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Review of the Toadfish Genera (Teleostei: Batrachoididae)

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The family Batrachoididae is represented by 25 genera and 78 species occurring worldwide between about 51°N and 45°S along continents in marine and brackish waters, occasionally entering rivers, with several freshwater species in South America. They have limited dispersal ability because they have demersal eggs and lack pelagic larvae. A phylogenetic analysis using Paup with 50 informative characters and *Draconetta*, *Ogilbia*, *Raniceps*, and *Synchiropus* as outgroups, resulted in the recognition of two major clades, New World and Old World. The subfamilies Porichthyinae and Thalassophryninae are retained; however the subfamily Batrachoidinae is restricted to the New World and a new subfamily, Halophryninae, is recognized for the Old World genera. *Triathalassothia*, which occurs in southeastern South America, is regarded as *incertae sedis* being either basal to the New World or Old World clade. There is close correspondence between various recognized clades and their geographic locations. *Batrichthys felinus* Smith is removed to *Chatrabus*.

The family Batrachoididae is the only family in the order Batrachoidiformes (Haplodoci). These small to medium-sized fishes (to 57 cm) are easily recognized by their characteristic shape, with a large, broad, flattened head, often with barbels and/or fleshy flaps around their large mouths, and a tapering body. The eyes are on top of the head and directed upwards. Moderately strong teeth are present in the jaws and on the roof of the mouth. Spines are present on the opercle and often the subopercle. There are two separate dorsal fins, the first with two or three spines, and the second long with up to 40 soft rays. The anal fin is somewhat shorter than the second dorsal with up to 39 rays. The pectoral fins are large and broad based and the pelvic fins are jugular in position with one spine and three soft rays. Glandular tissue may be present in the opercular region and pectoral-fin axil or between the pectoral-fin rays. The skin may be scaly or naked. The lateralis system is very well developed, with either single or multiple lateral lines, each pore usually surrounded by two tentacles. Gill openings are usually, but not always, small and restricted to the sides of the body. The number of vertebrae ranges from 25 to 47. The swimbladder is well developed, and used for sound production in many species. Species of *Porichthys* have photophores along their sides and ventral surface. Species in the subfamily Thalassophryninae have hollow, venomous spines in their first dorsal fin and opercles. *Bifax lacinia* has a flap with an eye spot at the end of the maxilla on each side of the mouth. Toadfishes usually are rather drab colored, often brownish with darker saddles, bars, or spots; however, some species in the Atlantic genus *Sanopus* are bright-

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ly colored as is *Bifax lacinia* from the Gulf of Oman. Maximum size of species ranges from 56 mm to at least 570 mm standard length.

The toadfishes, called frogfishes in Australia, are found worldwide between about 51ºN and 45º S along continents in marine and brackish waters, occasionally entering rivers, with several freshwater species in South America. They are found from the shoreline down to a depth of at least 366 m, often burying in the sand or under rocks or coral heads where they function as ambush predators feeding on crabs, shrimps, mollusks, sea urchins, and fishes. Although usually benthic, species of *Porichthys* feed in the water column at night.

The only known toadfish fossil is *Halobatrachus didactylus* from the Miocene Messinian deposits of the Oran region of Algeria (Carnevale 2004).

History of The Classification of the Batrachoididae

Higher Classification.— When Linnaeus described the first toadfish in 1758, he placed it in the Thoracici. In 1801 Bloch and Schneider placed the toadfishes in the Jugularies. Cope (1871) erected the suborder Haplodoci for the toadfishes based on its simple post-temporal (not bifurcate). The history of proposed relationships of the toadfishes is long and varied, starting with Starks (1905) who associated them with the gobiesociforms. Ogilby (1908:44) stated that they were "related on the one hand to the Blenniidae and on the other to the Congrogadidae." Regan (1912) was the first to link the batrachoidiforms with the lophiiforms, placing the toadfishes in the suborder Batrachoidea of the order Pediculati which contained the toadfishes and the Lophioidea with the Lophiiformes, the Antennariiformes, and the Ceratiiformes. Starks (1923:266) later stated that "The Batrachoid fishes doubtless are allied to the Uranoscopoids…." Briggs (1955) believed that the gobiesociforms were most closely allied to the toadfishes, but also showed some resemblance to the Callionymoidea. McAllister (1968) also suggested a relationship between clingfishes and toadfishes. Greenwood et al. (1966) later united the Batrachoidiformes with the Percopsiformes, Gobiesociformes, Lophiiformes, and Gadiformes under their new superorder Paracanthopterygii. Later, Rosen and Patterson (1969) referred to the batrachoidiform lineage, which included the Batrachoidiformes, Lophiiformes, and Gobiesociformes. Lauder and Liem (1983) followed Rosen and Patterson (1969) in placing the batrachoidiforms as the sister group of the lophiiforms and both the sister group of the gobiesociforms. Gosline (1970) questioned the inclusion of the gobiesociforms in the Paracanthopterygii, suggesting they were related to the callionymoids. Later, Patterson and Rosen (1989) agreed with Gosline as did Winterbottom (1993), and Johnson and Patterson (1993) as summarized by Johnson (1993).

Wiley et al. (2000) reported that a batrachoidiform was grouped with an ophidiiform when using molecular techniques. Earlier, Rosen and Patterson (1989, fig. 5), had shown that the ophidioids and batrachoidids shared a unique caudal-fin structure. Miya et al. (2005), using mitochondrial DNA, found the toadfishes to be the sister of a mastacembelid. Smith and Wheeler (2006), using molecular techniques in investigating venom evolution, presented a cladogram that showed toadfishes to be the sister group of the dragonets.

Genera and species.— The first toadfish to be described was *Cottus grunniens* by Linnaeus in 1758, a species from the East Indies now known as *Allenbatrachus grunniens.* Next was *Gadus tau* Linnaeus (1766) from the eastern coast of the United States, now in the genus *Opsanus*. Since that time, the number of valid species described has increased steadily to 78 (Fig. 1).

Ogilby (1908) was the first to revise the family Batrachoididae, recognizing ten genera and 35 species. Miranda-Ribeiro (1915) erected the family Thalassophrynidae for *Thalassophryne* and *Thalassothia* and the family Porichthyidae for *Porichthys*, but subsequent workers have recognized only the family Batrachoididae for the toadfishes. Smith (1952) was next to deal with toadfish genera on a world-wide basis. In a key to the genera, he recognized three subfamilies, Batrachoidinae, Porichthyinae, and Thalassophryninae. He also recognized 20 genera, four new in this paper, and three others he had described earlier. The subfamily Thalassophryninae contains two genera, *Daector* and *Thalassophryne* (Collette, 1966), and the subfamily Porichthyinae contains *Aphos* and *Porichthys* (Walker and Rosenblatt, 1988). The remaining toadfish genera have been placed in the Batrachoidinae (Greenfield 2006). Since Smith's (1952) summary, Roux and Whitley (1972) described the genus *Perulibatrachus*, Greenfield et al. (1994) described *Bifax*, Collette (1995) described *Potamobatrachus*, Greenfield (1997) described *Allenbatrachus*, and Greenfield (2006) described *Vladichthys* and *Colletteichthys*. Twenty-five genera are currently considered to be valid.

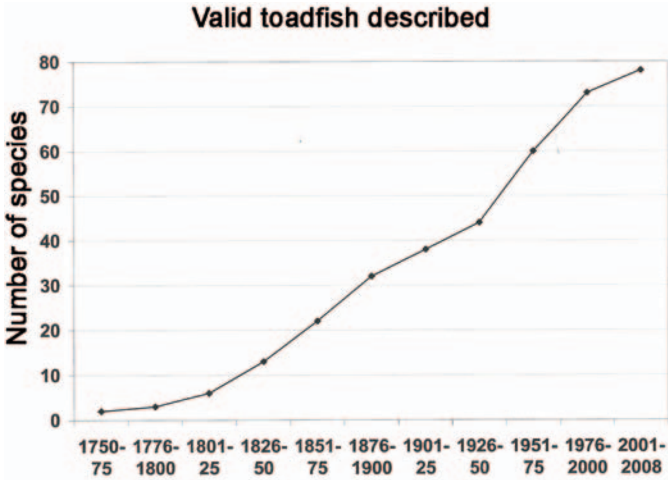


FIGURE 1. Number of valid species described over time.

METHODS

All counts and measurements follow Hubbs and Lagler (1964) except that the last two fin rays are not counted as one unless it is clear that they are joined at the base. Measurements were made to the nearest 0.1 mm using dial calipers. All measurements are expressed as thousandths of standard length (SL). Some counts were made from radiographs. Nomenclatural information is from Eschmeyer (1998 and 2008). Institutional abbreviations are as listed in Leviton et al. (1985). A list of all material examined is given in Appendix 1. At least one species from each genus was cleared and stained. Cleared and stained specimens of *Chatrabus felinus* and *Batrichthys apiatus* were available for comparison, but due to the rarity of *Batrichthys albofasciatus*, only a preserved specimen was available for comparison and various bones were exposed by dissection. Drawings of additional bones of each genus not illustrated here are archived at the California Academy of Sciences.

One of the most difficult aspects of this study was identifying an appropriate outgroup(s) for the Batrachoididae. As discussed above under Higher Classification, proposed relationships have varied greatly. Patterson and Rosen (1989:23–24) reviewed the arguments for the relationship between the lophiiforms and batrachoidiforms, a position that has been accepted by most workers, and provided four putative synapomorphies linking the two taxa. The problem, however, is that the highly derived morphology of the lophiiforms means that most of the bones are so different from the toadfishes that there usually are no shared character states, resulting in little polarization of batrachoid variation. In 1985, Rosen suggested that batrachoids, lophiiforms, gadiforms and bythitoids appeared to form a monophyletic group, based on the shared presence of cartilaginous cores connecting the tips of the exoccipital facets and the prezygapophyses of the first vertebra, rather than the bone-to-bone of most acanthopterygians. He noted further that this condition differed from that found in ophidioids. Patterson and Rosen (1989:23) suggested that lophiiforms and batrachoidiforms were monophyletic, sharing two apomorphies (elongate proximal radials in the pectoral-fin base and the reduction or loss of the first pharyngobranchial and the suspensory tip of the first epibranchial, and, if present, their lateral displacement away from the second and third pharyngobranchials. They added two further "probable" apomorphies: convergence of the ventral gill arches on a very short copula (basibranchial series), which is unossified or poorly so, and the insertion of the prezygapophyses of the first vertebra into elongate, hollow exoccipital tubes that extend beyond the basioccipital. In addition, they cited (*op. cit*., fig. 16, legend) another three apparent synapomorphies from Regan (1912: no endo [=meso] pterygoid, post-temporal fused to skull, no pleural ribs) and two from Monod (1960: no intercalary, partially/completely independent ascending process of the premaxillary process). They linked these two taxa (their Pediculati) to the gadiforms, because they share a third pharyngobrancial with three finger-like uncinate processes that articulate with the tips of epibranchials 2–4. They reiterated Rosen's (1985) view that bythitoids (excluding ophidioids) were related to this group; however, Rosen and Patterson (1969:370, legend to Fig. 5), had reported that the ophidioids and batrachoidids shared a unique caudal-fin structure, with the upper hypurals fused with the second ural centrum, the lower hypurals fused with the parhypural, and the uroneurals lost. They cautioned that this was a structural, rather than "phyletic", lineage, and the possible phylogenetic implications were not reflected in their cladogram, nor discussed further in Patterson and Rosen (1989). Markle stated (1989:84) that there "is reason to suggest that they [gadiforms] are more closely related to batrachoidiforms than to any other group (including the Pediculati)" and that "one is justified in considering batrachoidiforms as the appropriate outgroup for gadiform phylogenetic studies since the alternative (lophiiforms) is such a derived group." Markle (1989) placed the Ranicipitidae as basal to other gadiforms. In their monumental work on dorsal gill-arch musculature, Springer and Johnson (2004) pointed out the shared characters between *Raniceps* and *Opsanus*; however, they stated that they did not think this relationship was correct. Although *Raniceps* shares several character states with toadfishes, the bones of the neurocranium, pelvic girdle and caudal-fin structure bear no resemblance to the character states in toadfishes. These characters therefore cannot be polarized when using *Raniceps* as the sole outgroup. Teletchea et al. (2006), however, suggested that *Raniceps* is perhaps part of the Phycinae, and thus not basal among the gadiforms.

Recent molecular phylogenetic studies have also resulted in suggested relationships that provided possibilities for other outgroups for batrachoids, although not without the introduction of considerable differences from each other and from the various morphological hypotheses. For example, Wiley et al. (2000), Miya et al. (2005) and Smith and Wheeler (2006) all report gadiforms as the sister group of zeiforms, and relatively basal in the acanthomorph tree. With somewhat limited taxonomic sampling of the groups of interest here, Wiley et al. (2000) found batrachoids as the sister group to ophidioids, which together form the sister group of pleuronectiforms. Miya et al. (2005) placed the mastacembelids plus *Indostomus* as the sister group of batrachoids, these two being related to an eclectic mix of blennioids, gobiesociforms and various atherinomorphs. The batrachoid lineage is three nodes removed from the ophidioids plus bythitoids (monophyletic), and seven nodes removed from the lophiiformes. Finally, Smith and Wheeler (2006) reported that the draconettids were the sister group of the batrachoids, with callionymids being the next group (i.e. callionymoids are not monophyletic). The sister group to this assemblage was the lophiiform lineage, and the next lineage was comprised of two ophidioid taxa as the sister group of the champsodontids (their exemplar of a bythitoid failed to amplify). Smith (pers. comm., Dec. 2006) also stated "you might want to look at the Callionymioidei for sister-group relationships [to batrachoids]. I don't know whether Draconettidae + Callionymidae will ever form a clade without the inclusion of the toadfishes." As mentioned earlier, Briggs (1955) also had cited the Callionymoidea along with the toadfishes when discussing the gobiesociforms. We note that toadfishes have one to three long flexible filaments on the subopercle, a character we thought might be unique to toadfishes; however, a single long filament is present in *Synchiropus* and *Draconetta* (Fig. 2). The pectoral fin of toadfishes has elongate pectoral-fin radials with the distal end usually expanded. *Draconetta* also has elongate, expanded radials (Fig. 3). The New World toadfishes have a unique pelvic bone with a foramen in the median process that is also present in *Draconetta* (Fig. 4), but which is absent in callionymids and Old World toadfishes. The neurocranium of toadfishes differs greatly from that found in gadiforms or lophiiforms, but is very similar to those in the Callionymidae (Nakabo 1983, figs. 1–9) (Fig. 5). Toadfishes have either two or three dorsal-fin spines. *Draconetta* also has three spines, whereas all of our other outgroups have more. We also note, however, that callionymids lack the two morphological apomorphies and two putative apomorphies listed by Patterson and Rosen (1989–listed above). They do, however, lack an ossified endopterygoid, pleural ribs and intercalar, the post-temporal is rigidly attached to the skull, and the ascending process of the premaxilla is long and slender.

From the diversity of evidence and conclusions outlined above, we somewhat, but not entirely, arbitrarily chose to use a basal gadiform (*Raniceps*), a bythitoid (*Ogilbia*) and a callionymid (*Synchiropus*) as outgroups for our analysis of the intra-relationships of the batrachoids, based on morphological conclusions. To these we added *Draconetta*, based on the molecular evidence and the number of morphological characters shared with toadfishes.

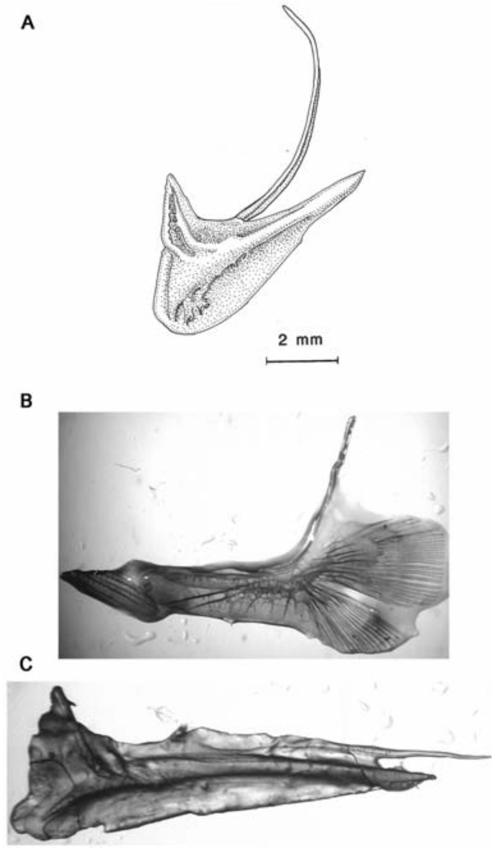


FIGURE 2. Subopercular bones with filaments (left lateral view). A. *Vladichthys gloverensis* FMNH 91036; B. *Synchiropus atrilabiatus*, CAS 168910, 73.0 mm SL; C. *Draconetta oregoni* CAS 168909, 89.4 mm SL.

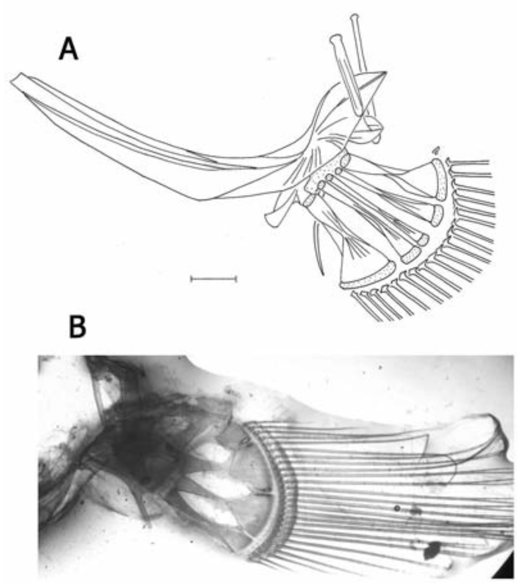


FIGURE 3. Pectoral girdle (left lateral view). A. *Aphos porosus* CAS 65051, scale equal 2 mm; B. *Draconetta oregoni*. CAS 168909, 89.4 mm SL.

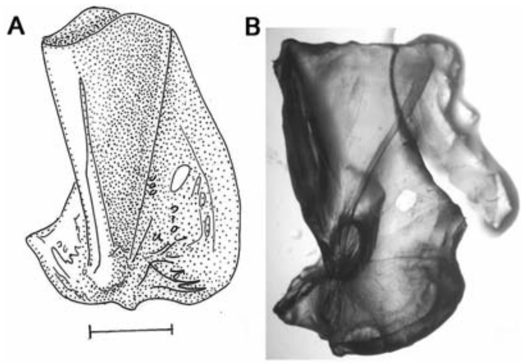


FIGURE 4. Pelvic bones (dorsal view of left pelvic bone). A. *Opsanus tau*, CAS 223821, scale equal 1 mm; B. *Draconetta oregoni*. CAS 168909, 89.4 mm SL.

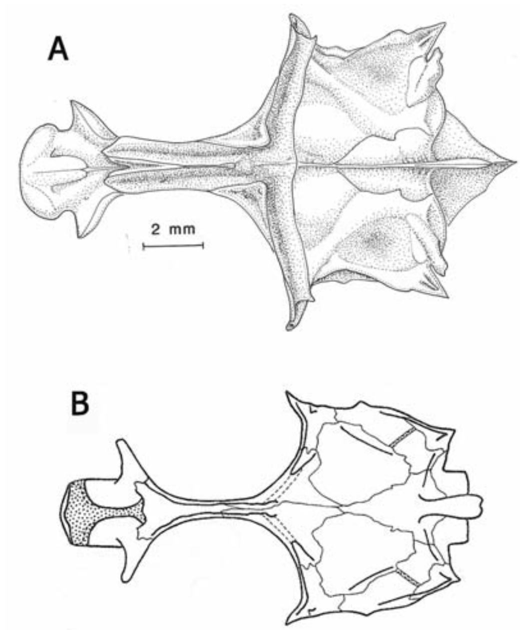


FIGURE 5. Dorsocranium. A. *Chatrabus felinus*, SAIAB 75-25; B. *Paracallionymus costatus* from Nakabo (1983).

