



Molecular phylogeny, analysis of character evolution, and submersible collections enable a new classification of a diverse group of gobies (Teleostei: Gobiidae: *Nes* subgroup), including nine new species and four new genera

LUKE TORNABENE^{1,2*}, JAMES L. VAN TASSELL³, RICHARD G. GILMORE⁴,
DAVID ROSS ROBERTSON⁵, FORREST YOUNG⁶ and CAROLE C. BALDWIN²

¹College of Science and Engineering, Texas A&M University – Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412, USA

²National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013–7012, USA

³Department of Ichthyology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024–5192, USA

⁴Estuarine, Coastal and Ocean Science, Inc., 5920 First Street SW, Vero Beach, FL 32968, USA

⁵Smithsonian Tropical Research Institute, Balboa, Panama, Unit 9100, Box 0948, DPO, AA 34002, USA

⁶Dynasty Marine Associates, Inc., 10602 7th Avenue Gulf, Marathon, FL 33050, USA

Received 13 November 2015; revised 9 January 2016; accepted for publication 9 January 2016

The *Nes* subgroup of the Gobiomatini (Teleostei: Gobiiformes: Gobiidae) is an ecologically diverse clade of fishes endemic to the tropical western Atlantic and eastern Pacific oceans. It has been suggested that morphological characters in gobies tend to evolve via reduction and loss associated with miniaturization, and this, coupled with the parallel evolution of adaptations to similar microhabitats, may lead to homoplasy and ultimately obscure our ability to discern phylogenetic relationships using morphological characters alone. This may be particularly true for the *Nes* subgroup of gobies, where several genera that are diagnosed by ‘reductive characters’ have been shown to be polyphyletic. Here we present the most comprehensive phylogeny to date of the *Nes* subgroup using mitochondrial and nuclear sequence data. We then evaluate the congruence between the distribution of morphological characters and our molecular tree using maximum-likelihood ancestral state reconstruction, and test for phylogenetic signal in characters using Pagel’s λ tree transformations (*Nature*, **401**, 1999 and 877). Our results indicate that all of the characters previously used to diagnose genera of the *Nes* subgroup display some degree of homoplasy with respect to our molecular tree; however, many characters display considerable phylogenetic signal and thus may be useful in diagnosing genera when used in combination with other characters. We present a new classification for the group in which all genera are monophyletic and in most cases diagnosed by combinations of morphological characters. The new classification includes four new genera and nine new species described here, many of which were collected from rarely sampled deep Caribbean reefs using manned submersibles. The group now contains 38 species in the genera *Carrigobius* gen. nov., *Chriolepis*, *Eleotrica*, *Gobulus*, *Gymneleotris*, *Nes*, *Paedovaricus* gen. nov., *Pinnichthys* gen. nov., *Psilotris*, and *Varicus*. Lastly, we provide a key to all named species of the *Nes* subgroup along with photographs and illustrations to aid in identification.

© 2016 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2016

doi: 10.1111/zoj.12394

ADDITIONAL KEYWORDS: ancestral state reconstruction – Caribbean – coral reef fish – deep reefs – gobies – Gobiidae – systematics.

*Corresponding author. E-mail: luke.tornabene@gmail.com

[Version of Record, published online 09 May 2016]

INTRODUCTION

Fishes belonging to the family Gobiidae (*sensu* Gill & Mooi, 2012) are among the most evolutionarily successful lineages of vertebrates in terms of species richness as well as ecological and morphological novelty (Patzner *et al.*, 2011). With close to 1800 species that occur in nearly every marine and coastal freshwater habitat on earth, gobies have become a model group for studying the role of microhabitat and ecology in speciation and adaptive radiation (Rüber, Van Tassell & Zardoya, 2003; Yamada *et al.*, 2009; Polgar, Sacchetti & Galli, 2010; Tornabene *et al.*, 2013a). Specifically, gobies belonging to the tribe Gobiosomatini (Birdsong, 1975) represent one of the best-known examples of adaptive radiation in marine fishes (Rüber *et al.*, 2003). The tribe Gobiosomatini, often referred to as the American seven-spined gobies, is a diverse clade comprising more than 130 species in 27 genera endemic to the western Atlantic and eastern Pacific oceans. Species of Gobiosomatini are well adapted to a plethora of marine and coastal freshwater microhabitats, and many species have developed obligate or facultative symbiotic relationships with other marine species such as alphaeid shrimp, sea urchins, sponges, corals, other larger reef fishes (via ectoparasite removal), and, as recorded for the first time in this paper, with the Yellowhead Jawfish, *Opistognathus aurifrons* (D.S. Jordan & J.C. Thompson, 1905). Several new species and new genera of seven-spined gobies have been described in recent years (Joyeux, Van & Macieira, 2009; Victor, 2010, 2014; Tornabene, Van Tassell & Robertson, 2012; Van Tassell, Tornabene and Colin, 2012; Hastings & Findley, 2013, 2015), and many more new taxa are known and await formal description.

STATUS OF GOBIOSOMATINI SYSTEMATICS:
THE EMERGENCE OF POLYPHYLETIC GENERA

The monophyly of the Gobiosomatini is supported by both morphological and molecular data (Birdsong, Murdy & Pezold, 1988; Thacker & Roje, 2011; Agorreta & Rüber, 2012; Agorreta *et al.*, 2013; Tornabene, Chen & Pezold, 2013b). In addition to nearly all members possessing seven dorsal-fin spines, the tribe possesses the following morphological synapomorphies: (1) 11 precaudal and 16 or 17 caudal vertebrae; (2) first dorsal-fin pterygiophore insertion pattern of 3-221110 (following the terminology of Birdsong *et al.*, 1988); (3) scapula unossified; and (4) first two anal-fin pterygiophores inserted anterior to the first haemal spine (Birdsong, 1975). Some of these characters are absent or variable in some species of Gobiosomatini (e.g. the specialized sponge-dwelling *Evermannichthys spongicola* (Radcliffe 1917) has six dorsal-fin

spines and a different dorsal pterygiophore pattern, and a few species have one anal-fin pterygiophore anterior to the first haemal spine), but these are considered secondarily derived characteristics (i.e. reversals) rather than retentions of plesiomorphic conditions. Birdsong *et al.* (1988) subsequently divided the Gobiosomatini into the *Microgobius* group and *Gobiosoma* group, both of which are well supported by molecular and morphological data (Rüber *et al.*, 2003; Thacker & Roje, 2011; Agorreta & Rüber, 2012; Van Tassell, Tornabene & Collin, 2012; Agorreta *et al.*, 2013; Tornabene *et al.*, 2013b).

The *Gobiosoma* group was subsequently divided into several subgroups (Van Tassell *et al.*, 2012), based largely on clades recovered from a mitochondrial DNA (mtDNA) analysis by Rüber *et al.* (2003). Among these subgroups were the *Barbulifer* subgroup (*Aruma*, *Barbulifer*, *Elactinus*, *Evermannichthys*, *Ginsburgellus*, *Gobiosoma*, *Risor*, and *Tigrogobius*) and the *Nes* subgroup (*Nes*, *Psilotris*, *Gobulus*, *Gymneleotris*, *Pycnomma*, *Chriolepis*, and *Varicus*). Van Tassell *et al.* (2012) noted that most species in the *Nes* subgroup have pelvic fins that are partially or completely separated, reduced or absent cephalic lateralis canals, and hypural fusion, and they lack adductor mandibulae 1 γ (the dorsal subdivision of the adductor mandibulae 1 that originates on the anterior process of the sphenotic and inserts on the maxilla). Within these subgroups, many of the genera have been shown to be para- and polyphyletic. For example, the phylogeny in Rüber *et al.* (2003) revealed the non-monophyly of *Gobiosoma* and *Tigrogobius*, indicating that some of the morphological characters used in delimiting genera and subgenera warranted re-evaluation (Tornabene & Van Tassell, 2014). A more recent molecular phylogeny by Agorreta *et al.* (2013) also indicated that the genera *Chriolepis*, *Psilotris*, and *Pycnomma* (all of the *Nes* subgroup) are not monophyletic. The non-monophyly of genera within the *Gobiosoma* group arises in large part from genera being defined in the absence of shared derived characters because of a poor understanding of the underlying phylogeny of the group. This problem was acknowledged by many authors (Böhlke & Robins, 1968; Findley, 1983; Greenfield, 1993; Smith & Baldwin, 1999), and the scope of the taxonomic issues within the *Gobiosoma* group has continued to grow in recent years as new species are described and provisionally placed in genera that are demonstrably polyphyletic. For example, Hastings & Findley (2013, 2015) recently described two western Atlantic species and tentatively placed them in the paraphyletic *Chriolepis*, and thus genera like *Chriolepis* have continued to serve as ‘catch-all’ genera for many species that may not form natural groups.

The characters that have routinely been used to classify groups within the *Gobiosoma* group include reductions in the extent of scales on the body and caudal peduncle, loss of cephalic lateralis canals and pores on the head, reduction in the membrane connecting pelvic fins, and reduction in the extent of branching of the pelvic-fin rays. The extent of phylogenetic information in these characters is unclear: all of the characters above have potential for homoplasy because of the apparent repeated trend of reduction and independent loss associated with miniaturization in gobies, coupled with the possible convergent evolution of morphological features associated with parallel adaptation to similar microhabitats. For example, head pore patterns have been shown to be homoplastic in many groups of closely related gobies (Tornabene *et al.*, 2013a; Tornabene & Van Tassell, 2014), and sometimes are geographically variable or associated with unique microhabitats (Ahnelt & Scattolin, 2003; Ahnelt *et al.*, 2004). The connection between the pelvic fins has also been reduced or lost several times independently in many groups of reef-associated gobies, including several genera that have undergone miniaturization (some species of *Coryphopterus*, *Eviota*, and *Trimma*, etc.).

Conducting a detailed search for more informative osteological characters has also proved challenging for members of the *Nes* subgroup, as specimens of many species are too rare in collections to clear and stain or dissect (many species are known solely from types), and frequently small specimens are in poor condition as a result of being trawled from considerable depths (below 200 m for some species). Thus, to date, the biggest challenges in resolving the classification within the *Nes* subgroup have been the lack of comparative material and a poor understanding of the phylogenetic information contained in the characters traditionally used to diagnose and classify species.

DEEP-REEF COLLECTIONS FACILITATE A REVISION OF THE *NES* SUBGROUP

Many additional specimens from the *Nes* subgroup have accumulated over the last several decades, largely as a result of two independent research programmes exploring deep reefs in the Caribbean. Recent collections from the Smithsonian Deep Reef Observation Project (DROP) via the manned submersible *Curasub* have produced several deep-reef goby specimens that represent undescribed species within the *Nes* subgroup. Specimens from DROP were also tissue sampled, enabling subsequent molecular phylogenetic analysis, and specimens were photographed prior to preservation, allowing comparisons of colour patterns. Many other deep-reef goby specimens were also collected by the Johnson

Sea Link submersibles in the 1980–1990s. Included in these collections were several undescribed species, but the taxonomic issues within the group coupled with a lack of available comparative material had postponed their description. Collectively these deep-reef collections combined with existing museum material for shallow-water species provide adequate data for the first comprehensive review of the *Nes* subgroup.

In this taxonomic review, we first use a molecular phylogeny from mitochondrial and nuclear DNA sequence data to infer relationships within the *Nes* subgroup. We then use the molecular tree as an independent phylogenetic hypothesis to assess the distribution of morphological characters and evaluate the phylogenetic information contained within them. Specifically, we use ancestral state estimation coupled with a model-fitting approach using Pagel's λ (Pagel, 1999) to evaluate the congruence between our morphological characters and the molecular tree, and to measure phylogenetic signal in characters. Traits with significant phylogenetic signal are deemed most useful for morphologically diagnosing the monophyletic groups recovered in our phylogeny, and are likely to be the most helpful in determining the placement of other species that are not included in our molecular tree because of a lack of available tissue samples. Collectively, the morphological and molecular data serve as a framework for a revised classification of the *Nes* subgroup that includes nine new species and the erection of four new genera. For each genus recognized here, we provide morphological diagnoses, justification for the inclusion of species not represented in our molecular tree, and, when relevant, a brief synopsis of the past and present taxonomic issues regarding species in that genus. The results of our study will hopefully lead to a more stable phylogenetic classification of this diverse group of fishes. Lastly, this study represents the latest contribution towards understanding the biology of American seven-spined gobies – a model group for studying ecological speciation and adaptive radiation – and demonstrates the utility of using multiple independent data sets in unravelling relationships among ecologically diverse, rapidly speciating groups of reef fishes.

MATERIAL AND METHODS

MATERIAL

Our list of material examined includes 197 lots from the *Nes* subgroup, of which 27 specimens were cleared and stained for cartilage and bone, 87 had lateral radiographs, and 39 had tissue or DNA samples available (Table S1). Our material includes type

specimens for most species in the *Nes* subgroup. The deep-reef gobies collected by DROP were obtained using the methods described by Baldwin & Robertson (2014). Several specimens captured by DROP were brought to the surface alive and photographed in aquaria by Barry B. Brown (Substation Curacao). Many additional specimens were captured with manned deep-sea submersibles during seven expeditions directed by R.G. Gilmore (chief scientist) from 1982 to 1997 in the Bahama Islands, West Indies, Central America, and Cuba using both Johnson-Sea-Link (JSL-I and JSL-II) submersibles. Innovative capture, hydraulic, and suction systems, along with pure crystalline rotenone-injection systems (Gilmore, Hastings & Kulczycki, 1981), had been developed over a period of 7 years, which finally allowed the active chase and capture of mobile fish using manned submersibles in 1982. The wide field of visibility offered by the JSL acrylic spheres along with effective emulsifiers for 100% rotenone, primarily dimethyl sulfoxide, allowed the capture of over 2000 fish specimens and over 100 undescribed fish species in a variety of phylogenetic groups during these expeditions. The multiple directional thrusters with experienced pilots capable of moving rapidly in three dimensions were indispensable in capturing highly mobile specimens. Specimens captured by JSL submersibles were stored in rotating individual numbered capture bins based on the capture site, time, and depth, and *in situ* photos and video were taken of the habitat along with audio narration from scientists. Water temperature and current profiles were maintained for all dives. Photos and or drawings were made of fresh dead specimens before fixation in 10% buffered formalin. Lastly, several new species described here resulted from shallow water collections in the Florida Keys by Dynasty Marine Associates, and from closed-circuit re-breather dives off Espirito Santo, Brazil, by Thiony Simon and Hudson T. Pinheiro. All specimens from this study that were captured alive were eventually killed with a lethal dose of MS-222 or quinaldine.

All measurements were taken with digital calipers and proportional measurements are expressed in percentage standard length (SL) or percentage head length (HL). An asterisk indicates the count of the holotype. The dorsal pterygiophore formula used is that of Birdsong *et al.* (1988), cephalic canal pore terminology follows Akihito, Hayashi & Yoshino (1988), and patterns of sensory papillae are described according to Sanzo (1911), with the following additions: we divide row *p* into *pb'*, *pc'*, and *pe'* to indicate the cephalic canal pores (B, C, E) which are replaced by papillae in the corresponding locations. Institutional acronyms follow Sabaj Pérez (2014). Definitions of other morphological characters follow Böhlke &

Robins (1968), as modified by Van Tassell *et al.* (2012). Specifically, we differ from Böhlke & Robins (1968) in that we differentiate the unsegmented spine and segmented rays of the second dorsal and anal fins using the Roman numeral 'I' for the spine followed by Arabic numbers for the soft rays. When pectoral-fin-ray counts differ on each side of a specimen, counts for both sides are given as 'left side/right side'.

MOLECULAR PHYLOGENETIC ANALYSIS AND CHARACTER EVOLUTION

New sequence data used in this study were supplemented with data from additional Gobiosomatini species from Agorreta *et al.* (2013). The alignment contained 72 specimens from the Gobiosomatini, including 45 from the *Nes* subgroup (Table S1). The matrix consisted of 4,402 characters from one mitochondrial gene (cytochrome *b*) and three nuclear genes (*Rag1*, *sreb2*, and *zic1*). Primers and polymerase chain reaction (PCR) conditions are identical to those used in Agorreta *et al.* (2013). Phylogenetic relationships were inferred using Bayesian inference in the program MrBayes 3.2 (Ronquist *et al.*, 2012). Substitution model choice and best partitioning scheme were assessed simultaneously using PartitionFinder (Lanfear *et al.*, 2012). The analysis was run four times, each analysis consisting of two parallel Markov chain Monte Carlo (MCMC) runs (four chains each), with each MCMC running for 10 million generations. Burn-in, convergence, and mixing were assessed using TRACER 1.5 (Rambaut & Drummond, 2007) and AWTY (Wilgenbusch, Warren & Swofford, 2004).

To generate an ultrametric time-calibrated phylogeny we used relaxed molecular-clock methods in BEAST 2.2.3 (Bouckaert *et al.*, 2014), as our data led us to reject the null hypothesis of a strict molecular clock (likelihood ratio test, $P < 0.05$). To incorporate appropriate fossil calibration points, we expanded our data set to include 107 total taxa, including species from throughout the families Gobiidae, Eleotridae, Butidae, Rhyacichthyidae, and Odontobutidae. These families (plus Milyeringidae and Thalasseleotrididae, neither of which were available for this study) collectively comprise the Gobioidi and represent appropriate out-groups for our analysis (Thacker, 2009; Gill & Mooi, 2012; Thacker *et al.*, 2015). We used the following three calibration points: (1) following Thacker (2015), we set the crown age of all gobioid fishes (root age of the tree) to a minimum of 52 Myr, with a very soft upper bound (prior settings: exponential distribution; mean, 10; offset, 52), based on the oldest known fossil gobioid, an Eocene otolith that could not be taxonomically placed within a gobioid family with confidence (Bajpai & Kapur,

2004; Gierl *et al.*, 2013); (2) the most recent common ancestor of *Kribia nana* (Boulenger, 1901) and *Bostrychus zonatus* Weber, 1907 was set to a minimum of 23 Myr, with a soft upper maximum (prior settings: lognormal distribution; mean, 1.5; standard deviation, 0.8; offset, 23), based on a well-preserved whole-body fossil of an upper Oligocene Butidae species that is hypothesized to be a close relative of *Kribia* (Gierl *et al.*, 2013); (3) the most recent common ancestor of the Atlantic and Pacific species of *Gobulus* was set to a minimum age of 2.8 Myr, with a conservative soft upper maximum (prior settings: exponential distribution; mean, 6; offset, 2.8), based on the most recent estimate of final closure of the Isthmus of Panama, which marks the latest point at which this split could have occurred. A maximum-clade credibility tree was generated from the BEAST analysis, and taxa were removed from this tree to include only single representatives of each species from the *Nes* subgroup. The resulting 26-species phylogeny was then used for downstream analysis of character evolution.

To examine the evolution of several morphological characters (Table 1) and assess their agreement with our molecular phylogenetic hypothesis, we fitted models of discrete trait evolution to the time-calibrated tree and calculated marginal ancestral character state reconstructions in the software language R (R Core

Team, 2014), using the function ‘rerootingMethod’; (Yang, Kumar & Nei, 1995) in the PHYTOOLS package (Revell, 2012). This likelihood-based method can accommodate uncertainty in character states at the tips of the phylogeny, making it well suited for species where certain morphological features could not be observed, or were variable within the species. For this approach we assumed a Markov model of discrete trait evolution with a symmetrical rate matrix, such that initial character transformations and subsequent reversals were equally probable. To assess how well our models of character evolution agreed with our molecular tree (evaluate phylogenetic signal of each trait), we employed a model-fitting approach using Pagel’s λ (Pagel, 1999). Pagel’s λ is a tree transformation parameter that removes phylogenetic structure from a given tree by manipulating internal branch lengths, such that $\lambda = 0$ transformation results in a completely unresolved tree (a ‘star phylogeny’) and $\lambda = 1$ is an untransformed (original) tree (Pagel, 1999). For each morphological character, we fitted our model of trait evolution to a $\lambda = 0$ transformed tree (unresolved) and our original tree to examine whether the morphological characters evolved fit our empirical tree significantly better than a tree with little or no phylogenetic signal. Lambda transformations were performed in the R package GEIGER (Harmon *et al.*, 2008). The $\lambda = 0$ transformed and untransformed

Table 1. Summary of model fit statistics for each character on original tree and unresolved tree, and comparison between models

Morphological character	Log likelihood for characters fit to molecular tree	Log likelihood for characters fit to unresolved tree	Likelihood ratio test <i>P</i> -value (χ^2 , d.f. = 1)
Papillae rows 5i and 5s connected or disjunct	−11.0612	−17.328	<0.001***
Body Scales present or absent	−12.0319	−17.3286	0.001**
Pelvic fins connected by well developed membrane or not	−6.780	−11.162	0.003**
Basicaudal Scales present or absent	−13.449	−17.329	0.005**
Anal-fin pterygiophores before haemal arch	−13.86	−17.328	0.008**
Fifth pelvic branched or not	−13.436	−16.048	0.022*
Head canals present or absent	−9.437	−9.298	1.000
Interorbital papillae present or absent	−16.582	−16.029	1.000

Asterisks indicate significantly better fit to molecular tree than the unresolved tree, indicating strong phylogenetic signal.

models were compared with one another using likelihood ratio tests (chi-square distribution, d.f. = 1).

The following characters were used in the analysis of ancestral character states and to evaluate phylogenetic signal: the presence or absence of lateral scale rows on the body; presence or absence of modified ctenoid scales at the dorsal and ventral base of the caudal-fin rays (hereafter 'modified basicaudal scales'; Fig. 1); fifth pelvic-fin ray branched or unbranched; pelvic fins with or without anterior frenum connecting spines; presence of one versus two anal-fin pterygiophores inserted anterior to haemal spine (Fig. 2); papillae rows 5i and 5s connected as a single row (or nearly so) or as well-separated rows (Fig. 3); presence or absence of interorbital papillae; and presence or absence of cephalic lateralis canals and associated head pores. The extent of branching of pelvic-fin rays 1–4 has been used in the past to diagnose species and genera within the *Nes* subgroup, and is considered here to have some taxonomic utility; however, the high number of distinct branching morphologies (Fig. 4) and the variation within species make this character poorly suited for likelihood-based analysis of discrete character traits with a phylogeny of this size, thus it is not included in our phylogenetic signal analyses.

RESULTS

The molecular phylogeny shows strong support (Bayesian posterior probability >0.97) for most clades in the *Nes* subgroup (Fig. 5). The major exceptions include the placement of *Psilotris amblyrhynchus* Smith & Baldwin, 1999; *Psilotris batrachoides*

Böhlke, 1963; and *Nes longus* (Nichols, 1914), and the position of *Varicus imswe* Greenfield, 1981 + *Gymneleotris* relative to the clade that contains *Pycnomma* and the Pacific species of *Chriolepis*. Of the five genera of the *Nes* subgroup that contain more than one species, only *Gobulus* is monophyletic, indicating a need for substantial taxonomic revision.

Our analysis of character evolution shows that every character mapped on the phylogeny, including the major characters that have been used to diagnose genera within the *Nes* subgroup, exhibit some level of homoplasy across the tree (Figs 6–9); however, the extent of homoplasy varies considerably, and all but two characters show significant levels of phylogenetic signal (Table 1). The presence of interorbital papillae and the presence of cephalic lateralis canals and pores on the head had no significant phylogenetic signal: models of trait evolution fitted to our unresolved phylogeny for those characters were not significantly better than models fitted to our empirical molecular tree (Table 1). The presence of a branched fifth pelvic-fin ray had only marginally significant phylogenetic signal ($P = 0.022$). Additional characters that have not previously been used to diagnose genera, such as the number of anal-fin pterygiophores inserted before the haemal spine and the connection of papillae rows 5i and 5s (Fig. 6), also show low levels of homoplasy and strong phylogenetic signal ($P = 0.008$ and <0.001 , respectively), and thus may be useful characters for a morphological classification.

Based on the presence of widespread polyphyletic genera under the existing classification scheme, we propose a new classification of the genera in the *Nes* subgroup (Fig. 5; Table 2) that renders each genus

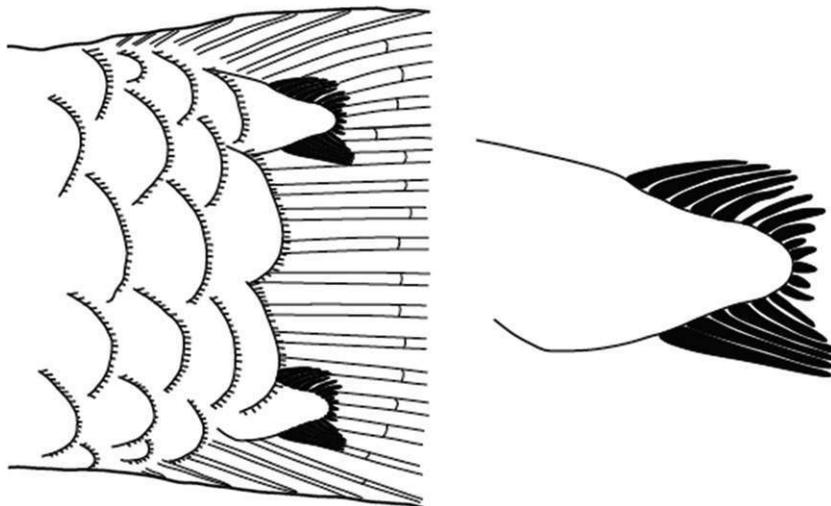


Figure 1. Modified ctenoid basicaudal scales showing position on caudal peduncle and a single scale. Species may possess two (as shown here) or as many as four modified scales.

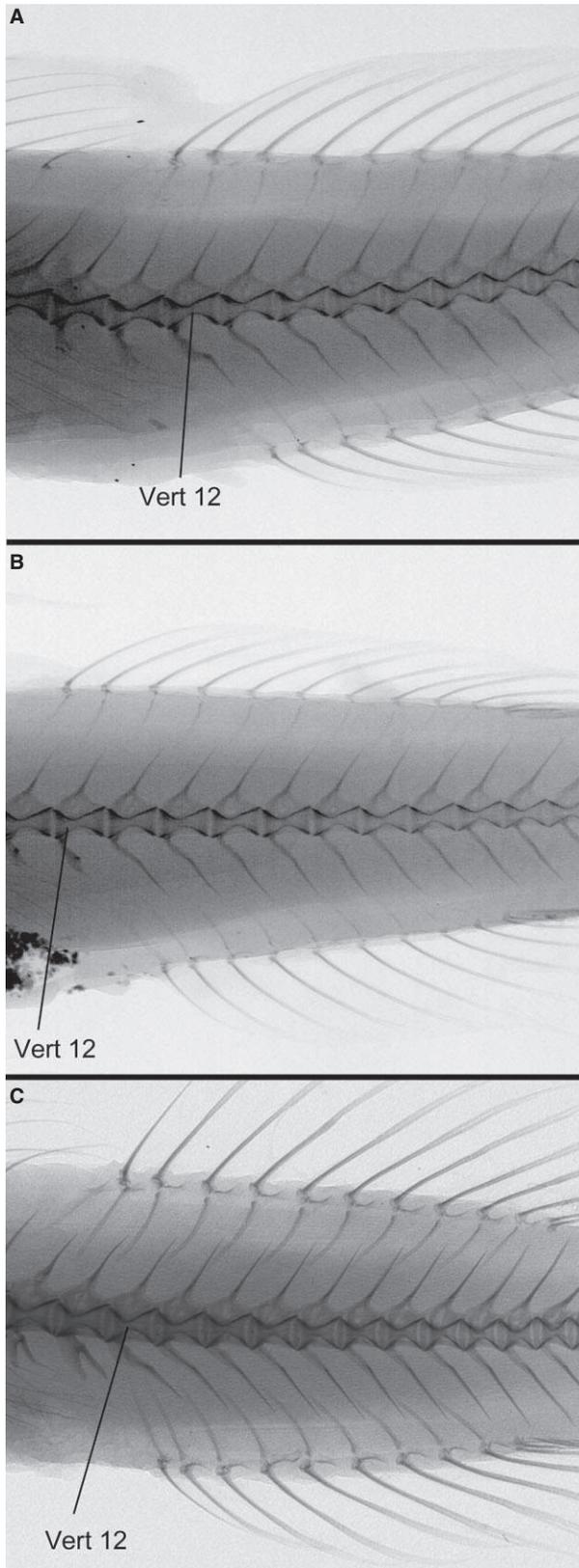


Figure 2. Anal-fin pterygiophore insertion patterns. (A) One anal-fin pterygiophore inserted anterior to first haemal spine (*Varicus cephalocellatus* paratype, USNM 427227); (B) rare pattern in which haemal spine on vertebra 12 is reduced, and first elongate haemal spine appears on vertebra 13, giving the appearance of two anal-ptyerygiophores inserted before first haemal spine. This pattern is considered homologous to pattern depicted in A, and occurs only in species in which the pattern from A is also observed (*Varicus cephalocellatus* paratype, USNM 427227); (C) two anal-fin pterygiophores inserted anterior to first haemal spine (*Chriolepis lepidota* holotype USNM 211456).

monophyletic. The new classification includes four new genera for three previously described species and one new species, reassigns four species to different existing genera, and leaves the generic status of 20 previously described species unchanged. The nine new species described here are placed into three genera. One species, *Chriolepis fisheri* Herre, 1942, is *incertae sedis*. Many of the genera circumscribed here are not diagnosed by a single morphological synapomorphy, because of widespread homoplasy revealed in the morphological characters (although all are strongly supported with shared derived molecular character states); however, nearly all of the genera are unambiguously diagnosed by a combination of characters, many of which possess moderate to significant phylogenetic signal based on the results of our character analysis (Table 1).

SYSTEMATICS

CARRIGOBIUS VAN TASSELL, TORNABENE & GILMORE
GEN. NOV.

TYPE SPECIES: *CARRIGOBIUS AMBLYRHYNCUS*
(SMITH & BALDWIN, 1999: 434, FIGS 1–3,
DESCRIBED AS *PSILOTRIS AMBLYRHYNCUS*)

[http://zoobank.org/urn:lsid:zoobank.org:pub:
E952647E-1571-4A14-8BD4-54D1746760D0](http://zoobank.org/urn:lsid:zoobank.org:pub:E952647E-1571-4A14-8BD4-54D1746760D0)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays (inter-radial

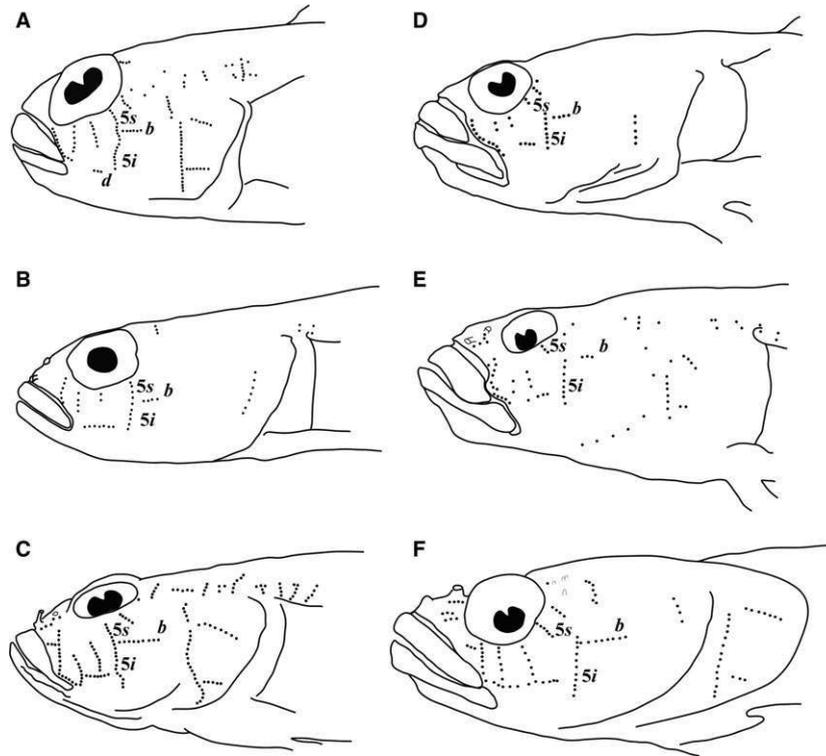


Figure 3. Examples of papillae patterns in which rows 5i and 5s are connected (A–C) or distinctly separate (D–F). (A) *Varicus bucca*, UMML 7119; (B) *Pinnichthys prolata*, AMNH 87272; (C) *Psilotris celsa*, USNM 98429; (D) *Chriolepis minutilla*, USNM 322595; (E) *Chriolepis zebra*, CAS 31001; (F) *Gobulus crescentalis*, USNM 48258.

membrane better developed in larvae); pelvic-fin rays 1–5 branched (fifth ray branched only in mature adults), without fleshy or flattened tips; pelvic-fin rays extending posteriorly to about halfway to anus or slightly further, but never reaching anus; body lacking scales (modified basicaudal scales absent); two anal-fin pterygiophores inserted before first haemal spine; cephalic sensory canals absent; second dorsal-fin rays I,10–11; anal-fin rays I,8–10; body with diffuse dark saddles and a series of evenly spaced midlateral blotches on side of body; anterior profile of head blunt, nearly vertical. The one known species occurs in the western Atlantic Ocean.

