

A REVIEW OF THE SPINYCHEEK SLEEPERS, GENUS *ELEOTRIS*  
(TELEOSTEI: ELEOTRIDAE), OF THE WESTERN HEMISPHERE, WITH  
COMPARISON TO THE WEST AFRICAN SPECIES

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ABSTRACT

Species of the genus *Eleotris* from the eastern Pacific and western Atlantic are reviewed. Three species are recognized from the eastern Pacific region. The wide-ranging *Eleotris picta* Kner, *Eleotris tubularis* Heller and Snodgrass (endemic to Cocos Island), and *Eleotris tecta* Bussing (limited to Costa Rica, Panama and Colombia) are distinguishable by scale counts (size), cephalic neuromast features and morphology of the urogenital papilla. Three western Atlantic species are recognized. *Eleotris pisonis* (Gmelin) is a continental South American species ranging from southern Brazil to the Orinoco River delta in eastern Venezuela. A second primarily continental species, *E. amblyopsis* (Cope), is distributed from Brazil through the Caribbean basin and Gulf of Mexico to North Carolina. *Eleotris perniger* (Cope), largely Caribbean in distribution, is the prevalent species in the Antilles and Quintana Roo, but is also sympatric with *E. amblyopsis* in Central America. The three western Atlantic species differ in scale counts and cephalic neuromast patterns. *Eleotris daganensis* Steindachner of West Africa is morphologically indistinguishable from *E. amblyopsis*. Lacking evidence of connectivity between eastern Atlantic populations of *E. daganensis* and western Atlantic populations of *E. amblyopsis*, the species are not synonymized. *Eleotris annobonensis* Blanc, Cadenat and Stauch is similar to *E. perniger* and North American populations of *Eleotris amblyopsis*. The remaining three West African species of *Eleotris* are most similar to *E. picta* of the eastern Pacific. *Eleotris* and *Erotelis* are recognized as distinct genera.

## INTRODUCTION

Spinycheek sleepers in the genus *Eleotris* are sit-and-wait predators characterized by a distinctive eleotrid morphology - moderately blunt large head, torpedo-like body form, broad, rounded caudal fin and prominent lower jaw (Fig. 1). In the tropics and subtropics, they are a common element in estuaries, insular freshwater streams and small continental streams with poorly developed freshwater ichthyofaunas. Although they are not important as food fishes in most places, spinycheek sleepers are likely an important component of these subtropical and tropical ecosystems, both as predators and, in the larval stage, as a food source (e.g. Nordlie, 1979, 1981; Perrone and Vieira, 1990, 1991). Despite the growing interest in their ecological roles in freshwater and estuarine communities, little attention has been given to the systematics of *Eleotris* species beyond the description of new species. The lack of significant interest is likely the synergistic result of the cosmopolitan distribution of the genus, a plethora of nominal species, few diagnostic characters with which to work and a confusing amount of state variation for those characters.

When it was extricated from *Gobius* 200 years ago, species included in the genus *Eleotris* were distinguished in that they lacked a cup-like base formed by joined pelvic fins, although the pelvic fins were described as connected by membranes (Bloch and Schneider, 1801). Through time the genus came to be identified with gobioid species with separate pelvic fins; species characterized by that feature were routinely tossed into the *Eleotris* bin throughout the 1800's and early 1900's (more than 200 species [Eschmeyer, 1998]). Although most of these species have been removed in turn to other genera, and in some cases families, the genus has never been revised or reviewed in its entirety and a number of nominal taxa remain for which validity has never been tested. Only two regional reviews have been accomplished. Akihito (1967) examined species from Japan and compared them to several other Indo-Pacific species. His study was particularly important in demonstrating the significance of the free neuromast patterns on the head for diagnosing species. More recently, Miller (1998) reviewed species from the eastern Atlantic. As did Akihito, he found cephalic free neuromast patterns and differences in squamation the most useful characters in separating species. Miller also offered what he termed a phenetic diagnosis of the genus based on the antrorse spine on the preoperculum, axial osteology and features of the cephalic lateralis system. He proposed that the genus *Erotelis* was a junior synonym of *Eleotris* as the former's two included species shared these diagnostic features.

This paper reports the results of a review of *Eleotris* species from the Western Hemisphere, the eastern Pacific and western Atlantic basins. Species are compared to West African *Eleotris* and a key is provided to the species of the



Figure 1. *Eleotris amblyopsis*, from Tortuguero, Costa Rica, NLU 69723.

western Atlantic and eastern Pacific oceans. *Eleotris* and *Erotelis* are distinguished and their separate recognition is recommended.

#### METHODS

Meristic and mensural characters and procedures follow Hubbs and Lagler (1958), except for the following: preanal length, postanal length, head width at the preopercle, length of the urogenital papilla, body width at pectoral fin base, and body width at second dorsal fin origin. Preanal length is the least distance from the vent to the tip of the snout, and postanal length is the least distance from the vent to the hypural of the caudal peduncle. Head width is the greatest lateral distance through the fish at the preopercle. Urogenital papilla length was measured from the vent to the distal tip of the papilla. Body widths are the greatest distance through the body at the bases of the left and right pectoral fins, and the greatest distance through the body at the origin of the second dorsal fin. Head length, head width at preopercle, pre-dorsal length, nape height, preanal length, postanal length, caudal peduncle length, body width at pectoral fin base, body width at second dorsal fin origin, urogenital papilla length, pectoral fin length, pelvic fin length, and caudal fin length are reported as proportions of standard length (SL). Interorbital width, upper jaw length, orbit length, and snout length are reported as proportions of head length (HL). First dorsal fin pterygiophore insertion pattern formulas are as given in Birdsong et al. (1988). Meristic information is reported as mode (range).

Principal component analyses were used to separately investigate morphological and meristic variation among species. Principal component scores derived from untransformed morphological variables were regressed against standard length. To remove size as a factor in the analyses, residual values for each specimen were then used in the scatter plots. Preliminary analysis disclosed no sexual dimorphism for morphological features other than urogenital papilla form, which was not included in the analysis. Males and females were pooled in subse-

quent analyses. Samples of the wide-ranging species *Eleotris amblyopsis* and *E. picta* were studied for geographic variation. For these analyses, *Eleotris picta* samples were subdivided into roughly equal latitudinal regions because there are no obvious geographic barriers or restrictions to movement throughout its range. *Eleotris amblyopsis* samples were subdivided into natural geographic units based upon regional current patterns, land mass distributions and distribution patterns observed for other gobioid fishes in the western Atlantic (e.g. Pezold and Grady, 1989).

Cephalic neuromast distribution patterns and urogenital papilla anatomy were examined and illustrated using a dissecting microscope and camera lucida. Cephalic neuromast patterns are described using terminology developed by Sanzo (1911) with modifications employed by Miller and Wongrat (1991). Transverse suborbital rows are designated with Arabic numbers and major horizontal rows on the cheek are indicated with the letters *b* and *d*. To simplify references to the particular transverse suborbital rows crossing row *d*, a formula of row numbers separated by periods is used. For example, if rows 2, 3 and 4 cross row *d*, this condition is represented by the formula "2.3.4." Similarly, the notation "2.4" indicates rows 2 and 4 cross *d*. Some species had incompletely formed rows, termed "segments." To be considered a "row" instead of a "segment," a line of papillae would have to reach at least half the distance between the eye and horizontal row *d*. Transverse opercular rows are labeled *ot* and *ot'*. Upper and lower longitudinal rows on the operculum are labeled *os* and *oi*, respectively (Fig.2).

Decisions of species limits were rooted in the Evolutionary Species Concept (Wiley and Mayden, 2000). Operational applications differed for sympatric and allopatric populations. Reproductive isolation was inferred from concordant patterns of variation of at least two morphological characters in sympatric population samples (Brown and Wilson, 1952; Grady and Quattro, 2000). For species determinations of allopatric population samples, the degree of morphological differentiation between samples was compared to that observed among sympatric samples. In the latter case, the possibility for gene flow through dispersion or dispersal, and probable length of separation were also considered.

Museum acronyms follow Leviton et al., 1985 and Leviton and Gibbs, 1988, except where noted in the list of materials examined.

## RESULTS

**EASTERN PACIFIC.** Three species of *Eleotris* are easily distinguished in the eastern Pacific basin using meristic features, cephalic neuromast patterns, urogenital papillae and pigmentation. Morphological variation was largely uninformative within or among species with the exception of the urogenital papilla (Table 1). Although some differences among species appeared in the simple examination of relative proportions presented in Table 1, no significant interspecific distinctions



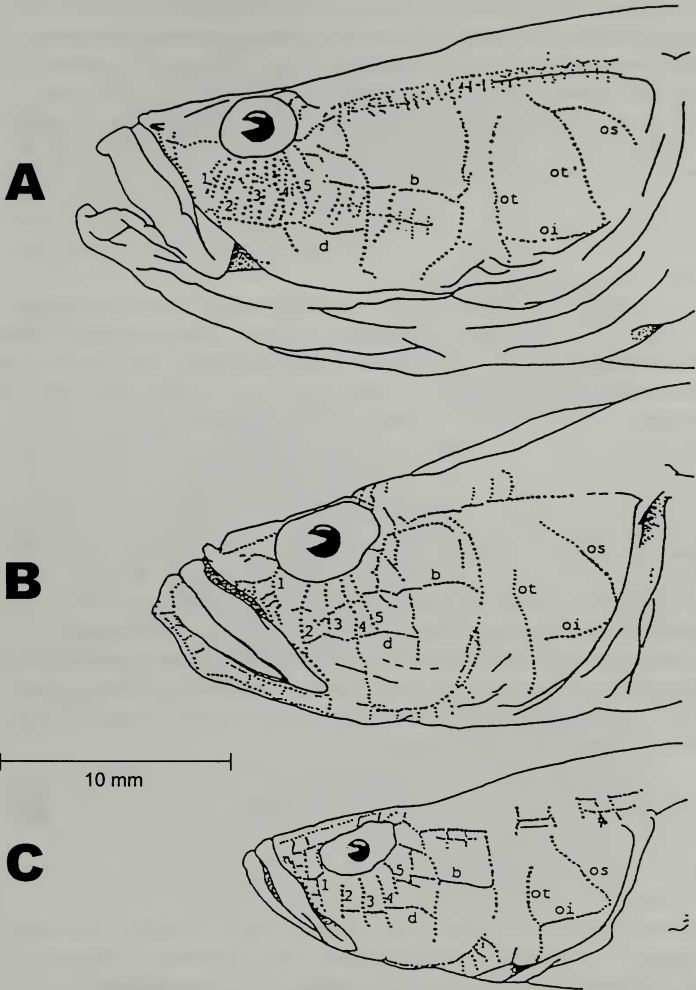


Figure 2. Cephalic free neuromast patterns of eastern Pacific *Eleotris* species. a) *Eleotris picta* b) *Eleotris tubularis* c) *Eleotris tecta*.

were retained in the multivariate analysis after principal component scores were corrected for size correlations. The urogenital papilla of female *Eleotris picta* is different from that of both *E. tubularis* and *E. tecta*. The posterior margin is not as rounded and has a fringe of finger-like projections that flare in the largest females (Fig. 3). Females of *E. tecta* and *E. tubularis* have robust, round urogenital papillae with fewer fringes. The urogenital papillae of female specimens of *Eleotris picta* develop more slowly than their smaller relatives. Among female specimens of *E. tecta* and *E. tubularis*, urogenital papillae vary little other than the development of longer pre-vent furrows in *E. tubularis* (Fig. 3). Urogenital papillae development in males occurs at a smaller size in *Eleotris tubularis* and *E. tecta* compared to *E. picta* (Fig. 4).

Principal components analysis of meristic features clearly separated the three species (Fig. 5). *Eleotris picta* has more predorsal scales than either eastern Pacific congener (Table 2). It also has more lateral scale rows than the others, but does overlap with *E. tecta*. *Eleotris tubularis* has a lower lateral scale count than either eastern Pacific congener (Table 2). When comparing transverse scale counts, *E. picta* has a much higher count than *E. tubularis*, whereas *E. tecta* has an intermediate range. *Eleotris tecta* is distinct from *E. picta* in having a lower range for caudal peduncle scale count, but is not distinguished by that feature from *E. tubularis* (Table 2). Although overlap occurs, the means and modes for pectoral-fin elements are distinct for each species. Modes observed were 18 for *Eleotris picta*, 17 for *E. tecta* and 16 for *E. tubularis* (Table 2). Principal components analysis of meristic characters among the regional samples of *Eleotris picta* suggested clinal variation from high values in the region of Guatemala-Costa Rica to lower values both southward and northward. The pattern reflected variation primarily of transverse scale row counts and caudal peduncle scale counts (Table 3). Specimens from Mexico (regions 1 and 2 in Table 3) also had higher numbers of lateral and predorsal scales.