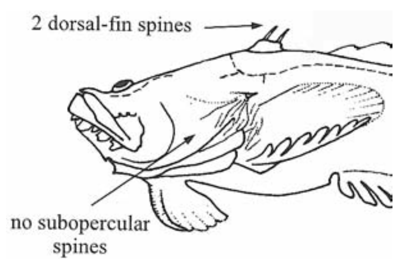


FIGURE 6. Head of *Thalassophryne*. Courtesy of FAO.

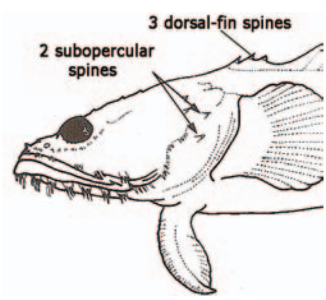


FIGURE 7. Head of *Batrachoides*. Courtesy of FAO.

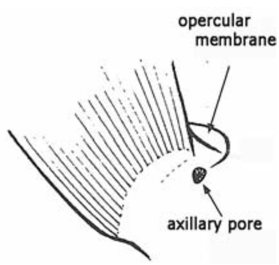


FIGURE 8. Axillary pore. Courtesy of FAO.

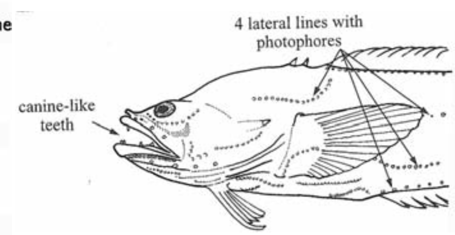


FIGURE 9. *Porichthys*. Courtesy of FAO.

PHYLOGENETIC ANALYTICAL METHODS

Individual data sets, autapomorphies removed, for the ingroup (batrachoids) and each of the outgroups (*Ogilbia*, *Raniceps*, *Synchiropus*, and *Draconetta*) as well as for virtually all combinations of the outgroups (*O* + *R*, O + R + S, R + D, *R* + *S*, R + S + D, and *S* + *D*) were analyzed with Paup 4.0b10 (Swofford, 2000) using PaupUp graphical interface (Calendini and Martin, 2005). All analyses were run with the character states unordered. Heuristic searches with stepwise addition of 10,000 replicates were performed, and strict consensus trees as well as the Consistency Index (CI), Retention Index (RI) and Rescaled Consistency Index (RC) were generated. Bremer support (Decay) indices were obtained by using MacClade ver. 4.0 (Maddison and Maddison, 2000).

Artificial Key to the Genera of Toadfishes (Batrachoididae)

1a. Dorsal-fin spines 2; subopercular spines absent; body naked; no axillary pore behind pectoral fins; canine-like teeth and photophores present or absent (Fig. 6.) .2
1b. Dorsal-fin spines 3; 1 to 3 subopercular spines present; body with or without scales; axillary pore behind pectoral fins present or absent; canine-like teeth and photophores absent (Batrachoidinae and Halophryninae) (Figs. 7 & 8) 5

2a. Dorsal and opercular spines solid with no venom glands under them; several lateral lines present; canine teeth present; pectoral glands present (Porichthyinae) (Figs. 9 & 10) 3
2b. Dorsal and opercular spines hollow with venom glands present under them; lateral line single or absent; canine teeth absent; pectoral glands present or absent (Thalassophryninae) 4

3a. Photophores present; no canines on vomer . . . . *Porichthys* (Fig. 21)
3b. Photophores absent; canines on vomer . . . .*Aphos* (Fig. 20)

4a. Second dorsal-fin rays 17–21; anal-fin rays 16–20; no discrete glands present on pectoral fin, but glandular tissue scattered on fins (Fig. 11) . . . .*Thalassophryne* (Fig. 22)
4b. Second dorsal-fin rays 22–33; anal-fin rays 21–30; 3 to 7 discrete glands located between the bases of the uppermost pectoral rays . . . .*Daector* (Fig. 23)

5a. Body completely naked 6
5b. Body with at least some scales (may be embedded and difficult to see) 19

6a. A flap with an eye spot at end of maxilla on each side of mouth . . . . *Bifax* (Fig. 35)
6b. Maxillary flaps absent 7

7a. No axillary foramen or pocket 8
7b. Axillary foramen or pocket present (Figure 12) 15

8a. Three subopercular spines . . . .*Potamobatrachus* (Fig. 27)
8b. Fewer than three subopercular spines 9

9a. Fewer than 24 dorsal-fin rays; teeth conical or blunt 10
9b. More than 24 dorsal-fin rays (28–29); (teeth short and blunt; a prominent plumose supraorbital tentacle present; venetian blind gland in pectoral-fin axil of adults) (Fig. 13) . . . . *Amphichthys* (Fig. 24)

10a. One subopercular spine 11
10b. Two subopercular spines 12

11a. Dorsal-fin rays 20–21; anal-fin rays 15–17; upper lateral-line pores 15–16; lower lateral-line pores 13–19; epaxial trunk musculature not extending forward to cover entire dorsocranium behind orbits (Fig. 14) . . . .*Vladichthys* (Fig. 29)
11b. Dorsal-fin rays 14–17; anal-fin rays 11–13; upper lateral-line pores 25–31; lower lateral-line pores 23–31; epaxial trunk musculature extending forward to cover entire dorsocranium behind orbits (Fig. 15) . . . .*Triathalassothia* (Fig. 48)

12a. Supraorbital tentacle or tentacles present (Fig. 16); gill openings less or greater than pectoral-fin base 14
12b. No tentacles above eye; gill openings not less than pectoral-fin base 13

13a. Pelvic fins reach vent; head deep, 20% SL or greater; eye equal to or greater than interorbital width . . . . *Chatrabus* (in part- *C. felinus*) (Fig. 37)
13b. Pelvic fins not reaching vent; head shallow, depressed, 17 % or less SL; eye less than interor obital width . . . . *Batrichthys* (Fig. 34)

14a. Head rounded with lower and upper jaws about equally terminal; eye diameter greater than snout length; interorbital width equal to or less than eye diameter; gill opening clearly above lower margin of pectoral-fin base (Fig. 17) . . . . *Halophyrne* (Fig. 45)
14b. Head more pointed and flattened with lower jaw protruding; eye diameter less than snout length; interorbital width greater than eye diameter; gill opening either at or below pectoral-fin base (Fig. 18) . . . . *Allenbatrachus* (Fig. 30)

15a. Axillary foramen or pocket at top of pectoral-fin axil; soft dorsal-fin rays 19–24, usually fewer than 24 16
15b. Axillary foramen near center of pectoral-fin axil; soft dorsal-fin rays 23–32, usually 24 or more 18

16a. Supraorbital tentacles present and others on head; anterior nasal tentacle not elongate 17
16b. Supraorbital tentacles absent and few on head; anterior nasal tentacle long . . . . *Austrobatrachus* (Fig. 31)

17a. Opening at top of pectoral-fin axil a distinct round hole, not funnel shaped and lacking glandular tissue on ventral margin; lower gill opening at lower pectoral-fin base; subopercle with one strong spine . . . . *Batrachomoeus* (Fig. 33)
17b. Opening at top of pectoral-fin axil a funnel-shaped pit with glandular tissue inside and extending from ventral margin onto axil; lower gill opening well below lower pectoral-fin base; subopercle with two spines, upper one large and lower one smaller . . . . *Colletteichthys* (Fig. 43)

18a. Soft dorsal-fin rays 23–27; anal-fin rays 19–23; discrete glands present on interior surface of pectoral fin between bases of upper fin rays . . . . *Opsanus* (Fig. 26)
18b. Soft dorsal-fin rays 29–32; anal-fin rays 24–26; no discrete glands present on interior surface of pectoral fin between bases of upper fin rays . . . . *Sanopus* (Fig. 28)

19a. No small, round, foramen in pectoral-fin axil, but a funnel-shaped pocket might be present 20
19b. Small, round foramen present on upper part of pectoral axil beneath upper edge of opercular membrane; (fewer than 24 dorsal-fin rays; no tentacle above eye) . . . *Halobatrachus* (Fig. 44)

20a. A more or less funnel-shaped pocket (deep or shallow) present on upper part of pectoral-fin axil 21
20b. Pectoral axil without a pocket. 22

21a. No obvious tentacles above eye . . . . *Perulibatrachus* (Fig. 46)
21b. One or more prominent tentacles above eye 23

22a. Anal-fin rays 18 or fewer, nasal barbels present (Fig. 19 a.) . . . . *Chatrabus* (in part) (Fig. 36)
22b. Anal-fin rays 19–27, nostrils tubular, no nasal barbels (Fig. 19 b.) . . . *Batrachoides* (Fig. 25)

23a. Scales on body extending forward to first dorsal-fin base; anal-fin rays 13–14; pectoral fin spotted; anterior nostril with a single pointed tentacle . . . . *Barchatus* (Fig. 32)
23b. Scales on body restricted to posterior half; anal-fin rays 15–17; pectoral fin without spots; anterior nostril with a large tuft of tentacles . . . . *Riekertia* (Fig. 47)

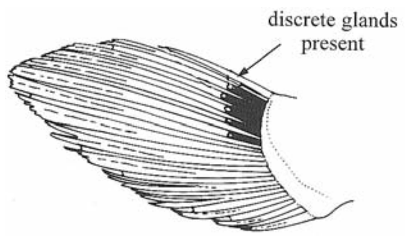


FIGURE 10. Pectoral-fin glands – distinct. Courtesy of FAO.

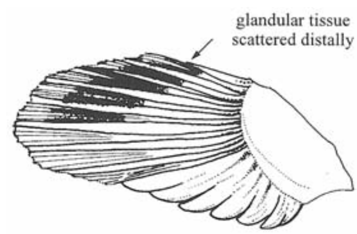


FIGURE 11. Pectoral-fin glands – scattered. Courtesy of FAO.

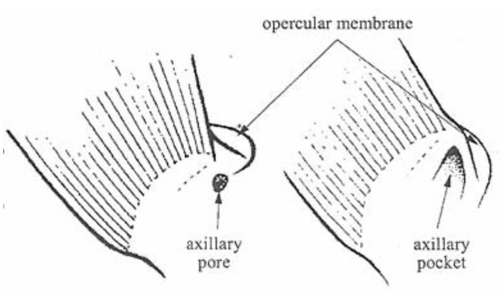


FIGURE 12. Axillary pore and pocket. Courtesy of FAO.

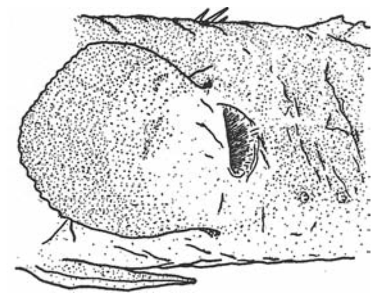


FIGURE 13. Venetian blind gland in pectoral-fin axil of *Amphichthys* (from Breder 1925).

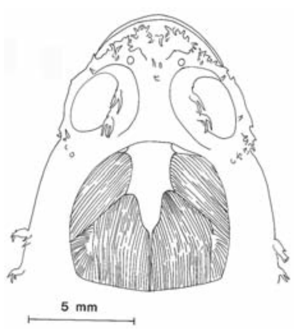


FIGURE 14. Head of *Vladichthys gloverensis* (from Greenfield 2006)

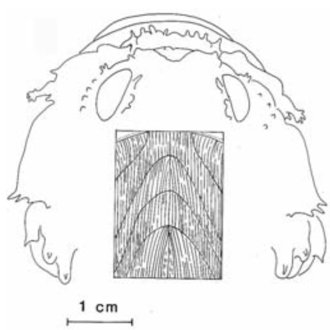


FIGURE 15. Head of *Triathalassothia argentinus* (from Greenfield 2006)

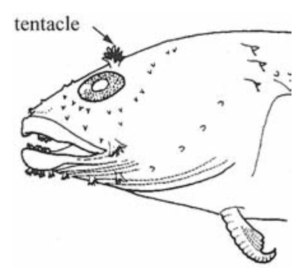


FIGURE 16. Supraorbital tentacle. Courtesy of FAO.

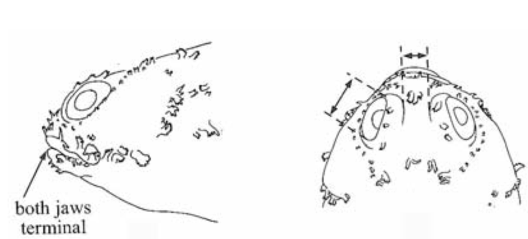


FIGURE 17. Head of *Halophryne*. Courtesy of FAO.

FIGURE 18. Head of *Allenbatrachus*. Courtesy of FAO.

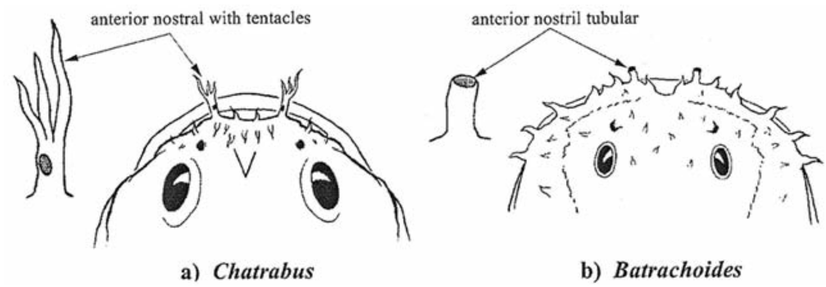


FIGURE 19. Nostrils of : a. *Chatrabus;* b. *Batrachoides*. Courtesy of FAO.

Subfamily Porichthyinae

Two solid dorsal-fin spines with no venom glands, subopercular spines absent, canine teeth present.

Genus *Aphos* Hubbs and Schultz, 1939

Aphos Hubbs and Schultz, 1939, Proc. U.S. Nat. Mus., 86 (3060):476. TYPE-SPECIES: *Batrachus porosus* Valenciennes, by original designation and monotypy.

SYNONYMS.— none.

SPECIES.— Single species, *Aphos porosus* (Valenciennes 1837), Pacific coast of South America.

DIAGNOSIS.— A member of the subfamily Porichthyinae with canines on the vomer and no photophores.

MAJOR REFERENCE.— Hubbs and Schultz (1939).

Genus *Porichthys* Girard, 1854

Porichthys Girard, C. F., 1854. Proc. Acad. Nat. Sci. Phil. 7:141–142. TYPE-SPECIES: *Porichthys notatus* Girard, 1854 by subsequent designation of Jordan and Gilbert, 1883.

SYNONYMS.— *Nautopaedium* Jordan, 1919: 342. TYPE-SPECIES: *Batrachus porosissimus* Valenciennes 1837: 501.

SPECIES.— Pacific Ocean, eight species: *P. analis* Hubbs and Schultz, 1939; *P. ephippiatus* Walker and Rosenblatt, 1988; *P. greenei* Gilbert and Starks, 1904; *P. margaritatus* (Richardson 1844); *P. mimeticus* Walker and Rosenblatt, 1988; *P. myriaster* Hubbs and Schultz, 1939; *P. notatus* Girard, 1854; *P. oculellus* Walker and Rosenblatt, 1988. Canada to Ecuador. Atlantic Ocean, five species: *P. bathoiketes* Gilbert, 1968; *P. kymosemeum* Gilbert, 1968; *P. oculofrenum* Gilbert, 1968; *P. pauciradiatus* Caldwell and Caldwell, 1963; *P. porosissimus* (Valenciennes 1837). Virginia, United States to Argentina.

DIAGNOSIS.— A member of the subfamily Porichthyinae with photophores and no canines on vomer.

MAJOR REFERENCES.— Hubbs and Schultz (1939), Gilbert (1968), Walker and Rosenblatt (1988).

Subfamily Thalassophryninae

Two dorsal-fin spines, no subopercular spines, dorsal and opercular spines hollow and connected to venom glands, canine teeth absent.

Genus *Thalassophryne* Günther, 1861

Thalassophryne Günther, 1861, Cat. Fishes v. 3: 174. TYPE-SPECIES: *Thalassophryne maculosa* Günther, 1861 by monotypy.

SYNONYMS.— *Thalassothia* Berg, 1895:66. TYPE-SPECIES: *Thalassophryne montevidensis* Berg, 1893 by monotypy.

SPECIES.— Six species, all western Atlantic: *T. amazonica* Steindachner, 1876 (freshwater); *T. maculosa* Günther, 1861; *T. megalops* Bean and Weed, 1910; *T. montevidensis* Berg, 1893; *T. nattereri* Steindachner, 1876; *T. punctata* Steindachner, 1876. Panama to Brazil.

DIAGNOSIS.— A member of the subfamily Thalassophryninae with no distinct glands present on pectoral fins; second dorsal-fin rays 17–21; anal-fin rays 16–20.

MAJOR REFERENCE.— Collette (1966).

Genus *Daector* Jordan and Evermann, 1898

Daector Jordan and Evermann, 1898, Bull. U.S. Natl. Mus. (47): 2313, 2325. TYPE-SPECIES: *Thalassophryne dowi* Jordan and Gilbert, 1887 by original designation and monotypy.

SYNONYMS.— none.

SPECIES.— Four species, all eastern Pacific: *D. dowi* (Jordan and Gilbert 1887); *D. gerringi* (Rendahl 1940); *D. quadrizonatus* (Eigenmann 1923); *D. reticulata* (Günther 1864); *D. schmitti* Collette, 1968. Costa Rica to Peru.

DIAGNOSIS.— A member of the subfamily Thalassophryninae with distinct glands located between the bases of the uppermost pectoral-fin rays; second dorsal-fin rays 22–33; anal-fin rays 21–30.

MAJOR REFERENCES.— Collette (1966, 1968, 1973).

Subfamily Batrachoidinae — New World Clade

Three dorsal-fin spines, no hollow dorsal and opercular spines connected to venom glands; one to three subopercular spines; lacks photophores and canine teeth; foramina in median process of pelvic bone; median process of pelvic bone connected to pelvic bone its entire length; upper accessory pectoral-fin radial fully ossified, medial suture between the epihyal and ceratohyal; ventral edge of cratohyal rounded where it joins epihyal; dorsal side of joint between dentary and articular about equal height and rounded; dorsal edge of quadrate flat all the way across where it meets the metapterygoid.

Genus *Amphichthys* Swainson, 1839

Amphichthys Swainson, 1839, Nat. Hist. & Class. V. 2: 184, 282. TYPE-SPECIES: *Amphichthys rubigenes* Swainson by monotypy.

SYNONYMS.— *Marcgravia* Jordan, 1887, TYPE-SPECIES: *Batrachus cryptocentrus* Valenciennes 1837, by original designation. *Marcgravichthys* Miranda-Ribeiro, 1915, TYPE-SPECIES: *Batrachus cryptocentrus* Valenciennes 1837, type by being a replacement name.

SPECIES.— One species, Atlantic: *A. cryptocentrus* (Valenciennes 1837). North coast of South America, from Panama to Brazil.

DIAGNOSIS.— A member of the subfamily Batrachoidinae lacking scales; no axillary foramen or pocket, one subopercular spine and one filament; 28–29 dorsal-fin rays; teeth short and blunt; a prominent plumose supraorbital tentacle present; venetian blind gland in pectoral-fin axil in adults.