Remarks

Carrigobius is erected for *Psilotris amblyrhynchus* Smith & Baldwin, 1999. *Psilotris amblyrhynchus* was described from a series of specimens collected off Carrie Bow Cay, Belize. It was tentatively placed in *Psilotris* based on the absence of scales and cephalic lateral canals and the presence of separate pelvic fins (Smith & Baldwin, 1999); however, in agreement with observations by Greenfield (1993), Smith & Baldwin (1999) recognized that the species of *Psilotris* were probably not a monophyletic group. Specifically, *Psilotris amblyrhynchus* stood out from the other members

of the genus in having a head with a steep blunt profile versus a gradually sloping pointed profile.

The type series of *Psilotris amblyrhynchus* included many larval specimens, two of which were reared through metamorphosis (Smith & Baldwin, 1999). The developmental series for this species enables observation of several ontogenetic changes that may provide some insight into the evolution of morphological features of the *Nes* group as a whole. First, the membrane uniting the pelvic fins begins as a well-developed connection in larvae and juveniles, resembling the adult condition found in some species of *Gobulus* and *Nes*. By 14.2 mm SL the pelvic membrane was completely reduced and fins were entirely free from one another. In addition, the pelvic-fin rays are originally unbranched and become branched throughout development, with rays 1–4 branching first and ray 5 becoming branched only in adults. Similar development of pelvic ray branching was observed in *Nes*.

Our phylogenetic hypothesis shows ambiguous placement of this species (Bayesian posterior probabilities <0.80), but it was consistently resolved outside the well-supported clade containing other all *Psilotris* species except *Psilotris batrachodes* Böhlke, 1963 (now as *Cryptopsilotris* gen. nov.). To reconcile

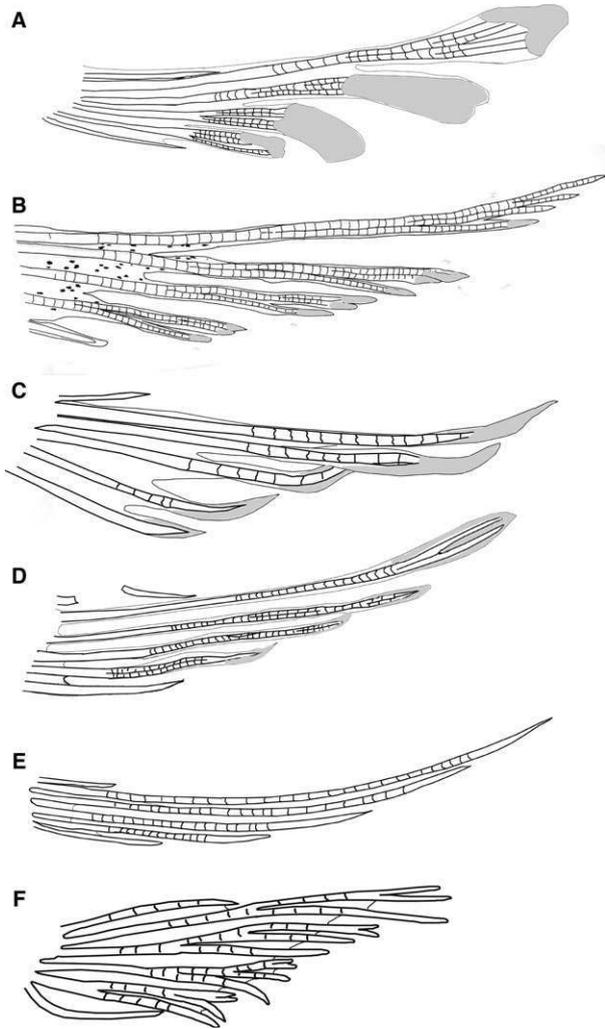


Figure 4. Variation in branching pattern of pelvic rays 1–4 in the Nes subgroup. (A) branched but united at tips as a flattened, spatulate fleshy pad, *Varicus adamsi*, USNM 220985; (B) branched to the tips, some branches with minute fleshy tips, *Varicus vespa*, paratype (USNM 221524); (C) rays unbranched, or branched internally and re-fused (as in ray 3), tips with fleshy pads, *Varicus bucca*, holotype ANSP 93083; (D) rays branched, mostly internally and re-fused, tips with fleshy pads, *Varicus* sp., USNM 199060; (E) all rays unbranched without fleshy tips, *Varicus veliguttatus* USNM 220982; (F) all rays branched, not re-fused and no fleshy tips, *Psilotris boehlkei*, USNM 427234.

the polyphyly of *Psilotris*, the new genus *Carrigobius* is erected. Important distinguishing features that separate it from *Psilotris* and *Cryptopsilotris* are the blunt profile of the head and the presence of a branched fifth pelvic-fin ray in adults. This latter feature, as well as the presence of two anal-fin pterygiophores before the first haemal spine, distinguishes

this species from the scale-less members of the genus *Varicus*. For additional descriptive information on *Carrigobius amblyrhynchus* see Smith & Baldwin (1999).

Etymology

The name *Carrigobius* is formed from the Latin *gobius* (goby or gudgeon) and Carrie, in reference to Carrie-Bow Cay, Belize, home of the Smithsonian Institution's field station, where many specimens of *Carrigobius amblyrhynchus* were collected.

CHRIOLEPIS GILBERT, 1892

TYPE SPECIES: *CHRIOLEPIS MINUTILLA* GILBERT, 1892 (ORIGINAL SPELLING *CHRIOLEPIS MINUTILLUS*), BY MONOTYPY
PYCNOMMA RUTTER, 1904

TYPE SPECIES: *PYCNOMMA SEMISQUAMATUM* RUTTER, 1904, BY MONOTYPY

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (seven-first dorsal-fin spines, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–4 branched, never with flattened or fleshy tips; fifth pelvic-fin ray unbranched in some species, branched or variable in others; pelvic-fin rays extending posteriorly to anus, never reaching origin of anterior anal-fin rays; body with scales, modified basicaudal scales present; two anal-fin pterygiophores inserted before first haemal spine; papillae rows 5i and 5s separate; cephalic lateralis canals and pores absent in all but two species *Chriolepis roosevelti* (Ginsburg, 1939), *Chriolepis semisquamata* (Rutter, 1904); second dorsal-fin rays I, 8–11; anal-fin rays I, 8–10. Colour patterns variable among species: uniformly drab, with cryptic mottling and spotting, or with prominent narrow black vertical bars on white body. All but one known species occur in the tropical eastern Pacific Ocean.

Remarks

Chriolepis received its first formal taxonomic treatment when Findley (1983) reviewed the Pacific members of the genus in an unpublished PhD dissertation. This review provided a robust overview of the diversity within the Pacific members of the group (including several apparently new species that have yet to be described). Findley also recognized that the genus could be divided into two sub-

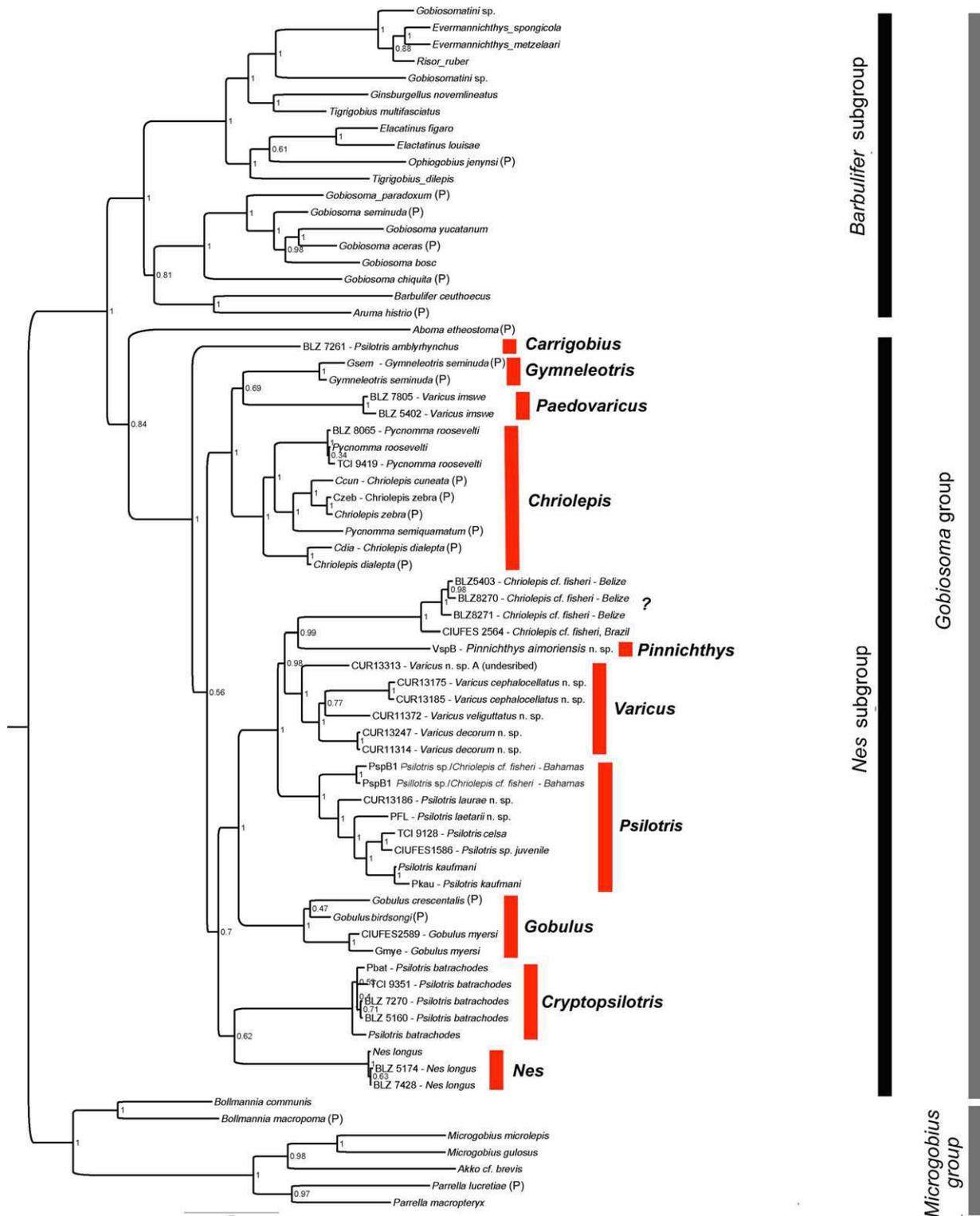


Figure 5. Bayesian phylogeny from MrBayes analysis of the Gobiosomatini. Tip labels follow classification recognized prior to this study. Red bars indicate new classification from this study (Table 2). Support values at nodes are Bayesian posterior probabilities. The “?” for *Chriolepis cf. fisheri* refers to the *incertae sedis* status of this species (see “Remarks” section for *Chriolepis*). Species from the eastern Pacific are denoted with “(P)”.

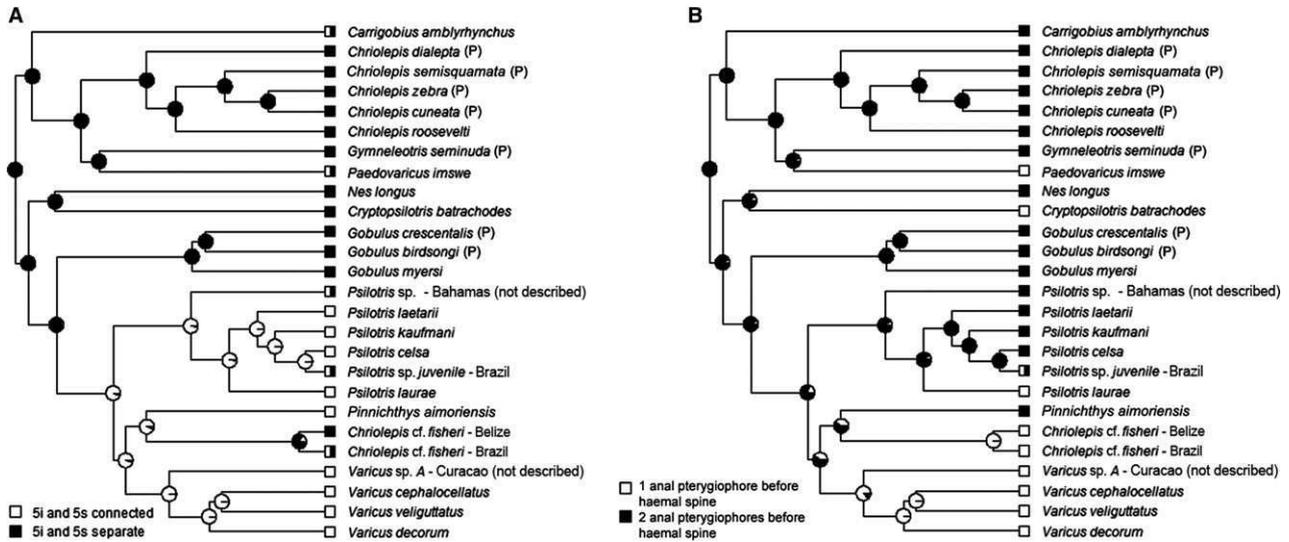


Figure 6. Ancestral character estimation for (A) papillae row 5i and 5s pattern and (B) anal-fin pterygiophore insertion pattern. Pies at nodes represent posterior probabilities for ancestor's character state. Tips with both black and white reflect variation or uncertainty in our knowledge of that species' character state. Species from the eastern Pacific are denoted with "(P)".

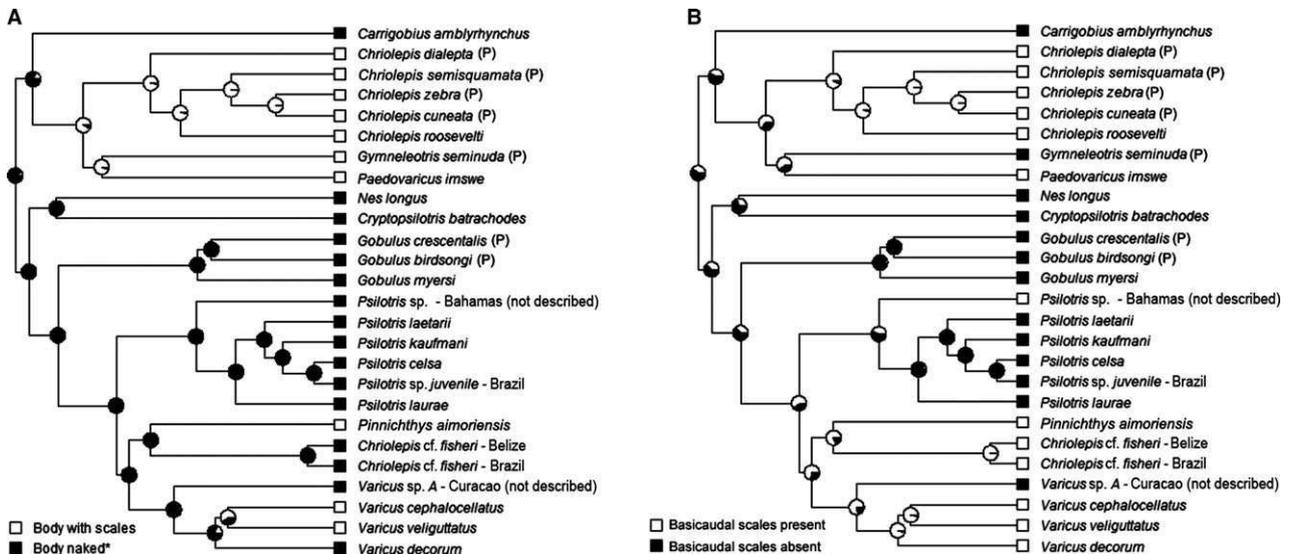


Figure 7. Ancestral character estimation for (A) the presence/absence of body scales (not including basicaudal scales) and (B) and presence/absence of modified basicaudal scales. Pies at nodes represent posterior probabilities for ancestor's character state. Species from the eastern Pacific are denoted with "(P)".

genera that were originally described by Ginsburg (1938) as *Chriolepis chriolepis* and *Chriolepis electriculus*. Findley (1983) made no formal inferences regarding the relationships to the Atlantic species of *Chriolepis* or *Varicus*; however, he acknowledged that *Chriolepis* as currently described was not likely to be monophyletic and was probably a 'catch-all' genus for unrelated species. Our molecular phylogeny supports this. The Pacific members of *Chriolepis* have no close relatives in the Atlantic

except for *Pycnomma roosevelti* (here as *Chriolepis roosevelti*). Even with the exclusion of Atlantic taxa, the Pacific species of *Chriolepis* themselves are not monophyletic, and form two distinct groups that agree well with Findley's (1983) subgeneric arrangement, with subgenus *Chriolepis* being represented here by *Chriolepis dialepta* Bussing, 1990, and subgenus *Electriculus* represented by *Chriolepis zebra* Ginsburg, 1938 and *Chriolepis cuneata* Bussing, 1990. *Chriolepis minutilla* is the type species of

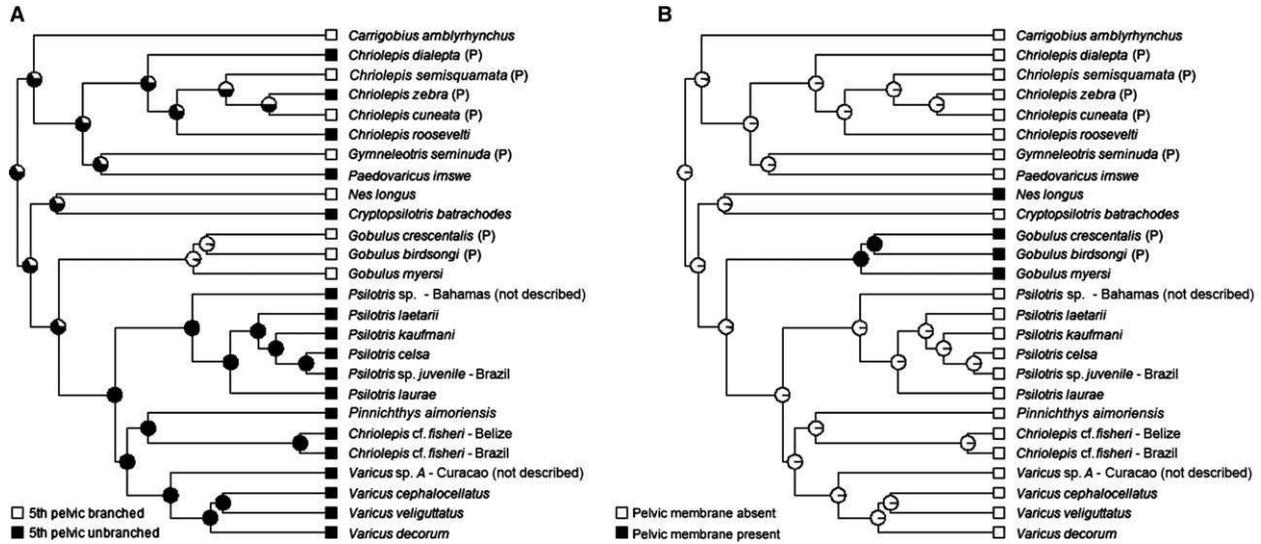


Figure 8. Ancestral character estimation for (A) branched versus unbranched 5th pelvic ray and (B) presence/absence of a well-developed membrane connecting the innermost pelvic rays. Pies at nodes represent posterior probabilities for ancestor’s character state. Species from the eastern Pacific are denoted with “(P)”.

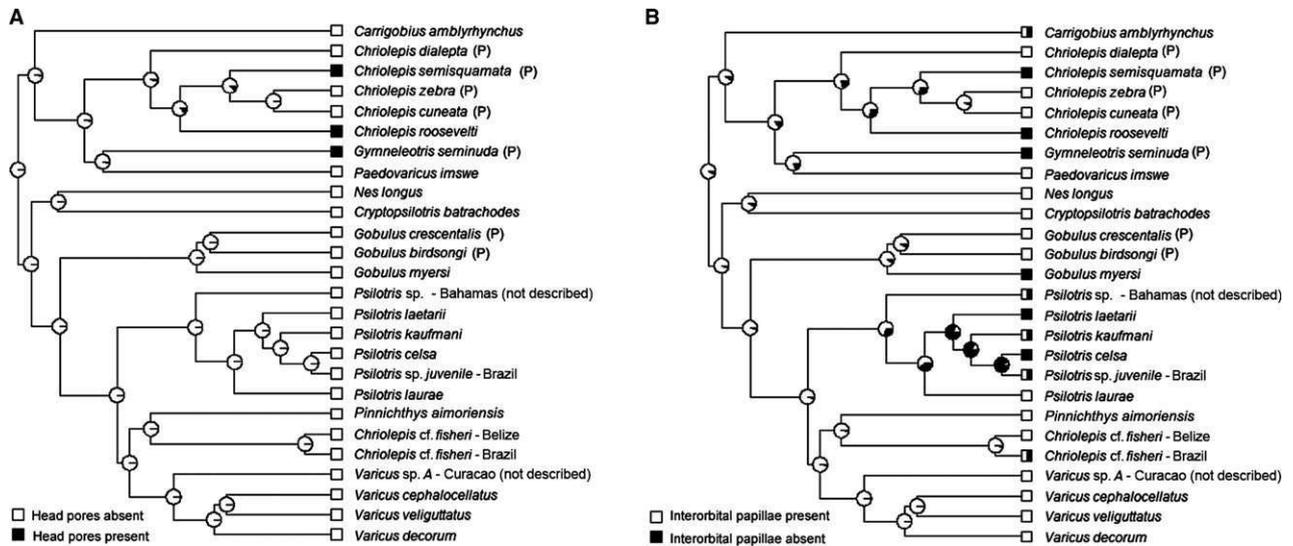


Figure 9. Ancestral character estimation for (A) the presence/absence of cephalic lateralis pores and canals, and (B) presence/absence of interorbital papillae. Pies at nodes represent posterior probabilities for ancestor’s character state. Tips with both black and white reflect variation or uncertainty in our knowledge of that species’ character state. Species from the eastern Pacific are denoted with “(P)”.

the genus, and Findley (1983) recognized many similarities between *Chriolepis minutilla*, *Chriolepis dialepta*, and *Chriolepis lepidota* Findley, 1975, placing all three in the subgenus *Chriolepis*. We agree with this assessment and conclude that *C. minutilla* and *C. lepidota* are likely to be part of the clade containing *C. dialepta*. *Chriolepis tagus* Ginsburg, 1953, known only from the holotype, is of uncertain affinity, but we provisionally retain it

within *Chriolepis* pending future analysis of additional specimens.

Nested between the two lineages of *Chriolepis* are the species of *Pycnomma*, a genus previously separated from *Chriolepis* by the presence of cephalic lateralis canals and pores; however, our analysis shows that the absence of cephalic lateralis canals may actually be a plesiomorphic condition across the *Nes* group, and that the presence of pores in *Pycnomma*

Table 2. New classification of the *Nes* subgroup

Present study		Van Tassell, 2011; Eschmeyer, 2015		Common name
<i>Carrigobius</i>	<i>amblyrhynchus</i>	<i>Psiilotris</i>	<i>amblyrhynchus</i>	Blunt-snout goby
<i>Chriolepis</i>	<i>atrimela</i> *	<i>Chriolepis</i>	<i>atrimelum</i>	Black-cheek goby
<i>Chriolepis</i>	<i>cuneata</i>	<i>Chriolepis</i>	<i>cuneata</i>	Rail-goby
<i>Chriolepis</i>	<i>dialepta</i>	<i>Chriolepis</i>	<i>dialepta</i>	White-starred goby
<i>Chriolepis</i>	<i>lepidota</i>	<i>Chriolepis</i>	<i>lepidotus</i>	Pretty goby
<i>Chriolepis</i>	<i>minutilla</i> *	<i>Chriolepis</i>	<i>minutilus</i>	Rubble goby
<i>Chriolepis</i>	<i>tagus</i>	<i>Chriolepis</i>	<i>tagus</i>	Mystery goby
<i>Chriolepis</i>	<i>zebra</i>	<i>Chriolepis</i>	<i>zebra</i>	Gecko goby
<i>Chriolepis</i>	<i>roosevelti</i>	<i>Pycnomma</i>	<i>roosevelti</i>	Roosevelt's goby
<i>Chriolepis</i>	<i>semisquamata</i>	<i>Pycnomma</i>	<i>semisquamatum</i>	Secret goby
<i>Eleotrica</i>	<i>cablae</i>	<i>Eleotrica</i>	<i>cablae</i>	Cable goby
<i>Gobulus</i>	<i>birdsongi</i>	<i>Gobulus</i>	<i>birdsongi</i>	Fin-joined goby
<i>Gobulus</i>	<i>crecensalis</i>	<i>Gobulus</i>	<i>crecensalis</i>	Crescent goby
<i>Gobulus</i>	<i>hancocki</i>	<i>Gobulus</i>	<i>hancocki</i>	Sand-top goby
<i>Gobulus</i>	<i>meyersi</i>	<i>Gobulus</i>	<i>meyersi</i>	Paleback goby
<i>Gymneleotris</i>	<i>seminuda</i>	<i>Gymneleotris</i>	<i>seminuda</i>	Split-banded goby
<i>Nes</i>	<i>longus</i>	<i>Nes</i>	<i>longus</i>	Orange spotted goby
<i>Cryptopsilotris</i>	<i>batrachoides</i>	<i>Psiilotris</i>	<i>batrachodes</i>	Toadfish goby
<i>Paedovaricus</i>	<i>imswe</i>	<i>Varicus</i>	<i>imswe</i>	Whiteband goby
<i>Psiilotris</i>	<i>alepis</i>	<i>Psiilotris</i>	<i>alepis</i>	Scaleless goby
<i>Psiilotris</i>	<i>boehlkei</i>	<i>Psiilotris</i>	<i>boehlkei</i>	Boehlkei's goby
<i>Psiilotris</i>	<i>celsa</i> *	<i>Psiilotris</i>	<i>celsus</i>	Highspine goby
<i>Psiilotris</i>	<i>kaufmani</i>	<i>Psiilotris</i>	<i>kaufmani</i>	Kaufman's goby
<i>Psiilotris</i>	<i>laetarii</i> sp. nov.			Burrow splitfin goby
<i>Psiilotris</i>	<i>laurae</i> sp. nov.			Thin-barred goby
<i>Pinnichthys</i>	<i>prolata</i>	<i>Chriolepis</i>	<i>prolata</i>	Platform goby
<i>Pinnichthys</i>	<i>bilix</i>	<i>Chriolepis</i>	<i>bilix</i>	Double-filament goby
<i>Pinnichthys</i>	<i>aimoriensis</i> gen. et sp. nov.			Thiony's goby
<i>Pinnichthys</i>	<i>saurimimica</i> gen. et sp. nov.			Lizardfish goby
<i>Varicus</i>	<i>adamsi</i> sp. nov.			Twilight goby
<i>Varicus</i>	<i>benthonis</i>	<i>Chriolepis</i>	<i>benthonis</i>	Deepwater goby
<i>Varicus</i>	<i>bucca</i>	<i>Varicus</i>	<i>bucca</i>	Puffed cheek goby
<i>Varicus</i>	<i>cephalocellatus</i> sp. nov.			Ocellated splitfin goby
<i>Varicus</i>	<i>decorum</i> sp. nov.			Decorated splitfin goby
<i>Varicus</i>	<i>marylinae</i>	<i>Varicus</i>	<i>marylinae</i>	Orangebelly goby
<i>Varicus</i>	<i>nigritus</i> sp. nov.			Banded splitfin goby
<i>Varicus</i>	<i>veliguttatus</i> sp. nov.			Spotted-sail goby
<i>Varicus</i>	<i>vespa</i>	<i>Chriolepis</i>	<i>vespa</i>	Wasp goby
<i>incertae sedis</i>		<i>Chriolepis</i>	<i>fisheri</i>	Translucent goby

*Spelling corrected to match gender of genus.

may represent independent apomorphic reversals. Rather than divide the clade containing the Pacific *Chriolepis* and *Pycnomma* into several genera, we synonymize *Pycnomma* with *Chriolepis* and restrict *Chriolepis* to the Pacific members of the group (except *Chriolepis atrimela* Bussing, 1997) plus the two species of *Pycnomma*.

Our genetic sampling did not include the Atlantic species *Chriolepis benthonis* Ginsburg, 1953; *Chri-*

olepis bilix Hastings & Findley, 2013; *Chriolepis prolata* Hastings & Findley, 2015; or *Chriolepis vespa* Hastings & Bortone, 1981; however, these four species have several characters that differentiate them from each other and from most Pacific *Chriolepis*, and are herein assigned to either the genus *Varicus* (for *Chriolepis vespa* and *Chriolepis benthonis*) or *Pinnichthys* gen. nov. (for *Chriolepis bilix* and *Chriolepis prolata*). The Atlantic species previ-

ously classified as *Chriolepis* have either one anal-fin pterygiophore inserted before the haemal spine, as in *Chriolepis benthonis* and *Chriolepis vespa*, or have papillae rows 5i and 5s connected and are heavily scaled, as in *Chriolepis bilix* and *Chriolepis prolata* Hastings & Findley, 2015. The Pacific *Chriolepis atrimela*, a deep-reef species from the Galápagos Islands, is also assigned to *Pinnichthys* based on morphological features. Further discussion on the reassignment of *Chriolepis atrimela* and the other aforementioned Atlantic species of *Chriolepis* are given in the remarks sections for *Varicus* and *Pinnichthys* below.

The generic assignment of the Atlantic species *Chriolepis fisheri* is uncertain. This species lacks body scales except for two modified basicaudal scales on each side of the caudal peduncle, has one anal-fin pterygiophore inserted before the first haemal spine, and the connection of papillae rows 5i and 5s is unknown. Our molecular analysis includes two species that superficially agree with *Chriolepis fisheri* in that they possess only basicaudal scales. These species are recovered in two different lineages on the molecular phylogeny. One lineage from Belize and Fernando de Noronha, Brazil, is sister to *Pinnichthys* and possesses I,10–11 second dorsal-fin rays, I,9–11 anal-fin rays, and one anal-fin pterygiophore inserted before the haemal spine, all of which agree to some extent with the holotype of *Chriolepis fisheri* (I,10 second dorsal, I,9 anal). The second lineage is represented by two specimens from the Bahamas, and is nested among several species of *Psilotris* (labelled as *Psilotris* sp./*Chriolepis* cf. *fisheri* in Fig. 5). These specimens have I,9 second dorsal-fin rays, I,8 anal-fin rays, and the one cleared-and-stained specimen has one anal-fin pterygiophore anterior to the haemal arch but two pterygiophores inserted in the subsequent interhaemal space. A survey of additional museum specimens labelled as *Chriolepis fisheri* from throughout the Caribbean has revealed a complex mix of specimens possessing a variety of combinations of second-dorsal and anal-fin counts, as well as pterygiophore insertion patterns, often co-occurring in the same locality (Table S1). Furthermore, all of the *Chriolepis fisheri* material examined in this study comes from shallow reefs, whereas the holotype of *Chriolepis fisheri* was collected from a depth of 82 m. Therefore, it is possible that the true *Chriolepis fisheri* may be a more rare, deep-reef species, not represented by either of the two lineages in our tree. Based on this information, the status of *Chriolepis fisheri* is still unresolved, and an in-depth study of the various forms throughout the western Atlantic is needed to clarify this species (or group of species). Given the

uncertainty regarding this species, rather than provisionally erect a new genus for the lineage that we tentatively decide is *Chriolepis fisheri* (thus preventing a polyphyletic *Chriolepis*), all with the likelihood that this may very well change in the near future, we instead consider *Chriolepis fisheri incertae sedis* pending further investigation.

CRYPTOSILOTRIS VAN TASSELL, TORNABENE & GILMORE GEN. NOV.

TYPE SPECIES: *CRYPTOSILOTRIS BATRACHODES* (BÖHLKE, 1963: 6, FIG. 2, DESCRIBED AS *PSILOTRIS BATRACHODES*)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group [first dorsal-fin spines VII (rarely five or six), pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal (occasionally 11 and 15 or 12 and 15), hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural]; pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–4 branched, without flattened or fleshy tips; pelvic-fin rays extending posteriorly half-way to anus or slightly further, never reaching anus; body without scales (modified basicaudal scales absent); one anal-fin pterygiophore inserted before haemal spine (in anomalous cases where first haemal spine is on vertebra 13 rather than vertebra 12, two anal-fin pterygiophores inserted before haemal spine); papillae rows 5i and 5s not connected; cephalic lateralis canals and pores absent; second dorsal-fin rays I,8–9; anal-fin rays I,6–7; a broad dark diagonal brown band on head passing through eye and onto preopercle; dorsal surface of body uniformly dark brown in contrast to ventral two-thirds of body, which has dark spots or mottling on pale background; first dorsal fin with dark wide diagonal band, second dorsal fin with two dark wide diagonal bands, and caudal fin with crescent-shaped dark band. The one known species occurs in the western Atlantic Ocean.

