Java, Indonesia; syntypes of *Apocryptes polyophthalmus* BMNH 1867.2.23.11-12, 2 males (87.3–99.9 mm), China; syntype of *Apocryptes serperaster* BMNH 1965.8.12.51, male (117.9 mm), China; holotype of *Apocryptodon wirzi* NMB 4218, female (73.7 mm), Terama River, Papua New Guinea; *Apocryptodon wirzi* NTM S.15267-004, 2 males (96.3–104.9 mm), mouth, east of East Alligator River, Australia; holotype of *Apocryptodon punctatus,* ZUMT 26306, male (60.5 mm), Ariake Sound, western Kyushu, Japan; *Apocryptodon wirzi* AMS I.23943-007, 2 males (58.7–62.6 mm), 2 females (56.8–60.9 mm), mouth of Buffalo Creek, Beagle Gulf, Australia; syntype of *Boleophthalmus tenuis* BMNH 1889.21.34.82, female (124.5 mm), Sind, India; *Parapocryptes serperaster* USNM 86957, 2 males (97.5–99.2 mm), Foochow, Fukien Province, China; *Scartelaos histophorus* USNM 243433, 3 undet. (C&S, 55.0–84.2 mm), Indonesia.

Specimen repositories

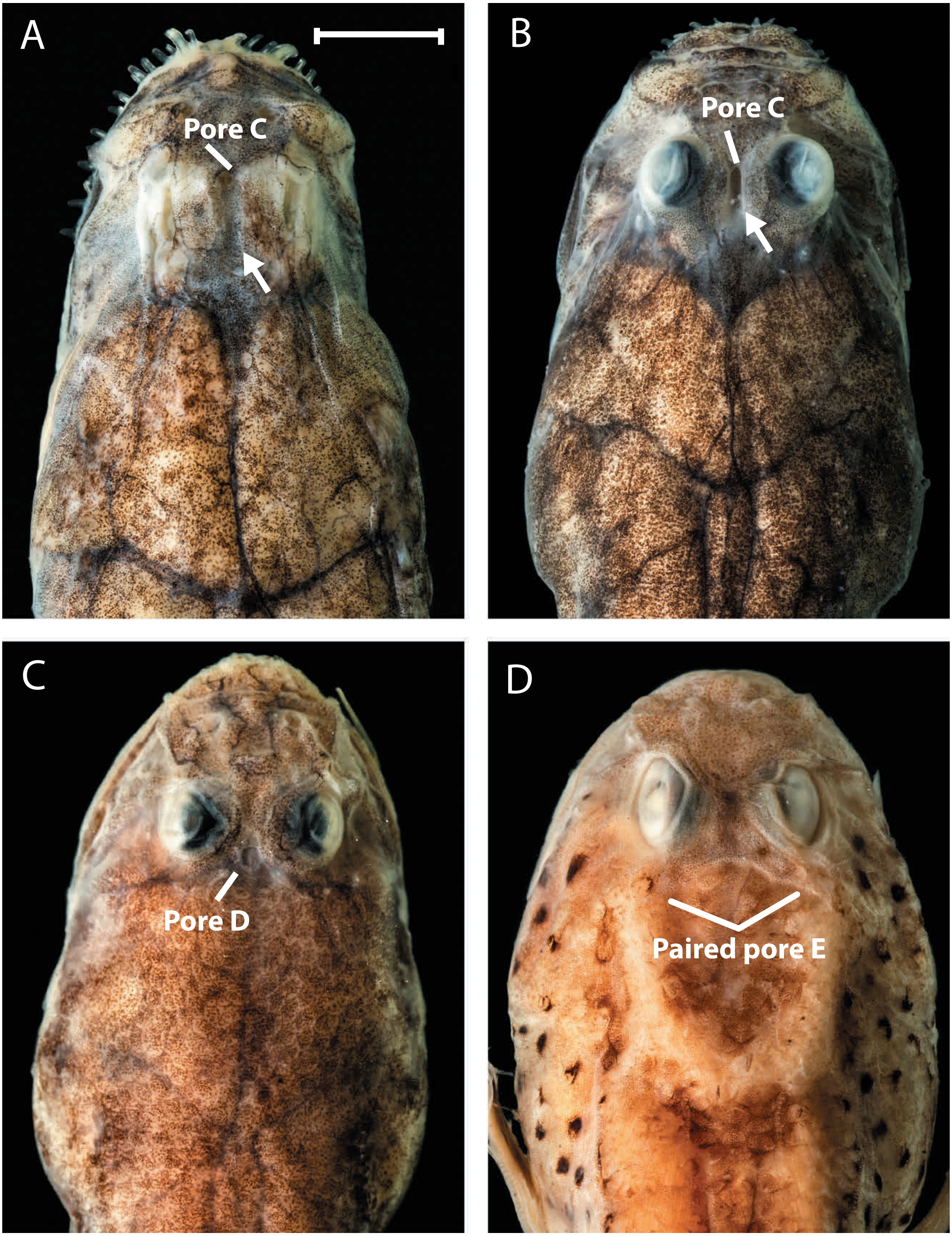
Material used in this study is housed at these institutions: Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania (ANSP); Australian Museum, Sydney (AMS); California Academy of Sciences, San Francisco (CAS and CAS-SU); Lee Kong Chian Natural History Museum, Singapore (ZRC); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum and Art Gallery of the Northern Territory, Darwin (NTM); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); National Museum of Nature and Science, Tokyo (NSMT-P); Natural History Museum, London (BMNH); Naturalis Biodiversity Center, Leiden (RMNH.PISC); Naturhistorisches Museum Basel, Basel (NMBA); and The University Museum, University of Tokyo (ZUMT).

RESULTS

Soft anatomy

Skin on the head

The two species of *Oxuderces* (*O. dentatus* and *O. nexipinnis*) recognized here share a unique morphology of the skin on the head. A fleshy, external trough, or deep groove, runs from anterior to posterior between the eyes (Fig. 3A, B). The trough is lined by a thin dermis and a correspondingly thick epidermis, and is supported internally by expanded medial margins of the medially fused frontal bones


A
Pore C
B
Pore C
C
Pore D
D
Paired pore E

that curve towards the midline (Figs 4A, 5A). A single, median sensory pore (pore C) sits in the anterior portion of the trough. A thick epidermis covers the eyes, especially dorsally (Fig. 5A); this epidermis contains a prominent middle or swollen cell layer (Park, Kim & Lee, 2006: fig. 2). In contrast, there is no open trough on the top of the head of *A. wirzi* or *A. glyphisodon* (Fig. 3C, D). Furthermore, the heads of these two species of *Apocryptodon* are covered by a thick, dermal stratum compactum (e.g. Genten, Terwindhe & Danguy, 2009) and relatively thin epidermal layer, which is almost imperceptible in histological sections (Figs 4B, 5B). The medial margins of the frontal bone of *A. wirzi* are covered by skin perforated posteriorly by a median sensory pore D (Figs 3C, 5B). In *A. glyphisodon* (Fig. 3D) there are paired sensory pores E, but no sensory pore D.

Dermal invagination

Dermal invaginations are rare in gobioid fishes. *Oxuderces nexipinnis* has a conspicuous dermal invagination just posterior to the point of attachment of the pelvic-fin base. Lateral to the base of the pelvic fin, the skin is invaginated and forms a discrete, shallow cavity lined with thin skin laterally and at the base (Fig. 6). The function of the invagination is unclear; we are unaware of any previous mention of this structure in *Oxuderces* or other gobioid fishes. It is absent in *Oxuderces dentatus*.

Another kind of dermal invagination is known in five amblyopine genera: *Amblyotrypauchen*, *Ctenotrypauchen*, *Paratrypauchen*, *Trypauchen* and *Trypauchenichthys*. In these taxa, in contrast to *O. nexipinnis*, the skin is invaginated on each side of the dorsal surface of the head lateral to the posttemporal bone and dorsal to the operculum. As with *O. nexipinnis*, the structure and function of the paired cavities in amblyopines is unknown (Murdy, 2006: fig. 1).

Osteology

Dentition

The oral jaw teeth of both species of *Oxuderces* are restricted to the premaxilla and the dentary; vomerine and palatine teeth are absent. In both species, the teeth are impressive: most are long and fang-like and jut out of the mouth (Fig. 7A). The specific epithet of the type species, *O. dentatus*, refers to the presence of large caninoid teeth on the upper oral jaw. Murdy (1989: fig. 76) proposed the presence of one fang-like canine tooth on each side of the premaxillary symphysis as a synapomorphy of *Oxuderces*. Both species of *Oxuderces* have two or more fang-like canine teeth on each side of the premaxillary symphysis. These teeth are markedly longer than the posteriorly adjacent teeth in most specimens, a character also shared with other oxudercine genera such as *Boleophthalmus* and *Parapocryptes*. Species of *Oxuderces* do not possess a canine tooth on each side of the symphysis internal to the anterior margin of the lower jaw; absence of these canine teeth is a character shared with only two other genera of oxudercine gobies: *Periophthalmodon* and *Periophthalmus*.