*Eleotris* from the eastern Pacific differ consistently in cephalic free neuromast patterns (Fig. 2). Though intraspecific variation can be observed, species are distinguished by the number and specificity of transverse suborbital rows extending ventrally beyond horizontal row *d*, the presence of row *ot'*, and the union or separation of opercular rows *os* and *oi*. The transverse suborbital rows of *Eleotris picta* and *E. tubularis* have the same configuration, rows 2 and 4 extend well ventral to horizontal row *d* in both species (2.4 pattern), but additional segments, incompletely formed superficial rows occur between the transverse rows in *E. picta*. In contrast to its two congeners, transverse suborbital row 3 crosses horizontal row *d* in *E. tecta* (Fig. 2). The cephalic neuromast pattern of *E. picta* is also distinguished from those of *E. tecta* and *E. tubularis* by the addition of an opercular posterior vertical row *ot'*. In *Eleotris picta*, *ot'* connects with opercular row *os* to form a fork on the upper posterior portion of the opercle. Row *ot* continues obliquely to the margin of the opercle where it connects

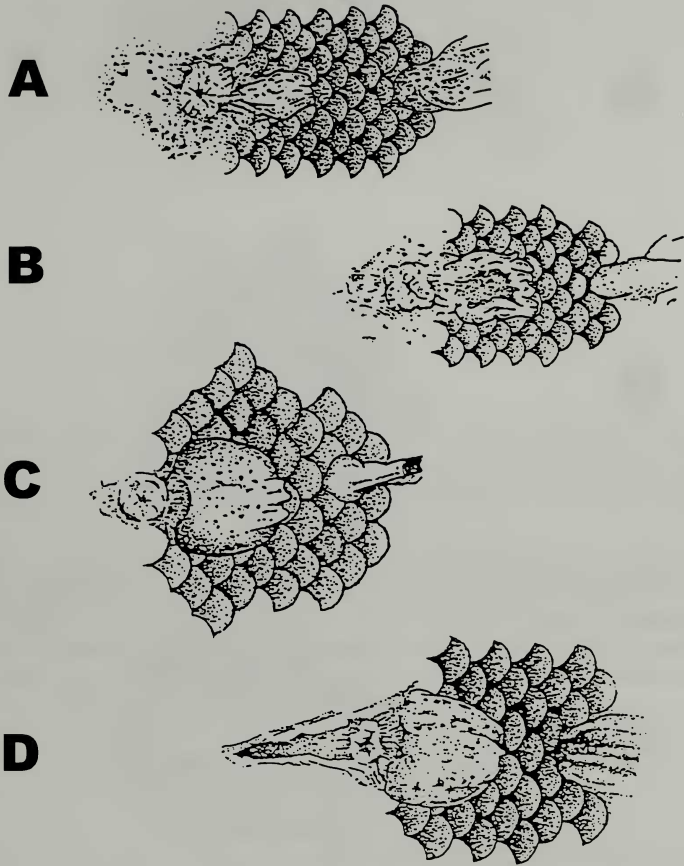


Figure 3. Comparison of the urogenital papillae among females of eastern Pacific *Eleotris*. a) *Eleotris picta* 63.7 mm SL (TNHC 14755) b) *Eleotris picta*, 63 mm SL (USNM 293478) c) *Eleotric tecta*, 55.1 mm SL (CAS 137539) d) *Eleotris tubularis*, 58.7 mm SL (LACM 200047).

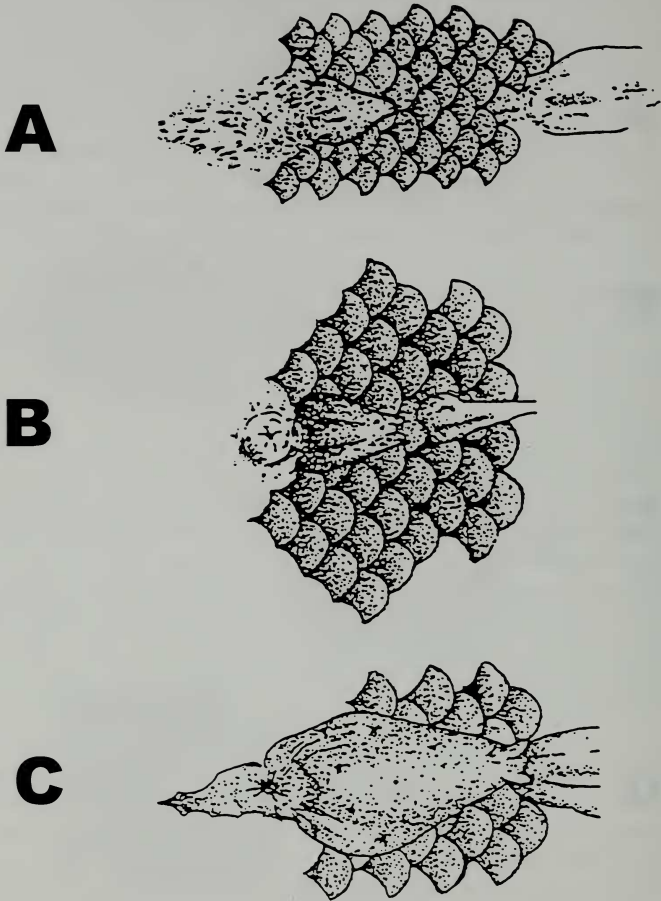


Figure 4. Comparison of urogenital papillae among males of eastern Pacific *Eleotris*. a) *Eleotris picta*, 51.4 mm SL (ANSP 144132) b) *Eleotris tecta*, 42.0 mm SL (CAS 66639) c) *Eleotris tubularis*, 50.5 mm SL (LACM 25806).

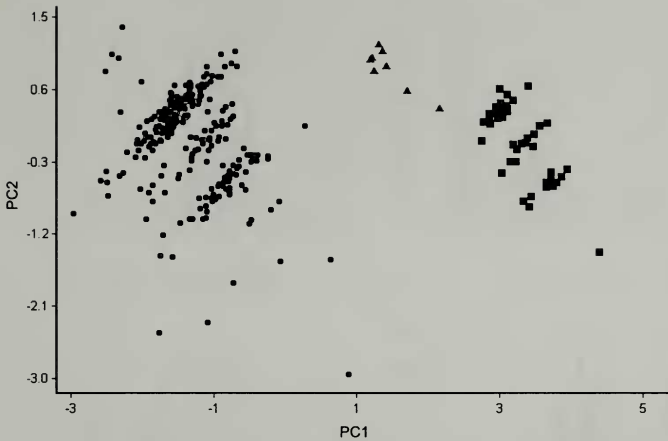


Figure 5. Principal components analysis of eastern Pacific *Eleotris* populations using meristic features (transverse scale rows, lateral scale rows, caudal peduncle scale rows, pectoral fin rays and predorsal scales). Dots = *Eleotris picta*, triangles = *E. tecta*, and squares = *E. tubularis*.

with lower longitudinal row *oi* (Fig. 2). *Eleotris tubularis* and *E. tecta* lack *oi* altogether. The relationship between rows *os* and *oi* differs between *Eleotris tubularis* and *E. tecta*. The upper row *os* in *E. tecta* shifts obliquely downward to meet the posterior end of lower longitudinal row *oi* on the lower right posterior margin of the opercle. Intersection of upper row *os* and lower longitudinal row *oi* was not observed in specimens of *E. tubularis* (Fig. 2).

Although all three species have a basic brown body color, pigmentation varies among the species. *Eleotris tecta* has horizontal rows of spots along the sides and a prominent spot on the upper pectoral fin base. *Eleotris tubularis* lacks both well-defined rows of spots along the sides and the spot on the upper pectoral fin base. *Eleotris picta* has a dark band or row of blotches along the upper flanks, lacks the dark spot on the upper pectoral fin base and often has a mottled body.

WESTERN ATLANTIC. The three western Atlantic species are not so easily delineated, but a combination of meristic, neuromast patterns and subtle pigmentation differences does allow their distinction. As with the eastern Pacific species, morphometry was of little help in distinguishing taxa, even with principal components analysis (Table 4).

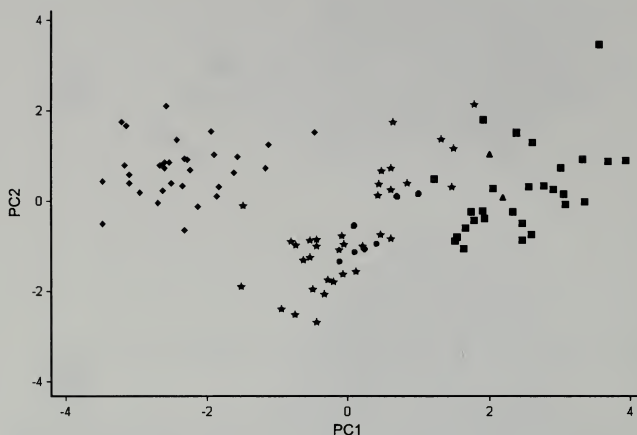


Figure 6. Principal components analysis of western Atlantic *Eleotris* populations using meristic features (transverse scale rows, lateral scale rows, caudal peduncle scale rows, pectoral fin rays and predorsal scales) and cephalic suborbital neuromast patterns. Diamonds = *Eleotris perniger*, stars = *E. pisonis*, dots = *E. amblyopsis* from the Gulf of Mexico, triangles = *E. amblyopsis* from SE Florida, and squares = *E. amblyopsis* from Central and South America.

Meristic and cephalic neuromast features clearly separate *Eleotris amblyopsis* and *E. perniger* (Fig. 6). The meristic differences are best illustrated by a comparison of lateral scale row counts (Table 5). *Eleotris amblyopsis* ranged from 40-58 with a mean of 49. *Eleotris perniger* had 54-68 with a mean of 60. The distinction between these two species is pronounced however, where they are sympatric in the Caribbean Basin; *E. amblyopsis* counts from that region ranged from 40-52 (Fig. 7 and 8). Lateral scale row number ranged from 47-63 with a mean of 54 for *Eleotris pisonis*. Although there was broad overlap with *E. amblyopsis*, *E. pisonis* counts were usually 50-54 in Guianas and eastern Venezuela where the two species are sympatric (Figs. 7 and 8). *Eleotris amblyopsis* counts ranged from 41- 46 in that region.

Cephalic free neuromast patterns distinguish *Eleotris perniger* from its two western Atlantic congeners (Fig. 9). Whereas *E. perniger* typically has a 2.4.6 transverse suborbital row pattern, the other two species have a 2.3.4 pattern.



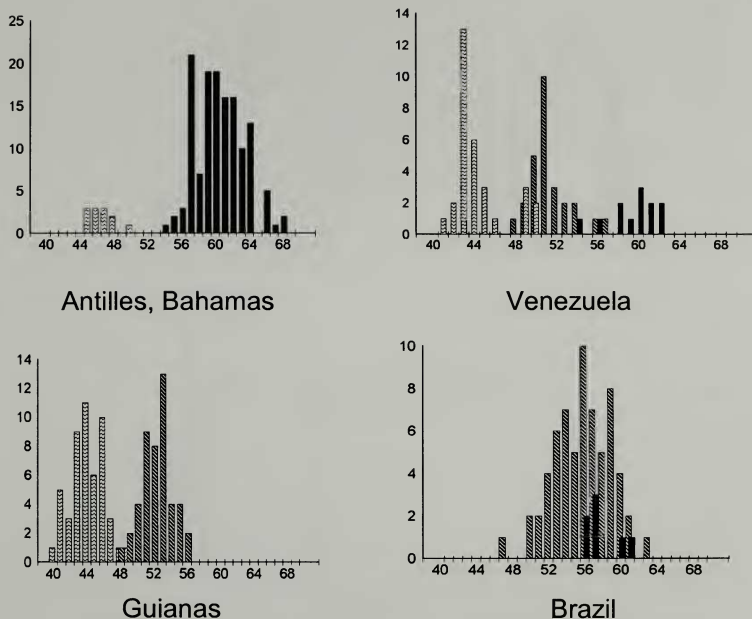


Figure 7. Frequency distributions of lateral scale counts (x axis) for western Atlantic *Eleotris* from South America, the insular Caribbean Basin and the Bahamas. Solid bars = *Eleotris perniger*, diagonal bars = *Eleotris pisonis* and wavy horizontal bars = *Eleotris amblyopsis*.

*Eleotris perniger* may also develop additional short segments between the primary rows. *Eleotris amblyopsis* from North America, particularly specimens seen from North Carolina, may have an additional row developed on one side of the head or the other. Many specimens from the Gulf of Mexico and the Carolinas also had occasional short segments developing between the primary rows. Intraspecific variation is detailed in the species accounts below. None of the western Atlantic species exhibit opercular row  $ot'$  and  $os$  and  $oi$  are generally connected although this may be variable within species.