MAJOR REFERENCE.— Greenfield and Greenfield (1973).

Genus *Batrachoides* Lacepède, 1800

Batrachoides Lacepède, 1800, Hist. nat. poissons, vol. 2: 451. TYPE-SPECIES: *Batrachoides tau* Lacepède, = *Batrachus surinamensis* Bloch and Schneider, not *Gadus tau* Linnaeus, by subsequent designation of Jordan and Evermann, 1896:466.

SYNONYMS.— *Batrictius* Rafinesque, 1815.

SPECIES.— Nine species: *B. boulengeri* Gilbert and Starks, 1904; *B. gilberti* Meek and Hildebrand, 1928; *B. goldmani* Evermann and Goldsborough, 1902; *B. liberiensis* (Steindachner 1867); *B. manglae* Cervigón, 1964; *B. pacifici* (Günther 1861); *B. surinamensis* (Bloch and Schneider 1801); *B. walkeri* Collette and Russo, 1981; *B. waltersi* Collette and Russo, 1981. Pacific, Mexico to Peru; W. Atlantic, Mexico to Brazil; freshwater (Central America); and E. Atlantic, Senegal to Angola.

DIAGNOSIS.— A member of the subfamily Batrachoidinae with scales; no foramen or funnel-shaped pocket in pectoral-fin axil; 2–19 glands present between fin rays; anal-fin rays 19–27; subopercle with two spines and one filament.

MAJOR REFERENCE.— Collette and Russo (1981).

Genus *Opsanus Rafinesque*, 1818

Opsanus Rafinesque, 1818, Am. Monthly Mag. Crit. Rev. 2(3):203. TYPE-SPECIES: *Opsanus cerapalus* Rafinesque by original designation.

SYNONYMS.— None.

SPECIES.— Six species: *O. beta* Goode and Bean, 1880; *O. brasiliensis* Rotundo, Spinelli, and Zavala-Camin, 2005; *O. dichrostomus* Collette, 2001; *O. pardus* Goode and Bean, 1880; *O. phobetron* Walters and Robins, 1961; *O. tau* (Linnaeus 1766). Gulf of Maine, United States south to Belize, including Bahamas and Cuba, and a disjunct species in São Paulo, Brazil.

DIAGNOSIS.— A member of the subfamily Batrachoidinae lacking scales; axillary foramen near center of pectoral-fin axil; one subopercular spine and one filament; dorsal-fin rays 23–27; anal-fin rays 19–23; discrete glands present between upper rays on posterior surface of pectoral fin.

MAJOR REFERENCES.— Walters and Robins (1961), Collette (2001, 2003).

DISCUSSION.— *Opsanus brasiliensis* was described from São Paulo, Brazil (Rotundo et al. 2005) far south of the distribution other species in the genus (Collette 2003). It is apparently very similar to *O. beta*, differing only in color. We have not been able to examine specimens of this species and think it is probably based on an introduction from the Gulf of Mexico.

Genus *Potamobatrachus* Collette, 1995

Potamobatrachus Collette, 1995, Ichthyol. Explor. Freshwaters, 6(4):334. TYPE-SPECIES: *Potamobatrachus trispinosus* Collette, 1995 by original designation and monotypy.

SYNONYMS.— None.

SPECIES.— One species: *P. trispinosus* Collette, 1995. Freshwater, Rio Araguaia and Rio Tocantins, Brazil.

DIAGNOSIS.— A member of the subfamily Batrachoidinae lacking scales; no axillary foramen or pocket; three subopercular spines and one filament.

MAJOR REFERENCE.— Collette (1995).

Genus *Sanopus* Smith, 1952

Sanopus Smith, 1952, Ann. Mag. Nat. Hist., ser. 12, 5:314. TYPE-SPECIES: *Opsanus barbatus* Meek and Hildebrand by original designation.

SYNONYMS.— None.

SPECIES.— Six species: *S. astrifer* (Robins and Stark 1965); *S. barbatus* (Meek & Hildebrand 1928); *S. greenfieldorum* Collette, 1983; *S. johnsoni* Collette and Stark, 1974; *S. reticulatus* Collette, 1983; *S. splendidus* Collette, Stark, and Phillips, 1974. Yucatán, Mexico south to Panama.

DIAGNOSIS.— A member of the subfamily Batrachoidinae lacking scales; axillary foramen near center of pectoral-fin axil; one subopercular spine and one filament; dorsal-fin rays 29–l34; anal-fin rays 24–28; no discrete glands present on posterior surface of pectoral fin between bases of upper fin rays.

MAJOR REFERENCES.— Collette (1974, 1983, 2003).

Genus *Vladichthys*, Greenfield, 2006

Vladichthys Greenfield, 2006 Proc. Calif. Acad. Sci., ser. 4, 57(32): 946. TYPE-SPECIES: *Triathalassothia gloverensis* Greenfield and Greenfield, 1973 by original designation and monotypy.

SYNONYMS.— None.

SPECIES.— One species: *V. gloverensis* (Greenfield and Greenfield 1973). Belize and Bay Islands, Honduras.

DIAGNOSIS.— A member of the subfamily Batrachoidinae lacking scales; no axillary foramen or pocket; one subopercular spine and one filament; dorsal-fin rays 20–21; anal-fin rays 15–17; upper lateral-fine pores 15–16; lower lateral-line pores 13–19; epaxial trunk musculature not extending forward to cover entire dorsocranium behind orbits.

MAJOR REFERENCES.— Greenfield and Greenfield (1973), Collette (2003), Greenfield (2006).

Subfamily Halophryninae – Old World Clade

New subfamily, Type-genus *Halophryne* Gill, 1863

Three dorsal-fin spines; no hollow dorsal and opercular spines connected to venom glands; one to two subopercular spines and one to three filaments; lacks photophores and canine teeth; no foramina in median process of pelvic bone; median process of pelvic bone not joined to pelvic bone along its entire length; ventral edge of ceratohyal square where it joins epihyal; dorsal edge of quadrate not flat all the way across where it meets the metapterygoid.

Genus *Allenbatrachus* Greenfield, 1997

Allenbatrachus Greenfield, 1997, Pac. Sci. 51(3):307. TYPE-SPECIES: *Cottus grunniens* (Linnaeus 1758) by original designation.

SYNONYMS.— None.

SPECIES.— Three species, all Indo-Pacific: *A. grunniens* (Linnaeus 1758); *A. meridionalis* Greenfield and Smith, 2004; *A. reticulatus* (Steindachner 1870).

DIAGNOSIS.— A member of the subfamily Halophryninae with body naked; no maxillary flaps, no axillary foramen or pocket; two subopercular spines and one filament; supraorbital tentacles present; gill opening at or below pectoral-fin base; eye diameter less than snout length; interorbital width greater than eye diameter; head more pointed and flattened with lower jaw protruding;

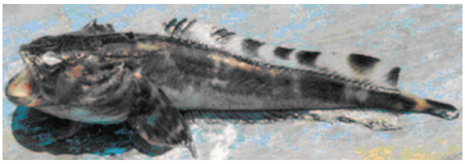


FIGURE 20. *Aphos porosus*. Photograph courtesy of R.J. Eakins.

FIGURE 21. *Porichthys notatus*. Photograph courtesy of J. Tashjian.

FIGURE 22. *Thalassophryne maculosa*. Photograph courtesy of P. Humann.

FIGURE 23. *Daector reticulata*. Photograph courtesy of G.R. Allen.

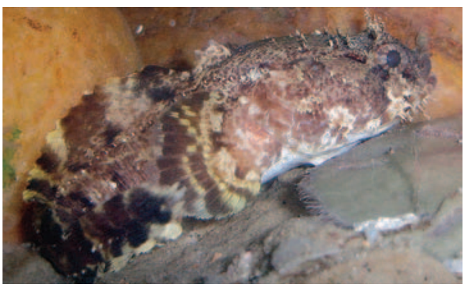


FIGURE 24. *Amphichthys cryptocentrus*. Photograph courtesy of J.L. Silva-Nunes.

FIGURE 25. *Batrachoides pacifici*. Photograph courtesy of G.R. Allen.

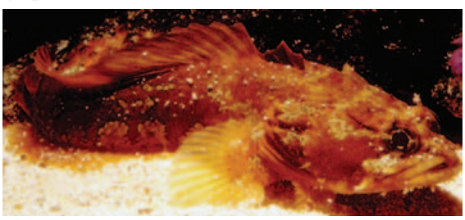


FIGURE 26. *Opsanus beta*. Photograph courtesy of S.W. Michael.

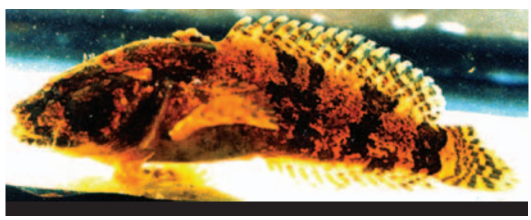


FIGURE 27. *Potamobatrachus trispinosus*. Photograph courtesy of R. Stawikowski.

FIGURE 28. *Sanopus splendidus*. Photograph courtesy of R. Whitworth.

FIGURE 29. *Vladichthys gloverensis*. Photograph by D.W. Greenfield.

epaxial trunk musculature covers entire dorsocranium; a foramen on each side of neurocranium behind eyes bordering sphenotic and frontal bones; accessory upper pectoral-fin radial totally ossified.

Major references.— Greenfield (1997), Greenfield and Smith (2004).

Genus *Austrobatrachus* Smith, 1949

Austrobatrachus Smith, 1949, Sea Fishes, 423. Type-species: *Pseudobatrachus foedus* Smith, 1947 by original designation and monotypy.

Synonyms.— None.

Species.— One species: *A. foedus* (Smith 1947). South Africa

Diagnosis.— A member of the subfamily Halophryninae lacking scales and a maxillary flap; a foramen at top of pectoral-fin axil; one subopercular spine and two filaments; supraorbital tentacles absent; anterior nasal tentacle long; dorsal-fin rays fewer than 24.

Major reference.— Smith (1952).

Genus *Barchatus* Smith, 1952

Barchatus Smith, 1952, Ann. Mag. Nat. Hist., Ser. 12, 5:332. Type-species: *Batrachus cirrhosus* Klunzinger, 1871 by original designation and monotypy.

Synonyms.— None.

Species.— One species: *B. cirrhosus* Klunzinger, 1871. Red Sea.

Diagnosis.— A member of the subfamily Halophryninae with scales extending forward to first dorsal-fin base; funnel-shaped pocket present on upper part of pectoral-fin axil; accessory pectoral-fin radial not ossified; two subopercular spines and two filaments; prominent tentacles above eyes; anterior nostril with single pointed tentacle; anal-fin rays 13–14; pectoral fin spotted.

Major reference.— Smith 1952.

Discussion.— Klunzinger (1871) described *Batrachus cirrhosus*, the only known toadfish species from the Red Sea. In 1952, Smith erected the genus *Barchatus* for that species, apparently without ever seeing a specimen. Dor (1984) then used the genus *Thalassothia* Berg (1895) for the Red Sea species, and that name has been used since (Fricke 2005), including Fish Base; however, Collette (1966) regarded the genus *Thalassothia* as a synonym of *Thalassophryne* Günther (1861), a New World genus in the subfamily Thalassophryninae. The Red Sea species is in the subfamily Halophryninae.

As stated in Eschmeyer (1998, 2008), the genus *Batrachus* (Klein 1776), used by Klunzinger (1871) to describe *B. cirrhosus*, is not available because it was published in a work that does not conform to the principle of binominal nomenclature. Prior to that, Schaeffer (1760) used the name *Batrachus*, but that publication is on the Official List of rejected works. Walbaum (1792) reprinted in a condensed form the genera of Klein, but did not accept them. D. S. Jordan (ICZN, 1910a) submitted a case to the International Commission on Zoological Nomenclature concerning the validity of Klein's genera. The Commission ruled that an earlier ruling (ICZN 1910b) on the status of pre-Linnaean names reprinted subsequent to 1757 applied, and thus the Klein names in Walbaum were not available. *Batrachus* was later used by Bloch and Schneider (1801) for *B. surinamensis*, but Collette and Russo (1981) regarded *Batrachus* as a synonym of *Batrachoides* Lacepède (1800). *Batrachus* Rafinesque (1814) is a junior synonym of the amphibian genus *Bufo* Laurenti (1768). Thus, the genus *Batrachus* is not available for the Red Sea toadfish and the valid name is *Barchatus cirrhosus*.

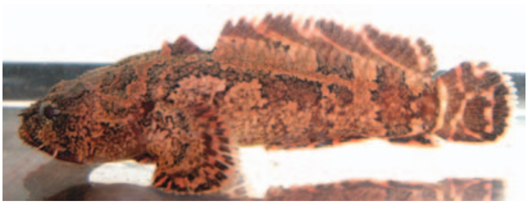


Figure 30. *Allenbatrachus meridionalis*. Photograph courtesy of P. Loiselle.

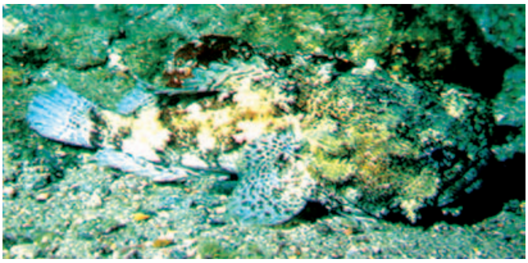


FIGURE 32. *Barchatus cirrhosus*. Photograph courtesy of E. Brokovich.

FIGURE 34. *Batrichthys apiatus*. Photograph courtesy of G. Zsilavecz.

FIGURE 36. *Chatrabus melanurus*. Photograph courtesy of P.C. Heemstra.

FIGURE 31. *Austrobatrachus foedus*. Photograph courtesy of J. Swanepoel.

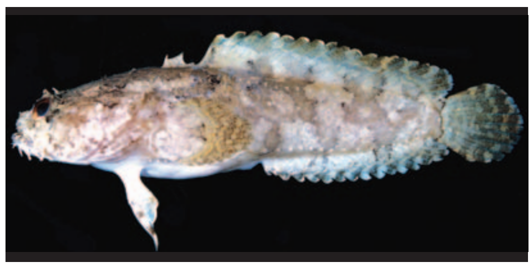


FIGURE 33. *Batrachomoeus trispinosus*. Photograph courtesy of J.E. Randall.

FIGURE 35. *Bifax lacinia*. Photograph courtesy of J.E. Randall.

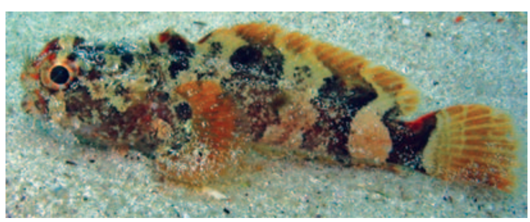


FIGURE 37. *Chatrabus felinus*. Photograph courtesy of G. Zsilavecz.

Genus *Batrachomoeus* Ogilby, 1908

Batrachomoeus Ogilby, 1908, Ann. Queensl. Mus. 9(pt. 2):46. TYPE-SPECIES: *Batrachomoeus minor* Ogilby, 1908 by subsequent designation of McCulloch 1929:358.

SYNONYMS.— *Pseudobatrachus* Castelnau, 1875; *Pelophiletor* Ogilby, 1906.

SPECIES.— Five species: *B. dahli* (Rendahl 1922); *B. dubius* (Shaw 1790); *B. occidentalis* Hutchins, 1976; *B. rubricephalus* Hutchins, 1976; *B. trispinosus* (Günther 1861). Australia north through Indo-Australian Archipelago to Thailand.

DIAGNOSIS.— A member of the subfamily Halophryninae lacking scales; no maxillary flap; foramen at top of pectoral-fin axil a distinct round hole, not funnel shaped and lacking glandular tissue on ventral margin; supraorbital tentacles present and others on head; anterior nasal tentacle not elongate; lower gill opening at lower pectoral-fin base; subopercle with one strong spine and one filament.

MAJOR REFERENCE.— Hutchins (1976).

Genus *Batrichthys* Smith, 1934

Batrichthys Smith, 1934, Trans. Roy. Soc. S.A., 22:98. TYPE-SPECIES: *B. albofasciatus* Smith, by original designation.

SYNONYMS.— *Gymnobatrachus* Smith, 1949.

SPECIES.— Two species: *B. albofasciatus* Smith, 1934; *B. apiatus* Valenciennes, 1837 South African coast.

DIAGNOSIS.— A member of the subfamily Halophryninae lacking scales; no maxillary flap; no axillary foramen or pocket; two subopercular spines and one filament; 22 or fewer dorsal-fin rays; no tentacles above eye; gill opening not less than pectoral-fin base; head depressed, 17% or less SL; eye less than interorbital width.

MAJOR REFERENCE.— Smith (1952).

DISCUSSION.— *Batrichthys felinus* Smith was previously in this genus, but has been removed to *Chatrabus*.

Genus *Bifax* Greenfield, Mee and Randall, 1994

Bifax Greenfield, Mee, and Randall, 1994, Fauna Saudi Arabia 14:277. TYPE-SPECIES: *Bifax lacinia* Greenfield, Mee, and Randall, 1994 by original designation and monotypy.

SYNONYMS.— None.

SPECIES.— One species: *B. lacinia,* Greenfield, Mee and Randall, 1994. Oman, Arabian Sea.

DIAGNOSIS.— A member of the subfamily Halophryninae lacking scales; a flap with an eye spot at end of maxilla on each side of mouth.

MAJOR REFERENCE.— Greenfield, Mee, and Randall (1994).

Genus *Chatrabus* Smith, 1949

Chatrabus Smith, 1949, Sea Fishes S. A.: 423. TYPE-SPECIES: *Batrachoides melanurus* Barnard, 1927 by original designation.

SYNONYMS.— *Tharbacus* Smith, 1952. TYPE-SPECIES: *Tharbacus vanecki* Smith, 1952.

Four species: *C. damaranus* (Barnard 1927); *C. felinus* (Smith 1952); *C. melanurus* (Barnard 1927); *C. hendersoni* (Smith 1952). West Africa Angola to Namibia and South Africa.

Diagnosis.— A member of the subfamily Halophryninae with scales present or absent; no foramen or pocket in pectoral-fin axil; two subopercular spines and two or three filaments; nasal barbels present; no supraorbital tentacles; anal-fin rays 18 or fewer.

Major references.— Smith (1952), Hutchins (1986).

Discussion.— *Chatrabus felinus* was previously in the genus *Batrichthys*, but our cladistic analysis has shown that it should be moved to the genus *Chatrabus*. The genus *Batrichthys* contained three species, *B. apiatus* (=*ophiocephalus*), *B. albofasciatus*, and *B. felinus*. The pelvic fins in both *B. apiatus* and *B. albofasciatus* are short, not reaching the vent, whereas they are longer and reach the vent in *C. felinus*. *Chatrabus felinus* has a deeper head that is not depressed (20% SL or greater) versus a depressed head (17% or less SL) in *Batrichthys* species. The interorbital is wider in *Batrichthys* species (eye less than interorbital width) versus narrower in *C. felinus* (eye equal to or greater than interorbital width). The median process of the pelvic bone is short in *C. felinus* (Fig. 38 A), whereas it is long in both *Batrichthys* species (Fig. 38 B). The ventral process of the urohyal is deep and rounded in *C. felinus* (Fig. 39 A) whereas it is more slender and elongate in both *Batrichthys* species (Fig. 39 B). The distal end of the maxilla is square and its articular head rounded in *C. felinus* (Fig. 40 A), whereas the distal end is rounded and there is a gap between the anterolateral and anteromedial process of the articular head in both *Batrichthys* species (Fig. 40 B). *Chatrabus felinus* has two subopercular filaments (Fig. 41 A) whereas both *Batrichthys* species have one (Fig. 41 B). In a comparison of the length of the skull anterior to the sphenotics to the length posterior to them, *C. felinus* is shorter behind (Fig. 42 A) whereas it is longer behind in *Batrichthys* species (Fig. 42 B). Thus, *C. felinus* differs from the species in the genus *Batrichthys* in many features.

