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Classification and relationships of *Assiculus* and *Assiculoides* (Teleostei: Pseudochromidae)

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Abstract

The monotypic Australian pseudochromid fish genera *Assiculus* and *Assiculoides* had been previously included in the subfamily Pseudochrominae on the basis of symplesiomorphic characters. Osteological synapomorphies are identified in support of a closer relationship to the remaining pseudochromid subfamilies. Two synapomorphies (five or fewer infraorbital bones, haemal spine of preural vertebra 2 attached to centrum) diagnose a clade consisting of *Assiculoides*, Pseudoplesiopinae, Anisochrominae and Congrogadinae. Two additional synapomorphies (parhypural not separate from hypurals 1+2, total caudal-fin rays modally 27 or fewer) diagnose a more inclusive clade that also includes *Assiculus*. Two new subfamilies are erected to reflect these relationships.

Key words: osteology; Assiculoidinae new subfamily; Assiculinae new subfamily; Australia; systematics

Introduction

The Indo-Pacific reef-fish family Pseudochromidae is currently divided into four subfamilies, three of which are demonstrably monophyletic: Anisochrominae (Gill & Fricke 2001); Congrogadinae (Godkin & Winterbottom 1985); Pseudoplesiopinae (Gill & Edwards 1999). The fourth subfamily, Pseudochrominae, is by far the largest with 10 genera and nearly 100 described species, but is diagnosed only by symplesiomorphic characters (Gill 2004): pelvic-fin rays I,5 (versus I,4 or fewer); all segmented pelvic-fin rays branched (vs. at least some rays unbranched); lateral line consisting of two series, one anterodorsal and the other posterolateral (vs. only anterodorsal series present, though additional lateral lines are secondarily present in some derived congrogadines; see Winterbottom 1986). The derived states for each of these characters are synapomorphic for a clade consisting of the remaining three subfamilies (Springer *et al.* 1977, Godkin & Winterbottom 1985, Figure 1). Further synapomorphies support, in turn, a sister relationship between Anisochrominae and Congrogadinae (Godkin & Winterbottom 1985, Figure 1).

In describing the new genus and species *Assiculoides desmonotus*, Gill and Hutchins (1997) presented evidence that the taxon and the pseudochromine genus *Assiculus* Richardson (1846) form successive sister groups to the clade consisting of the Anisochrominae, Congrogadinae and Pseudoplesiopinae. However, Gill and Hutchins tentatively included both genera in the Pseudochrominae. Although the biogeographic area relationships implied by the two genera were discussed by Mooi and Gill (2004: 195, fig. 9b), subsequent publications have retained both genera in the Pseudochrominae (e.g., Gill 2004, Gill *et al*. 2006). As part of my ongoing studies on pseudochromid relationships and classification, I herein reiterate character evidence for the phylogenetic relationships of the two genera, and erect two new subfamilies to reflect those relationships.

Materials and methods

Character information on pseudochromids are based on published information (as noted) and on observations on extensive specimens listed in my other publications (including x-radiographs and specimens prepared by clearing

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and staining, following the methods of Taylor & Van Dyke 1985): *Assiculoides, Assiculus* and pseudochromine specimens listed by Gill (2004); anisochromine specimens listed by Gill and Fricke (2001); pseudoplesiopine specimens listed by Gill and Edwards (1999, 2004); congrogadine specimens listed by Gill (1998), Gill *et al.* (2000), Gill and Zajonz (2003) and Mooi and Gill (2004). Caudal peduncle length was measured from the anal-fin termination to the ventral edge of caudal peduncle at the vertical through the posterior edge of the lower hypural plate.

Phylogenetic Relationships

Phylogenetic relationships are summarised in Figure 1.

***Assiculus* + *Assiculoides* + Pseudoplesiopinae + Anisochrominae + Congrogadinae**

A relationship of *Assiculus* and *Assiculoides* to the Pseudoplesiopinae + Anisochrominae + Congrogadinae clade is supported by the following two synapomorphies.

