



## An overview of the dwarfgobies, the second most speciose coral-reef fish genus (Teleostei: Gobiidae: *Eviota*)

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### Abstract

An overview of the dwarfgobies in the genus *Eviota* is presented. Background information is provided on the taxonomic history, systematics, reproduction, ecology, geographic distribution, genetic studies, and speciation of dwarfgobies. Future research directions are discussed. A list of all valid species to date is included, as well as tables with species included in various cephalic sensory-canal pore groupings.

**Key words:** review, taxonomy, systematics, ichthyology, ecology, behavior, reproduction, evolution, coloration, Indo-Pacific Ocean, gobies.

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### Introduction

The gobiid genus *Eviota*, known as dwarfgobies, is a very speciose genus of teleost fishes, with 113 valid described species occurring throughout the Indo-Pacific Ocean (Table 1), and many more awaiting description. It is the fifth most speciose saltwater teleost genus, and second only to the 129 species in the eel genus *Gymnothorax* in the coral-reef ecosystem (Eschmeyer *et al.* 2017). Information on the systematics and biology of the species of the genus is scattered in the literature, often in obscure references, and, other than the taxonomic key to all the species in the genus (Greenfield & Winterbottom 2016), no recent overview of the genus exists. It is the purpose of this review to draw this information together for more easy access. This paper is not intended to be an in-depth discussion of the various topics, but rather to provide an overview of the topics and key references for further investigation.

The genus *Eviota* was described by Jenkins (1903) based on *Eviota epiphanes* from Hawai‘i. No etymology was given, however Christopher Scharpt (pers. comm. 2017) has suggested that *Eviota* is the Latinization of *eu*, meaning true, and *iota* meaning anything very small; the combination would suggest “truly very small”. Jenkins said *Eviota* was “the smallest vertebrate that has to this time been described”, making this interpretation plausible. The species are tiny (< 35.7 mm SL, 43% of the species are less than 18.0 mm SL, and 27% less than 15.0 mm SL), with some maturing at only 8.9 mm SL (Lachner & Karnella 1980: 99).

Two species belonging to *Eviota* had been described before Jenkins erected the genus in 1903, and he included them in the new genus. The first was described as *Eleotris prasina* Klunzinger, 1871, from the Red Sea, and the second as *Asterropteryx abax* Jordan & Snyder, 1901, from Japan. From 1903 up to 1978, the number of valid described species worldwide increased to 19. In 1978, Lachner & Karnella published a paper on the species of *Eviota* in the Red Sea in which they included descriptions of three new species, raising the total number of species to 22. Two years later, their landmark review of the genus added 8 new species (Lachner & Karnella 1980), and, in Karnella & Lachner (1981), they described three additional new species. In their final collaboration (Jewett [née Karnella] & Lachner 1983), they added 7 more species, which brought the total number of *Eviota* species to 40. These important papers laid the groundwork for all future work on the genus, as they established both standardized methodological procedures and terminology.

For the next 16 years, no new species were added, until Greenfield & Randall’s paper in 1999 describing two new species from the Hawaiian Islands. Up until then, *Eviota* species descriptions had utilized only drawings or black-and-white photographs of specimens, but the situation soon changed. Between 2001 and 2008, 8 more *Eviota* species were described by various authors, raising the total to 50; notably, some of those papers included color photographs of fresh specimens and three included color photographs of live individuals. This transition in the manner of illustration initiated a change in *Eviota* systematics in that advances in underwater photography, particularly digital photography, and the affordability of color photographic printing now allowed for better and more detailed descriptions as well as comparisons of individuals from different localities. For example, the availability of live color descriptions revealed that some species that had been described only from preserved material actually were composed of two or more species, often with restricted distributions (Greenfield & Randall 2010a, 2011, Greenfield & Winterbottom 2016, Greenfield *et al.* 2017). The number of described *Eviota* species began to rise, and between 2009 and 2017, 63 additional species had been added, for a new total of 113 (Table 1). In 2016, a key to all 107 of the species of *Eviota* described until then was published by Greenfield & Winterbottom (2016).

## Ecology

The species of *Eviota* appear to be relatively abundant on coral reefs, although their small size makes them difficult to observe, for which reason they have been included in a group referred to as cryptobenthic reef fishes (Depczynski & Bellwood 2003). Their presence has been recognized mostly as the result of broadcast chemical-collecting techniques. For example, nearly all of the 322 rotenone collections made at Fiji by Greenfield & Randall (2016) contained at least one species of *Eviota*, with 28 *Eviota* species taken overall. In the Hawaiian Islands, larval *Eviota* constitute the most abundant species in the plankton (Boehlert & Mundy 1996) and, on the island of O‘ahu, *E. epiphanes* is the most abundant cryptic fish species in the spur-and-groove habitat of Kan‘eohe Bay (Longenecker 2001, 2007). In Australia’s cryptobenthic coral-reef fish communities, *E. queenslandica* was found to be one of the 4 species occurring in all 4 microhabitat types studied, as well as one of the two most abundant species overall (Depczynski & Bellwood 2004). Further, in a recent survey of fish assemblages across the Great Barrier Reef, three goby species accounted for 55.9% of all specimens, two of which were *E. queenslandica* and *E. variola* (Goatley *et al.* 2016). In addition, in Sulawesi, Indonesia, collections yielding 50 species from 13 families of cryptobenthic fishes revealed that *E. cf. queenslandica* was the most common species, comprising 38% of the total abundance (Ahmadia *et al.* 2012).

One species of *Eviota*, *E. sigillata*, has the shortest lifespan known for any vertebrate, living a maximum of 8 weeks in a large sample, the first three of which are in the pelagic larval phase (Depczynski & Bellwood 2005). Depczynski & Bellwood (2006) showed that this species exhibits rapid linear growth, produces several broods of offspring during its short lifetime, and experiences exceptionally high daily mortality.

Table 1

Species	Common Name	Authors	Holotype mm SL
<i>E. abax</i>	Sand-table	(Jordan & Snyder, 1901)	35.7
<i>E. afelei</i>	Afele's	Jordan & Seale, 1906	18.2
<i>E. algida</i>	Upwelling	Greenfield & Erdmann, 2014	16.5
<i>E. albolineata</i>	White-line	Jewett & Lachner, 1983	24.7
<i>E. ancora</i>	Hookcheek	Greenfield & Suzuki, 2010	14
<i>E. aquila</i>	Dark	Greenfield & Jewett, 2014	22
<i>E. asymbasia</i>	Inconsistent	Greenfield & Jewett, 2016	16.8
<i>E. atriventris</i>	Blackbelly	Greenfield & Suzuki, 2012	18.2
<i>E. bifasciata</i>	Twostripe	Lachner & Karnella, 1980	22.5
<i>E. bilumula</i>	Crescent	Greenfield & Suzuki, 2016	10.9
<i>E. bimaculata</i>	Twin-occipital	Lachner & Karnella, 1980	22.7
<i>E. bipunctata</i>	Variable	Greenfield & Jewett, 2016	17.2
<i>E. brahmi</i>	Brahm's	Greenfield & Tornabene, 2014	17.5
<i>E. cometa</i>	Comet	Jewett & Lachner, 1983	18.5
<i>E. deminuta</i>	Diminutive	Tornabene, Ahmadi & Williams, 2013	
<i>E. disrupta</i>	Brokenbar	Karnella & Lachner, 1981	16.1
<i>E. distigma</i>	Twospot	Jordan & Seale, 1906	20.3
<i>E. dorsimaculata</i>	Dorsal-spot	Tornabene, Ahmadi & Williams, 2013	
<i>E. dorsogilva</i>	Creamback	Greenfield & Randall, 2011	17
<i>E. dorsopurpurea</i>	Purple	Greenfield & Randall, 2011	21.9
<i>E. epiphanes</i>	Divine	Jenkins, 1903	15.7
<i>E. epistigmata</i>	Twinspot	Greenfield & Jewett, 2014	15.5
<i>E. erdmanni</i>	Erdmann's	Tornabene & Greenfield, 2016	11.8
<i>E. eyreae</i>	Eyre's	Greenfield & Randall, 2016	10.9
<i>E. fallax</i>	Twin	Greenfield & Allen, 2012	18.2
<i>E. fasciola</i>	Barred	Karnella & Lachner, 1981	19.1
<i>E. filamentosa</i>	Threadfin	Suzuki & Greenfield, 2014	10.9
<i>E. flavipinnata</i>	Yellowfin	Suzuki, Greenfield & Motomura, 2015	16.6
<i>E. flebilis</i>	Tearful	Greenfield, Suzuki & Shibukawa, 2014	10.3
<i>E. geminata</i>	Geminate	Greenfield, Bogorodsky & Mal, 2014	13.9
<i>E. guttata</i>	Spotted	Lachner & Karnella, 1978	18.5
<i>E. herrei</i>	Herre's	Jordan & Seale, 1906	13.6
<i>E. hinanoae</i>	Hinano's	Tornabene, Ahmadi & Williams, 2013	
<i>E. hoesei</i>	Hoese's	Gill & Jewett, 2004	19.7
<i>E. imitata</i>	Imitator	Greenfield, Tornabene & Erdmann, 2017	13.9
<i>E. indica</i>	Indian	Lachner & Karnella, 1983	15.4
<i>E. infulata</i>	Shouldermark	(Smith, 1956)	19.5
<i>E. inutilis</i>	Chestspot	Whitley, 1943	25
<i>E. irrasa</i>	Unpolished	Karnella & Lachner, 1981	17.6
<i>E. japonica</i>	Japanese	Jewett & Lachner, 1983	24.1
<i>E. jewettae</i>	Jewett's	Greenfield & Winterbottom, 2012	12.4
<i>E. karaspila</i>	Eastern Headspot	Greenfield & Randall, 2010	17.9
<i>E. kermadecensis</i>	Kermadec	Hoese & Stewart, 2012	24
<i>E. korechika</i>	Korechika's	Shibukawa & Suzuki, 2005	24.4
<i>E. lachdeberae</i>	Lachdeberae's	Giltay, 1933	21
<i>E. lacrimae</i>	Teared	Sunobe, 1988	14.6
<i>E. lacrimosa</i>	Weeping	Tornabene, Ahmadi & Williams, 2013	
<i>E. lateritea</i>	Laterite	Greenfield & Winterbottom, 2016	16
<i>E. latifasciata</i>	Brownbanded	Jewett & Lachner, 1983	14.7
<i>E. maculibotella</i>	Spotted Dick	Greenfield & Winterbottom, 2016	15.8
<i>E. masudai</i>	Masuda's	Matsuura & Senou, 2006	32.4
<i>E. melanosphena</i>	Wedge	Greenfield & Jewett, 2016	13.3
<i>E. melasma</i>	Headspot	Lachner & Karnella, 1980	26.6
<i>E. mikiae</i>	Miki's	Allen, 2001	19.1
<i>E. mimica</i>	Mimic	Greenfield & Randall, 2016	13.3
<i>E. minuta</i>	Minute	Greenfield & Jewett, 2014	13.5