Remarks

Greenfield (1993) and Smith & Baldwin (1999) noted that the species of *Psilotris* are quite dissimilar from one another, and probably do not represent a natural group. *Psilotris batrachodes* is the most distinctive of these species both in meristics (lowest anal-fin ray count) and in coloration, and indeed our molecular phylogeny shows this species as being a distinct lineage separate from other *Psilotris* species. For this

reason, we erect the new genus *Cryptopsilotris* for this species.

Etymology

The genus name is formed from '*Psilotris*', the genus the type species was formerly classified under, and the root 'crypto-', which is taken from the Greek 'kruptos' meaning hidden. The name is in reference to the cryptic coloration of the type species.

ELEOTRICA GINSBURG, 1933

TYPE SPECIES: *ELEOTRICA CABLEAE* GINSBURG, 1933 (p. 10, by Original Designation)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–4 branched and never with flattened or fleshy tips, fifth pelvic-fin ray sometimes branched once near tip; pelvic-fin rays extending posteriorly to anus, never reaching origin of anterior anal-fin rays; side of body without scales (modified basicaudal scales present); two anal-fin pterygiophores inserted before first haemal spine; papillae rows 5i and 5s separate; cephalic sensory canals present, pores B', D, F, and H' present on raised short tubes; second dorsal-fin rays I,11; anal-fin rays I,9–10; body variously mottled with numerous small white spots on head and body, background colours generally with light tones that match the substrate from which it was collected, sometimes with a series of horizontally paired small dark spots along lateral midline. The one known species occurs in the eastern Pacific Ocean from the Galápagos Islands.

Remarks

The single species in this genus, *Eleotrica cableae*, is known only from the Galápagos Islands. It is generally a shallow water species that occurs from tide pools to depths of around 21 m, although a single record exists from a depth of 48 m off Santa Cruz (CAS 54523), which we have not examined. The phylogenetic placement of this species is uncertain. *Eleotrica* has the distinctive apomorphic feature of raised tubes at the opening of the cephalic sensory canal pores. It possesses a number of

plesiomorphic characters, including two anal-fin pterygiophores, inserted before the first haemal spine, and separate papillae rows 5i and 5s. The loss of body scales and the presence of cephalic lateralis canals are characters shared with *Gobulus*; however, it is uncertain whether this is a result of common ancestry or possibly convergent adaptation to a similar microhabitat (both occur in shallow, exposed habitats). Besides the Pacific members of *Gobulus*, no other Pacific species in the *Nes* subgroup completely lack body scales; however, the extent of squamation is variable across *Chriolepis*, and many species lack scales anteriorly. We were unable to obtain tissue samples for *Eleotrica* for molecular analysis, and we maintain *Eleotrica* as a valid genus pending further phylogenetic investigation.

GOBULUS GINSBURG, 1933

TYPE SPECIES: *GOBULUS CRESCENTALIS* (GILBERT, 1892) (GINSBURG, 1933: 12, BY ORIGINAL DESIGNATION)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins partially united with each other by a well-developed membrane along at least one-third of their length, pelvic spines sometimes connected by a weakly developed anterior frenum; anterior pelvic frenum connecting pelvic spines absent or reduced to a thin membrane, not extending to tips of spines; pelvic-fin rays 1–5 branched; pelvic-fin rays not extending posteriorly to anus; side of body without scales (modified basicaudal scales absent); two anal-fin pterygiophores inserted before first haemal spine; papillae rows 5i and 5s separate; cephalic lateralis canals and pores absent; second dorsal-fin rays I,9–I,13; anal-fin rays I,7–I,12; body with distinct reverse counter-shading, with lightly coloured dorsal surface and dark-brown lateral and or ventral surfaces. The four species are known from both the western Atlantic Ocean and eastern Pacific Ocean.

Remarks

The genus *Gobulus* was the only genus delimited prior to this study that was recovered as monophyletic in our tree. The four species in *Gobulus* are very similar in overall appearance and general biol-

ogy, and were reviewed in detail by Hoese & Reader (2001). The molecular phylogeny shows strong support for a sister relationship between *Gobulus* and the clade containing the western Atlantic genera *Psilotris*, *Varicus*, and *Pinnichthys*.

GYMNELEOTRIS BLEEKER, 1874

TYPE SPECIES: *GYMNELEOTRIS SEMINUDUS* (GÜNTHER, 1864: 304, DESCRIBED AS *ELEOTRIS SEMINUDUS* GÜNTHER, 1864, BY ORIGINAL DESIGNATION)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and the *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–5 branched and never with flattened or fleshy tips; pelvic-fin rays extending posteriorly to anus, never reaching origin of anterior anal-fin rays; side of body with scales (modified basicaudal scales absent), scales embedded anteriorly; two anal-fin pterygiophores inserted before first haemal spine; papillae rows 5i and 5s separate; cephalic sensory canals present, pores B', F, and H' present; second dorsal-fin rays I,10; anal-fin rays I,9; body dark brown to black with prominent narrow white vertical or diagonal bars on head, body, and dorsal fins. The one known species occurs in the eastern Pacific Ocean.

Remarks

The monotypic *Gymneleotris* was recovered in a clade with the genera *Chriolepis*, *Pycnomma* (now as *Chriolepis*), and *Varicus imswi* (now as *Paedovaricus* gen. nov.). Its position within this clade is unclear, as the sister relationship between *Gymneleotris* and *Paedovaricus* is weakly supported (Bayesian posterior probability of 0.69). Morphologically there is little evidence for a sister relationship between the two genera. At present, the only character distinguishing *Gymneleotris* from *Chriolepis* (as circumscribed herein) is the absence of modified basicaudal scales in *Gymneleotris*. The inclusion of additional eastern Pacific taxa and or phylogenetically informative characters may help resolve the position of this taxon and ultimately support a closer relationship (or nested relationship) with *Chriolepis*. Pending further investigation *Gymneleotris* is maintained here as a valid genus.

NES GINSBURG, 1933

TYPE SPECIES: *NES LONGUS* (NICHOLS, 1914) (GINSBURG, 1933: 25, DESCRIBED AS *GOBIOSOMA LONGUM* NICHOLS, 1914, BY ORIGINAL DESIGNATION; PROPOSED AS A SUBGENUS OF *GOBIOSOMA*)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins united completely to form round to oval disc, with well-developed anterior frenum uniting pelvic spines; pelvic-fin rays 1–5 branched; pelvic-fin rays extending posteriorly to point halfway to anus or slightly further, never reaching anus; side of body without scales (modified basicaudal scales absent); two anal-fin pterygiophores inserted before first haemal spine; papillae rows 5i and 5s separate; cephalic lateralis canals and pores absent; second dorsal-fin rays I,10–13; anal-fin rays I,10–12; body variously mottled and with distinct series of horizontally paired dark spots along lateral midline. The one known species occurs in the western Atlantic Ocean.

Remarks

The genus *Nes* contains one species, *Nes longus*. The ecology and behaviour of this species has been extensively studied because of its interesting association with *Alpheus* snapping shrimp (Randall, Lobel & Kennedy, 2005; Kramer, Van Tassell & Patzner, 2009). It is the only species in the *Nes* subgroup of the Gobiosomatini to have a fully developed pelvic disc. The phylogenetic position of *Nes* based on our molecular tree is unclear. A sister relationship between *Nes* and *Psilotris batrachoides* (now assigned to *Cryptopsilotris* gen. nov.) is shown in Fig. 5, but support is weak (Bayesian posterior probability = 0.62).

PAEDOVARICUS VAN TASSELL, TORNABENE & GILMORE GEN. NOV.

TYPE SPECIES: *PAEDOVARICUS IMSWE* (GREENFIELD, 1981: 269, DESCRIBED AS *VARICUS IMSWE*)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent

with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–5 unbranched, without flattened or fleshy tips; pelvic-fin rays very long, fourth ray extending posteriorly to origin of last anal-fin ray or beyond; body with scales (modified basicaudal scales present); one anal-fin pterygiophore inserted before first haemal spine; cephalic lateralis canals and pores absent; second dorsal-fin rays I,7; anal-fin rays I,7; body, head, and fins with light yellowish orange hue, diffuse dark vertical bars alongside of body, and very dark wide vertical band over posterior end of caudal peduncle and on base of caudal rays. The one known species occurs in the western Atlantic Ocean.

Remarks on the genus Paedovaricus

We erect the new genus *Paedovaricus* for *Varicus imswae* Greenfield, 1981; which was described based on two specimens from 21 to 25 m depth off Carrie-Bow Cay, Belize. This species is recovered outside of the well-supported clade containing all other species now considered to belong to *Varicus*. It was originally placed in *Varicus* based primarily on the presence of body scales, the absence of cephalic lateralis pores, and the presence of separate pelvic-fin rays with unbranched tips. The absence of cephalic lateralis pores is apparently a plesiomorphic condition within the *Nes* subgroup, and we now know that *Varicus* species may have pelvic-fin rays that are branched, unbranched, flattened at the tips, or with fleshy pads, and that there may be an ontogenetic component to these features (Gilmore, 1979; Hastings & Bortone, 1981). *Paedovaricus imswae* also shares with *Varicus* the presence of a single anal-fin pterygiophore inserted anterior to the first haemal spine, a character that overall shows some significant phylogenetic signal (Fig. 6B; Table 1), but has apparently evolved independently in *Varicus*, *Paedovaricus*, and *Cryptosilotris*. The distinguishing features separating *Paedovaricus* from *Varicus* are the length of the pelvic-fin rays (extending to base of last anal-fin ray in *Paedovaricus*; never extending past base of fourth ray in *Varicus*), lower pectoral-ray counts (15 or fewer in *Paedovaricus*; 16 or more in *Varicus*) and second dorsal-fin rays (I,7 in *Paedovaricus*; I,8 or more in *Varicus*). The depth range for *Paedovaricus* is 15–32 m, whereas all other *Varicus* species occur from deeper waters (typically >60 m, with most species found >150 m); however, *Paedovaricus* may be more common in deeper water but rarely collected because of its small size. The largest known specimen is 13.5 mm SL, and individuals are apparently sexually mature at 8.0 mm SL (Williams & Gilbert, 1983). In

comparison, *Varicus* reach much larger sizes, which may be associated with different selective pressures associated with living at greater depths. For example, the largest and deepest known species of *Varicus*, *Varicus adamsi* sp. nov., was collected at a depth of 435 m and was 61 mm SL.

According to our molecular phylogenetic analysis (Fig. 5) the closest relative to *Paedovaricus* is the eastern Pacific species *Gymneleotris seminuda* (Günther, 1864); however, the statistical support for this sister relationship is low (0.69 posterior probability), and these two species differ in most of the phylogenetically informative morphological characters examined here. *Gymneleotris* lacks the modified basicaudal scales that are present in *Paedovaricus*. All pelvic rays are unbranched in *Paedovaricus*, whereas all rays (including the well-developed fifth pelvic ray) are branched in *Gymneleotris*. Head pores are present in *Gymneleotris* and lacking in *Paedovaricus*. *Gymneleotris* has two anal-fin pterygiophores inserted before the haemal spine, whereas *Paedovaricus* has one. Lastly, the two species have very different coloration, with *Paedovaricus* being cryptically mottled with an overall yellowish orange tone (Fig. S5D), and with *Gymneleotris* having prominent alternating black and white vertical bars over the head and body (Figs S6B and S7F). Thus, we maintain the two as separate monotypic genera.

Etymology

The genus name *Paedovaricus* is formed from the root ‘paed-’ (the English spelling of the Greek root ‘ped-’, meaning ‘child’) and *Varicus*. The name is in reference to the small size of the type species *Paedovaricus imswae* and its general similarity to the genus *Varicus*.

PINNICHTHYS VAN TASSELL, TORNABENE & GILMORE GEN. NOV.

TYPE SPECIES: *PINNICHTHYS AIMORIENSIS* VAN TASSELL, TORNABENE & GILMORE SP. NOV

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal, hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–4 branched, sometimes with flattened tips, fifth pelvic-fin ray unbranched; pelvic-fin rays extending posteriorly to

anus or beyond, rarely reaching origin of first anal-fin ray; body with scales (modified basicaudal scales present); two anal-fin pterygiophore inserted before haemal spine; papillae rows 5i and 5s connected, or nearly so, separated by the absence of a single papilla in one species; cephalic lateralis canals and pores absent; second dorsal-fin rays I,10–11; anal-fin rays I,10–11; first dorsal-fin spine elongate in two species; coloration in life known only for two species (*Pinnichthys aimoriensis* gen. et sp. nov. and *Pinnichthys saurimimica* gen. et sp. nov.), and consists primarily of four or five dark-brown or brownish yellow blotches along lateral midline, with four or five pairs of short narrow saddles along dorsal midline; in preservation, side of body pale with series of evenly-spaced dark spots, saddles, or broken saddles. Four species occur in the western Atlantic Ocean and one species occurs in the eastern Pacific Ocean.

Remarks on the genus *Pinnichthys*

The genus *Pinnichthys* is erected based on the type species *Pinnichthys aimoriensis* gen. et sp. nov., a new species collected from a depth of 70 m near the edge of the continental slope off Espirito Santo, Brazil. Our phylogeny shows *Pinnichthys aimoriensis* gen. et sp. nov. nested within a clade of western Atlantic species that also includes a monophyletic *Varicus* clade, a monophyletic *Psilotris* clade, and specimens tentatively identified as *Chriolepis fisheri* (Fig. 5). An alternative phylogenetic classification to the one proposed here would be to include *Pinnichthys aimoriensis* gen. et sp. nov. and *Chriolepis* cf. *fisheri* as part of *Varicus*. *Pinnichthys aimoriensis* gen. et sp. nov. (and the other four species assigned here to *Pinnichthys*) differs from *Varicus* in several ways, however: (1) the body of *Pinnichthys* has more scales than *Varicus* (lateral scale rows 0–27 vs. 30–53); (2) the counts in the anal fin are higher in *Pinnichthys* than in *Varicus* (I,10–11 vs. I,7–9); and (3) *Pinnichthys* has two anal-fin pterygiophores inserted anterior to the haemal spine, whereas *Varicus* has one.

Pinnichthys is morphologically most similar to *Chriolepis*. The two genera share the plesiomorphic characters of two anal-fin pterygiophores inserted before the haemal spine, and cephalic lateralis pores absent. *Pinnichthys* and *Chriolepis* also possess body scales, although these may have been independently gained in each group (Fig. 7A). In general, *Chriolepis* is less heavily scaled than *Pinnichthys*, as most species of *Chriolepis* have fewer than 30 lateral scale rows (with *Chriolepis dialepta* occasionally possessing up to 35), and the scales never extend past the middle of the first dorsal fin (well short of this in most species). *Chriolepis* are also generally found in shallow water (<40 m), whereas *Pinnichthys*

occur from depths of 70 m or more. Lastly, all *Chriolepis* have papillae rows 5i and 5s distinctly separate, with row 5s dorsal and well anterior of row 5i (Fig. 3D–F), whereas *Pinnichthys* has rows 5i and 5s connected or nearly so (separated by the space of one papilla in *Pinnichthys aimoriensis* gen. et sp. nov.).

In addition to the type species, *Pinnichthys aimoriensis* gen. et sp. nov., the genus also includes the new species *Pinnichthys saurimimica* gen. et sp. nov., and three species previously assigned to *Chriolepis*: the eastern Pacific species *Chriolepis atrimela*, and the Atlantic species *Chriolepis bilix* and *Chriolepis prolata*. These three species all occur from deep reefs and have two anal-fin pterygiophores anterior to the first haemal spine, extensively scaled bodies, high anal-fin ray counts, and papillae rows 5i and 5s that are connected as a single row. The authors did not examine the papillae pattern for *Chriolepis atrimela*, but C. Thacker (pers. comm. 2015) at the Los Angeles County Museum of Natural History examined the holotype and confirmed the connection of 5i and 5s.

Etymology

The name *Pinnichthys* is formed from the roots *pinna* (Latin, feminine; fin) and *ichthys* (Latinized form of the Greek acronym *ichthus*; fish). The name is given in reference to the high number of fin rays in the second dorsal fin and anal fin of all species in the genus.

PINNICHTHYS AIMORIENSIS VAN TASSELL & TORNABENE SP. NOV. THIONY'S GOBY FIGS 10–12

Holotype

CIUFES 2414, 22.4 mm SL, male, plataforma Peroá, Espirito Santo, Brazil, –19.577S –39.264W, 70 m depth, 13 April 2012, T. Simon & H.T. Pinheiro.



Figure 10. *Pinnichthys aimoriensis* holotype, prior to preservation, 22.4 mm SL, CIUFES 2414. Photo by Hudson Pinheiro.



Figure 11. *Pinnichthys aimoriensis* in preservation. (A) holotype, 22.4 mm SL, CIUFES 2414; (B) paratype, 16.4 mm SL, AMNH 265021. Photos by J.L. Van Tassell.

Paratypes

AMNH 265020, 17.4 mm SL, male, collected at type locality, 13 April 2012, T. Simon & H.T. Pinheiro; AMNH 265021, 16.4 mm SL, female, cleared and stained, collected at type locality, 7 February 2014, T. Simon and H.T. Pinheiro.

Diagnosis

Side of body with 40–47 scale rows extending anteriorly to pectoral base; modified basicaudal scales present; first dorsal fin VII, without notably elongate spines, second dorsal I,10; anal fin I,10, rays fork only once near tips; pelvic fins well separated, no anterior frenum and no membrane connecting base of innermost rays; fifth pelvic-fin ray half the length of fourth and unbranched; pelvic-fin rays 1–4 branched, without fleshy tips; papillae rows 5s and 5i separate, lacking a papilla that would result in their forming a single continuous transverse row; interorbital papillae row pb', pc', and pe' present; head and preopercle canals and pores absent; two anal-fin pterygiophores inserted anterior to haemal arch.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII (3), spines 2–5 nearly equal in length, none notably elongate or filamentous; second dorsal fin I,10 (3), soft rays branch only once near tips; anal fin I,10 (3), soft rays branch only once near tips; pectoral-fin rays 19/18* (1), 18/18 (1) 18/? (1); pelvic fin 1,5 (3); pelvic fins well separated, lacking both anterior frenum and membrane connecting bases of innermost rays; fourth pelvic-fin ray longest, extending posteriorly beyond anus but falling short of anal-fin origin; first pelvic-fin ray branched once at midpoint; pelvic-fin rays 2–4 branched twice; fifth pelvic-fin ray unbranched, short, half length of fourth pelvic-fin ray; tips of pelvic-fin rays not ending in fleshy pads; caudal-fin rounded to slightly truncate; branched caudal-fin rays 14 (3); segmented caudal-fin rays 17 (3).

Scales: Trunk of body covered with ctenoid scales, extending anteriorly to pectoral base; 40–47 scales in lateral series (some scales missing anteriorly in holotype); eight or nine transverse scale rows; scales on abdomen cycloid (absent in female paratype); no scales on head and predorsal region; two modified basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base.

Head: Jaw extending posteriorly to a vertical through the anterior margin of eye; anterior nare a short tube; posterior nare an opening with raised rim; no cephalic lateralis pores on head or preopercle; eyes 29.1–32.6% HL, dorsolateral, extending above profile of head, interorbital narrow, 7.0–10.7% HL; snout profile steep; operculum opening extending only length of pectoral-fin base; upper jaw with three or four rows at anterior, outer row enlarged and teeth spaced further apart; rows reduce to a single row, extending to posterior of premaxilla; lower jaw with four or five rows of conical teeth, outer two rows slightly larger, all teeth

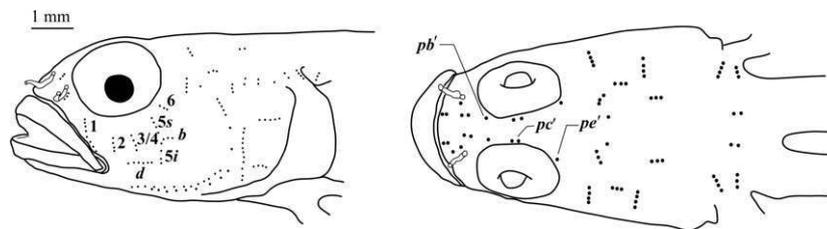


Figure 12. *Pinnichthys aimoriensis* papillae pattern, composite from AMNH 265020 and CIUFES 2414. Illustration by J.L. Van Tassell.

Table 3. Morphometrics of new species. Values are ranges followed by mean

	<i>Pinnichthys aimorien-</i> <i>sis</i> gen. et sp. nov.		<i>Pin-</i> <i>nichthys</i> <i>saurimim-</i> <i>ica</i> gen. et sp. nov.		<i>Psilotris</i> <i>lau-</i> <i>rae</i> sp. nov.		<i>Psilotris lae-</i> <i>tarii</i> sp. nov.		<i>Varicus</i> <i>adamsi</i> sp. nov.		<i>Varicus cephalocel-</i> <i>latus</i> sp. nov.		<i>Varicus deco-</i> <i>rum</i> sp. nov.		<i>Varicus</i> <i>nigri-</i> <i>tus</i> sp. nov.		<i>Varicus veligutta-</i> <i>tus</i> sp. nov.	
Eye diameter % SL	8.6–9.15	8.8	8.2	8.2	9.0	9.0	6.8–7.8	7.2	8.1–11.4	9.4	7.5–11.5	9.5	7.6–10.0	8.8	7.3	7.3	9.6–12.6	11.0
Eye diameter % HL	29.0–32.7	31.0	30.9	30.9	30.1	30.1	24.1–29.2	25.9	30.6–41.2	36.5	26–37.2	31.5	26.5–45.5	33.3	23.7	23.7	30.7–41.6	36.3
Jaw length % SL	9.6–11.5	10.3	10.6	10.6	11.9	11.9	8.9–10.3	9.8	10.1–11.4	10.9	11.8–13.9	12.7	9.4–11.0	10.1	9.3	9.3	10.9–12.4	11.7
Jaw length % HL	34.4–39.0	36.1	40.0	40.0	39.8	39.8	31.8–37.6	35.0	39.3–42.2	40.9	39.2–44.7	42.1	31.09–49.3	37.8	30.3	30.3	35.6–40.9	38.5
Head length % SL	27.9–29.5	28.5	26.5	26.5	29.9	29.9	26.8–28.8	28.0	27.7–28.5	28.0	28.8–31.7	30.1	20.1–30.2	26.9	30.7	30.7	27.2–32.5	30.2
Post orbital length % SL	13.5–16.6	15.0	15.0	15.0	14.9	14.9	13.2–15.6	14.6	12.5–13.6	13.2	13.4–17.1	14.7	13.715.7	14.7	15.3	15.3	12.7–15.8	14.0
Depth at first dorsal origin % SL	15.8–16.5	16.2	15.9	15.9	18.1	18.1	18.4–20.9	19.7	14.9–18.3	16.8	16.6–19.1	17.6	16.1–19.9	17.8	18.2	18.2	15.5–22.2	18.8
Depth at anal- fin origin % SL	14.6–17.3	16.4	15.5	15.5	17.4	17.4	16.2–18.6	17.0	14.5–16.9	16.0	15.1–16.8	15.8	14.6–17.6	16.3	15.4	15.4	15.68–18.8	17.2
Width at anal- fin origin % SL	8.3–9.7	9.0	9.6	9.6	10.7	10.7	8.0–13.5	11.1	8.4–10.8	9.8	10.6–12.5	11.3	8.0–11.0	9.6	8.0	8.0	10.4–14.0	12.0
Caudal peduncle depth % SL	10.4–12.5	11.4	11.2	11.2	11.9	11.9	11.6–13.5	12.7	10.1–11.3	10.6	10.8–12.1	11.2	9.9–12.4	11.1	10.0	10.0	10.1–12.9	11.9
Caudal peduncle length % SL	18.8–23.0	21.4	18.8	18.8	19.3	19.3	16.0–19.1	17.3	20.2–21.2	20.7	7.2–19.6	15.8	20.7–27.0	22.8	22.6	22.6	20.6–24.4	22.7
Caudal fin length % SL	6.3–27.8	18.5	24.4	24.4	24.5	24.5	27.9–33.1	30.2	25.4–26.5	26.0	20.8–24.4	22.8	24.9–29.6	26.9	23.8	23.8	22.4–26.7	24.7
Snout length % SL	5.2–7.0	6.0	6.1	6.1	7.1	7.1	7.4–8.8	7.9	4.3–6.7	5.5	5.4–6.5	5.9	6.1–7.5	6.6	7.0	7.0	5–6.9	5.9
Interorbital width % SL	2.0–3.1	2.6	1.6	1.6	2.1	2.1	2.9–4.4	3.7	1.2–1.4	1.3	1.1–1.4	1.3	0.8–2.2	1.3	2.6	2.6	1.1–1.7	1.4
Interorbital width % HL	7.0–10.7	9.0	6.0	6.0	7.1	7.1	10.7–14.5	12.6	4.3–4.5	4.4	3.4–4.6	4.2	3.0–7.6	4.9	8.5	8.5	3.6–5.4	4.5
Pectoral fin length % SL	19.8–25.0	21.9	24.9	24.9	26.5	26.5	24.3–28.7	26.0	32.8–33.9	33.4	23.9–30.6	27.4	25.6–39.5	31.0	36.3	36.3	21.66–25.3	23.8

closely packed, tips slightly recurved; reducing to a single row extending to posterior of dentary.

Genitalia: Male urogenital papilla short, thin, and pointed; female urogenital papilla rounded and bulbous.

Colour in life (Fig. 10): Background colour of body and fins white; four large squarish brown spots along midline between level of anus and end of base of dorsal fin; first spot beneath pectoral fin, second spot below origin of second dorsal fin, third spot below middle of second dorsal fin, and fourth spot on caudal peduncle; an upper row of paler, more irregular, partly interconnected brownish yellow blotches along dorsal surface of body, extending forwards to under first dorsal fin, and partly interconnected with the mid-flank row; head pale with indistinct yellow marks on lower jaw, between eyes, and on nape; head behind eye to pectoral-fin base and abdomen with a yellowish pink hue; first dorsal fin translucent whitish at base, a wide yellow-brown stripe across middle of fin, distal quarter of fin white, outer half of fin heavily peppered with melanophores; second dorsal fin peppered with melanophores, with yellowish brown spots or broken stripes and white distal margin; caudal fin pale with yellow-brown spots and irregular vertical bars; anal fin dusky brown, with whitish basal stripe and distal margin; pectoral fins with no obvious pigmentation; pelvic fins with brownish base, distal three-quarters of fin white.

Colour in preservation (Fig. 11): Body with four dark blotches along lateral aspect of trunk, positioned as described above; in holotype, the pale space between each two spots with a narrow vertical bar of melanophores, bars lighter in intensity than squarish spots; body mostly pale below blotches; above blotches, four or five weakly separated dorsal saddles present that may connect to blotches; nape uniformly covered with dense peppering of melanophores; side of head with light scattering of melanophores; upper margin of pectoral-fin base with patch of dark melanophores, lower half unpigmented; pectoral rays unpigmented; first dorsal fin with dark lateral stripe across interspinous membranes, stripe with concentrated patches of melanophores over second, fourth, and fifth spines; second dorsal fin and caudal fin with several distinct, circular, dark spots on a pale background, spots on second dorsal of smallest paratype roughly arranged in three or four diagonal rows; anal fin with a pale horizontal stripe at base of rays, remainder of rays uniformly covered with dark

melanophores, appearing uniformly grey to black; pelvic fins pale.

Sensory papillae (Fig. 12): A transverse pattern with abbreviated transverse rows; rows 1, 2, 3/4, 5s, 5i, and 6 present; rows 2–6 represented by three or four papillae; row 5s not reaching the level of row b and missing a complete connection to 5i by a single papilla; interorbital papillae row pb', pc', and pe' present.

Vertebral skeleton: Dorsal pterygiophore formula 3–221110; two anal-fin pterygiophores inserted anterior to first haemal arch; second neural spine expanded and slightly spatulate at tip; hypurals 1 and 2 fused with hypurals 3 and 4 along at least half of their length; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: Collected from the seafloor near the Peroá natural gas platform. The substrate was predominately rhodoliths and other calcareous substrate.

Distribution: Known only from the margin of the continental shelf of Brazil off Espírito Santo.

Etymology: The species epithet *aimoriensis* is an adjective formed from the proper noun Aimorés, an indigenous warrior people from the lands now belonging to the Brazilian states Espírito Santo, Bahia, and Minas Gerais. The Aimorés people were virtually extirpated by European settlers during the Aimorés War (1555–1673), and much of their native forest has been replaced by agriculture. The type locality for *Pinnichthys aimoriensis* gen. et sp. nov. is adjacent to the Peroá natural gas platform, and the nearby coastal region is facing rapid development from the petroleum industry and mining of rhodolith beds (carbonates) for agriculture, and may be under threat of losing biodiversity before it can be adequately studied and described. This situation is analogous to the loss of Aimorés culture and the forest biodiversity that inhabited their native lands of the Central Brazilian coast.

The common name of Thiony's Goby is given in honor of Thiony Simon. Thiony collected the type series of this species while scientific diving with friend and fellow ichthyologist Hudson Pinheiro. Together Thiony and Hudson pioneered scientific diving below 45 meters in the Central Brazilian coast, which contributed immensely to our knowledge of the regional biodiversity, and was key to discovering *P. aimoriensis*. Thiony, a promising young ichthyologist that in recent years stood out in the Brazilian ichthyological community, passed away at the age of 30 in a diving accident while this manuscript was in preparation.

Comparisons: *Pinnichthys aimoriensis* gen. et sp. nov. can be distinguished from *Pinnichthys bilix* comb. nov. and *Pinnichthys prolata* comb. nov. by having fewer lateral scale rows (40–47 vs. 30–27). *Pinnichthys aimoriensis* gen. et sp. nov. lacks the elongate first dorsal-fin spines of *Pinnichthys bilix* comb. nov. and the eastern Pacific *Pinnichthys atrimela* comb. nov. Lastly, *Pinnichthys aimoriensis* gen. et sp. nov. is distinguished from *Pinnichthys saurimimica* gen. et sp. nov. by having I,10 second dorsal-fin and anal-fin rays (versus I,11 in *Pinnichthys saurimimica* gen. et sp. nov.).

PINNICHTHYS SAURIMIMICA GILMORE,
VAN TASSELL & TORNABENE SP. NOV.
LIZARDFISH GOBY
FIGS 13–16

Holotype

USNM 427228, 55.4 mm SL, female, Cockburn Town, Riding Rock, San Salvador, Bahamas, 24.04833N, -74.5375W, Johnson Sea Link I, Dive JLS-I 2024, 282 m depth, 3 May 1987, R.G. Gilmore & D. Liberatore.

Diagnosis

Body scaled with 47–53 ctenoid scales, modified basi-caudal scales present; first dorsal VII, no elongate filamentous spines present; second dorsal I,11; anal I,11; pectoral 20; pelvic fins I,5, separate, rays 1–4 branched between two and four times, fifth pelvic-fin ray long and unbranched, three-quarters length of fourth pelvic-fin ray, no fleshy tips present on pelvic-fin rays; head and preopercle canals and pores absent; a transverse sensory papillae pattern with row 5s/5i connected, interorbital papillae pc' and pe' present; two anal-fin pterygiophores inserted anterior to haemal arch.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII, spines 1, 2, and 3 successively longer, spines 4 and 5 longest, spines 2–5 extending slightly beyond membrane; second dorsal fin I,11, soft rays branch two or three times beginning midway along each ray; anal fin I,11, soft rays branch two or three times beginning midway along each ray; pectoral-fin rays 20; pelvic fin I,5; pelvic fins well separated, lacking anterior frenum, short membrane connecting fifth rays basally, fourth ray longest, extending three-quarters distance to anus when extended posteriorly, rays 1–4 branched between two and four times, fifth long, unbranched, three-quarters length of fourth ray; tips of pelvic-fin rays not ending in fleshy pads;

caudal fin oval; branched caudal-fin rays 14; segmented caudal-fin rays 17.

Scales: Trunk of body covered with ctenoid scales from beneath pectoral fin nearly to caudal-fin base, anterior scales with reduced ctenii; 53/47 (left/right) scales in lateral series; 11 transverse scale rows; cycloid scales on lateral and posterior portions of abdomen, scales absent on mid- and anterior portions of abdomen; a naked upper area from posterior end of first dorsal-fin base to upper pectoral-fin base; a naked lower area extending from abdomen near anus to lower pectoral-fin base; two modified basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base.

Head: Jaw extending posteriorly to a vertical through anterior end of pupil; anterior nare an elongate tube, posterior nare a short tube, no flaps on edges; no cephalic lateralis pores on head or preopercle; eyes 30.9% HL, dorsolateral, extending above profile of head, interorbital narrow, 6.04% HL; snout profile steep; operculum opening extending length of pectoral-fin base; teeth in upper jaw arranged in four or five rows, outer row with enlarged widely spaced teeth continuing to near posterior of premaxilla, inner rows smaller and more numerous with slightly recurved tips; teeth in lower jaw in three or four rows, outer row with eight or nine large teeth, widely spaced, restricted to anterior of jaw, teeth in remaining rows smaller with slightly recurved tips.

Genitalia: Female (only known specimen) with short, rounded bulbous papilla, no melanophores present.