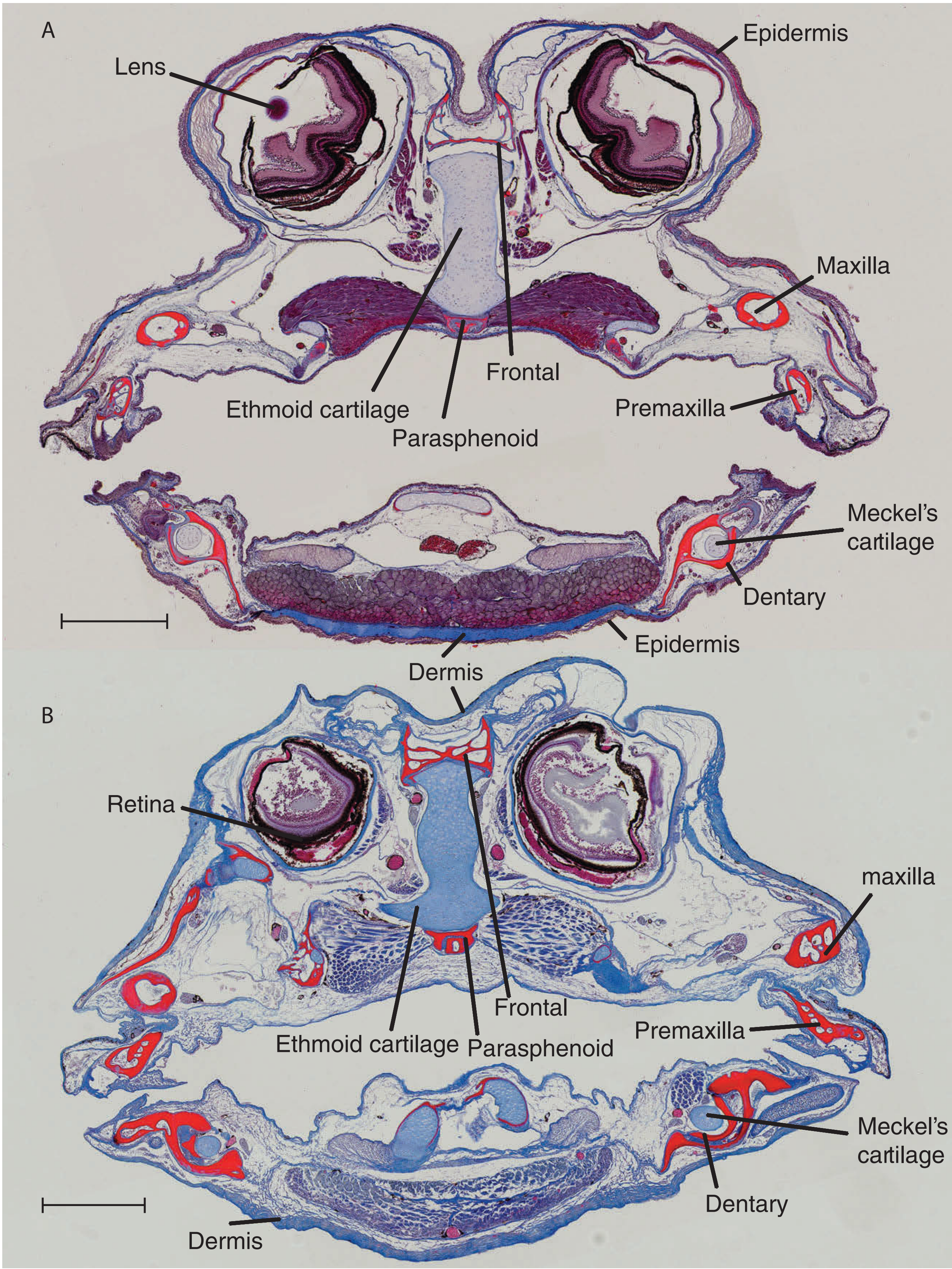
Jaw and jaw suspensorium

The gape of both species of *Oxuderces* is wide and extends about 3–4 eye lengths posterior to the orbit whereas the gape of most other oxudercine gobies only extends posteriorly to about the posterior margin of the eye. One character that is correlated with this structure is the angle between the metapterygoid–symplectic–quadrate strut and the anguloarticular. This angle is acute in *Oxuderces* (Fig. 7A) but obtuse in all other oxudercine gobies and other gobioid taxa examined (Fig. 7B). Furthermore, the preopercle is uniquely thin and subcrescent-shaped in both *O. dentatus* and *O. nexipinnis* (Fig. 7A), whereas it is broader and more distinctly crescent-shaped in other oxudercines and other gobioid taxa examined, such as *Gnatholepis* (Fig. 7B) and *Microgobius* (Birdsong, 1975: fig. 1a).

Hyoid bar

In gobioid fishes, the generalized shape of the anterior ceratohyal is broad and quadrangular, and in some taxa square (e.g. Birdsong, 1975; Fig. 8C). In *Oxuderces*, the anterior ceratohyal posterior to the insertion of the fourth branchiostegal ray is elongate and notched, a synapomorphy of the genus (Fig. 8A). Murdy (1989) reported this configuration only in *O. dentatus*, but he also unknowingly examined specimens that we now identify as *O. nexipinnis*. He reported an elongate portion of the anterior ceratohyal in *O. wirzi* (*A. wirzi* in our study) and proposed the elongation of the anterior ceratohyal posterior to the insertion of the fourth branchiostegal ray as a

Figure 3. Dorsal view of the head including interorbital region of (A) *Oxuderces dentatus* (ZRC 53939) and (B) *Oxuderces nexipinnis* (ZRC 53919). Arrow points to interorbital trough or groove. A sensory pore C sits in the anterior portion of the trough. C, *Apocryptodon wirzi* (AMS I23993.007), there is a single sensory pore D, and no trough; D, *Apocryptodon glyphisodon* (USNM 99874), there is a paired sensory pore E and no trough. Scale bar = 3 mm.


A
Lens
Epidermis
Maxilla
Frontal
Ethmoid cartilage
Parasphenoid
Premaxilla
Meckel's cartilage
Dentary
Epidermis
Dermis
B
Retina
maxilla
Frontal
Ethmoid cartilage
Parasphenoid
Premaxilla
Meckel's cartilage
Dentary
Dermis

synapomorphy of *Oxuderces*. We observe this region of the anterior ceratohyal to be relatively elongate and without a notch in other mudskipper genera, such as *Parapocryptes*, in addition to *A. wirzi* (Fig. 8B).

Many gobioid species, including all gobioid taxa examined herein, have five branchiostegal rays (Hoese & Gill, 1993: 416). A relatively thin anterior ray articulates with the anterior ramus of the anterior ceratohyal followed posteriorly by three rays that articulate with the posterior ramus of the anterior ceratohyal. The posteriormost fifth ray articulates with the posterior ceratohyal (Fig. 8). Branchiostegal rays 3–5 are distinctly thinner in some oxudercine gobies (Fig. 8A, B) and also clustered on the anterior portion of the posterior ramus of the anterior ceratohyal. In the gobionelline *Gnatholepis* (Fig. 8C), branchiostegal rays 3–5 are relatively thicker than in the two oxudercines illustrated here and the fifth ray articulates with the anterior ceratohyal closer to where it articulates with the posterior ceratohyal (Fig. 8A, B).

Frontal bones

The generalized condition of the frontal bones of gobioid fishes is separate and paired (Birdsong, 1975: table 2), and is characteristic of primitive gobioid taxa such as the genus *Rhyacichthys*. At the same time, Birdsong (1975) reported the frontal bones fused as the most frequent condition, logically rejecting the notion that common equals primitive. In his study of *Microgobius signatus*, Birdsong (1975: 141) reported that the paired 'frontal bones form a synostosis where they meet along the mid-line' and later in the same paragraph alluded to the frontals being fused. Based on our histological sections, the frontal bones are separate (not fused) in the gobionelline *Hemigobius hoevenii*, but fused in the oxudercines *O. nexipinnis*, *A. wirzi* and *Pseudapocryptes elongatus*. The medial margins of the fused frontal bones in *Oxuderces* curve dorsally and medially, towards the midline, but do not meet (Fig. 5A). The medial margins of the frontal bones in *Apocryptodon* are expanded dorsally, but do not curve towards the midline (Fig. 5B).

Axial skeleton

In both species of *Oxuderces*, the neural spine of the fourth vertebra is broad and spatulate and directed posteriorly (Fig. 9A), whereas the other neural spines are relatively narrow and attenuate. The spatulate neural spine comprises a rigid, thick and narrow ramus and a ventral laminar extension that is dorsoventrally broad and thin. A spatulate neural spine of the fourth vertebra is also observed in the gobiid genus *Gobionellus* (Pezold, 2004: fig. 5). In most other gobioid fishes, all the neural spines, including that on the fourth vertebra, are narrow and attenuate (Fig. 9B); in some gobionelline taxa, the neural spines are variably broadened (see Larson, 2001: fig. 11; Pezold & Larson, 2015: 8).

The first hemal spine extends ventrally to approximately the mid-length of the first anal-fin pterygiophore in *O. dentatus* (Fig. 10A; we examined one cleared and stained specimen and radiographs of three specimens). In contrast, in *O. nexipinnis*, the first hemal spine terminates dorsal to the mid-length and near to the proximal tip of the first anal-fin pterygiophore (Fig. 10B; we examined four cleared and counterstained specimens and radiographs of five specimens).

SYSTEMATICS

Genus *Oxuderces* Eydoux & Souleyet, 1848

Oxuderces Eydoux & Souleyet, 1848: 181 (type species *Oxuderces dentatus* Eydoux & Souleyet, 1848, type by monotypy)

Composition: Two allopatric species: *O. dentatus* Eydoux & Souleyet, 1848 (Figs 3A, 11, 12) and *O. nexipinnis* (Cantor, 1849) (Figs 2, 3B, 6, 14). The distribution of each species is shown in Figure 13.

Differential diagnosis: Oxuderces is differentiated from all other oxudercine gobies by five putative synapomorphies: (1) single, anterior interorbital pore C that sits in a fleshy, interorbital trough supported internally by expanded, curved medial margins of the frontal bones and lined externally with a thick epidermis and thin dermis (vs. no fleshy, interorbital trough, medial margins of the frontal bones expanded but not curved, and epidermis extremely thin and dermis thick); (2) highly thickened epidermis over the eye (vs. a thickened dermis); (3) neural spine of the fourth vertebra broad and spatulate (vs. narrow and pointed); (4) anterior ceratohyal elongate and notched posterior to insertion of fourth branchiostegal (vs. not elongate, or elongate but not notched); and (5) acute angle

Figure 4. Histological sections through the head of (A) *Oxuderces nexipinnis* (USNM 427099) and (B) *Apocryptodon wirzi* (USNM 432509). The paired adductor arcus palatini lie on either side of the parasphenoid and the intermandibularis spans the lower jaw and connects the dentaries. Bone is bright red, cartilage light blue, muscle and connective tissue dark blue to purple. Scale bar = 0.5 mm.