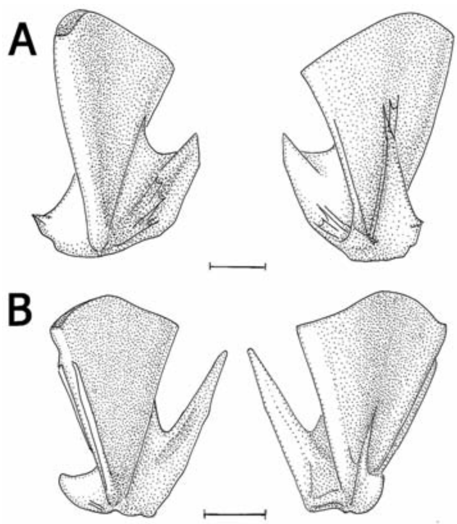


FIGURE 38. Pelvic bones (ventral view on right side of plate, dorsal view on left side of plate). A. *Chatrabus felinus*; B. *Batrichthys apiatus*.

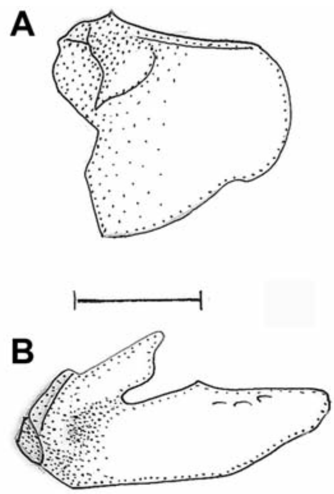


FIGURE 39. Urohyal (left lateral view). A. *Chatrabus felinus*; B. *Batrichthys apiatus*.

The genus *Tharbacus* Smith, based on *T. vanecki* Smith (1952), was placed in synonymy of *Chatrabus* by Hutchins 1986. The genus *Tharbacus* was distinguished from *Chatrabus* by having scales extending forward on the top of the head to the rear edge of the orbits and in advance of the pelvic-fin insertion, whereas scales did not extend this far forward in *Chatrabus* (Smith 1952). Hutchins (1986) did not consider the difference in squamation to be of sufficient sig-

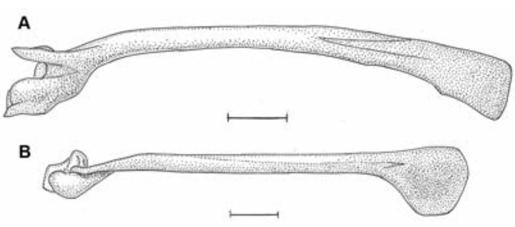


FIGURE 40. Maxilla (left lateral view). A. *Chatrabus felinus*; B. *Batrichthys apiatus*.

nificance to warrant generic recognition. The inclusion of *B. felinus* in the genus *Chatrabus* extends this variability to the complete loss of scales. *Chatrabus felinus* differs from the other species in the genus by lacking scales and by having two rather than three subopercular filaments. Other osteological characters agree with *Chatrabus*. The cladistic analysis placed *C. felinus* as the sister of the other two *Chatrabus* species. *Chatrabus felinus* is known only from Port Alfred and False Bay, South Africa (Penrith and Penrith 1971; Smith 1952; Winterbottom 1978).

Genus *Colletteichthys* Greenfield, 2006

Colletteichthys Greenfield, 2006, Proc. Calif. Acad. Sci., Ser. 4, 57(32): 949. TYPE-SPECIES: *Batrachus dussumieri* Valenciennes 1837 by original designation and monotypy.

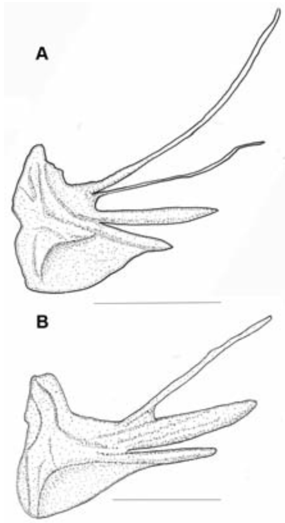


FIGURE 41. Suboperculum (left lateral view). A. *Chatrabus felinus*; B. *Batrichthys apiatus*.

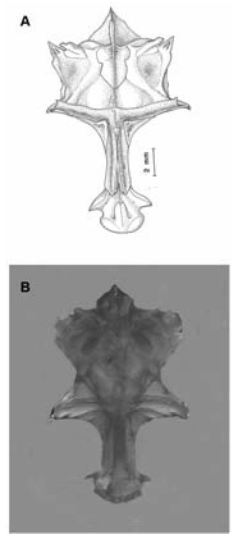


FIGURE 42. Dorsocranium. A. *Chatrabus felinus;* B. *Batrichthys apiatus*.

SYNONYMS.— None.

SPECIES.— One species: *C. dussumieri* (Valenciennes 1837). Arabian Gulf to India and Sri Lanka.

DIAGNOSIS.— A member of the subfamily Halophryninae lacking scales; no maxillary flaps; a funnel-shaped pit with glandular tissue inside and extending from ventral margin onto pectoral-fin axil; supraorbital tentacles present and others on head; anterior nasal tentacle not elongate; lower gill opening well below lower pectoral-fin base; subopercle with two spines, upper one large and lower one smaller and two filaments.

MAJOR REFERENCE.— Greenfield (2006).

Genus *Halobatrachus* Ogilby, 1908

Halobatrachus Ogilby, 1908, Ann. Queensl. Mus. 9(pt. 2):46, 53. TYPE-SPECIES: *Batrachus didactylus* Bloch and Schneider, 1801 by original designation

SYNONYMS.— None.

SPECIES.— One species: *H. didactylus* (Bloch and Schneider 1801). Portugal south to Angola.

DIAGNOSIS.— A member of the subfamily Halophryninae with scales; small, round foramen present on upper part of pectoral axil; one subopercular spine and two filaments; 20–21 dorsal-fin rays; no tentacles above.

MAJOR REFERENCES.— Collette, Greenfield and Costa (2006), Collette and Greenfield (in press).

Genus *Halophryne* Gill, 1863

Halophryne Gill, 1863, Proc. Acad. Nat. Sci. Phila. 15:170, TYPE-SPECIES: *Batrachoides diemensis* Lesueur, 1824 by original designation.

SYNONYMS.— *Coryzichthys* Ogilby, 1908.

SPECIES.— Four species*:* *H. diemensis* (Lesueur 1824); *H. hutchinsi* Greenfield, 1998;

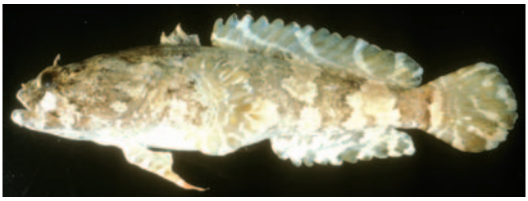


FIGURE 43. *Colletteichthys dussumieri*. Photograph courtesy of J.E. Randall.

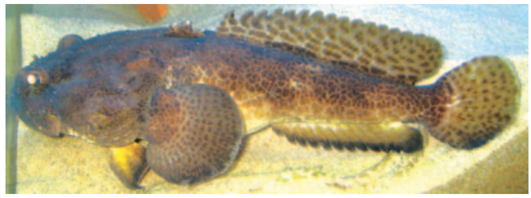


FIGURE 44. *Halobatrachus didactylus*. Photograph courtesy of T. Pereira.

FIGURE 45. *Halophryne hutchinsi*. Photograph courtesy of K. Atack, I. Larsen, and C. Lee.

FIGURE 46. *Perulibatrachus rossignoli*. Photograph courtesy of A. Oddgeir.

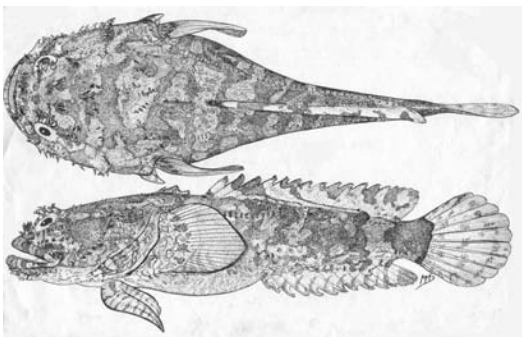


FIGURE 47. *Riekertia ellisi*. Drawing courtesy of P.C. Heemstra.

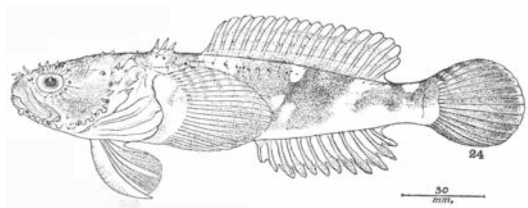


FIGURE 48. *Triathalassothia argentinus*. From Fowler (1943, figs. 23–25 of *T. devincenzii*).

H. ocellatus Hutchins, 1974; *H. queenslandiae* (DeVis 1882). Australia through New Guinea north to the Philippine Islands.

DIAGNOSIS.— A member of the subfamily Halophryninae lacking scales; no maxillary flaps; no axillary foramen or pocket; two subopercular spines and one filament; supraorbital tentacles present; gill opening clearly above lower margin of pectoral-fin base; head rounded with lower and upper jaws about equally terminal; eye diameter greater than snout length; interorbital width equal to or less than eye diameter; all bones of the branchial arches very slender.

MAJOR REFERENCES.— Hutchins (1976),Greenfield (1998).

Genus *Perulibatrachus* Roux and Whitley, 1972

Perulibatrachus Roux and Whitley, 1972, Bull. Mus. Natl. Hist. Nat. Zool. (6) [1971]:349. TYPE-SPECIES: *Batrachus elminensis* Bleeker, a replacement name for *Parabatrachus* Roux, 1971.

SYNONYMS.— *Parabatrachus* Roux.

SPECIES.— Four species: *P. aquilonarius* Greenfield, 2005; *P. elminensis* (Bleeker 1863); *P. kilburni* Greenfield, 1996; *P. rossignoli* Roux, 1957. West coast of Africa from Ghana south to Namibia; Natal, South Africa; and India.

DIAGNOSIS.— A member of the subfamily Halophryninae with scales; funnel-shaped pocket present on upper part of pectoral-fin axil; two subopercular spines and two filaments; no obvious tentacles above eyes.

Major references.— Roux and Whitley (1972), Roux (1981), Greenfield (1996, 2005).

Genus *Riekertia* Smith, 1952

Riekertia Smith, 1952, Ann. Mag. Nat. Hist., Ser. 12, 5: 325. Type-species: *Riekertia ellisi* Smith, 1952 by monotypy and original designation.

Synonyms.— None.

Species.— One species: *R. ellisi* Smith, 1952. South Africa.

Diagnosis.— A member of the subfamily Halophryninae with scales restricted to posterior half of body; a funnel-shaped pocket present on upper part of pectoral-fin axil; two subopercular spines and three filaments; accessory pectoral-fin radial totally ossified; prominent tentacles above eye; anterior nostril with large tuft of tentacles; anal-fin rays 15–17; pectoral fin without spots.

Major reference.— Smith (1952).

Discussion.— Although differing in osteological characters, *R. ellisi* is very similar externally to *Barchatus cirrhosus* from the Red Sea. Both species have very broad, depressed heads; a deep pit in the upper portion of the pectoral-fin axil with a venetian blind-like gland below; much glandular tissue on the body under the pectoral fin; three well developed cirri above the eye; patches of small cirri on the head behind the eye; and a body with scales. The only external differences between the two species are the extent of squamation on the sides of the body, the number tentacles on the anterior nostril, the number of anal-fin rays, and the pigmentation of the pectoral fin.

Genus *Triathalassothia* Fowler, 1943

Triathalassothia Fowler, 1943, Proc. Acad. Nat. Sci. Phila. 95:330. Type-species: *T. devincenzii* (= *T. argentina*) by original designation and monotypy.

Synonyms.— None.

Species.— Two species: *T. argentina* (Berg 1897); *T. lambaloti* Menezes and Figueiredo, 1998. Brazil and Argentina.

Diagnosis.— A member of the subfamily Halophryninae lacking scales; no maxillary flaps; no axillary foramen or pocket; one subopercular spine and two filaments; dorsal-fin rays 14–17; anal-fin rays 11–13; upper lateral-line pores 23–31; lower lateral-line pores 13–19; epaxial trunk musculature extending forward to cover entire dorsocranium behind orbits.

Major references.— Greenfield and Greenfield (1973), Menezes and Figueiredo (1998).

Osteology

Illustrations of the overall osteology are presented here, whereas illustrations of specific bones mentioned in various character states are presented in the Phylogenetic Analysis section. Most of the illustrations are of a paratype of *Potamobatrachus trispinosus*, USNM 330064, 48.0 mm SL, unless otherwise noted, and were drawn by S.G. Monden, with some enhancements by Greenfield and Winterbottom. Figures 49–59.

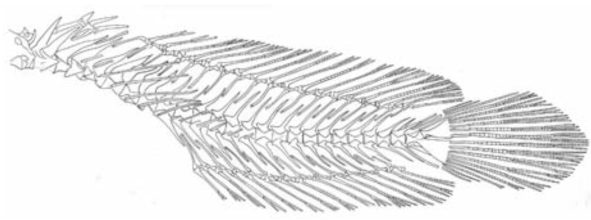


FIGURE 49. Axil skeleton of *Potamobatrachus trispinosus* (left lateral view).

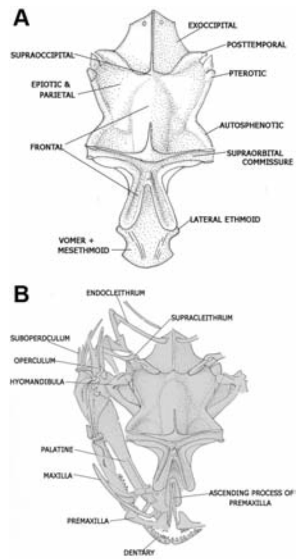


FIGURE 50. Dorsal view of head of *Potamobatrachus trispinosus*.

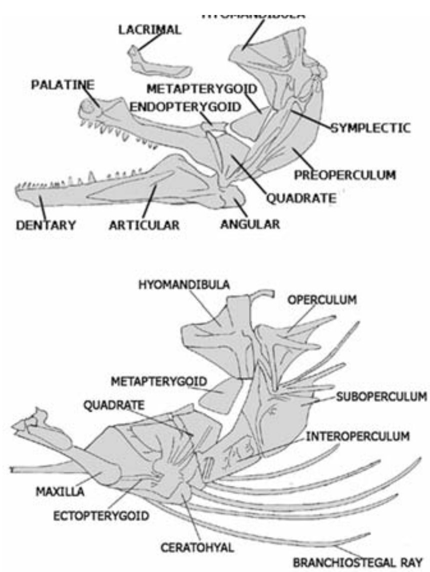


FIGURE 51. Schematic left lateral view of head skeleton of *Potamobatrachus trispinosus*, opercular series removed from upper figure.

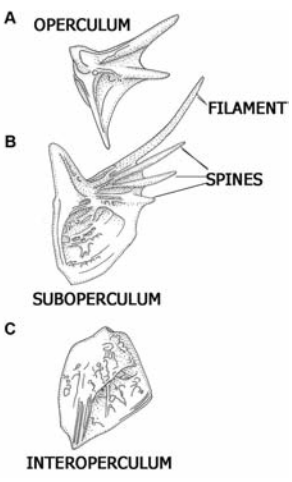


FIGURE 52. Opercular series of *Potamobatrachus trispinosus* (left lateral view).

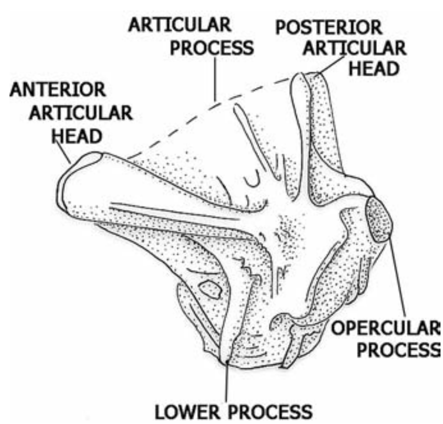


FIGURE 53. Hyomandibula of *Potamobatrachus trispinosus* (left lateral view).

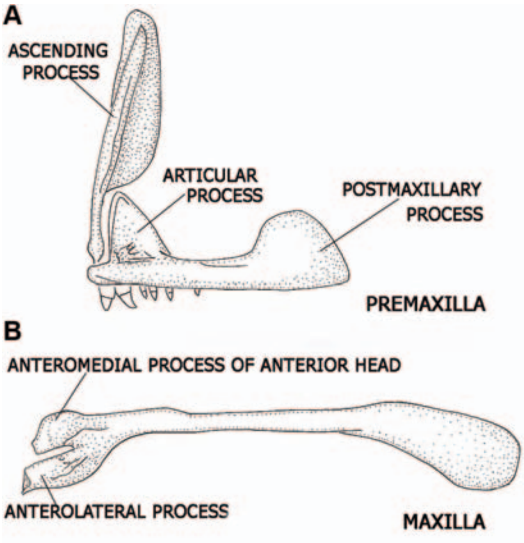


FIGURE 54. Maxilla and premaxilla of *Potamobatrachus trispinosus* (left lateral view).

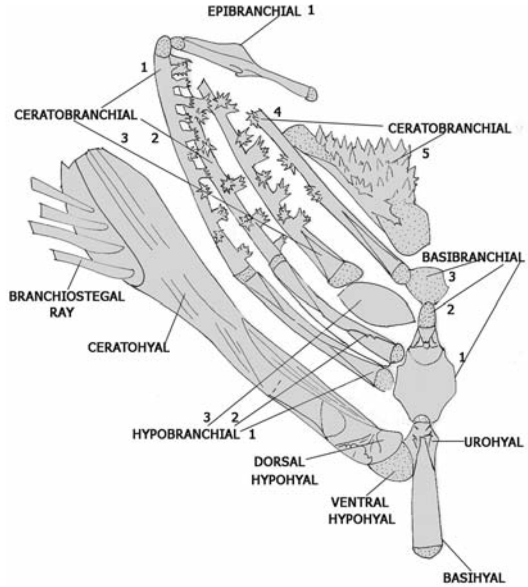


FIGURE 55. Branchial basket of *Potamobatrachus trispinosus* (left ventral portion in dorsal view; dorsal portion in ventral view).

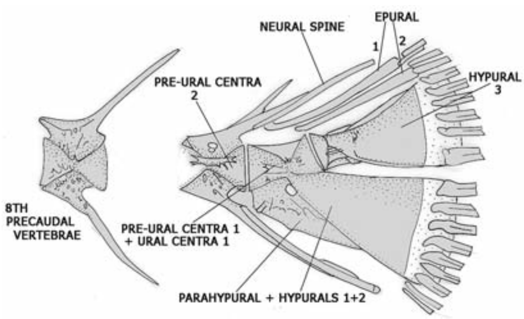


FIGURE 56. Caudal fin and eighth precaudal vertebrae of *Potamobatrachus trispinosus* (left lateral view).

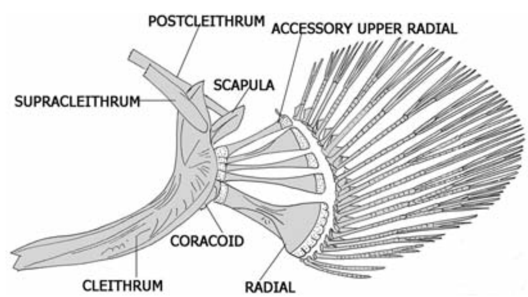


FIGURE 57. Pectoral girdle of *Potamobatrachus trispinosus* (left lateral view).