Table 1 cont.

<i>E. monostigma</i>	Singlespot	Fourmanoir, 1971	27
<i>E. natalis</i>	Christmas	Allen in Allen, Steene & Orchard, 2007	
<i>E. nebulosa</i>	Nebulous	Smith, 1958	17.4
<i>E. nigramembrana</i>	Blackbar	Greenfield & Suzuki, 2013	17.2
<i>E. nigripinna</i>	Blackfin	Lachner & Karnella, 1980	14
<i>E. nigrispina</i>	Blackspine	Greenfield & Suzuki, 2010	15
<i>E. nigriventris</i>	Redbelly	Giltay, 1933	14.3
<i>E. notata</i>	Barhead	Greenfield & Jewett, 2012	15.4
<i>E. occasa</i>	Sunset	Greenfield, Winterbottom & Suzuki, 2014	
<i>E. ocellifer</i>	Ocellated	Shibukawa & Suzuki, 2005	18.4
<i>E. oculopiperita</i>	Pepperminteye	Greenfield, Bogorodsky & Mal, 2014	11.9
<i>E. pamae</i>	Pam's	Allen, Brooks & Erdmann, 2013	17.7
<i>E. pardalota</i>	Leopard	Lachner & Karnella, 1978	18.8
<i>E. partimacula</i>	Dividedspot	Randall, 2008	17.9
<i>E. pellucida</i>	Transparent	Larson, 1976	20.9
<i>E. pictifacies</i>	Paintedface	Greenfield & Erdmann, 2017	17
<i>E. pinocchio</i>	Pinocchio	Greenfield & Winterbottom, 2012	16.5
<i>E. piperata</i>	Peppered	Greenfield & Winterbottom, 2014	20.5
<i>E. prasina</i>	Greenbubble	(Klunzinger, 1871)	30.9
<i>E. prasites</i>	Hairfin	Jordan & Seale, 1906	21.3
<i>E. pseudostigma</i>	False Singlespot	Lachner & Karnella, 1980	20.6
<i>E. punctulata</i>	Dotted	Jewett & Lachner, 1983	23.1
<i>E. punyit</i>	Punyit	Tornabene, Valdez, Erdmann & Pezold, 2016	
<i>E. queenslandica</i>	Queensland	Whitley, 1932	24.3
<i>E. raja</i>	Raja	Allen, 2001	23.8
<i>E. randalli</i>	Randall's	Greenfield, 2009	18.3
<i>E. readerae</i>	Reader's	Gill & Jewett, 2004	17.9
<i>E. richardi</i>	Rick's	Greenfield & Randall, 2016	16.7
<i>E. rubra</i>	Red	Greenfield & Randall, 1999	12.8
<i>E. rubrimaculata</i>	Redspot	Suzuki, Greenfield & Motomura, 2015	12
<i>E. rubriceps</i>	Redhead	Greenfield & Jewett, 2011	13.5
<i>E. rubriguttata</i>	Redspotfin	Greenfield & Suzuki, 2011	13.2
<i>E. rubrisparsa</i>	Redspeckled	Greenfield & Randall, 2010	19.5
<i>E. saipanensis</i>	Saipan	Fowler, 1945	26.3
<i>E. santanae</i>	Santana's	Greenfield & Erdmann, 2013	12.8
<i>E. sebreei</i>	Sebree's	Jordan & Seale, 1906	20.4
<i>E. shibakawai</i>	Shibukawa's	Suzuki & Greenfield, 2014	9.9
<i>E. shimadai</i>	Shimadai's	Greenfield & Randall, 2010	15.6
<i>E. sigillata</i>	Adorned	Jewett & Lachner, 1983	21
<i>E. singula</i>	One-spot	Greenfield & Winterbottom, 2016	12.2
<i>E. smaragdus</i>	Emerald	Jordan & Seale, 1906	22.6
<i>E. sodwanaensis</i>	Sodwana	Greenfield & Winterbottom, 2016	17.8
<i>E. sparsa</i>	Speckled	Jewett & Lachner, 1983	21.3
<i>E. specca</i>	Dusted	Greenfield, Suzuki & Shibukawa, 2014	21.1
<i>E. spilota</i>	Spottedfin	Lachner & Karnella, 1980	24.9
<i>E. springeri</i>	Springer's	Greenfield & Jewett, 2012	16.9
<i>E. storthynx</i>	Storthynx	Rofen, 1959	20.9
<i>E. susanae</i>	Susan's	Greenfield & Randall, 1999	18.5
<i>E. teresae</i>	Terry's	Greenfield & Randall, 2016	21.1
<i>E. tetha</i>	Tetha's	Greenfield & Erdmann, 2014	11.6
<i>E. thamani</i>	Thaman's	Greenfield & Randall, 2016	10.1
<i>E. tigrina</i>	Tiger	Greenfield & Randall, 2008	21.7
<i>E. toshiyuki</i>	Toshiyuki's	Greenfield & Randall, 2010	18
<i>E. variola</i>	Finspot	Lachner & Karnella, 1980	21.5
<i>E. winterbottomi</i>	Winterbottom's	Greenfield & Randall, 2010	16.2
<i>E. zebrina</i>	Zebra	Lachner & Karnella, 1980	19
<i>E. zonura</i>	Zoned	Jordan & Seale, 1906	20.4

Because of their relative abundance, rapid growth, and high turnover, these small fishes play an important role in coral-reef ecology, and may be an important link between small invertebrates (their prey) and larger piscivorous fishes (as predators) in the coral-reef ecosystem (Depczynski & Bellwood 2003). *Eviota* species feed primarily on small invertebrates; for example, Kramer *et al.* (2013) found that between 49.5% and 100% of the gut contents of *E. zebrina* consisted of harpacticoid copepods, and that they consume an average of 249 copepods per square meter of reef surface. Longenecker (2001, 2007) found that *E. epiphanes* at Kan‘eohe Bay, on O‘ahu, Hawai‘i, fed mainly on harpacticoid copepods, tanaids, and amphipods, as well as a large variety of other small invertebrates. Depczynski & Bellwood (2003) found that *E. queenslandica* in addition consumes detritus, contributing to a major trophic pathway on coral reefs. Species of *Eviota*, in turn, serve as food for larger fishes, such as snappers (Wen *et al.* 2012) and serranids (St. John 1995), and even for sea snakes (Voris 1972).

