A review of the gobioid fish genus *Gobioides*

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Abstract The gobioid genus *Gobioides* Lacepède, 1800 shares with the amblyopine gobies (Gobiidae: Amblyopinae) an eel-like, elongate body with a continuous dorsal fin and an affinity for shallow water, muddy bottom habitats. Due to similarities in external morphology and habitat requirements, some workers considered *Gobioides* allied with amblyopine gobies. Others, however, dispute a close relationship between *Gobioides* and the Amblyopinae; morphological and ecological similarities are considered to be homoplasious. Results of this study concur with placing *Gobioides* separate from amblyopine gobies and within the gobiid subfamily Gobionellinae. *Gobioides* is easily distinguished from the Amblyopinae by its larger eyes (small in *Gobioides* vs. inconspicuous in the Amblyopinae), fewer dorsal and anal-fin rays (14–20 vs. 27–48), and different fin element to vertebra ratios (1 : 1 vs. 2 : 1). *Gobioides* reaches lengths of 500 mm SL or greater whereas amblyopines rarely exceed 300 mm SL. *Gobioides* comprises five species (*G. africanus*, *G. broussoneti*, *G. grahamae*, *G. peruanus*, and *G. sagitta*). Although these gobies occupy habitats with similar conditions, *Gobioides* and amblyopines are nowhere sympatric. *Gobioides* occurs in tropical and subtropical coastal waters of the eastern and western Atlantic as well as the tropical eastern Pacific Ocean. In the eastern Atlantic, *Gobioides* is known from Senegal to Zaire. In the western Atlantic, *Gobioides* is reported from South Carolina to southern Brazil. In the eastern Pacific, *Gobioides* is known from Mexico to Peru.

Key words. — *Gobioides*; vertebral counts; species; distribution; relationships.

The gobioid genus *Gobioides* Lacepède, 1800, and amblyopine gobies (Gobiidae: Amblyopinae) share an eel-like, elongate body with a continuous dorsal fin and an affinity for shallow water, muddy bottom habitats. Due to similarities in external morphology and habitat requirements, some workers (Bleeker, 1874; Jordan, 1923; Koumans, 1931; Palmer, 1952; Norman, 1966; Hoese, 1984; Nelson, 1984, 1994) considered *Gobioides* allied with the Amblyopinae; others have considered *Gobioides* synonymous with one or more amblyopine genera (Günther, 1861; Weber, 1913; Hora, 1924). Others (Miller, 1973; Birdsong et al., 1988; Harrison, 1989; Pezold, 1993), however, dispute a close relationship between *Gobioides* and the Amblyopinae; they considered morphological and ecological similarities to be homoplasious.

Gobioides has been placed in various gobioid groups (Table 1): the Amblyopodini (Bleeker, 1874); the Gobioididae (Jordan, 1923; Nelson, 1984); the Taenioninae (Hora, 1924); the Taenioininae (Koumans; Norman, 1966); the Taenioidinae (Palmer, 1952); and the Amblyopinae as a subfamily of the Gobiidae (Hoese, 1984; Nelson, 1994). Günther's (1861) Amblyopina comprised only *Amblyopus*; Günther considered *Gobioides* a synonym of *Amblyopus*. Bleeker's (1874) grouping comprised a new genus (*Odontamblyopus*) and four other genera: *Brachyamblyopus*, *Gobioides*, *Taenioides*, and *Trypauchen*. Jordan (1923) established the family Gobioididae that comprised 12 genera including *Gobioides*. The Taenioididae of Hora (1924) comprised two subfamilies, the Taenioninae and the Trypaucheninae, with all the genera of Jordan's Gobioididae being members of Hora's Taenioninae as well as two others, *Trypauchenopsis* and *Trypauchenophrys*. Hora went on to state that eight of these genera (including *Gobioides*) were probably synonyms of *Taenioides*, a view shared by Weber (1913). Koumans (1931) and Norman (1966) divided the Taenioididae into the same subfamilies as did Hora, but made a minor spelling change from Taenioninae to Taenioininae. Koumans' Taenioininae comprised eight genera: *Brachyamblyopus*, *Gobioides*, *Nudagobioides*, *Odontamblyopus*, *Paragobioides*, *Sericagobioides*, *Taenioides*, and *Tyntlastes*. Nor-

man's Taenioininae also comprised eight genera, six contained in Koumans' grouping: *Brachyamblyopus*, *Gobioides*, *Odontamblyopus*, *Sericagobioides*, *Taenioides*, and *Tyntlastes* and two others, *Paratyntlastes* and *Pseudotrypauchen*. Citing the International Rules of Zoological Nomenclature, Palmer (1952) changed the spelling of Taenioininae to Taenioidinae. Palmer's group comprised six genera: *Brachyamblyopus*, *Gobioides*, *Nudagobioides*, *Odontamblyopus*, *Pseudotrypauchen*, and *Taenioides*. Nelson (1984) stated that his Gobioididae comprised eight genera, but he listed only the following seven: *Brachyamblyopus*, *Caragobioides*, *Gobioides*, *Nudagobioides*, *Odontamblyopus*, *Taenioides*, and *Tyntlastes*. Hoese's (1984) Amblyopinae contained 10 unnamed genera. Nelson (1994) followed Hoese's usage of Amblyopinae and also stated that the subfamily comprised 10 genera; Nelson went further than Hoese, however, and listed several amblyopine genera including *Gobioides*. However, Nelson (1994) also included *Gobioides* in the Gobionellinae indicating a lack of certainty as to its most appropriate placement. Pezold (1993) transferred *Gobioides* from the Amblyopinae to the Gobionellinae; that placement is followed here for reasons discussed below.