Pigmentation is remarkably similar among the three western Atlantic species, and actually throughout the genus. Preserved specimens of all three species are basically tawny in body color with a light colored abdomen. *Eleotris perniger* tends to have well-developed horizontal rows of spots on the flanks that in some specimens appear as continuous lines. Of the other two species, *E.*

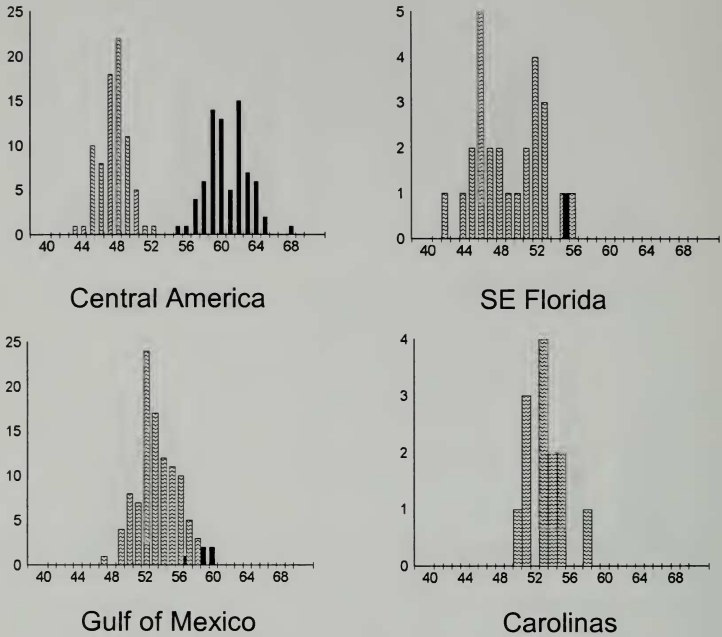


Figure 8. Frequency distributions of lateral scale counts (x axis) for western Atlantic *Eleotris* from North and Central America. Solid bars = *Eleotris perniger* and wavy horizontal bars = *Eleotris amblyopsis*.

*amblyopsis* may have horizontal rows of spots, but less regularly arranged or contrasted as in *E. perniger*. Most often, *E. amblyopsis* shows scattered spots along the upper flanks which may not be arranged in rows. *Eleotris pisonis* specimens were seen with the scattered spots as in *E. amblyopsis*, but sometimes spots on the sides were entirely lacking. *Eleotris perniger* and *E. amblyopsis* both have a dark spot on the upper pectoral-fin base. This spot was generally not observed in *E. pisonis*, but when it was expressed it was poorly contrasted and not as pronounced as dark pigment above the pectoral-fin base on the side of the nape. Individuals of any of these species or the eastern Pacific species may shift to a two-tone appearance of the trunk in which a light dorsum is sharply and evenly contrasted with dark flanks.

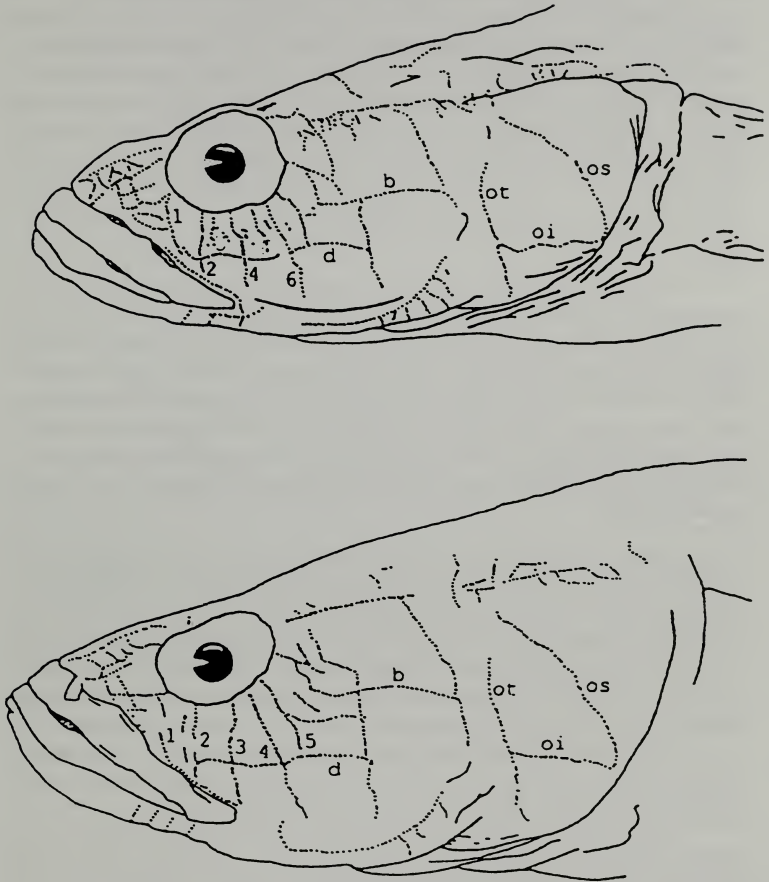


Fig. 9 Cephalic free neuromast patterns of western Atlantic *Eleotris* species, *E. perniger* (above) 57.5 mm SL, NLU 69725 and *E. amblyopsis* (below) 60.7 mm SL, NLU 69723. The suborbital free neuromast configuration of *Eleotris pisonis* (not illustrated) is the same as that shown for *E. amblyopsis*.

## DISCUSSION

Our findings support the recognition of six *Eleotris* species in the Western Hemisphere. Bussing (1996) and Miller (1998) have previously noted the conservative morphology of the genus. The only significant morphometric variation we observed was that of the form of the urogenital papilla, which is useful in determining the sex of individuals. Eye size was a major distinguishing feature in Jordan and Gilbert's (1896) original description of *E. abacurus* and a relatively larger eye size has been used since then to separate *E. amblyopsis* from *E. perniger* (referred to in most works as *E. pisonis*) in keys to eleotrids of the western Atlantic (e.g. Villa, 1982). We found no concordance between eye size variation and the other features determined diagnostic for the western Atlantic species.

Despite the importance of meristic characters in delimiting the species, some meristic features regarded as diagnostic in the literature were uninformative. Jordan and Evermann (1898) used the extent of cheek squamation to distinguish *E. amblyopsis* (including *E. abacurus*, a synonym herein) and *E. pisonis* from *E. perniger*. *Eleotris amblyopsis* and *E. pisonis* were described as having fully scaled cheeks, while those of *E. perniger* were only ½ scaled. We found cheek squamation highly variable within species. The extent of squamation on the snout and interorbital region, characters examined by Akihito (1967), were also of no utility.

COMPARISONS WITH WEST AFRICAN SPECIES. *Eleotris daganensis* Steindachner, 1869 of the eastern Atlantic is indistinguishable from *E. amblyopsis* from the Caribbean Basin. The free neuromast patterns, number of lateral scale rows and body and fin pigmentation are similar in type and variation. The number of scales in a lateral series ranged from 44 - 53 with a mean of 48 in 48 specimens of *E. daganensis* examined. Specimens of that species typically had a 2.3.4 suborbital neuromast pattern, but of 38 examined one had a 2.3.5 pattern and another 2.3.4.5. Undoubtedly, *E. amblyopsis* and *E. daganensis* are closely related and possibly sister species. Their relationship to *E. annobonensis*, *E. perniger* and *E. pisonis* is close and undecipherable from comparative morphology.

*Eleotris annobonensis* from the eastern Atlantic islands of Equatorial Guinea and Pagalu (Annobon) is similar to *E. perniger*. Pigmentation is comparable between these two species and lateral scale row numbers are the same. Suborbital free neuromast patterns differ slightly in the extent of supernumerary row development. Whereas 2.4.6 is the predominant pattern in *E. perniger*, 2.3.4 with intervening segments was the most common pattern observed in the 22 specimens of *E. annobonensis* we examined, including types. Only 3 specimens had a 2.4.6 pattern; one specimen had a 2.4 pattern and another a 2.5.8 pattern.

Of all the *Eleotris* species in the eastern Pacific and Atlantic basins, *Eleotris picta* is most similar to *E. senegalensis*, *E. feai* and *E. vittata* from West Africa. All four species have the forked neuromast pattern on the upper operculum. All are large species for the genus, with *E. picta* possibly reaching the largest size. *Eleotris picta* is similar in lateral scale row number to *E. vittata* and *E. feai*. Twenty specimens of *E. vittata* had a range of 57-65 and a mean of 61. Two paratypes of *E. feai* had counts of 62 scales. Although *E. senegalensis* has larger scales (and therefore a lower count), most specimens examined exhibited a 2.4 suborbital neuromast row pattern as in *E. picta*. There was variation observed for this feature in both *E. vittata* and *E. senegalensis*, however. The 19 specimens of *E. vittata* examined for the character showed five patterns - 2 (15 specimens), 3 (1), 2.3 (1), 2/2.5 (1) and 2.4/2.5 (1). The *E. feai* paratypes had 2 and 2/2.5 patterns. Twenty-one specimens of *E. senegalensis* showed 2 character states - 2 (3) and 2.4 (18). A low degree of variation for this feature was also observed in *E. picta*; out of 255 specimens examined, four had 2.3.4 and one a 2.3.4.5 pattern. Of the four with the 2.3.4 pattern, only one had the aberrant pattern on both cheeks. Clearly, the phylogenetic lines of *Eleotris* hypothesized by Miller (1998) based upon differences in suborbital neuromast patterns may be confused when variation is considered. The potential for homoplasy is great.

*Eleotris amblyopsis* is not synonymized with *E. daganensis* and *E. perniger* is not synonymized with *E. annobonensis*. The allopatric distributions of these taxa make it difficult to evaluate the relationships of the amphi-Atlantic species pairs considering the scant, subtle and overlapping morphological variation of diagnostic characters observed among the western Atlantic taxa. For example, although North American populations of *E. amblyopsis* approach a morphology that could be confused with that observed in *E. perniger*, sympatric populations of the two species in the Caribbean Basin are clearly distinguished. Additionally, the distinctive compositions of the west African and western Atlantic gobioid faunas suggest that gene flow between gobioid fishes of these two long-isolated regions is unlikely, even considering the pelagic larval stage of these species. It is most parsimonious and consistent with the Evolutionary Species Concept not to synonymize the species pairs. There is considerable circumstantial evidence to suspect that these taxa have had independent evolutionary histories for millions of years and continue on distinct evolutionary trajectories. We also believe that application of the Morphological Species Concept to this genus of cryptic species is inappropriate because of the concept's insensitivity to the diversity the genus comprises.

The gobioid fauna of tropical West Africa comprises about 28 genera, including 8 that are endemic to that region and two others endemic to Africa (Birdsong et al., 1988). Three genera are shared with the Indo-Pacific (discounting the introduced *Prionobutis*) and four genera are shared only with the north-eastern Atlantic/Mediterranean region (Table 6). Five genera are shared only with

the Western Hemisphere. Five other genera are more cosmopolitan, occurring in the Western Hemisphere, Indo-Pacific and eastern Atlantic. Thus, of the 28 gobioid genera in West Africa, 10 are shared with the Western Hemisphere. One goby species possibly common to the eastern and western Atlantic, *Bathygobius soporator* (Miller and Smith, 1989), doesn't increase the likelihood of ongoing gene flow among other gobioids. It merely suggests a lack of differentiation despite a long period of isolation and offers no evidence of even an intermittent mechanism for larval transport east to west across the Atlantic. It should also be noted that there are five species of *Eleotris* in the eastern Atlantic, three of which (*E. feai*, *E. senegalensis* and *E. vittata*) have no counterpart in the western Atlantic. It seems unlikely that there should be any link between populations of *E. daganensis* or *E. annobonensis* and their New World counterparts, and not the other three species if east to west surface currents are the potential vehicle.