Colour in life (Figs 13 and 14): Background colour of body and fins white; five large yellow–brown spots with dense concentrations of melanophores along lateral midline trunk, first (largest) under first dorsal-fin spines 3–6, second under anterior rays of second dorsal fin, third under second dorsal-fin rays 6–8, fourth equidistant between third and fifth spot, fifth (smallest) on caudal peduncle; four yellow–brown double bars stippled with melanophores along back

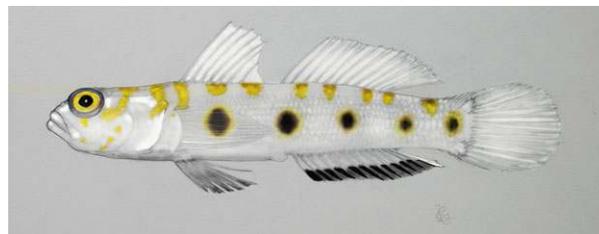


Figure 13. *Pinnichthys saurimimica*, illustration of live holotype, 55.5 mm SL, USNM 427228 by R.G. Gilmore.

positioned between the mid-lateral spots, crossing dorsal midline, bars lighter in colour than mid-lateral spots, single yellow bar on back before caudal peduncle; nape with three yellow bars, the first extending anterioventrally to the lower posterior margin of orbit, second nape bar extending to upper opercular margin, the third bar extending from near dorsal midline ventrally to upper pectoral base; yellow spot below eye near maxilla, other spots on cheek; iris bright yellow; prominent white pigment over both dorsal fins; caudal fin brilliant white, middle of anal fin white to base and distal margin, with black pigment along ventral one-third of fin; pelvic fins black; pectoral fins translucent white.

Colour in preservation (Fig. 15): Body light brown with five large spots just below lateral midline, positioned as described above; a small spot on posterior portion of caudal peduncle, near base of caudal-fin rays; a series of wide, double bars along dorsal portion of trunk, bars lighter in colour than body spots, first pair under first dorsal fin, second pair under second dorsal-fin rays 2–5, and third at posterior end of second dorsal; a single bar on caudal peduncle, ending at bases of caudal procurent rays; dark pigment on nape where the three yellow bars are as described above; pectoral, first dorsal, second dorsal, and caudal fin translucent; pelvic fin with a few scattered melanophores; anal fin with a band of melanophores from middle to outer region of fin.

Sensory papillae (Fig. 16): A transverse pattern with rows 1, 2, 3/4, 5s/5i, and 6 present; rows 2 and 3/4 short; row 5s/5i joined forming a single row and extending below the level of row d; row b short with five or six papillae, ending anteriorly at row 5s/5i; interorbital row pc' with two papillae, row pe' with a single papilla.

Vertebral skeleton: Dorsal pterygiophore formula 3–221110; two anal-fin pterygiophores inserted anterior to first haemal arch; hypurals 1 and 2 fused to hypurals 3 and 4 along one-quarter of length; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: Holotype was collected on a calcareous sand and dead *Halimeda* spp. algal rubble zone, with scattered shallow calcareous rock ledges.

Distribution: Known only from San Salvador, Bahamas, the type locality.

Etymology: The name *saurimimica* is derived from 'saurus', a genus of lizard fish and the Greek 'mimic', as the colour pattern closely resembles that of a lizard fish.

Comparisons: Pinnichthys

saurimimica gen. et sp. nov. is most similar to *Pinnichthys bilix* comb. nov. Both species have counts of I,11 in the second dorsal and anal fins, and both occur off the Bahamas. *Pinnichthys saurimimica* gen. et sp. nov. differs from both *Pinnichthys bilix* comb. nov. and *Pinnichthys prolata* comb. nov. in having more lateral scale rows (47–53 vs. 30–37). *Pinnichthys saurimimica* gen. et sp. nov. also lacks the elongate first dorsal-fin spines that are present in *Pinnichthys bilix* comb. nov. and the eastern Pacific *Pinnichthys atrimela* comb. nov. Lastly, *Pinnichthys saurimimica* gen. et sp. nov. is distinguished from *Pinnichthys aimoriensis* gen. et sp. nov. by the presence of I,11 second dorsal-fin and anal-fin rays versus I,10, and in having slightly more lateral scale rows (42–47 in *Pinnichthys saurimimica* gen. et sp. nov. versus 47–53 in *Pinnichthys aimoriensis* gen. et sp. nov.).

PSILOTRIS GINSBURG, 1953

TYPE SPECIES: *PSILOTRIS ALEPIS* GINSBURG, 1953
(BY ORIGINAL DESIGNATION)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and the *Gobiosoma* group



Figure 14. *Pinnichthys saurimimica*, holotype. 55.5 mm SL, USNM 427228, in situ at 282 m, Bahamas, photo by R.G. Gilmore, from the Johnson Sea Link II submersible.



Figure 15. *Pinnichthys saurimimica* holotype, 55.4 mm SL, USNM 427228, preserved. Photo by J.L. Van Tassell.

(first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110; 27 vertebrae – 11 precaudal and 16 caudal; hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays 1–4 branched, typically without fleshy or flattened tips (sometimes slightly fleshy in *Psilotris boehlkei* Greenfield, 1993), fifth pelvic-fin ray unbranched; pelvic-fin rays extending posteriorly from about halfway to anus to anus, but never beyond anus; body lacking scales (modified basicaudal scales present in one undescribed species; see Remarks below); two anal-fin pterygiophores inserted before first haemal spine in all but one species (*Psilotris laurae* sp. nov., Van Tassell, Tornabene & Baldwin, 2016), which has one anal-fin pterygiophore inserted before first haemal spine; papillae rows 5i and 5s connected in some species, not connected in others; cephalic lateralis canals and pores absent; second dorsal-fin rays I,9–10; anal-fin rays I,7–10; body coloration highly variable (presumably for camouflage with a specific substrate type), but frequently with vertical bars (broken or continuous, yellow to dark brown or black) or saddles over body and head, some species with prominent spots or mottling over side of body. All six valid species occur from the western Atlantic Ocean.

Remarks

Psilotris was described by Ginsburg (1953) for *Psilotris alepis*. Like *Chriolepis*, *Psilotris* was considered by Ginsburg as belonging to the Eleotridae for the split pelvic fins lacking a connective membrane and anterior frenum, a character now known to have evolved multiple times in Gobiidae. In addition to the split pelvic fins, *Psilotris* lacks cephalic lateralis pores and body scales – two characters that appear multiple times across the Gobiosomatini. The scale-less and pore-less *Psilotris celsa* Böhlke, 1963 and *Psilotris batrachoides* were added to the genus, and Böhlke noted that the three species were ‘more different in appearance than members of most shore-fish genera’ (Böhlke, 1963: 2). Later, *Psilotris kauf-*

mani Greenfield, Findley & Johnson, 1993; *Psilotris boehlkei* Greenfield, 1993; and *Psilotris amblyrhynchus* Smith & Baldwin, 1999 were also added to the genus.

Smith & Baldwin (1999) and Greenfield (1993) recognized that the species of *Psilotris* probably do not form a monophyletic group. In addition to not being united by unique shared derived characters, *Psilotris batrachodes* has a colour pattern and general appearance that is strikingly different from the other members of the genus, and *Psilotris amblyrhynchus* has a notably different body shape, with a blunt anterior profile versus a gradually sloped or pointed anterior profile. In our molecular phylogeny (Fig. 5), *Psilotris amblyrhynchus* and *Psilotris batrachodes* are recovered well outside the clade containing *Psilotris celsa*, *Psilotris kaufmani*, and several other undescribed species. The new genera *Carrigobius* and *Cryptopsilotris* are erected for *Psilotris amblyrhynchus* and *Psilotris batrachodes*, respectively (see remarks section of each genus for additional information). The steep anterior profile and branched fifth pelvic-fin ray (in adults) distinguish *Carrigobius* from *Psilotris*, and the body coloration and low anal-fin ray counts (I,6–7) distinguish *Cryptopsilotris* from *Psilotris*.

The loss of body scales and cephalic lateralis pores have apparently occurred multiple times within the *Nes* subgroup (Figs 7A and 9A). In addition to *Psilotris*, *Carrigobius*, and *Cryptopsilotris* possessing these losses, at least two species in the genus *Varicus* are also naked and without pores (*Varicus decorum* sp. nov. and an undescribed species). Because of the parallel loss of scales (or conversely, the regaining of scales in some members of *Varicus*), we know of no characters that unambiguously distinguish *Varicus* from *Psilotris*. Although there are general trends in several characters, there are exceptions for all of them. For example, of the ten species of *Varicus* recognized in this study (nine named herein plus one undescribed), eight possess scales on the body, whereas all species of *Psilotris* are naked. Of the six species of *Psilotris* considered valid in this study, all but one, *Psilotris laurae* sp. nov., have two anal-fin pterygiophores inserted before the haemal arch,

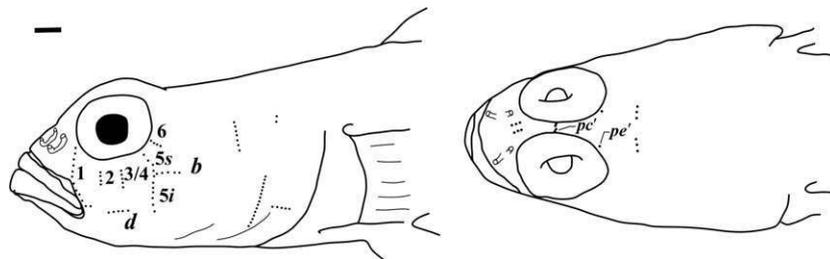


Figure 16. *Pinnichthys saurimimica* papillae pattern, drawn from holotype, USNM 427228. Illustration by J.L. Van Tassell.

whereas all *Varicus* have one. All species of *Psilotris* have pelvic-fin rays 1–4 branched without expanded fleshy tips, whereas only two of the ten known species of *Varicus* [*Varicus benthonis* (Ginsburg, 1953) and *Varicus vespa* Hastings & Bortone, 1981] have pelvic-fin rays that are branched to the tips (although these two have very small fleshy pads at the tips of some branches). Lastly, all ten of the known species of *Varicus* occur at or below 60 m, whereas only one species of *Psilotris* (*Psilotris laurae* sp. nov.) occurs on deep reefs. Despite partial overlap in all morphological characters examined here, the two genera form distinct clades in our molecular phylogeny with strong support (Bayesian posterior probability = 1.0).

In addition to the two new species of *Psilotris* described here (*Psilotris laurae* sp. nov. and *Psilotris laetarii* sp. nov.), there are two additional lineages in the *Psilotris* clade that are of uncertain identity. One juvenile specimen of *Psilotris* from Brazil is recovered as sister to *Psilotris celsa*. It is not clear whether this specimen is truly *Psilotris celsa*, which would expand the range of the species considerably, or if it represents an undescribed species. Another lineage comprises two specimens from the Bahamas, and could represent an undescribed species. This latter species differs from all other *Psilotris* in possessing two modified basicaudal scales, which makes it superficially resemble the *incertae sedis* species *Chriolepis fisheri*. The second dorsal-fin ray and anal-fin ray counts (I,9 and I,8, respectively) of this species do not match that of the *Chriolepis fisheri* holotype (I,10 and I,9). The *Psilotris* specimens from the Bahamas may be the same species as the '*Chriolepis* cf. *fisheri*' described by Smith-Vaniz & Jelks (2014). These specimens from the Bahamas also superficially resemble another species in our phylogeny that is recovered as sister to *Pinnichthys*. This latter species also possesses only basicaudal scales and has second dorsal-fin and anal-fin ray counts more closely matching those of the *Chriolepis fisheri* holotype; however, additional specimens and genetic data are needed to resolve the status of *Chriolepis fisheri* and the putatively new species of *Psilotris* from the Bahamas (see the remarks section for *Chriolepis* above).

PSILOTRIS LAETARII VAN TASSELL &
YOUNG SP. NOV.
BURROW SPLITFIN GOBY
FIGS 17–19

Holotype

AMNH 261272, 23.5 mm SL, female, Marathon, Florida, USA, 24.39.470N –81.00.397W, 7.6 m depth, 20 September 2012, John 'Bucky' Wile III.

Paratypes

AMNH 264217, 21.5 mm SL, male, collected with holotype; AMNH 257973, 23.27 mm SL, male, Marathon, Florida USA, 24.39.470N –81.00.397W, 7.9 m depth, 10 September 2014, Warren 'Skip' Wohlers; AMNH 257974, 19.3 mm SL, male, Marathon, Florida USA, 24.39.470N –81.00.397W, 7.9 m depth, 15 June 2013, John 'Bucky' Wile III.

Diagnosis

Side of body and head without scales; no modified basicaudal scales present; first dorsal fin VII, without elongate spines; second dorsal I,9–10; anal fin I,7–8; pelvic fins well separated, anterior frenum absent, membrane connecting fifth pelvic-fin rays absent or very low; fifth pelvic-fin ray unbranched and half the length of fourth; pelvic-fin rays without fleshy tips; papillae row 5s and 5i connected forming a single row, interorbital papillae row pc' present; head and preopercle canals and pores absent; two anal-fin pterygiophores inserted anterior to haemal arch.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII(4), spines 1–3 about equal in length, spines 4–6 slightly shorter, spine 7 three-quarters the length of first spine; second dorsal fin I,9*(1), I,10(3); anal fin I,7*(1), I,8(3); pectoral-fin rays 15(1), 16(2), 17*(1), elongate, extending to a vertical through second dorsal-fin ray 1 or 2; pelvic fin I,5(4); pelvic fins well separated, lacking anterior frenum, membrane connecting fifth rays absent or very low; fourth pelvic-fin ray longest, extending three-quarters distance to anus; rays 1–4 branched two or three times, fifth ray unbranched and half the length of fourth ray; tips of pelvic-fin rays not ending in fleshy pads; caudal fin ovate; branched caudal-fin rays 15 (3); segmented caudal-fin rays 17(4).

Scales: Scales on head and trunk absent.

Head: Jaw extending posteriorly to a vertical through the anterior margin of eye; anterior nare a short tube, posterior nare an opening with raised rim; no cephalic lateralis pores on head or preopercle; eyes 24.1–29.1% HL, dorsolateral; interorbital narrow, 10.7–14.4% HL; upper jaw with two or three rows of teeth at anterior, outer row extending to posterior end of premaxilla, teeth large but slightly smaller than teeth in lower jaw, conical with recurved tips; lower jaw with two or three rows at anterior, slightly larger than upper teeth, pointed conical and slightly recurved, inner row with four larger teeth at mid-dentary.



Figure 17. *Psilotris laetarii* holotype, prior to preservation, 23.6 mm SL, AMNH 261272. Photo by J.L. Van Tassell.

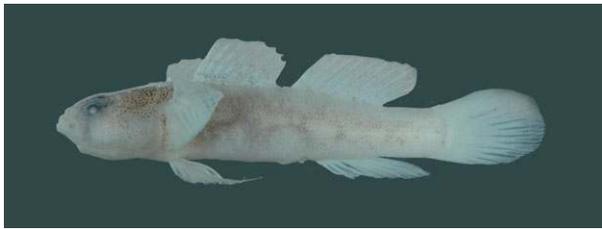


Figure 18. *Psilotris laetarii* holotype, preserved, 23.6 mm SL, AMNH 261272. Photo by J.L. Van Tassell.

Genitalia: Male urogenital papilla conical and pointed; female urogenital papilla short, round, bulbous with small villi around edge.

Colour in life (Fig. 17): Background colour of body and head whitish; head with three dark yellowish–orange bars, a vertical bar under eye extending to jaw, an oblique bar extending from eye to lower edge of preopercle, a third bar extending from rear of the eye to top corner of opercle; top of head with reticulating yellow–orange lines; trunk with a reticulum of dark yellow–orange lines, darker at the anterior, becoming lighter posteriorly; numerous scattered small dark concentrations of melanophores on head and trunk, more numerous on nape and on dorsal trunk under first dorsal fin, the concentrations of melanophores superimposed on the yellow–orange reticulum are larger and dark; first dorsal fin with three irregular, transverse bands of

yellow spots, one at base of fin ending between fifth and sixth spine, a central band along middle of fin, upper band not extending to upper margin of fin; distal margin of fin clear; entire first dorsal fin with scattered melanophores, particularly concentrated on and adjacent to the yellow bands; second dorsal fin clear with five thin oblique light-yellow bands with scattered small melanophores, bands equally spaced along dorsal extent of fin but not extending to dorsal margin, which lacks pigment; anal fin unpigmented with a few widely scattered small melanophores; caudal fin translucent with five thin, irregular pale yellow bars; pectoral fin translucent, base of fin whitish with scattered melanophores and a yellow–brown spot at dorsal corner of base; pelvic fin lacking pigment.

Colour in preservation (Fig. 18): Background colour of head and body yellowish pale; all areas with yellowish–orange colour before preservation, now light brown or grey, and peppered with dark melanophores, including stripes on head, and reticulations on nape and trunk; first dorsal fin peppered with melanophores, loosely concentrated to form two lateral stripes, stripes less apparent posteriorly; second dorsal fin with very small and sparsely spaced irregular patches of melanophores; caudal fin immaculate; anal fin with very light dusting of small melanophores; pelvic fin immaculate.

Sensory papillae (Fig. 19): Sensory papillae in a transverse pattern; transverse row 1 long, extending from orbit to row d; rows 2 and 3/4 short, extending from mid-cheek to near row d; rows 5s and 5i connected, extending from orbit to below level of row d; row b short, anterior end not reaching row 5s/5i; interorbital row pc' with two papillae present.

Vertebral skeleton: Dorsal pterygiophores formula 3–221110; two anal-fin pterygiophores inserted anterior to first haemal arch; hypurals 1 and 2 fused to hypurals 3 and 4 along approximately one-half of their length; 27 vertebrae – 13 precaudal and 14 caudal.

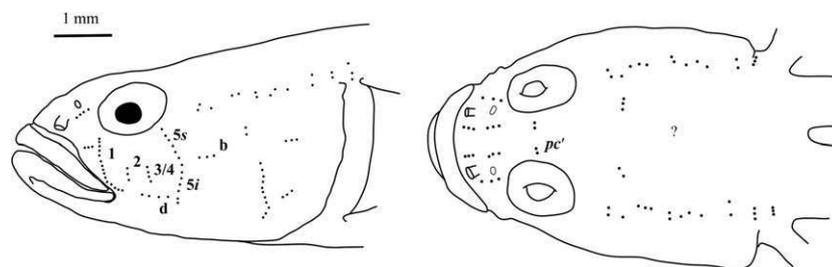


Figure 19. *Psilotris laetarii* papillae pattern, composite from type series. Illustration by J.L. Van Tassell.

Habitat: Types were collected from a sand and rubble substrate, rubble about 0.5–10.0 cm in diameter, located 45–90 m from the gradual reef drop-off. Found in or near burrows of *Opistognathus aurifrons* (Jordan & Thompson, 1905) (yellowhead jawfish) at depths of 8.5 m.

Types were collected solely during dedicated collections of *Opistognathus aurifrons* (yellowhead jawfish) by use of a 1% quinaldine solution (2-methylquinoline) at depths of 6.0–8.5 m. The only observance and collection of this species has been from within the yellowhead jawfish burrows. There appears to be some relationship between the two species, as this new goby is found in no other situation that the authors are aware of, but further research will be necessary to establish what that relationship may involve. The authors have not seen *Psilotris laetarii* sp. nov. exit from any other kind of burrow; such burrows are common among the back-reef rubble habitat. This is not an abundant species but can be found on a regular basis from April to November, when the jawfish are seasonally abundant.

Distribution: Known only from the type series collected off the south shore of Marathon, Florida.

Etymology: Named in honor of Heath Jens Laetari, 28 years old, Vice President of Dive Operations, Partner & Acquisition Manager for Dynasty Marine, who was lost at sea on 14 September 2006, doing what he loved to do.

Comparisons: *Psilotris laetarii* sp. nov. is the only known *Psilotris* species to have a reticulating yellowish orange pattern on the body. *Psilotris celsa* has vertical yellowish orange bars on the side of the body (Fig. S4C), similar in colour to that of the reticulations on *Psilotris laetarii* sp. nov.; however, the shape of the overall pattern is different. In addition to the colour pattern, *Psilotris laetarii* sp. nov. differs from *Psilotris alepis* and *Psilotris boehlkei* in having papillae rows 5i and 5s connected (separate in *Psilotris alepis* and *Psilotris boehlkei*). This species can be further distinguished from *Psilotris boehlkei* in having fewer anal-fin rays (I,7–8 vs. I,9 in *Psilotris boehlkei*), and in having a jaw that does not extend posteriorly past a vertical through the pupil. Both *Psilotris laurae* sp. nov. and *Psilotris kaufmani* have bicoloured pectoral fins, whereas the pectoral fin in *Psilotris laetarii* sp. nov. is uniformly unpigmented. *Psilotris laetarii* sp. nov. is distinguished from the scaleless *Varicus* species *Varicus decorum* sp. nov. both in colour pattern (yellow–orange reticulations versus round yellow spots in *Varicus decorum* sp. nov.) and in having pelvic-fin rays 1–4 that branch to the tips without

fleshy pads (tips either unbranched or branched and re-fused, with fleshy tips in *Varicus decorum* sp. nov.).

PSILOTNIS LAURAE VAN TASSELL, TORNABENE &
BALDWIN SP. NOV.
THIN-BARRED GOBY
FIGS 20–22

Holotype

USNM 426779, 26.8 mm SL, male, off Bonaire City Dock, Kralendijk, Bonaire 12.15N –68.2829W, 30 May 2013, 114–137 m, B. Van Bebber, A. Schrier, C.C. Baldwin & T. Christiaan.

Diagnosis

No scales on sides of body or head; no modified basicaudal scales; first dorsal fin VII, with spines 1–4 slightly elongate; second dorsal fin I,9; anal fin I,8; elongate pointed pectoral fin with 18 rays; pelvic fins



Figure 20. *Psilotris laurae*; (A) holotype, prior to preservation 26.8 mm SL, USNM 426779. Photo by D.R. Robertson and C. Baldwin; (B) holotype, live, photo by Barry Brown.



Figure 21. *Psilotris laurae* holotype, preserved, 26.8 mm SL, USNM 426779. Photo by J.L. Van Tassell.

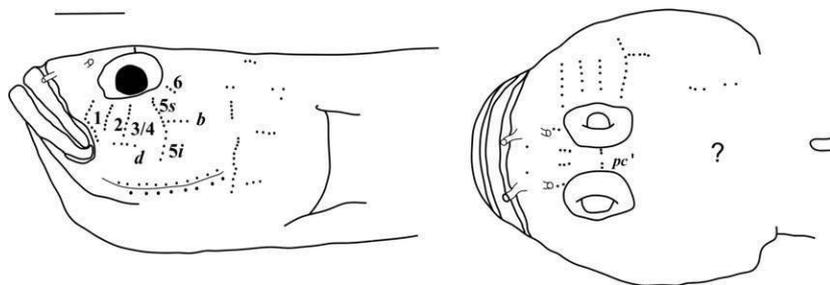


Figure 22. *Psilotris laurae* papillae pattern, drawn from holotype, USNM 426779. Illustration by J.L. Van Tassell.

separate, no anterior frenum or membrane connecting fifth rays, rays 1–4 branched once, fifth ray unbranched and one-quarter the length of fourth ray; papillae row 5s/5i connected forming a single row at the anterior of row b, interorbital papillae row pc' with two papillae; head and preopercle canals and pore absent; one anal-fin pterygiophore inserted anterior to haemal arch; a distinct colour pattern with five conspicuous thin bars along trunk, bars bright yellow in life or black in preserved specimens.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII, spines 1–4 slightly elongate, second spine longest, tips of spines projecting from membrane; second dorsal fin I,9; anal fin I,8; pectoral fin 18, elongate, pointed, extending to second or third ray of anal fin; pelvic fins I,5; pelvic fins well separated, lacking both anterior frenum and membrane connecting bases of innermost pelvic-fin rays; fourth pelvic-fin ray longest, extending posteriorly to anus; rays 1–4 branched once, fifth ray unbranched and one-quarter the length of fourth ray; tips of pelvic-fin rays not ending in fleshy pads; caudal fin rounded; branched caudal-fin rays 15; segmented caudal-fin rays 17.

Scales: Scales on head and trunk absent.

Head: Jaw extending posteriorly to a vertical at anterior of eye; anterior nare an elongate narrow tube; posterior nare an opening with raised rim; no cephalic lateralis pores on head or preopercle; eyes 30.1% HL, dorsolateral, extending above head profile; interorbital narrow, 7.09% HL; snout profile steep; operculum opening extending slightly wider than vertical of pectoral-fin base; teeth in upper jaw in three or four rows, teeth in outer row enlarged, extending along most of premaxilla, teeth in inner rows small and more numerous; teeth in lower jaw in three or four rows, teeth in outermost and innermost rows slightly enlarged, middle rows

smaller and more numerous, two enlarged recurved canines in inner row at midpoint of dentary.

Genitalia: Male with conical pointed papilla, no melanophores present; female unknown.

Colour in life (Fig. 20): Head and body translucent white (with a yellow cast to body after death), with distinct thin yellow–brown bars; head with four distinct bands radiating from eye; first band, with few melanophores, extending from anterior of eye forwards and down across both jaws; second band, with numerous melanophores, extending posteroventral corner of eye onto middle of preopercle; third band with many melanophores and dark edges, originates at posterodorsal corner of eye, extending posteriorly where it meets with corresponding band from opposite side of head, forming U–shape across the top of head; fourth band a short thin yellow interorbital bar connecting the anterodorsal corners of the two eyes; snout light yellow with a few scattered melanophores; trunk with five narrow, yellow–brown bars with scattered melanophores, densest along edges; first trunk bar across nape, connecting the upper corners of the pectoral fins; second trunk bar originating under dorsal-fin spines 4–6, extending to abdomen; third trunk bar extending from anterior of second dorsal fin to abdomen; fourth trunk bar originating under posterior one-third of second dorsal fin; fifth trunk bar over mid-caudal peduncle; first dorsal fin with bright-white stripe along outer edge and three yellow–brown bands; lower band on first dorsal fin dark yellow–brown, extending from lower anterior edge of fin to midpoint of base, where it joins the first body bar; second band on first dorsal fin extending diagonally from near mid-point of first spine to near posterior of fin base, yellow–brown with dense melanophores at front, broken into spots posterior to fifth spine; third and outermost band on first dorsal fin broad, yellow, with dark melanophores concentrated along first spine, colour becoming lighter posteriorly; second dorsal fin translucent white, with broad bright-white dorsal

edge, with a row of yellow–brown spots under the rear third of that white band, and four yellow–brown transverse bands with numerous melanophores; first band extending only from first to third spine before coalescing with the third trunk bar, second band extending from first spine to seventh ray before coalescing with the fourth bar on trunk; third and fourth bands narrow, extend entire width of fin; caudal fin translucent white with rear margin broadly bright white, and with four thin yellow–brown vertical bars with numerous melanophores, bars equally spaced, anterior bar at base of caudal-fin rays; lower one-fifth of caudal fin yellow with black margin; pectoral fin translucent to white on lower two-thirds of fin, bright yellow on upper one-third, with bright-yellow band coalescing with the first trunk bar; anal fin translucent with dark distal margin; anal fin translucent with blackish outer margin, rear edge yellowish; pelvic fin colour not known.

Colour in preservation (Fig. 21): Background colour of body and head yellowish pale; all bright-yellow markings from life still evident as dark concentrations of melanophores, including dark streak on upper third of pectoral fin, and dark stripes on head, nape, body, and dorsal and caudal fins; anal fin with dark posterior margin; pelvic fin immaculate.

Sensory papillae (Fig. 22): A transverse pattern with rows 1, 2, and 3/4 extending most of the distance from orbit to row d; row 5s/5i connected and at the anterior of row b; row b short, composed of four papillae; row d short, about four papillae located midway between rows 1 and 5s/5i; interorbital papillae row pc' with two papillae present.

Vertebral skeleton: Dorsal pterygiophores formula 3–221110; one anal-fin pterygiophore inserted anterior to first haemal arch; second neural arch expanded, forked at tip; hypurals 1 and 2 fused to hypurals 3 and 4 along half of their length; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: The only known specimen was found inside a glass bottle collected along a sandy slope between 114 and 137 m depth. There is no additional information on the natural microhabitat of this species.

Distribution: Known only from the type location off Bonaire.

Etymology: Named after Laura Albini, wife of Adriaan 'Dutch' Schrier, the owner of Substation Curacao, through whose efforts new, tropical, deep-

water species are being discovered. Laura has generously fed and hosted numerous researchers during their visits to Curacao.

Comparison: *Psilotris laurae* sp. nov. is the only deep-water species of *Psilotris* known at this time, and the only species with one anal-fin pterygiophore inserted anterior to the haemal spine. It can be distinguished from all other *Psilotris* species except *Psilotris kaufmani* by possessing a bicoloured pectoral fin. *Psilotris laurae* sp. nov. differs from *Psilotris kaufmani* in having distinct narrow vertical bars on the body and caudal fin versus small round spots and mottling (Fig. S3D). The distinct vertical bars also serve to separate *Psilotris laurae* sp. nov. from the morphologically similar *Varicus decorum* sp. nov., which possess distinct yellow circles and spots along the side of the body and dorsal surface. In addition, *Psilotris laurae* has pelvic-fin rays 1–4 branched to the tips, whereas rays 1–4 are either unbranched or branched and re-fused as fleshy pads in *Varicus decorum* sp. nov.

VARICUS ROBINS & BÖHLKE, 1961

TYPE SPECIES: *VARICUS BUCCA* ROBINS & BÖHLKE, 1961 (P. 47, FIGS 1–3, BY ORIGINAL DESIGNATION)

Diagnosis

Possesses all taxonomic characters present in most members of Gobiosomatini and the *Gobiosoma* group (first dorsal-fin spines VII, pterygiophore insertion pattern of 3–221110, 27 vertebrae – 11 precaudal and 16 caudal (rarely 12 and 15), hypurals 1 and 2 fused to some extent with hypurals 3 and 4 and the terminal vertebral element, one epural); pelvic fins well separated, lacking both anterior frenum and well-developed membrane connecting innermost rays; pelvic-fin rays highly variable among species (Fig. 4A–E), with rays 1–4 unbranched, branched internally and re-fused with pointed fleshy pads, or branched to tips with flat, spatulate fleshy pads, fifth pelvic-fin ray always unbranched; pelvic-fin rays generally extending posteriorly to anus and sometimes to origin of rays 1–4 of anal fin; body with scales in all but one species (*Varicus decorum* sp. nov.) (modified basicaudal scales present in all but one species, which awaits description; see remarks below); one anal-fin pterygiophore inserted before first haemal spine (in anomalous cases where first haemal spine is on vertebra 13 rather than 12, two anal-fin pterygiophores inserted before haemal spine); papillae rows 5i and 5s connected in all but three species (*Varicus benthonis*, *Varicus vespa*, and variable in *Varicus cephalocellatus* sp. nov.); cephalic lateralis canals and pores absent; second dorsal-fin rays I,8–

10; anal-fin rays I,7–9 (rarely I,6 in one species); body coloration variable, but generally with yellow spots or stripes on dorsal and caudal fins, bright-yellow spots, bands, or saddles on dorsal and lateral surface of body, and in several species, dark vertical bars or bands along side of body. The ten species in this genus are known only from the western Atlantic Ocean.

Remarks on the genus *Varicus*

Varicus was described by Robins & Böhlke (1961) for *Varicus bucca*. Since then *Varicus* has been loosely distinguished from *Chriolepis* based on *Varicus* having unbranched pelvic-fin rays (rays branched to the tips in *Chriolepis*), having a bilobed tongue (rounded in *Chriolepis*), and in lacking a low fleshy ridge between the innermost pelvic-fin rays (ridge present in *Chriolepis*); however, as more species from both genera were subsequently described, mostly from the Atlantic (e.g. *Chriolepis vespa*, *Varicus marilynae* Gilmore, 1979, and *Varicus imswe*), the generic distinctions began to blur, and the aforementioned characters proved to be of little use in separating species into two clearly delineated groups (Hastings & Bortone, 1981). Birdsong *et al.* (1988) noted that *Varicus* and the Atlantic members of *Chriolepis* (*Chriolepis vespa*, *Chriolepis fisheri*, and *Chriolepis benthonis*) are the only species of Gobiosomatini to have one anal-fin pterygiophore inserted anterior to the first haemal spine (two in all other species), indicating a possible close relationship between the two groups and a potential distinction between the Atlantic and Pacific species of *Chriolepis*; however, this link between the pterygiophore pattern and the divide between Atlantic and Pacific species became less apparent when Hastings & Findley (2013, 2015) described two Atlantic species that have two anal-fin pterygiophores anterior to the first haemal spine, tentatively placing both in *Chriolepis*.