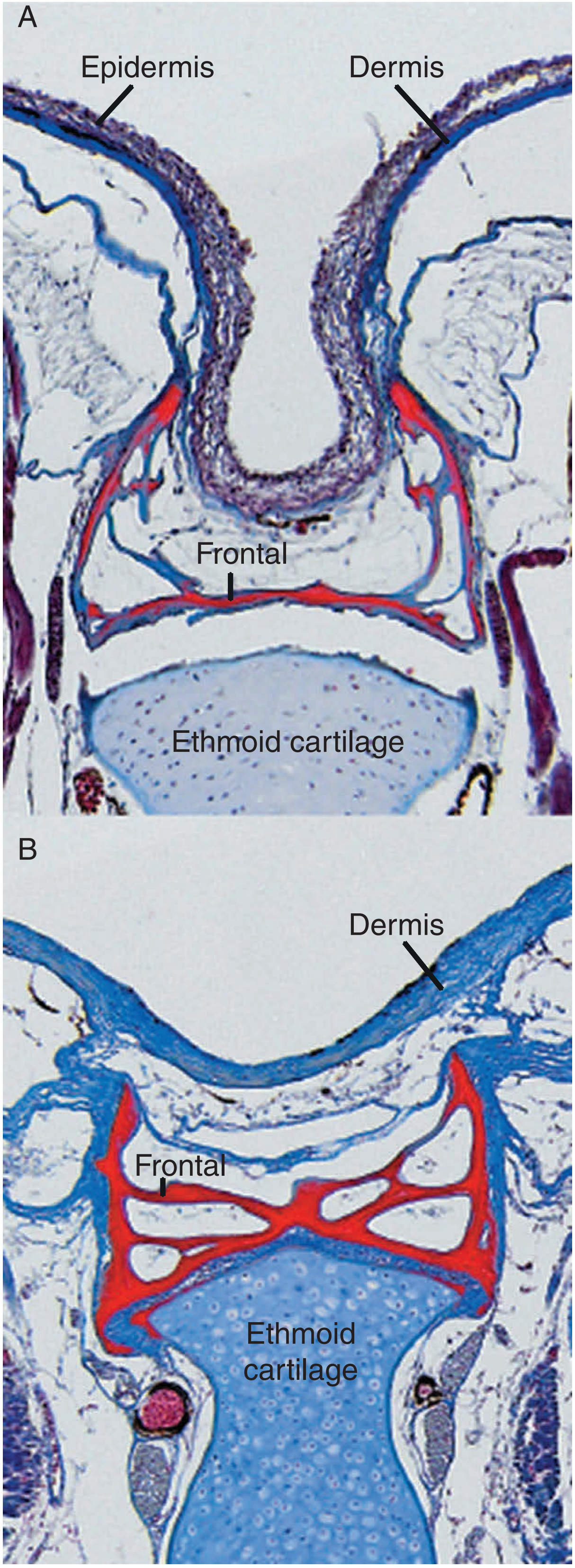


Figure 5. Enlargement of the histological sections of Figure 4 through the mid-dorsal region of (A) *Oxuderces nexipinnis* (USNM 427099) and (B) *Apocryptodon wirzi* (USNM 432509). Bone is bright red, cartilage light blue, muscle and connective tissue dark blue to purple.

between metapterygoid–symplectic–quadrate strut and the anguloarticular (vs. angle obtuse).

Description: Anterior portion of head markedly depressed; snout profile broadly pointed; gape wide; distinct notch in middle of upper lip between two medial premaxillary teeth; lips thick, posterior lower lip protruding distally. Roof of mouth with fleshy palp that is elliptical and with pointed tips, palp studded with papillae. Teeth in both premaxilla and dentary in single row; one or two prominent, elongate canine teeth on each side of premaxillary symphysis, canine teeth extending slightly anteroventrally and projecting beyond lower jaw when mouth closed, all teeth on premaxilla caninoid; dentary with discontinuous caninoid teeth; no canine tooth on each side of symphysis internal to anterior margin of dentary; dentary with small dorsally directed flange on each side just posterior to posterior-most tooth. Maxillo-dentary ligament with finger-like projections on dorsoposterior sides of lower lip; dentary with ligament on each side attaching medially just posterior to posterior-most tooth and antero-medially to flange (Murdy, 1989: fig. 73). Gill opening restricted, beginning from the region anterior to midpoint of pectoral-fin base, coursing anteroventrally, and ending just dorsal to pelvic-fin origin. Eyes positioned anterodorsally but not meeting medially, no dermal cup or membrane covering ventral portion of eye. Thickened dermal layer (or secondary cornea) over dorsal portion of eye, extending, and gradually thinning out ventrally and posteriorly (Figs 4, 5). Single anterior interorbital sensory pore (pore C) at anterior edge of fleshy trough or groove; trough covered externally by thickened dermal layer extending from dorsal area of eyes; a pair of anterior oculoscapular canal pores present. Posterior nostril large, anteroventral to eye; anterior nostril opening ventrally at tip of pendulous short tube overlapping upper jaw. Sphenotic bones small, not contacting eyes. Frontal bone elongate; lateral processes on medial portion of frontal distinct; frontal bone fused, forming interorbital bridge, slightly curved, not overlapping ethmoid anteriorly (Fig. 5A). Maxilla and premaxilla terminating posterior to eye, maxilla not reaching retroarticular. Palatine terminating before mid-

Table 1. Counts and measurements for *Oxuderces dentatus* and *Oxuderces nexipinnis*

	O. dentatus									*O. nexipinnis*										
	Holotype MNHN A-1822	CAS-SU 25524	CAS-SU 61139	USNM 85846		USNM 86378		USNM 86954	Range (*N* = 7)	ANSP 63091	RMNH 12091		USNM 119547	USNM 278447	USNM 279359				ZRC 39777	Range (*N* = 10)
Counts																				
First dorsal fin	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI	VI
Second dorsal fin	27	25	25	27	27	25	25	26	25–27	26	25	26	26	26	26	25	26	26	26	25–26
Anal fin	27	25	26	26	24	25	25	26	24–26	26	25	24	26	26	26	26	26	25	26	24–26
Pectoral fin (left)	24	22	22	23	22	22	22	23	22–23	22	21	21	21	22	23	24	21	22	23	21–24
Longitudinal scales	54	54	52	56	59	53	51	57	51–59	50	50	53	51	50	50	52	DNT	DNT	54	50–54
Predorsal midline scales	0	0	29	24	0	16	0	16	0–29	0	0	0	0	0	0	0	DNT	DNT	14	0–14
Vertebrae number	DNT	DNT	DNT	10 + 16	10 + 16	DNT	DNT	10 + 16	10 + 16	10 + 16	10 + 16	10 + 16	10 + 16	DNT	DNT	DNT	10 + 16	10 + 16	10 + 16	10 + 16
Standard length (SL, mm)	77.5	65.0	75.3	80.3	80.2	67.3	54.3	78.7		73.2	73.0	66.8	64.0	43.6	30.8	31.5	47.9	35.7	80.6	
Gender	Female	Female	Male	Male	Female	Female	Female	Male		Male	Female	Male	Female	Female	Female	Female	Female	Male	Male	
Measurements (%SL)																				
Head length	24.5	27.7	25.1	26.8	27.2	25.7	27.3	26.9	25.1–27.7	29.5	27.7	27.4	28.1	30.3	27.3	29.2	28.8	29.1	28.2	27.3–30.3
Predorsal length	25.7	30.8	28.7	28.8	29.7	36.8	31.9	31.3	28.7–36.8	29.6	31.6	30.5	31.6	31.4	30.2	30.5	30.5	28.6	28.2	28.2–31.6
D1 and D2 base length	59	57.7	58.4	59.8	57.6	58.2	59.7	59.0	57.6–59.8	58.6	57.8	58.4	59.4	58.7	56.8	56.5	57.0	54.9	56.8	54.9–59.4
Anal-fin base length	36.8	39.1	40.8	38.6	36.4	39.2	37.6	42.8	36.4–42.8	39.6	35.9	38.0	39.5	37.6	36.0	39.0	36.7	36.7	40.4	35.9–40.4
Pelvic-fin length	NA	15.2	14.5	18.4	16.3	14.4	16.0	15.8	14.4–18.4	16.8	14.0	15.0	17.2	17.2	18.2	14.3	14.4	16.0	15.4	14.0–18.2
Pectoral-fin length	16.8	16.3	15.0	17.4	15.6	14.6	18.8	16.1	14.6–18.8	15.7	17.8	18.9	16.6	14.0	19.2	18.1	15.7	17.6	14.9	14.0–19.2
Caudal-fin length	18.7	25.4	DNT	20.5	21.8	21.4	25.4	21.6	20.5–25.4	23.6	20.8	24.0	23.6	24.8	22.7	22.5	24.6	26.3	21.5	20.8–26.3
Body depth at anus	9.3	11.1	12.5	12.2	11.3	11.1	10.7	11.9	10.7–12.5	9.3	12.3	11.5	11.7	8.7	9.1	8.6	10.6	10.4	12.9	8.6–12.9
Body width at anus	2.9	5.5	6.9	6.1	5.2	5.6	6.3	6.6	5.2–6.9	4.5	7.3	6.1	5.9	5.0	4.9	5.1	5.2	4.5	6.8	4.5–7.3
Measurements (%HL)																				
Head width	41.6	42.8	47.1	44.2	46.3	41.6	35.8	48.1	35.8–48.1	42.1	41.1	41.0	44.4	32.6	42.9	41.3	41.3	38.5	43.2	32.6–44.4
Head depth	34.2	37.2	42.3	33.5	39.9	39.9	32.4	42.5	32.4–42.5	33.8	37.6	38.3	36.7	31.1	33.3	30.4	36.2	32.7	42.7	30.4–42.7
Snout length	10.5	13.9	17.5	14.4	14.2	16.2	12.8	15.6	12.8–17.5	12.5	DNT	12.0	12.8	14.4	15.5	15.2	14.5	14.4	13.7	12.0–15.5
Interorbital distance	4.7	3.9	3.7	3.7	4.6	4.6	5.4	4.7	3.7–5.4	4.2	DNT	4.4	4.4	3.0	3.6	3.3	DNT	4.8	4.8	3.0–4.8
Eye diameter	8.9	11.1	10.6	9.3	8.7	13.3	10.1	13.7	8.7–13.7	15.3	DNT	10.9	15.6	11.4	15.5	16.3	11.6	8.7	15.9	8.7–16.3
Jaw length	48.4	55.6	57.1	48.8	48.2	45.7	44.6	44.8	44.6–57.1	59.7	54.5	55.7	52.2	49.2	45.2	41.3	50.0	42.3	59.0	41.3–59.7

If a specimen was damaged or abnormal (e.g. it has obvious parasites), we did not record data; this is noted in the table by the abbreviation DNT. Data for the holotype of *O. dentatus* are not included in the range reported for the species.