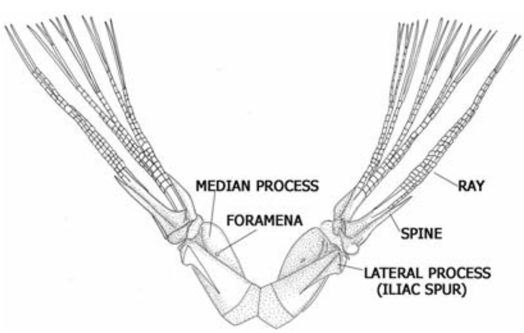


FIGURE 58. Pelvic girdle of *Potamobatrachus trispinosus* (left lateral view).

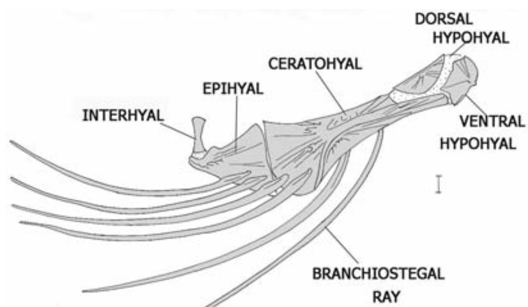


FIGURE 59. Hyoid apparatus of *Chatrabus hendersoni* SAIAB 8611 (left lateral view). Scale equals 1 mm.

Phylogenetic Analysis

The outgroup taxa chosen for the present analysis are discussed in the Methods section under Phylogenetic Analytical Methods. Many of the nodes in most of the trees are poorly supported (Bremer Support = 1), and the trees are poorly resolved. In almost all cases, there are numerous putative apomorphies (n) per node listed in the apomorphy list generated by PAUP, but the next most parsimonious tree(s) has(have) n-1 such apomorphies. We believe that these results are a function of the number of ingroup taxa (25) versus the number of informative characters in the data set (50). Consequently, we have chosen to present only the two most completely resolved trees here. These are the strict consensus trees using a) *Draconetta* and b) *Raniceps* + *Synchiropus* as the outgroups. We note, however, that several putative monophyletic subgroups appear in all, or many, of the total number of analyses conducted.

Toadfish Characters

Character Data Set

[1] Two dorsal-fin spines: 0 = no; 1 = yes.
[2] Dorsal-fin spines hollow: 0 = no; 1 = yes.
[3] Number of subopercular spines present: 0 = none; 1 = one; 2 = two; 3 = three.
[4] Scales present: 0 = absent; 1 = present.
[5] Upper accessory pectoral-fin radial cartilage: 0 = ossified; 1 = not ossified (Fig. 60).
[6] Medial suture between epihyal and ceratohyal: 0 = no; 1 = yes (Fig. 61).
[7] Foramina in skull behind eyes: 0 = no; 1 = yes (Fig. 62).
[8] Upper accessory pectoral-fin radial expanded and wide: 0 = no; 1 = yes (Fig. 60).
[9] Pectoral pore (foramina) in center of pectoral-fin axil: 0 = no; 1 = yes.
[10] Exposed bone on top of skull: 0 = no; 1 = yes (Fig. 14).
[11] Pectoral pore (foramina) top of pectoral-fin axil: 0 = no; 1 = yes (Fig. 8).
[12] Funnel-shaped pit at top of pectoral-fin axil: 0 = no; 1 = yes (Fig. 12).
[13] Ceratohyal width of expanded end equal to depth of center of ceratohyal: 0 = equal; 1 = greater.
[14] Ceratohyal at lower joint with epihyal square or round: 0 = square; 1 = round.
[15] Ceratohyal depth- depth into length of ceratohyal. 0 = 2.7; 1 = 5.3–6.4; 2 = 6.8–7.9; 3 = 8.0–8.9; 4 = 9.2–9.8; 5 = 10.6–11.9; 6 = 13.7–15.8.
[16] Maxillary flange: 0 = absent; 1 = present (Fig. 63).
[17] Maxilla bent and flange high and narrow at bend: 0 = present; 1 = absent (Fig. 64).
[18] Anterior pointing hook at distal end of maxilla: 0 = absent; 1 = present (Fig. 65).
[19] Length of premaxilla into length of maxilla: 0 = very short - 2.4–2.7; 1 = short - 2.0–2.1; 2 = medium - 1.5–1.9; 3 = long - 1.2–1.4.
[20] Shape of postmaxillary process on premaxilla: 0 = short, rounded, and symmetrical; 1 = short, rounded but not symmetrical; 2 = pointed (Fig. 66).
[21] Ascending process of premaxilla into premaxillary length: 0 = longer than premaxilla - 0.7–0.9; 1 = equal or slightly longer - 1.0–1.1; 2 = medium - 1.2–1.3; 3 = short - 1.4–2.1; 4 = very short - 4.0.
[22] Articular process of premaxilla: 0 = base wider than height; 1 = less than height.
[23] Ascending process of premaxilla, width into length: 0 = short and fat - 2.3; 1 = medium width - 4.5; 2 = slender - 6.0 and greater.
[24] Shape of articular head of maxilla: 0 = rounded; 1 = no gap between anterolateral and anteromedial process; 2 = anterolateral process long and pointed; 3 = a gap between the anterolateral

and anteromedial process (Fig. 67).

[25] Pelvic bone- foramina in median process: 0 = absent Figure 38); 1 = present (Fig. 58).

[26] Pelvic bone-distance of anterior point of median process to its joining place on pelvic bone divided into pelvic-bone length: 0 = none, connected entire length; 1 = short - 5.2–10.8; 2 = medium - 3.1–5.0; 3 = long - 2.1–2.9.

[27] Pelvic bone-length of median process divided into pelvic-bone length: 0 = long - 1.1; 1 = 1.2; 2 = 1.3; 3 = 1.4; 4 = 1.5; 5 = 1.6; 6 = 1.7; 7 = short - 1.9 or >.

[28] Hyomandibula: 0 = not rounded; 1 = rounded (Fig. 68).

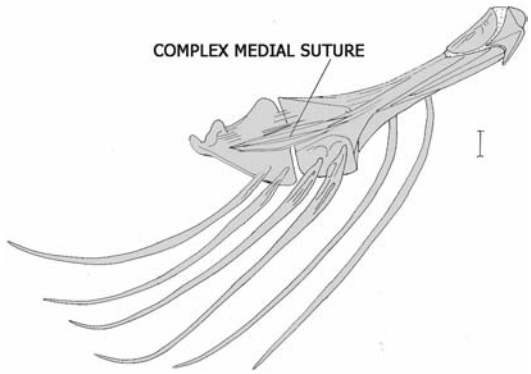


FIGURE 61. Hyoid apparatus of *Riekertia ellisi* SAIAB 12738 showing complex medial suture (left lateral view).

[29] Hyomandibula - angle of anterior articular head: 0 = anterior articular head angled up from a straight line across from opercular process;1 = anterior articular head in a straight line across from the opercular process (Fig. 68).

[30] Hyomandibula - lower process: 0 = square (Figure 68); 1 = round (Fig. 53).

[31] Angular - shape of distal end: 0 = slant posterior, about 65 degrees - bump and cup present; 1 = slant posterior, about 80–82 degrees - bump present; 2 = slant posterior, about 65 degrees - bump rounded; 3 = straight up no bump or cup; 4 = rounded and symmetrical; 5 = straight up- small bump sticks out; 6 = slants forward 98–103 degrees; 7 = slants more forward, 109–112 degrees, deep cup (Fig. 69).

[32] Lower jaw-joint of dentary and articular - dorsal side: 0 = dentary highest, pointed and triangular - often gap (Fig. 69C); 1 = dentary highest, but rounded; 2 = about equal height and rounded (Fig. 70A); 3 = dentary only at high point, articular reduced, triangular (Fig. 70B); 4 = dentary highest, and flat (Fig. 70C); 5 = articular higher, and pointed (Fig. 69A).

[33] Dentary shape: 0 = bent down with no tip (Fig. 69C); 1 = sharp bend down with obvious tip down at end (Fig. 70C); 2 = straight with obvious tip at end; 3 = straight, no tip at end; 4 = curved up (Fig. 69A).

[34] Extent of endopterygoid onto quadrate: 0 = extends well up onto or past quadrate (Fig. 71A); 1 = does not extend onto quadrate (Fig. 71B).

[35] Ectopterygoid attachment to quadrate: 0 = full anterior face attached (Fig. 71A); 1 = top notch on anterior face only (Fig. 71B).

[36] Quadrate shape: 0 = flat on top all the way across where it meets metapterygoid Fig. 71A); 1 = part flat at top, but is trangular shaped; 2 = top rounded, fan-like shape (Fig. 71B).

[37] Flange on anterodorsal face of metapterygoid; 0 = absent (Figure

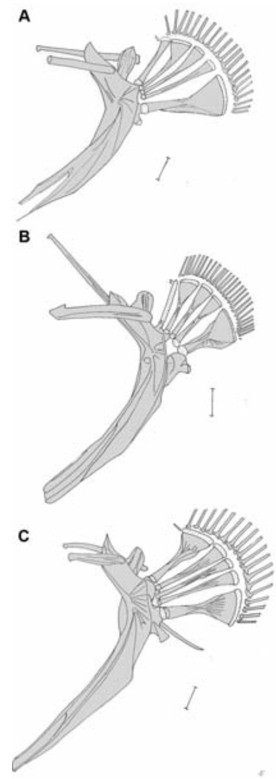


FIGURE 60. Upper accessory pectoral-fin radial character states (left lateral view). A. *Batrachoides gilberti* (FMNH 84549), fully ossified and not expanded; B. *Halobatrachus didactylus* (USNM 205066), not ossified and not expanded; C. *Porichthys notatus*, (CAS 223822), fully ossified and expanded. Scale equals 2 mm.

72B), 1 = present (Fig. 72A).

[38] Shape of dorsal end of metapterygoid: 0 = single head, straight up, no hook or bend; 1 = double head straight up (Fig. 72A); 2 = narrow club-shaped with slight anterior bend; 3 = sharp angle anteriorly and narrow (Fig. 71B); 4 = narrow sharp sickle-shaped point- anterior; 5 = small, broad anterior hook; 7 = anterior curve, multi points.

[39] Number of subopercular filaments: 0 = absent; 1 = one (Fig. 41); 2 = two (Fig. 41); 3 = three.

[40] Opercular spine number: 0 = two; 1 = one.

[41] Width into length of urohyal: long, 0 = 1.1 or >; 1 = short 1.0 or <.

[42] Hypobranchial III, number of heads: 0 = 2 heads (Fig. 73A); 1 = one head (Fig. 73B).

[43] Hypobranchial III, shape of anterior end: 0 = square (Fig. 74A); 1 = rounded (Fig. 74B); 2 = narrow point (Fig. 74C); 3 = wide point (Fig. 74D); 4 = reduced different from preceding (Fig. 74E).

[44] Hypobranchial I, shape of narrower anterior end: 0 = flat (Figure 75A); 1 = spine (Fig. 75B).

[45] Epibranchial I, length of uncinate process compared to length of proximal end of epibranchial (where pharyngobranchial I would attach) measured from base of uncinate process: 0 = distal end of epibranchial longer than uncinate process; 1 = both symmetrical; 2 = uncinate process twice as long as distal end of epibranchial; 3 = same as 2, but with no bump-like expansion on medial side of epibranchial; 4 = distal end of epibranchial very short and directed towards pharyngobranchial II, and uncinate long and straight; 5 = distal end of epibranchial very short, but directed laterally, and uncinate long and straight; 6 = distal end of epibranchial pointed towards ceratobranchials, and uncinate long and straight.

[46] Sphenotic shape on side of skull; 0 = cut in towards center of skull (Fig. 76A); 1 = straight and flat (Fig. 76B).

[47] Interorbital width divided by skull width at sphenotics: 0 = narrow, 5.1–7.5; 1 = medium, 3.4–5.0; 2 = wide, 1.1–3.3.

[48] Skull width at sphenotics into length: 0 = wide - 1.3–1.5; 1 = narrower- 1.6 or > .

[49] Comparison of length of skull in front of sphenotics to length in back: 0 = front greater than back, 1 = front equals back, 2 = front less than back.

[50] Caudal fin- shape of parhypural: 0 = anteroventral surface flat against neural spine for short distance and then up posteriorly abruptly; 1 = anteroventral surface broad, gentle, concave curve; 2 = anteroventral surface broad, gentle, convey curve up to anterior bend; 3 = anteroventral surface gently concave with double points at bend; 4 = anteroventral surface short and rounded with single spine, parhypural very narrow; 5 = anteroventral surface straight to slightly concave, parhypural very narrow, almost missing; 6 = anteroventral surface with radiating spines.

The data set is presented with character distributions in tabular form in Table 1.

Results.— The two consensus trees are given in Fig. 77 (*Draconetta* as outgroup – hereafter referred to as 'D') and Fig. 78 (*Raniceps* + *Synchiropus* as outgroups –'RS'). Figure 79 gives the visual concensus of these two trees. Several clades are present in both trees. In the ensuing discussion, putative apomorphies (hereafter referred to as 'PAs') in both PAUP analyses are listed along with the character state changes at that node. Unambiguous synapomorphies are referred to as unreversed, or listed with a CI of 1. References to the characters in the character data set list above will be referred to as '# X'.

The uppermost clade in the figures links six of the ten New World taxa, *Opsanus* through *Vladichthys*, in a monophyletic group. The D analysis lists four PAs supporting the clade, the RS has five. While there are no characters common to the two lists, the change in state of # 32 in the

TABLE 1. Data Matrix for Toadfish taxa with *Raniceps*, *Synchiropus* and *Draconetta* as outgroups

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Amphichthys cryptocentrus	0	0	1	0	0	1	0	0	0	1	0	0	1	0	2	1	0	0	0	0	0	0	2	1	1	0	0	0	1	1	4	2	3	0	0	0	1	0	1	1	0	1	2	0	3	1	1	1	1	2
Aphos porosus	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	3	2	3	1	2	2	1	0	1	0	0	0	5	5	2	0	0	0	1	5	2	0	0	1	3	0	2	0	1	0	0	6
Daector reticulata	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	2	1	1	0	2	1	1	1	7	5	4	0	0	0	1	0	2	0	0	1	3	0	5	0	0	0	0	3
Batrachoides gilberti	0	0	2	1	0	1	0	0	0	0	0	0	1	1	5	1	0	0	0	1	0	0	2	1	1	0	0	0	1	1	4	2	3	0	0	0	1	4	1	1	0	1	2	0	2	0	1	1	1	0
Opsanus tau	0	0	1	0	0	1	0	0	1	0	0	0	1	1	4	1	0	0	1	0	0	0	2	1	1	0	0	0	0	1	4	2	3	0	0	0	1	1	1	1	0	1	2	0	2	0	1	1	0	4
Potamobatrachus trispinosus	0	0	3	0	0	1	0	0	0	0	0	0	1	1	2	0	0	0	2	1	1	0	1	3	1	0	0	0	1	1	4	2	3	0	0	0	1	0	1	1	0	1	2	0	5	0	2	1	1	2
Porichthys notatus	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	3	2	3	1	2	2	1	0	2	0	0	0	5	5	2	0	0	1	1	5	2	0	1	1	3	0	2	0	1	0	0	6
Sanopus barbatus	0	0	1	0	0	1	0	0	1	1	0	0	1	1	2	1	0	0	1	0	1	0	2	1	1	0	0	0	1	1	4	2	3	0	0	0	1	1	1	1	0	1	2	0	2	1	2	1	1	2
Thalassophryne megalops	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	2	0	2	1	1	0	1	1	0	1	7	5	4	0	0	0	1	0	2	0	0	0	2	0	5	0	0	0	2	2
Vladichthys gloverensis	0	0	1	0	0	1	0	0	0	1	0	0	1	0	3	1	0	0	1	0	1	0	2	1	1	0	2	0	1	1	4	2	3	0	0	0	1	7	1	1	0	1	2	0	1	1	1	1	2	0
Triathalassothia argentinus	0	0	1	0	1	0	0	0	0	0	0	0	1	0	4	0	0	0	2	2	2	0	2	3	0	2	4	0	0	0	0	0	0	0	0	1	1	6	2	1	0	1	1	1	1	0	0	0	0	2
Allenbatrachus grunniens	0	0	2	0	0	1	1	0	0	0	0	0	1	0	5	1	0	0	1	1	0	0	2	3	0	2	5	0	1	0	6	3	2	1	1	1	1	0	1	1	1	0	0	0	1	0	2	1	2	0
Austrobatrachus foedus	0	0	1	0	1	1	0	0	0	0	0	1	1	0	3	0	0	0	2	2	3	0	2	3	0	3	3	0	1	0	1	0	1	1	1	2	0	3	2	1	1	1	1	1	4	0	1	0	2	1
Barchatus cirrhosus	0	0	2	0	0	1	0	0	0	0	0	1	1	0	3	0	0	0	2	2	3	0	2	3	0	3	3	0	1	0	6	0	2	1	1	2	0	3	2	1	1	1	2	1	4	0	1	0	0	5
Riekertia ellisi	0	0	2	0	1	1	0	0	0	0	0	1	1	0	3	0	0	0	2	2	1	0	2	3	0	3	1	0	1	0	6	0	2	1	1	2	0	3	3	1	1	1	0	1	4	0	1	0	0	5
Batrachomoeus trispinosus	0	0	1	0	0	1	1	0	0	0	1	0	1	0	2	1	0	0	2	1	1	0	2	3	0	1	7	0	0	0	6	3	2	1	1	1	1	4	1	1	0	1	2	0	6	0	1	0	2	0
Chatrabus felinus	0	0	2	0	0	0	0	0	0	0	0	0	1	0	3	0	0	1	2	2	3	0	2	3	0	1	6	0	0	0	1	0	2	1	1	2	0	4	2	1	1	1	2	1	2	0	0	0	0	0
Batrichthys apiatus	0	0	2	0	1	0	0	0	0	0	0	0	1	0	5	0	0	0	2	2	3	0	2	0	0	3	2	0	1	0	1	1	1	1	0	2	0	3	1	1	0	1	2	1	2	0	1	0	2	5
Bifax lacinia	0	0	2	0	0	1	0	0	0	0	0	0	1	0	5	0	0	0	2	2	2	0	2	3	0	2	4	0	1	1	4	0	2	1	1	2	0	2	1	1	1	1	2	0	4	0	2	0	2	0
Chatrabus hendersoni	0	0	2	1	0	0	0	0	0	0	0	0	1	0	3	0	0	1	2	2	1	0	2	3	0	2	4	0	1	0	1	0	1	1	1	2	0	3	3	1	1	1	2	1	2	0	0	0	0	1
Chatrabus melanurus	0	0	2	1	0	0	0	0	0	0	0	0	1	0	3	0	0	1	2	2	2	0	2	3	0	3	7	0	1	0	1	0	1	1	1	2	0	3	3	1	1	1	2	1	2	0	0	0	0	1
Colletteichthys dussumieri	0	0	2	0	0	1	0	0	0	0	0	1	1	0	6	0	0	0	2	1	2	0	2	3	0	2	5	0	0	0	6	0	2	1	1	2	0	3	2	1	1	1	2	1	4	0	0	0	0	0
Halobatrachus didactylus	0	0	1	1	1	1	0	0	0	0	1	0	1	0	4	0	0	0	2	2	2	0	2	3	0	3	3	0	0	0	3	4	1	1	1	2	0	3	2	1	1	1	1	1	4	0	1	0	0	3
Halophryne diemensis	0	0	2	0	0	1	1	0	0	0	0	0	1	0	4	0	0	0	0	2	0	0	2	0	0	2	6	0	1	1	2	3	2	1	1	1	1	0	1	1	1	1	4	0	1	0	0	0	0	0
Perulibatrachus elminensis	0	0	2	1	1	1	0	0	0	0	0	1	1	0	5	0	0	0	2	2	3	0	2	3	0	3	2	0	1	0	3	4	1	1	1	2	0	2	2	1	1	0	0	0	4	0	2	0	2	0
Synchiropus atrilabiatus	0	0	0	0	-	0	0	-	0	0	0	0	1	0	1	0	0	0	3	1	0	0	2	3	0	0	4	0	1	0	0	0	1	1	0	?	1	?	1	?	0	1	0	0	4	0	0	0	0	2
Raniceps raninus	0	0	0	1	-	0	0	-	0	0	0	0	1	0	0	0	0	0	3	1	4	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
Draconetta oregona	0	0	1	0	-	0	0	-	0	0	0	0	1	1	5	0	1	0	3	2	0	1	1	3	1	0	0	0	0	0	6	1	1	1	1	2	0	0	1	1	0	1	1	1	4	0	0	1	0	4

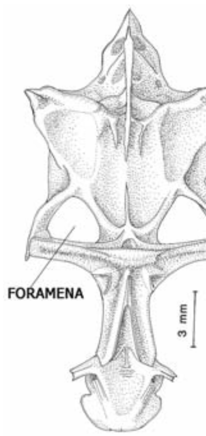


FIGURE 62. Foramina in dorsocranium of *Allenbatrachus reticulatus* CAS-SU 30658.