Our phylogenetic analysis includes only one named species of *Varicus* (*Varicus imswe*); however, several other deep-reef Caribbean species are included in our tree that are very similar to the type species, *Varicus bucca*, and are likely to be much closer relatives to *Varicus bucca* than to *Varicus imswe*. The four species in our tree that are similar to *Varicus bucca* are the new species *Varicus cephalocellatus* sp. nov., *Varicus decorum* sp. nov., and *Varicus veliguttatus* sp. nov., plus one undescribed species (*Varicus* sp. A in Fig. 5). The four species form a well-supported monophyletic group, and all have one anal-fin pterygiophore inserted before the first haemal spine, pelvic-fin rays that are either unbranched or branched internally, and pelvic-fin rays with fleshy tips. Those morphological characters are shared with *Varicus bucca* and *Varicus marilynae*. *Varicus*

imswe is distinct from these four species both genetically and morphologically, and is herein assigned to a new genus *Paedovaricus* (see remarks section for *Paedovaricus* above for justification). In addition to the aforementioned species in our tree, two other new species are described here without molecular data and placed in *Varicus* (*Varicus adamsi* sp. nov. and *Varicus nigrinus* sp. nov.). These two also possess one anal-fin pterygiophore before the first haemal spine and pelvic-fin rays that are either unbranched or are branched but have fleshy tips. The anal-fin pterygiophore character is not entirely free of homoplasy (Fig. 6B), but it nevertheless contains considerable phylogenetic information (Table 1); thus, it may be of some utility in classifying species, if not by itself then in combination with other characters (e.g. pelvic-fin branching pattern, fin-ray counts, papillae pattern, etc.). In addition, most species in this group have papillae rows 5i and 5s connected to form a single continuous row (variable in *Varicus cephalocellatus* sp. nov., separate in *Varicus vespa* and *Varicus benthonis*, see paragraph below). This character is apparently derived in the *Nes* subgroup and is shared among several lineages of Atlantic species. Another important characteristic of the species in our *Varicus* clade is that, like *Varicus bucca* and *Varicus marilynae*, all species occur on continental or insular slopes at or below 60–100 m depth. Collectively, despite lacking a single unambiguous morphological synapomorphy, we recognize the five new species described here plus *Varicus marilynae* and *Varicus bucca* as belonging to the genus *Varicus* based on the combined molecular, morphological, and ecological information presented above.

Of the five Atlantic species of *Chriolepis*, two are now referred to the new deep-reef genus *Pinnichthys* based on the presence of two anal-fin pterygiophores before the first haemal spine (versus one in *Varicus*), a high number of lateral scale rows (≥ 30 vs. ≤ 27 in *Varicus*), and more anal-fin rays (I,10 vs. I,9 or fewer in *Varicus*). The status of *Chriolepis fisheri* remains unclear (see remarks section for *Chriolepis* above). The two remaining species, *Chriolepis vespa* and *Chriolepis benthonis*, are considered here to belong to *Varicus* rather than *Pinnichthys* or *Chriolepis* based on the presence of one anal-fin pterygiophore inserted before the first haemal spine, a low number of lateral scales (≤ 12), low anal-fin ray counts (I,8 or fewer), and the fact that both are deep-water species. This assignment is tentative, however, as papillae rows 5i and 5s are separate in both species (nearly connected in *Varicus vespa*), and both species possess highly branched pelvic-fin rays (some rays in *Varicus vespa* and *Varicus benthonis* with minute fleshy tips at the end of some branches, Fig. 4B). *Varicus ben-*

thonis is known only from the holotype, which is in poor condition. Additional fresh specimens and molecular data from these species may ultimately prove helpful in verifying their taxonomic placement. Lastly, *Varicus* overlaps with *Psilotris* to some extent for virtually every morphological feature examined here. Details on morphologically differentiating *Psilotris* and *Varicus* are given in the remarks section for *Psilotris*.

Remarks on the type species Varicus bucca and unidentified Varicus specimens

With the recent accumulation of many new specimens of *Varicus* and the discovery of multiple new species in this genus, we have re-examined the type series of *Varicus bucca* and come to several conclusions. First, the type series probably contains multiple species, given the wide range of second dorsal-fin and anal-fin counts present among specimens. Furthermore, several of the paratypes have broken pelvic and pectoral rays, and the pigmentation for all specimens has faded, making identification difficult. For these reasons we consider only specimens with I,9 second dorsal-fin rays and I,7–8 anal-fin rays to be *Varicus bucca*, and some of those only tentatively so. We provide an annotated list of *Varicus* specimens that are confidently identified as *Varicus bucca* as well as those that are of questionable identity, including some paratypes of *Varicus bucca* (Table S1).

VARICUS ADAMSI GILMORE, VAN TASSELL &
TORNABENE SP. NOV.
TWILIGHT GOBY
FIGS 23–26

Holotype

USNM 427226, 60 mm SL, male, Johnson Sea Link I Dive JLS-I-2027, 23.957833N –74.57066W, Sand Point, San Salvador, Bahamas, 435.1 m depth, 4 May 1987, R.G. Gilmore & M. Adams.

Paratype

USNM 427225, 44.5 mm SL, female, Johnson Sea Link I Dive JLS-I-2022, 24.050833N –74.53933W, Cockburn Town, Riding Rock, San Salvador, Bahamas, 280 m depth, 2 May 1982, R.G. Gilmore & M. Adams; USNM 220985, 32.5 mm SL male, R/V *Oregon* Cruise 94, Station 5021, 11.3533N –60.645W, north of Tobago, tumbler dredge, Trinidad and Tobago, 165–183 m depth, 21 September 1964.

Diagnosis

Side of body typically with ctenoid scales from caudal peduncle to pectoral-fin base, ctenii reduced or lack-

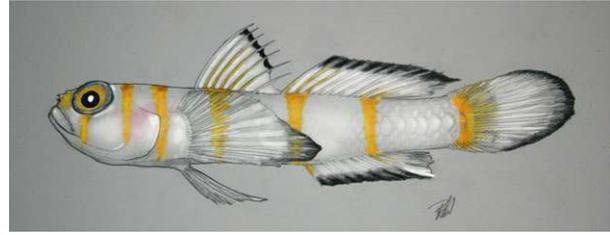


Figure 23. *Varicus adamsi*, illustration of holotype, 61.0 mm SL, USNM 427225, based on notes and photos of live coloration, by R.G. Gilmore.



Figure 24. *Varicus adamsi*, 61.0 mm SL, USNM 427225, in situ at 435 m, Bahamas, photo by R.G. Gilmore and Michael Adams from the Johnson Sea Link II submersible (original photo out of focus – no additional photos available).



Figure 25. *Varicus adamsi* paratype, 44.5 mm SL, preserved, USNM 427226. Photo by J.L. Van Tassell.

ing anteriorly; six or seven very enlarged ctenoid scales on caudal peduncle; two modified basicaudal scales with enlarged ctenii on dorsal and ventral margins of caudal-fin base; first dorsal-fin spines VII, no elongate spines; second dorsal-fin rays I,9; anal-fin rays I,8; pectoral fin extending to third element of second dorsal fin; pelvic fins well separated, fifth ray one-quarter length of fifth ray, rays 1–4 branched several times with spatulate, fleshy tips; papillae rows 5s and 5i connected as a continuous transverse row; interorbital papillae row pc' with two papillae; no cephalic lateralis pores on head or preopercle; anterior nostril with dorsal bilobed flap, posterior with simple triangular flap; one anal-fin

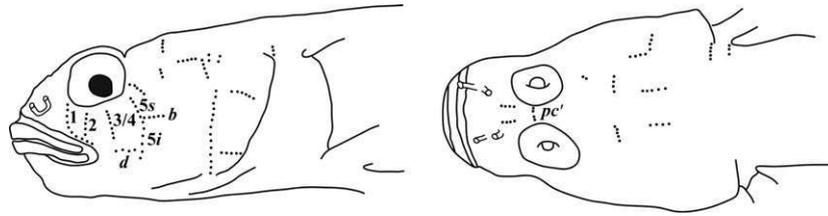


Figure 26. *Varicus adamsi* papillae pattern, composite from type series. Illustration by J.L. Van Tassell.

pterygiophore inserted anterior to haemal arch; pectoral, spinous dorsal and caudal fins with brilliant white pigment adjacent to black fin margins, body white with seven conspicuous yellow bars situated under eye, on cheek, behind opercular margin, below middle of dorsal fin, below origin of second dorsal fin, below middle of second dorsal fin, and on posterior margin of caudal peduncle.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal-fin spines VII (3), spines 2–4 extending slightly from membrane, none notably elongate or filamentous; second dorsal fin I, 9(3); anal fin I, 8*(2), I, 7(1); pectoral-fin rays 18 (3), rays 13 and 14 longer than others, extending to vertical through third ray of second dorsal fin; pelvic fin I, 5(3); pelvic fins well separated, lacking anterior frenum and membrane connecting bases of innermost rays; fourth pelvic-fin ray longest extending to anus, pelvic-fin rays 1–4 branched several times, tips of branches united with fleshy spatulate pads (Fig. 4A), fifth pelvic-fin ray unbranched, short, one-quarter length of fourth pelvic-fin ray; caudal fin lanceolate in male, truncate in female; branched caudal-fin rays 14(3); segmented caudal-fin rays 17(3).

Scales: Trunk of body with ctenoid scales, length of ctenii reduced anteriorly; six or seven very enlarged ctenoid scales on caudal peduncle; 21–24 lateral scale rows extending to beneath pectoral fin in holotype (USNM 427226, male), male paratype (USNM 220985) with 23 lateral scale rows extending to beneath pectoral fin, female paratype (USNM 427225) with only enlarged scales on caudal peduncle, remainder of body abraded; two enlarged modified basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base.

Head: Jaw extending posteriorly to a vertical through either the anterior margin of eye or the anterior margin of pupil; anterior nare as a short tube with dorsal bilobed flap; posterior nare an

opening with simple triangular flap; no cephalic lateralis pores on head or preopercle; eyes 30.6–41.8% HL, dorsolateral, extending above head profile; interorbital narrow 4.3–5.1% HL; snout profile steep; operculum opening extending only length of pectoral-fin base; teeth (observed from USNM 220985) in both jaws consisting of multiple irregular rows of small conical teeth, no enlarged canines.

Genitalia: Male genitalia pointed and triangular; female as bulbous pore; no melanophores present on either sex.

Colour in life (Figs 23 and 24): Background of body pale white; trunk with four narrow bright yellow bars that traverse the dorsal midline, diameter greater than pupil but less than eye; first trunk bar located below middle of first dorsal fin; second trunk bar below origin of second dorsal fin; third trunk bar below middle of second dorsal fin; last trunk bar over posterior end of caudal peduncle; head with three narrow vertical yellow bars; first vertical bar on head directly below eye; second vertical bar on head extending ventrally from anterior nape onto margin of preopercle; third vertical bar on head extending ventrally from posterior nape onto upper opercular margin; iris of eye golden yellow; tip of snout yellow; opercle pale pink.

Coloration of fins in the male holotype differs from female paratype. The following description is based on the male: first dorsal fin covered with white pigment except on spines, with yellow–orange pigment on basal third of spines opposite the first vertical yellow body bar, distal margin black; second dorsal with faint yellow coloration on basal portion of rays at location of vertical yellow body bars; black distal margin; caudal fin white; fin margin with black pigment; anal fin with black on lower third of fin; rays adjacent to yellow body bars with yellow pigment; distal third of pectoral fin with black pigment, remainder of fin with white pigment. Female pectoral fins and anal fin lack black pigment and dorsal and caudal fins have much reduced black pigment compared with the male.

Colour in preservation (Fig. 25): Background colour tan with faint vertical melanic bars at locations where yellow bars were observed on head and trunk of fresh specimens; dusky distal margins of dorsal, anal, and caudal fins retaining pigment in some specimens, faded in others.

Sensory papillae (Fig. 26): A transverse pattern with rows 1, 2, 3/4, 5s/5i, and 6 present; row 5s/5i joined forming a single row and extending below the level of row d; row b short with four or five papillae, ending anteriorly at row 5s/5i; interorbital row pc' with two papillae.

Vertebral skeleton: Dorsal pterygiophore formula 3–221110; one anal-fin pterygiophore inserted anterior to first haemal arch; hypurals 1 and 2 fused with hypurals 3 and 4 along one-quarter of their length; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: This is the deepest occurring goby of the genus *Varicus*, and possibly the deepest occurring goby in the world, and has been captured at depths of 280 and 435.1 m during manned submarine dives, JSL – II, 2022 and 2027 off the western shore of San Salvador, Bahamas. The substrate at the type locality principally consists of limestone outcroppings and boulders with an occasional thin layer of calcareous oolite sands and *Halimeda* spp. algal rubble (see *in situ* photo of the holotype at 435 m off Sandy Point, San Salvador; Fig. 24). Bare sedimentary rock surface and boulders predominate in this region at depths of 250–500 m.

Distribution: Known only from the western shore of San Salvador, Bahamas and from Tobago.

Etymology: Named for the late famed research submersible pilot, Mr. Michael Adams, who painstakingly captured both Bahamas specimens during a 30–45 min chase using a 26 ton submarine (JSL – II) in simultaneous multiple thrust, multi-directional mode to allow this description. Mr. Adams was one of the five original research submersible pilots within the United States.

Comparisons: *Varicus adamsi* sp. nov. is distinctive in that it is the only species of *Varicus* to have highly branched pelvic-fin rays 1–4 that terminate in flattened, spatulate fleshy tips (Fig. 4A). The I,9 count for second dorsal-fin rays further distinguishes *Varicus adamsi* sp. nov. from *Varicus cephalocellatus* sp. nov. (I,10) and from *Varicus marilynae*, *Varicus benthonis* and *Varicus veliguttatus* sp. nov. (all with I,8). *Varicus adamsi* sp. nov. is further distinguished from *Varicus nigritus* sp. nov. in lacking prominent black wide

bands along the body. The presence of body scales easily distinguish *Varicus adamsi* sp. nov. from *Varicus decorum* sp. nov. *Varicus adamsi* sp. nov. is likely most closely related to *Varicus vespa*. The two species have similar meristic counts and nearly identical coloration (Figs 23, 24, and Fig. S4D). Both *Varicus adamsi* sp. nov. and *Varicus vespa* have branched pelvic rays, although rays in *Varicus vespa* never have the distinct spatulate tips. *Varicus vespa* is a relatively small species (types <30 mm SL) known only from the Gulf of Mexico where it occurs over mud, whereas *Varicus adamsi* sp. nov. is larger (reaching 61 mm SL) and is known from the Bahamas and Tobago where it occurs over hard calcareous substrate. The differences in distribution, maximum size, habitat association, and pelvic-fin morphology support that the two represent distinct species.

VARICUS CEPHALOCELLATUS N. SP., GILMORE,
VAN TASSELL, AND BALDWIN
FIGS 27–30
OCELLATED SPLITFIN GOBY

Holotype

USNM 427232, 28.2 mm SL, female, Paynes Bay, Barbados, West Indies, 13.162N –59.658W, Johnson Sea Link II Dive JLS-II 1755, 159 m depth, 1 May 1989, C.L. Smith & C. Caddigan.

Paratypes

USNM 426788, 30.4 mm SL, female, Bonaire City Dock, Kralendijk, Bonaire, Lesser Antilles, 12.15N, –68.2829W, tissue CUR13185, 114–137 m depth, 5 May 2013, Dive 2 CURASUB submersible, B. Van Bebber, A. Schrier, C. Baldwin, T. Christiaan; USNM 426736, 39.8 mm SL, female, Bonaire City Dock, Kralendijk, Bonaire, Lesser Antilles, 12.15N, –68.2829W, tissue CUR13175, 122–140 m depth, 5 May 2013, Dive 1, CURASUB submersible, B. Van Bebber, A. Schrier, C. Baldwin, & T. Christiaan; USNM 427227, 37.2/37.08 mm SL, 1 male and 1 female, Johnson Sea Link II Dive JSL-II 1772,

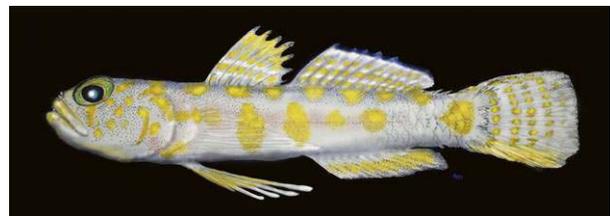


Figure 27. *Varicus cephalocellatus*, illustration of holotype, 28.2 mm SL, USNM 427232, based on notes of live coloration, by R.G. Gilmore.

13.34N –61.2266W, Larikai Point, St. Vincent, 144 m depth, 9 May 1989, R.G. Gilmore & C. Caddigan.

Diagnosis

Side of body with 12–23 ctenoid scales extending anteriorly to between vertical under the middle of the second dorsal fin, to just posterior of pectoral-fin base, scales becoming smaller with reduced ctenii anteriorly; modified basicaudal scales present; first dorsal-fin spines VII; second dorsal-fin rays I,10; anal-fin rays I,9; pectoral fin with 19–20 rays, (23.9–30.6% SL), with rays 13–16 greatly extended, reaching base of anal-fin rays 1–3, giving fin asymmetrical appearance; fleshy exertions on tips of spinous dorsal, first six rays of second dorsal; pelvic fins well separated lacking anterior frenum and membrane connecting innermost rays, 5th pelvic-fin ray 1/4–1/5 length of 4th ray, all rays unbranched or branched internally and re-fused, with flattened fleshy tips, longest ray extending posteriorly to anal-fin origin or reaching origin of 2nd anal-fin ray; sensory papillae rows 5s and 5i connected as a continuous transverse row, separated by a space of 1–2 papillae in two specimens; interorbital papillae *pc'* and *pe'* present; no cephalic lateralis pores on head or preopercle; one anal-fin pterygiophore inserted anterior to haemal arch; series of 3–5 conspicuous yellow ocelli on head extending from mouth to nape over dense field of numerous red, brown and gold chromatophores.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal-fin spines VII (5), spines 2–4 nearly equal in length, no elongate spines, fleshy exertions present on holotype and two paratypes; second dorsal fin I,10(5), spine and rays of second dorsal fin with 1–4 with exerted fleshy tips (holotype and two paratypes), soft rays 1–4 undivided or with minor terminal bifurcation, remainder of second dorsal-fin rays bifurcated for 30–50% of element length; anal fin I,9(5); pectoral-fin rays 20*(4), 19(1), rays 13–16 greatly extended beyond remainder of fin reaching vertical through anal-fin rays 1 to 3; pelvic-fin rays I,5(5); pelvic fins well separated, lacking both anterior frenum and membrane connecting bases of innermost rays; 4th pelvic-fin ray longest extending to anal-fin origin or 2nd anal-fin ray, reaching origin of 2nd anal-fin ray in one specimen; 5th pelvic-fin ray 1/4–1/5 length of 4th ray; all pelvic-fin rays unbranched, or branched internally but re-fused at tips, all tips generally with single fleshy pads; caudal fin rounded to truncate or slightly emarginate; branched caudal rays 14*(4) 15

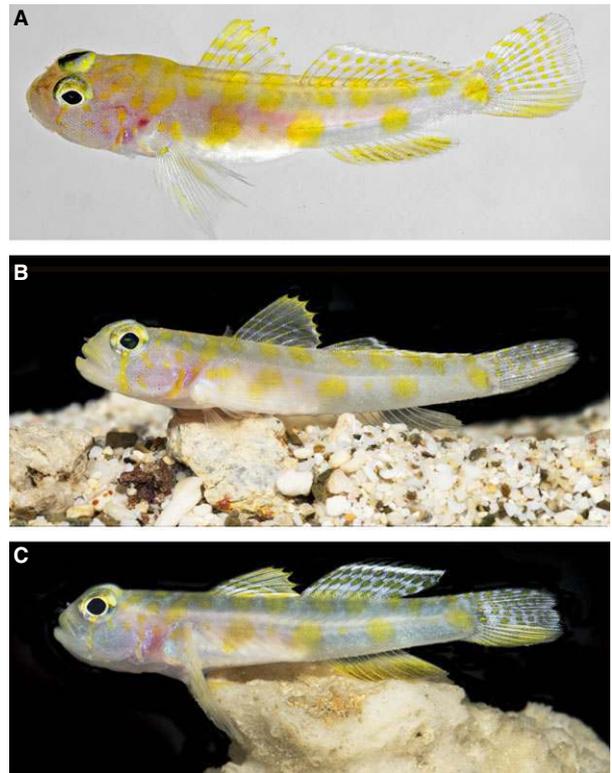


Figure 28. *Varicus cephalocellatus*; (A) paratype, 30.4 mm SL, USNM 426788, prior to preservation, photo by C. Baldwin and D.R. Robertson; (B, C) paratype, 39.8 mm, USNM 426736, live, photos by Barry Brown.



Figure 29. *Varicus cephalocellatus*, preserved. (A) holotype, 28.2 mm SL, USNM 427232; (B) paratype, 37.1 mm SL, USNM 427227. Photos by J.L. Van Tassell.

(1); segmented caudal rays 17(5) with 6–7 strong procurent rays.

Scales: Trunk of body with 12*–23 lateral ctenoid scale rows extending anteriorly in wedge to a vertical below middle of second dorsal fin, or anterior to a point just posterior to pectoral-fin base; 5–10 transverse scale rows; no scales on abdomen, head or predorsal region; two modified

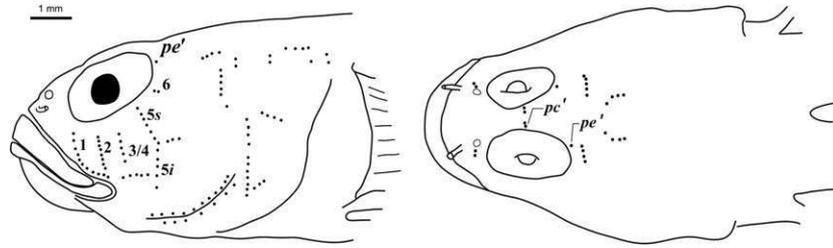


Figure 30. *Varicus cephalocellatus* papillae pattern, drawn from paratype USNM 426788. Illustration by J.L. Van Tassell. Note that two paratypes USNM 427227 have papillae rows 5i and 5s separated by the space of 1 or two papillae.

basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base; 4–5 pre-caudal scales along dorsal caudal peduncle with enlarged ctenii.

Head: Jaw extending posteriorly to vertical through the middle of eye; anterior nare on a long tube, posterior nare an opening with a raised rim; no head or preopercle pores; eyes large, 26–37.2% HL, dorsolateral, extending slightly above head profile; interorbital moderate, 3.4–8.2% HL; snout profiles steep; operculum opening extending only length of pectoral-fin base; teeth in upper jaw arranged in 2–3 rows, teeth in middle row smallest and most numerous, teeth in inner row slightly larger, teeth in outer row largest and recurved, widely space and continuing along most of premaxilla; teeth in lower jaw in 5–6 rows, teeth in outer row enlarged, restricted to anterior of dentary (USNM 426736) or extending to mid-dentary (USNM 426788), inner row slightly smaller, and middle row very small and numerous.

Genitalia: Male urogenital papilla triangular and pointed; female urogenital papillae round and bulbous with a few melanophores at tip.

Colour in life (Figs 27 and 28): Head and body largely translucent with red background cast on head and front of body due to internal blood; head and anterior body with numerous tiny red, yellow and black melanophores/chromatophores; head with numerous distinct bright yellow markings, loosely arranged into one subocular bar and a series of yellow ocelli surrounded by darker melanophores scattered from the lower cheek to the nape; preopercular margin with a yellow vertical bar; nape with 2–3 irregular yellow cross-bars; iris iridescent greenish yellow; body with four large mid-lateral yellow oval blotches declining in size to caudal peduncle with a small yellow spot between each of them on lateral midline, first large spot under middle of first dorsal fin, second large spot below origin of second dorsal fin, third large spot below second dorsal-fin rays 8–10, fourth large spot on

posterior caudal peduncle; dorsal midline with seven yellow saddles, three under spinous dorsal, three under soft dorsal, one dorsal before the peduncle; first dorsal fin with 3 yellow lateral stripes, upper stripe broad, covering margin, areas of iridescent white pigment between lateral stripes; second dorsal with yellow spots on each ray in 2–3 rows parallel with body axis, with three iridescent white bands, the submarginal band most conspicuous; the margins of all vertical fins are outlined with black melanophores; caudal fin translucent, with 4–6 yellow bars formed by vertical rows of yellow spots separated by white pigment, lower 5–6 caudal rays broadly yellow; anal-fin membrane between rays with dark melanophore and yellow pigment; pectoral-fin base with a large yellow hour-glass shaped blotch above, a small yellow spot below, fin with white pigment on rays with yellow pigment extending from upper P1 base blotch; pelvic fins with yellow pigment on inner membrane, exerted flattened rays with brilliant white pigment.

Specimens captured on a recent pyroclastic flow at Larikai Point, St. Vincent, W.I (USNM 427227; Fig. 29B), deposited in a volcanic eruption ten years prior to capture, were more heavily pigmented, darker, than Barbados and Bonaire specimens captured on sedimentary sediments (Figs 27, 28 and 29A). The yellow lateral blotches were dark melanic blotches in the St. Vincent fish and the body was gray in colour, yet the yellow ocelli were still present on the cheek and head.

Colour in preservation (Fig. 29): Background tan with dusting of very fine faint melanophores over entire body and larger faint melanophores on head and cheek. The St. Vincent specimens are darker with melanic bars and spots persisting on head and body.

Sensory papillae (Fig. 30): A transverse pattern with rows 1, 2, 3/4, 5s/5i and 6 present (7 present on two specimens); row 5s/5i joined forming a single row in 3 specimens, separated by the space of 1–2 papillae in two paratypes, extending below the level

of row *d*; row *b* short represented by 3–4 papillae, ending anteriorly at row 5*s*/5*i*; interorbital papillae row *pc*' with two papillae and *pe*' with one papilla.

Vertebral skeleton: Dorsal pterygiophore formula 3-221110; single anal-fin pterygiophore inserted anterior to first haemal arch; hypurals 1 and 2 fused with hypurals 3 and 4 along 1/4–1/2 of their length; 27 vertebrae, 11 precaudal and 16 caudal; one paratype from USNM 427227 with haemal spine on vertebra 12 greatly reduced, giving appearance of 12 precaudal vertebrae and 15 caudal vertebrae, and thus also giving the appearance of two anal-ptyerygiophores inserted before the first haemal spine (which is actually the haemal spine of the vertebra 13; Fig. 2B).

Habitat: The holotype was captured on the west Barbados shelf on a gentle sloping calcareous sand bottom with scattered small calcareous rocks and ledges while the St. Vincent specimens were captured on fresh volcanic deposits, a submerged pyroclastic flow, mostly rock with thin layer of dark sediments, scattering of small rocks, ledges and various sessile invertebrates. The recently deposited volcanic substrate differed from the surrounding older volcanic substrates and the sessile invertebrate and fish faunas differed between these habitats as a result. Substrate not recorded for Bonaire specimens.

Distribution: All specimens are known from southern Lesser Antilles, St. Vincent, Barbados and Bonaire.

Etymology: Named for series of ocelli on head extending from mouth diagonally to nape.

Comparisons: *Varicus cephalocellatus* sp. nov. can be distinguished from all other *Varicus* species in having I, 10 dorsal-fin rays (I, 9 or less in all other species), and I, 9 anal-fin rays (I, 8 or less in all other species). In addition, *Varicus cephalocellatus* sp. nov. lacks the distinct black bands on the body present in *Varicus nigrinus* sp. nov., and the dark spots on the first dorsal fin present in *Varicus veliguttatus* sp. nov. The presence of scales on the body distinguishes *Varicus cephalocellatus* sp. nov. from *Varicus decorum* sp. nov.

VARICUS DECORUM N. SP., VAN TASSELL,
BALDWIN AND TORNABENE
FIGS 31–33
DECORATED SPLITFIN GOBY

Holotype

USNM 432000, 42.5 mm SL, female, CURASUB15-26, slope off Playa Forti, Westpoint, leeward side,

Curacao, 12.083 N, –68.899 W, 165 m, 29 September 2015, C. Baldwin, B. Van Bebber, D. Robertson & L. Tornabene.

Paratype

USNM 426692, 40.2 mm SL, female, tissue CUR 13247, CURASUB13-13, east of downline at Substation Curacao, 12.0832N –68.8991W, 99 m depth, 8 Aug 2013, C. Baldwin, R. Robertson, C. Castillo, B. Brandt & L. Rocha; USNM 406314, 41.2 mm SL male, tissue CUR11314, CURASUB11-04, near Substation Curacao, 12.083197N –68.899058W, 197–251 m depth, 27 May 2011, A. Schrier, B. Brandt, M. van der Huls, C. Baldwin & A. Driskell. USNM 432001, 2 (20.45 mm SL female, 35.86 mm SL male), CURASUB15-30, slope off Playa Forti, Westpoint, leeward side, Curacao, 12.368 N, –69.155 W, 180 m (for female) and 172 m (male) depth, 29 September 2015, C. Baldwin, B. Brandt, D. Robertson & L. Tornabene; USNM 436466, 45.53 mm SL, female, tissue CUR15131, CURASUB15-26, slope off Playa Forti, Westpoint, leeward side, Curacao, 12.083 N, –68.899 W, 161 m depth, 29 September 2015, C. Baldwin, B. Van Bebber, D. Robertson & L. Tornabene.

Diagnosis

Body and head entirely naked except for two modified ctenoid scales with enlarged ctenii present on each side of caudal-fin base; first dorsal fin VII, without notably elongate spines; second dorsal fin I, 9; anal fin I, 7–8; pectoral fin with 17 rays, 5th and 6th rays from ventral very elongate, extending well beyond other rays of fin, giving pectoral fin distinctly asymmetrical shape; pelvic fins I, 5, well separated with 5th pelvic-fin ray approximately 1/3–1/5 length of 4th, all pelvic-fin rays unbranched and some may have flattened fleshy tips; interorbital papillae row *pb*' and *pc*' present; no cephalic lateralis pores on head or preopercle present; one anal-fin pterygiophore inserted anterior to haemal arch; first dorsal fin with scattered with yellow spots in life, some with small dark centers; dorsal surface of body with distinct round yellow circles of varying sizes; side of head with two distinct narrow yellow vertical stripes, one through eye and one through posterior margin of preopercle.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII(7), spines 2–4 nearly equal in length; second dorsal fin I, 9(7); anal fin I, 8*(4), I, 7(3); pectoral rays 17(7), 5th and 6th rays from bottom of fin greatly elongate, extending to a vertical through origin of second

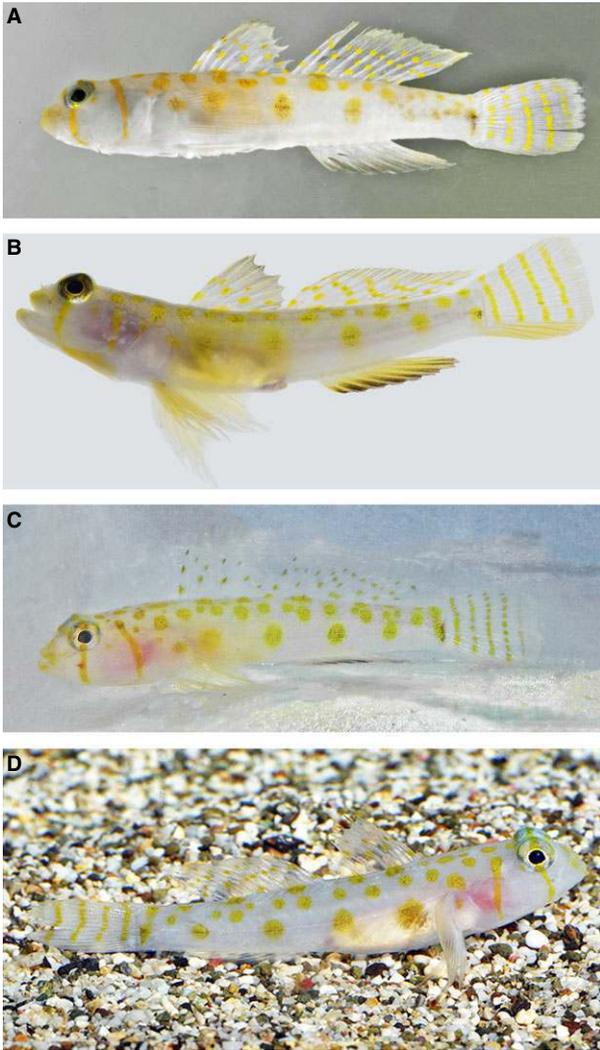


Figure 31. *Varicus decorum*; (A) paratype, 41.2 mm SL, USNM 406314, prior to preservation, photo by D.R. Robertson and C. Baldwin; (B) holotype, 42.5 mm SL, USNM 432000, prior to preservation, photo by D.R. Robertson and C. Baldwin; (C, D) paratype, USNM 406314, live, photos by Barry Brown.



Figure 32. *Varicus decorum*, paratype, 40.2 mm SL, USNM 426692, preserved. Photo by J.L. Van Tassell.

dorsal fin, giving fin a distinctly asymmetrical shape; pelvic fins I,5(7); pelvic fins well separated, lacking both anterior frenum and membrane connecting

bases of innermost rays; 4th pelvic-fin ray longest, extending to between anus and anal-fin origin in 6 of 7 specimens, including holotype, and extending to origin of anal fin in one paratype; 5th pelvic-fin ray approximately 1/3 to 1/5 the length of 4th ray; all pelvic-fin rays unbranched, rays becoming wider and flattened near tips, appearing as a pointed fleshy tip in holotype; caudal fin rounded; branched caudal-fin rays 13(1), 14*(4), 15(2); segmented caudal-fin rays 17(7).