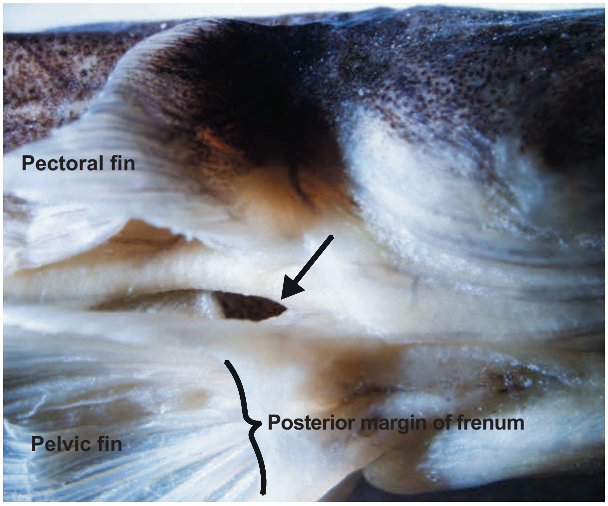


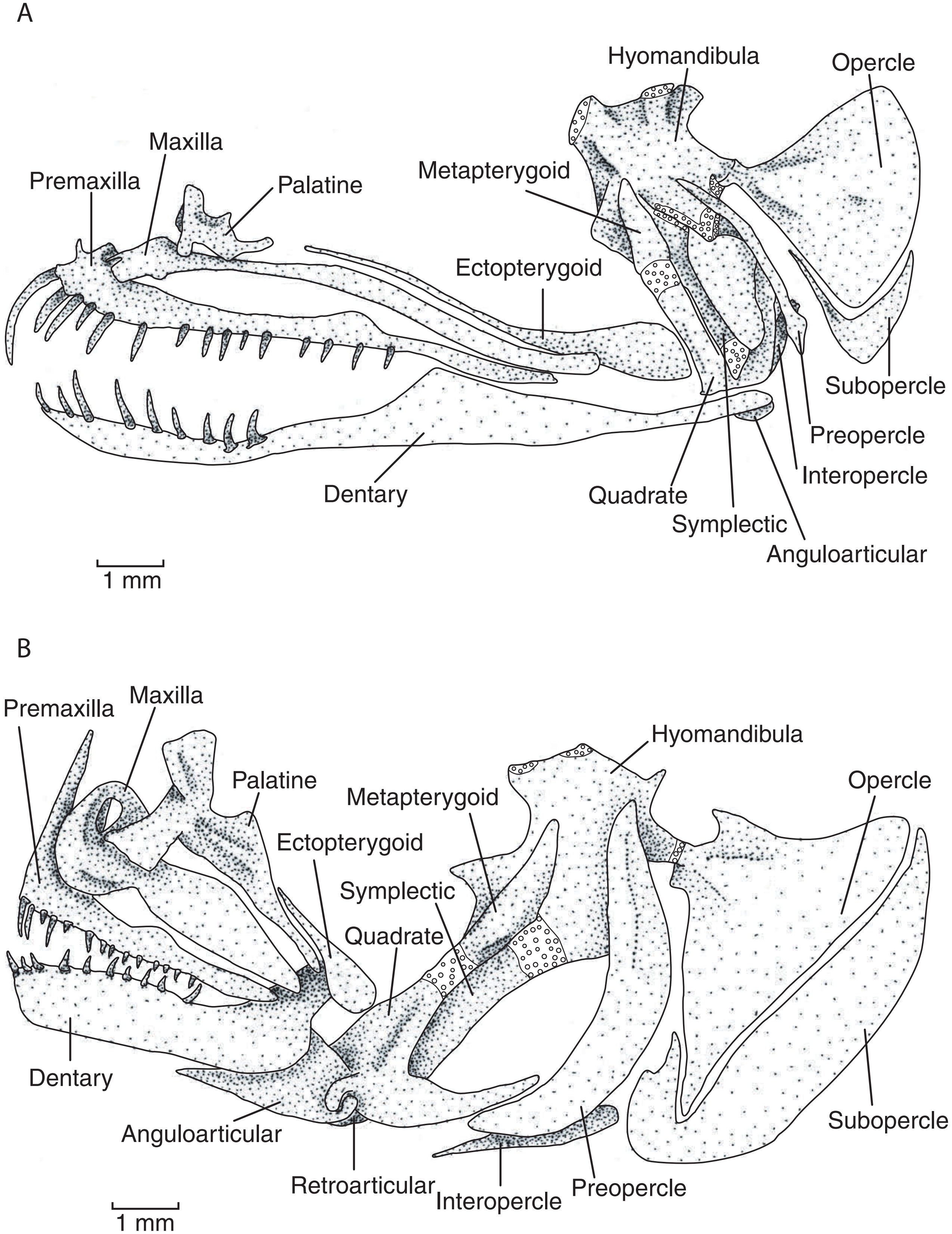
Figure 6. Dermal invagination or pouch (arrow) at point of attachment of the pelvic-fin base in *Oxuderces nexipinnis* (ZRC 53919, 53.2 mm SL). Anterior is to the right.

ectopterygoid. Ectopterygoid thin and elongate, meeting with quadrate posteriorly (Fig. 7A). Metapterygoid terminating at hyomandibular junction; angle between metapterygoid–symplectic–quadrate strut and anguloarticular acute (vs. angle obtuse). Preopercle subcrescent-shaped, thin, meeting hyomandibula dorsally. Basihyal bone triangular with continuous cartilaginous anterior margin. Branchiostegal rays 5, rays thin. No laminar processes on parapophyses of fourth vertebrae; neural spine of fourth vertebra broad and spatulate. D1 and D2 connected by membrane for entire height, shallow indentation separating D1 and D2 due to varying height of fin elements. No membrane connecting D2 or A to caudal fin. D1 with six spinous elements, each spine with associated pterygiophore; spaces between first five D1 spines subequal, base of sixth spine positioned approximately midway between base of fifth D1 spine and first element of D2; all elements in D2 and A fins are segmented rays; penultimate and ultimate rays of D2 and A fins supported by single pterygiophore; caudal fin lanceolate, with 17 segmented rays; pelvic fin short and rounded, not reaching genital papilla. Caudal peduncle cartilage elongate, reaching anterior extent of penultimate vertebra. Vertebrae slightly elongate, vertebrae number 10 + 16, two epural bones present. Dense network of capillaries close to epidermal surfaces, especially on head. Males with triangular, conical genital papilla, with posterior tip pointed; females with bulbous, rectangular genital papilla. No other observed external sexual dimorphism.

Etymology: Greek in origin, derived from the word '*oxyderkes*' meaning 'sharp-sighted' (Murdy, 1989). Gender masculine.

Remarks: The genus *Oxuderces*, and type species *O. dentatus*, was first described by Eydoux and Souleyet based on a single specimen collected from Macao along with some 200 other fish species aboard the corvette *La Bonite* between 1836 and 1837 (Bauchot, Whitehead & Monod, 1982; Figs 1, 11). The unique character of the holotype that prompted its description as a new genus and species (Eydoux & Souleyet, 1848:181) was a peculiar gill opening interpreted by Springer (1978:1) as '... continuous across the isthmus and restricted to the ventral surface of the head'. The holotype and, until 1978, the sole scientific specimen identified as *O. dentatus* also lacks pelvic fins (Fig. 12A; Springer, 1978: fig. 4b). Springer (1978) concluded that the absence of pelvic fins in the holotype was abnormal, although it was not considered so by Eydoux & Souleyet (1848) who compared *Oxuderces* to the 'anarrhiques', the French vernacular for wolffishes, currently classified as the family Anarhichadidae, which typically lack pelvic fins. Although Eydoux & Souleyet (1848) placed their new genus in the family Gobioides, congruent with the modern Gobiidae, classification of *Oxuderces* has been unstable (Springer, 1978). It has been subsequently placed in its own family, the Oxudercidae (Günther, 1861; Gill, 1872, 1893; Reeves, 1927; Chu, 1931), which was classified alternatively as a trachinoid (Berg, 1940; Fowler, 1956; Schultz, 1960; Golvan, 1965; Lindberg, 1971), blennioid (Gosline, 1968) or gobioid fish (Günther, 1880; Boulenger, 1904; Jordan, 1905). Many of these ichthyologists who reclassified *O. dentatus* did not examine the holotype or, even if they did, were probably diverted to a search for close relatives among other fishes that also lacked pelvic fins, such as the wolffishes. No other specimen of *Oxuderces* has been identified without pelvic fins.