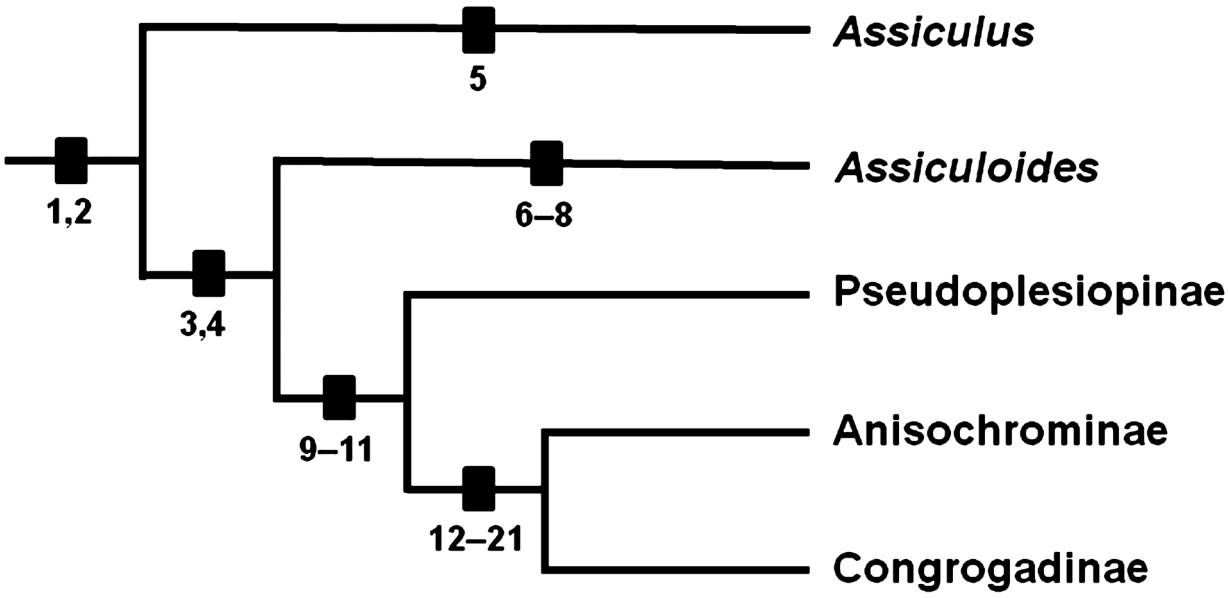

FIGURE 1. Cladogram of relationships discussed in the text. Numbers indicate autapomorphies of *Assiculus* and *Assiculoides*, and unambiguous synapomorphies relating terminal taxa (modified from Springer *et al.* 1977, Godkin & Winterbottom 1985). Character: 1, parhypural not separate from hypurals 1+2; 2, total caudal-fin rays 27 or fewer; 3, infraorbital bones five or fewer; 4, pu2 haemal spine attached to centrum; 5, opercle with prominent serrations ventral to subopercle junction; 6, anteroventral scale rows on posterior body and caudal peduncle oriented almost vertically; 7, dorsal fin connected to caudal fin by membrane; 8, hypural 5 reduced or absent; 9, pelvic-fin rays I,4 or fewer; 10, at least some pelvic-fin rays unbranched; 11, only anterodorsal lateral line present; 12, hypochordal longitudinalis muscle inserts on only two caudal-fin rays; 13, palatine teeth absent; 14, lateral extrascapula attached firmly to skull; 15, posterior tip of infraorbital 5 does not contain anterior continuation of pterotic laterosensory canal; 16, supraoccipital crest reduced to ridge of bone; 17, pectoral-fin rays 15 or fewer; 18, opercular spine present; 19, epibranchial 1 plate-like; 20, branchiostegal membranes united; 21, caudal vertebrae 22 or more.

1. Parhypural not separate from hypurals 1+2: Plesiomorphically in acanthomorphs, the parahypural is an autogenous element. In all pseudochromines except *Assiculus* and *Assiculoides* the parhypural is autogenous, although closely applied to hypurals 1+2 (Figure 2A). In *Assiculus, Assiculoides*, pseudoplesiopines, and anisochromines it is undifferentiated from hypurals 1+2 (Figures 2B, 3A–B; Springer *et al.* 1977, Gill & Edwards 1999, Gill & Fricke 2001). As is often the case for eel-like fishes (in which the caudal skeleton is reduced in size, thus prone to developmental truncation with corresponding variation in the degree of consolidation of bony elements), congrogadines vary for this character. Although the parhypural is undifferentiated from hypurals 1+2 in most species, it is autogenous in *Haliophis* Rüppell (1829), and variably autogenous or undifferentiated in *Rusichthys* Winterbottom (1979), *Halidesmus* Günther (1872) and *Halimuraena* Smith (1952) (Godkin & Winterbottom 1985, Winterbottom 1996, Gill *et al.* 2000, Gill & Zajonz 2003). This character was previously identified by Godkin and Winterbottom (1985) as a synapomorphy of the Pseudoplesiopinae + Anisochrominae + Congrogadinae.

2. Total caudal-fin rays modally 27 or fewer: With the exception of *Assiculoides* and *Assiculus*, pseudochromines are plesiomorphic in having a relatively high number of caudal-fin rays. Depending on species, total caudal-fin ray counts vary from 26–34 (Gill 2004: appendix table 1c). However, counts of 27 or fewer are rare: only three of nearly 100 pseudochromine species have been recorded with 26 rays and then only rarely (four [2%] of 197 specimens of the three species), and only 10 species have been recorded with 27 or fewer rays (32 [5%] of 594 specimens of the 10 species). *Assiculoides* and *Assiculus* are derived in having low counts: 23–25, rarely 25 in *Assiculoides*; 25–27, rarely 25 or 27 in *Assiculus* (Gill 2004: appendix table 1c). Other pseudochromid subfamilies also have low counts: 23–30, modally 25–27 in pseudoplesiopine species (except modally 29 in the relatively derived *Chlidichthys johnvoelckeri* Smith 1953, Gill & Edwards 1999, 2004); 23–27, modally 25 in anisochromines (Gill & Fricke 2001); and 10–18 in congrogadines (Godkin & Wintebottom 1985: tab. 1).