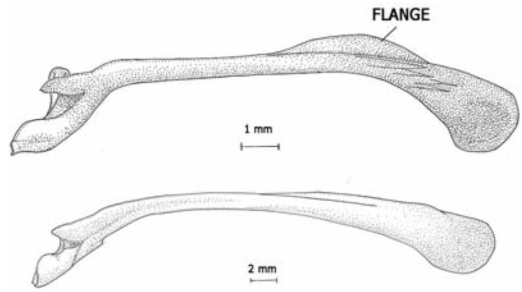


FIGURE 63. Maxilla of – A. *Allenbatrachus grunniens* CAS-SU 26909 with flange; B. *Trithalassothia argentinus* USNM 214438 without flange (left lateral view).

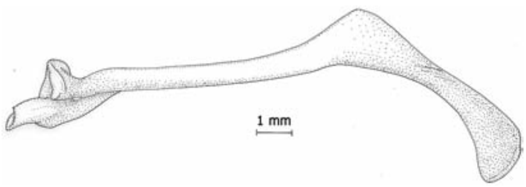


FIGURE 64. Maxilla of *Thalassophryne maculosa* USNM 199524 with bend and flange (left lateral view).

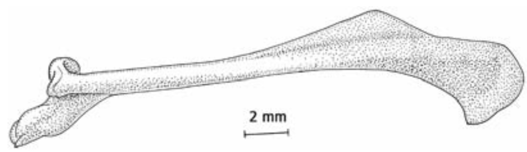


FIGURE 65. Maxilla of *Vladichthys gloverensis* FMNH 91036 with distal hook (left lateral view).

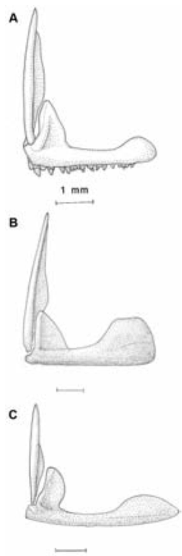


FIGURE 66. Shape of postmaxillary process of premaxilla (left lateral view). A. *Amphichthys cryptocentrus* USNM 144888, short, rounded, and symmetrical; B. *Batrachoides gilberti* FMNH 84549, short, rounded, but not symmetrical; C. *Batrichthys apiatus* SAIAB 75-25, pointed.

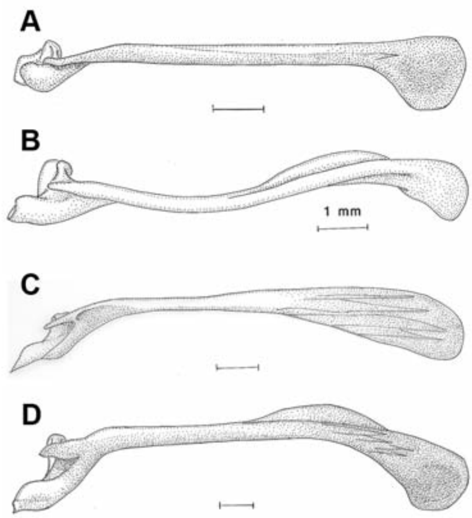


FIGURE 67. Shape of articular head of maxilla (left lateral view). A. *Batrichthys apiatus* SAIAB 75-25, rounded; B. *Amphichthys cryptocentrus* USNM 144888, no gap between anterolateral and anteromedial process; C. *Aphos porosus* CAS 65051, anterolateral process long and pointed; D. *Allenbatrachus grunniens* CAS-SU 26909, gap between anterolateral and anteromedial process.

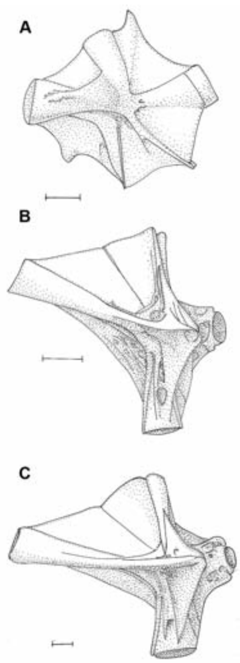


FIGURE 68. Hyomandibula (left lateral view). A. *Daector reticulata* GCRL 16194, rounded; B. *Halobatrachus didactylus* USNM 205066, not rounded, anterior articular head angled up; C. *Perulibatrachus elminensis* MNHN 1970-43, not rounded, anterior articular head straight across. Scale equals 1 mm.

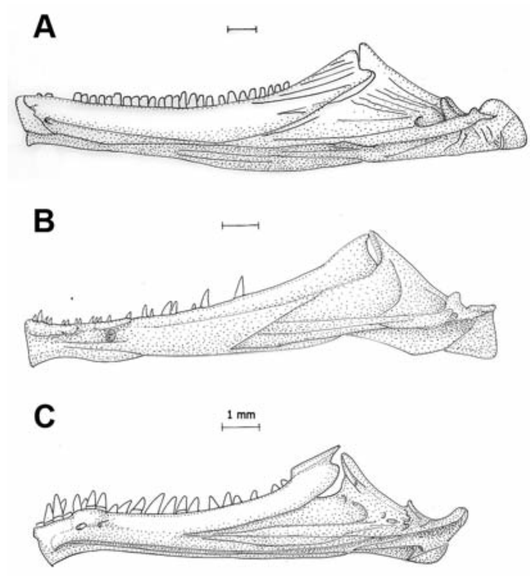


FIGURE 69. Orientation of distal end of angular (left lateral view). A. *Thalassophryne maculosa* USNM 199524, anterior; B. *Aphos porosus* CAS 65051, straight up; C. *Triathalassothia argentinus* USNM 214438, posterior.

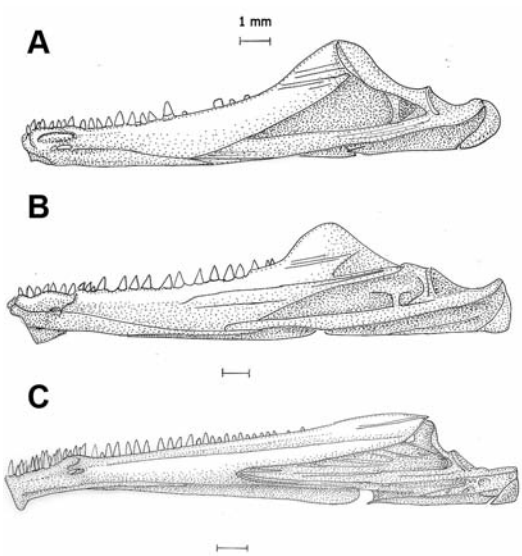


FIGURE 70. Dorsal joint of dentary and articular (left lateral view). A. *Opsanus tau* CAS 223821, equal height and rounded; B. *Allenbatrachus grunniens* CAS-SU 26909, dentary only at high point, articular reduced, triangular; C. *Halobatrachus didactylus* USNM 205066, dentary highest and flat.

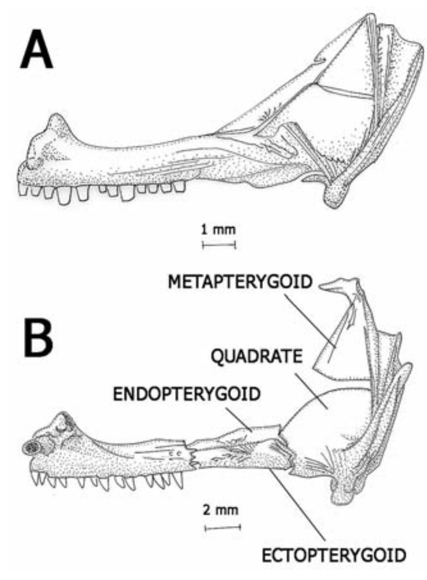


FIGURE 71. Extent of endopterygoid onto quadrate (left lateral view). A. *Amphichthys cryptocentrus* USNM 144888, extends well up onto or past quadrate; B. *Riekertia ellisi* SAIAB 12738, does not extend onto quadrate.

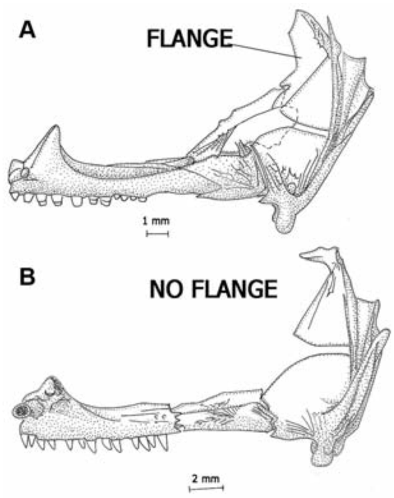


FIGURE 72. Metapterygoid flange (left lateral view). A. *Sanopus barbatus* SIO 6745, flange present; B. *Riekertia ellisi* SAIAB 12738, no flange.

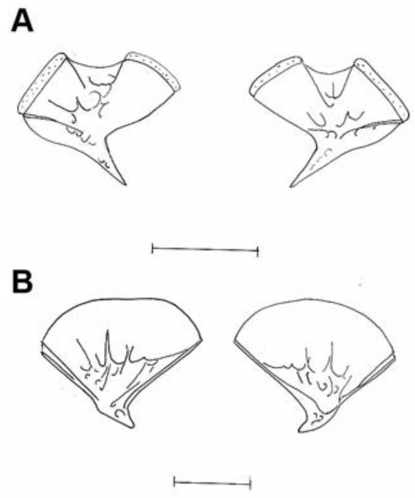
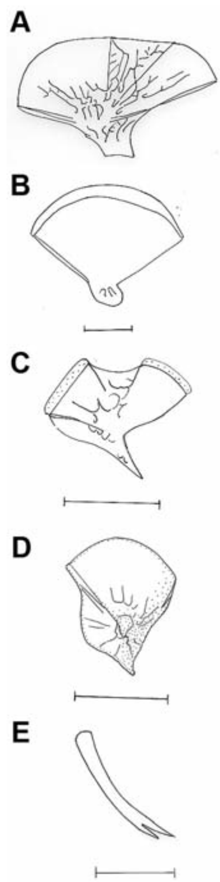


FIGURE 73. Hybobranchial III, number of heads (dorsal view of left side on right side of plate, ventral view on right side of plate). A. *Thalassophryne maculosa* USNM 199524, two heads; B. *Chatrabus felinus* SAIAB 75-25, one head. Scale equals 1 mm.



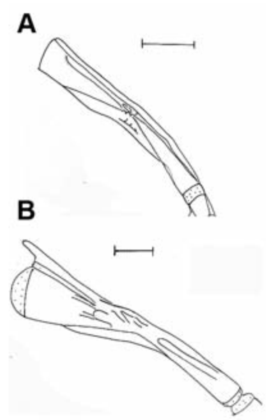


FIGURE 75. Hypobranchial I, shape of anterior end. (Dorsal view of right side). A. *Amphichthys cryptocentrus* USNM 144888, flat; B. *Chatrabus hendersoni* SAIAB 8611, spine. Scale equal 1 mm.

FIGURE 74. Hypobranchial III, shape of anterior end (left ventral view). A. *Perulibatrachus elminensis* MNHN 1970-43, square; B. *Triathalassothia argentnius* USNM 214438, rounded; C. *Thalassophryne maculosa* USNM 199524, narrow point; D. *Aphos porosus* CAS 65051, wide point; E. *Halophryne diemensis* NTMS 10005-019, reduced.

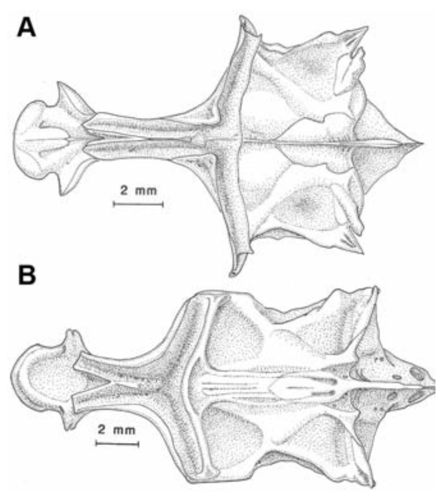


FIGURE 76. Autosphenotic shape on side of dorsocranium. A. *Chatrabus felinus* SAIAB 75-25, cut in towards center of skull; B. *Vladichthys gloverensis* FMNH 91036, straight and flat.

RS analysis is an unreversed synapomorphy for the clade (state 5→2). In both analyses, *Opsanus* is the first taxon to diverge, and is autapomorphic based on four character states, three of which are shared. These are the homoplastic states of #9 and #38 (both 0→1) and the unreversed state of # 50 (2→4). The remaining five genera share two putative homoplastic apomorphies in both analyses (#s 29 and 49, both 0→1). *Batrachoides*, the next taxon to diverge, is defined by the same five putative synapomorphies in both analyses, # 3 (1→2), # 4 (0→1), # 19 (1→0), # 38 (0→4) and # 50 (2→0). The four remaining taxa share two PAs in the D analysis, and one in the RS. One of these is shared between the two trees - #21 (0→1). Both analyses find *Potamobatrachus* as sister to the remaining three taxa, and defined by the same six autapomorphic states. These are # 3 (1→3), # 16 (1→0), # 19 (1→0), # 23 (2→1), # 24 (1→3), and # 45 (2→5). Of these, both analyses recognize # 3 as an unreversed autapomorphy (CI = 1) and # 23 is also accorded this status in the RS list. The other three taxa are defined by two unreversed synapomorphies in both analyses: # 10 (0→1) and # 46 (0→1), and a further homoplastic PA is listed by the RS. *Sanopus* is defined by two homoplastic states (# 9, 0→1, # 38, 0→1). *Amphichthys* and *Vladichthys* are sister groups based on a single homoplastic character state (# 14, 0→1). Two autapomorphies define *Amphichthys* (# 19, 1→0, # 21, 1→0). *Vladichthys* has five autapomorphies: # 15 (2→3), # 27 (0→2), # 38 (0→7), # 49 (1→2), and # 50 (2→0), of which only # 38 has a CI = 1.

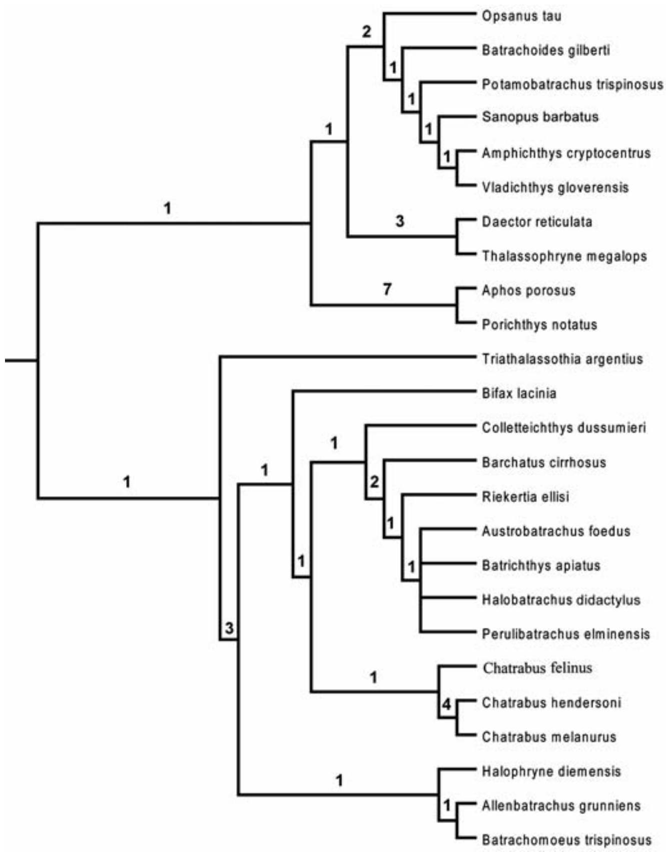


FIGURE 77. Strict consensus tree with *Raniceps* and *Synchiropus* as outgroups. Numbers above the lines represent Bremmer Support Values.

Both analyses recognize *Aphos* and *Porichthys* as a monophyletic group based on seven putative synapomorphies, six of them common between them. These are: # 8 (0→1, CI = 1); # 13 (1→0, CI = 1); # 21 (2→3 in D, 0/2→3 in RS); # 22 (0 →1, homoplastic in D but unreversed in RS); # 38 (0→5, CI = 1); and # 50 (2→6, CI = 1). The D analysis also lists # 30 (0→1), and the RS lists # 43 (2→3). Two autapomorphies are listed in both analyses that define *Porichthys*, but both exhibit homoplasy (# 36 (0→1) and # 41 (0→1). None are given for *Aphos*. Similarly, both analyses recognize *Daector* and *Thalassophryne* as sister taxa. In the D analyses, the group is defined by eight putative synapomorphies, and three of these are unreversed: # 2 (0→1, CI = 1), # 16 (0→1), # 17 (0→1), # 20 (2→1), # 28 (0→1, CI = 1), # 30 (0→1), # 33 (2→4, CI = 1), and # 45 (2→5). The RS analysis list four of the above, three of which are unreversed (#'s 2, 17, 28 and

45, with # 17 now interpreted as unreversed).