Figure 7. Line drawings of the jaw and jaw suspensorium of (A) *Oxuderces nexipinnis* (USNM 279359) and (B) *Gnatholepis* sp. (USNM 287166). Angle between metapterygoid–symplectic–quadrate strut and anguloarticular is acute in *O. nexipinnis*, in which the preopercle is relatively thin and subcrescent-shaped. In contrast, the angle between the strut and the anguloarticular is obtuse, and the preopercle is wider and broadly crescent-shaped in *Gnatholepis* sp. Bone is stippled, cartilage is represented by open circles.



A
Hyomandibula
Opercle
Maxilla
Premaxilla
Palatine
Metapterygoid
Ectopterygoid
Subopercle
Preopercle
Interopercle
Dentary
Quadrate
Symplectic
Anguloarticular
1 mm
B
Premaxilla
Maxilla
Hyomandibula
Palatine
Metapterygoid
Opercle
Ectopterygoid
Symplectic
Quadrate
Dentary
Subopercle
Anguloarticular
Retroarticular
Interopercle
Preopercle
1 mm

After examining the holotype, Springer (1978) returned *Oxuderces dentatus* to the family Gobiidae, a decision followed by all subsequent workers (e.g. Hoese, 1984; Murdy, 1989; Pezold, 1993).

The monotypic *Apocryptichthys* Day, 1876, allied historically with *Oxuderces*, was described for *Apocryptes cantoris* Day, 1871. Confusion surrounding the identity of *Apocryptichthys cantoris* stemmed from the inconsistent descriptions in the literature and figures by Day (1871, 1876, 1889; and see Springer, 1978: 10 for a tabulated summary). These descriptions varied from publication to publication. The original description of *Apocryptichthys* and the figure included of the type specimen *Apocryptes cantoris* (Day, 1876) conform to *Oxuderces* (probably referring to AMS B.8336 from Madras), whereas the original description of *Apocryptes cantoris* (probably referring to BMNH 1870.5.18.23 from the Andaman Islands) conforms to *Scartelaos histophorus* (Valenciennes, 1837). Springer (1978) designated a lectotype for *Apocryptes cantoris* Day, 1871 (BMNH 1870.5.18.23) from an unspecified number of syntypes and classified the species in the genus *Boleophthalmus* Valenciennes, 1837. Murdy (1989) reclassified this species in *Scartelaos* Swainson, 1839, a decision with which we concur, as does V. G. Springer (pers. comm.). As the original description of *Apocryptichthys* may be interpreted to include *Oxuderces,* we have included *Apocryptichthys*, in part, in our treatment of *Oxuderces*.

Ecological note: Published information on the biology and natural history of *Oxuderces* may refer to what we now recognize as three allopatric species classified in two genera. We interpret information on specimens from eastern China to refer to *O. dentatus*, that on specimens from the Indo-West Pacific, excluding China, to refer to *O. nexipinnis*, and that on specimens from northern Australia and New Guinea to refer to *Apocryptodon wirzi*. General information on *O. dentatus* may refer to either one of the species of *Oxuderces*.

OXUDERCES DENTATUS EYDOUX & SOULEYET, 1848
FIGURES 1, 3A, 10A, 11, AND 12; TABLE 1

Oxuderces dentatus Eydoux & Souleyet, 1848: 182 (type locality, Kwantung, near Macao, China)

Apocryptichthys sericus Herre, 1927: 264 (type locality, Amoy, China)

Apocryptes pellegrini Wu, 1931: 48 (type locality, Foochow, China)

Holotype (examined): MNHN A-1822, female, 77.5 mm SL, 91.0 mm TL, Kwantung, near Macao, China, by *La Bonite*, 1837.

Other material examined: Eight specimens, 54.3–93.8 mm SL: CAS-SU 25524, female (65.0 mm), Xiamen, China; CAS-SU 61139, male (75.3 mm), Macao, China; USNM 85846, male (80.3 mm), female (80.2 mm), Fengsien, Nanking (near Shanghai), China; USNM 86378, 2 females (54.3–67.3 mm), Foochow and nearby Fukien, China; USNM 86954, male (78.7 mm), 1 undet. (C&S, 93.8 mm), Foochow, Fujian, China.

Differential diagnosis: Oxuderces dentatus is differentiated from its sole congener *O. nexipinnis* in having: first hemal spine extending ventrally to a point approximately mid-length of first anal-fin pterygiophore (vs. terminating dorsal to mid-length of first anal-fin pterygiophore; see Fig. 10); mouth terminal (vs. superior); no conspicuous dermal invagination posterior to point of attachment of pelvic-fin base (vs. present); and head relatively short (25.1–27.7%SL vs. 27.3–30.3%SL).

Description: Head markedly depressed, wider than deep, head length 25.1–27.7%SL, head width 35.8–48.1%HL, head depth 32.4–42.5%HL. Eye diameter 8.7–13.7%HL; interorbital narrow, interorbital distance 3.7–5.4%HL, eye without dermal cup. Snout profile broadly pointed, snout length 12.8–17.5%HL. Mouth terminal; gape wide; jaw length 44.6–57.1% HL; distinct notch in middle of upper lip between two medial teeth. Teeth in premaxilla and dentary caninoid, unevenly spaced, in single row; one or two prominent and elongate canine tooth/teeth on each side of premaxillary symphysis, canine teeth on premaxilla extending anteroventrally beyond lower jaw when mouth closed, teeth decreasing in length posteriorly; teeth in dentary more uniform in size, all teeth shorter than medial canine teeth of premaxilla, teeth absent posteriorly, no canine tooth on each side of symphysis internal to anterior margin of dentary. Body compressed and stout, body depth at anus 10.7–12.5%SL, body width at anus 5.2–6.9%SL. Predorsal long, predorsal length 28.7–36.8%SL. D1 and D2 connected by membrane for entire height, base of D1 and D2 57.6–59.8%SL; base of anal fin 36.4–42.8%SL. No membrane connecting D2 or A to caudal fin. Pelvic fin rounded, not reaching genital papilla, pelvic-fin length 14.4–18.4% SL. Pectoral-fin length 14.6–18.8%SL. Caudal fin long, lanceolate, 20.5–25.4%SL. First dorsal fin (D1) with six spinous rays (VI); all elements of D2 and A fins segmented, D2 with 25–27 elements, A fin with 24–26 elements; pectoral rays 22–23; caudal fin segmented rays 17; dorsal procurrent rays 5, ventral procurrent rays 4. Two epural bones. Lateral longitudinal scale count 51–59. Predorsal midline with 0–29 scales, scales may be small and embedded in skin. In specimens without predorsal scales, entire dorsal region anterior to D1 as well as the isthmus, pectoral-fin base and ventral region of head without scales; scales on body small and embedded in skin anteriorly, and increasing in size posteriorly. Raised free-neuromast rows on head.

Coloration: Eydoux & Souleyet (1848:183) described the colour of the holotype: 'Ce poisson est d'un brun verdâtre supérieurement et sur les côtés; inférieurement, il est d'une couleur blanchâtre. Les nageoires sont grisâtres [This fish is greenish-brown on the dorsal surface and on the sides; on the ventral surface, it is whitish. The fins are grayish]'. Wu (1931) reported live specimens with a bluish throat and abdomen and a black line on the upper lip. Preserved specimens are uniformly light brown with a dark brown to black upper lip and pectoral-fin base. There is a diffuse, dark brown spot at half of ray height, on the posterior distal end of D2; the spot lies between the 20^{th} and the penultimate rays. Eydoux & Souleyet (1848) did not mention nor did they illustrate the spot, although Springer (1978) reported it in examination of the holotype. Only Herre (1927: 265–266) reported the presence of seven to eight brown dorsal cross bands posteriorly in his smallest specimen (41.0 mm).

Etymology: Latin, '*dentatus*' meaning 'toothed', in reference to prominent canines on the upper jaw.

Distribution and ecological note: Known from isolated localities in coastal China, from Shanghai south to Macao (Fig. 13). Ecology poorly known; reports on the natural history of *O. dentatus* may refer to *O. nexipinnis*.

Remarks: Data associated with the holotype indicate that it was collected from Kwantung (Guangdong), China, the province adjacent to Macao, although all other reports identify the type locality as Macao. The precise locality of collection of the holotype is probably unknowable. The holotype is in poor condition, with most teeth lost and pelvic fins abnormally absent (Figs 11, 12A). Various dates have been cited for the description of *O. dentatus*: 1842 in Springer (1978), or 1848 in Murdy (1989). In an attempt to standardize the dates of publication, Bauchot *et al.* (1982) inadvertently introduced more confusion. In the abstract presented in English, the authors wrote that fishes described by Eydoux & Souleyet were '...published as late as 1850' (Bauchot *et al.*, 1982: 59). In the abstract presented in French, they wrote 'La publication est postérieure à 1848 et peut avoir été aussi tardive que 1850 [The publication was made after 1848, and may have been as late as 1850]' (Bauchot *et al.*, 1982: 59). Elsewhere in the paper, and in English, they concluded that the volume describing fishes from the voyage '...were published after March 1848' (Bauchot *et al.*, 1982: 63). We use 1848 following Murdy (1989) and the earliest year within the range proposed by Bauchot *et al.* (1982).

Oxuderces nexipinnis (Cantor, 1849)
Figures 2, 3B, 4A, 5A, 6, 7A, 8A, 9A, 10B, 14; Table 1

Apocryptes nexipinnis Cantor, 1849: 1170 (type locality, Sea of Penang, Malaysia)

Apocryptes cantoris not Day, 1871 (in part Day, 1876, specimens from Madras, India)

Apocryptichthys livingstoni Fowler, 1935: 162 (type locality, Paknam, Thailand)

Syntypes examined: BMNH 1860.3.19.568-69, 2 undet., 65.0–67.8 mm SL, Sea of Penang, Malaysia.

Other type material examined: Apocryptichthys livingstoni holotype: ANSP 63091, male, 73.2 mm SL, mouth of Me Nam Chao Praya, Paknam, Thailand.