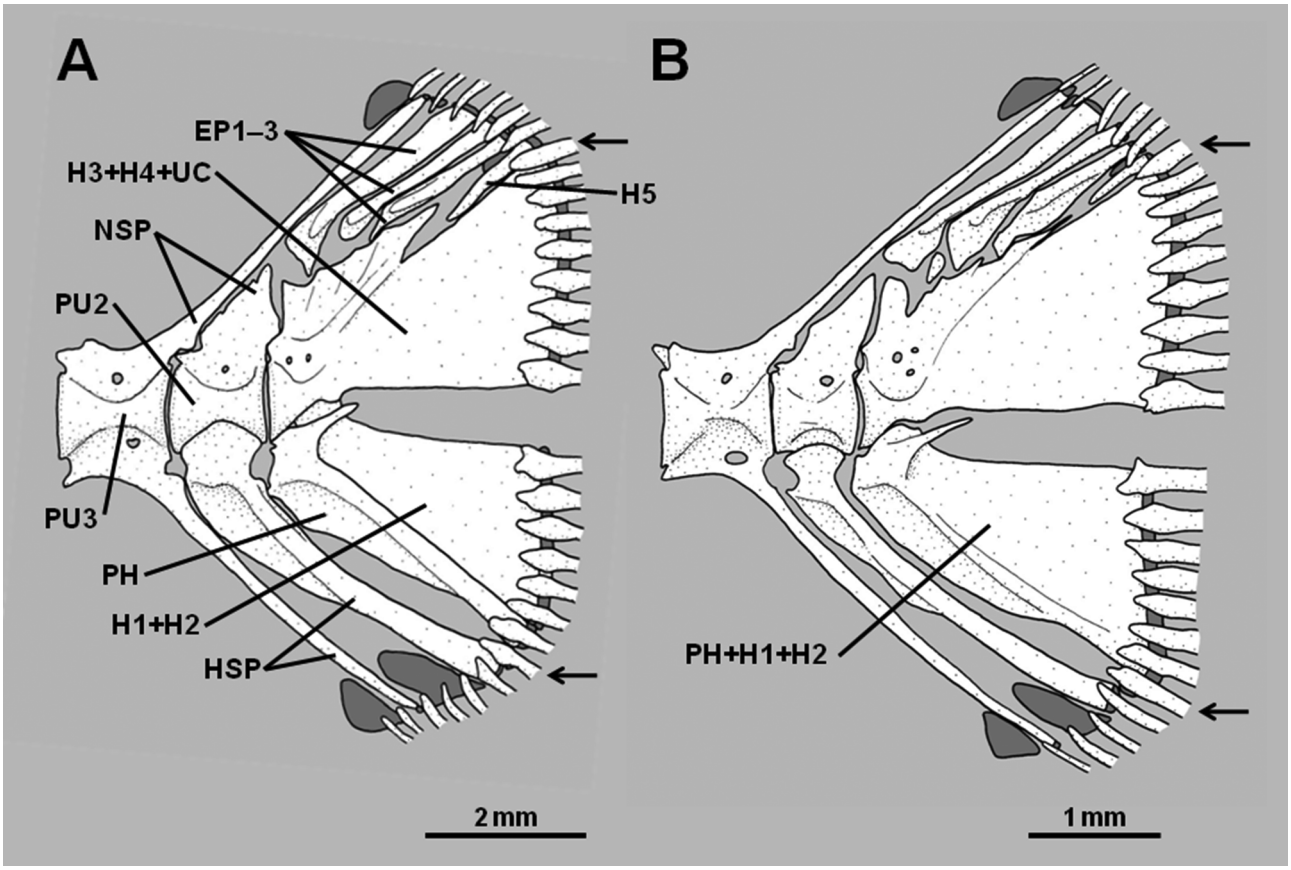

FIGURE 2. Left lateral view of caudal skeletons of: (A) *Pseudochromis fuscus* Müller & Troschel (1849) (Pseudochrominae), AMS I.18469-044, 48.0 mm SL; (B) *Assiculus punctatus*, NTM S.10016-009, 32.2 mm SL. Cartilage shown in dark grey. Outer principal caudal-fin rays indicated by arrows. Abbreviations: EP1–3, epurals 1–3; H1–5, hypurals 1–5; HSP, haemal spines; NSP, neural spines; PH, parhypural; PU2–3, preural centra 2–3; UC, compound urostylar complex.

Assiculoides + Pseudoplesiopinae + Anisochrominae + Congrogadinae

A relationship of *Assiculoides* to the Pseudoplesiopinae + Anisochrominae + Congrogadinae clade is supported by the following two synapomorphies.

3. Infraorbital bones five or fewer: Although Godkin and Winterbottom (1985: 641) reported that pseudochromines have five infraorbitals, *Assiculus* and other pseudochromines except *Assiculoides* are plesiomorphic in having six infraorbital bones (which includes the dermosphenotic and "lachrymal") (Figure 4A). *Assiculoides* and the other subfamilies are derived in having fewer infraorbitals: five in *Assiculoides* (Figure 4B); four or five in pseudoplesiopines (Gill & Edwards 1999: fig. 10, Gill & Edwards 2004: fig. 2); three to five in anisochromines (Springer *et al.* 1977); one to five in congrogadines (Godkin & Winterbottom 1985, Winterbottom 1996). Comparison of the construction of infraorbitals (particularly the consistent – and plesiomorphic – presence of a prominent suborbital shelf on infraorbital 3) and the relative sizes of posterior infraorbitals suggests that the reduction from a six infraorbital condition is a result of "fusion" of infraorbitals 4 and 5.