Gobioides is easily distinguished from the Amblyopinae by its larger eyes (small in *Gobioides* vs. inconspicuous in the Amblyopinae), fewer dorsal and anal-fin rays (14–20 in *Gobioides* vs. 27–48 in the Amblyopinae), and a different fin element to vertebra ratio (1 : 1 vs. 2 : 1). *Gobioides* can reach lengths of 500 mm SL or greater whereas amblyopines rarely exceed 300 mm SL. Although these taxa occupy habitats with similar conditions, *Gobioides* and amblyopine gobies are nowhere sympatric. Amblyopine gobies are found in the Indian and Western-Central Pacific Oceans. *Gobioides* is found in tropical and subtropical coastal waters of the eastern and western Atlantic as well as the tropical eastern Pacific Ocean. In the eastern Atlantic, *Gobioides* is known from Senegal to Zaire (Fig. 1). In the western Atlantic, *Gobioides* is reported from South Carolina to southern Brazil (Lee et al., 1980) including the Gulf Coast of the U.S., Cuba, Mexico, Puerto Rico, Colombia, Guyana, Surinam, and French Guiana. In the eastern Pacific, *Gobioides* is known from Mexico to Peru.

The only previous species-level review of *Gobioides* was Palmer (1952). Palmer included *Gobioides*

Table 1. Placement of *Gobioides* in various gobioid groupings

Amblyopodini-Bleeker, 1874	Gobioididae-Jordan, 1923	Taenioninae-Hora, 1924	Taenioininae-Koumans, 1931
Gobioides	*Gobioides*	*Gobioides*	*Gobioides*
Brachyamblyopus	*Amblyopus*	*Amblyopus*	*Brachyamblyopus*
Odontamblyopus	*Brachyamblyopus*	*Brachyamblyopus*	*Nudagobioides*
Taenioides	*Cayennia*	*Cayennia*	*Odontamblyopus*
Trypauchen	*Gymnurus*	*Gymmurus*	*Paragobioides*
	Odontamblyopus	*Odontamblyopus*	*Sericagobioides*
	Ognichodes	*Ognichodes*	*Taenioides*
	Paragobioides	*Paragobioides*	*Tyntlastes*
	Plecopodus	*Plecopodus*	
	Psilosomus	*Psilosomus*	
	Taenioides	*Taenioides*	
	Tyntlastes	*Trypauchenopsis*	
		Trypauchenophrys	
		Tyntlastes	

Taenioidinae-Palmer, 1952	Taenioininae-Norman, 1966	Gobioididae-Nelson, 1984	Amblyopinae-Nelson, 1994
Gobioides	*Gobioides*	*Gobioides*	*Gobioides*
Brachyamblyopus	*Brachyamblyopus*	*Brachyamblyopus*	*Amblyotrypauchen*
Odontamblyopus	*Odontamblyopus*	*Caragobioides*	*Brachyamblyopus*
Nudagobioides	*Paratyntlastes*	*Nudagobioides*	*Odontamblyopus*
Pseudotrypauchen	*Pseudotrypauchen*	*Odontamblyopus*	*Taenioides*
Taenioides	*Sericagobioides*	*Taenioides*	*Tyntlastes*
	Taenioides	*Tyntlastes*	4 unnamed genera
	Tyntlastes	1 unnamed genus	

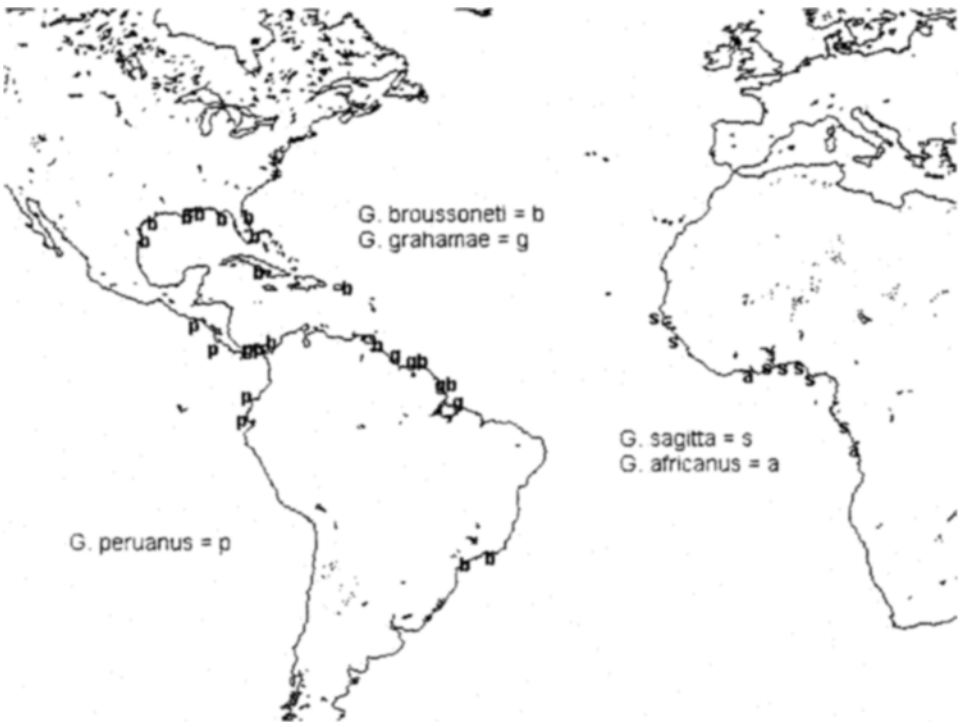

Fig. 1. Geographic distributions of the five species of *Gobioides*. Points may indicate more than one collection or specimen. Two localities for *G. broussoneti* in west Texas are based on data, rather than specimens, provided by the Texas Cooperative Wildlife Collection at Texas A&M University.

in the Taenioidinae and compared *Gobioides* to the other five genera within that subfamily. Palmer also provided a key to the eight species of *Gobioides* that he recognized and gave brief accounts of each. Newly discovered information relevant to the taxonomy and distribution of *Gobioides* has prompted this review of the genus.