Miller (1998) suggests that a subsurface equatorial countercurrent could allow dispersal from west to east across the Atlantic. Studies of larval gobiids have shown a typical duration of 20 - 40 days (Breitburg, 1989; Brothers et al., 1983; McFarland et al., 1985). This is a much shorter period than the 96 days estimated as necessary for cross Atlantic subsurface transport at the equator (Scheltema and Hall, 1975). The western Atlantic has more than 120 gobioid species (Birdsong et al., 1988) and an entire tribe, the Gobiosomini, that is shared only with the more recently conjoined eastern Pacific. This degree of taxonomic distinction is consistent with the limitations on larval transport that may be inferred from the few studies mentioned above. However, a much longer larval period was observed by Radtke et al. (1988) for the Hawaiian freshwater gobiids *Stenogobius genivittatus* and *Awaous stamineus* that would span the 96 days estimated above. Studies of shore fishes of the St. Paul's Rocks (Lubbock and Edwards, 1981), St. Helena (Edwards and Glass, 1987) and Ascension Islands (Lubbock, 1980) are informative. No gobioid fishes were taken at St. Pauls' Rocks. Two gobies are known from Ascension and St. Helena, the western Atlantic *Gnatholepis thompsoni* and the endemic *Priolepis ascensionis*. One specimen of an *Eleotris* species was captured at St. Helena and referred to *E. pisonis*. This species' identity has not been checked by us. These mid-Atlantic tropical islands are more interesting for the gobioid species they lack, than for those that are present. The lack of more of the rocky reef-associated goby fauna suggests a passage too long or stressful for most gobioid fishes. Where is *Bathygobius soporator*? As for the single sleeper at St. Helena, was it a ballast introduction as we presume for the *Eleotris picta* specimen we have observed from Venezuela?

There is limited information available about the status of tropical Atlantic species within the ten gobioid genera common to both sides of the ocean, but it generally suggests isolation of the shore fauna. The only other shared eleotrid genus is *Dormitator*; the common west African species, *D. lebretonis*, is distinct



from the common western Atlantic species, *D. maculatus* (unpubl. data). The species limits and relationships within *Sicydium*, the only sicydiine genus common to streams in both the Caribbean Basin and Gulf of Guinea, are unclear, but Harrison (1993) observed that *S. bustamantei* from West Africa and specimens identified as *S. plumieri* from the Antilles were very similar and suggested that they could be amphi-Atlantic conspecifics as has been suggested for *Bathygobius soporator*. Watson (2000) redescribed *S. plumieri*, but did not include *S. bustamantei* in the synonymy. Although he indicated some familiarity with West African species, he did not list any comparative material from West Africa, so the question of species distinction remains unanswered. Among the shared gobiionelline genera, *Awaous*, *Ctenogobius*, *Gnatholepis*, *Gobioides* and *Gobionellus*, information on species status is available for three genera. In a recent review of the genus *Gobioides*, Murdy (1998) recognized two African species distinguished from western Atlantic species. *Gobionellus* and *Ctenogobius* are each represented by a single species in West Africa not found in the western Atlantic (Pezold, 1984). Reports of *Gobionellus oceanicus* from (e.g. Miller and Harrison, 1992) the Gulf of Guinea are presumed to be based on misidentifications of *G. occidentalis* as no specimens of this species were found from West Africa during an exhaustive review of the genus (Pezold, 1984). The gobiine genus *Priolepis* has not been reviewed for its Atlantic species.

The phylogenetic relationships of species within the 10 shared genera are for the most part unknown. Murdy (1998) offers evidence that *Gobioides africanus* is the sister group to the other species of the genus. Preliminary data also indicate that *Dormitator lebretonis* is the primitive sister group to the Western Hemisphere species (unpubl. data). These observations further support a long break between gobioid populations on the two sides of the Atlantic.

Instead of any active genetic exchange across the Atlantic we suggest that *Eleotris* is simply morphologically conservative. Similar morphotypes to those seen in the Western Hemisphere and the eastern Atlantic pop up in other tropical estuaries and insular streams, albeit ever so slightly different. Present circumglobal distributions suggest that several basic lines were separated long ago. This perspective is reinforced by the phylogenetic study of gobioid fishes using mtDNA by Akihito et al. (2000). The several species of *Eleotris* included in their analysis, *E. acanthopoma*, *E. fusca*, *E. melanosoma* and *E. oxycephala* were separated by greater genetic distances than were specimens in the morphologically distinct pairs of genera *Dormitator* and *Hypseleotris*, and *Calumia* and *Gobiomorphus*. The four species of *Eleotris* are distinguishable by cephalic free neuromast patterns and various meristic combinations similar to those seen in the Western Hemisphere.

PHYLOGENETIC RELATIONSHIPS. Miller (1998) subdivided *Eleotris* into clusters of nominal species based upon cephalic neuromast patterns. Although there is

heuristic value in his approach, cephalic free neuromast patterns must be used with caution in any phylogenetic reconstruction. The suborbital row patterns vary additively and ontogenetically, and that variation is significant, as can be seen in the species descriptions that follow. Variation among species also exists for the presence or absence of the *ot'* row that Miller regarded as a synapomorphy for *Leptophilypnus* and *Eleotris* (including *Erotelis*). In addition to the variation among *Eleotris* species as noted by Miller, it appears in only one of the two *Leptophilypnus* species; *Leptophilypnus fluviatilis* has it, but *L. panamensis* does not. The appearance of both states of the single proposed synapomorphy in *Leptophilypnus* increases the homoplasy inherent in any phylogenetic reconstruction and weakens the argument for recognizing *Leptophilypnus* as the sister group to an *Eleotris* clade on the basis of that character alone. Before an unequivocal phylogeny of intrageneric relationships can be developed, more polarized characters are needed, and this demands a better understanding of eleotrid relationships. Another major problem confronting any attempt at phylogenetic reconstructions of intrageneric *Eleotris* relationships at this time is that morphological variation within and among Indo-Pacific species requires attention. The seminal work by Akihito (1967) was only a beginning.

#### SYSTEMATICS

##### *Eleotris* Bloch and Schneider, 1801

- Eleotris*, Bloch and Schneider (1801): 65. Type species: *Gobius pisonis* Gmelin 1789, South America (Brazil). Type established by ICZN by use of plenary powers (Opinion 93, Direction 56) and *Eleotris* Gronow 1763 listed as a name published in a rejected work (Opinion 417).
- Eleotrides*, Bory de Saint-Vincent, 1825: 417. Type species: *Gobius pisonis* Gmelin 1789.
- Culius*, Bleeker, 1856: 385, 411. Type species: *Cheilodipterus culius* Hamilton 1822, Bengal, India, by absolute tautonymy, not *Culius fuscus* Bleeker 1856 (= *Poecilia fusca* Bloch and Schneider, 1801 = *Eleotris nigra* Quoy and Gaimard, 1824, 259, pl 60 fig 2, Waigeo, Indonesia) as subsequently designated in Bleeker 1874: 303.
- Kieneria*, Maugé, 1984: 98 (subgenus of *Eleotris*). Type species: *Kieneria vomerodentata* Maugé, 1984, Madagascar, by original designation and monotypy.

DIAGNOSIS. Eleotrid fishes with transverse suborbital free neuromast rows, no cephalic lateralis canals, a spine on the angle of the preopercle, and equal numbers of fin elements in the second dorsal and anal fins (1,8).

DESCRIPTION. Head broad and flattened, body low, and torpedo-like. Mouth large and oblique, posterior margin of upper jaw to vertical through middle of eye or rear margin of orbit, lower jaw projecting. Upper and lower jaws with multiple rows of small teeth, a few caniniform teeth in some species. Tubular anterior nares overhanging upper lip, posterior nares open pits. Stout antrorse spine at angle of preopercle. Small eyes high on head. Interorbital broad, frequently three times eye width. Gill opening moderately broad, extending to below preoperculum. Almost completely scaled, cycloid scales on nape, cheek, opercle, interorbital, pectoral-fin base, pre-pelvic region, abdomen, and in one or two rows bordering median fins, ctenoid scales covering sides of trunk. Urogenital papilla in females rounded, bulb-shaped with orifice equal to anus in size, elongate and tapered in males. Pectoral fins longer than pelvic fins, variably reaching to vertical through urogenital base to vertical through anal-fin origin. Pelvic fins separate, I, 5, generally not reaching anus (variable within *E. amblyopsis*, may reach anus in some populations). Two separate dorsal fins, first dorsal fin with six flexible spines, second dorsal fin with single leading flexible spine followed by eight soft rays. Anal fin with single flexible spine followed by eight soft rays. Appressed median fins not reaching caudal-fin base. Caudal fin rounded, preceded by 8-10 procurrent fin rays that extend forward no further than above the penultimate caudal vertebra. Caudal fin not extended forward along the caudal peduncle. No lateral line canals. Rows of transverse and longitudinal free neuromasts (sensory papillae) on head; disconnected short vertical rows of free neuromasts along sides of trunk; three diverging rows of free neuromasts on caudal fin, central row horizontal, upper and lower rows angled posterodorsally and posteroventrally respectively. Dorsal-fin pterygiophore formula 3-1221 or 3-12210,  $10 + 15 = 25$  vertebrae, two epurals, 2 or 3 preanal hemal pterygiophores (Birdsong et al., 1988).

REMARKS. *Eleotris* was placed in the Official List of Generic Names and *Gobius pisonis* Gmelin, 1789 was established as the type species by the International Commission on Zoological Nomenclature by use of plenary powers for the suspension of rules in Opinion 93, Direction 56, 1926. The summary lists *E. gyrinus* Cuvier and Valenciennes as type species in error. Opinion 93 also notes that *Gobiomoroides*, Lacepède, 1800: 592, is not a synonym of *Eleotris* as the dried type specimen has a "single dorsal of 45 rays and canine teeth." *Epiphthalmus*, Rafinesque-Schmaltz, 1815: 86, an unnecessary substitute name for *Gobiomoroides*, is also removed from synonymy.

Miller (1998) synonymized *Erotelis* with *Eleotris* because they share an antrorse spine on the preoperculum, have the same number of precaudal and caudal vertebrae, agree in first dorsal-fin pterygiophore pattern and have similar cephalic sensory systems. He stated that they only differ in squamation. *Erotelis* has small cycloid scales covering the body, while *Eleotris* has larger scales and those on the lateral trunk are ctenoid. In actuality, *Erotelis* also differs in having a

derived condition of the caudal fin. The caudal fin is tapered and has 12-14 unsegmented procurent rays before the hypural both dorsally and ventrally that extend forward above and below the third caudal vertebra from the terminus. The procurent rays are elongate and support well-developed fin margins along the rear portion of the caudal peduncle. In *Eleotris*, there are about eight to ten rays in advance of the hypural extending no farther forward than above and below the penultimate caudal vertebra and the caudal fin is rounded. The procurent rays of *Eleotris* also quickly taper to rudiments and are not associated with extensive fin membranes as seen in *Erotelis*. *Erotelis* also has a much more oblique jaw, a more elongate body, more segmented rays in the second dorsal and anal fins, one more ray in the second dorsal fin than the anal fin (as opposed to equal numbers) and a highlighted myomeric pattern of pigmentation on the sides (Dawson, 1969; Ginsburg, 1953; Jordan and Evermann, 1898). We assume that Miller's purpose in synonymizing the two genera was to establish a monophyletic *Eleotris* based upon the shared possession of a preopercular spine. As none of the other characters of the axial skeleton and cephalic lateralis are unique to *Eleotris*, the genus remains undefined by a synapomorphy. The number of elements in the second dorsal fin and anal fin, as a combination, may be synapomorphic, but this character cannot be polarized until an outgroup is unequivocally identified. Accepting the preopercular spine as a synapomorphy of the two genera, the three *Erotelis* taxa (two species and a subspecies) are characterized by several derived features: many small cycloid scales covering the body, the lanceolate caudal fin, the forward extensions of the caudal fin and their numerous associated procurent rays and probably the myomeric pigmentation on the sides. Polarity of the other characters described for *Erotelis* is less certain. Considering the conservative nature of morphological variation within *Eleotris* and other genera of eleotrids, the distinction of *Erotelis* from *Eleotris* is outstanding. Synonymization will only obscure the distinctions. If we were to apply the same rationale to gobioid fishes as a whole, that is ignoring identified monophyletic groups if it results in a sister group diagnosed by plesiomorphic traits, we would only have two families, Rhyacichthyidae and Gobiidae with all but a couple of the roughly 2000 gobioids in the latter family (Miller, 1973). Obviously much information is less readily available in a classification developed with that approach and many of our advances in understanding of gobioid relationships would be less apparent (e.g. Hoese and Gill, 1993; Pezold, 1993). We recognize the two genera as distinct and valid.