Scales: Body and head entirely naked except for two modified ctenoid scales with enlarged ctenii present on each side of caudal-fin base; body often covered with a thick mucous, making it difficult to observe basicaudal scales; basicaudal scales proportionally larger and more evident in smaller specimens.

Head: Jaw extending posteriorly to a vertical through middle of eye; anterior nare a long tube; posterior nare an opening with raised rim; no cephalic lateralis pores on head or preopercle; tongue truncate or slightly bilobed; eyes large, 26.45–45.52% HL, dorso-lateral, interorbital narrow, 3.02–7.57% HL; snout profile steep; operculum opening extending only length of pectoral-fin base; teeth in upper row in 3–4 rows, teeth in outer row enlarged and widely spaced, teeth in inner rows smaller with slightly recurved tips; teeth in lower jaw in 6–7 rows, outer row with enlarged teeth restricted to anterior of dentary, remaining teeth in inner rows smaller with slightly recurved tips.

Genitalia: Male urogenital papilla short, thin and pointed; female urogenital papilla rounded and bulbous.

Colour in life (Fig. 31): Background of body and head white; lateral portion of trunk with 4 round to oval yellow spots that have heavy speckling of melanophores; first lateral spot below anterior half of first dorsal fin; second lateral spot below origin of second dorsal fin; third lateral spot beneath middle of second dorsal fin; fourth lateral spot (may be faint) on anterior half of caudal peduncle; dorsal third of body with numerous irregularly-spaced circular yellow spots, approximately the size of pupil, sometimes forming loose clusters; head with two narrow yellow bars, first bar extending vertically through eye to ventral surface of head, second bar curving from nape ventrally to posterior margin of preopercle onto branchiostegal rays; two thin yellow crossbars between front and center of eyes; tips of upper and lower jaws bright yellow; iris of eye iridescent, outer margin of eye and interorbital area faintly green; first dorsal fin translucent, with dusky

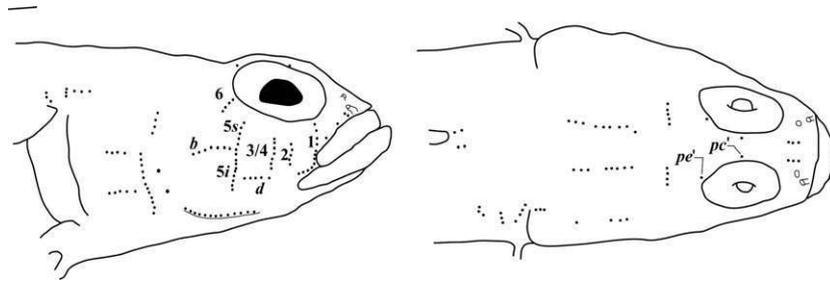


Figure 33. *Varicus decorum* papillae pattern, drawn from paratype, USNM 426692. Illustration by J.L. Van Tassell.

distal margin, small yellow spots (sometimes with very small dark centers) arranged in 2 irregular diagonal rows; second dorsal fin translucent, with small yellow spots loosely arranged in 2–4 diagonal rows; caudal-fin base with a yellow bar with an indistinct blackish bar superimposed on lower half, fin translucent white, with lower 2–4 rays of caudal fin uniformly bright yellow in paratype, pale in holotype, remainder of caudal fin with 5 narrow bright yellow vertical bars separated by wider pale interspaces; anal-fin rays pale (holotype) or yellow (paratype), with dusky to black distal margin; pectoral-fin base with a bright yellow spot on upper corner, fin rays yellow; pelvic-fin rays yellow.

Colour in preservation (Fig. 32): Background colour of body pale to light yellow; side of body with four faint spots of melanophores along trunk and one dark blotch at base of caudal fin, spots of melanophores corresponding to yellow spots in life; dorsal half of body with a very faint dusting of melanophores, pigment more concentrated in some areas where yellow dorsal spots existed in life; nape uniformly covered with light peppering of melanophores, most prominent immediately behind eyes; side of head and preopercle pale, upper half of opercle with light scattering of melanophores; pectoral-fin base and rays unpigmented; first dorsal fin uniformly washed with minute melanophores except for distal margin of membrane between rays 1–5, which is more heavily pigmented, some spines with small concentrated patches of melanophores that correspond to yellow spots in life; second dorsal fin with light scattering of melanophores on interradiial membranes, some spines with dark concentrations of pigment that correspond to diagonal rows of yellow spots in life; caudal-fin rays with faint concentrations of pigment on rays that together represent form bars that correspond to vertical yellow bars in life; anal fin with a pale horizontal stripe at base of rays, remainder of rays uniformly covered with dark melanophores, appearing uniformly dark grey to black; ventral surface of body and pelvic fins pale.

Sensory papillae (Fig. 33): Sensory papillae in a transverse pattern; transverse papillae rows short with upper end at eye (row 1) or well below eye (rows 2–4); transverse row 1 longest, intersecting with anterior part of row *d*; papillae row *b* short ending under posterior of eye; papillae row *5s/5i* continuous, attached to anterior of *b* and extending ventrally below level of row *d* by 3–4 papillae; papillae row *d* not continuous; interorbital papillae *pc'* and *pe'* present.

Vertebral skeleton: Dorsal pterygiophores formula 3-221110; 1 anal-fin pterygiophore inserted anterior to first haemal arch; second neural spine expanded and slightly spatulate at tip; hypurals 1 and 2 fused with hypurals 3 and 4 along at least half of their length; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: This species has been collected from sand habitats with scattered rocks and calcareous rubble, from depths of 99 m to at least 197 m, and possibly 251 m. It has been observed perching on open sand and retreating into crevices when disturbed.

Distribution: Known only from deep reefs off Curacao.

Comparisons: *Varicus decorum* sp. nov. differs from all other named species of *Varicus* in that it lacks scales on the body except for two modified basicaudal scales. An undescribed species of *Varicus* (*Varicus* sp. A in Fig. 5) also possesses a scaleless trunk but the only known specimen is in poor condition and thus the species awaits formal description. Because of the lack of body scales, *Varicus decorum* sp. nov. is morphologically similar to species of the genus *Psilotris*. It can be distinguished from all species of *Psilotris* in having pelvic-fin rays 1–4 that are either unbranched, or if branched, are re-fused with tips forming a single fleshy pad (Fig. 4C, E), versus having rays branched to the tips in *Psilotris* (Fig. 4F). In addition, all but one species of *Psilotris* have two anal-ptyerygiophores inserted anterior to the haemal spine, whereas *Varicus decorum* sp. nov.,

like all species of *Varicus*, has one pterygiophore inserted before the haemal spine. The only species of *Psilotris* that is the exception to this is *P. laurae* sp. nov. – a species that can be easily distinguished from *Varicus decorum* sp. nov. in having yellow vertical stripes on the body, as opposed to yellow round circles and spots as in *Varicus decorum* sp. nov., and in lacking basicaudal scales (two basicaudal scales present in *Varicus decorum* sp. nov.).

Etymology: The specific epithet *decorum* is Latin for “decorated”, “adorned”, “beautiful” or “elegant” and is in reference to the beautiful round yellow markings on the dorsal surface of the body.

VARICUS NIGRITUS SP. NOV. N. SP., GILMORE,
VAN TASSELL, AND BALDWIN
FIGS 34–36
BANDED SPLITFIN GOBY

Holotype

USNM 427233, 35.4 mm SL, male, Johnson Sea Link-I Dive JSL-I 1512, Rocky Pt., San Salvador, Bahama Islands, 24.10833N –74.5333W, 244 m depth, 31 October 1983, R.G. Gilmore & D. Liberatore.

Diagnosis

No scales on body of preserved specimen, though small embedded ctenoid scale at first dorsal-fin base; modified basicaudal scales present; first dorsal fin with small filaments extending beyond membrane on spine tips, spines 2–4 nearly equal; second dorsal fin I,9; anal fin I,8; pectoral fin with 17 rays, rays 14–15 elongate extending to a vertical through 5th second dorsal-fin ray, past the anal origin to vertical through anal rays 4–5; pelvic fins well separated, all rays unbranched without flattened fleshy tips, long ray extending past anus to anal fin origin; papillae rows 5s and 5i connected as a continuous transverse row; interorbital papillae row *pc'* and *pe'* present; no cephalic lateralis pores on head or preopercle; 1 anal-fin pterygiophore inserted anterior to haemal arch; seven black bars from below eye to caudal peduncle.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII, spines 2–4 nearly equal, with filamentous exertions on all spines; second dorsal fin I,9 without fleshy exertions; anal fin I,8; pectoral rays 17, rays 14–15 elongate, extending to a vertical through 4th or 5th anal-fin ray or through 6th second dorsal-fin ray; pelvic fins I,5; pelvic fins well separated, lacking both anterior

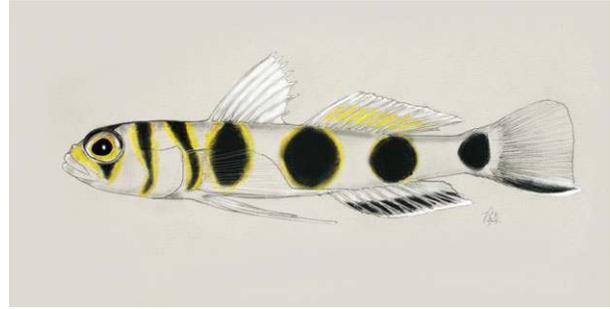


Figure 34. *Varicus nigritus*, holotype, 35.4 mm SL, USNM 427233, illustration of live coloration by R.G. Gilmore.



Figure 35. *Varicus nigritus*, holotype, 35.4 mm SL, USNM 427233; (A) preserved, photographed in 2014, photo by J.L. Van Tassell; (B) preserved, photographed several days after collection, photo by R.G. Gilmore.

frenum and membrane connecting bases of innermost rays; 4th pelvic-fin ray longest extending to anal-fin origin, all pelvic-fin rays unbranched, 5th pelvic-fin ray short, approximately 20% of 4th ray; caudal-fin rounded; branched caudal-fin rays 14; segmented caudal-fin rays 17, 7 dorsal and 5 ventral strong procurent rays.

Scales: No scales present over the lateral portion of trunk of preserved specimen, 1–2 small ctenoid scales remain on base of first dorsal fin, photograph of fresh holotype indicates scales or scale pockets present over most lateral surface of body; 2 modified basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base.

Head: Jaw extending posteriorly to a vertical through anterior margin of pupil; anterior nare an elongate tube, posterior nare a short tube; no cephalic lateralis pores on head or preopercle; eyes 23.7% HL, dorsolateral; interorbital narrow, 8.47% HL; snout profile steep; operculum opening restricted to width of pectoral-fin base; both jaws with multiple rows of

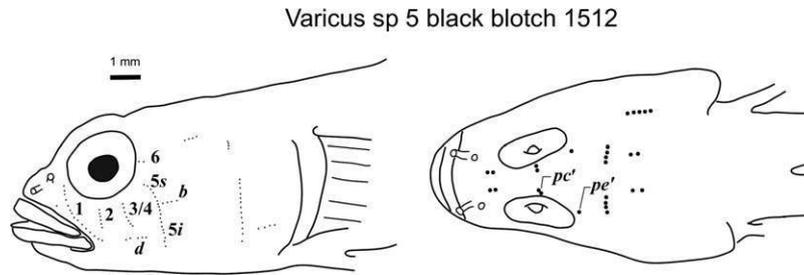


Figure 36. *Varicus nigritus* papillae pattern, drawn from holotype, USNM 427233. Illustration by J.L. Van Tassell.

teeth, outermost and innermost rows with enlarged and conical teeth, middle rows small and irregular.

Colour in life (Fig. 34): Background of body and head pale, somewhat translucent; body and head with seven black bars; first three bars on head, including one below the eye, a second from nape to lower margin of preoperculum, and a third extending diagonally from nape to over pectoral base; body with four black bars, width of 1st, 2nd and 3rd bars wider than eye diameter, first body bar extending ventrally from below first dorsal-fin rays 2–4 to abdomen, second body bar a very broad oval, extending from origin of soft dorsal fin to near the anal-fin origin, the third body bar (also broad) extending from posterior 3–4 rays of the second-dorsal fin to the anal fin, and the final bar on caudal base; anteriormost first five of seven black bars margined in yellow pigment; first dorsal fin, most of caudal fin, inner portion of the anal fin and pelvic fin are entirely brilliant white; lower margin of caudal fin and ventral one-third of anal fin with jet black pigment; a yellow stripe extending along center of second dorsal fin.

Colour in preservation (Fig. 35): Background of head and body light yellowish tan; parts of body and head dark brown with dense melanophores concentrations where the seven dark bars are located in life; pigment faded on fins.

Sensory papillae (Fig. 36): A transverse pattern with rows 1, 2, 3/4, 5s/5i and 6 present; row 5s/5i joined forming a single row and extending below the level of row d; row b short with 4–5 papillae, ending anteriorly at row 5s/5i; interorbital row pc' with two papillae, row pe' a single papilla.

Vertebral skeleton: Dorsal pterygiophore formula 3-221110; single anal-fin pterygiophore inserted anterior to first haemal arch; 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: The holotype was captured off Rocky Point along the northwest shore of San Salvador, Bahama

Islands on a steep rocky slope (45° slope) with thin and sparse calcareous *Halimeda* rubble layer mixed with scattered flat rock outcroppings, hard rock unlayment and scattered rock boulders 1–30 m in diameter.

Distribution: A single specimen captured at 243.8 m off San Salvador, Bahama Islands.

Etymology: The epithet *nigritus* sp. nov., Latin for “black”, is given in reference to the diagnostic dark black wide bars on the trunk of this species.

Comparisons: *Varicus nigritus* sp. nov. is distinguished from all other species of *Varicus* by the presence of prominent black wide bands along the body. It can be distinguished from *Varicus adamsi* sp. nov. by having pelvic-fin rays 1–4 that are unbranched versus branched with wide, spatulate fleshy pads. The presence of I,9 dorsal-fin rays further distinguishes *Varicus nigritus* sp. nov. from *Varicus cephalocellatus* sp. nov. (I,10), and from *Varicus marilynae*, *Varicus benthonis* and *Varicus veliguttatus* sp. nov. (all with I,8). *Varicus nigritus* sp. nov. also possesses a very long pectoral fin with an asymmetrical shape, in which the ventral portion of the fin has rays that extend posteriorly to above the origin of the 4th or 5th anal-fin ray. The pectoral fin is shorter in the other *Varicus* species with I,9 second dorsal-fin rays, including *Varicus bucca*, *Varicus vespa*, and *Varicus decorum* sp. nov. An asymmetrically shaped pectoral fin with extended ventral rays is also present in *Varicus decorum* sp. nov. and *Varicus cephalocellatus* sp. nov., but not *Varicus bucca* or *Varicus vespa*.

VARICUS VELIGUTTATUS SP. NOV. N. SP.,
VAN TASSELL, BALDWIN AND GILMORE
FIGS 37–39
SPOTTED-SAIL GOBY

Holotype

USNM 427224, 45 mm SL, female, Dive JLS-I-2018, Johnson Sea Link I, East of Catto Cay, NE, San Sal-

vador, Bahamas, 24.1443N –74.4591W, 287.6 m depth, 30 April 1987, R.G. Gilmore & M. Adams.

Paratypes

USNM 406372, 39.2 mm SL, male, DNA CUR11372, CURASUB #11-05, eastward out of Substation Curacao, Curacao, 12.083197N –68.899058W, 152 m, 30 May 2011, D. Robertson, B. Brandt, R. Loendersloot, A. Driskell & K. Stewart; USNM 431697, 41.5 mm SL, male, DNA CUR14089, CURASUB #14-09, east of downline at Substation Curacao, Curacao, 12.0832N –68.8991W, 225 m depth, 24 Jun 2014, C.C. Baldwin, B. Brandt, & A. Schrier; USNM 220982, 28 mm SL, male, Oregon Cruise Station 4834, east of Puerto Cabezas, off Nicaragua, 14.2367N –80.475W, 274–293 m depth, 12 May 1964; USNM 432003, 39.69 mm SL, female, CURASUB15-30, slope off Playa Forti, Westpoint, leeward side, Curacao, 12.368 N, –69.155 W, 186 m depth, 29 September 2015, C. Baldwin, B. Brandt, D. Robertson & L. Tornabene; USNM 434795 39.3 mm SL, female, DNA CUR15115, CURASUB14-15, east of downline at Substation Curacao, Curacao, 12.0832N –68.8991W, 187 m depth, 1 September 2015, C. Baldwin, B. Brandt, A. Schrier; USNM 436648, 27.7 mm SL, male, DNA CUR15133, CURASUB15-26, slope off Playa Forti, Westpoint, leeward side, Curacao, 12.083 N, –68.899 W, 191 m depth, 29 September 2015, C. Baldwin, B. Van Bebber, D. Robertson & L. Tornabene.

Diagnosis

Side of body with 23–34 lateral scales extending anteriorly to beneath pectoral fin; 2 modified basicaudal scales present; first dorsal fin VII, without notably elongate spines, spines 2–4 nearly equal; second dorsal fin I,8; anal fin I,6–7; pectoral fin with 17–18 rays; pelvic fins well separated with 5th ray approximately 1/4–1/5 length of 4th, rays 1–4 unbranched or slightly branched near end of ray with tips of branches joining as flattened fleshy tips, 4th pelvic-fin ray very long, extending to base of anal-fin rays 3 or 4; one anal-fin pterygiophore inserted anterior to haemal arch; first dorsal fin with scattered prominent black spots bordered with yellow in life, two prominent small black spots on first dorsal-fin spine.

Description

Morphometric data are presented in Table 3.

Median and paired fins: First dorsal fin VII(7), spines 2–4 nearly equal in length; second dorsal fin I,8(7); anal fin I,6 (1), I,7*(6); pectoral-fin rays 17(1), 18*(5), 19(1); pelvic fins I,5(7); pelvic fins well separated, lacking both anterior frenum and membrane connecting bases of innermost rays; 4th

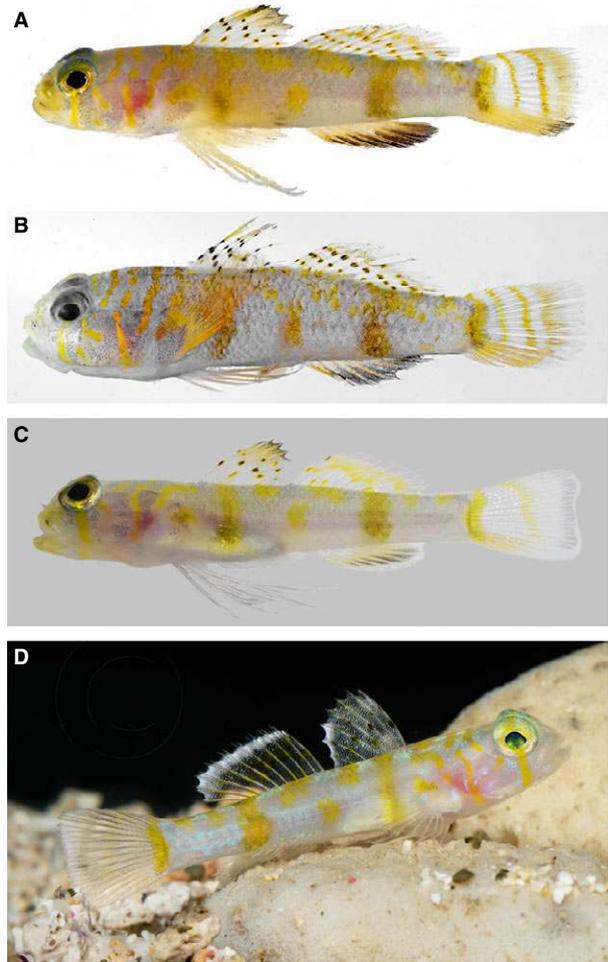


Figure 37. *Varicus veliguttatus*; (A) paratype, 39.2 mm SL, USNM 406372, prior to preservation; (B) paratype, 41.5 mm SL, USNM 431697, prior to preservation; (C) paratype, 27.7 mm SL, USNM 436648, prior to preservation; (D) paratype, USNM 436648, live; photos by D.R. Robertson and C. Baldwin (A–C) and Barry Brown (D).

pelvic-fin ray longest, extending to origin of 3rd or 4th anal-fin-ray; pelvic-fin rays 1–2 unbranched, rays 3–4 either unbranched or slightly branched internally near end of ray, with tips of branches being rejoined as a single fleshy tip; 5th pelvic-fin ray unbranched, approximately 1/5 to 1/4 length of 4th ray; caudal fin rounded; branched caudal-fin rays 14*(5), 15(1), segmented caudal-fin rays 16(1), 17*(5).

Scales: Trunk of body with ctenoid scales, extending anteriorly to axis of pectoral fin and underneath origin of first dorsal, ctenii becoming reduced or in some cases absent on scales immediately below spinous dorsal fin and beneath anterior portion of pectoral fin; 32* scales in lateral series (approximately 26–34 in paratypes); transverse scale rows 11(2), 10 (2), 9*(2), 7(1); scales on abdomen



Figure 38. *Varicus veliguttatus*; (A) paratype, 39.2 mm SL, USNM 406372, preserved; (B) holotype, 45.0 mm SL, USNM 427224, preserved, photos by J.L. Van Tassell.

cycloid or with reduced ctenii; predorsal region with 0(1), 2–3*(1), 5(1), 10(1) scales, in heavily scaled specimen predorsal scales extending anteriorly to halfway between origin of first dorsal fin and posterior margin of eyes; side of head without scales; 2 modified basicaudal scales with enlarged ctenii present at dorsal and ventral margins of caudal-fin base.

Head: Jaw extending posteriorly to a vertical through middle of eye; anterior nare a long tube; posterior nare an opening with raised rim; no cephalic lateralis pores on head or preopercle; eyes large, dorsolateral, extending above head profile, 30.6–41.6% HL; interorbital narrow 3.55–5.38% HL; teeth in both jaws arranged in 3 rows, outer row consisting of distinct recurved canines, larger in upper jaw than in lower jaw, inner two rows of both jaws smaller and irregularly spaced.

Genitalia: Male urogenital papilla short, thin and pointed; female urogenital papilla rounded and bulbous.

Colour in life (Fig. 37): Background of body and head white; body with 2 yellow vertical bars

extending from dorsal midline to well below lateral midline, bars with superimposed dark pigment on their lower halves, first bar under middle of first dorsal fin, second bar under posterior half of second dorsal fin; an elongate yellow oval with a dark center midway between two vertical bars, situated below origin of second dorsal fin; dorsal surface of body 5–6 bright yellow saddles that do not extend ventrally to lateral midline; nape with 3–4 narrow transverse bright yellow bars separated by wide white spaces, center two bars extending onto and down operculum and preoperculum; side of head with 2 additional narrow bright yellow vertical bars, first bar below pupil, second bar broken and below posterior margin of eye, background colour of opercle light pink; tip of upper and lower jaws bright yellow; iris of eye bright gold, outer margin of eye and interorbital area bright green; first dorsal fin translucent whitish, with a broad yellow distal margin peppered with melanophores, fin with irregular rows of scattered black spots margined with bright yellow; second dorsal fin translucent white with black and yellow spots similar to first dorsal fin, arranged in 3–4 diagonal rows; caudal fin with wide vertical yellow bar partly overlaid by blackish pigment at base, another broad fainter yellow submarginal bar at rear of fin, two narrow yellow vertical bars between the 2 broad bars, lower one-third of caudal fin bright yellow with a pale to dusky tip; anal-fin rays bright yellow, inter-radial membranes pale or yellow at base, dusky to black on remainder of fin; upper pectoral-fin base bright yellow, lower pectoral-fin base pale with a scattering of melanophores, pectoral rays uniformly yellow; pelvic-fin rays yellow.

Colour in preservation (Fig. 38): Background of body and head pale yellow; dorsal half of body uniformly covered with a light scattering of melanophores, pigmentation becoming sparse to pale ventrally; two concentrations of melanophores resembling remnants of dark vertical bars present, one immediately behind pectoral fin and one below last rays of second dorsal fin, no other prominent markings on side of body; nape with concentrations

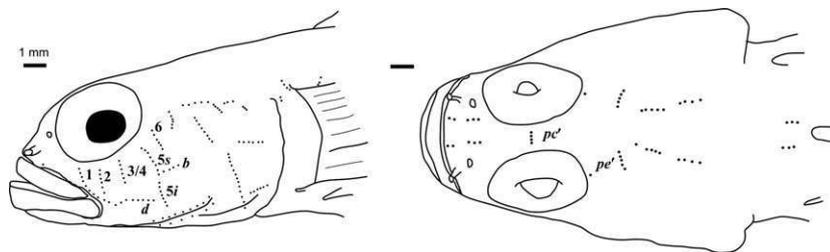


Figure 39. *Varicus veliguttatus* papillae pattern, drawn from paratype, USNM 406372. Illustration by J.L. Van Tassell.

of melanophores roughly corresponding to three transverse bars, the middle being the widest and longest, extending onto upper half of operculum; spines and rays of dorsal fins each with 1–3 dark spots, interradial membranes, where still intact, lacking pigment; side of head, pectoral-fin base, pectoral fins, abdomen, and pelvic fins immaculate; anal fin and caudal fin both with dusky distal margin in one paratype (Fig. 33A), immaculate in other specimens.

Sensory papillae (Fig. 39): A transverse pattern with rows 1, 2, 3/4, 5s/5i and 6 present; row 5s/5i joined forming a single row and extending below the level of row *d*; row *b* short with 4–5 papillae, ending anteriorly at row 5s/5i; interorbital row *pc*' extending across interorbital, *pe*' with 1–4 papillae.

Vertebral skeleton: Dorsal pterygiophore formula 3-221110; 1 anal-fin pterygiophore inserted anterior to first haemal arch; one paratype, USNM431697, haemal spine on vertebrae 12 greatly reduced, giving appearance of 12 precaudal vertebrae and 14 caudal vertebrae, and thus also giving the appearance of two anal-ptyerygiophores inserted before the first haemal spine (which is actually the haemal spine of vertebra 13; as in Fig. 2B); 27 vertebrae – 11 precaudal and 16 caudal.

Habitat: In the Bahamas this species was collected from oolite sedimentary rock at 287.6 m depth. In Curacao this species was collected at depths between 152 m and 225 m, over sand habitats with rubble, gravel and shells.

Distribution: Known from San Salvador, Bahamas, Curacao, and Tobago.

Etymology: The specific epithet *veliguttatus* sp. nov. is formed from the Latin roots *veli-* (sail) and *guttatus* (spotted or speckled). The scientific name and common name refer to the scattered black markings on the first dorsal fin.

Comparisons: *Varicus veliguttatus* sp. nov. can be distinguished from all other *Varicus* species in having a long pelvic fin that extends posteriorly to the base of anal-fin ray 3 or 4, whereas the pelvic fin is shorter in other species (typically reaching anus or anal-fin origin, sometimes reaching origin of 2nd anal-fin ray in *Varicus cephalocellatus* sp. nov.). The low second dorsal-fin ray count of I,8 distinguishes *Varicus veliguttatus* sp. nov. from *Varicus cephalocellatus* sp. nov. (I,10), and from *Varicus decorum* sp. nov., *Varicus adamsi* sp. nov., *Varicus nigrinus* sp. nov., *Varicus vespa*, and *Varicus bucca* (all with I,9). The two other species with

I,8 second dorsal-fin rays, *Varicus benthonis* and *Varicus marilynae*, have fewer lateral scale rows (less than 16 in *Varicus benthonis* and *Varicus marilynae* versus 26–34 in *Varicus veliguttatus* sp. nov.).

SUMMARY OF SYSTEMATIC CHANGES

Based on our combined analysis of molecular data from mtDNA, nuclear genes, and morphological characters, we have made the following changes in the classification of the *Nes* subgroup in order to render all groups monophyletic (see Table 2). We synonymize the genus *Pycnomma* with *Chriolepis*. Two Atlantic species previously belonging to *Chriolepis* (*C. vespa* and *C. benthonis*) are now reassigned to the genus *Varicus*, which now also contains five new species described here (*Varicus adamsi* sp. nov., *Varicus cephalocellatus* sp. nov., *Varicus decorum* sp. nov., *Varicus nigrinus* sp. nov., *Varicus veliguttatus* sp. nov.). The genus *Pinnichthys* is erected for the new species *Pinnichthys aimoriensis* gen. et sp. nov., and also contains three other species formerly included in *Chriolepis* (*C. atrimela*, *C. bilix*, *C. prolata*). The new genus *Paedovaricus* is erected for *Paedovaricus imswe* (formerly *Varicus imswe*), and the new genus *Carrigobius* is erected for *Carrigobius amblyrhynchus* (formerly *Psilotris amblyrhynchus*). *Chriolepis fisheri* is considered *incertae sedis*, as its phylogenetic position is either sister to *Pinnichthys*, or nested within *Psilotris*. The latter genus now includes the two new species *P. laetarii* sp. nov. and *P. laurae* sp. nov.

KEY TO THE SPECIES OF THE *NES* SUBGROUP OF THE GOBIOSOMATINI

The following artificial identification key is based on external features for all named species in the *Nes* subgroup. Anal-fin pterygiophore insertion pattern may also be useful in distinguishing species but, since that cannot be observed without radiographs or clearing and staining, it is not included. As discussed above, we know of several additional undescribed taxa beyond those considered here, as well as several specimens of uncertain taxonomic placement (Table S1). Information for these species was not considered when designing this key. Note that *Varicus bucca* in this key refers only to specimens with I,9 second dorsal-fin rays, as specimens with I,8 rays (including two *Varicus bucca* paratypes) are of questionable identity; see “Remarks” section for *Varicus* above and Supplementary Table S1. Sections of this key use characters and couplets modified from other identification keys (Findley, 1983; Greenfield, 1993; Smith & Baldwin, 1999; Hoese & Reader, 2001). Information regarding whether the specimen is from

the Atlantic or Pacific Ocean is helpful in identifying many species, and this information is included in the key where relevant. Photos of most *Nes* subgroup species are included either in the body of this paper (for all new species) or in Figs S1–S7 (most remaining species) to aid in identification. Photos of freshly caught *Pinnichthys prolata* were not available, although Hastings & Findley (2015) include photos of a long-preserved specimen that lacks colour. Photos of *Chriolepis tagus* also are not available due to the poor state of the holotype, the only known specimen.