Other material examined: Sixty-four specimens, 19.9–80.6 mm SL. RMNH.PISC 12091, male (66.8 mm), 2 females (65.9–73.0 mm), east coast Java Island, Indonesia; RMNH.PISC 12092, 5 males (63.0–76.4 mm), 14 females (60.0–79.9 mm), east coast Java Island, Indonesia; RMNH.PISC 12433, female (55.6 mm), Java Island, Indonesia; RMNH.PISC 12750, female (79.4 mm), Surabaya, Indonesia; RMNH.PISC 33844, female (57.6 mm), Indonesia; RMNH.PISC 17382, female (72.0 mm), Pulau Weh, Sumatra, Indonesia; USNM 119547, female (64.0 mm), off Tachalon, Gulf of Thailand; USNM 278447, female (43.6 mm), southern side of river mouth, Muar river, Johore, Malaysia; USNM 279359, 12 males (19.9–50.0 mm; 1 C&S, 35.7 mm), 14 females (22.1–31.5 mm; 1 C&S, 47.9 mm); USNM 288662, 1 male (C&S, 39.7 mm), 2 females (C&S, 21.6–26.8 mm), southern side of river mouth, Muar river, Johore, Malaysia; ZRC 39777, male (80.6 mm), Sungai Selising, Matang mangroves, Perak, Malaysia; ZRC 53919, 3 males (50.3–53.2 mm), 3 females (33.4–53.3 mm), Matla mudflats, Jharkali, South 24 Parganas, West Bengal, India.

Differential diagnosis: Oxuderces nexipinnis is differentiated from *O. dentatus* by the following characters: first hemal spine terminating above mid-length of first anal-fin pterygiophore (vs. extending ventrally below mid-length of first anal-fin pterygiophore; Fig. 10); mouth superior (vs.

terminal); conspicuous dermal invagination posterior to the point of attachment of pelvic-fin base (vs. dermal invagination absent; Fig. 6); head relatively long (27.3–30.3%SL vs. 25.1–27.7%SL).

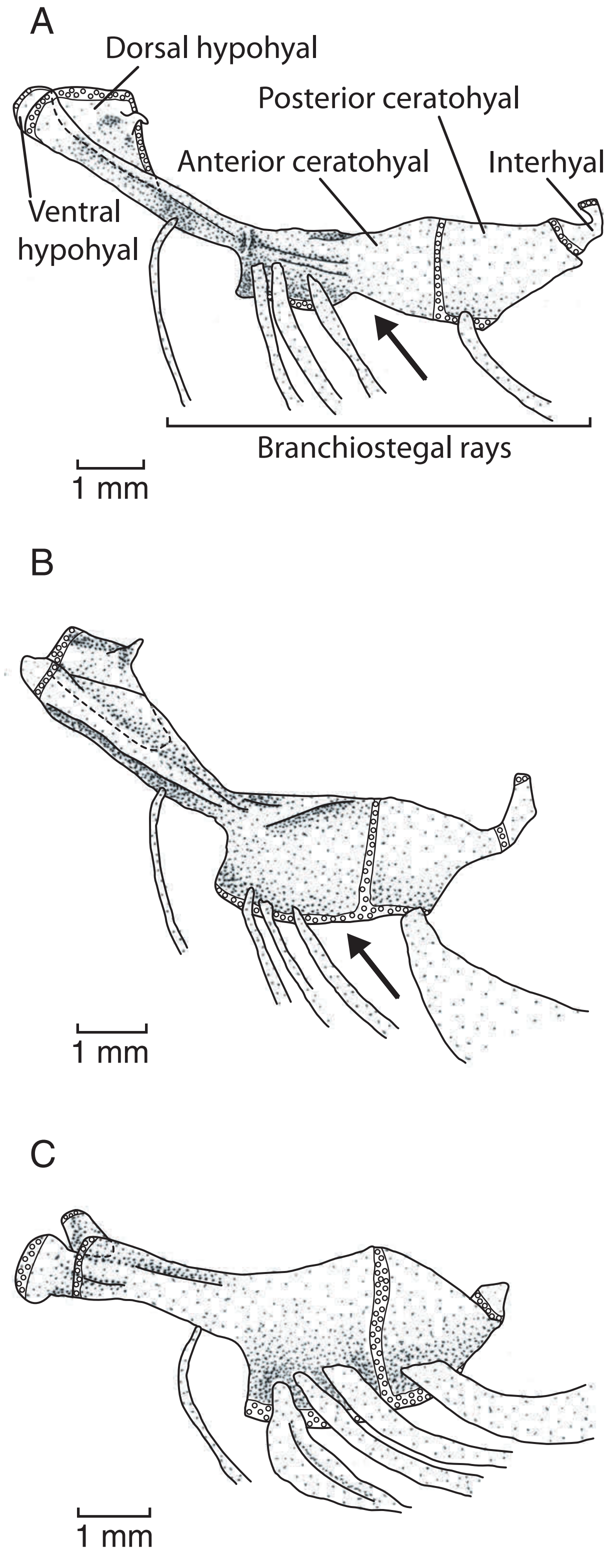


Figure 8. Line drawings of the hyoid bar in (A) *Oxuderces nexipinnis* (USNM 279359), (B) *Apocryptodon wirzi* (USNM 287292) and (C) *Gnatholepis* sp. (USNM 287166). The anterior ceratohyal posterior to insertion of the fourth branchiostegal ray is elongate and notched (arrow) in *O. nexipinnis*, elongate and not notched (arrow) in *A. wirzi*, and not elongate and not notched in *Gnatholepis* sp. Branchiostegal rays 3–5 are distinctly thinner in A and B. Bone is stippled, cartilage is represented by open circles. Only the proximal portion of the five branchiostegal rays is drawn.

Description: Head markedly depressed, wider than deep, head length 27.3–30.3%SL, head width 32.6–44.4%HL, head depth 30.4–42.7%HL. Eye diameter 8.7–16.3%HL; interorbital distance 3.0–4.8%HL, eye without dermal cup. Snout profile pointed, snout length 12.0–15.5%HL. Mouth superior, lower jaw terminating just anterior to upper jaw, gape wide; jaw length 41.3–59.7%HL; distinct notch in middle of upper lip between two medial teeth. Teeth in both jaws caninoid, unevenly spaced, in single row; one or two prominent and elongate canines on each side of premaxillary symphysis, canine teeth extending slightly anteroventrally and reaching beyond lower jaw when mouth closed, teeth decreasing in length posteriorly; teeth in lower jaw more uniform in size, teeth all shorter than medial canine teeth of upper jaw, teeth absent posteriorly, no canine tooth on each side of symphysis internal to anterior margin of lower jaw. Body compressed and gracile; body depth at anus 8.6–12.9%SL, body width at anus 4.5–7.3% SL. Predorsal long, predorsal length 28.2–31.6%SL. D1 and D2 connected by membrane for entire height, base of D1 and D2 54.9–59.4%SL; base of anal fin 35.9–40.4%SL. No membrane connecting D2 or A to caudal fin. Pelvic fin short and rounded, not reaching genital papilla, pelvic-fin length 14.0–18.2% SL. Pectoral-fin length moderate, 14.0–19.2%SL. Caudal fin long, lanceolate, 20.8–24.8%SL. D1 with six spinous dorsal rays (VI); all elements of D2 and A fins segmented; D2 with 25–26 elements, A fin with 24–26 elements; pectoral rays 21–24; caudal fin segmented rays 17; dorsal procurrent rays 5, ventral procurrent rays 4. Two epural bones. Lateral longitudinal scale count 50–54, scales on body small and embedded in skin anteriorly, and increasing in size posteriorly. All specimens without scales on dorsal region anterior to D1, ventral region of the head, cheek, operculum and pectoral-fin base except for largest specimen examined (ZRC 39777, 80.6 mm) which has cheek scales and 14 predorsal midline scales; all scales small and embedded. Raised and distinct free-neuromast rows on head. Conspicuous dermal invagination posterior to point