#### KEY TO *ELEOTRIS* SPECIES OF THE WESTERN HEMISPHERE

1. a. Teeth heteromorphic, several rows of fine teeth in both jaws with larger canine teeth present laterally towards rear in outer row

- and/or medially near symphysis in inner rows; opercular free neuromast row *ot'* absent.....2
- b. All teeth fine, no canine teeth present; opercular vertical row *ot'* present.....*E. picta*  
(eastern Pacific; Mexico to Peru and the Galapagos)
2. a. Dark spot present on upper pectoral-fin base (may be covered by opercular membrane), darker than markings on nape at opercular margin.....3
- b. No dark spot present on upper pectoral-fin base or if present not strongly-contrasted and not as dark as pigment on nape.....4
3. a. Second and some combination of two of third, fourth or fifth transverse suborbital neuromast rows extend below longitudinal row *d* (usually third and fourth).....5
- b. Second, fourth and sixth transverse suborbital neuromast rows extend below longitudinal row *d*.....*E. perniger*  
(western Atlantic; Caribbean Basin, Mexico, Bermuda)
4. a. Only second and fourth transverse suborbital neuromast rows on cheek extend below longitudinal row *d* (2.4 pattern)...*E. tubularis*  
(eastern Pacific; Cocos Island)
- b. Second, third and fourth transverse suborbital neuromast rows on cheek extend below longitudinal row *d* (2.3.4 pattern)...*E. pisonis*  
(western Atlantic; Brazil to Orinoco delta)
5. a. Scales in lateral series 40-58 over range, 43-52 in Caribbean Basin.....*E. amblyopsis*  
(western Atlantic; primarily continental, Guianas through North Carolina, Cuba, occasional other Antilles)
- b. Scales in lateral series 54-60.....*E. tecta*  
(eastern Pacific; Costa Rica through Colombia)

*Eleotris amblyopsis* (Cope, 1871)

*Eleotris gyrinus*, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).

*Culius amblyopsis* Cope, 1871: 473, Surinam.

*Eleotris (Culius) belizianus* Sauvage, 1880: 56, Belize, (in part).

*Eleotris abacurus* Jordan and Gilbert, 1896: 228, Charleston, South Carolina.

*Eleotris isthmensis* Meek and Hildebrand, 1916: 356, 359, Mindi, Panama Canal Zone.



**DIAGNOSIS.** Scales in lateral series 40 - 58, generally 41- 46 in NE South America, 45 - 49 in Caribbean Basin, 50 - 56 in North America. Second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (2.3.4 pattern); lacking *ot'* neuromast row on upper opercle. Dark blotch present on upper pectoral-fin base; sides of trunk usually with scattered spots along dorsum and no regular rows of spots of uniform intensity forming horizontal pinstripes.

**DESCRIPTION.** Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canine teeth present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

**Meristics.** First dorsal fin VI; second dorsal fin I,8 (I,7-I,9); pectoral fins 16 (15-18); pelvic fins I, 5; anal fin I,8 (I,7-I,8). Scales in lateral series 49 (40-58), generally 43-46 in NE South America, 45-49 in Caribbean Basin, 50-56 in North America; predorsal scales 36 (29 - 46); transverse scale rows 14 (11 - 18); caudal peduncle scale rows 15 (11 - 24).

**Cephalic lateralis.** Fig. 9. Five transverse suborbital free neuromast rows of which 2nd, 3rd and 4th extend ventrally beyond horizontal row *d* (2.3.4 pattern). Short supernumerary segments may occur between two or more transverse rows in specimens from North America, occasionally with an extra row on one or both sides such that 2nd, 3rd and 5th (2.3.5) or 2nd 4th and 5th rows (2.4.5) extend below row *d*, extra rows especially common in specimens from Atlantic coast of US. No *ot'* row on upper opercle, row *os* connects with row *oi* at ventroposterior margin of opercle.

**Coloration in alcohol.** Based on specimens from Costa Rica (NLU 69723), Florida (UF 87886), and Mexico (UMMZ 209724). Body dark brown laterally, lighter along the dorsum or tan with rows of spots on sides of varying intensity; abdomen and gular region lighter. Cheek with two dark streaks radiating posteriorly from eye, one along sulcus between nape and cheek and operculum. Large spot on upper pectoral-fin base which may be covered by the opercular membrane; two elongate spots extending from pectoral-fin base onto pectoral-fin rays seen in some specimens. First dorsal fin with dark band along base and another reticulate band through middle of fin, dark spots generally present on spines above mid-level band, but not at tips, bands generally converging posteriorly; second dorsal fin with 5 to 8 wavy diagonal bands, sometimes over dusky membrane; anal fin dusky or with as many as seven wavy rows of spots; caudal fin with 10 to 14 vertical bars formed by small spots on rays against a dusky mem-



brane; pectoral fins peppered with small spots on rays, membrane may be clear or dusky, pelvic fins similar but with fewer rows of spots.

**DISTRIBUTION.** Common in continental estuaries from French Guiana to North Carolina, but also known from Brazil and the Antilles. Enters freshwater streams in the Caribbean Basin.

**COMMENTS.** This species reaches a smaller maximum size than *E. perniger* and matures at a size of 50-60 mm (Hildebrand, 1938). The largest specimen collected by Greenfield and Thomerson (1997) in Belize was just over 73 mm SL and Bussing (1996) reported it to reach 80 mm SL in Costa Rica. The largest specimens observed in our study were 83 mm SL from the Caribbean Basin and 113 mm SL from North America.

Dawson (1969) noted the ability of this species to change color pattern from uniformly dark to dark laterally with a light dorsum, a trait that seems to be common to a number of *Eleotris* species. This is most likely the species from Mexico karyotyped by Uribe et al. (1994), as *E. perniger*, though known from that region, is not the common species. Karyotypes revealed heteromorphic sex chromosomes; 44 acrocentric and two metacentric chromosomes.

This species is known from both estuaries and streams in Central America (Gilbert and Kelso, 1971; Greenfield and Thomerson, 1997; Nordlie, 1979) where it often co-occurs with *E. perniger* and estuaries in North America (Dawson, 1969; Schwartz, 1999). In Belize, it was the primary species on the mainland (only one specimen of *E. perniger* was taken), but both species were regularly found together in Saint George's Cay on the barrier reef (Greenfield and Thomerson, 1997). Greenfield collected both species in Honduras, where *E. amblyopsis* was most common in estuaries and *E. perniger* (reported as *E. pisonis*) was found more often in freshwater. Gilbert and Kelso (1971) and Bussing (1998) found *E. amblyopsis* the more common species in Costa Rica. Although Gilbert and Kelso (1971) took both species together from estuaries and streams, Nordlie (1979) reported *E. perniger* (as *E. pisonis*) more common in freshwater than *E. amblyopsis*, but *E. amblyopsis* the more abundant by far in the Tortuguero estuary. Bussing (1998) also noted it in estuaries and streams to 15m elevation. In Panama *E. amblyopsis* was reported by Hildebrand (1938) (as *E. isthmensis*) to be less common than *E. perniger* (identified as *E. pisonis*). Although usually noted from low salinity estuaries in North America (e.g. Dawson, 1969), Gilmore and Herrema (1981) found them most common in freshwater in east-central Florida. Microhabitat preferences that have been noted included mangroves in Mexico (Britton and Morton, 1989), mangrove channels in Belize (Greenfield and Thomerson, 1997) and hyacinth roots in Costa Rica (Gilbert and Kelso, 1971). In Louisiana, the first author has collected this species associated with hyacinth roots and *Phragmites* marshes in oligohaline estuaries at

the mouth of the Mississippi River. Others have been captured in a channel in a *Spartina* marsh using traps composed of oyster shells in plastic crates. *Eleotris amblyopsis* is a carnivorous species that feeds on arthropods and fishes (Bussing, 1998; Nordlie, 1981). Nordlie observed no change in diet associated with position in the estuary or size.

*Eleotris perniger* (Cope, 1871)

*Eleotris gyrinus*, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).

*Culius perniger* Cope, 1871: 473, St. Martin, West Indies.

*Eleotris maltzani* Hilgendorf, 1889: 53, Haiti.

*Eleotris hilgendorfi* Pietschman, 1913: 182. replacement name for *E. maltzani* Hilgendorf (not Steindachner)

DIAGNOSIS. Scales in lateral series 54-68, usually about 60. Second, fourth and sixth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (2.4.6 pattern), with numerous short segments above row *d* between transverse rows, sometimes an additional row formed resulting in 2.4.7 pattern or other variants; lacking *ot'* neuromast row on upper opercle. Dark blotch present on upper pectoral-fin base, sides of trunk usually with regular rows of spots or stripes.

DESCRIPTION. Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canine teeth present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

*Meristics*. First dorsal fin VI; second dorsal fin I,8 (I,7-I,8); pectoral fins 18 (16-19); pelvic fins I, 5; anal fin I, 8. Scales in lateral series 60 (54-68); predorsal scales 49 (39 - 62); transverse scale rows 20 (17-23); caudal peduncle scale rows 17 (13 - 21).

*Cephalic lateralis*. Fig. 9. Adults with six transverse suborbital free neuromast rows of which 2nd, 4th, and 6th extend ventrally beyond horizontal row *d* and many short supernumerary segments often present between transverse rows (2.4.6 pattern). Often one or two complete extra rows formed on one or both sides such that 2nd, 4th and 7th rows extend below row *d* (2.4.7), occasionally other patterns produced including 2.5.7, 2.5.8, 2.4.5, 2.4.8, 2.5.9, 2.6.8, 3.5.7 and 3.5.10. No *ot'* row on upper opercle, row *os* connects with row *oi* at ventroposterior margin of opercle. Early juveniles with five transverse suborbital rows forming 2.3.4 pattern and no intervening segments.

*Coloration in alcohol.* Based on specimens from Costa Rica (NLU 60725), Honduras (UF 16325, UF 16333), Mexico (UMMZ 196529), Panama (ANSP 104096, ANSP 104158, ANSP 104400), Puerto Rico (ANSP 115625, ANSP 144626). Body dark brown laterally, lighter along the dorsum or tan with rows of dark brown spots on sides sometimes forming thin horizontal pinstripes; abdomen and gular region lighter. Cheek with two dark streaks radiating posteriorly from eye, one along sulcus between nape and cheek and operculum. Large spot on upper pectoral-fin base which may be covered by the opercular membrane. Other pigment as observed in *E. amblyopsis*.

**DISTRIBUTION.** Common in the Caribbean Basin, predominant species in the Antilles, also known from Bermuda and Rio de Janeiro.

**COMMENTS.** Recent references to *Eleotris pisonis* from the Caribbean Basin (e.g. Bussing, 1998; Greenfield and Thomerson, 1997) in which large-scaled species (*E. amblyopsis*) and small-scaled species (*E. pisonis*) were distinguished refer to this species. This is the largest species native to the western Atlantic. Bussing reported that *E. perniger* reaches 120 mm SL. The largest specimen observed in our study was 177 mm SL. Doug Smith (pers. comm.), University of Massachusetts at Amherst, photographed a specimen captured on St. John Island, VI, that was approximately 250 mm TL. Considering that the caudal fin in this species averages 26% SL, the specimen was about 200 mm SL.

Greenfield and Thomerson (1997) reported a single juvenile specimen from freshwater in continental Belize where *E. amblyopsis* is the more abundant species. Hildebrand (1938) reported *E. perniger* as the common species in Panama. It is the only species known from Bermuda where Smith-Vaniz et al. (1999) reported two specimens from oligohaline waters: Walsingham Cave Pool and Fern Sink Cave Pool. Bohlke and Chaplin (1993) noted two juveniles from a shallow tidal creek on the south shore of New Providence Island. The specimens were collected over a substrate of sand and rocks amid mangrove roots. They stated that it was also known from freshwater Lake Killarney on that island. Bussing (1998) regarded *E. perniger* as uncommon in Costa Rica. He also said that it occurred in stagnant waters, or low velocity rivers and creeks. He found the species in water of 25-28 C and although most abundant near the coast, it occurs at least 60 m above sea level (which puts it farther inland than *Eleotris amblyopsis*). Like *E. amblyopsis*, it feeds primarily on fishes and shrimps. Nordlie (1979) found them mostly in freshwaters of the Rio Tortuguero system.

*Eleotris picta* Kner, 1863

*Eleotris picta* Kner, 1863:223. Rio Bayano, Panama.

*Eleotris pictus* Kner and Steindachner, 1864:18, Plate 3, fig. 1,

Rio Bayano, Panama. (spelled *Eleotris picta* on plate).

*Culius aequidens* Jordan and Gilbert, 1882:461, Rio Presidio near Mazatlan, Mexico.

**DIAGNOSIS.** Scales in lateral series 56-68, mode of 61. Neuromast configuration with second and fourth suborbital vertical rows extending ventrally past horizontal row *d* (2.4 pattern); opercular vertical rows *os* and *ot'* intersect on posterior opercle forming an acute fork opening towards posterior margin. Urogenital papillae small and square in shape in young females; distal margin fringed and flared in adult females; pre-vent furrow not well developed.

**DESCRIPTION.** Body morphology is as described for the genus, although the head is flatter and narrower compared to *Eleotris tubularis*. Broad bands of fine teeth in both jaws, no canine teeth. Urogenital papillae small and square in shape in young females; distal margin fringed and flared in adult females; pre-vent furrow not well developed. Proportional measurements are shown in Table 1.