- 1a. Innermost rays of each pelvic fin united by well-developed membrane along at least 1/3 of their length; pelvic spines with or without a well-developed anterior frenum.....2
- 1b. Innermost rays of each pelvic fin not connected by well-developed membrane, although sometimes with very low vestigial membrane at base of innermost rays; pelvic spines without a well-developed anterior frenum6
- 2a. Pelvic frenum connecting pelvic spines extending to tips of spines; body pigment not countershaded as in 2b, but variously mottled and with series of vertically paired dark spots or short vertical bars along lateral midline; often found in shallow water associated with *Alpheus* shrimp burrows; western Atlantic.....*Nes longus* (Figs S5C and S7C)
- 2b. Pelvic frenum connecting pelvic spines absent or reduced to a thin membrane, not extending to tips of spines; body with reverse countershading, lower 2/3 of head and body dark and dusky, upper 1/3 of head and body distinctly lighter.....3 (*Gobulus*)
- 3a. Two dorsal fins partly connected; second dorsal fin I,13; anal fin I,12–13; eastern Pacific...*Gobulus birdsongi* (Fig. S2A)
- 3b. Two dorsal fins completely separate; second dorsal fin I,10–11; anal fin I,9–10.....4
- 4a. Pelvic interspinal membrane present but reduced; eye small (less than 0.8 into snout); countershading junction well above lateral midline in adults; pectoral-fin rays typically 16; eastern Pacific.....*Gobulus hancocki* (Fig. S2C)
- 4b. Pelvic interspinal membrane rudimentary or absent; eye larger (at least 0.8 of snout); countershading junction at lateral midline in adults (countershading may be obscure in large specimens); pectoral-fin rays 15 or 17, rarely 16.....5
- 5a. Pectoral fin usually 15, rarely 16; second dorsal fin I,9–10; western Atlantic.....*Gobulus myersi* (Fig. S2D)
- 5b. Pectoral fin usually 17; second dorsal fin usually I,10–11; eastern Pacific.....*Gobulus crescentalis* (Fig. S2B)
- 6a. Cephalic lateralis pores present.....7
- 6b. Cephalic lateralis pores absent.....10
- 7a. Side of body without scales; eastern Pacific.....*Eleotrica cableae* (Fig. S6A)
- 7b. Side of body with scales.....8
- 8a. Second dorsal fin I,9; anal fin I,8; western Atlantic.....*Chriolepis roosevelti* (Fig. S1E)
- 8b. Second dorsal fin I,10; anal fin I,9; eastern Pacific.....9
- 9a. Modified basicaudal scales absent; lateral scale rows more than 30; body and fins with distinct dark vertical or diagonal bars separated by narrow white bars, without speckling or mottling; posterior interorbital pore D absent; Eastern Pacific.....*Gymneleotris seminuda* (Figs S6B and S7F)
- 9b. Modified basicaudal scales present; lateral scale rows 26 or fewer; body and head cryptically coloured, with brown and white speckling or mottling, with brown markings often forming approximately 6 dark wide bars over side of body; posterior interorbital pore D present; Eastern Pacific.....*Chriolepis semisquamata* (Fig. S1F)
- 10a. Scales present, may be restricted to posterior half of body but always in multiple lateral rows; Western Atlantic and Eastern Pacific.....11
- 10b. Scales absent or present only as 2–4 modified basicaudal scales on base of caudal fin; Western Atlantic.....30
- 11a. Anal fin I,10 or more.....12
- 11b. Anal fin I,9 or fewer.....17
- 12a. Scales extending anteriorly to below posterior end of first dorsal fin, not reaching well beneath pectoral fin; Eastern Pacific.....*Chriolepis tagus*
- 12b. Scales extending anteriorly underneath pectoral fin, reaching the base of the fin or nearly so13 (*Pinnichthys*)
- 13a. Lateral scale rows fewer than 37; Western Atlantic.....14
- 13b. Lateral scale rows more than 41; Western Atlantic and Eastern Pacific.....15
- 14a. First dorsal-fin spines I-II; belly scaled; lower jaw without well-developed canine teeth.....*Pinnichthys bilix* (Fig. S4E)
- 14b. First dorsal fin without notably elongate spines; belly naked; lower jaw with well-developed canine teeth.....*Pinnichthys prolata*
- 15a. First dorsal-fin spines I-III notably elongate; Eastern Pacific.....*Pinnichthys atrimela* comb. nov. (Fig. S4F)

- 15b. First dorsal fin without notably elongate spines; Western Atlantic.....16
- 16a. Second dorsal fin I,11; anal fin I,11; lateral scale rows 47–53..... *Pinnichthys saurimimica* gen. et sp. nov. (Figs 13 and 14)
- 16b. Second dorsal fin I,10; anal fin I,10; lateral scale rows 42–47..... *Pinnichthys aimoriensis* gen. et sp. nov. (Fig. 10)
- 17a. Anal fin I,9; Atlantic and Pacific.....18
- 17b. Anal fin I,8 or fewer; Atlantic.....23
- 18a. Second dorsal fin I,10–11; head not dorsoventrally depressed; Eastern Pacific and Western Atlantic.....19
- 18b. Second dorsal fin I,8–9; head strongly dorsoventrally depressed; Eastern Pacific.....22 (*Chriolepis*, in part)
- 19a. Pelvic fins extending to or beyond anus; 5th pelvic-fin ray short, 1/3 length of 4th ray or shorter; Western Atlantic.....*Varicus cephalocellatus* sp. nov. (Figs 27 and 28)
- 19b. Pelvic fins not reaching anus; 5th pelvic-fin ray at least 3/4 length of 4th ray; Eastern Pacific.....20 (*Chriolepis*, in part)
- 20a. Scales extend anteriorly to below origin of first dorsal fin.....*Chriolepis lepidota* (Fig. S1C)
- 20b. Scales reach no further forwards than below middle of first dorsal fin.....21
- 21a. Pectoral fin 19–21 (rarely 17 or 22); scales on body may extend forwards to below middle of first dorsal fin.....*Chriolepis dialepta* (Fig. S1B)
- 21b. Pectoral fin 13–16; scales on body usually restricted to caudal peduncle.....*Chriolepis minutilis* (Fig. S1D)
- 22a. Body with 7–8 vertical black bars on white background; caudal fin with 3–5 narrow vertical black bars spaced evenly over entire fin.....*Chriolepis zebra* (Figs S1G and S7D, E)
- 22b. Body with 5–6 vertical black bars; caudal fin with only 1 broad black band, over base of fin.....*Chriolepis cuneata* (Fig. S1A)
- 23a. Second dorsal fin I,7; 4th pelvic-fin ray extends to origin of last anal-fin ray or beyond.....*Paedovaricus imswe* (Fig. S5D)
- 23b. Second dorsal fin I,8–9; 4th pelvic-fin ray does not reach beyond base of 3rd anal-fin ray.....24 (*Varicus*, in part)
- 24a. Pelvic-fin rays 1–4 branched multiple times, with tips fused into spatulate, flattened, fleshy pads (Fig. 4A).....*Varicus adamsi* sp. nov. (Figs 23 and 24)
- 24b. Pelvic-fin rays 1–4 branched or unbranched, tips of any branched rays without wide, spatulate pads (Fig. 4B–F).....25
- 25a. Scales on side of body extend anteriorly only to below middle of second dorsal fin; pelvic-fin rays 1–4 branched to tips, no tips fused to form pointed fleshy pads (Fig. 4B or Fig. 4F).....26
- 25b. Scales on side of body extend anteriorly at least to below first dorsal fin; pelvic-fin rays 1–4 unbranched, or if branched, some branches usually with tips fused to form fleshy pads (Fig. 4C–E).....27
- 26a. Second dorsal fin I,8; tongue rounded; posterior 6–8 lateral scales on body cycloid or weakly ctenoid.....*Varicus benthonis* (Fig. S4A)
- 26b. Second dorsal fin I,9; tongue indented; posterior scales on body distinctly ctenoid.....*Varicus vespa* (Fig. S4D)
- 27a. Longest pelvic-fin ray extends posteriorly to base of 3rd ray of anal fin; second dorsal I,8.....*Varicus veliguttatus* sp. nov. (Fig. 37)
- 27b. Longest pelvic-fin ray extends to anus or to origin of anal fin but falls well short of 3rd ray; second dorsal I,8 or I,9.....28
- 28a. Side of body with 4 broad (nearly twice eye diameter) dark bars or large vertically oriented ovals; second dorsal fin I,9; anal fin I,8; pectoral fin long, longest ray extending to or beyond base of anal-fin ray 3–4.....*Varicus nigritus* sp. nov. (Fig. 34)
- 28b. Side of body without dark bars, or with 3 narrow (less than eye diameter) dark bars; second dorsal fin I,8–9; anal fin I,7–8; pectoral fin not extending posteriorly past origin of first anal-fin ray.....29
- 29a. Second dorsal fin I,8; anal fin I,7; lateral scale rows 18–19.....*Varicus marilynnae* (Fig. S4C)
- 29b. Second dorsal fin I,9; anal fin I,7 or I,8; lateral scale rows 22–27.....*Varicus bucca* (Fig. S4B; see note at beginning of key regarding *Varicus bucca* paratypes)
- 30a. Base of caudal fin with two modified scales with elongate cteni.....31
- 30b. Base of caudal fin without modified scales.....32
- 31a. Second dorsal fin I,9; anal fin I,7 or I,8; pelvic-fin rays 1–4 unbranched, or if branched, with fused tips bearing a single pointed fleshy pad (Fig. 4C,E).....*Varicus decorum* sp. nov. (Fig. 31)
- 31b. Second dorsal-fin I,10; anal fin I,9; pelvic-fin rays 1–4 branched.....*Chriolepis fisheri* (Fig. S5E, F)

- 32a. Anal fin typically I,6, rarely I,7; body; a broad dark diagonal bar through eye and onto preopercle, first dorsal fin with dark wide diagonal bar, second dorsal fin with two dark wide diagonal bars, a dark crescent shaped bar across pectoral fin and base of caudal fin. *Cryptopsilotris batrachodes* (Figs S5B and S7A,B)
- 32b. Anal fin typically I,7 or more; body not as above.33
- 33a. Pectoral fin distinctly bicoloured, with upper 1/3–1/2 bright yellow or brown in life, lower part white.34 (*Psilotris*, in part)
- 33b. Pectoral fin not bicoloured.35
- 34a. Body with 5 prominent golden-yellow narrow bars; caudal fin with 3–4 dark vertical bars; second dorsal fin I,9; anal fin I,8. *Psilotris laurae* sp. nov. (Fig. 20)
- 34b. Body uniformly covered with round yellow spots (spots with dark melanophores, sometimes appearing brown); second dorsal fin I,10 (rarely I,9); anal fin I,10 (rarely I,9); *Psilotris kaufmani* (Fig. S3D)
- 35a. Head with blunt, nearly vertical anterior profile; 5th pelvic-fin ray branched in adults; first dorsal-fin rays I,10–11; caudal fin with 3 oblique dark bars. *Carrigobius amblyrhynchus* (Fig. S5A)
- 35b. Head with pointed or gradually sloping anterior profile, 5th pelvic-fin ray unbranched in adults; caudal fin without three oblique dark bars.36 (*Psilotris*, in part)
- 36a. Jaw extending to or past a vertical through the middle of pupil; papillae rows 5*i* and 5*s* not connected (Fig. 3D–F); anal fin I,9. *Psilotris boehlkei* (Fig. S3B)
- 36b. Jaw not reaching a vertical through the middle of pupil; papillae rows 5*i* and 5*s* connected or not connected; anal in I,7–10.37
- 37a. Body and nape white with yellowish orange mottling and reticulations; anal fin I,7–8; papillae rows 5*i* and 5*s* connected as a continuous row (Fig. 18) *Psilotris laetarii* sp. nov. (Fig. 17)
- 37b. Body with dorsal saddles and vertical bars, some vertical bars being aligned with dorsal saddles and others being interspaced between them; anal fin I,7–10; papillae rows 5*i*5*s* connected or not connected.38
- 38a. Anal fin typically I,9–10 (infrequently I,8); pectoral-fin rays 16–17; papillae rows 5*i* and 5*s* connected as a single continuous row (Fig. 3C). *Psilotris celsa* (Fig. S3C)

- 38b. Anal fin I,7–8; pectoral-fin rays 15; papillae rows 5*i* and 5*s* not connected (Fig. 3D–F). *Psilotris alepis* (Fig. S3A)

ACKNOWLEDGEMENTS

This paper is dedicated to Heath Laetari and Thiony Simon, two young and promising scientists and divers who passed away tragically, doing what they loved. We thank Frank Pezold helping support this research during the initial stages of the project. A great many individuals helped us in examining, borrowing, x-raying, clearing and staining, and tissue sampling specimens from their respective collections. Specifically, we thank Cristina Castillo, Diane Pitassy, Jeffrey Williams and Sandra Raredon (USNM), Barbara Brown, Radford Arrindell and Bob Schelly (AMNH), Christine Thacker and Rick Feeney (LACM), Dave Catania (CAS), Rob Robins (UF), Mark Sabaj Pérez and Kyle Luckenbill (ANSP), Leo Smith (formerly FMNH, now KU), and Jean-Christophe Joyeux and Rafael Macieira (CIUFES). Gerry Allen, Jeffrey Williams, Raphael Macieira, Phil Hastings, Lloyd Findley, Alex Kerstitch, and William Smith-Vaniz graciously provided photographs. We sincerely thank Thiony Simon and Hudson Pinheiro for collecting and photographing the type series of *Pinnichthys aimoriensis* gen. et sp. nov. This project would not have been possible without the support of Adriaan ‘Dutch’ Schrier, Barry Brown and the entire staff of Substation Curacao, as well as the various research teams from Harbor Branch Oceanographic Institute that helped orchestrate the Johnson Sea Link submersible dives in the 1980–1990s. The project was funded in part by the American Museum of Natural History Lerner-Gray Award and the Smithsonian Peter Buck Fellowship to Luke Tornabene, and by the Smithsonian Schultz Fund to James Van Tassell. This is Ocean Heritage Foundation/Curacao Sea Aquarium/Substation Curacao contribution number OHF/CSA/SC #22.

REFERENCES

- Agorreta A, Rüber L. 2012.** A standardized reanalysis of molecular phylogenetic hypotheses of Gobiodei. *Systematics and Biodiversity* **10**: 375–390.
- Agorreta A, San Mauro D, Schliewen U, Van Tassell JL, Kovacic M, Zardoya R, Rueber L. 2013.** Molecular phylogenetics of Gobiodei and phylogenetic placement of European gobies. *Molecular Phylogenetics and Evolution* **69**: 619–633.
- Ahnelt H, Scattolin G. 2003.** The lateral line system of the blind goby, *Typhlogobius californiensis* Steindachner, 1879 (Teleostei: Gobiidae). *Annalen des Naturhistorisches Museums in Wien Serie B Botanik und Zoologie* **104B**: 11–25.

- Ahnelt H, Goschl J, Dawson MN, Jacobs DK. 2004.** Geographical variation in the cephalic lateral line canals of *Eucyclogobius newberryi* (Teleostei, Gobiidae) and its comparison with molecular phylogeography. *Folia-Zoologica* **53**: 385–398.
- Akihito P, Hayashi M, Yoshino T. 1988.** Suborder Gobioidaei. In: Masuda K, Amaoka C, Araga C, Uyeno Y, Yoshino T, eds. *The fishes of the Japanese Archipelago*, 2nd edn. Tokyo: Tokai University Press, 228–289.
- Bajpai S, Kapur VV. 2004.** Oldest known gobiids from a vastan lignite mine (early Eocene), Surat district, Guajarat. *Current Science* **87**: 433–435.
- Baldwin CC, Robertson DR. 2014.** A new *Liopropoma* sea bass (Serranidae, Epinephelinae, Liopropomini) from deep reefs off Curacao, southern Caribbean, with comments on depth distributions of western Atlantic liopropomins. *ZooKeys* **409**: 71–92.
- Birdsong R. 1975.** Osteology of *Microgobius signatus* Poey (Pisces: Gobiidae), with comments on other gobiid fishes. *Bulletin of the Florida State Museum, Biological Sciences* **19**: 135–187.
- Birdsong R, Murdy E, Pezold F. 1988.** A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* **42**: 174–214.
- Böhlke J. 1963.** The species of the west Atlantic gobioid fish genus *Psilotris*. *Notulae Naturae* **362**: 2–10.
- Böhlke J, Robins C. 1968.** Western Atlantic seven-spined gobies, with descriptions of ten new species and a new genus, and comments on Pacific relatives. *Proceedings of the Academy of Natural Sciences of Philadelphia* **120**: 45–174.
- Bouckaert R, Heled J, Kuhnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014.** BEAST 2: a software platform for bayesian evolutionary analysis. *Plos Computational Biology* **10**: e1003537. [Epub ahead of print].
- Eschmeyer WN (ed). 2015.** Catalog of fishes: Genera, Species, References. (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>). Electronic version accessed 20 July 2015.
- Findley LT. 1983.** A revision of the Easter Pacific species of the gobiid genus *Chriolepis* (Teleostei: Gobioidae). Unpublished PhD Dissertation, University of Arizona.
- Gierl C, Reichenbacher B, Gaudant J, Erpenbeck D, Pharisant A. 2013.** An extraordinary gobioid fish fossil from southern France. *PLoS One* **8**: e64117.
- Gill A, Mooi R. 2012.** Thalasseleotrididae, new family of marine gobioid fishes from New Zealand and temperate Australia, with a revised definition of its sister taxon, the Gobiidae (Teleostei: Acanthomorpha). *Zootaxa* **3266**: 41–52.
- Gilmore RG. 1979.** *Varicus marilynae*, a new gobiid fish from Florida. *Copeia* 126–128.
- Gilmore RG, Hastings PH, Kulezycski GR. 1981.** Crystalline rotenone as a selective fish toxin. *Florida Scientist* **44**: 193–203.
- Ginsburg I. 1938.** Eight new species of gobioid fishes from the American Pacific coast. *Allan Hancock Pacific Expedition 1932–40, Los Angeles* **2**: 109–121.
- Ginsburg I. 1953.** Ten new American gobioid fishes in the United States National Museum, including additions to a revision of *Gobionellus*. *Journal of the Washington Academy of Sciences* **43**: 18–26.
- Greenfield DW. 1981.** *Varicus imswe*, a new species of gobiid fish from Belize. *Copeia* 269–272.
- Greenfield DW. 1993.** New goby, *Psilotris boehlkei* (Pisces, Gobiidae), from the Western Atlantic, with a key to the species. *Copeia* 771–775.
- Greenfield DW, Findley LT, Johnson RK. 1993.** *Psilotris kaufmani* n.sp. (Pisces, Gobiidae), a 4th Western Atlantic species of *Psilotris*. *Copeia* 183–186.
- Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008.** GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.
- Hastings PA, Bortone S. 1981.** *Chriolepis vespa*, a new species of gobiid fish from the Northeastern Gulf of Mexico. *Proceedings of the Biological Society of Washington* **94**: 427–436.
- Hastings PA, Findley LT. 2013.** *Chriolepis bilix*, a new species of goby (Teleostei: Gobiidae) from deep waters of the western Atlantic. *Zootaxa* **3745**: 596–600.
- Hastings PA, Findley LT. 2015.** *Chriolepis prolata*, a new species of Atlantic goby (Teleostei: Gobiidae) from the North American continental shelf. *Zootaxa* **3904**: 589–595.
- Hoese DF, Reader S. 2001.** Revision of the eastern Pacific species of *Gobulus* (Perciformes: Gobiidae), with description of a new species. *Revista de Biología Tropical* **49**: 169–176.
- Joyeux JC, Van Tassell JL, Macieira RM. 2009.** *Barbulifer enigmaticus*, a new seven-spined goby (Pisces: Teleostei: Gobiidae) from the southwestern Atlantic. *Zootaxa* **2022**: 58–68.
- Kramer A, Van Tassell JL, Patzner RA. 2009.** A comparative study of two goby shrimp associations in the Caribbean Sea. *Symbiosis* **49**: 137–141.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012.** PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**: 1695–1701.
- Pagel M. 1999.** Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Patzner RA, Van Tassel JL, Kovacic M, Kapoor B. 2011.** *The biology of gobies*. Enfield, NH: Science Publishers.
- Polgar G, Sacchetti A, Galli P. 2010.** Differentiation and adaptive radiation of amphibious gobies (Gobiidae: Oxudercinae) in semi-terrestrial habitats. *Journal of Fish Biology* **77**: 1645–1664.
- R Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rambaut A, Drummond AJ. 2007.** Tracer Version 1.5. Available at <http://tree.bio.ed.ac.uk/software/tracer/>.
- Randall JE, Lobel PS, Kennedy CW. 2005.** Comparative ecology of the gobies *Nes longus* and *Ctenogobius saepepallens*, both symbiotic with the snapping shrimp *Alpheus floridanus*. *Environmental Biology of Fishes* **74**: 119–127.

- Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Robins C, Böhlke J. 1961.** A new gobioid fish from the Antilles and comments on *Ctenogobius fasciatus* and *C. curtisi*. *Copeia* **1961**: 46–50.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012.** MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.
- Rüber L, Van Tassell JL, Zardoya R. 2003.** Rapid speciation and ecological divergence in the American seven spined gobies (Gobiidae: Gobiosomatini) inferred from a molecular phylogeny. *Evolution* **57**: 1584–1598.
- Sabaj Pérez MH 2014.** *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference*. Version 5.0 (22 September 2014). Electronically accessible at <http://www.asih.org/>, Washington, DC: American Society of Ichthyologists and Herpetologists.
- Sanzo L. 1911.** Distribuzione delle papille cutanee (organi ciatiformi) e suo valore sistematico nei Gobi. *Mittheilungen aus der Zoologischen Station zu Neapel* **20**: 251–328.
- Smith DG, Baldwin CC. 1999.** *Psilotris amblyrhynchus*, a new seven-spined goby (Teleostei: Gobiidae) from Belize, with notes on settlement-stage larvae. *Proceedings of the Biological Society of Washington* **112**: 433–442.
- Smith-Vaniz WF, Jelks HL. 2014.** Marine and inland fishes of St. Croix, U. S. Virgin Islands: an annotated checklist. *Zootaxa* **3803**: 1–120.
- Thacker CE. 2009.** Phylogeny of GObioidei and placement within Acanthomorpha, with a new classification and investigation of diversification and character evolution. *Copeia* **2009**: 93–104.
- Thacker CE. 2015.** Biogeography of goby lineages (Gobiiformes: Gobiodei): origin, invasions and extinction throughout the Cenozoic. *Journal of Biogeography* **42**: 1615–1625.
- Thacker CE, Roje DM. 2011.** Phylogeny of Gobiidae and identification of gobiid lineages. *Systematics and Biodiversity* **9**: 329–347.
- Thacker CE, Satoh TP, Katayama E, Harrington RC, Eytan RI, Near TJ. 2015.** Molecular phylogeny of Percomorpha resolves Trichonotus as the sister lineage to Gobiodei (Teleostei: Gobiiformes) and confirms the polyphyly of Trachinoidei. *Molecular Phylogenetics and Evolution* **93**: 172–179.
- Tornabene L, Van Tassell JL. 2014.** Redescription of the goby genus *Gobiosoma* (Teleostei: Gobiidae: Gobiosomatini), with the synonymy of the genus *Enypnias*. *Journal of Natural History* **48**: 1413–1437.
- Tornabene L, Van Tassell JL, Robertson DR. 2012.** *Microgobius urraca* (Teleostei: Gobiidae), a new species of goby from the tropical eastern Pacific. *Zootaxa* **3447**: 41–55.
- Tornabene L, Ahmadi GN, Berumen ML, Smith DJ, Jompa J, Pezold F. 2013a.** Evolution of microhabitat association and morphology in a diverse group of cryptobenthic coral reef fishes (Teleostei: Gobiidae: *Eviota*). *Molecular Phylogenetics and Evolution* **66**: 391–400.
- Tornabene L, Chen YJ, Pezold F. 2013b.** Gobies are deeply divided: phylogenetic evidence from nuclear DNA (Teleostei: Gobiodei: Gobiidae). *Systematics and Biodiversity* **11**: 345–361.
- Van Tassell JL. 2011.** Gobiiformes of the Americas. In: Patzner RA, Van Tassell JL, Kovacic M, Kapoor B, eds. *The biology of gobies*. Science Publishers: Enfield, NH, 139–176.
- Van Tassell JL, Tornabene L, Collin P. 2012.** Review of the western Atlantic species of *Bollmannia* (Teleostei: Gobiidae: Gobiosomatini) with the description of a new allied genus and species. *Aqua, International Journal of Ichthyology* **18**: 61–94.
- Victor B. 2010.** The Redcheek Paradox: the mismatch between genetic and phenotypic divergence among deeply-divided mtDNA lineages in a coral-reef goby, with the description of two new cryptic species from the Caribbean Sea. *Journal of the Ocean Science Foundation* **3**: 1–16.
- Victor BC. 2014.** Three new endemic cryptic species revealed by DNA barcoding of the gobies of the Cayman Islands (Teleostei: Gobiidae). *Journal of the Ocean Science Foundation* **15**: 25–60.
- Wilgenbusch JC, Warren DL, Swofford DL 2004.** AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. <http://ceb.csit.fsu.edu/awty>.
- Williams J, Gilbert C. 1983.** Additional information on the gobiid fish *Varicus imswe*, with comments on the nominal species of *Varicus*. *Northeast Gulf Science* **6**: 185–189.
- Yamada T, Sugiyama T, Tamaki N, Kawakita A, Kato M. 2009.** Adaptive radiation of gobies in the interstitial habitats of gravel beaches accompanied by body elongation and excessive vertebral segmentation. *BMC Evolutionary Biology* **9**, 45. [Epub ahead of print].
- Yang ZH, Kumar S, Nei M. 1995.** A new method of inference of ancestral nucleotide and amino-acid-sequences. *Genetics* **141**: 1641–1650.

SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article.

Figure S1. Species of *Chriolepis*.

Figure S2. Species of *Gobulus*.

Figure S3. Species of *Psilotris*.

Figure S4. Species of *Varicus* and *Pinnichthys*.

Figure S5. The monotypic genera and incertae sedis species of the Nes subgroup in the Atlantic Ocean.

Figure S6. The monotypic genera of the Nes subgroup, Pacific Ocean species.

Figure S7. Select live photographs of Nes subgroup species.

Table S1. All material examined.

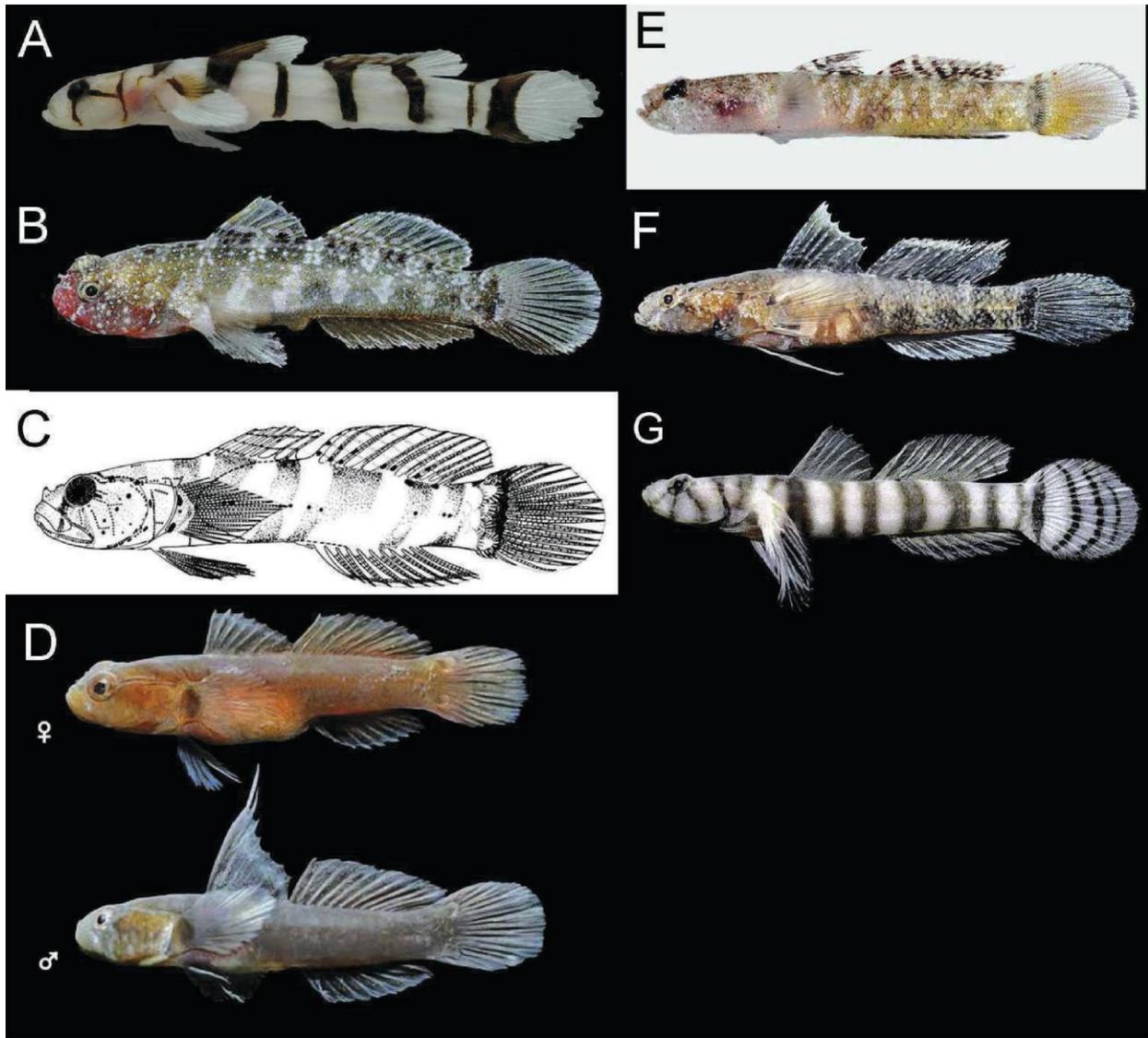


Figure S1. Species of *Chriolepis*. A) *Chriolepis cuneata*, AMNH 256651; B) *Chriolepis dialepta*, AMNH 257515; C) *Chriolepis lepidota*, drawing by Lloyd Findley from Findley (1975); D) *Chriolepis minutilla*, female above, male below; E) *Chriolepis roosevelti*; F) *Chriolepis semisquamata*; G) *Chriolepis zebra*. Photos or illustrations by James Van Tassell (A, E), D. Ross Robertson (B), Lloyd Findley (from Findley 1975; C), and Gerry Allen (D, F, G).

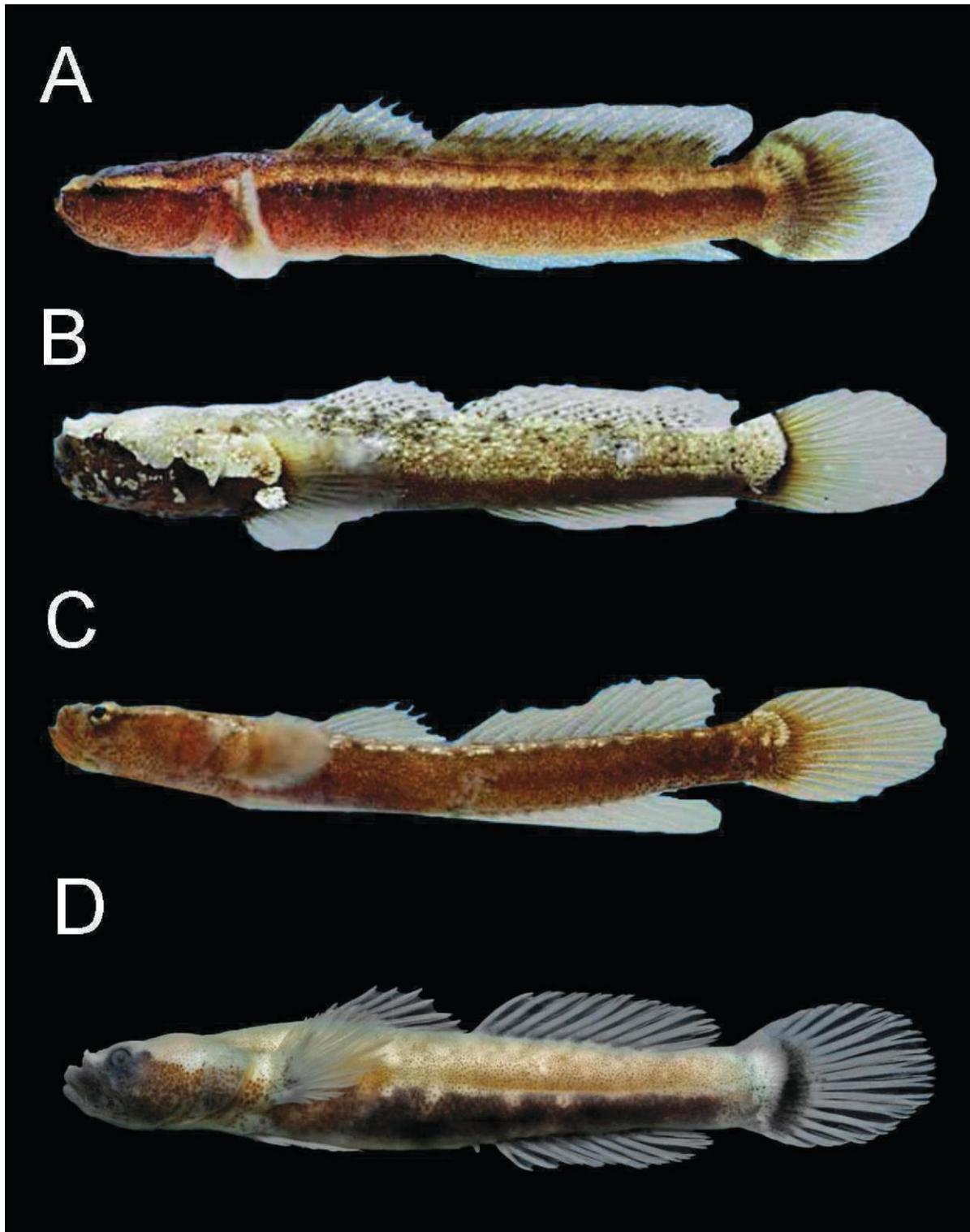


Figure S2. Species of *Gobulus*. A) *Gobulus birdsong*, AMNH 233163; B) *Gobulus crescentalis*, AMNH 256713; C) *Gobulus hancocki*, USNM 322696; D) *Gobulus myersi*, CIUFES 2589. Photos by Ross Robertson (A, B), James Van Tassell (C), and Raphael Macieira (D).



B



C



D



Figure S3. Species of *Psilotris*. A) *Psilotris alepis*, UF collection; B) *Psilotris boehlkei*, USNM 404966; C) *Psilotris celsa*, USNM 411968; D) *Psilotris kaufmani*, AMNH 243300. Photos by L. A. Rocha (A), James Van Tassell (B, D), Jeff Williams (C).