## Habitat

Most species of *Eviota* are found resting on the substrate, but in the *E. nigriventris* complex (including at least 4 species), and *E. atriventris*, *E. bifasciata*, *E. pamae*, and *E. raja*) the fishes hover in the water above the coral, often in groups and between the branches of *Acropora* corals. Of those species that rest on the substrate, many appear to have some habitat specificity. For example, Shibukawa & Suzuki (2005) reported that *E. ocellifer* was found only at the mouth of a river in an estuary. *Eviota susanae* is found only in fouling communities on docks or on sheltered reefs surrounded by silt and mud (Greenfield & Randall 1999). Some species have been found to be most often associated with hard coral, whereas others usually occur over rubble or rubble/sand substrates (Tornabene *et al.* 2013a). Of the 5 *Eviota* species that they surveyed in the Red Sea, Herler & Hilgers (2005) found some were more common on coral rock and others on various species of living coral. In Fiji, *E. cometa* has been found over a wide range of habitats, including well-developed coral reef, dead coral covered with algae, rock, sand, and silt, whereas others were found to be more selective and occupying a limited range of substrates, i.e. dead reef, dead reef with silty sand, silt, and also fine sand in *E. punctulata*; in very shallow water, often including tidepools in *E. smaragdus*; and on near-shore reefs with strong currents in *E. fasciola* (Greenfield & Randall 2016). On the Great Barrier Reef in Australia, *E. queenslandica* and *E. variola* were found to vary substantially in mean density between the inner-shelf, mid-shelf, and outer-shelf, an example of pronounced differences in species assemblages among these zones (Goatley *et al.* 2016). Specific microhabitat associations also have been found for 5 different *Eviota* species in Sulawesi, Indonesia (Ahmadia *et al.* 2012). This kind of microhabitat specificity, in both gobies and blennioid fishes, has been reported in the past for western Caribbean fauna, and was found to contribute to the composition of different fish assemblages across various habitats (Greenfield & Johnson 1990, 1999), underscoring the importance of incorporating cryptobenthic fishes in assessments of assemblage structure on all scales, including across oceans.

## Distribution

The genus *Eviota* is restricted to the Indo-Pacific Ocean. In the Pacific Ocean, they are found as far north as Japan, where 23 species have been recorded, 9 of which are endemic. To the east, there are 13 species recorded from the Marshall Islands and 10 from the Gilbert Islands. To the northeast, three species occur at the Hawaiian Islands, and to the southeast, 11 species have been found at the Tuamotu Archipelago and Society, Marquesas, Austral, and Pitcairn Islands, with two species extending as far east as Ducie Atoll. Towards the west-central Pacific, the number of species increases, with at least 28 species found in Fiji and 28 in Tonga. The northeastern coast of Australia has at least 29 species, with two having been recorded as far south as Sydney Harbor in NSW. The greatest number of species are found in what has been called the Coral Triangle, or the Indo-Australian Archipelago, including the Philippines, Indonesia, Malaysian Borneo, Timor-Leste, Papua New Guinea, and the Solomon Islands (Vernon *et al.* 2009); for example, West Papua in Indonesia has at least 37 species and other locations may have more.

The Indian Ocean has a lower diversity of *Eviota* species compared to the Pacific Ocean. In the far south, along the South African coast, only two species are found: *E. prasina* and *E. sodwanaensis*. Farther north along the east

coast of Africa, including Mozambique, Kenya, Madagascar, and the offshore islands of the Comoros, Mauritius, Reunion, and Cargados Carajos Shoals, only 9 species have been recorded. In the north-central Indian Ocean, the Seychelles and Chagos Archipelago together have 12 species. Farther north, there are 8 species recorded from the Red Sea. In the northern Indian Ocean, in the Bay of Bengal, 18 species have been recorded from the Andaman Islands. In the southeast Indian Ocean, the west coast of Australia has 25 species, one of which (*E. bimaculata*) extends all the way to Australia's south coast. Increasing proximity to the Coral Triangle correlates with increasing numbers of species, except for the isolated islands of Christmas and Cocos-Keeling which have, respectively, only 4 and two species. The increase in the number of species approaching the Coral Triangle mirrors what is found in the Pacific Ocean; however, the Indian Ocean has not experienced the same level of collecting, especially of gobies, that has taken place in the Pacific Ocean.

The number of fish species recorded from different locations reflects the intensity of broad-based collections, mostly using ichthyocides (usually rotenone). The distribution, intensity, and methodology of those collections has varied greatly from one area to another, with relatively few collections being made in more remote and isolated areas. Furthermore, collecting methods in some areas included only wading or snorkeling in relatively shallow water, whereas in other areas SCUBA gear was used to make collections at greater depths. This variation in collecting sites and methods, in addition to the very small size of *Eviota* specimens, made them easy to overlook in early collection efforts. More recently, collections have been made specifically targeting *Eviota* (for example, Mark V. Erdmann's recent collections in the Coral Triangle), and these have yielded many species not taken in earlier collections. Additional intensive collecting efforts focusing on gobies undoubtedly will result in increasing numbers of *Eviota* species being recorded in many areas, especially in the Indian Ocean.

The greater diversity of *Eviota* species in the Coral Triangle and adjacent areas follows the pattern found for many other marine taxa. Various hypotheses have been proposed to explain this high diversity, including the center-of-origin hypothesis, the accumulation hypotheses and the center-of-overlap hypothesis. All of these hypotheses relate to the position of the Indo-Australian Archipelago between the Pacific and Indian Oceans where sea-level changes have taken place. Tornabene *et al.* (2015, 2016) suggest that both geological features and the biology of various species have contributed to this diversity, with support for different hypotheses depending on the species being investigated; for example *E. punyit* and *E. sebrei* appear to fit the center-of-overlap hypothesis whereas species in the *E. nigriventris* and *E. bifasciata* complexes are better explained by the center-of-origin hypothesis.

Relatively few *Eviota* species are thought to have a wide geographic distribution. *Eviota albolineata* originally was described as ranging from the east coast of Africa eastward across Australia and the Indo-Pacific Ocean to the Tuamotu Archipelago (Jewett & Lachner 1983); however, Greenfield & Randall (2010b) subsequently demonstrated that the species is restricted to the Society Islands, Tuamotus, and Line Islands. The specimens in the western part of the originally identified range, i.e., from the east African coast to the western Pacific Ocean, were identified by them as *E. guttata*, using the name of the Red Sea species. Later Greenfield & Randall (2016) restricted *E. guttata* to the Red Sea population and re-named the western Pacific population *E. teresae*. Similarly, whereas *E. sebrei* was described from American Samoa and also recorded from various areas in the Indian Ocean, Tornabene *et al.* (2016) demonstrated that two species were involved, and described one as *E. punyit*.

Three other *Eviota* species are thought to widely range from the Indian Ocean to French Polynesia: *E. distigma*, *E. nebulosa*, and *E. zebrina*. However, given the results of Tornabene *et al.* (2013b, 2016) and Greenfield & Tornabene (2014), which show that closer examination of specimens, combined with DNA sequencing, can divide what was thought to be a single species into two or more species, those three species would appear to be excellent candidates for further study. The relatively short pelagic larval duration of 23–27 days (Depczynski & Bellwood 2005), combined with a short lifespan and rapid turnover, provide the necessary ingredients for the development of restricted-range endemic species. For example, studies of two *Eviota* species on Australia's Great Barrier Reef and of another goby genus (*Elacatinus*) in the Caribbean, have suggested that, despite larval stages of several weeks and the potential for long-distance dispersal, most goby larvae can be retained and settle on the reef on which they were spawned, or nearby, rather than dispersing broadly (Palumbi & Warner 2003, Farnsworth *et al.* 2010, D'Aloia *et al.* 2015). Indeed, Farnsworth *et al.* (2010) found a genetically distinct population of *E. queenslandica* at a single island, nearby to many others within the reef lagoon at the Great Barrier Reef.

## Reproduction

Studies on reproduction in the dwarf gobies have been conducted on only a few *Eviota* species, and have focused primarily on courtship, spawning, and mate preference; fecundity and embryonic and larval development; the morphology of the urogenital papillae; and the occurrence of sequential hermaphroditism.

### Courtship, spawning, and mate preference

Taru & Sunobe (2000, 2002) working with *E. abax*, endemic to Japan, reported that males exhibited a non-territorial home range, using small holes, rock cracks, or empty oyster shells as a spawning nest. Nevertheless, they did have aggressive interactions with other males, with behavior including heads up, open mouth, expanded fins, and lateral displays that could result in biting. Males approached a female's home range, displayed, and then led the female to the nesting area, after which she entered the nest and spawning took place. The female then left and the male guarded the eggs, cleaning them with his mouth and ventilating them with his pectoral and caudal fins.