The objectives of this study are to (1) revise and define *Gobioides* using derived characters, (2) to provide characters for reorganizing the included species, (3) to list synonyms for all valid forms, and (4) to provide and analyze distributional and ecological data. Specimens were examined at or obtained from the following institutions (abbreviations in parentheses): Academy of Natural Sciences, Philadelphia (ANSP); Biological Laboratory of the Imperial Household, Tokyo (BLIH); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS-SU); Harvard University, Cambridge (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Naturhistorika Riksmuseet, Stockholm (NHRM); National Science Museum, Tokyo (NSMT); Scripps Institution of Oceanography, La Jolla (SIO); Florida Museum of Natural History, University of Florida, Gainesville (UF); and National Museum of Natural History, Washington (USNM).

Methods

All measurements are straight-line distances made with dial calipers and recorded to the nearest millimeter. All fish lengths given are standard lengths (SL) except where noted as total length (TL).

The spinous elements of the dorsal and anal fins are soft and flexible. The last two rays of each of these fins are very close together, share the ultimate pterygiophore, and, as is common practice, counted as a single element. The count of scales in a longitudinal series was begun at the dorsoposterior attachment of the opercular membrane, continued on a posteroventral diagonal to the tip of the pectoral fin, and then in a straight line along the midline of the body to the posterior edge of the hypural plate, determined externally. Gill-raker counts were made on the outer face of the first arch and include the raker (if present) at the angle of the arch plus those on the lower limb of the arch. The vertebral count is separated into precaudal and caudal counts, the latter including the terminal vertebral element; counts were taken from radi-

ographs and cleared and stained material. The methods of Birdsong et al., (1988) were used in describing the relationship between the spinous dorsal fin pterygiophores and the underlying vertebrae.

All specimens examined are listed in the material examined section and grouped by major geographic areas. The total number of specimens and size range follow each catalog number. Data referring to type specimens, including those pertaining to synonyms, are listed by specific name and type category.

Gobioides Lacepède, 1800

Gobioides Lacepède, 1800: 576 (type species, *Gobioides broussoneti* Lacepède 1800: 580, subsequent designation by Bleeker, 1874: 329).

Plecopodus Rafinesque, 1815: 87 (unneeded replacement name for *Gobioides* Lacepède, 1800).

Ognichodes Swainson, 1839: 183 (objective synonym of *Gobioides* Lacepède, 1800).

Tyntlastes Günther, 1862: 194 (type species, *Amblyopus sagitta* Günther, 1862, by original designation).

Cayennia Sauvage, 1880: 57 (type species, *Cayennia guichenoti* Sauvage, 1880, by monotypy).

Paratyntlastes Giltay, 1935: 11 (type species, *Paratyntlastes africanus* Giltay, 1935, by original designation).

Diagnosis. Body greatly elongate with a continuous dorsal fin. Only genus of gobioid fishes that possesses a spinous dorsal-fin pterygiophore formula of 3-12201.

Included Species. Five species are assigned to *Gobioides*: *G. africanus*, *G. broussoneti*, *G. grahamae*, *G. peruanus*, and *G. sagitta*.

Description. Elongate, body depth 9–14% SL; head length 15–21% SL; head width 5–8% SL; continuous dorsal fin, VI-I, 14–15 or 19; spines flexible; dorsal-fin base long, broadly joined with base of caudal fin (except in *G. africanus* where dorsal fin not connected to caudal fin). Precaudal vertebrae 10, caudal vertebrae 16–17, or 21. Anal fin I, 13–15, or I, 19, segmented rays branched; anal-fin spine much reduced; height of anal fin moderate, less than height of dorsal fin; anal-fin membrane broadly joined to base of caudal fin (except in *G. africanus* where anal fin not connected to caudal fin). Two anal-fin pterygiophores anterior to first hemal spine. Pectoral fin with 15–20 rays; rounded and tapered posteriorly, terminating at point anterior to vertical from posteriormost margin of pelvic fin. Pelvic fin I, 5; frenum present; basal membrane uniting fins present; broadly rounded posteriorly. Caudal fin with 17 segmented rays; procurrent rays 6 dorsally, 5–6 ventrally. Scales cycloid, difficult to count with accuracy; present on body and cheeks, largest posteriorly. In some species, scales embedded and extremely small. Teeth caninoid; lower-jaw teeth in 1–3 rows laterally, one row medially; outer row teeth 9–42, much larger, more pointed than teeth of inner rows; upper jaw teeth in 1–3 rows, inner, medial row smaller, 8–16, outer row, 12–46. Tongue slightly bilobed; basihyal bifid. Gape wide, mouth oblique; posterior tip of maxilla extending to vertical below posterior half of eye; posteriorly near tip of maxilla, upper lip expanded into large fold that joins similar lower lip fold at rictus, latter fold completely covers posterior part of jaws even when agape. Interorbital space broad. Eyes small, approximately twice diameter of posterior nostril, covered by skin; posterior nostril located anterior to eye; anterior nostril smaller than posterior nostril, located anterior to it near upper jaw; cephalic sensory pores and cutaneous papillae as in Figure 2. Ventral margin of first gill arch with 8–11 gill rakers; gill rakers short and blunt; gill opening narrow.