4. Haemal spine of preural vertebra 2 attached to centrum: *Assiculus* and other pseudochromines except *Assiculoides* are plesiomorphic in having the haemal spine of pu2 autogenous (Figures 2A–B). It is also autogenous in some specimens of the congrogadine genera *Natalichthys* Winterbottom (1980) and *Halidesmus*, but it is attached to the pu2 centrum in all other congrogadines and in *Assiculoides*, anisochromines and pseudoplesiopines (Figures 3A–B, Springer *et al.* 1977, Godkin & Winterbottom 1985, Gill & Edwards 1999, Gill & Fricke 2001). Variation within the Congrogadinae is not unexpected given their eel-like shape (see discussion of character 1). This character was previously identified by Godkin and Winterbottom as a synapomorphy of the Pseudoplesiopinae + Anisochrominae + Congrogadinae.

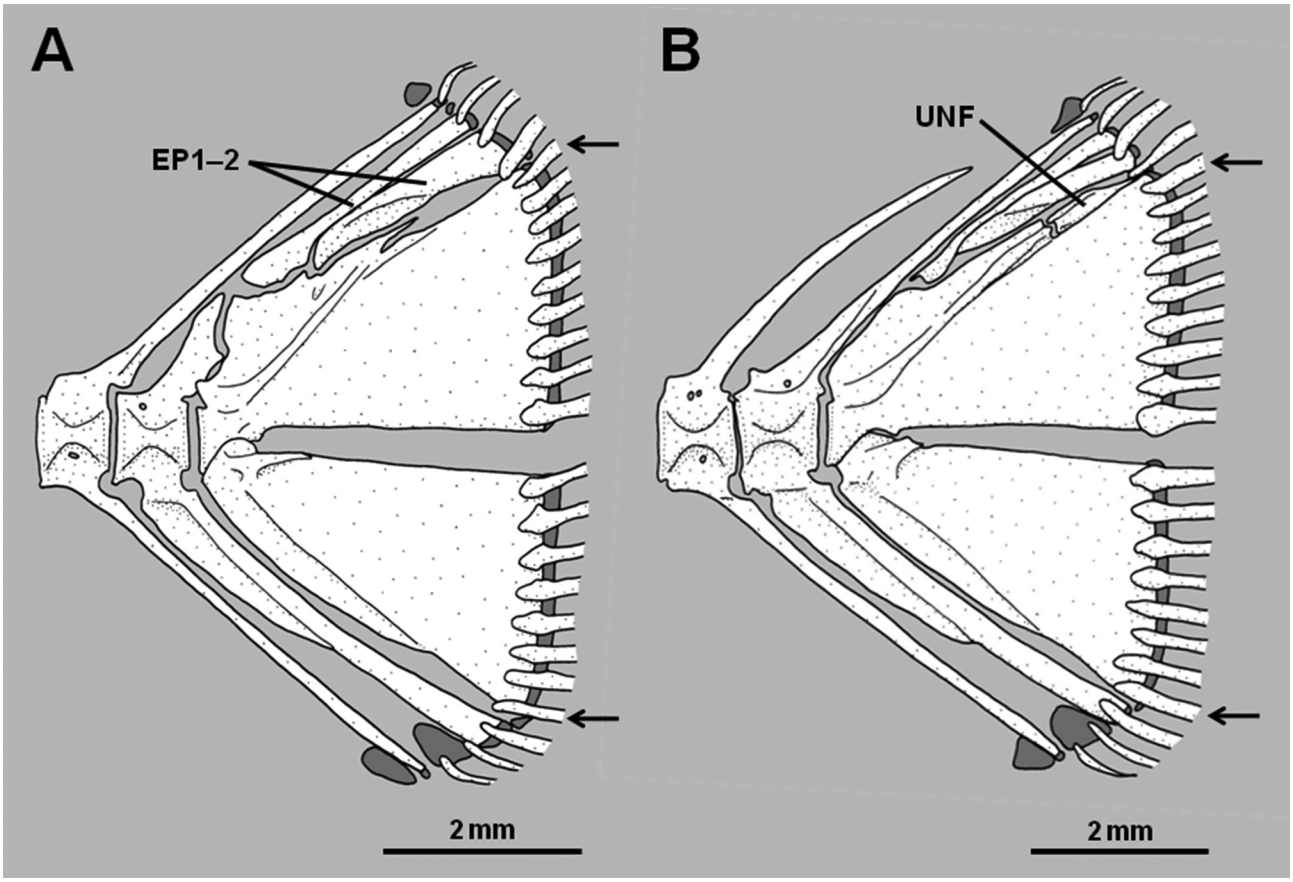

FIGURE 3. Left lateral view of caudal skeletons of *Assiculoides desmonotus*: (A) WAM P.30929-008, 41.3 mm SL, paratype, with short pu2 neural spine; (B) WAM P.30929-008, 46.2 mm SL, paratype, with long pu2 neural spine.UNF, uroneural fragment. Other methods of presentation follow Figure 2.

Revised Classification

The above relationships necessitate removal of *Assiculoides* and *Assiculus* from the Pseudochrominae and the erection of two new subfamilies.

Assiculinae new subfamily

Type genus. *Assiculus* Richardson 1846.