Sunobe (1998) further described the courtship and spawning behaviors of several *Eviota* species in the aquarium, including *E. abax*, *E. melasma*, *E. prasina*, *E. prasites*, *E. queenslandica*, and *E. storthynx*. The species differed in their courtship behaviors, especially in the ways they positioned their dorsal fins and moved their heads, but all of them displayed the same spawning behavior, i.e. the males scooped out sand and cleaned the ceiling preparing the nest; males then courted females until a female entered the nest; both male and female then turned upside down, moving back and forth across the ceiling while laying and fertilizing the eggs. Spawning repeated on a regular cycle; spawning periodicity appears to be semilunar (14 days) for *E. queenslandica*, *E. sigillata*, and *E. melasma* (Depczynski & Bellwood 2006).

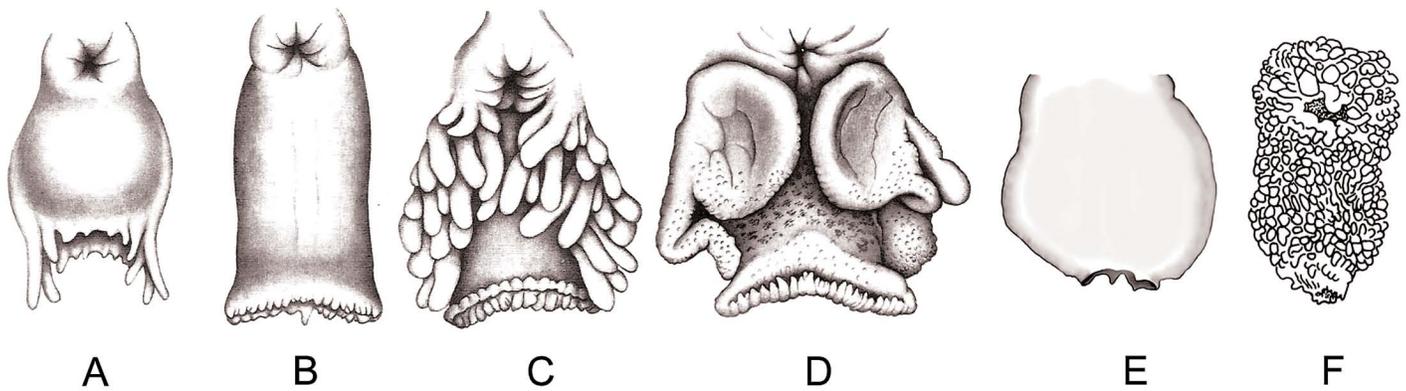
Female preference for males was investigated in aquarium experiments for two species of *Eviota* in relation to the length of the first dorsal-fin spine in males. Kitamura *et al.* (2002) cut down the first spine of males of *E. abax* and found that females preferred males with longer spines during the first phase of courtship. Sekiya & Karino (2004) conducted similar studies with *E. prasina*, where the male also has an elongate dorsal-fin spine that is used in the courtship display, but utilized males with natural spines of different lengths instead of cutting down the spines. They also found that females preferred males with longer dorsal-fin spines, and hypothesized that males with longer spines may signal better body condition, thus enhancing their chances of successfully defending and caring for the eggs. This hypothesis was examined by a subsequent study (Karino & Aria 2006) investigating the relationship between sexually-selected traits of males of *E. prasina*, including dorsal-fin spine length, body size, and courtship frequency, and the resulting hatching success of eggs between nests. They found that hatching success did not show a significant correlation with the presumably sexually-selected traits; rather, it showed a positive correlation with the time spent by males fanning eggs.

### Fecundity and embryonic and larval development

Fecundity has been studied for several *Eviota* species (Depczynski & Bellwood 2006, Sunobe & Nakazono 1987). The studies showed fecundity ranges from about 100 to over 300 eggs per brood, i.e. *E. abax* with 250–350; *E. storthynx*, 200–250; *E. sigillata*, 108–163; *E. queenslandica*, 160–374; and *E. melasma*, 104–270.

Sunobe & Nakazono (1987) further described the embryonic development and larvae of *E. abax* and *E. storthynx*. Hatching was found to take place 129 hours after fertilization in *E. abax* and 110 hours after fertilization in *E. storthynx*, in both cases occurring after sunset.

Little is known about the duration of the pelagic larval stage after hatching on the reef, although all goby species are presumed to have a larval stage that disperses in the plankton. Pelagic larval duration has been reported for only a few species: an average of 24.2 days for *E. queenslandica*, 24.7 days for *E. sigillata*, 26.2 days for *E. melasma* (Depczynski & Bellwood 2006), and 26.5 days for *E. epiphanes* in Hawai'i (Reagan 2013).



**Figure 1.** Examples of five types of urogenital papillae in mature *Eviota*. A) bulbous papilla of female; B) nonfimbriate condition in male; C) fimbriate condition in male; D) cup-shaped papilla of male [A–D after Lachner & Karnella (1980), drawn by J.R. Schroeder]; E) flat, rounded, plate-like papilla of male from Greenfield & Winterbottom (2016); F) rugose papilla of male *E. susanae* from Fig. 3 of Greenfield & Randall (1999), drawn by S.G. Monden.

### Urogenital papillae and sequential hermaphroditism

The female urogenital papilla is mostly similar across *Eviota* species, being a short and smooth bulbous structure, about as wide as long, with finger-like projections on the end (Fig. 1A). The sole exception is *E. susanae* where the sides are not smooth, but rather rugose.

The structure of the male urogenital papilla varies between species and has been used as a character in *Eviota* systematics. There are at least five different basic types of urogenital papillae in *Eviota* males. The most common is the nonfimbriate papilla, a variable-length, elongate, smooth structure with an expanded distal end that often is fringed with small finger-like projections, usually much shorter than those found in females (Figs. 1B & 2). A second type consists of a fimbriate papilla, in which the exterior is not smooth but instead has many finger-like projections (Fig. 1C), found in a group of four species including *E. partimacula*, *E. prasina*, *E. thamani*, and *E. zonura*. A third type is a cup-shaped papilla (Fig. 1D), found in *E. hinanoae*, *E. minuta*, and *E. saipanensis*. The fourth type is a plate-like papilla (Fig. 1E), found in two species, *E. mimica* and the undescribed *E. cf. specca* from Fiji. The fifth type is a rugose papilla (Fig. 1F), and is characteristic of *E. rubra* and *E. susanae*. Notably, within species with the basic smooth papilla, there can be variation in the shape of the distal end (Fig. 2).

Evidence of sequential hermaphroditism has been found in several *Eviota* species including *E. epiphanes*, where a captive female in an aquarium was observed to transform into a male during a 13-day period (Cole 1990). Depczynski & Bellwood (2006) proposed that the strong predominance of females in their studies of *E. melasma*, *E. queenslandica*, and *E. sigillata* could be the result of protogynous hermaphroditism.

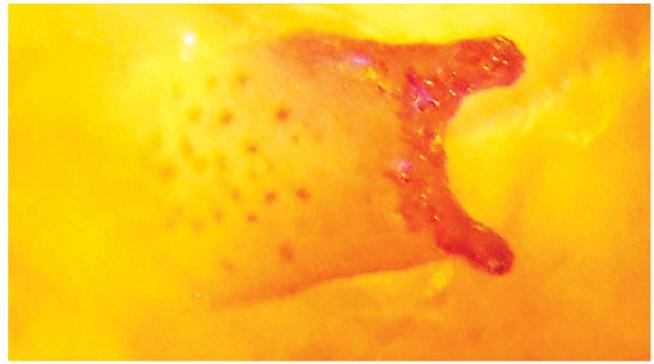
### Post-settlement stage

*Eviota* species seem to have very short life spans; in fact, Depczynski & Bellwood (2005) reported that *Eviota sigillata* has the shortest lifespan of any vertebrate, with a maximum lifespan of 59 days, based on otolith aging of a sample of 319 specimens from the Great Barrier Reef. Reagan (2013) found the maximum life span for *E. epiphanes* to be similarly short, at 60.5 days. Some other species have longer maximum life spans including 97 days for *E. melasma* and 99 days for *E. queenslandica* (Depczynski & Bellwood 2005).

Predictably, the postsettlement portion of the life span is very short, on average 34.0 days for *E. epiphanes*, 34.3 days for *E. sigillata*, 70.8 days for *E. melasma*, and 73.8 days for *E. queenslandica*. In addition, sexual maturity is reached rapidly after settlement in the species studied: *E. sigillata* matures in about 11 or 12 days, *E. melasma* in about 17 days, *E. queenslandica* in about 26 days (all from Depczynski & Bellwood 2006), and *E. epiphanes* matures 14.4 days after settlement (Reagan 2013).