Fifteen taxa comprise the Old World sampling, and the trees from the two analyses are identical (although the support may not be). The D analysis lists six putative synapomorphies supporting the monophyly of this group: # 14 (1→0), # 19 (1/3→2), # 25 (1→0, CI = 1), # 26 (0→2), # 36 (0→1), and # 45 (2→1). The RS lists four such characters, three of which also occur in the D analysis: (# 19 (3→2), # 26 (0→2), # 36 (0→1), and # 40 (0→1). *Triathalassothia* forms the sister group to the other 14 taxa, and is defined in the D tree seven autapomorphies: # 5 (0→1), # 6 (1→0), # 15 (5→4), # 31 (6→0, CI = 1), # 33 (2→0, CI = 1), # 38 (0→6, CI = 1), and # 44 (0→1). There are four such character states given in the RS: #'s 5, 38 and 44 as above, and # 43 (2→1). Six putative synapomorphies, none unreversed, define the remaining taxa in both trees. In D, these are: # 3 (1→2), # 29 (0→1), # 34 (0→1), # 35 (0→1), # 41 (0→1), and # 50 (2→0). The list is the same for RS, except that # 3 drops away, and # 31 (0→6) is added. There are two monophyletic subgroups in the remaining 14 taxa. *Allenbatrachus*, *Batrachomoeus* and *Halophryne* form a clade, based on # 7 (0→1, CI = 1), # 21 (2→0), and # 32 (0→3, CI = 1) in the D analysis and #s 7 and 32 in the RS. The sister group to this, the remaining taxa, is defined by three character states in the D: # 36 (1→2), # 37 (1→0) and # 45 (1→4) and by the first two in the RS, in which # 36 is unreversed. In the first clade, the first two genera form a monophyletic group based on three homoplastic character states in both analyses: # 16 (0→1), # 20 (2→1) and # 49 (0→2). *Halophryne* is defined by six autapomorphies in the D analysis: # 15 (5→4), # 19 (2→0), # 24 (3→0), # 30 (0→1), # 31 (6→2) and # 43 (2→4) and by five of the same states (# 15 absent) in the RS. Character states # 31 and # 43 have a CI of one. In both analyses, *Allenbatrachus* is characterized by four homoplastic autapomorphies: # 19 (2→1), # 42 (1→0), # 43 (2→0), and # 48 (0→1). *Batrachomoeus* is defined by eight autapomorphies in both hypotheses: # 3 (2→1), # 11 (0→1), # 21 (0→1), # 26 (0→1), # 29 (1→0), # 38 (0→4), # 41 (1→0) and # 45 (1→6, CI = 1). In addition, the D analysis lists # 15 (5→2).

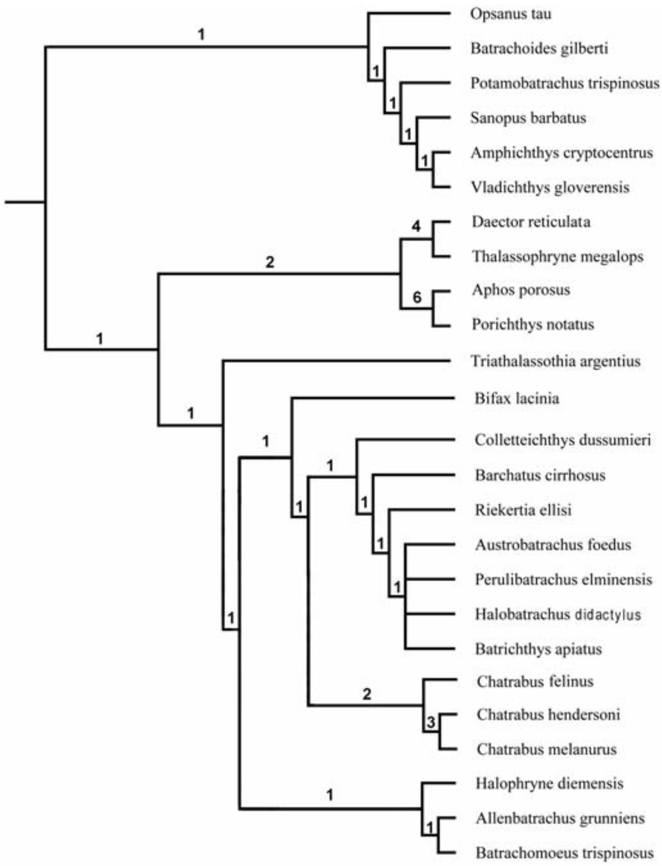


FIGURE 78. Strict consensus tree with *Draconetta* as outgroup. Numbers above the lines represent Bremmer Support Values.

The remaining clade of 11 entities is divided into *Bifax* (autapomorphies in both analyses: # 30 (0→1), # 31 (6→4), # 47 (0→2) and # 49 (0→2), and the remaining 10 taxa, defined by two homoplastic states (# 15, 5→3, and # 44, 0→1) in the D analysis and by only the second of these

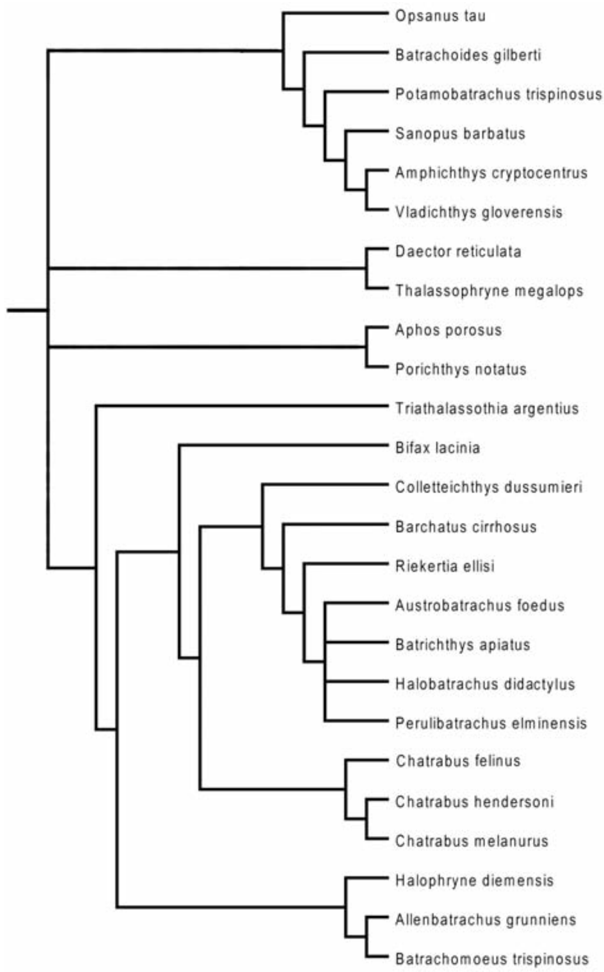


FIGURE 79. Visual consensus tree of figures 77 and 78.

in the RS. This clade is divided into two monophyletic subsets, one containing the two species of *Chatrabus* plus *Pseudobatrichthys* and the other the remaining taxa. The former is defined by the same four putative synapomorphies in both analyses: # 6 (0→1), # 18 (0→1, CI = 1), # 31 (6→1), and # 45 (4→2). Both analyses list the same five autapomorphies for *Pseudobatrichthys* (# 21, 2→3, # 26, 2→1, # 27, 4→6, # 29, 1→0, and # 38 3→4), and four putative synapomorphies for the two species of *Chatrabus* (# 4, 0→1, # 33, 2→1, # 39, 2→3, and # 50, 0→1). *Chatrabus melanurus* has two autapomorphies (# 26, 2→3, and # 27, 4→7) and *C. hendersoni* one (# 21, 2→1). Within the remaining clade, *Colletteichthys* (# 15, 3→6, CI = 1, # 20, 2→1, and # 29, 1→0) is the sister group to the remaining six taxa (# 26, 2→3, # 47, 0→1, and # 50, 0→5) in both analyses. *Barchatus* (no autapomorphies) is the sister group to the last five taxa, which are united by a single, homoplastic character state (# 5, 0→1). *Riekertia* is defined by three homoplastic character states (# 21, 2/3→1, # 27, 3→1, and # 39, 2→3), and the remaining four taxa form a group also based on three putative but homoplastic synapomorphies: # 31 (6→1), # 33 (2→1), and # 49 (0→2). No further resolution of these four genera was present in either analysis.

DISCUSSION.— In addition to the two trees detailed above, eight other analyses were performed with the following outgroups or combinations of outgroups selected from the potential taxa mentioned under Phylogenetic Analytical Methods: *Draconetta*, *Ogilbia*, *Raniceps*, and *Synchiropus* (here abbreviated to the first letter of the taxon name): O only, R only, S only, D + R, D + S, D + S + R, O + R + S, and O + S. The trees vary considerably in resolution, from almost completely resolved (e.g. S as outgroup) to almost no resolution (e.g. D + R as outgroups). Figure 80 gives the R + S tree with the number of trees congruent with the node separated by a "/" from the total number of trees that were informative about that node. There are three contentious nodes. The New World (NW) taxa, with the exception of *Triathalassothia*, form a monophyletic clade in the R + S tree and in a total of five of the six analyses for which information about this node is present (Fig. 80). The only analysis which disagrees with this is the D tree, which places ((*Daector* + *Thalassophryne*) + (*Aphos* + *Por-ichthys*)) as the sister group to the Old World (OW) taxa. The second disagreement involves the sister group status of the two pairs of genera above, which is found in two of the eight trees with information on this node. The R + S tree forms part of a group of six of the eight informative trees in which *Aphos* + *Porichthys* forms the sister group to the rest of the NW taxa (as defined above), and *Daector* + *Thalassophryne* forms the sister group to remaining six NW taxa. The final incongruence is in the tree generated using S as the only outgroup, which places *Triathalassothia* as the basal taxon of the NW taxa. While this results in congruence with other NW taxa, four of the other analyses have this genus in a basal tri- or poly-chotomy, and are thus uninformative; the other five all place it as the basal taxon to the rest of the OW taxa. *Triathalassothia* is located on the southeastern coast of South America, closer geographically to other OW taxa in Africa than any of the NW taxa.

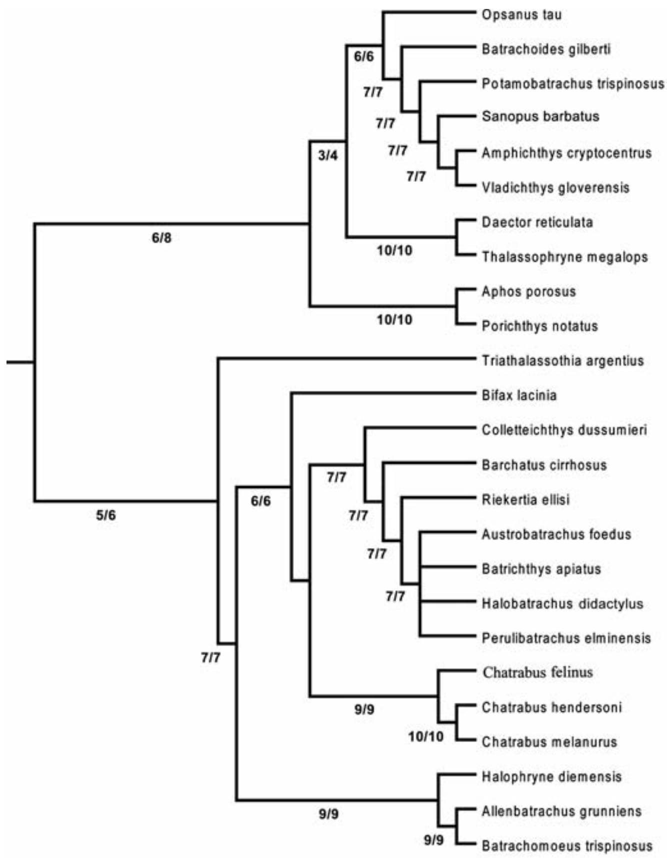


FIGURE 80. *Raniceps*/*Synchiropus* consensus tree with % congruence with other trees.

It must be stressed here that, despite the congruence of numerous trees based on different outgroups (or combinations thereof), most of the nodes are poorly supported by the available evidence (see Bremer Support indices in Figs. 77 and 78). This is especially true in the basal portions of the trees, and is further compromised by the fact that most of the supporting character states for these nodes exhibit a disturbing amount of homoplasy (occasionally as low as CI = 0.125). Despite this, the perfect congruence for those analyses yielding information for all the nodes except those discussed above is perhaps suggestive.

The only published phylogenetic reconstruction with information pertinent to toadfish intrarelationships is that of Smith and Wheeler (2006). They included representatives of six genera of toadfishes as part of a much broader study of acanthomorphs. Their results indicate that the OW taxa are paraphyletic with respect to a monophyletic NW group, and that this latter grouping exhibits a different structure from any of those developed in our analyses. The relationships they found can be expressed as (*Perulibatrachus* (*Allenbatrachus* (*Porichthys* (*Opsanus* (*Thalassophryne*, *Daector*))))). We do not explore this hypothesis further, other than to suggest that a possible reason for the discrepancy may be due to taxon sampling (6 vs. our 25), and to express some concerns regarding the validity of the implied alignments generated by the POY algorithm they used.

In summary, we believe our results as presented in Fig. 79 represent the best hypothesis of toadfish relationships available to date. We are also inclined to accept that (*Daector* + *Thalas-*

sophryne) and (*Aphos* + *Porichthys*) nest with the remaining NW taxa, although whether this is as a monophyletic sister group to them, or as sequential sister groups is unclear.

We remain uncertain as to the relationships of *Triathalassothia* because the basal batrachoid relationships are so weakly supported and because of its South American provenance. However, because five of the six informative trees place it basal to the OW taxa, with which it shares a number of character states not found in any of the NW taxa, we have placed it in that clade in our classification. We recommend the retention of the existing supra-specific taxonomy for the subfamilies Porichthyinae and Thalassophryninae, restricting the use of the Batrachoidinae to the six NW genera in the *Opsanus* – *Vladichthys* clade, erecting a new subfamily for the OW taxa (Halophryninae), and leaving *Triathalassothia* as *incertae sedis* until reliable information on its phylogenetic position becomes available.

Biogeographical Relationships

A key factor in the biogeography of any group of organisms is their ability to disperse from one geographic area to another, which in turn, is related to their mode of reproduction and dispersal. Toadfishes have demersal eggs that are laid in a nest that is guarded by the male. After hatching, unlike most other demersal spawners, the larvae do not move up into the water column to disperse, but rather stay attached to the substratum until most of the yolk sac has been absorbed, at a size of about 12 to 16 mm total length (Gill 1907; Collette 2005) (Fig. 81).

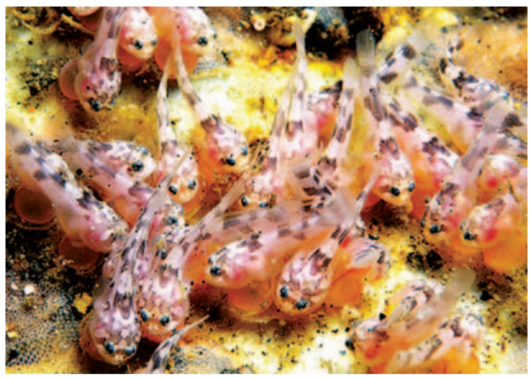


Figure 81. Larval *Thalassophryne maculosa*, Cubuga, Venezuela. Photograph courtesy of P. Humann.

This greatly reduced dispersal ability should increase the probability for genetic isolation between those individuals that manage to disperse some distance and form a founding population and those in the original population. The results of such potential isolation can be seen in some toadfish genera such as *Sanopus,* where the species have rather limited distributions. *Sanopus* has six species, all occurring in the tropical western Atlantic. *Sanopus reticulatus* is known only from Progresso on the northern coast of Yucatán, Mexico, *S. johnsoni* and *S. splendidus* are known only from Isla Cozumel off the east coast of Yucatán, Mexico, *S. greenfieldorum* and *S. astrifer* are both only known from Belize, but *S. greenfieldorum* is only known from the barrier reef, and *S. astrifer* only from the atolls about 10—20 kilometers farther off shore. *Sanopus barbatus* ranges from southern Belize south to Panama (Collette 2003). Adding to the limited distribution of species in this area, *Vladichthys gloverensis* is only known from the barrier reef and atolls of Belize and the adjacent Bay Islands of Honduras.

Species of *Opsanus* in the western Atlantic also show limited distributions; *Opsanus tau* ranges from the Gulf of Maine south to Florida; *O. pardus* occurs along part of the western coast of Florida in the Gulf of Mexico; *O. beta* is found from Florida through the Gulf of Mexico to Belize; *O. phobetron* ranges from the Bahamas to northern Cuba, and *O. dichrostomus* is found from the southwestern coast of Cuba to the Yucatán Peninsula and Belize. Avise et al. (1987) used mitochondrial DNA to evaluate the population-genetic structures of two *Opsanus* species, *O. tau* and *O. beta*. They found that, even within the relatively limited geographic distributions of these two species, significant mtDNA structure was present, with *O. tau* divided into northern and southern genetic forms, and *O. beta* into Florida and Mississippi-Louisiana populations. They further stated that the divergence values in toadfishes were slightly greater than those found for restricted geographic assemblages of freshwater fish populations. As discussed earlier under genus *Opsanus*, the validity of a disjunct species of *Opsanus* in Brazil (*O. brasiliensis*) is doubtful.

The genus *Thalassophryne* along the Atlantic coast of South America demonstrates a series of species replacements going from north to south: *T. megalops*, *T. maculosa*, *T. nattereri, T. punctata*, and *T. montevidensis* (Collette 1966).

In the Pacific Ocean the species in the genus *Porichthys* show a pattern of species replacement from the north in Canada south to Ecuador with minimal overlap (Walker and Rosenblatt 1988), and several Atlantic species show limited distributions (Collette 2003). The genus *Aphos*, the sister genus of *Porichthys*, occurs from Peru to Chile, to the south of *Porichthys* species except for *P. margaritatus* with which it overlaps in northern Peru. The genus *Batrachoides* in the Pacific also shows a north-south replacement of species with *B. waltersi* from Mexico to Costa Rica; *B. walkeri* and *B. boulengeri* only from the Bay of Panama; and *B. pacifici* from Panama south to Peru (Collette and Russo 1981).

Similar restricted distributions are found in species of Old World genera. Hutchins (1976, Fig. 17) has shown replacement of the four species of *Batrachomoeus* around Australia. Hutchins (1976, Fig. 8), also showed *Halophryne queenslandiae* being restricted to the east coast of Australia, *H. ocellatus* to the west coast, and *H. diemensis* to the north coast. Greenfield (1998) documented the distribution of *H. diemensis* to extend from Indonesia south through New Guinea to Australia, but is replaced in Pulau Waigeo, Indonesia and the Philippine Islands by *H. hutchinsi*. In South Africa similar limited distributions have been described for many of the species.

Toadfishes are, however, able to disperse as demonstrated by the presence of *Porichthys margaritatus* at the Galápagos Islands, 972 km from Ecuador. Toadfishes do occur on other islands, but all of these have been connected to the mainland at one time or another. Kricher (2002) points out that during the rainy season the Guayas River of Ecuador, with its many islands of floating vegetation, could be carried by the Humboldt Current to the Galápagos. Whether this is a possible mechanism of transport that could be used by toadfishes is unknown. The depth of water between South America and the Galápagos Islands is 2000 m, so movement along the bottom is unlikely. *Porichthys* does, however, unlike other toadfishes, move up into the water column at night to feed on zooplankton, so movement across open water is possible, but unlikely, for species in this genus. In reviewing early stages of fishes found in the California Current region, Watson (1996:546) states "However, newly released juveniles, primarily *P. notatus*, occasionally are taken in CalCOFI samples." In discussing dispersal abilities of toadfishes, Walters and Robins (1961:20) reported "Robins observed several individuals of another batrachoidid (*Porichthys*) rafting on logs 25 miles from land in the Gulf of Panama during the summer of 1957..." They also stated "In addition, young *O. beta* often hide in sponges, which in stormy weather may be torn free from the bottom and float suspended in the water, pushed onward in advance of the storm."

The limited distributions of species from so many different toadfish genera and the population structure within *Opsanus* species, clearly demonstrates the increased potential for isolation resulting from their limited dispersal ability. In addition, two studies on the movement of *Opsanus tau* (Isaacson 1964; Schwartz 1974) found that the adults had restricted movements. These factors also explain the continental distribution of toadfishes, their having failed (with the exception of the Galápagos) to reach islands that were not at one time connected to a continental area or very close during previous sea level drops. What is seen at the species level should be kept in mind when considering biogeographical relationships of the genera.