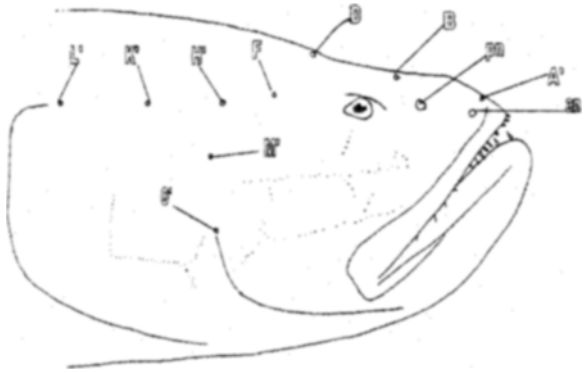

Fig. 2. Sensory pore and cutaneous papillae from the right side of the head of *Gobioides broussoneti* (BLIH 1980131). Sensory pores labeled as in Pezold (1993). Sensory pores C, E, G, I, J, N are absent. Sensory pore D is unpaired. Terminal pores indicated by'. *an*—anterior nostril; *pn*—posterior nostril.

Key to the species of *Gobioides*

1a. D. VI-I, 14 and, typically, A. I, 14, rarely A. I, 13; caudal vertebrae 16 2

1b. D. VI-I, 15 or 19; A. I, 15 or 19; caudal vertebrae 17 or 21 3

2a. Dorsal and anal fins not joined by membrane to caudal fin; one row of teeth in lower jaw; tips of segmented dorsal and anal-fin rays blackish; body whitish; found only in the tropical eastern Atlantic (Ghana and Zaire) . . . . . *Gobioides africanus*

Fig. 3. *Gobioides africanus*, MRAC 56249, 78 mm SL, 101 mm TL, Vista, Zaire.

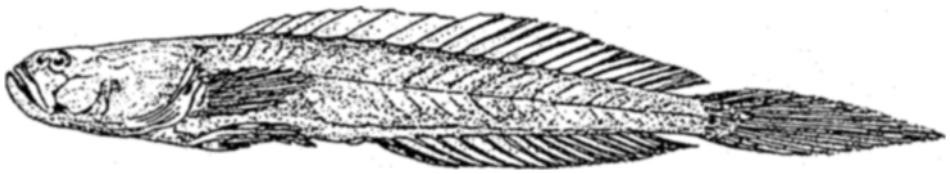

Fig. 4. *Gobioides africanus* from Giltay (1935).

2b. Dorsal and anal fins joined by membrane to caudal fin; two rows of teeth in lower jaw; tips of segmented dorsal and anal-fin rays without pigment; body uniformly pinkish purple; found only in the tropical western Atlantic (Guyana, French Guiana, and Brazil) . . . . . *Gobioides grahamae*

3a. D. VI-I, 15; A. I, 15; caudal vertebrae 17 4

3b. D. VI-I, 19; A. I, 19; caudal vertebrae 21 . . . . . *Gobioides sagitta*

4a. Mouth very oblique with anterior tip of lower jaw on a horizontal with ventral margin of eye; maxilla terminating at or near a vertical with posterior margin of eye; body tannish brown; found only in the eastern Pacific (Mexico to Peru) . . . . . *Gobioides peruanus*

4b. Mouth oblique with anterior tip of lower jaw ventral to a horizontal with ventral margin of eye; maxilla terminating ventroposterior to eye; body purplish brown; found only in the western Atlantic (Florida to Brazil) . . . . . *Gobioides broussoneti*

Gobioides africanus (Giltay, 1935)
(Figs. 3, 4)

Paratyntlastes africanus Giltay, 1935: 11, fig. 3 (type locality Moanda, Zaire).

Material examined. (6 specimens from 2 localities, size range 47–135): Ghana, Accra: BMNH 1939.7.12.33, 1 : 135. Zaire: MRAC 38278, holotype of *Paratyntlastes africanus* Giltay, 64; MRAC 39279-280, paratypes of *Paratyntlastes africanus* Giltay, 2: 47–55; MRAC 56191, 1 : 70; MRAC 56249, 1 : 77.

Description. As for genus except as noted. Dorsal and anal fins not joined by membrane to caudal fin.

Meristics. — Dorsal fin VI-I, 14; anal fin I, 14; caudal vertebrae 16; pectoral-fin rays 15–19. One complete row of teeth in each jaw.

Coloration. — Based on the original description, the color of live specimens is uniformly white with the tips of the second dorsal and anal fins black. Fresh material was not available for this study.

Ecology. Inshore marine species according to Harrison and Miller (1992).

Distribution. Preserved material for this study was available from collections made in Ghana and Zaire. Additionally, this species is reported to occur off islands in the Gulf of Guinea (Maugé, 1986).