**Meristics.** First dorsal fin VI; second dorsal fin I,8; pectoral fin 18 (11-19); pelvic fins I, 5; anal fins I,8 (I,8-I,9). Scales in lateral series 61 (56-68); predorsal scales 61 (53-65); transverse scale rows 24 (20-31); caudal peduncle scale rows 18 (13-23).

**Cephalic lateralis.** Fig. 2. Five suborbital transverse rows of which the 2nd and the 4th extend below horizontal row *d* (2.4 pattern). Supernumerary segments occur between the 5 transverse rows. Opercular vertical row *ot'* is present, connecting with horizontal row *os* to form an acute fork opening toward the posterior margin of the opercle.

**Coloration in Alcohol.** Based on specimens from Honduras (TU 186087) and Costa Rica (TU 84544, TU 24181, TU 84587, TU 84687 and TU uncat.). Color dark tan or brown with darkest pigment laterally on trunk. Abdomen pale. Entire body often mottled. Two dark postocular stripes present, more distinct in young; uppermost postocular stripe extends horizontally from orbit to posterior opercular margin; lower postocular stripe extends to upper preopercular margin. Pigmentation on lateral scales may form dark band, especially in juveniles, continuous or broken into series of large blotches, band being formed from horizontal rows of spots; often with dark speckles on top of head highlighting longitudinal rows of free neuromasts. All fins possess wavy, dusky bands of spots. Dorsal and ventral spots sometimes present above and below hypural.

**DISTRIBUTION.** Common from Mexico to continental Ecuador and the Galapagos

Islands, also known from Cocos Island and Salton Valley of California.

COMMENTS. This is the largest species of *Eleotris* in the Western Hemisphere. Bussing (1998) stated that it reaches 320 mm SL. The largest specimen we examined was 276 mm SL. Uribe and Diaz (1996) described the karyotype for this species as 52 acrocentric chromosomes.

Bussing (1998) described life colors of *Eleotris picta* as grayish black dorsally, with pale gray sides occasionally marked with irregular yellow blotches, and a tan abdomen with yellow or white blotches on young and subadults. He also stated that juveniles are often pale yellowish brown above with spotted sides and have a black tail with transparent margin. The fins in this species were noted as dark with transparent spots producing bands, although he notes that this pattern is less apparent in larger specimens. Grove and Lavenberg (1997) described the species as being dark greenish brown with a light abdomen with dusky fins "with dark speckles, [and] undulating stripes on the dorsal and anal fins". Juveniles were described as "mottled with blue and dark brown speckles, without stripes or bars."

Grove and Lavenberg (1997) reported one specimen 94 mm SL from a freshwater stream near Playa Negra, on Floreana in the Galapagos Islands. Bussing (1998) found them in waters ranging from stagnant to high velocity rivers. He reported them most abundant near the coast, but inhabiting streams up to 100 m above sea level, with larger individuals upstream. Temperatures at capture were from 25-33 C.

According to Bussing (1998), this is a lie-and-wait benthic predator, like others in the genus, that feeds on fishes and shrimps. It lurks under stones and overhanging shorelines. Winemiller and Morales (1989) found the diet comprised about 32% aquatic insect larvae, 39% shrimps and 9% fishes in Corcovado National Park, Costa Rica. The condition of seven specimens examined by Hildebrand (1938) suggested that spawning occurs during the dry season.

A single specimen of *Eleotris picta* was discovered during this study from San Juan de los Cayos, Falcon State, Venezuela. This is the first report of this species in the western Atlantic. It most likely resulted from introduction via ship's ballast water.

#### *Eleotris pisonis* (Gmelin, 1789)

*Gobius pisonis*, Gmelin, 1789:1206, South America (based on *Eleotris capite plagioplateo* of Gronow; after Marcgrave and Piso, Hist. Brasil, IV. 166, 1648; Brazil).

*Gobius amorea* Walbaum, 1792: 205, western Atlantic.

*Eleotris gyrinus*, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).

*Eleotris (Culius) belizianus* Sauvage, 1880: 56, Belize, (in part).

*Eleotris carvalhois* Starks, 1913: 65, pl.9, Brazil.



**DIAGNOSIS.** 47-63 lateral scale rows, usually 50-54 in NE South America and 54-59 in Brazil. 2.3.4 suborbital free neuromast pattern. Spot on upper pectoral fin base lacking or poorly defined, not as dark as patch of pigment above opercle on edge of nape; no well-defined rows of spots or stripes on flanks

**DESCRIPTION.** Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canines present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

**Meristics.** First dorsal fin VI; second dorsal fin I, 8; pectoral fins 17 (15-19); pelvic fins I, 5; anal fin I, 8. Scales in lateral series 54 (47-63), usually 50-54 in Guianas and eastern Venezuela, 54-59 in Brazil; predorsal scales 40 (32-49); transverse scale rows 16 (14-20); caudal peduncle scale rows 17 (13 - 25).

**Cephalic lateralis.** Fig. 9. Five transverse suborbital free neuromast rows of which 2nd, 3rd and 4th extend ventrally beyond horizontal row *d* (2.3.4 pattern). Short supernumerary segments rarely observed. No *ot'* row on upper opercle, row *os* connects with row *oi* at lower rear margin of opercle.

**Coloration in alcohol.** Based on specimens from Brazil (AMNH 20743), Guyana (AMNH 14420, AMNH 72129, AMNH 72151), and Venezuela (MHNLS 9805, MHNLS 9945). Body tan to dark brown, often with a few scattered brown spots on upper flanks, not forming regular rows or thin stripes; dorsum occasionally lighter than flanks; abdomen and gular region lighter. Two streaks radiating across cheek posteriorly from eye, another along sulcus between nape and cheek and operculum, expanding into patch of dark brown pigment on nape along edge of operculum, more pronounced than pigment on upper pectoral-fin base. Spot or dark patch variably present on upper pectoral-fin base, if present not highly defined and not as dark as pigment on side of nape; other pigment as observed in *E. amblyopsis*.

**DISTRIBUTION.** Brazil to the Orinoco Delta of eastern Venezuela.

**COMMENTS.** *Eleotris pisonis* reaches a maximum size similar to *E. amblyopsis*. The largest we examined was a 113 mm SL individual from Brazil. Teixeira (1994) mentioned that this species was a common element of the ichthyofauna in estuaries of northeastern Brazil. The species was taken in salinities ranging from 0.1-18.2 ppt at temperatures of 25-33 C. It was most abundant in the fall in channels in regions of fluctuating salinity. Perrone and Vieira (1990) found that marginal vegetation served as the primary shelter and feeding area for this species in another Brazilian river system during the wet season.



Teixeira (1994) discovered *E. pisonis* primarily fed on snails (*Neritina virginea*), polychaetes, shrimps and fishes. *Neritina* were the principal food resource throughout the year; secondary foods changed with season and ontogeny. Smaller spinycheek sleepers ate polychaetes, larger individuals fed on fishes and shrimps. In another Brazilian estuary, this species ate mostly dipteran larvae in the wet season and carideans and fishes in the dry season (Perrone and Vieira, 1991). Seasonal changes in diet were associated with fluctuation in the abundance of marginal vegetation, a preferred habitat when it is present. As with the study by Teixeira, there were ontogenetic differences in diet. Juveniles fed mostly on dipterans, while adults ate more fishes and crustaceans.

Size at maturity for this species has been reported as 57 mm TL for males and 43 mm TL for females (Teixeira, 1994). He observed no clearly defined reproductive period for males, but noted an April surge for females. Perrone and Vieira (1990) gave a size at maturity of 35 mm SL for females (in agreement with that above) and suggested a reproductive period linked to the wet season, summer in southeastern Brazil and winter in the northeast.

#### *Eleotris tecta*, Bussing 1996

*Eleotris tecta* Bussing, 1996: 252, Rio Banegas, Puntarenas, Costa Rica.

**DIAGNOSIS.** Scales in lateral series 54-60, mode of 59. Neuromast configuration with 2nd, 3rd, and 4th suborbital rows extending ventrally past horizontal row *d*. Urogenital papillae round and blunt in females, long and acuminate in males.

**DESCRIPTION.** Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canines present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 1.

**Meristics.** First dorsal fin VI; second dorsal fin I,8 (I,7- I,8); pectoral fins 17 (16-17); pelvic fins I, 5; anal fin I,8 (I,7-I,8). Scales in lateral series 59 (54-60), predorsal scales 38 (38-43); transverse scale rows 18 (17-21); caudal peduncle scale rows 14 (13-14).

**Cephalic lateralis.** Fig 2. Second, 3rd, and 4th suborbital vertical rows intersecting horizontal row *d* (2.3.4 pattern). No *ot'* row on upper opercle, opercular rows *os* and *oi* join at ventroposterior margin of preopercle.

**Coloration in Alcohol.** Based on specimens available. Body straw color, darker on dorsum, lighter on belly; mottling present in a few specimens; pigmentation

on lateral scales forming series of interrupted lines six to seven scales in depth extending from pectoral-fin base to caudal peduncle, more distinct posteriorly. Dark spot present on upper base of pectoral fin; dorsal and anal fins with wavy, dusky bands parallel or diagonal to body axis; bars on the caudal, pectoral, and pelvic fins perpendicular to body axis, some specimens lacking dusky bars on pectoral and pelvic fins. Cheek with small dark dots; interrupted interorbital bar; two postocular stripes, top stripe extends to the posterior margin of the opercle, bottom stripe extends to or slightly past the posterior margin of the preopercle; bar connecting two postocular stripes along seam of opercle and preopercle in a few specimens.

DISTRIBUTION. Pacific versant of Colombia, Panama and Costa Rica.

COMMENTS. Bussing (1998) stated that this species reaches 80 mm SL. The largest specimen we observed was 62 mm SL. The holotype of the species is female, not male as originally described by Bussing (1996). There was also some confusion in Figs. 2 and 3 of the original description. Cephalic neuromast drawings in Fig. 2 are from top to bottom *Eleotris picta* (c in legend), *E. tecta* (a in legend) and *E. tubularis* (b in legend). In Fig. 3, the illustrations are *Eleotris picta* in the upper left corner, *E. tecta* in the upper right and *E. tubularis* on the bottom.

From Bussing (1998) we know that *Eleotris tecta* inhabits streams with little to high current up to 75 m above sea level, and has been taken in waters with temperatures of 25-29 C. It is known to be sympatric, but not syntopic, with *E. picta*. He also stated that it is carnivorous.

*Eleotris tubularis*, Heller and Snodgrass, 1903

*Eleotris tubularis* Heller and Snodgrass, 1903: 210, Plate 10, Cocos Island, Costa Rica.

DIAGNOSIS. Scales in lateral series 48-53, mode of 50. Neuromast configuration with 2nd and 4th suborbital vertical rows extending ventrally past horizontal row *d*. Urogenital papilla round and blunt in females; urogenital papilla long and acuminate in males, tip extending past anal fin origin in adults; long pre-vent furrow.

DESCRIPTION. Body morphology as described for genus. Head is less robust than *Eleotris tubularis*. Proportional measurements given in Table 1.

*Meristics*. First dorsal fin VI; second dorsal fin I,8 (I,8-I,9); pectoral fins 16 (14-16); pelvic fins I, 5; anal fin I,8. Scales in lateral series 50 (48-53), predorsal

scales 36 (34-40); transverse scale rows 16 or 17(14-17); caudal peduncle scale rows 13 (12-16).

*Cephalic lateralis*. Fig. 2. Second and fourth suborbital vertical rows intersect horizontal row *d*. No *ot'* row on upper opercle, opercular rows *os* and *oi* do not meet at posterior opercular margin.

*Coloration in Alcohol*. Based on specimens available. Body olive brown with head region slightly darker; ventral surface lighter than dorsal surface. No dark spot on pectoral base; dorsal and anal fins with dusky bands parallel or diagonal to body axis; pectoral, pelvic, and caudal fins with dusky bars perpendicular to body axis.

DISTRIBUTION. Endemic to Cocos Island, Costa Rica.

COMMENTS. The holotype is desiccated but counts on measurements were taken where possible. This is also a small species, the largest individual observed in this study was 85 mm SL.