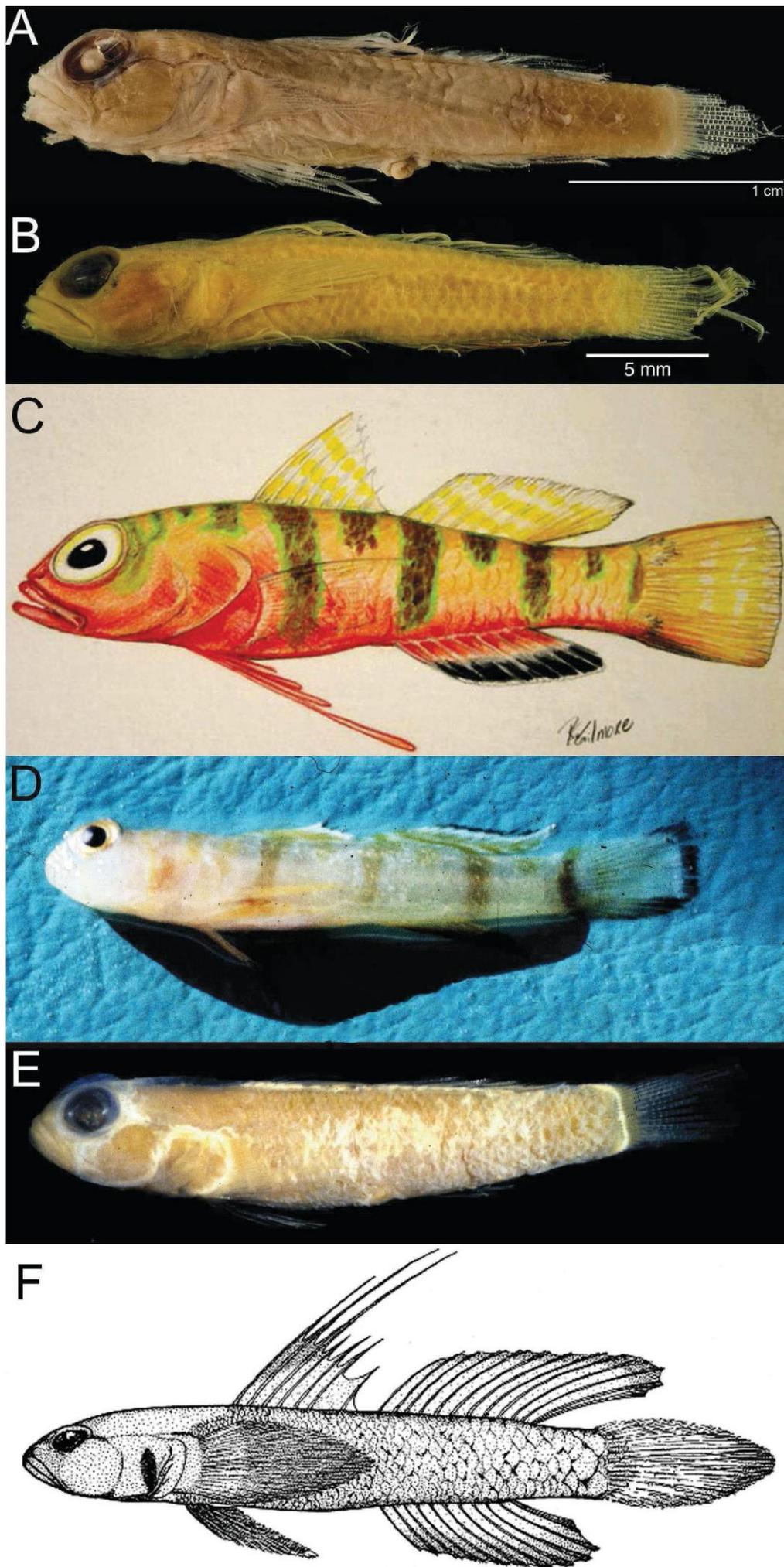


Figure S4. Species of *Varicus* and *Pinnichthys*. A) *Varicus benthonis*, holotype, USNM 47641; B) *Varicus bucca*, holotype, ANSP 93083; C) *Varicus marilynae*, holotype, USNM 218406; D) *Varicus vespa*, paratype, USNM 221524; E) *Pinnichthys bilix*, holotype, USNM 199058; F) *Pinnichthys atrimela*, holotype, LACM 32264-10. Photos and illustrations by Sandra Raredon (A), Kyle R. Luckenbill (B), R. Grant Gilmore (C), the crew of the R/V *BELLOWS* (D), Phil Hastings (E), and William Bussing (F) from Bussing (1997).

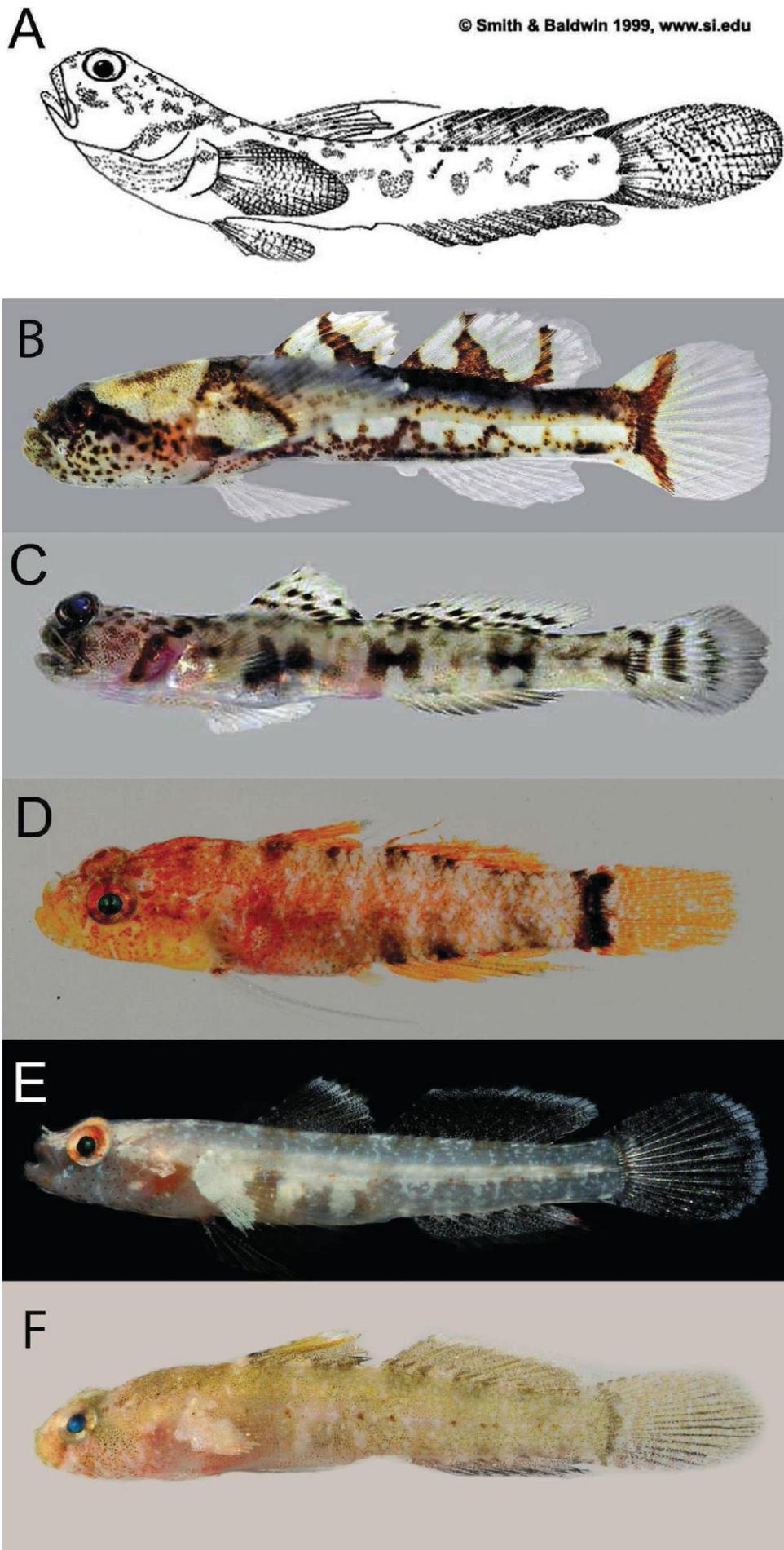


Figure S5. The monotypic genera and *incertae sedis* species of the *Nes* subgroup in the Atlantic Ocean. A) *Carrigobius amblyrhynchus*, holotype, USNM 321019; B) *Cryptopsilotris batrachodes*, AMNH 248374; C) *Nes longus*; D) *Paedovaricus imswe*, USNM 416106; E) *Chriolepis cf. fisheri*, *incertae sedis*, Brazil, CIUFES 2564; F) *Chriolepis cf. fisheri*, *incertae sedis*, Belize, 20 mm SL, USNM 415296. Photos or illustrations by David G. Smith and Carole Baldwin (from Smith & Baldwin 1999), Ross Robertson (B,C), Carole Baldwin (D, F), and Raphael Macieira (E).



Figure S6. The monotypic genera of the *Nes* subgroup, Pacific Ocean species. A) *Eleotrica cableae*; B) *Gymneleotris seminuda*. Photos by Ross Robertson (A) and Gerry Allen (B).

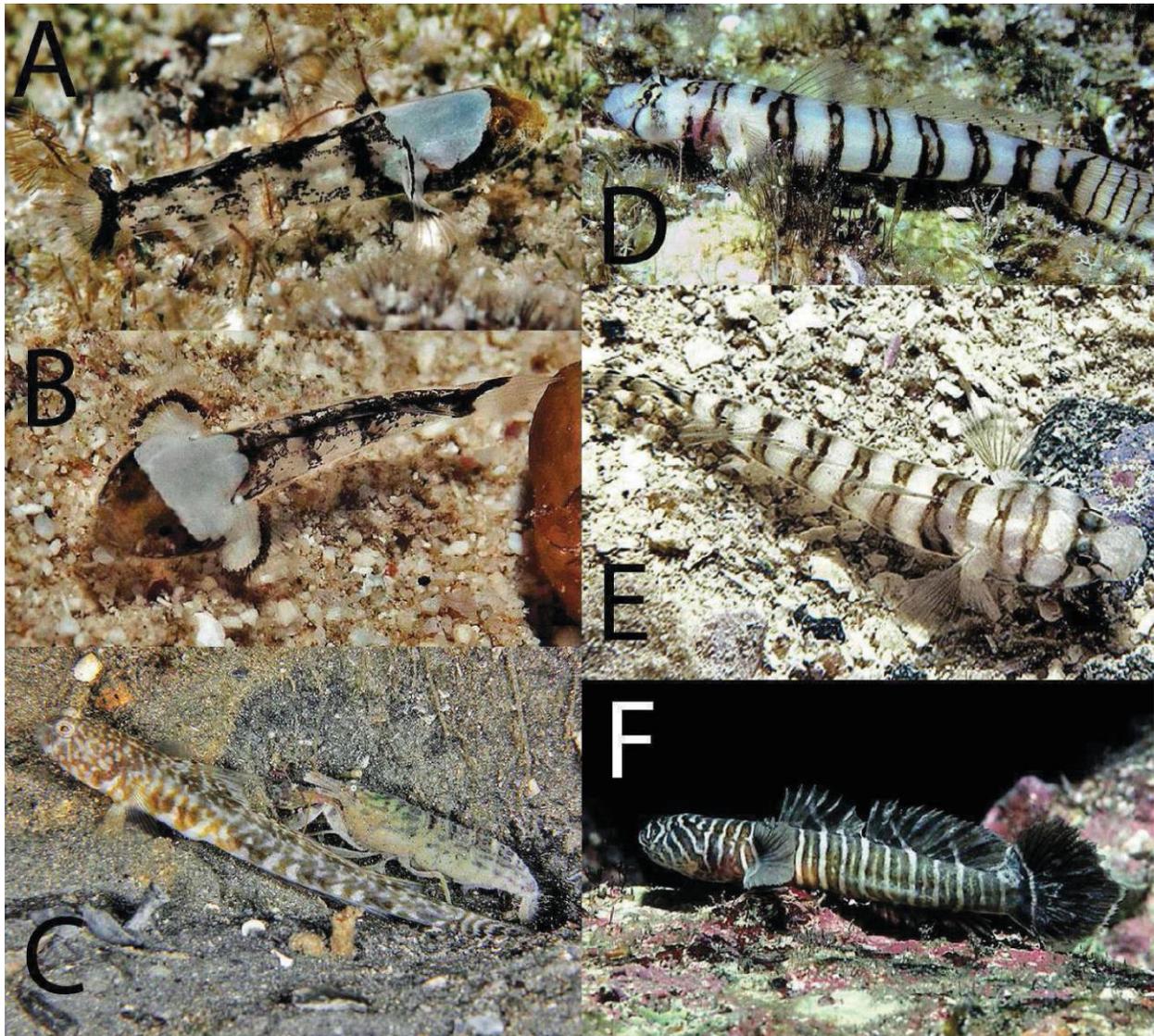


Figure S7. Select live photographs of *Nes* subgroup species; A, B) *Cryptopsilotris batrachodes*, photos by Everet Turner; C) *Nes longus* and alpheid snapping shrimp; D) *Chriolepis zebra*, photo by Ross Robertson; E) *Chriolepis zebra*, photo by Lloyd Findley; F) *Gymneleotris seminuda*, photo by Alex Kerstitch.

Catalog number	Genus	Species	Type status	Osteological data	Tissue label*	Notes on identification*
AMNH 256651	<i>Chriolepis</i>	<i>cuneata</i>			Ccun	
LACM 32499-47	<i>Chriolepis</i>	<i>cuneata</i>	paratype	radiograph		
AMNH 257515	<i>Chriolepis</i>	<i>dialepta</i>			Cdia	
LACM 32254-34	<i>Chriolepis</i>	<i>dialepta</i>		cleared and		
LACM 32283-25	<i>Chriolepis</i>	<i>dialepta</i>	paratype			
CAS 37262	<i>Chriolepis</i>	<i>fisheri</i>	holotype	radiograph		
AMNH 30191	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,11(I,12?)/I,10; AP=1; May be <i>C. fisheri</i> ; Bahamas
CIUFES 2564	<i>Chriolepis</i>	<i>cf. fisheri</i>			2564	D2/A = I,12/I,11; AP=?; May be <i>C. fisheri</i> ; Brazil, Fernando de Noronha
UF 100857	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,9/I,8; AP=2; May be same as <i>Psilotris sp.</i> in phylogeny; Cayman Islands
UF 100858	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,9/I,8; AP=2; May be same as <i>Psilotris sp.</i> in phylogeny; Cayman Islands
UF 100859	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,10/?; AP=1; May be <i>C. fisheri</i> ; Cayman Islands
UF 100860	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,11/I,10; AP=1; May be <i>C. fisheri</i> ; Cayman Islands
UF 13498	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,10-11/I,9-10; AP=1; May be <i>C. fisheri</i> ; Bahamas
UF 13726	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,10/?; AP=1; May be <i>C. fisheri</i> ; Bahamas
UF 13934	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,10-11/I,9-10; AP=1; May be <i>C. fisheri</i> ; Bahamas
UF 164707	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph		D2/A = I,9/I,8, Smith-Vaniz & Jelks (2014) say I,9; AP=2; May be same as <i>Psilotris</i>
UF 16667	<i>Chriolepis</i>	<i>cf. fisheri</i>				
UF 17643	<i>Chriolepis</i>	<i>cf. fisheri</i>				
USNM 415296	<i>Chriolepis</i>	<i>cf. fisheri</i>			BLZ 8270	Posterior half of specimen missing; D2/A(from photo) = I,10; may be <i>C. fisheri</i> ; Belize
USNM 415297	<i>Chriolepis</i>	<i>cf. fisheri</i>			BLZ 8271	Posterior half of specimen missing; genetic match to USNM 415297; may be <i>C. fisheri</i> ;
USNM 416079	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph	BLZ 7329	D2/A (from photo) \approx I,10/I,9; photo resembles USNM 415296 and 415297; may be <i>C.</i>
USNM 420302	<i>Chriolepis</i>	<i>cf. fisheri</i>		radiograph	BLZ 5403	D2/A (from radiograph) \approx I,10/?; AP=1; may be <i>C. fisheri</i> ; Belize
USNM 211456	<i>Chriolepis</i>	<i>lepidotus</i>	holotype	radiograph		
USNM 211457	<i>Chriolepis</i>	<i>lepidotus</i>	paratype			
CAS 30966	<i>Chriolepis</i>	<i>minutillus</i>				
LACM 20148	<i>Chriolepis</i>	<i>minutillus</i>		C&S		
USNM 322595	<i>Chriolepis</i>	<i>minutillus</i>		radiograph		
USNM 48261	<i>Chriolepis</i>	<i>minutillus</i>	holotype	radiograph		
AMNH 256897	<i>Chriolepis</i>	<i>cf. minutillus</i>				May be undescribed species from Findley (1983); Pacific Mexico
AMNH 87272	<i>Chriolepis</i>	<i>prolata</i>	paratype			
USNM 230001	<i>Chriolepis</i>	<i>prolata</i>	holotype			
FMNH 101362	<i>Chriolepis</i>	<i>roosevelti</i>				
FMNH 83964	<i>Chriolepis</i>	<i>roosevelti</i>				
FMNH 96484	<i>Chriolepis</i>	<i>roosevelti</i>				
FMNH 96487	<i>Chriolepis</i>	<i>roosevelti</i>				
UF 149179	<i>Chriolepis</i>	<i>roosevelti</i>				
USNM 107108	<i>Chriolepis</i>	<i>roosevelti</i>	paratype	radiograph		
USNM 108139	<i>Chriolepis</i>	<i>roosevelti</i>	holotype	radiograph		
USNM 346493	<i>Chriolepis</i>	<i>roosevelti</i>				
USNM 387961	<i>Chriolepis</i>	<i>roosevelti</i>				
USNM 388585	<i>Chriolepis</i>	<i>roosevelti</i>				
USNM 404054	<i>Chriolepis</i>	<i>roosevelti</i>				
USNM 404965	<i>Chriolepis</i>	<i>roosevelti</i>				

USNM 412954	<i>Chriolepis</i>	<i>roosevelti</i>			TCI 9419
USNM 415215	<i>Chriolepis</i>	<i>roosevelti</i>			BLZ 8065
ANSP 111201	<i>Chriolepis</i>	<i>semisquamatum</i>		cleared and	
ANSP 111201	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 214509	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 322594	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 322622	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 322623	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 322624	<i>Chriolepis</i>	<i>semisquamatum</i>			
USNM 123232	<i>Chriolepis</i>	<i>tagus</i>	holotype	radiograph	
AMNH 28802	<i>Cryptopsilotri</i>	<i>batrachodes</i>		cleared and	
AMNH 29052	<i>Cryptopsilotri</i>	<i>batrachodes</i>			
AMNH 29067	<i>Cryptopsilotri</i>	<i>batrachodes</i>			
ANSP 191896	<i>Cryptopsilotri</i>	<i>batrachodes</i>			Pbat
ANSP 98418	<i>Cryptopsilotri</i>	<i>batrachodes</i>	paratype	cleared and	
USNM 321048	<i>Cryptopsilotri</i>	<i>batrachodes</i>		cleared and	
USNM 404139	<i>Cryptopsilotri</i>	<i>batrachodes</i>		radiograph	
USNM 413099	<i>Cryptopsilotri</i>	<i>batrachodes</i>			TCI 9351
USNM 413099	<i>Cryptopsilotri</i>	<i>batrachodes</i>		radiograph	
USNM 415040	<i>Cryptopsilotri</i>	<i>batrachodes</i>			BLZ 7270
USNM 419356	<i>Cryptopsilotri</i>	<i>batrachodes</i>			BLZ 5160
CAS 23723	<i>Eleotrica</i>	<i>cableae</i>		cleared and	
CAS 31203	<i>Eleotrica</i>	<i>cableae</i>			
USNM 278977	<i>Eleotrica</i>	<i>cableae</i>		cleared and	
USNM 65517	<i>Eleotrica</i>	<i>cableae</i>	holotype	radiograph	
AMNH 233163	<i>Gobulus</i>	<i>birdsongi</i>		radiograph	Gbir
LACM 32549-61	<i>Gobulus</i>	<i>creescentalis</i>			
LACM 32562-49	<i>Gobulus</i>	<i>creescentalis</i>		cleared and	
USNM 48258	<i>Gobulus</i>	<i>creescentalis</i>			
CAS 118449	<i>Gobulus</i>	<i>hancocki</i>			
LACM 31579-36	<i>Gobulus</i>	<i>hancocki</i>		cleared and	
AMNH 250453	<i>Gobulus</i>	<i>myersi</i>		radiograph	Gmye
CIUFES 2589	<i>Gobulus</i>	<i>myersi</i>			2589
AMNH 256714	<i>Gymneleotris</i>	<i>seminuda</i>		cleared and	
AMNH 258720	<i>Gymneleotris</i>	<i>seminuda</i>			
AMNH 259330	<i>Gymneleotris</i>	<i>seminuda</i>			Gsem
ANSP 134939	<i>Gymneleotris</i>	<i>seminuda</i>		cleared and	
CAS 157881	<i>Gymneleotris</i>	<i>seminuda</i>			
uncatalogued	<i>Gymneleotris</i>	<i>seminuda</i>			
AMNH 256944	<i>Nes</i>	<i>longus</i>			Nes
ANSP 133224	<i>Nes</i>	<i>longus</i>		cleared and	
ANSP 147247	<i>Nes</i>	<i>longus</i>			
USNM 416042	<i>Nes</i>	<i>longus</i>			BLZ 7428
USNM 419365	<i>Nes</i>	<i>longus</i>			BLZ 5174

USNM 328243	<i>Paedovaricus</i>	<i>imswe</i>		cleared and	
USNM 416106	<i>Paedovaricus</i>	<i>imswe</i>			BLZ 7805
USNM 420303	<i>Paedovaricus</i>	<i>imswe</i>			BLZ 5402
AMNH 265020	<i>Pinnichthys</i>	<i>aimoriensis</i>	paratype	radiograph	
CIUFES 2414	<i>Pinnichthys</i>	<i>aimoriensis</i>	holotype	radiograph	VspB
AMNH 265021	<i>Pinnichthys</i>	<i>aimoriensis</i>	paratype	cleared and	
LACM 32264-10	<i>Pinnichthys</i>	<i>atrimela</i>	holotype	radiograph	
USNM 199058	<i>Pinnichthys</i>	<i>bilix</i>	holotype	radiograph	
AMNH 87272	<i>Pinnichthys</i>	<i>prolata</i>	paratype	radiograph	
USNM 230001	<i>Pinnichthys</i>	<i>prolata</i>	holotype	radiograph	
USNM 427228	<i>Pinnichthys</i>	<i>sauremimica</i>	holotype	radiograph	
UF 158491	<i>Psilotris</i>	<i>alepis</i>			
UF 158493	<i>Psilotris</i>	<i>alepis</i>			
UF 12343	<i>Psilotris</i>	<i>alepis</i>		radiograph	
USNM 123231	<i>Psilotris</i>	<i>alepis</i>	holotype	radiograph	
USNM 192402	<i>Psilotris</i>	<i>alepis</i>		radiograph	
USNM 197515	<i>Psilotris</i>	<i>alepis</i>		radiograph	
USNM 321019	<i>Psilotris</i>	<i>amblyrhynchus</i>	holotype	radiograph	
USNM 350087	<i>Psilotris</i>	<i>amblyrhynchus</i>		cleared and stained	
USNM 350094	<i>Psilotris</i>	<i>amblyrhynchus</i>		cleared and	
USNM 415039	<i>Psilotris</i>	<i>amblyrhynchus</i>			BLZ 7261
ANSP 124619	<i>Psilotris</i>	<i>boehlkei</i>	paratype	cleared and	
UF 160122	<i>Psilotris</i>	<i>boehlkei</i>		radiograph	
USNM 404966	<i>Psilotris</i>	<i>boehlkei</i>		radiograph	
AMNH 31210	<i>Psilotris</i>	<i>celsa</i>			
ANSP 98431	<i>Psilotris</i>	<i>celsa</i>	paratype	cleared and	
UF 160124	<i>Psilotris</i>	<i>celsa</i>			
UF 205393	<i>Psilotris</i>	<i>celsa</i>	paratype		
UF 212926	<i>Psilotris</i>	<i>celsa</i>			
UF 234400	<i>Psilotris</i>	<i>celsa</i>			
UF 24889	<i>Psilotris</i>	<i>celsa</i>			
UF 25815	<i>Psilotris</i>	<i>celsa</i>			
University of Alabama	<i>Psilotris</i>	<i>celsa</i>			
University of Alabama	<i>Psilotris</i>	<i>celsa</i>			
USNM 360607	<i>Psilotris</i>	<i>celsa</i>			
USNM 411968	<i>Psilotris</i>	<i>celsa</i>			TCI 9128
USNM 98429	<i>Psilotris</i>	<i>celsa</i>			
AMNH 21298	<i>Psilotris</i>	<i>cf. alepis</i>			
USNM 427234	<i>Psilotris</i>	<i>boehlkei</i>		radiograph	
AMNH 243300	<i>Psilotris</i>	<i>kaufmani</i>		radiograph	Pkau
UF 21336	<i>Psilotris</i>	<i>kaufmani</i>	paratype		
USNM 426779	<i>Psilotris</i>	<i>laurae</i>	holotype	radiograph	CUR 13186
AMNH 257973	<i>Psilotris</i>	<i>laetarii</i>	paratype	cleared and	
AMNH 257974	<i>Psilotris</i>	<i>laetarii</i>	paratype	radiograph	PFL

AMNH 261272	<i>Psilotris</i>	<i>laetarii</i>	holotype	radiograph	
AMNH 264217	<i>Psilotris</i>	<i>laetarii</i>	paratype	radiograph	
ANSP 191897	<i>Psilotris</i>	<i>sp.</i>			Pspb1, Pspb2D2A=I,9/I,8; AP=2; body scales absent but 2 basicaudal scales present.
CIUFES 1586	<i>Psilotris</i>	<i>sp. juvenile</i>			1586
UF 234392	<i>Robinsichthys</i>	<i>arrowsmithensis</i>	paratype	cleared and	
UF 234393	<i>Robinsichthys</i>	<i>arrowsmithensis</i>	paratype		
UF 172648	<i>Varicus</i>	<i>sp.</i>		radiograph	D2/A = I,10/I,8; AP= 2, but haemal spine is on vertebra 13 instead of 12, total vertebrae 27; pelvic rays 1-4 branched; 10-12 lateral scale rows extending to beneath posterior 1/3 of D2; tentatively referred to <i>C. vespa</i> (= <i>V. vespa</i>) by Hasting and Bortone (1981), we disagree. May be variant of <i>V. cephalocellatus</i> or new species.
USNM 220985	<i>Varicus</i>	<i>adamsi</i>		radiograph	
USNM 427225	<i>Varicus</i>	<i>adamsi</i>	paratype	radiograph	
USNM 427226	<i>Varicus</i>	<i>adamsi</i>	holotype	radiograph	
USNM 47641	<i>Varicus</i>	<i>benthonis</i>	holotype	radiograph	
ANSP 93083	<i>Varicus</i>	<i>bucca</i>	holotype	radiograph	
UF 213873	<i>Varicus</i>	<i>bucca</i>			
USNM 199060	<i>Varicus</i>	<i>bucca</i>		radiograph	
USNM 427229	<i>Varicus</i>	<i>bucca</i>		radiograph	
USNM 427230	<i>Varicus</i>	<i>bucca</i>		radiograph	
USNM 427231	<i>Varicus</i>	<i>bucca</i>		radiograph	
USNM 426736	<i>Varicus</i>	<i>cephalocellatus</i>	paratype	radiograph	CUR13175
USNM 426788	<i>Varicus</i>	<i>cephalocellatus</i>	paratype	radiograph	CUR13185
USNM 427232	<i>Varicus</i>	<i>cephalocellatus</i>	holotype	radiograph	
USNM 427227	<i>Varicus</i>	<i>cephalocellatus</i>	paratype	radiograph	
USNM 427227	<i>Varicus</i>	<i>cephalocellatus</i>	paratype	radiograph	
ANSP 151291	<i>Varicus</i>	<i>sp.</i>		radiograph	Specimen in poor condition; Bermuda
USNM 406314	<i>Varicus</i>	<i>decorum</i>	holotype	radiograph	CUR 11314
USNM 426692	<i>Varicus</i>	<i>decorum</i>	paratype	radiograph	CUR 13247
UF 24757	<i>Varicus</i>	<i>marilynae</i>	paratype	radiograph	
USNM 218406	<i>Varicus</i>	<i>marilynae</i>	holotype	radiograph	
USNM 427233	<i>Varicus</i>	<i>nigritus</i>	holotype	radiograph	
USNM 179154	<i>Varicus</i>	<i>sp.</i>		radiograph	D2/A=I,10/I,9; AP=1; pectoral and pelvic fins destroyed; papillae rows 5i and 5s just short of being complete; 10 lateral scale rows; may be <i>V. cephalocellatus</i> ; Caribbean
FMNH 65608	<i>Varicus</i>	<i>sp.</i>	paratype of <i>V. bucca</i>		D2/A=I,8/I,7; AP=1; 27 lateral scale rows; may be <i>V. veliguttatus</i>
UF 207114	<i>Varicus</i>	<i>sp.</i>	paratype of <i>V. bucca</i>	cleared and stained	D2/A=I,8/I,7; AP=2, 28 total vertebrae (11+17); 27 lateral scale rows; may be <i>V. veliguttatus</i> ; Puerto Rico
USNM 143022	<i>Varicus</i>	<i>sp.</i>	paratype of <i>V. bucca</i>	radiograph	D2/A = I,9/I,8; AP=1; pectoral fins broken; pelvic fins partly broken, rays that are intact unbranched without fleshy tips; may be <i>V. bucca</i> or <i>V. nigritus</i> ; Cuba
USNM 214518	<i>Varicus</i>	<i>sp.</i>			D2/A = I,9/I,7?; pectoral and pelvic fins destroyed; ≈27 lateral scales (pockets); could be <i>V. bucca</i> , <i>V. adamsi</i> , <i>V. vespa</i> or <i>V. nigritus</i> ; Caribbean (Oregon Station 4931)
USNM 220983	<i>Varicus</i>	<i>sp.</i>		radiograph	Specimen in poor condition, broken in half; unable to identify; Montserrat

USNM 220984	<i>Varicus</i>	<i>sp.</i>		radiograph		D2/A = I,9/I,8; AP=1; pelvic rays 1-4 with fleshy tips, ray 4 branched once internally and refused; pectoral fin destroyed; 26 lateral scales; could be <i>V. bucca</i> or <i>V. nigrinus</i> ; Colombia (Isla de Providencia)
USNM 438231	<i>Varicus</i>	<i>sp.</i>		radiograph		D2/A=I,10/I,8; AP=2 but haemal spine is on vertebra 13 instead of 12, total vertebrae 27; all pelvic fin-rays unbranched and not fleshy; ≈23 lateral scale rows (only pockets remain); could be <i>V. bucca</i> or <i>V. nigrinus</i> , pectoral fin extends above anal-fin origin;
USNM 414960	<i>Varicus</i>	<i>cf. bucca</i>		radiograph	CUR 12021	D2/A (from photo) = I,9/I,8; all pelvic-fin rays unbranched and not fleshy; specimen in poor condition; photograph shows no black bands as in <i>V. nigrinus</i> ; Smithsonian DNA barcoding suggests distinct from all species sequenced here, four genes here failed to sequence; may be <i>V. bucca</i> ; Curacao
USNM 430025	<i>Varicus</i>	<i>sp. A</i>		radiograph	CUR13313	D2/A = I,9/at least I,6, anal fin damaged; AP=1; pelvic-fin rays may be branched; specimen in poor condition; scales absent; most likely undescribed species; Curacao
USNM 342859	<i>Varicus</i>	<i>sp.</i>		cleared and stained		D2/A = I,8/I,7; pelvic fin broken; AP=1; may be <i>V. benthonis</i> , <i>V. marylinae</i> or <i>V. veliguttatus</i> ; locality as "Vessel Eastward" no other data
USNM 220982	<i>Varicus</i>	<i>veliguttatus</i>	paratype	radiograph		
USNM 406372	<i>Varicus</i>	<i>veliguttatus</i>	paratype	radiograph	CUR 11372	
USNM 427224	<i>Varicus</i>	<i>veliguttatus</i>	holotype	radiograph		
USNM 431697	<i>Varicus</i>	<i>veliguttatus</i>	paratype	radiograph	CUR 14089	
UF 28037	<i>Chriolepis</i>	<i>vespa</i>	paratype			
UF 28038	<i>Chriolepis</i>	<i>vespa</i>	paratype			
UF 72110	<i>Chriolepis</i>	<i>vespa</i>		cleared and		
UF 72156	<i>Chriolepis</i>	<i>vespa</i>				
UF 72163	<i>Chriolepis</i>	<i>vespa</i>		cleared and		
USNM 221523	<i>Chriolepis</i>	<i>vespa</i>	holotype	radiograph		
USNM 221524	<i>Chriolepis</i>	<i>vespa</i>	paratype	radiograph		
AMNH 259394	<i>Chriolepis</i>	<i>zebra</i>			Czeb	
CAS 31001	<i>Chriolepis</i>	<i>zebra</i>				
LACM 9598-5	<i>Chriolepis</i>	<i>zebra</i>		cleared and		
SIO 65-186	<i>Chriolepis</i>	<i>zebra</i>				
USNM 322597	<i>Chriolepis</i>	<i>zebra</i>				
USNM 322599	<i>Chriolepis</i>	<i>zebra</i>				
USNM 322600	<i>Chriolepis</i>	<i>zebra</i>				