Remarks. Although this species was described and figured as not having its dorsal and anal fins joined with the caudal fin, this condition was questioned by Palmer (1952). As mentioned by Palmer

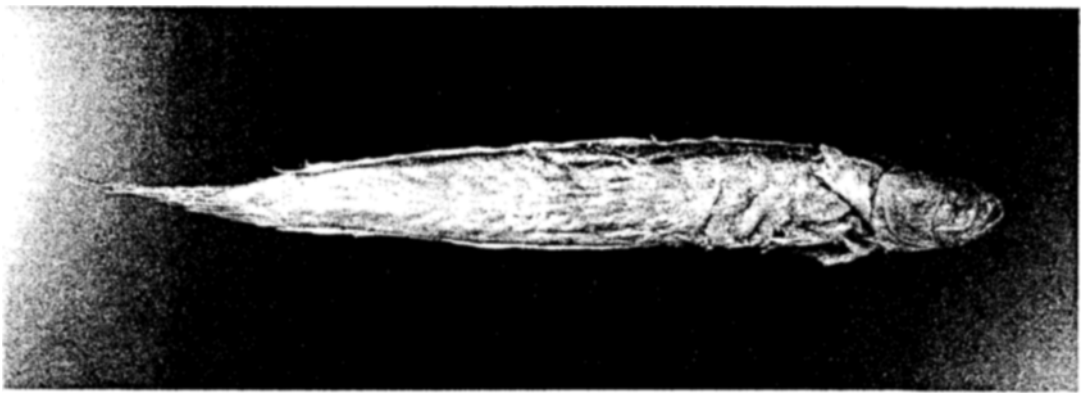

Fig. 5. *Gobioides grahamae*, UF 14805, 89 mm SL, 122 mm TL, Cayenne River estuary, French Guiana.

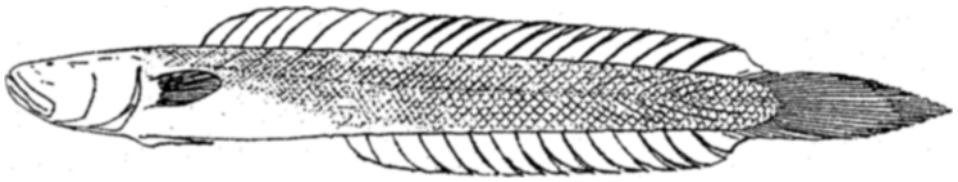

Fig. 6. *Gobioides grahamae* from Palmer and Wheeler (1955).

(1952), the membrane uniting the dorsal and anal fins with the caudal fin is thin and easily torn in congeners. Palmer wondered if this had occurred with the type specimens of *G. africanus*. I can only confirm that the specimens I examined did not have a membrane joining the median fins with the caudal fin, however, the specimens available to me were in poor condition. (P. J. Miller [pers. comm.] who examined the same specimens that I did also did not discern a membranous connection between the median fins and caudal fin.) Fresh material is needed to confirm this feature. If *G. africanus* does not have its dorsal and anal fins united with the caudal fin, then it is the only species in the genus to exhibit this condition. The lack of union between the median fins and the caudal fins was the primary reason Giltay erected *Paratyntlastes*.

This species typically does not exceed 130 mm TL according to Harrison and Miller (1992) whereas its congener in the eastern Atlantic, *G. sagitta*, can attain 500 mm TL.

Gobioides grahamae Palmer & Wheeler, 1955
(Figs. 5, 6)

Gobioides unicolor Palmer, 1952: 53 (type locality, Marajo Island, Brazil).

Gobioides grahamae Palmer & Wheeler, 1955: 68 (replacement name for *Gobioides unicolor* Palmer, 1952).

Material examined. (7 specimens from 4 localities, size range 71–173): Guyana, Georgetown: BMNH 1950.5.15.41, paratype of *Gobioides grahamae* Palmer & Wheeler, 123; BMNH 1959.3.17.161, 1 : 97. Surinam, Corantijn River: USNM 226242, 1 : 71. French Guiana, Cayenne River estuary: UF 14805, 2:89–96. Brazil, Marajo Island: BMNH 1925.10.28.464, holotype of *Gobioides unicolor* Palmer, and *Gobioides grahamae* Palmer & Wheeler, 173; BMNH 1925.10.28.465, paratype of *Gobioides unicolor* Palmer, and *Gobioides grahamae* Palmer & Wheeler, 164.

Description. As for genus except as noted. Mouth very oblique with anterior tip of lower jaw on a horizontal with ventral margin of eye; maxilla terminating near a vertical with posterior margin of eye.

Meristics. — Dorsal fin VI-I, 14; anal fin I, 13–14; caudal vertebrae 16; pectoral-fin rays 15–18. Scale rows in longitudinal series 77–89. Upper-jaw teeth in a single row, 23–29; lower-jaw teeth in two rows, outer row 33–35.

Coloration. — No fresh specimens were available for this study. Palmer and Wheeler (1955) noted that this species is uniformly pinkish purple in life. This species is brown in preservative with dusky pigment extending along the dorsal surface. The caudal fin is dusky posteriorly; other fins are translucent.

Fig. 7. *Gobioides sagitta*, MRAC 84-51-P-184-186, 113 mm SL, 145 mm TL, Calabar, Nigeria.

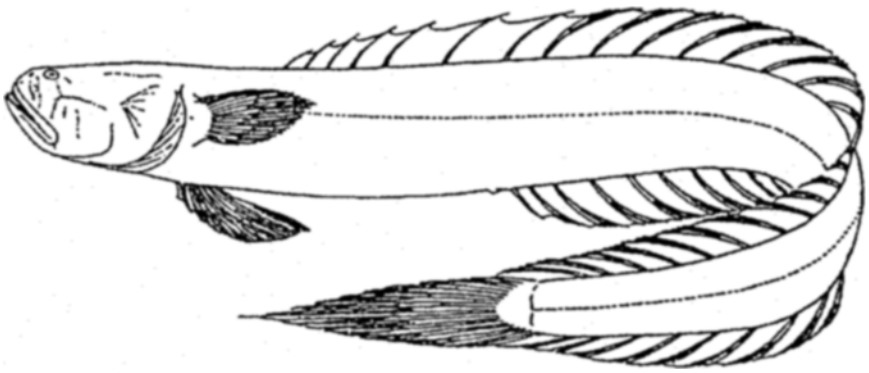

Fig. 8. *Gobioides sagitta* from Harrison and Miller (1992).