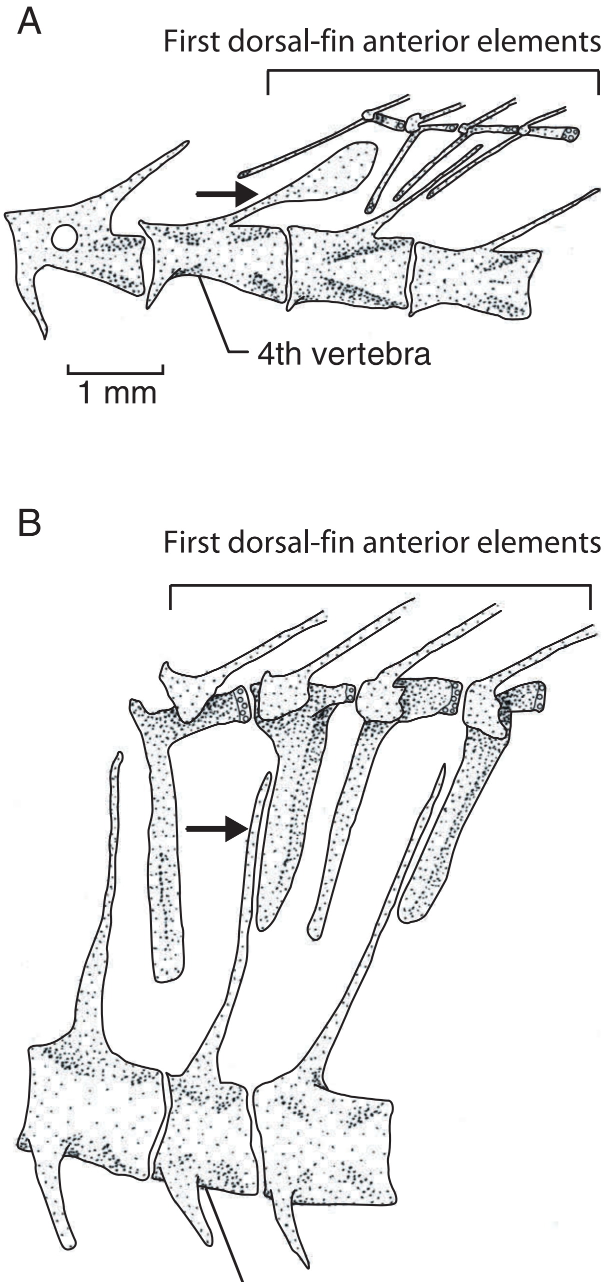


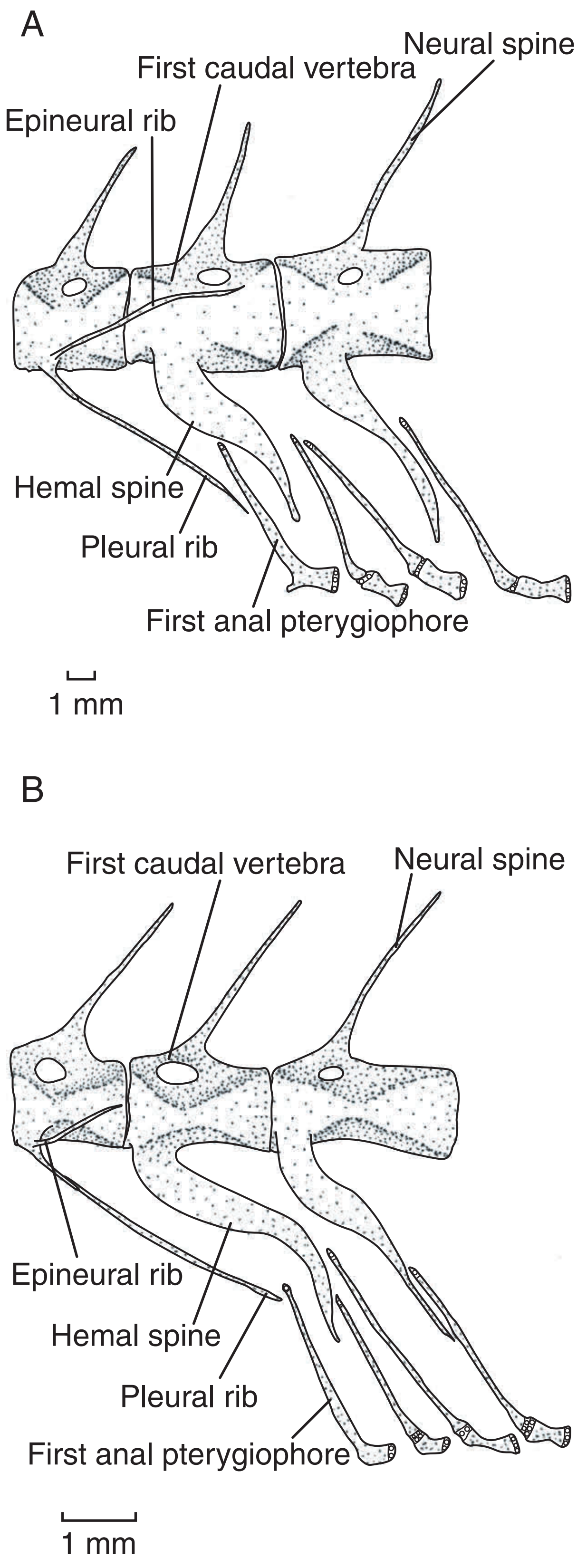
Figure 9. Line drawings of several anterior vertebrae and associated elements of the first dorsal fin in (A) *Oxuderces nexipinnis* (USNM 279359) and (B) *Gnatholepis* sp. (USNM 287166). The neural spine of the fourth vertebra (arrow) is broad and spatulate and directed posteriorly in *O. nexipinnis* and relatively thin and pointed and directed dorsally in *Gnatholepis*. Bone is stippled, cartilage is represented by open circles.

of attachment of pelvic-fin base, invagination deep and appearing as a 'pit' (Fig. 6).

Coloration: Preserved specimens uniformly light to dark brown with black spots on dorsal region of head and nape. Darkened brown to black upper lip and pectoral-fin base. Dark brown spot between 20th and penultimate rays, positioned at mid-height of D2. Murdy (1989: 20) based his description of live coloration on material from Peninsular Malaysia that he had identified as *O. dentatus* (=*O. nexipinnis* here): 'Head and trunk greyish blue; 7 greyish-blue spots along lateral midline starting at a point equal to origin of first dorsal fin and ending at a point equal to about 75% of the length of D2; a suffusion of shiny, bluish scales on posterior half of trunk; 6 dusky, saddle-like blotches on dorsum starting at terminus of D1 with 4 across the base of D2 and 1 on caudal peduncle; D1 translucent; D2 translucent except for a thin, faint dusky stripe through the median part of fin and a large black ocellus near distal tips of last 4 rays; caudal, anal and pelvic fins translucent; pectoral fin translucent but with a large, dusky blotch on upper base; nape with dusky reticulations; anterior nostril with a black anterior margin; venter shiny white.' In the Malacca Straits, along the western coast of Peninsular Malaysia, Takita, Agusnimar & Ali (1999: 132) identified *O. nexipinnis* (reported as *O. dentatus*) by the characteristic '. . .bright green eyes and depressed head, and a dark spot posteriorly on the dorsal fin'. They reported that *O. nexipinnis* occurs on the mudflats of Bengkalis and Penang islands in Peninsular Malaysia, at sites facing the sea and not influenced by freshwater inflow (Takita *et al.*, 1999). At Teluk Bahang in Penang Island, this species was found low on the intertidal zone, an area which was exposed for only several days per lunar cycle, prompting the hypothesis that *O. nexipinnis* is probably active underwater (Takita *et al.*, 1999). This hypothesis is corroborated by Polgar & Bartolino (2010) who found larger individuals of *O. nexipinnis* (reported as *O. dentatus*) in the lower intertidal zones (more aquatic) and smaller individuals in higher intertidal zones (more terrestrial) at their study site in Tanjung Piai, Johor, along the western coast of Peninsular Malaysia.

Etymology: Latin, '*nexus*' meaning 'tied together' and '*pinnis*' meaning 'fins', referring to the continuous dorsal fins.

Distribution and ecological note: Oxuderces nexipinnis is distributed in the Indo-West Pacific, here reported from the southern part of the South



China Sea, Gulf of Thailand, Java Sea, Andaman Sea and Bay of Bengal (Fig. 13). This species lives on intertidal soft-bottom habitats, predominantly mudflats. Adults have been observed to swim through the muddy substrate with only a thin film of water above them, through which they would occasionally poke their heads (Murdy, 1989, reported as *O. dentatus*). This species has been reported to store air in its burrows, especially in the spawning chambers (Ishimatsu *et al.*, 1998, reported as *O. dentatus*). In Malaysia, it is a common prey of homalopsine snakes such as *Bitia hydroides* (see Jayne, Ward & Voris, 1995, reported as *O. dentatus*) and *Cerberus rynchops* (see Jayne, Voris & Heang, 1988, reported as *O. dentatus*).

Remarks: Apocryptes nexipinnis, described by Cantor (1849), was classified in the genus *Oxuderces*, and synonymized with *O. dentatus* by Murdy (1989). We resurrect this name from synonymy as *Oxuderces nexipinnis*. The BMNH syntypes are the left sides (heads and bodies) of two individuals that have been dried, filleted and stuffed with cotton wool (Fig. 14). Cantor (1849) did not indicate the number of specimens he had on hand and reported the total length of the specimen (or specimens) on which he based his description as 3 3/8 inches, or 85.7 mm TL. He further indicated that the caudal fin comprised 1/5 of the TL, which would mean that the specimen (or specimens) was approximately 68 mm SL. The BMNH syntypes measure approximately 67.8 mm SL (possibly a male) and 65 mm SL (possibly a female). Although the larger specimen is closer in size to that given by Cantor (1849), we do not designate it as a lectotype because both specimens are extremely distorted, as well as incomplete, and we cannot identify either with certainty as the primary specimen on which the description was based.

DISCUSSION

Examination of type specimens and a review of the literature confirmed the hypothesis that *Oxuderces* comprises two distinct species. Specimens from

Figure 10. Line drawings of the last precaudal and the first two caudal vertebrae and associated elements of the anal fin in (A) *Oxuderces dentatus* (USNM 86954) and (B) *Oxuderces nexipinnis* (USNM 279359). In *O. dentatus*, the hemal spine extends to a point at about mid-length of the first anal-fin pterygiophore; in *O. nexipinnis* the hemal spine terminates closer to the proximal tip of the first anal-fin pterygiophore. Bone is stippled; cartilage is represented by open circles.

Figure 11. Holotype of *Oxuderces dentatus* Eydoux & Souleyet (1848), MNHN A.1822, 77.5 mm SL.