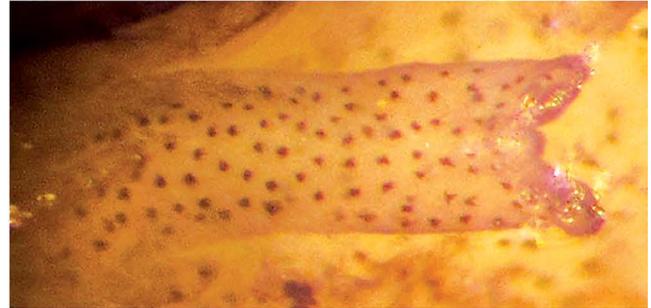
*E. punyit*



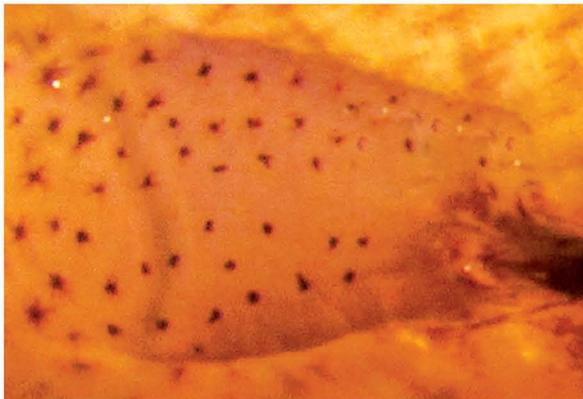
*E. atriventris*



*E. karaspila*



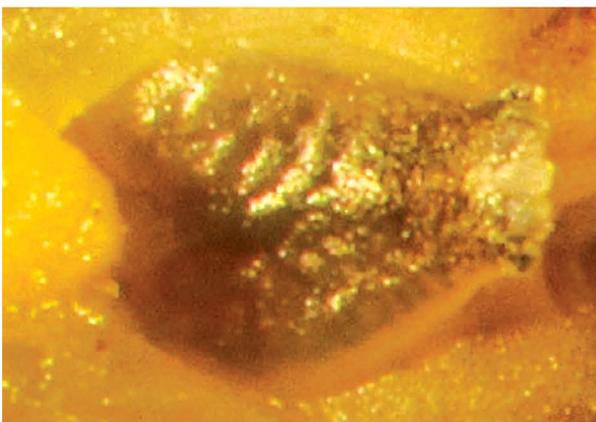
*E. dorsogilva*



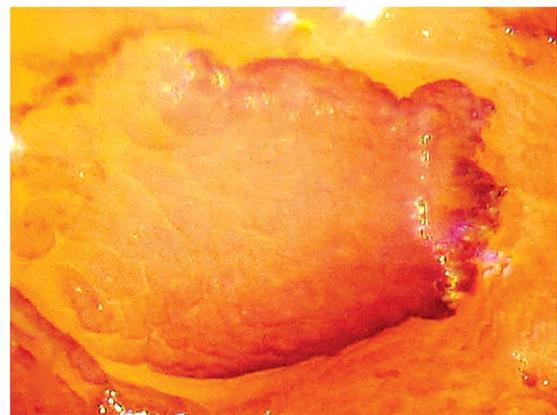
*E. maculibotella*



*E. bipunctata*



*E. algida*



*E. fasciola*

**Figure 2.** Various *Eviota* species with elongate and smooth-sided nonfimbriate male urogenital papillae (D.W. Greenfield; *E. punyit* by L. Tornabene).

## Coloration

Live coloration among *Eviota* species varies greatly. Some species, such as those at the periphery of the geographic distribution of the genus, where there may be only two or three species, do not appear to be as brightly colored as those found within the Coral Triangle, where as many as 37 species are found in one location, such as West Papua, Indonesia. For example, *E. epiphanes* and *E. susanae*, both endemic to the Hawaiian Islands, have rather subdued coloration. *Eviota sodwanaensis*, endemic to South Africa, co-occurs with only one other species (*E. prasina*), and is also not particularly brightly colored. In contrast, most of the species found in the Coral Triangle are brightly colored, as illustrated in Fig. 3. If coloration in *Eviota* is used in species recognition, then one would expect color variation to increase where the diversity of close relatives increases.

Coloration can change between live and freshly killed specimens. Greenfield & Suzuki (2010, Figs. 2 & 4) found that the distinctive golden-yellow line that curves across the black stripe over the abdomen in living *E. nigripinna* is no longer visible in freshly killed or preserved specimens. Coloration also has been observed to vary in live individuals, and the variety of appearances in underwater photographs of the same species indicate that they may be able to turn some coloration on or off, perhaps during intraspecific interactions (pers. obs.). Fluorescence may be another color feature that *Eviota* possess and could be of use in intraspecific interactions; Michiels *et al.* (2008) demonstrated that many fishes, including *E. atriventris* (as “*E. pellucida*”), *E. guttata*, *E. zebrina*, and *E. sebreei*, not only can produce red fluorescence but also are capable of seeing that fluorescence.

Eye-color patterns in *Eviota* species show perhaps more variation than in any other teleost genus (Fig. 4). A group of morphologically similar species of *Eviota* has been shown to have very different eye-color patterns (Greenfield & Erdmann 2017, Fig. 8). Considering that many of these species dwell in rock or coral crevices with only the front end protruding, the most prominent structure to be seen would be their eyes. The importance of living eye-color patterns in separating different species has been discussed by Greenfield & Tornabene (2014), Greenfield *et al.* (2014), and Greenfield & Randall (2016). In the field, different eye coloration may indicate an undetected species, and field names such as “starburst eyes” or “leopard-spot eyes”, among others, have been used in the field to distinguish specimens.

## Systematics

The genus *Eviota* is distinguished by a number of characteristics including the following: the pelvic fins are separate and the fifth pelvic-fin ray, if present, is unbranched; the membrane joining the fifth pelvic-fin rays from each side is weakly developed; the pelvic-fin rays are many-branched, often fringe-like; there are ctenoid scales on the body, but no scales on the head, nape, or pectoral-fin base; the breast is either lacking scales or with a few embedded cycloid scales; there are two or more rows of teeth in the upper jaw, and 1–3 enlarged, curved, canine-like teeth in the innermost row of the lower jaw just behind the jaw symphysis.

The most similar genus to *Eviota* is *Sueviota* Winterbottom & Hoese, 1988, but it differs from *Eviota* in having the fifth pelvic-fin ray branched vs. unbranched, if present. In describing *Sueviota*, Winterbottom & Hoese (1988) speculated that there might be two sister groups within the genus, and also stated that it was not clear whether *Sueviota* is the sister group of all species of *Eviota* or just some; they also questioned whether *Eviota* is monophyletic. In discussing the possible monophyly of *Eviota*, they mentioned the importance of the branched vs. unbranched pectoral-fin rays (note not pelvic-fin rays) of two natural groups, a character difference consistent with clades within *Eviota* (Tornabene *et al.* 2013b). As discussed by Allen & Erdmann (2017), the validity of the genus *Sueviota* as it relates to *Eviota* is under question, and is currently being studied by Luke Tornabene (University of Washington, Seattle, WA). Recent phylogenetic studies have suggested that *Eviota* forms a clade with *Gobiodon* and *Pleurosicya* (Thacker & Roje 2011, Tornabene *et al.* 2013b).

Lachner & Karnella (1980) established a number of morphological characters to identify the species of *Eviota*, including head-pore patterns, pectoral-fin-ray branching and the number of pectoral-fin rays, the presence or absence and length of the fifth pelvic-fin ray, urogenital-papilla structure, dorsal and anal soft fin-ray counts (D/A formula), and color patterns of preserved specimens. Some of these are discussed below.



*E. atriventris*



*E. pamae*



*E. pinocchioii*



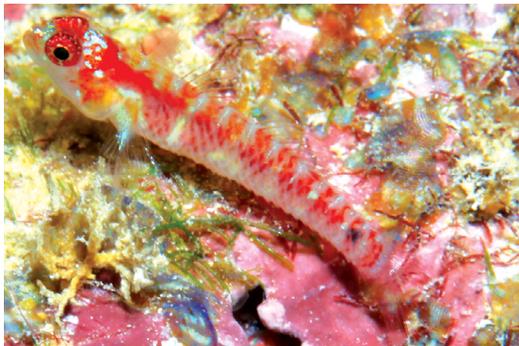
*E. rubriceps*



*E. brahmi*



*E. dorsopurpurea*



*E. santanai*



*E. teresae*



*E. cometa*



*E. prasites*

**Figure 3.** Underwater photographs of various *Eviota* species showing bright coloration (M.V. Erdmann; except *E. pamae* by G.R. Allen; *E. dorsogilva* by J.E. Randall; *E. prasites* by H. Kanehara; *E. teresae* & *E. cometa* by R. Whitworth).