Ecology. Palmer and Wheeler (1955) stated that this species is "found under stones in muddy places."

Distribution. Found coastally and up river mouths from Guyana to northern Brazil.

Remarks. As stated by Palmer and Wheeler (1955), *Cepola unicolor* Gray is a synonym of *Gobioides broussoneti* and, thus, the name *Gobioides unicolor* Palmer became a homonym. Consequently, Palmer and Wheeler (1955) proposed *Gobioides grahamae* to replace *Gobioides unicolor*. In his original description, Palmer (1952) described and figured the breast of *G. unicolor* as naked. In some specimens I examined, the breast was scaled. As scales are easily lost, I assume this species possesses breast scales. This species is not nearly as abundant in collections as the other congener in the Western Atlantic, *G. broussoneti*. The very similar meristics of this species and *G. africanus* leads me to conclude that these two species are closely related.

Gobioides sagitta (Günther, 1862) (Figs. 7, 8)

Amblyopus sagitta Günther, 1862: 193, pl. 27, fig. A (type locality, Calabar, Nigeria).

Tyntlastes sagitta Günther, 1862: 194 (new combination).

Gobioides ansorgii Boulenger, 1909: 431 (type locality, Port Mansoa, Guinea-Bissau).

Gobioides senegalensis Puyo, 1957: 185 (type locality, Ile de St. Louis, Senegal River, Senegal).

Material examined. (23 specimens from 9 localities, size range 72–397): Senegal, Casamance: MNHN 1987-1029, 1:303. Guinea-Bissau, Port Mansoa: BMNH 1909.10.29.110-112, syntypes of *Gobioides ansorgii* Boulenger, 3:159–222. Guinea: MNHN 1979-506, 1:190. Togo: MRAC 73-11-P-18, 1:413. Benin: MNHN 1919-480-484, 4:350–397; MRAC 179504, 1:320; MRAC 89-58-P-14, 1:238. Nigeria, Calabar: BMNH 1862.1.24.27-29, paratypes of *Amblyopus sagitta* Günther, 3:105–118; BMNH 1862.1.24.26, holotype of *Amblyopus sagitta* Günther, 182; MRAC 84-51-P-184-186, 2:72–123. Lagos Lagoon: BMNH 1968.11.15.77, 1:340. Kwa River: MRAC 89-51-P-185-186, 1:120; MRAC 91-10-P-937-938, 2:77–190. Congo, Pointe-Noire: MNHN 1979-506, 1:261.

Description. As for genus except as noted below.

Meristics. — Dorsal fin VI-I, 19; anal fin I, 19; caudal vertebrae 21; pectoral-fin rays 16–18. Lower jaw with two rows of teeth, upper jaw with one.

Coloration. — No fresh specimens were available for this study. Based on Boulenger's (1909) original description of *G. ansorgii*, the head and back are greyish whereas the rest of the body is yellowish; fins are white. According to Günther (1862), "Upper parts grey, lateral and lower silvery; an ovate spot before each dorsal ray; caudal grey." Preserved material is uniformly dark brown.

Ecology. Primarily brackish water/estuarine, but may ascend rivers according to Harrison and Miller (1992). Boulenger (1909) stated that his material was collected at low tide from exposed muddy, river banks.

Distribution. Material examined ranged from Senegal to the Congo. Harrison and Miller (1992) stated that this species extends as far south as Zaire.

Remarks. The original description is in error reporting 11 precaudal vertebrae; I counted 10 precaudal vertebrae from a radiograph of the holotype. Boulenger (1909) indicated a variable count of VI–VII, 19–21 for the dorsal fin. Based on counts of dorsal-fin elements from 18 radiographs of *G. sagitta*, all were VI–I, 19 (Table 2).

Günther (1862) mistakenly believed his new species was from California. According to Darrell Siebert, Curator of Fishes, BMNH, (pers. comm.) descriptions of fishes in Günther's paper were based on specimens deposited in the museum by a Mr. A. Murray and included fishes from both California and Old Calabar (Nigeria).

In the same paper that Günther (1862) described *Amblyopus sagitta*, he also erected *Tyntlastes*. Gunther's intention was to differentiate his new species (*A. sagitta*) that he believed was from California from both *Amblyopus* and *Gobioides*. Günther stated that both *Amblyopus* and *Gobioides* possessed bands of teeth in their jaws (vs. a single series in *Tyntlastes* according to Günther) and neither *Amblyopus* nor *Gobioides* occurred in California. However, Günther was mistaken in both the number of tooth rows in his new species as well as its origin.

Type material of *G. senegalensis* was not preserved (Bauchot et al., 1991). Maugé (1986) included *Gobioides senegalensis* Puyo, 1957, in the synonomy of *G. africanus*; Bauchot et al. (1991) did likewise. However, Harrison and Miller (1992) concluded that *G. senegalensis* is a junior synonym of *G. ansorgii* (=*G. sagitta*). Based on the information provided in the original description of *G. senegalensis*, I concur with Harrison and Miller.

Gobioides peruanus (Steindachner, 1880) (Fig. 9)

Amblyopus peruanus Steindachner, 1880: 94, pl. 2, figs. 2, 2a (type locality, Guayaquil, Ecuador).

Gobioides peruvianus: Clark, 1936: 391 (misspelling of *G. peruanus*).

Material examined. (10 specimens from 6 localities, size range 25–261): Ecuador, Guayaquil: NMW 76499, holotype of *Amblyopus peruanus* Steindachner, 249. Manabi Province: CAS 11566, 2 : 241–244. Panama, Yaviza: USNM 293271, 1 : 125. Miraflores: SIO 71-83, 1 : 261; USNM 123615, 1 : 188. Costa Rica: USNM 123616, 1 : 117. El Salvador: SIO 73-277, 2 : 25–36.