#### MATERIALS EXAMINED

*Eleotris amblyopsis*. Belize: FMNH 82078 (30); MNHN 27 (1), *Eleotris belizianus*, syntype; MNHN 2528 (2), *E. belizianus* syntypes. Brazil: AMNH 211135 (1); AMNH 20752 (1); Costa Rica: ANSP 140682 (1); ANSP 140683 (1); ANSP 174839 (2); ANSP 174841 (1); ANSP 174842 (1); NLU 69723 (8); Cuba: CAS 66647 (4); CAS 89139 (1); MCZ 32926 (2); MCZ 159203 (1). Florida: ANSP 71070 (5); ANSP 72915 (1); ANSP 72947 (1); ANSP 73105 (1); ANSP 144266 (1); MCZ 13435 (1); UF 59144 (5); UF 91947 (3); UF 87754 (1); UF 18133 (1); UF 47739 (1); UF 33977 (1); UF 87886 (8); UF 47003 (1). Guatemala: AMNH 32076 (3); AMNH 35114 (1). French Guiana: NLU 76503 (3); NLU 76504 (1); NLU 76505 (2); NLU 76506 (1). Guyana: FMNH 53923 (1); FMNH 53924 (1). Haiti: ANSP 83082 (1); AMNH 19315 (1); AMNH 19421 (1). Jamaica: CAS-SU 69780 (1). Louisiana: NLU 33488 (3); NLU 33614 (1); NLU 33958 (1); NLU 53287 (1); NLU 69722 (1); NLU 69736 (1); NLU 69843 (1); NLU 69844 (1); NLU 69845 (2); NLU 69846 (1); NLU 69851 (1); NLU 69852 (1); NLU 69853 (2); NLU 69854 (1); NLU 69900 (1); NLU 69901 (2); NLU 71488 (1). Mexico: CAS-SU 21122 (1); GCRL 2878 (6); UMMZ 167492 (1); UMMZ 178565 (3); UMMZ 184433 (4); UMMZ 184444 (3); UMMZ 184454 (1); UMMZ 238760 (1); UMMZ 184471 (1); UMMZ 184480 (8); UMMZ 184503 (2); UMMZ 184504 (1); UMMZ 186657 (1); UMMZ 194837 (23); UMMZ 194838 (4); UMMZ 194884 (2); UMMZ 196411 (14); UMMZ

194861 (4); UMMZ 209505 (5); UMMZ 209664 (1); UMMZ 209724 (2); UMMZ 209772 (2); UMMZ 213610 (1); UMMZ 213611 (3); UMMZ 213612 (9). Mississippi: GCRL 497 (2); GCRL 1456 (3); GCRL 2501 (20). North Carolina: UNC 8273 (1); UNC 10355 (5); UNC 11668 (1); UNC 14951 (6); UNC 15379 (1). Panama: ANSP 103393 (12); ANSP 104227 (1); ANSP 104291 (4); CAS 46149 (1); CAS-SU 50905 (1); CAS-SU 50317 (1); CAS 50318 (10); CAS-SU 50320 (5); CAS 214223 (1); (1); CAS 66651 (1); CAS 66652 (1). South Carolina: CAS-SU 2009 (1), *E. abacurus* holotype, specimen and radiograph. Surinam: AMNH 211136 (10); ANSP 10577-10579 (3), *E. amblyopsis* syntypes; CAS-SU 53292 (2); CAS-SU 53331 (5); MCZ 13429 (20); MNHN A.1672 (1), *E. gyrinus* syntype; MNHN A.1673 (3) *E. gyrinus* syntypes. Texas: TNHC 8115 (2). Trinidad: ANSP 144625 (1). Venezuela: CAS 50794 (2); ANSP 76244 (1); MCNG 19176 (1); MCNG 19245 (1); MCNG 13982 (1); SCN 1428 (11); SCN 1439 (1); SCN 1443 (4); SCN 1990 (1); SCN 9945 (1); SCN 14603 (3); SCN 14604 (2); SCN 14605 (1).

*Eleotris annobonensis*. Pagalu (Annobon): MNHN 1965.611 (4), paratypes; MNHN 1965.612 (4), paratypes; MNHN 1967.446 (1), holotype. Fernando Po: MRAC 7846p229 (1); MRAC 92089p0001-04 (4); MRAC 142100-01 (2); MRAC 7846p222-8 (7); MRAC 145418-20 (3).

*Eleotris daganensis*. Cameroun: MRAC 7302p2205-7 (3); MRAC 93083p0033-34 (2). Congo- Brazzaville: MRAC 8027p257-58 (2); MRAC 9057p2607 (1); MRAC 78027p256 (1). Gabon: MRAC 7660p126 (1). Guinea: MRAC 92059p4031 (1). Liberia: MRAC 7310p7385-91 (7); MRAC 7310p7392 (1); RMNH 24403 (6), *E. buttikoferi* paralectotypes. Namibia: RUSI 63257 (6). Nigeria: MRAC 8803p58-60 (3); MRAC 9019p529-33 (3); MRAC 9110p918-27 (10). Portuguese Congo: MRAC 1760 (1); MRAC 1764 (1). Rio Muni: MRAC 7846p235 (1); MRAC 173332-4 (3). Sierra Leone: MRAC 73406-8 (3); MRAC 73410-11 (2); MRAC 7310p7382-83 (2); MRAC 7310p7378-81 (4). Togo: MRAC 7313p429-31 (3).

*Eleotris feai*. Pagalu (Annobon): MNHN 1974.5.13.1 (1), paratype; MRAC 7445p1 (1), paratype.

*Eleotris perniger*. Bahamas: ANSP 98816 (1); ANSP 98817 (1); ANSP 148541 (1). Barbados: CAS-SU 37267 (7); MCZ 13283 (1). Bermuda: ANSP 150163 (1); ANSP 150164 (1). Brazil: ANSP 121269 (2); CAS-SU 69781 (1); MCZ 159204 (2). Cayman Islands: MCZ 52513 (1). Costa Rica: ANSP 163142 (1); ANSP 163772 (1); ANSP 163773 (2); ANSP 163774 (1); ANSP 163775 (2); NLU 69725 (4). Cuba: ANSP 39935 (1); ANSP 69214 (3); CAS-SU 1892 (3); CAS 66648 (2); MCZ 13342 (1); MCZ 13334 (1); MCZ 13355 (1); MCZ 13363 (1);

MCZ 13364 (4); MCZ 13366 (1); MCZ 13382 (1); MCZ 13384 (1). Dominican Republic: ANSP 10574 (1); MNHN A.1698 (3), *Eleotris gyrinus* syntypes. Florida: ANSP 55907 (1). Grenada: ANSP 52517 (3). Guadeloupe: MCZ 13440 (2). Haiti: ANSP 83082 (1); ANSP 83660 (1); CAS-SU 25604 (4). Honduras: CAS 35746 (1); GCRL 6003 (1); UF 16325 (6); UF 16333 (3). Jamaica: ANSP 112909 (1); ANSP 144716 (1); CAS-SU 4965 (8); MCZ 34030 (10); MCZ 58321 (8). Martinique: ANSP 152267 (1); MCZ 26070 (12); MNHN A.1597 (1), *E. gyrinus* syntype; NLU 75227 (3). Mexico: ECOCH (El Colegio de la Frontera Sur- Chetumal) 0243 (1); ECOCH 0505 (1); ECOCH 0573 (1); UMMZ 184467 (3); UMMZ 196529 (1); UMMZ 209702 (2). Panama: ANSP 99833 (3); ANSP 99915 (1); ANSP 104074 (6); ANSP 104096 (1); ANSP 104158 (2); ANSP 104302 (3); ANSP 104400 (5); CAS-SU 50277 (1); CAS 214224 (5); CAS-SU 50906 (5); CAS-SU 18578 (10); CAS-SU 18579 (11); CAS 66650 (1). Puerto Rico: ANSP 23552 (4); ANSP 23587 (1); ANSP 91914 (3); ANSP 115625 (1); ANSP 118559 (44); ANSP 144626 (3); CAS-SU 8243 (1); CAS-SU 8274 (2); CAS 78668 (2); CAS 11702 (1); MCZ 28871 (1); MCZ 34669 (1); MCZ 49411 (18). St. Martin: ANSP 10575 (1), *E. perniger* holotype. St. Vincent: MCZ 26103 (4); MCZ 26109 (1); MCZ 26111(11). Trinidad: ANSP 174843 (1). Venezuela: ex-MCNG 13982 (1); SCN 2451 (1); SCN 3958 (3); SCN 3966 (2); SCN 3968 (1); SCN 5969 (2); SCN 9245 (1); SCN 10001 (2); Virgin Islands: CAS 66645 (1); UMA (University of Massachusetts at Amherst) uncatalogued (1).

*E. perniger* x *E. amblyopsis* hybrids. Cuba: MCZ 13360 (2); MCZ 13365 (1); Mexico: ECOCH 0272 (1); ECOCH 0861 (1); UMMZ 124299 (1). Panama: ANSP 178003 (1); MCZ 45744 (1).

*Eleotris picta*. Colombia: NRM 28607 (1); NRM 28609 (1); NRM 10704 (1); FMNH 94689 (15); CAS 11691 (1); LACM 24320 (1); NRM 39516 (3); NRM 10705 (2). Costa Rica: ANSP 144126 (1); ANSP 144155 (5); ANSP 144132 (15); LACM 30109-5 (2); LACM 2887 (3); LACM 4859 (1); TNHC 15362 (5); TNHC 14789 (3); TNHC 15380 (1); TU uncat. (2); TU 84587 (1); TU 24181 (1); TU 84544 (1); TU 84687 (1); TNHC 14849 (5); TNHC 15350 (3); TNHC 11986 (1); TNHC 12006 (1); TNHC 11496 (1); TNHC 11505 (1); TNHC 15360 (1); TNHC 14755 (2); UCR 130.003 (12); UCR 936.006 (5); UCR 732.007 (5). Isla del Cocos, Costa Rica: LACM 26462 (2); UCR 736.005 (2). Ecuador: MCZ 58605 (1); MCZ 54970 (1); USNM 288041 (2); CAS 66643 (2); FMNH 56864 (2); CAS 66644 (1); FMNH 56865 (1). Ecuador, Galapagos Islands: UWZM 10688 (1); CAS 54585 (1); SIO 59-358-58B (1); LACM 43964-1 (1). Guatemala: UMMZ 194134 (3); UMMZ 197122 (1); UMMZ 188085 (5); UMMZ 190541 (2). Honduras: TU 186087 (1). Mexico: UMMZ 164635 (1); LACM 30369-2 (1); UMMZ 164646 (1); UMMZ 173605 (1); CAS-SU 2907 (5); UMMZ 164627 (1); UMMZ 164685 (1); UMMZ 172012 (1); UMMZ 172096



(1); UMMZ 172060 (3); UMMZ 183927 (1); UMMZ 172082 (1); UMMZ 183935 (1); UMMZ 172145 (1); UMMZ 184827 (5); UMMZ 184747 (1); UMMZ 178428 (1). Nicaragua: UCR 52.002 (10); UCR 272.003 (1); UCR 187.002 (7); UCR 270.006 (20). Panama: NMW 76866 (1), *E. picta* syntype; FMNH 27274 (1); FMNH 27280 (7); ANSP 146763 (1); USNM 226407 (2); FMNH 32313 (1); FMNH 32312 (1); FMNH 27283 (6); FMNH 27281 (3); FMNH 32314 (1); ANSP 104276 (2); ANSP 104277 (1); ANSP 104282 (1); ANSP 104189 (1); ANSP 104101 (1); ANSP 104403 (2); CAS 66637 (1); CAS 66638 (1); FMNH 27275 (1); ANSP 104165 (2); FMNH 36985 (1); USNM 270831 (10); USNM 260093 (3); USNM 293478 (4); NRM 35870 (1). Venezuela: SCN 2270 (1).

*Eleotris pisonis*. Brazil: AMNH 3764 (1), *Eleotris carvalhonis*, paratype; AMNH 20743 (2); ANSP 69641 (1); CAS-SU 22208 (5), *E. carvalhonis* paratypes; CAS-SU 22215 (1), *E. carvalhonis* holotype, specimen and radiograph; CAS 39109 (3); CAS-SU 52355 (15 of 62); CAS-SU 52356 (2); CAS-SU 52359 (1); CAS-SU 52360 (1); CAS 53478 (1); MCZ 1196 (1); MCZ 4627 (1); MCZ 13385 (1); MCZ 13386 (1); MCZ 13389 (2); MCZ 13391 (1); MCZ 13397 (5). French Guiana: MNHN A.2216 (3), *Eleotris belizianus* syntypes; MNHN A.2217 (5), *E. belizianus* syntypes. Guyana: AMNH 14420 (1); AMNH 72049 (1); AMNH 72129 (7); AMNH 72151 (1); AMNH 73056 (1); AMNH 14420 (1); CAS 51066 (1). Surinam: AMNH 54793 (31); MNHN A.1693 (1), *E. gyrinus* syntype. Venezuela: ANSP 149479 (1); SCN 1429 (7); SCN 1962 (1); SCN 9805 (11); SCN 13142 (4); SCN 13485 (2); SCN 14602 (2).