**Figure 4.** Live eye-color patterns of various species of *Eviota*: 1) *E. algida* (M.V. Erdmann); 2) *E. tetha* (M.V. Erdmann); 3) *E. teresae* (R. Whitworth); 4) *E. bilunula* (R. Whitworth); 5) *E. cometa* (R. Whitworth); 6) *E. fallax* (G.R. Allen); 7) *E. flebilis* (K. Yano); 8) *E. infulata* (J.E. Randall); 9) *E. melanosphena* (A. González-Cabello); 10) *E. natalis* (G.R. Allen); 11) *E. nigriventris* (M.V. Erdmann); 12) *E. piperata* (M.V. Erdmann); 13) *E. ancora* (H. Kanehara); 14) *E. dorsogilva* (J. Eyre); 15) *E. pamae* (G.R. Allen); 16) *E. karaspila* (J.E. Randall); 17) *E. korechika* (M.V. Erdmann); 18) *E. randalli* (D.W. Greenfield); 19) *E. winterbottomi* (M.V. Erdmann); 20) *E. cf. sigillata* (J.E. Randall); 21) *E. oculopiperita* (S.V. Bogorodsky); 22) *E. pellucida* (K. Kanehara); 23) *E. susanae* (J.E. Randall); 24) *E. rubriguttata* (H. Kanehara); 25) *E. atriventris* (R. Patzner); 26) *E. prasina* (S.V. Bogorodsky); 27) *E. rubriceps* (M.V. Erdmann); 28) *E. rubrisparsa* (J.E. Randall); 29) *E. zebrina* (S. V. Bogorodsky); 30) *E. dorsopurpurea* (J.E. Randall); 31) *E. santanai* (M.V. Erdmann); 32) *E. nigrispina* (H. Kanehara); 33) *E. pinocchio* (M.V. Erdmann); 34) *E. albolineata* (J.E. Randall); 35) *E. prasites* (H. Kanehara); 36) *E. mikae* (R. Patzner).

## Cephalic sensory-canal pores

The pattern of the sensory pores on the head has been used for many years in gobiid taxonomic studies. Takagi (1957) was the first to propose terminology for the pores and their utilization as a taxonomic character, followed by Hoese (1971). Lachner & McKinney (1974) later adapted terminology from many sources and included a drawing of *Barbuligobius boehlkei* with the pores labeled. Their drawing and terminology were the basis for the first labeled diagrams of the cephalic sensory-canal pore system of *Eviota* (Lachner & Karnella 1978) (see Fig. 5), and this terminology is used today in the United States; however, ichthyologists in Japan use a somewhat different terminology, as proposed by Masuda *et al.* (1984) (see Fig. 6).

Lachner & Karnella (1980) placed *Eviota* species into several groups according to their pattern of sensory pores, branching of the pectoral-fin rays, number of vertebrae, development of the fifth pelvic-fin ray, and a few other characters. More recently, only two main groups are being recognized, based just on sensory-pore pattern: Pattern 1 species have a complete cephalic sensory-canal pore system while Pattern 2 species lack the IT pore. Overall, 41 species have Pattern 1 (Table 2), all with branched pectoral-fin rays and 40 species have Pattern 2, of which 14 show no branching of the pectoral-fin rays and 26 show branching (Table 3).

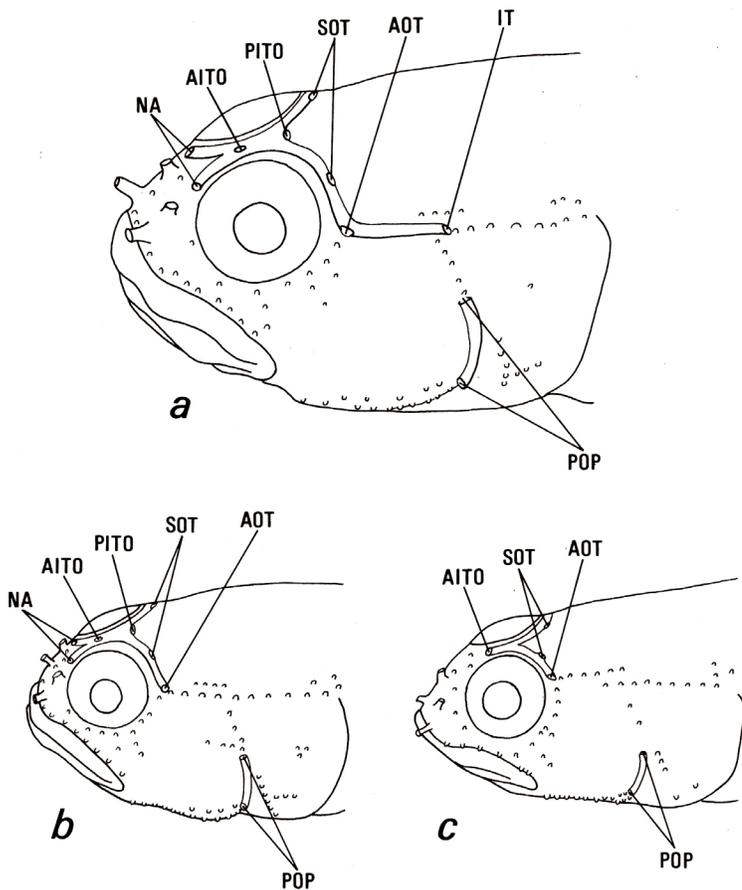


FIGURE 2.—Diagrammatic views of three patterns of cephalic sensory pore system and cutaneous papillae system in *Eviota*: a, pore pattern 1 and papillae pattern A, typical of *E. guttata* (see "Methods" for descriptions of these patterns); b, pore pattern 2 and papillae pattern B, sketched from *E. zebrina*; c, pore pattern 6 and papillae pattern C, sketched from *E. sebrei*.

Figure 5. Cephalic sensory-canal pore system of *Eviota* from Lachner & Karnella (1978).

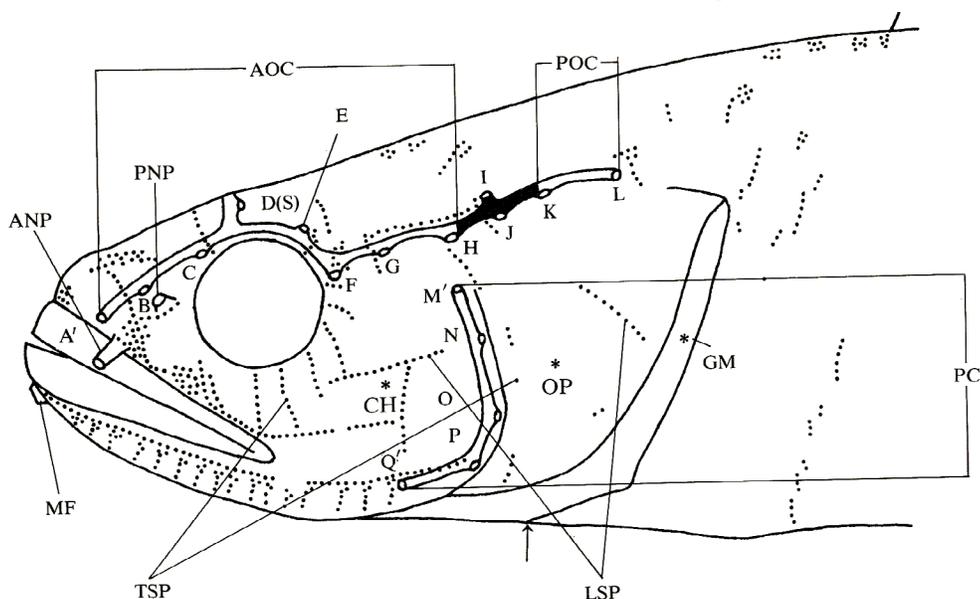


Fig. 36. Names of the parts of the head. The arrow showing the position where the gill membranes are attached to the isthmus. Black portion of the sensory canal indicates the part of the canal lost in the subfamily Gobiinae. A to Q indicate sensory canal pores.

ANP, anterior nasal pore; AOC, anterior oculoscapular canal; CH, cheek; GM, gill membrane; LSP, longitudinal sensory papillae; MF, mental flap; OP, operculum; PC, preopercular canal; PNP, posterior nasal pore; POC, posterior oculoscapular canal; TSP, transverse sensory papillae.