Description. As for genus except as noted. Mouth very oblique with anterior tip of lower jaw on a horizontal with ventral margin of eye; maxilla terminating at or near a vertical with posterior margin of eye.

Meristics. — Dorsal fin VI-I, 15; anal fin I, 15; caudal vertebrae 17; pectoral fin with 19–20 rays. Two or three rows of teeth in each jaw, outer row in upper jaw, 12–46, outer row in lower jaw, 9–42.

Coloration. — Based on Allen and Robertson

Table 2. Meristic data collected for species of *Gobioides*

Species\Meristics	Caudal vertebrae	Total dorsal-fin soft rays	Total anal-fin soft rays
G. africanus (6)	16	14	14
G. grahamae (6)	16	14	13–14
G. broussoneti (14)	17	15	15
G. peruanus (5)	17	15	15
G. sagitta (18)	21	19	19

Numeral in parentheses following species name is the number of specimens radiographed or cleared and stained.

Fig. 9. *Gobioides peruanus*, 140 mm SL, Aqua Dulce, Panama. Photograph by G. R. Allen.

(1994), the body is pale tan with a golden sheen on the gill cover and side of body; the dorsum is brown with brown, vertical bars extending ventrally, bars not distinct posterodorsally. In preservative, bars on body appear as purplish brown chevrons.

Ecology. Inhabits muddy burrows in brackish tidal rivers and freshwaters according to Allen and Robertson (1994). Based on an analysis of stomach contents, this species feeds on diatoms almost exclusively.

Distribution. Ranging from the Bay of Paita, southwest of Caleta Colan, Peru (Evermann and Radcliffe, 1917) northward to at least El Salvador and possibly as far north as Jalisco, Mexico (Cajiga, 1993). Has been collected by trawls from depths as great as 47m off the coast of Costa Rica.

Remarks. Günther (1862) stated the range of *Gobioides* as only "Coasts of Peru and Guayaquil," though no specimen was definitely listed from Peru. Evermann and Radcliffe (1917) is apparently the first definite Peruvian record. This species has matching meristics to a Western Atlantic congener (*G. broussoneti*); they are probably geminate species.

Hildebrand (1946) described a number of differences to distinguish *G. broussoneti* from *G. peruanus*. The only differences cited by Hildebrand that I believe have merit are: 1) degree of obliqueness of the mouth being greater in *G. peruanus* than in *G. broussoneti*; and 2) maxilla terminating ventroposterior to the eye in *G. broussoneti* whereas in *G. peruanus*, the maxilla terminates just before or at a vertical with the posterior margin of the eye.

Gobioides broussoneti Lacepède, 1800
(Figs. 10, 11)

Gobioides broussonnetii Lacepède, 1800: 576, 580, pl. 17, fig. 1 (species name emended based on Robins et al., 1980; type locality is presumably Surinam, "given by Holland to France").

Amblyopus brasiliensis Bloch & Schneider, 1801: 69 (based on a drawing commissioned by Johan Maurits of Nassau, Governor-General of Dutch Brazil from 1637–1644).

Gobius oblongus Bloch & Schneider, 1801: 548 (based on Lacepède).

Cepola unicolor Gray, 1854: 188 (synonymy proposed by Palmer and Wheeler, 1955, based on examination of the Gronovius collection of fish-skins).

Gobioides barreto Poey, 1860: 282 (type locality, Cuba).

Amblyopus broussonetii: Günther, 1861 (new combination).

Amblyopus mexicanus O'Shaughnessy, 1875: 147 (type locality, Mexico).

Cayennia guichenoti Sauvage, 1880:57 (type locality, Cayenne, French Guiana).

Material examined. (24 specimens from 12 localities, size range 68–459): Florida, Salerno: ANSP 71736, 1 : 440. Louisiana, Cameron: SU 21381, 1 : 119; Lake Borgne: USNM 156576, 1 : 189. Texas, Brazoria: ANSP 74023, 1 : 68. Cuba: MCZ 13246, holotype of *Gobioides barreto* Poey, 459. Puerto Rico: ANSP 144502, 1:180. Mexico, east coast ?: BMNH (unregistered), holotype of *Amblyopus mexicanus* O'Shaughnessey, 400. Colombia, Gulf of Uraba: UF 223836, 2:196-222. Venezuela, Orinoco River: USNM 233612, 4:92–132. Surinam?: MNHN 4209, holotype of *Gobioides broussoneti* Lacepède, 214. French Guiana, Cayenne: MNHN 6200, holotype of *Cayennia guichenoti* Sauvage, 334. Brazil: BLIH 1980131, 2 : 131–134. Atafona: ANSP 121256, 2 : 132–143. Cananeia: BLIH 1949006, 5:139-166.

Description. As for genus except as noted. Mouth oblique with anterior tip of lower jaw ventral to a horizontal with ventral margin of eye; maxilla terminating posteroventral to eye.

Meristics. — Dorsal fin VI-I, 15; anal fin I, 15; caudal vertebrae 17; pectoral fin with 17–20 rays.

Fig. 10. *Gobioides broussoneti*, 186 mm SL, female. Photograph courtesy of S. Poss, Gulf Coast Research Laboratory.

Fig. 11. *Gobioides broussoneti* from Bean and Bean (1894).

Scale rows in longitudinal series about 160. Two or three rows of teeth in each jaw.