Diagnosis. The Assiculinae is cladistically diagnosed by a single autapomorphy.

5. Opercle with prominent serrations ventral to junction with subopercle: In other pseudochromids there usually are no serrations ventral to the subopercle junction, although there may be one or more serrations on the posterodorsal edge of the opercle above the subopercle junction (Figure 5A). An exception is within the Pseudochrominae in *Pseudochromis quinquedentatus* McCulloch (1926) and its near relatives (Gill 2004, Gill &

Allen 2011), in which 1–3 small, indistinct serrations are sometimes present beneath the subopercle junction. *Assiculus* is unique among pseudochromids in having 1–5 prominent serrations on the opercle beneath the subopercle junction (Figure 5B, see also Gill 2004: fig. 6).

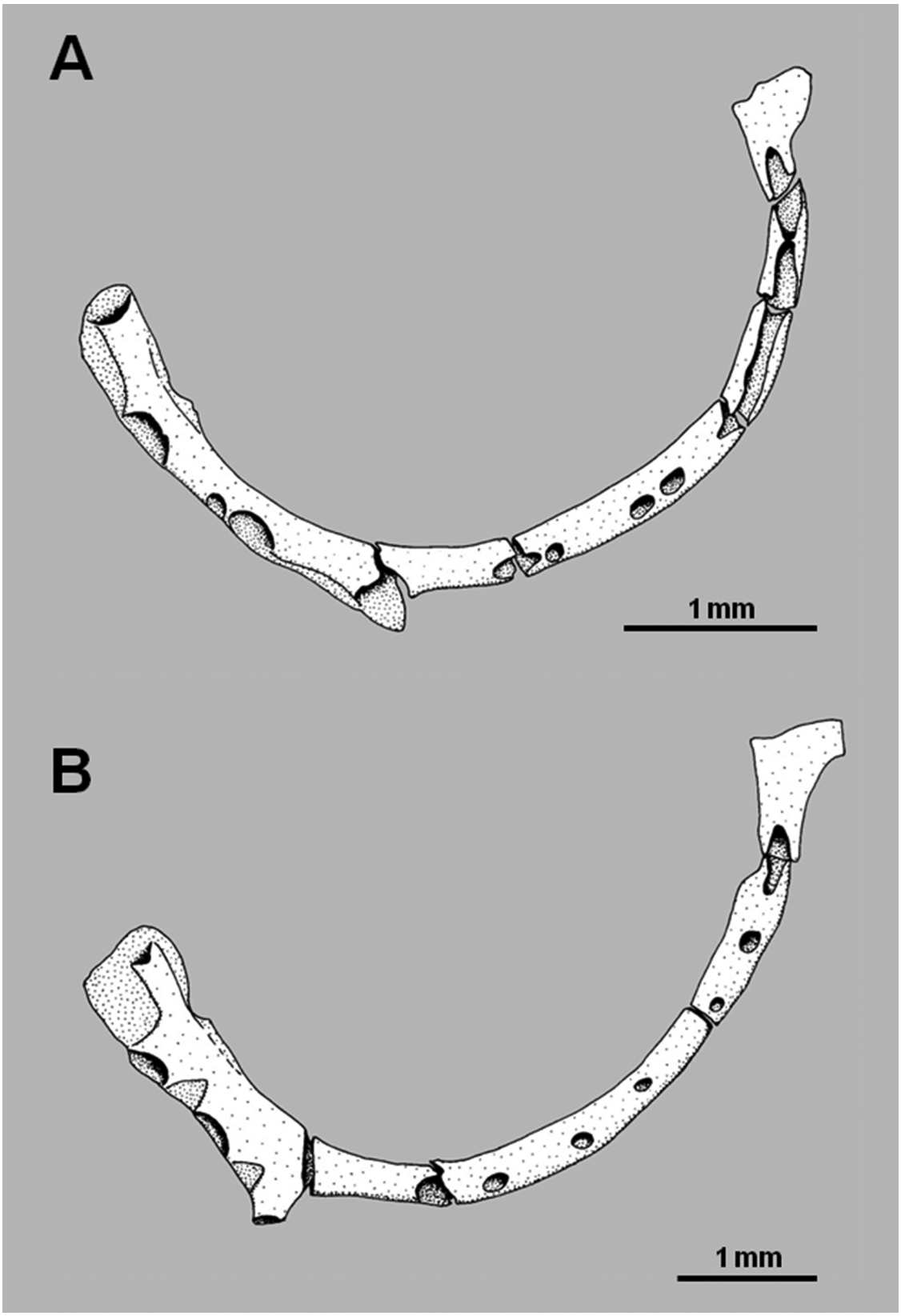

FIGURE 4. Lateral view of left infraorbital bones of: (A) *Assiculus punctatus*, NTM S.10016-009, 32.2 mm SL (redrawn from Gill & Hutchins 1997: fig. 1B); (B) *Assiculoides desmonotus*, WAM P.30929-008, 41.3 mm SL, paratype (redrawn from Gill & Hutchins 1997: fig. 1A).