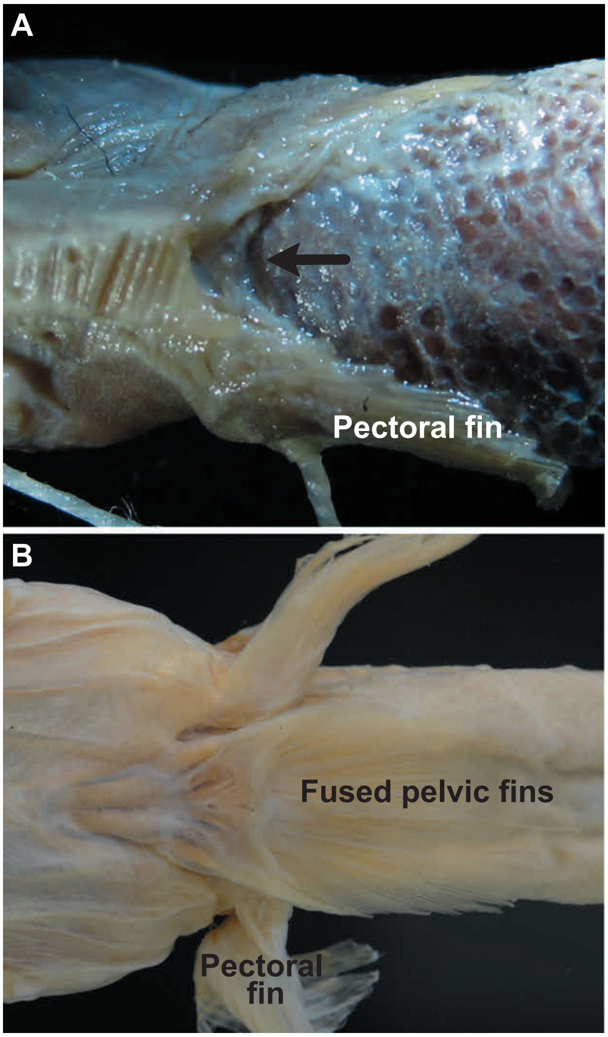


Figure 12. *Oxuderces dentatus*, head and anterior portion of the body in ventral view. A, MNHN A.1822 (holotype, 77.5 mm SL) has pectoral fins and lacks pelvic fins. B, USNM 85846 (80.3 mm SL) has fully formed pectoral and pelvic fins. The arrow in A points to the area where the pelvic fins have either been lost or never developed. Anterior is to the left.

coastal areas of southern China agree with the detailed description of the type specimen of *Oxuderces dentatus* (see Springer, 1978). Contra Springer (1978) and Murdy (1989), we consider *Apocryptes cantoris* Day, 1871 (in part) and *Apocryptichthys livingstoni* Fowler, 1935 to be synonyms of *Apocryptes nexipinnis* Cantor, 1849, rather than of *Oxuderces dentatus* Eydoux & Souleyet, 1848. Material from Peninsular Malaysia, Thailand, Indonesia and India agrees with the type specimens and original description of *Apocryptes nexipinnis* which we classify here as the second valid species of *Oxuderces*. Contra Murdy (1989), we do not classify *Apocryptodon wirzi* Koumans, 1937 in the genus *Oxuderces*. After examination of type and non-type specimens of *Apocryptodon wirzi*, we conclude that this species has characters diagnostic of the inferred sister genus *Apocryptodon* (Murdy, 1989; Agorreta *et al.*, 2013), and does not conform to our revised concept of *Oxuderces*. *Oxuderces nexipinnis* uniquely has a conspicuous dermal invagination of unknown function just posterior to the point of attachment of the pelvic-fin base.

The epidermal surfaces of all oxudercine gobies are barriers to the external environment and aid with respiration when individuals are near the surface or out of the water. Consequently, the skin of amphibious oxudercine gobies, such as *Boleophthalmus*, *Periophthalmodon*, *Periophthalmus* and *Scartelaos*, has been examined in detail to hypothesize adaptations to terrestriality (see Park *et al.*, 2003; Zhang *et al.*, 2003). In contrast, little is known of the form and function of the skin of the oxudercine gobies that do not readily emerge out of water, such as species of the genera *Apocryptodon*, *Oxuderces* and *Parapocryptes*. Here we report for the first time some of the modifications of the skin on the head of *Oxuderces*, in which the dorsal part of the head and the eyes are covered with a thick epidermis that gradually thins ventrally (Figs 4A, 5A). This differs from the epidermal layer in the dorsal region of the head in *Apocryptodon*, which is relatively thin (Figs 4B, 5B). In addition, *O. nexipinnis* uniquely has a conspicuous dermal invagination of unknown function just posterior to the point of attachment of the pelvic-fin base.

Swollen cells in the middle epidermal layer, hypothesized to inhibit desiccation while on land (Yokoya & Tamura, 1992; Suzuki & Hagiwara, 1994), were reported in *Boleophthalmus*, *Periophthalmodon*, *Periophthalmus* and *Scartelaos* (Suzuki, 1992; Zhang *et al.*, 2000, 2003; Park, 2002). We identify these cells in *Oxuderces*, but not in *Apocryptodon*. Dense networks of capillaries close to the epidermal surface have been reported in *Boleophthalmus*, *Periophthalmodon*, *Periophthalmus* and *Scartelaos* (Zhang *et al.*, 2000, 2003), assumed to aid in cutaneous respiration while out of water. We observed these capillaries in both *Apocryptodon* and *Oxuderces*. In many fish, a thickened epidermis and associated modifications to the epidermis are

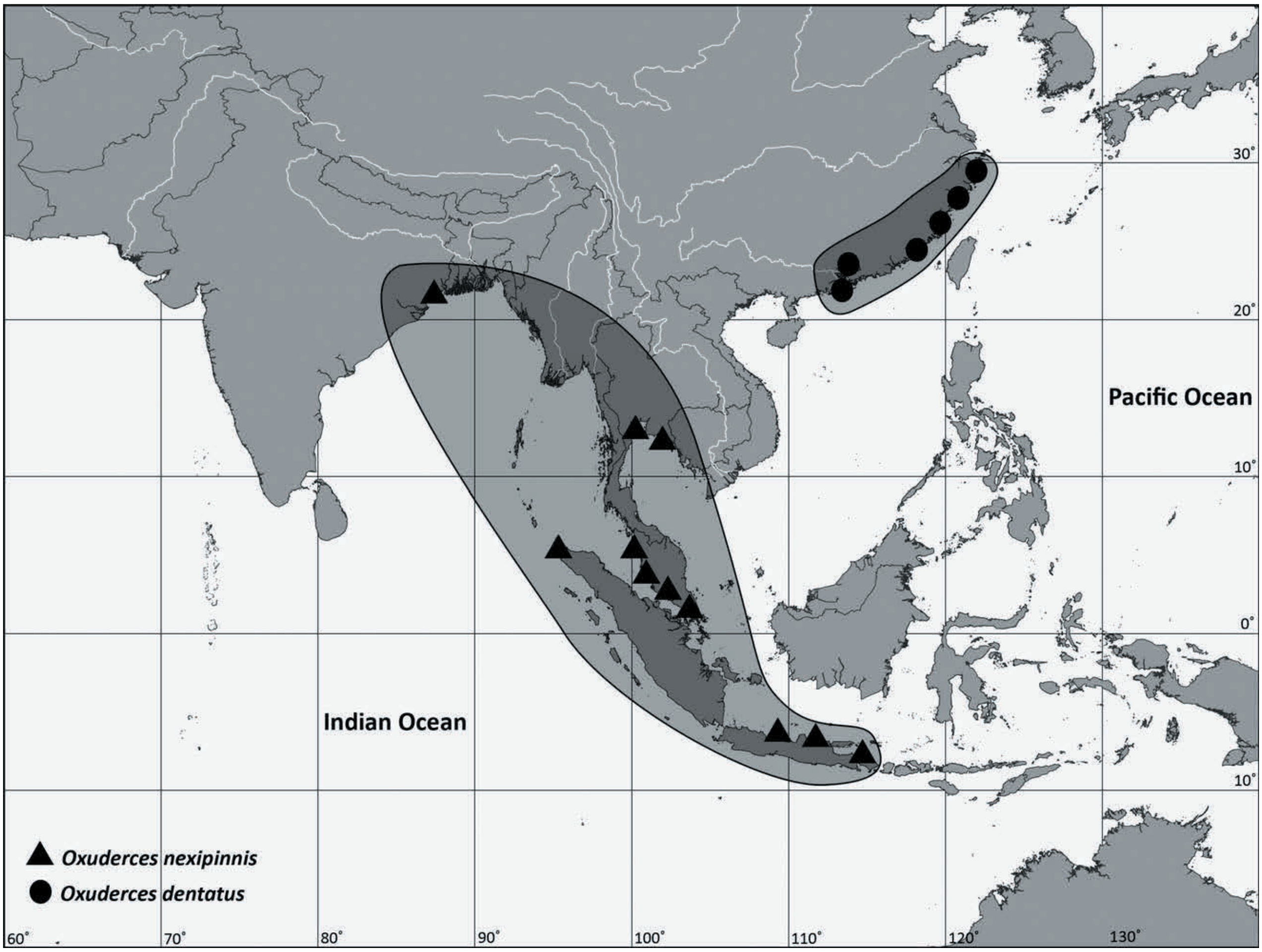


Figure 13. Distribution map of *Oxuderces dentatus* (solid circles) and *Oxuderces nexipinnis* (solid triangles). Each symbol represents one catalogued museum lot. Distributional limits are approximated by a solid line.

correlated with the ability to breathe atmospheric air (see Park, Kim & Kim, 2014: 206). *Periophthalmus*, for example, can undergo cutaneous respiration facilitated by the intraepithelial capillaries that characterize the thickened epidermis (Park, Kim & Kim, 2000). Likewise, the thickened epidermis in *Oxuderces* may function as an accessory respiratory organ for gaseous exchange, possibly aiding in respiration in hypoxic habitats.

Both species of *Oxuderces* further share a unique morphology: a fleshy, interorbital trough (Fig. 3A, B). The function of this trough is unknown, and it has not been reported in any other gobioid fishes. The presence and position of a single, median sensory pore C in the anterior part of the trough suggests that the function of the trough may be sensory-related. We are encouraged by the details revealed by histological preparation of the heads of oxudercine gobies, and plan to continue that examination as part of our larger study of oxudercine goby phylogeny.

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Figure 14. *Apocryptes nexipinnis* Cantor, 1849, syntypes, BMNH1860.3.19.568-69 (2), dried, filleted and stuffed with cotton wool. Anterior is to the left. Top: the larger of the two syntypes, approximately 67.8 mm SL. Middle: the same specimen as the top, rotated on the horizontal axis. Bottom: the smaller of the two syntypes, approximately 65 mm SL.

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