Coloration. — Fresh material was not available for this study. Based on Dawson (1969), "Dorsum, lateral head and body purplish-brown, variously interrupted with cream-white; lateral body with 25–30 anteriorly directed dark chevron-like markings, ventral head and abdomen generally pale; anterior margin of lower jaw and gular region dusky; caudal fin dusky; pectoral fins with 3–4 faint dusky vertical bars; pelvic and anal fins pale." Preserved specimens are tan to pale brown laterally, dorsum brown. Myomeres brownish. Pigment on dorsum courses along dorsal-fin elements. Caudal fin dusky grey, anal fin whitish.

Ecology. Occurs in low salinity (less than 1 ppt), muddy marsh habitats and offshore (50 fathoms) sand-bottom habitats (Dawson, 1969; Lee et al., 1980). Can ascend rivers.

Distribution. Ranging from Charleston, South Carolina (Lee et al., 1980) southward to Florida, along the Gulf of Mexico coasts of Alabama, Mississippi, Louisiana, and eastern-central Texas; along the Caribbean coast of Colombia, eastward to Venezuela, Surinam, Guyana, French Guiana, and Brazil as far south as Rio Grande do Sul, Brazil (Menezes and Figueiredo, 1985.)

Remarks. This species appears to overlap in distribution (Guyana to northern Brazil) with its Western Atlantic congener, *G. grahamae*. It is not known if these species are sympatric, however, it appears that they share similar ecological requirements.

Günther (1861) stated the range of *Amblyopus broussonetii* as the "Coasts of Peru and Guayaquil."

The only feature used by O'Shaughnessy (1875) to distinguish *Amblyopus mexicanus* from *G. broussoneti* was size and distribution of teeth; these characters are considered too variable for distinguishing species.

Comments on *Amblyopus brevis* Günther

Palmer (1952) recognized eight species of *Gobioides*, seven of which have been treated above. The other species not yet discussed here is *Amblyopus brevis* Günther (1864) from Panama that was considered by Palmer to be a species of *Gobioides*. (Jordan and Eigenmann [1887] assigned this species to *Tyntlastes*.) An examination of a radiograph of the holotype of *A. brevis* (BMNH 1864.1.26.416) revealed a pterygiophore formula of 3-22 1110 as well as 11 precaudal and 16 caudal vertebrae. Based on these two characters, this specimen is not a *Gobioides* as defined here. Using character distributions cited in Birdsong et al. (1988), *A. brevis* likely is either a member of the Gobiosoma or Microgobius groups and, thus, is best considered part of the Gobiinae (sensu Pezold, 1993).

Discussion of Relationships and Biogeography

A close relationship between *Gobioides* and amblyopine gobies has been accepted historically in the literature. Recent evidence suggests these genera are, at best, distantly related and that *Gobioides* belongs with the Gobionellinae rather than the Amblyopinae. The Gobionellinae is a non-monophyletic assemblage comprising *Gobionellus* and more than 50 other gobiid genera that are not assignable to any of the following gobiid subfamilies: Amblyopinae, Gobiinae, Oxudercinae, and Sicydiinae. Whereas the members of the Gobionellinae lack a synapomorphy, the Amblyopinae (sensu Pezold, 1993) possess the derived fin element to vertebra ratio of 2 : 1 (Birdsong et al., 1988). As noted by Pezold (1993), *Gobioides* has a fin element to vertebra ratio of 1 : 1 and, thus, its affinities are outside the Amblyopinae. As also noted by Pezold (1993), *Gobioides* shares with *Gobionellus* an extensive cephalic lateralis canal system with identical pore patterns and the posterior opercular row of sensory papillae intersects with the subopercular row; both of these conditions are considered derived. In addition, one species of *Gobionellus* (*G. liolepis*) has united dorsal fins as seen in *Gobioides* (F. Pezold, pers. comm.). Also, Harrison (1989) described an apomorphic palatine structure that unites *Gobioides*, *Gobionellus*, and several other gobionelline genera. Based on the above, *Gobioides* is best considered a member of the Gobionellinae.

Within the species of *Gobioides*, vertebral counts are stable (Table 2) and can be polarized. All species have a precaudal vertebral count of 10. Counts of caudal vertebrae vary according to species: 16 (*G. africanus* and *grahamae*); 17 (*G. broussoneti* and *peruanus*); and 21 (*G. sagitta*). Gobionelline gobies typically have caudal vertebral counts of 15 or 16, or, rarely, 17 (Birdsong et al., 1988). Therefore, caudal vertebral counts of 17 and 21 within *Gobioides* could be considered apomorphic in comparison to other gobionellines. It is likely that the caudal vertebral count of 21 can be used to define *G. sagitta* and 17 caudal vertebrae can be considered a synapomorphy for *G. broussoneti* and *G. peruanus*. In comparison to other gobionellines, the union of the medial fins with the caudal fin is considered apomorphic. Therefore, by its lacking this feature, *G. africanus* is the sister group to all other *Gobioides*. I speculate that a *Gobioides*-like ancestor was present in the proto-eastern Atlantic when South America separated from Africa 100 mya and that it may have had 16 or fewer caudal vertebrae when it migrated westward with the South American continent. This ancestor may have given rise to a *Gobioides* possessing 17 caudal vertebrae similar to *G. broussoneti* and *G. peruanus* today. *G. broussoneti* and *G. peruanus* represent sister-species, most likely resulting from the closure of the transisthmian seaway across Central America and subsequent isolation leading to speciation. In the eastern Atlantic, *G. sagitta* (21 caudal vertebrae) may also have evolved from an ancestor with 16 or fewer caudal vertebrae. The question of why there are no species of *Gobioides* with 18, 19, or 20 caudal vertebrae is intriguing.

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