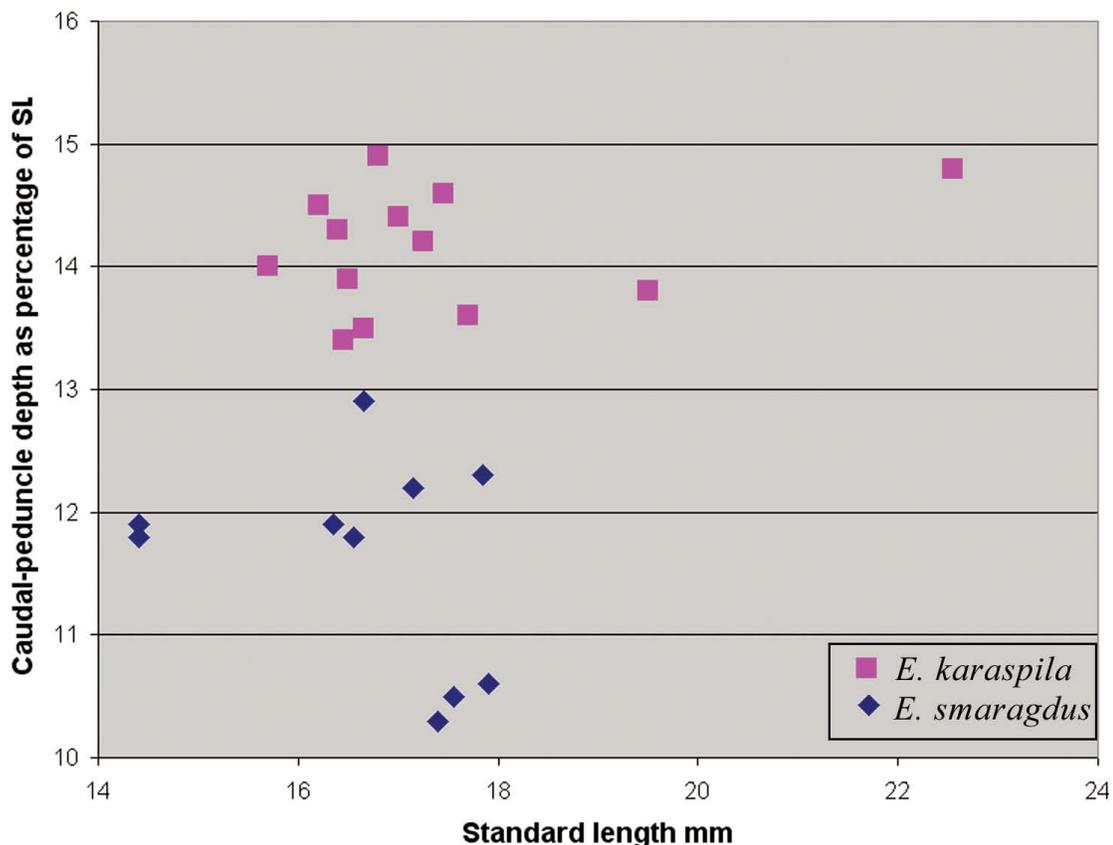
Figure 6. Cephalic sensory-canal pore system of *Eviota* from Masuda *et al.* (1984).

The remaining species have various combinations of missing pores (e.g., PITO & IT; IT & POP; NA, PITO & IT) or lack pores altogether (Greenfield & Winterbottom 2016) (Table 4). There are 6 *Eviota* species lacking all pores; of these, 5 reach a very small maximum size: *E. diminuta* (11.8 mm SL), *E. jewettae* (12.4 mm SL), *E. occasa* (10.6 mm SL), *E. singula* (12.2 mm SL), and *E. thamani* (10.1 mm SL), and one species, *E. laterita*, is larger, with a maximum size of 16.4 mm SL. Discussions of miniaturization of fishes (e.g. Rüber *et al.* 2007) have suggested that miniaturized fishes often are characterized by a reduction or simplification of various structures, and the very small size of the species lacking cephalic sensory-canal pores suggests that this hypothesis might apply here. Grouping of species by the pattern of cephalic sensory-canal pores is most helpful in constructing artificial keys to the species (e.g. Greenfield & Winterbottom 2016). However, they are only phenetic groupings, not reflecting genetic relationships; indeed Tornabene *et al.* (2013b) showed that branching of the pectoral-fin rays, and not pore patterns, correlated with phylogeny in the genus.

### Other taxonomic characters

Color pattern is another important character for separating *Eviota* species. Live coloration is very useful in recognizing species in underwater photographs and, as discussed earlier, has led to the realization that previously widespread species were really allopatric species complexes. Although live coloration is mostly lost after preservation, some of the darker pigment remains and can be used to distinguish species, i.e. the presence or absence of an occipital spot and the number of ventral post-anal spots, among others.

Other taxonomic characters used to separate species include dorsal/anal fin-ray formulas, branched vs. unbranched pectoral-fin rays, presence or absence of the fifth pelvic-fin ray, degrees of dorsal-fin-spine elongation, and type of male urogenital papilla. Morphometrics were not used as characters in earlier studies, presumably because *Eviota* species are so small, with the exception of the deep-bodied *E. herrei*; however, the author and others have found that several body measurements are in fact useful in separating some species, for example caudal-peduncle depth can separate *E. karaspila* from *E. smaragdus* (Fig. 7) and *E. nigrispina* from *E. rubriceps*



**Figure 7.** Plot of caudal-peduncle depth versus standard length (mm SL) for *E. karaspila* from Fiji and *E. smaragdus* from American Samoa and the Mariana Islands (after Fig. 8 from Greenfield & Randall [2010a]).

Table 2  
*Eviota* with cephalic sensory-canal pore system Pattern I (complete)  
dorsal/anal-fin formulas (D/A) and pectoral-fin ray branching

Species	D/A 7/7	D/A 8/7	D/A 8/8	D/A 9/8	D/A 10/8	D/A 10/9	pectoral rays
<i>E. notata</i>	X						branched
<i>E. pardalota</i>		X					branched
<i>E. rubriguttata</i>		X					branched
<i>E. sodwanaensis</i>		X					branched
<i>E. algida</i>			X				branched
<i>E. distigma</i>			X				branched
<i>E. epistigmata</i>			X				branched
<i>E. herrei</i>			X				branched
<i>E. mimica</i>			X				branched
<i>E. minuta</i>			X				branched
<i>E. monostigma</i>			X				branched*
<i>E. nebulosa</i>			X				branched
<i>E. nigramembrana</i>			X				branched
<i>E. nigripinna</i>			X				branched
<i>E. pseudostigma</i>			X				branched
<i>E. randalli</i>			X				branched
<i>E. specca</i>			X				branched
<i>E. winterbottomi</i>			X				branched
<i>E. albolineata</i>				X			branched
<i>E. aquila</i>				X			branched
<i>E. disrupta</i>				X			branched
<i>E. epiphanes</i>				X			branched
<i>E. fallax</i>				X			branched
<i>E. fasciola</i>				X			branched
<i>E. guttata</i>				X			branched
<i>E. inutilis</i>				X			branched
<i>E. irrasa</i>				X			branched
<i>E. karaspila</i>				X			branched
<i>E. korechika</i>			(X)	X			branched
<i>E. melasma</i>				X			branched
<i>E. natalis</i>				X			branched
<i>E. pictifacies</i>				X			branched
<i>E. readerae</i>				X			branched
<i>E. richardi</i>				X			branched
<i>E. rubrisparsa</i>				X			branched
<i>E. smaragdus</i>				X			branched
<i>E. teresae</i>				X			branched
<i>E. toshiyuki</i>				X			branched
<i>E. abax</i>					X		branched
<i>E. kermadecensis</i>					X		branched
<i>E. masudai</i>						X	branched

\*occasionally all unbranched

Table 3  
*Eviota* with cephalic sensory-canal pore system Pattern II (IT missing)  
dorsal/anal-fin formula (D/A) and pectoral-fin ray branching

Species	D/A 8/7	D/A 8/8	D/A 9/7	D/A 9/8	D/A 10/9	pectoral rays
<i>E. ancora</i>	X					unbranched
<i>E. atriventris</i>	X					unbranched
<i>E. bilunula</i>	X					unbranched
<i>E. flebilis</i>	X					unbranched
<i>E. imitata</i>	X					unbranched
<i>E. nigrispina</i>	X					unbranched
<i>E. prasites</i>	X					unbranched
<i>E. rubriceps</i>	X					unbranched
<i>E. springeri</i>	X					unbranched
<i>E. storthynx</i>	X					unbranched
<i>E. spilota</i>			X			unbranched
<i>E. cometa</i>	X			X		unbranched
<i>E. sigillata</i>				X		unbranched
<i>E. zebrina</i>	X			X		unbranched
<i>E. pellucida</i>	X					branched
<i>E. asymbasia</i>		X				branched
<i>E. bipunctata</i>		X				branched
<i>E. dorsimaculata</i>		X				branched
<i>E. indica</i>		X				branched
<i>E. lacrimosa</i>		X				branched
<i>E. latifasciata</i>		X				branched
<i>E. piperata</i>		X				branched
<i>E. rubra</i>		X				branched
<i>E. afelei</i>				X		branched
<i>E. bimaculata</i>				X		branched
<i>E. erdmanni</i>				X		branched
<i>E. flavipinnata</i>				X		branched
<i>E. hinanoae</i>				X		branched
<i>E. hoesei</i>				X		branched
<i>E. japonica</i>				X		branched
<i>E. melanosphena</i>				X		branched
<i>E. prasina</i>				X		branched
<i>E. punctulata</i>				X		branched
<i>E. queenslandica</i>				X		branched
<i>E. rubrimaculata</i>				X		branched
<i>E. saipanensis</i>				X		branched
<i>E. shibukawai</i>		X		X		branched
<i>E. zonura</i>				X		branched
<i>E. tigrina</i>					X	branched
<i>E. variola</i>					X	branched