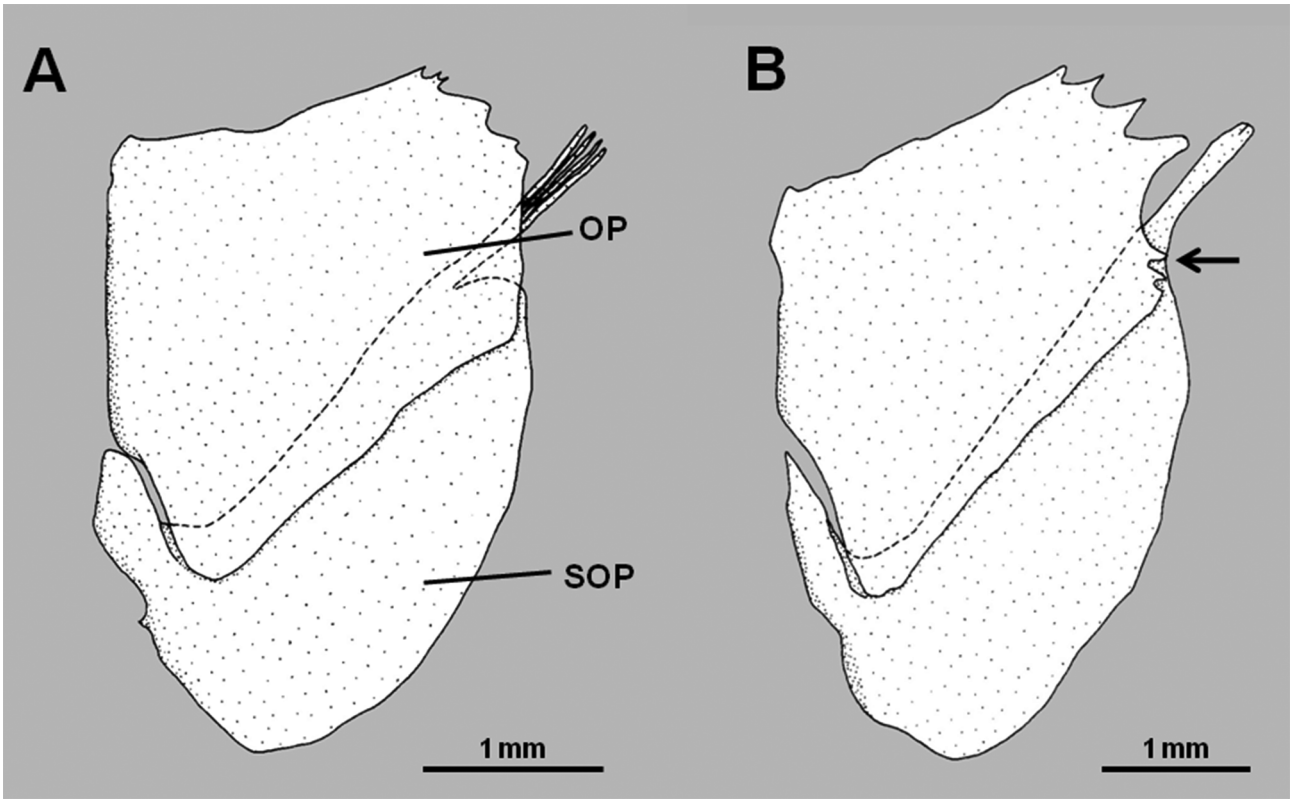

FIGURE 5. Lateral view (reversed) of right opercle (OP) and subopercle (SOP) of: (A) *Assiculoides desmonotus*, WAM P.30929-008, 41.3 mm, paratype (redrawn from Gill & Hutchins 1997: fig. 3A); and (B) *Assiculus punctatus*, NTM S.10016-009, 32.2 mm SL (redrawn from Gill & Hutchins 1997: fig. 3B). Dashed lines indicate obscured outline of subopercle. Arrow in B indicates uppermost opercular serration beneath subopercle junction.

In addition, the subfamily is readily identified from other pseudochromids by the following combination of external characters: dorsal-fin rays III,22–24 (usually III,23); anal-fin rays III,12–14 (usually III,13); upper and lower procurrent caudal-fin rays 4–5 (usually 5) and 3–5 (usually 4), respectively, total caudal-fin rays 25–27 (usually 26); pelvic-fin rays I,5, all segmented rays branched; lateral line represented by an anterodorsal and a posterolateral series of tubed scales; circumpeduncular scales 17-21; dorsal and anal fins without distinct scale sheaths; and lower lip complete.

Remarks. Includes only *Assiculus punctatus* Richardson 1846 from northern and north-western Australia. See Gill (2004) for a detailed description and synonymy of the species.

Assiculoidinae new subfamily

Type genus. *Assiculoides* Gill & Hutchins 1997.

Diagnosis. The Assiculoidinae is cladistically diagnosed by the following three autapomorphies:

6. Anteroventral scale rows on posterior part of body and caudal peduncle oriented almost vertically: In most pseudochromids the scale rows on the posterior part and caudal peduncle are arranged in an obviously anteroventral direction (Figure 6A). Uniquely among pseudochromids, in *Assiculoides* the scale rows on the posterior part of body and caudal peduncle are oriented almost vertically (Figure 6B).