Geographic Patterns

Probably the most unexpected result from the phylogenetic analysis was the emergence of two major clades, one composed wholly of New World genera (Batrachoidinae), and the other of Old World genera (Halophryninae) with the exception of *Triathalassothia*, with two species, that occurs on the southeastern coast of South America. One species of the New World genus *Batrachoides* occurs in the eastern Atlantic Ocean off Africa (*B. liberiensis*), but the other eight species are New World. The basal position of *Triathalassothia* to the Old World clade, or the New World clade, and its geographical position, being closest to South Africa, suggest a relationship between the two areas. Other such relationships between New and Old World taxa in the Western Atlantic have been discussed recently by Floeter et al. (2008).

The world-wide distribution of toadfishes, and the division of them into two separate clades, New World and Old World, suggest that toadfishes originated prior to the final closing of the Tethys seaway (about 20 mya, McKenzie 1991). *Halobatrachus didactylus*, a Recent species, is recorded under that name from the Miocene of Algeria (Carnevale 2004). Thus, it, or a member of that generic lineage, was present in the general area at that time. Because *Halobatrachus* is part of the terminal lineage of Old World toadfishes, toadfishes must have evolved before that time because there have been an absolute minimum of nine speciation events in toadfishes prior to this. An even earlier origin is suggested by the presence of *Allenbatrachus* in India and Madagascar, discussed below.

Old World (Halophryninae)

The clade containing three genera, *Halophryne*, *Allenbatrachus*, and *Batrachomoeus* occurs from Australia north through the Indo-Australia Archipelago to Thailand and the Philippines, with *Allenbatrachus* extending to India, with an isolated species at Madagascar. Both *Halophryne* and *Batrachomoeus* are restricted to Australia and the Archipelago, and no other toadfish genus occurs in this area. Considering the limited dispersal ability of toadfishes, the occurrence of *Allenbatrachus* in both India and Madagascar is particularly interesting. Both *Allenbatrachus grunniens*, found in India, and *A. meridionalis* in Madagascar, are species that occur in estuaries and enter fresh water. A similar distribution pattern occurs in cichlids, with species of the genus *Etroplus* in India and those of *Paretroplus* in Madagascar. In discussing the cichlid distribution, Sparks (2004:599) concludes that it is "congruent with prevailing paleogeographic hypotheses regarding the sequence of Gondwana fragmentation." India and Madagascar were close to each other until the Late Cretaceous, about 88 MYA (Hay et al. 1999). If in fact the distribution of *Allenbatrachus* is the result of this vicariance scenario, then this suggests this clade had evolved by that time.

The "Gondwana clade" is sister to a large clade of l0 genera all found off Africa or in the northwestern Indian Ocean. Basal to this clade is *Bifax lacinia*, a distinctive, brightly colored species with maxillary flaps with eye spots, found only in the Arabian Sea. *Bifax* is sister to a clade with two subdivisions, one with only *Chatrabus*, found in south and western Africa. The other subdivision contains seven genera. Basal to that latter clade is *Colletteichthys dussumieri*, a species ranging from the Arabian Sea to India and Sri Lanka. The next two genera branching off that clade are *Barchatus* and *Riekertia*, each monotypic. *Barchatus cirrhosus* occurs only in the Red Sea, being geographically adjacent to *Colletteichthys dussumieri*, and *Riekertia ellisi* is known only from Durban to Port St. Johns (Transkei), South Africa. Although there are osteological differences between *Barchatus* and *Riekertia*, externally they are very similar.

Santini and Winterbottom (2002) hypothesized that the Arabian and Red Seas together is the sister area of the whole rest of the Indo-West Pacific. The ancestor of the *Bifax* → *Chatrabus* clade inhabited this area, as well as the ancestor of the *Colletteichthys* → *Perulibatrachus* clade, suggesting a potential vicariant event congruent with their hypothesis.

Riekertia is the sister to an unresolved clade with four genera, *Austrobatrachus*, *Batrichthys*, *Halobatrachus*, and *Perulibatrachus*. Although unresolved phylogenetically, only *Halobatrachus* and *Perulibatrachus* occur on the west coast of Africa. Based on the close correlation between phylogenetic relationships and geography in other genera, this would suggest that *Halobatrachus* and *Perulibatrachus* might be sister taxa. *Halobatrachus didactylus* ranges from Straits of Gibraltar south to Nigeria with a fossil in Algeria. *Perulibatrachus elminensis* ranges from Ghana to Walvis Bay, Namibia, and *P. rossignoli* ranges from Gabon south to Walvis Bay, Namibia. *Halobatrachus didactylus* only overlaps slightly with *P. elminensis* in geographic distribution (Collette and Greenfield in press; Collette et al. 2006).

Besides occurring on the western coast of Africa (*P. elminensis* and *P. rossignoli*), the genus *Perulibatrachus* also occurs in Natal, southeastern South Africa and India (Greenfield 1996, 2005). *Perulibatrachus kilburni* is known only from Natal, and *P. aquilonarius* only from Madras, India. Whether the presence of these species in Africa close to Madagascar and in India is another possible example of Gondwana influence is not known.

Austrobatrachus and *Batrichthys* are both known only from South Africa. *Austrobatrachus* is monotypic, *A. foedus*, and is known only from Algoa Bay to Coffee Bay, Transkei, South Africa. *Batrichthys* has two species, *B. apiatus* and *B. albofasciatus*, both found in the Transkei area. Thus, the two genera are in close proximity and may overlap.

New World (Batrachoidinae)

Isthmus of Panama

The rise of the Isthmus of Panama, about 3.1–3.5 Ma (Coates and Obando 1996), had a significant impact on toadfish evolution. The sister genera, *Daector* and *Thalassophryne* clearly were separated by this barrier. *Daector* is represented by four species all found in the tropical eastern Pacific, whereas *Thalassophryne* has six species all in the tropical western Atlantic Ocean (with one in fresh water draining into the Atlantic). Different species of *Porichthys* and *Batrachoides* are found on both sides of the Isthmus: *Porichthys* has eight species in the Pacific and five in the Atlantic, and *Batrachoides* has four species in the Pacific and five in the Atlantic. Because there are no toadfishes in the south Pacific, and toadfishes have limited dispersal abilities, the species along the Pacific coast of the New World were derived from the Atlantic Ocean.

Western Atlantic

The genus *Opsanus* is basal to the rest of the Batrachoidinae in the New World, and has a distribution that is more northern than the rest of the genera, occurring from the Gulf of Maine to Belize, except for the questionable species described from Brazil (*O. brasiliensis*). Walters and Robins (1961:19), citing Breder (1941), suggested that "It is evidently the spawning threshold of 19°–20°C that limits the distribution of *Opsanus tau* and its relatives both in the north and the south."

The genus *Batrachoides* is the sister to the rest of the Western Atlantic batrachoidin genera, with the exception of *Opsanus*. It differs from all other Western Atlantic genera in having scales, a character apparently independently derived from other genera with scales in the Old World. The major distribution of this genus is south of that of *Opsanus*. *Batrachoides gilberti* is the northern-most species in the genus, occurring from the southern border of the Yucatán Peninsula with Belize south to Panama. Although occurring in Belize, this is a species that is restricted to the mainland, often entering fresh water, and not reaching the barrier reef or atolls where *Sanopus* and *Vladichthys* occur (Greenfield and Thomerson 1997). Other *Batrachoides* species extend south to Brazil.

The monotypic *Potamobatrachus* is the sister group to the remaining three genera. *Potamobatrachus trispinosus* is known only from the Río Tocantins, Para, Brazil. Its geographic position in northern Brazil, places it in an area where *Batrachoides* occurs.

The genus *Sanopus* is basal to *Amphichthys* and *Vladichthys*. *Sanopus* species range from the Yucatán, Mexico south to Panama, a distribution that is north of *Amphichthys* and adjacent to *Vladichthys*. *Sanopus* and *Vladichthys* species co-occur on both the barrier reef and atolls of Belize.

Amphichthys and *Vladichthys* are sister genera that are separated geographically. *Amphichthys cryptocentrus* ranges from Panama to Brazil, whereas *Vladichthys gloverensis* occurs only at the barrier reef and atolls of Belize and the Bay Islands of Honduras. *Vladichthys gloverensis* is a specialized, miniature species that because of its small size is able to live in coral-reef habitats not utilized by other toadfishes. Most other toadfishes are found on sand or mud bottoms, often burrowing under rocks or coral heads. It thus is possible that *Vladichthys* was derived from the more generalized *Amphichthys*, or they both evolved from the same ancestor.

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Appendix I

Material Examined

Cleared and Stained Specimens.— *Allenbatrachus grunniens*, CAS-SU 26909; *Allenbatrachus meridionalis* MNHN A-3777 (1); *Allenbatrachus reticulatus*, CAS-SU 30658; *Amphichthys cryptocentrus*, USNM 144888; *Aphos porosus*, CAS 65051; *Austrobatrachus foedus*, SAIAB 12748; *Barchatus cirrhosus*, HUJ 13711; *Batrachoides gilberti*, FMNH 84549; *Batrachomoeus trispinosus*, CAS 69938; *Batrichthys apiatus*, SAIAB 75-25; *Bifax lacinia*, BPBM 35843; *Chatrabus hendersoni*, SAIAB 8611; *Chatrabus felinus*, SAIAB 75-25; *Chatrabus melanurus*, SAIAB 12749; *Collettteichthys dussumieri*, USNM 147914; *Daector reticulata*, GCRL 16194; *Halobatrachus didactylus*, USNM 205066; *Halophryne diemensis*, NTMS 10005-019; *Halophryne hutchinsi*, CAS-SU 204-62; *Opsanus tau*, CAS 223821; *Perulibatrachus elminensis*, MNHN 1970-43; *Potamobatrachus trispinosus*, USNM 330064; *Porichthys notatus*, CAS 223822; *Riekertia ellisi*, SAIAB 12738; *Sanopus barbatus*, SIO 6745, MCZ 44549 (1); *Thalassophryne maculosa*, USNM 199524; *Thalassophryne megalops*, FMNH 66907; *Triathalassothia argentinus*, USNM 214438; *Vladichthys gloverensis* FMNH 91036.

Non-batrachoid specimens cleared and stained: *Draconetta oregoni* CAS168909 (1); *Synchiropus atrilabiatus*, CAS 168910 (5); *Foetorepus agassizi* USNM 188524 (1); *Raniceps raninus* CAS 225749 (1), USNM 35222 (1- parts only C & S); *Lophius americanus* MCZ 51259 (1); *Merluccius productus* CAS225753 (3), CAS 225754 (4); *Antennarius coccineus* CAS 225751 (1); *Gobiesox maeandricus* CAS 225752 (1); *Brachionichthys hirsutus* CAS 225750 (1); *Ogilbia robertsoni* CAS 81418 (1). .

Other Specimens.— *Allenbatrachus grunniens* CAS 75217 (2), CAS 75218 (1), CAS-SU 32944 (2), CAS-SU 27732 (4), CAS-SU 38261 (1), CAS-SU 38262 (1), CAS-SU 41321 (1), ANSP 48743 (1), ANSP 77373 (1), AMS B.8319 (1), USNM 047986 (1), USNM 148493 (1); *Allenbatrachus meridionalis* AMNH 233686 (holotype), AMNH 234024 (1), CAS 220508 (1), MNHN 1992-0670 (1), MNHN 1962-0197 (3) *Allenbatrachus reticulatus* CAS-SU 33701 (1), CAS-SU 35153 (2), CAS 82188 (neotype), CAS 66821 (1), CAS 75216 (1), CAS 17652 (1), CAS 88690 (7), CAS 225745 (3), CAS 225746 (4), AMS I.21036003 (2), USNM 333283 (5); *Amphichthys cryptocentrus* CAS-SU 52346 (2), CAS-SU 52347 (1),CAS 225744 (3), USNM 144888 (1); *Austrobatrachus foedus* RUSI 12744 (1); *Barchatus cirrhosus* USNM 221140(1); BPBM 18303 (1), TAU P-12259 (1- photographs only); *Batrachoides boulengeri* CAS-SU 6487 (holotype), CAS-SU 12815-6 (2), MCZ 12805 (1), USNM 80990-1 (3), USNM 220127 (4), LACM W58-304-1 (3); *Batrachoides gilberti* USNM 81002 (holotype), USNM 81002 (1), USNM 81003 (5), FMNH 71317 (1), FMNH 86588 (1), FMNH 84549 (14), ANSP 123884 (1), AMNH 35033 (1); *Batrachoides goldmani* USNM 50006 (holotype), USNM 219383 (4),UMMZ 144152 (1), UMMZ 144156 (6), AMNH 25623 (1), AMNH 24532 (1); *Batrachoides liberiensis* NHMV 5558 (holotype), USNM 205067 (1), USNM 193648 (2), USNM 219393 (5), ANSP 140358 (1), FMNH 83861 (1); *Batrachoides manglae* ANSP 102200 (5), USNM 218893 (1); *Batrachoides pacifici* BMNH 1860.6.18.11 (lectotype), MCZ 12755-57 (6), USNM 80999 (2), USNM 53486 (4), USNM 144882-3 (4), FMNH 26090-95 (6), SIO 70-366 (3), LACM 32732-1 (1), CAS-IU 15050 (2), CAS-SU 6872 (14) ; *Batrachoide*s *surinamensis* USNM 44463 (1),USNM 9368 (1), USNM 159249 (3), USNM 219462 (3), FMNH 84547 (1), FMNH 84548 (1), ANSP 37901 (1), AMNH 9319 (2), MCZ 30164 (1), MCZ 12773 (4); *Batrachoides walkeri* USNM 220128 (holotype); *Batrachoides waltersi* LACM 33806-64 (holotype), CAS-SU 57002 (1), USNM 219788 (3), USNM 219789 (2), FMNH 91905 (3), SIO 73-257 (19); *Batrachomoeus trispinosus* CAS 35620 (4), CAS 27537 (1), CAS 35620 (4), CAS 66820 (1), CAS 27436 (1), CAS 74966 (1), CAS 81633 (1), CAS 74965 (3), USNM 72724 (1), USNM 150909 (1), AMS I.28978007 (1); *Batrichthys albofasciatus* RUSI 29413 (1); *Batrichthys apiatus* SAIAB 12728 (7), SAIAB 2348 (1), SAIAB 2345 (1), SAIAB 2346 (1), SAIAB 12731 (3), SAIAB 12733 (15*); Bifax lacinia* BPBM 35949 (holotype), BMNH 1994.4.5.1 (1), BPBM 36210 (1), BPBM 35731 (1), CAS 81232 (1), USNM 329111 (1); *Chatrabus felinus* SAIAB 4341 (1), SAIAB 75-23 (1); *Colletteichthys dussumieri*, USNM 147914 (3), USNM 047986 (1), USNM 333284 (3), USNM 333281 (1), USNM 196473 (1), USNM 221342 (5), USNM 226512 (1), USNM 147913 (7), USNM 147915, CAS 23719 (1), CAS 29743 (1), BPBM 30509 (1), BPBM 29525, AMS B.8115 (1), AMS B.8112; *Daector dowi* USNM 128235 (holotype), USNM 39085 (1), USNM 41232 (2), USNM 188844 (11), CAS 58304 (14), SIO 64-386 (4), FMNH 62736 (2); *Daector gerringi* NRS 10651 (holotype); *Daector quadrizonatus* USNM 206335 (1); *Daector reticulata* BMNH 1864.1.26.342 (holotype), CAS-SU 14949 (1), CAS-SU 22287 (4), USNM 81698 (2), USNM 81699 (1),USNM 81700 (2), MCZ 41806 (3), ANSP 70346 (1); *Daector schmitti* USNM 144869 (holotype), CAS-SU 14949 (paratypes); *Halobatrachus didactylus* MCZ224-5 (2), MCZ 12787 (1), USNM 205060 (1), USNM 205062 (1), USNM 205063 (1), USNM 205064 (1), USNM 205065 (1), USNM 205066 (1),UMML 16893 (2), UMML 16854 (4); *Halophyrne diemensis* FMNH 23284 (1), USNM 221343 (1), USNM 174024 (1), AMS I.1564k002 (1), AMS I.18553001 (2), AMS S-10600-020 (2), NTMS 10600-020 (2); *Halophyrne hutchinsi* USNM 150899 (holotype), USNM 150927 (1), USNM 219797 (1), FMNH 47500 (1), FMNH 52489 (1), CAS-SU 38260 (1), CAS 126908 (11); *Halophyrne ocellatus* AMS I.7029 (1), WAM P25058-001 (1); *Halophyrne queenslandiae* CAS 120529 (1), AMS I.9500 (1); *Opsanus beta* USNM 21477 (1), USNM 23541 (1), UMMZ 184510 (2), ANSP 68629 (1); *Opsanus dichrostomus* USNM 361063 (holotype), USNM 361064 (3 paratypes), CAS 225748 (1) FMNH 110990 (1), FMNH 110991 (1), FMNH 110992 (2), UMMZ 102169 (1), UMMZ 184702 (1), UF 13365 (1); *Opsanus pardus* USNM 22217 (2), USNM 73173 (1), USNM 301941 (1), UF 204220 (1); *Opsanus phobetron*, USNM 170961 (paratype) USNM 170962 (1), ANSP 79480 (paratype), ANSP 79481 (paratypes), UF 2027128 (1), MCZ 34708 (1); *Opsanus tau* USNM 48976 (1), USNM 45460 (1), USNM 91202 (2), USNM 301995 (1); *Perulibatrachus aquilonarius* CAS-SU 41322 (holotype); *Perulibatrachus elminensis* MNHN 1967-909 (1); *Perulibatrachus kilburni* SAIAB 28203 (holotype); *Perulibatrachus rossignoli* CAS 223402 (1); *Potamobatrachus trispinosus* MZUSP 4335 (holotype), MNHG 2575.53 (1); *Riekertia ellisi* SAIAB 12739 (1), SAIAB 12742 (1); *Sanopus astrifer* USNM 259421-F1 (holotype), UMML 9415 (paratypes), ANSP 102736 (3-paratypes), FMNH 71318 (1), USNM 209720 (1); *Sanopus barbatus* FMNH 91031 (1), CAS 225747 (1), USNM 81009 (1), USNM 22522 (1), MCZ 44550 (1); *Sanopus greenfieldorum* USNM 213555 (holotype), USNM 261601 (paratypes), FMNH 94517 (paratypes); *Sanopus johnsoni* USNM 205945 (holotype); *Sanopus splendidus* USNM 205944 (holotype), ANSP 117316 (paratypes), UMML 29141 (paratypes), USNM 205606 (paratypes), USNM 205607 (paratypes), CAS 29110 (paratypes); *Thalassophryne amazonica* USNM 200560 (1), USNM 200559 (3); *Thalassophryne megalops* USNM 37669 (holotype), USNM 197643 (paratypes), USNM 200556 (2), FMNH 66832 (1), ANSP 103620 (2); *Thalassophryne montevidensis* MNH 37 (holotype), MACN 5267 (1), USNM 200350 (3); *Thalassophryne nattereri* MCZ 12726 (lectotype), BMNH 1924.7 (2), MNHN 03-40 (1), MNHN 04-19 (1), USNM 187975 (1), USNM 200555 (1), FMNH 66273 (1), FMNH 66275 (1), CAS-SU 2223 (holotype of *T. branneri*); *Thalassophryne punctata* MCZ 4632 (lectotype); *Triathalassothia argentinus*, USNM 86687 (1), USNM 214438 (1), ANSP 70373 (1); *Vladichthys gloverensis*, FMNH 71575 (holotype), Paratypes- FMNH 71576 (1), FMNH 71577 (2), FMNH 71578 (2), FMNH 71579 (1), FMNH 71580 (1), FMNH 91036 (1), USNM 318691 (1), USNM 208239 (3), ANSP 120499 (5), CAS 15409 (3), BMNH 197.10.10.97 (1)