*Eleotris senegalensis*. Cameroun: MRAC 7302p2208-09 (2); MRAC 7329p1630-31 (2). Congo: AMNH 17020 (1). Congo-Brazzaville: MNHN 1901.8.1.90-3 (1); MRAC 9057p2612-15. Gabon: MRAC 7302p2204 (1); MRAC 7660p125 (1). Guinea: MRAC 92059p4032-33 (2). Liberia: MRAC 7310p7567-68 (2); RMNH 5254 (1), *E. buttikoferi* lectotype. Nigeria: MRAC 9263p357-8 (2); MRAC 8608p42 (1); MRAC 9110p928 (1). Senegal: MRAC 771p640 (1). Sierra Leone: MRAC 7310p7556 (1).

*Eleotris tecta*. Colombia: NRM 43549 (1); CAS 66639 (1); CAS-SU 37538 (2); CAS-SU 37539 (2). Costa Rica: LACM 45893-1 (1), *E. tecta* holotype. Panama: USNM 357288 (3).

*Eleotris tubularis*. Isla del Cocos, Costa Rica: CAS-SU 6348 (1), *E. tubularis* holotype; LACM 25806 (23); LACM 20047 (20).

*Eleotris vittata*. Angola: AMNH 223211 (1); BMNH 1864.7.11.8 (1), *E. monteiri* type. Benin: MRAC 8958p15 (1). Cameroun: MRAC 7308p26 (1). Congo:



AMNH 43132 (2). Congo- Brazzaville: MRAC 9057p2416-17 (2). Cote D'Ivoire: MRAC 173598 (1). Fernando Po: MRAC 142099 (1). Gabon: MNHN a.1548 (1). Liberia: MRAC 7310p7384 (1). Nigeria: MRAC 8843p463-5 (3); MRAC 8803p56-57 (2); MRAC 9022p4 (1). Sierra Leone: MRAC 7310p7382-83 (2). Togo: MRAC 739p141 (1).

*Erotelis armiger*. Mexico: CAS-SU 3455 (1), *Alexurus armiger* holotype, specimen and radiograph.

*Erotelis smaragdus*. Florida: CAS 51044 (1). Louisiana: UNOVC (University of New Orleans Vertebrate Collections) 4295 (1). Panama: CAS-SU 19339 (2).

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Table 1. Eastern Pacific *Eleotris* morphometric data. Standard length reported to nearest 0.1 mm. P1 = pectoral fin, D2 = second dorsal fin, Orbit, interorbital, snout and upper jaw measurements expressed as per cent of head length, all others expressed as per cent of standard length (all rounded to nearest per cent).

character	<i>Eleotris picta</i>				<i>Eleotris tecta</i>				<i>Eleotris tubularis</i>			
	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range
standard length	95.9 (255)	89.9-101.9	30.5-276.0	47.9 (8)	41.5-54.4	37.0-61.6	60.5 (45)	56.6-64.3	31.6-85.0			
orbit length	19 (255)	18-19	11-37	22 (8)	21-24	20-24	24 (45)	23-24	21-28			
snout length	22 (255)	21-22	7-28	22 (8)	21-24	19-25	25 (45)	24-25	19-30			
interorbital width	27 (255)	26-27	16-37	25 (8)	21-29	18-32	28 (45)	26-29	20-26			
upper jaw length	42 (255)	41-42	30-52	43 (8)	41-45	39-46	48 (45)	47-49	42-54			
head length	29 (253)	29-30	25-34	27 (8)	26-28	24-30	29 (45)	28-29	22-32			
head width	21 (253)	20-21	12-36	18 (8)	17-19	16-20	22 (45)	21-22	16-26			
predorsal length	41 (253)	41-42	20-46	40 (8)	34-46	23-45	41 (45)	41-42	31-44			
nape depth	16 (253)	16	11-22	15 (8)	14-16	13-17	18 (45)	18-19	12-22			
body width P1 base	17 (253)	17-18	10-26	17 (8)	16-18	15-18	19 (45)	18-20	13-37			
body width D2 origin	13 (253)	13	8-17	12 (8)	11-13	10-14	14 (45)	13-14	8-17			
preanal length	58 (253)	57-58	48-64	56 (8)	55-57	55-59	55 (45)	54-56	43-59			
postanal length	44 (253)	44	30-54	45 (8)	44-46	44-48	46 (45)	45-47	35-49			
caudal peduncle length	25 (253)	25-26	18-32	26 (8)	24-28	22-29	26 (45)	26-27	24-29			
pectoral fin length	22 (254)	21-22	15-29	23 (8)	19-28	19-36	24 (45)	23-24	19-26			
pelvic fin length	16 (253)	16	12-21	17 (8)	14-21	14-28	17 (45)	17-18	12-20			
caudal fin length	25 (253)	25	16-30	22 (8)	21-24	20-24	24 (43)	23-24	20-26			

Table 2. Meristic characters for eastern Pacific *Eleotris*. Means and 95% confidence interval values rounded to the nearest whole number. Cpd = caudal peduncle scale rows. P1 = pectoral fin.

character	<i>Eleotris picta</i>					<i>Eleotris tecta</i>					<i>Eleotris tubularis</i>					
	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode
cpd scales	19 (255)	19	16-24	18	14(8)	13-14	13-14	14	14(45)	13-14	13-14	14	14(45)	13-14	12-16	13
lateral scales	62(255)	61-62	56-66	61	59(8)	57-60	54-60	59,60	50(45)	49-50	48-53	49	50(45)	49-50	48-53	49
transverse scales	25(255)	24-25	20-31	24	18(8)	17-19	17-21	18	16(45)	16	14-17	16,17	16(45)	16	14-17	16,17
predorsal scales	61(255)	60-61	53-65	61	38(8)	38-43	38-47	38	37(45)	36-37	34-40	37	37(45)	36-37	34-40	37
left P1 rays	18(255)	18	11-19	18	17(8)	16-17	16-17	17	16(45)	15-16	14-16	16	16(45)	15-16	14-16	16

Table 3. Geographic patterns of meristic variation in *Eleotris picta*. Regions are: 1) Baja California - Puerto Vallarta, Mexico, 2) Puerto Vallarta, Mexico - Guatemala Border, 3) Guatemala, Honduras, El Salvador, Nicaragua, 4) Costa Rica, Panama 5) Colombia, Ecuador, Galapagos Islands.

REGION	MEAN	LOW 95% CI	UP 95% CI	MODE
LATERAL SCALES				
1	63.00	61.97	64.03	65
2	63.00	61.92	64.08	64
3	61.72	61.26	62.18	61
4	61.18	60.90	61.46	60
5	61.95	61.44	62.47	61
PREDORSAL SCALES				
1	60.63	59.31	61.94	62
2	60.09	58.11	62.07	62
3	60.34	59.84	60.84	60
4	60.29	59.97	60.60	61
5	61.51	60.95	62.08	61
TRANSVERSE SCALES				
1	23.25	22.39	24.11	24
2	24.91	24.28	25.54	25
3	26.02	25.41	26.63	25
4	24.56	24.26	24.85	25
5	24.15	23.71	24.59	24
CAUDAL PEDUNCLE SCALES				
1	18.31	17.85	18.78	18
2	19.18	18.34	20.02	19
3	19.70	19.24	20.16	19
4	18.59	18.40	18.78	19
5	18.15	17.78	18.51	17,18
PECTORAL FIN RAYS (LEFT)				
1	17.56	17.29	17.84	18
2	17.82	17.55	18.09	18
3	17.74	17.59	17.89	18
4	17.66	17.53	17.80	18
5	17.36	17.18	17.55	17

Table 4. Western Atlantic *Eleotris* morphometric data. Standard length reported to nearest 0.1 mm. P1 = pectoral fin, D2 = second dorsal fin. Orbit, interorbital, snout and upper jaw measurements expressed as per cent of head length, all others expressed as per cent of standard length (all rounded to nearest per cent).

character	<i>E. amblyopsis</i>				<i>E. perniger</i>				<i>E. pisonis</i>			
	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range
standard length	48.2 (342)	46.0 - 50.3	10.9 - 112.6	66.7 (251)	66.7 - 75.3	14.6 - 176.6	58.4 (146)	54.8 - 62.0	17.2 - 112.7			
orbit length	19 (137)	19 - 20	14 - 25	19 (70)	18 - 20	13 - 26	18 (55)	18 - 19	14 - 24			
snout length	21 (63)	20 - 21	15 - 26	22 (56)	21 - 22	16 - 27	22 (40)	22 - 23	19 - 28			
interorbital width	25 (55)	23 - 27	12 - 36	26 (54)	24 - 28	16 - 35	27 (45)	26 - 28	20 - 35			
upper jaw length	39 (67)	38 - 40	31 - 48	42 (60)	40 - 43	33 - 51	42 (49)	41 - 43	33 - 49			
head length	32 (137)	32 - 32	27 - 36	31 (70)	31 - 31	27 - 36	31 (55)	31 - 32	28 - 34			
head width	21 (51)	20 - 21	16 - 26	22 (47)	21 - 23	16 - 31	21 (38)	20 - 21	16 - 27			
predorsal length	43 (83)	42 - 43	30 - 49	43 (45)	43 - 44	39 - 42	42 (39)	41 - 43	38 - 46			
nape depth	14 (51)	13 - 15	8 - 21	14 (45)	13 - 15	8 - 24	15 (37)	14 - 17	8 - 23			
body width P1 base	16 (51)	15 - 16	9 - 19	17 (44)	16 - 18	11 - 26	17 (37)	17 - 18	13 - 20			
body width D2 origin	11 (50)	11 - 12	8 - 15	13 (45)	12 - 14	6 - 17	13 (37)	12 - 14	9 - 18			
preanal length	57 (50)	56 - 58	41 - 65	59 (41)	58 - 60	53 - 64	57 (37)	56 - 57	54 - 61			
postanal length	44 (50)	43 - 44	40 - 48	42 (41)	42 - 43	38 - 46	44 (37)	43 - 44	40 - 47			
caudal peduncle length	25 (50)	24 - 26	19 - 33	25 (41)	24 - 25	22 - 27	25 (37)	25 - 26	21 - 28			
pectoral fin length	26 (136)	25 - 26	19 - 31	25 (70)	24 - 25	20 - 35	23 (55)	23 - 24	20 - 26			
pelvic fin length	20 (135)	20 - 21	12 - 26	18 (72)	18 - 19	14 - 25	18 (55)	18 - 18	15 - 22			
caudal fin length	29 (49)	28 - 30	13 - 33	26 (34)	26 - 27	22 - 31	27 (41)	26 - 27	20 - 31			

Table 5. Meristic characters for western Atlantic *Eleotris*. Means and 95% confidence interval values rounded to the nearest whole number. Cpd = caudal peduncle scale rows, P1 = pectoral fin.

character	<i>E. amblyopsis</i>				<i>E. perniger</i>				<i>E. pisonis</i>			
	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode
cpd scales	15 (53)	14-16	11-24	12	17 (46)	16-18	13-21	17	17 (45)	16-18	13-25	15
lateral scales	49 (316)	48-49	40-58	52	60 (235)	60-61	54-68	60	54 (139)	53-54	47-63	51,53
transverse scales	14 (53)	14-15	11-18	15	20 (48)	20-21	17-23	20	16 (44)	16-17	14-20	17
predorsal scales	36 (60)	35-37	29-46	33-35,39	49 (52)	47-50	39-62	47	40 (49)	39-42	32-49	40
left P1 rays	17 (161)	17	15-18	17	18 (104)	18	16-19	18	17 (71)	17	15-19	18

Table 6. Geographic affinities of West African genera of gobioid fishes. (\* Introduced)

West African Endemic	South African Endemic	Western Hemisphere	Northeast Atlantic/Mediterranean	Indo-Pacific	Global
<i>Hannoichthys</i>	<i>Caffrogobius</i>	<i>Dormitator</i>	<i>Gobius</i>	<i>Bostrychus</i>	<i>Eleotris</i>
<i>Kribia</i>	<i>Psamnogobius</i>	<i>Ctenogobius</i>	<i>Leseuerigobius</i>	<i>Prionobutis</i> *	<i>Awaous</i>
<i>Ebomegobius</i>		<i>Gobioides</i>	<i>Mauligobius</i>	<i>Parascyidium</i>	<i>Bathygobius</i>
<i>Gorogobius</i>		<i>Gobionellus</i>	<i>Thorogobius</i>	<i>Periophthalmus</i>	<i>Gnatholepis</i>
<i>Nematogobius</i>		<i>Sicydium</i>			<i>Priolepis</i>
<i>Porogobius</i>					
<i>Wheelerigobius</i>					
<i>Yongeichthyes</i>					