7. Dorsal fin connected to caudal fin by membrane: The dorsal fin is completely separate from the caudal fin in *Assiculus*, pseudochromines, anisochromines and pseudoplesiopines (Figure 6A). *Assiculoides* is derived in having the posteriormost dorsal-fin ray bound posteriorly by a low membrane to the dorsal edge of the caudal fin, the membrane interrupting the circumpeduncular scales so that the median row of scales along the dorsal edge of caudal peduncle is absent (Figure 6B). With the exception of *Rusichthys*, in which the dorsal fin is nonetheless connected to the caudal peduncle by a low membrane, the dorsal fins (and anal fins) of congrogadines are connected to the caudal fin by membrane. Depending on species, the membrane varies from low (connecting to

only the base of the final dorsal- and anal-fin rays) to high (with the three fins fully confluent). Such connection is common in eel-like fishes. Consideration of other characters that nest congrogadines within the Pseudochromidae as the sister group of the Anisochrominae (Figure 1) reveals the dorsal-fin connection in congrogadines to be non-homologous with the condition found in *Assiculoides*.

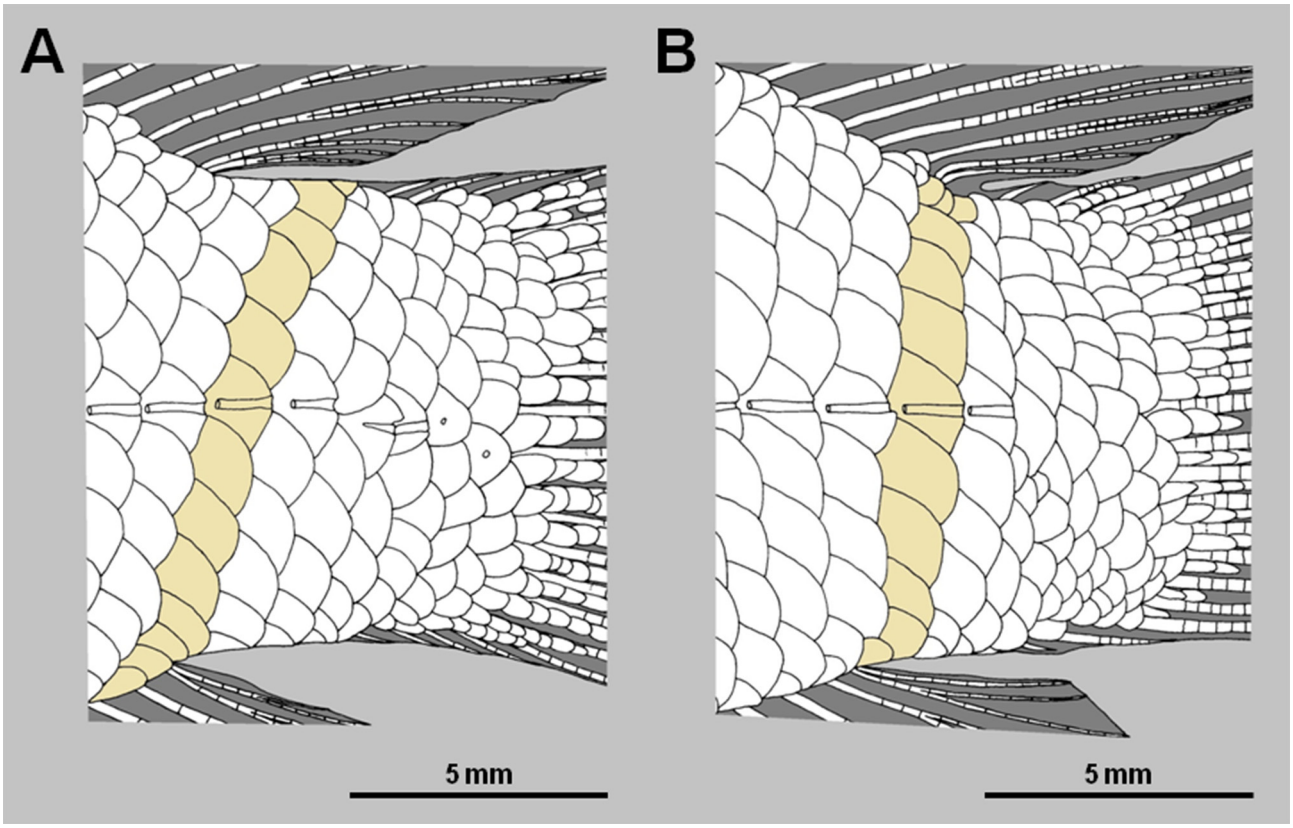

FIGURE 6. Left lateral view of caudal peduncle region of: (A) *Assiculus punctatus*, WAM P.31013-012, 51.3 mm SL (redrawn from Gill & Hutchins 1997: fig. 2B); and (B) *Assiculoides desmonotus*, WAM P.31085-009, 46.6 mm SL, holotype (redrawn from Gill & Hutchins 1997: fig. 2A). Fin membranes shown in dark grey; representative scale row shown in pale yellow. Anterior procurrent rays are obscured by scales.

8. Hypural 5 reduced in size or absent: A relatively well-developed hypural 5 is present in pseudochromines, *Assiculus*, pseudoplesiopines and anisochromines (Figures 2A–B, Springer *et al.* 1977, Gill & Edwards 1999). In *Assiculoides* it is either present as a tiny splint at the posterodorsal corner of hypurals 3+4, or absent (Figures 3A–B; note that the small bone in the approximate position of hypural 5 in Fig. 3B is actually an anomalous uroneural fragment). Hypural 5 is also absent in all congrogadines (Godkin & Winterbottom 1985, Winterbottom 1996). As for character 7, other characters reveal the absence of hypural 5 in *Assiculoides* and congrogadines to be independently derived (i.e., a homoplasy).

In addition, the following character combination allows ready identification of the subfamily: dorsal-fin rays III,25–27 (usually III,26); anal-fin rays III,14–16 (usually III,15); pelvic-fin rays I,5, all segmented rays branched; lateral line represented by an anterodorsal and a posterolateral series of tubed scales; caudal peduncle relatively short (5.2–7.9 % SL).

Remarks. Includes only *Assiculoides desmonotus* Gill & Hutchins 1997 from coastal regions of the Kimberley district of Western Australia. See Gill (2004) for a detailed description of the species.

Assiculoides desmonotus shows marked variation in the development of the pu2 neural spine. Of 58 specimens of *A. desmonotus* examined (see Gill 2004), 48 (83%) have a short pu2 neural spine that does not extend above the proximal tip of the first epural. The neural spine of the pu3 centrum is cartilage-tipped and long, extending to the dorsal margin of the caudal skeleton, and usually supports the anteriormost procurrent caudal-fin ray. The second epural is much broader than the first. The pu2 haemal spine is not forked distally (Figure 3A). The remaining 10 specimens (17% of total) have an elongate, cartilage-tipped pu2 neural spine, which extends to the dorsal margin of the caudal skeleton and usually supports the anteriormost procurrent caudal-fin ray, thus resembling the pu3 neural

spine of specimens with a short pu2 neural spine. The neural spine of the pu3 centrum is relatively short, comparable in length to those of more anterior vertebrae, and neither reaches to the dorsal margin of the caudal skeleton nor supports a ray. The second epural is only slightly broader than the first. The pu2 haemal spine is either forked or unforked distally (Figure 3B).

Anisochromines display similar variation in pu2 neural spine length. Springer *et al.* (1977, p. 4) noted that the pu2 neural spine of *Anisochromis straussi* Springer, Smith & Fraser (1977) is "usually short, occasionally long." My observations on the type specimens of *A. straussi*, and on specimens of the remaining two species in the Anisochrominae, *A. kenyae* Smith (1954) and *A. mascarenensis* Gill & Fricke (2001) (see Gill & Fricke 2001 for list of specimens examined), revealed the following variation: *A. straussi*, short in 65 specimens, moderately long (reaching above middle of first epural, but not extending to dorsal edge of caudal skeleton) in four specimens, and "full" in 13 specimens; *A. kenyae*, short in 39 specimens, moderately long in two specimens, and "full" in four specimens; *A. mascarenensis*, short in nine specimens, and moderately long in one specimen.

Artificial key to pseudochromid subfamilies based on external characters

1 Body elongate and eel-like, body depth at anal-fin origin less than 16% SL; segmented dorsal-fin rays 32–79; anal-fin spines absent; segmented anal-fin rays 26–66 . . . . . Congrogadinae
- Body oblong to moderately elongate, body depth at anal-fin origin greater than 17% SL (except in the elongate pseudoplesiopine *Lubbockichthys myersi* Gill & Edwards 2006); segmented dorsal-fin rays 20–38; anal-fin spines 1–3, though sometimes small and difficult to detect; segmented anal-fin rays 10–21 2

2 Single tubed lateral-line scale at shoulder. . . . . Pseudoplesiopinae
- Series of tubed lateral-line scales extending from shoulder along sides just below dorsal-fin base. 3

3 Dorsal fin with 1 weak spine and 25–27 segmented rays; anal fin with 1 weak spine and 17–19 rays; pectoral rays 13–15; pelvic rays I,4, the inner ray tiny and unbranched (other segmented rays branched); peduncular lateral line represented by centrally pitted scales; head naked . . . . . Anisochrominae
- Dorsal fin with 2 or 3 weak to strong spines and 20–38 segmented rays; anal fin with 2 or 3 weak to strong spines and 10–21 segmented rays; pectoral rays 14–20, usually 16–19; pelvic rays I,5, all segmented rays branched; peduncular lateral line represented by tubed scales (sometimes absent in juveniles); head scaled 4

4 Posteriormost dorsal-fin ray bound by membrane to dorsal edge of caudal fin, the membrane interrupting the circumpeduncular scales (median scale or row of scales along dorsal edge of caudal peduncle absent); caudal peduncle length 5.2–7.9 % SL; total caudal-fin rays 23–25, rarely 25 . . . . . Assiculoidinae
- Posteriormost dorsal-fin ray not bound to caudal fin by membrane and circumpeduncular scales not interrupted; caudal peduncle length 7.9–19.5 % SL; total caudal-fin rays 25–34, rarely 25. 5

5 Opercle with 1–5 distinct serrations ventral to junction with subopercle; total caudal-fin rays 25–27, rarely 25 or 27 . . . . . Assiculinae
- Opercle with at most indistinct serrations ventral to junction with subopercle; total caudal-fin rays 26–34, rarely 26 . . . . . Pseudochrominae

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