Table 4

Various cephalic sensory-canal pore system patterns in *Eviota*, dorsal/anal-fin formula (D/A) and pectoral-fin ray branching

**Lacking all pores**

Species	D/A 7/7	D/A 8/7	D/A 8/8	D/A 9/8	pectoral rays
<i>E. deminuta</i>		X			branched
<i>E. jewettae</i>			X		branched
<i>E. lateritea</i>				X	branched
<i>E. occasa</i>			X		branched
<i>E. singula</i>	X	X			branched
<i>E. thamani</i>			X		branched

**Lacking only the PITO & IT pores, with the AITO pore enlarged or paired**

Species	D/A 8/7	D/A 8/8	D/A 9/8	D/A 9/9	D/A 10/9	D/A 11/9	pectoral rays
<i>E. bifasciata</i>				X			unbranched
<i>E. brahmi</i>			x	x	X	x	unbranched
<i>E. dorsogilva</i>			X				unbranched
<i>E. dorsopurpurea</i>				X			unbranched
<i>E. lachdeberei</i>	X						unbranched
<i>E. nigriventris</i>			X				unbranched
<i>E. oculopiperita</i>		X					unbranched
<i>E. pamae</i>			X				unbranched
<i>E. partimacula</i>	X						unbranched
<i>E. raja</i>					X		unbranched
<i>E. shimadai</i>		X	X				unbranched

**Lacking only the PITO & IT pores, with the AITO pore normal sized, not enlarged or paired**

Species	D/A 7/7	D/A 8/8	pectoral rays
<i>E. eyraeae</i>	X		branched
<i>E. santanai</i>		X	branched

**Lacking only the IT & POP pores**

Species	D/A 8/7	D/A 8/8	D/A 9/8	pectoral rays
<i>E. lacrimae</i>		X		unbranched
<i>E. maculibotella</i>		X		unbranched
<i>E. ocellifer</i>	X			branched
<i>E. pinocchio</i>			X	unbranched
<i>E. sparsa</i>	X			branched

Table 5

Range of caudal-peduncle depth (as % SL) among some *Eviota* species

	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5
<i>E. geminata</i>				[.....]														
<i>E. randalli</i>		[.....x.....]																
<i>E. rubriceps</i>		[.....x.....]																
<i>E. notata</i>			[.....x.....]															
<i>E. teresae</i>			[.....x.....]															
<i>E. fallax</i>				[.....x.....]														
<i>E. karaspila</i>				[.....x.....]														
<i>E. tetha</i>				[.....x.....]														
<i>E. mimica</i>			[.....x.....]															
<i>E. rubrisparsa</i>				[.....x.....]														
<i>E. imitata</i>				[.....x.....]														
<i>E. lateritea</i>				[.....x.....]														
<i>E. santanai</i>					[.....x.....]													
<i>E. algida</i>								[.....x.....]										
<i>E. smaragdus</i>										[.....x.....]								
<i>E. occasa</i>									[.....x.....]									
<i>E. nigramembrana</i>											[.....x.....]							
<i>E. singula</i>														[.....x.....]				

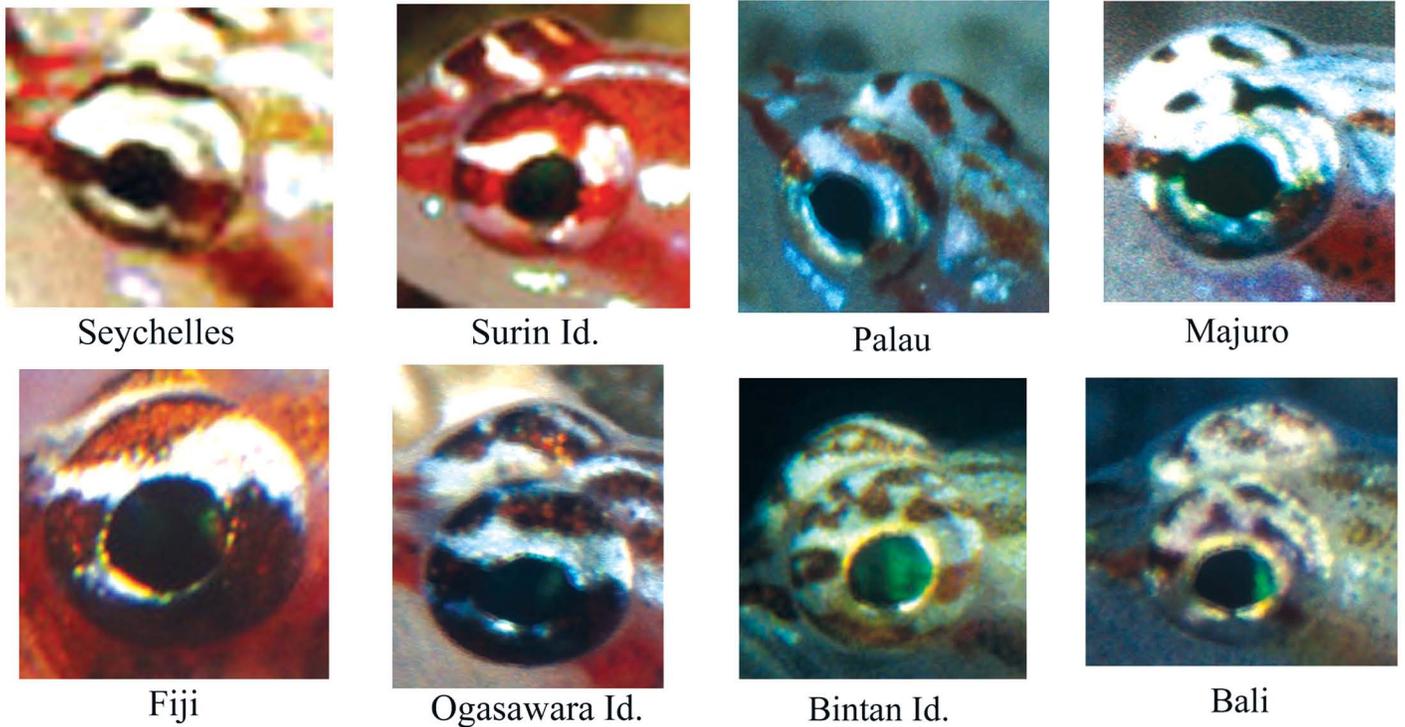
(Greenfield & Jewett 2011; Fig. 7), while eye size can separate *E. karaspila* from *E. melasma* (Greenfield & Randall 2010a; Figs. 7 & 8) and *E. dorsogilva* from *E. dorsopurpurea* (Greenfield & Randall 2011; Fig. 20). Table 5 shows variation in caudal-peduncle depth among various *Eviota* species.

## Molecular taxonomy

The use of DNA sequencing in taxonomic studies is having a major impact on *Eviota* systematics. Tornabene *et al.* (2013b) presented the first phylogeny for a group of *Eviota* species and found that they formed two distinct clades, correlating with pectoral-fin branching state rather than cephalic sensory-canal pore pattern, as had been previously assumed. Tornabene & Greenfield (2016) extended the analysis and found that three species with cup-like urogenital papillae are monophyletic within the “branched pectoral-fin ray” clade.

Greenfield & Tornabene (2014) investigated the *E. nigriventris* species complex, including specimens from the type locality of *E. nigriventris*, and split the complex, describing *E. brahmi* from Papua New Guinea and showing the complex comprised a single clade along with *E. dorsogilva* and *E. dorsopurpurea*. This was the first demonstration that *Eviota* species distinguished only by live coloration were, in fact, genetically distinct. In subsequent examples, Tornabene *et al.* (2016) demonstrated that the red and black morphs of *E. sebreei* were genetically distinct and described the red morph as *E. punyit*. Similarly, Greenfield *et al.* (2017), in describing *E. imitata*, found a single specimen with a different color pattern and showed that it was genetically distinct from *E. imitata*; description of the new species is pending based on securing additional material.

The fact that many species of *Eviota* show differences in live-color patterns in different parts of their range suggests that there are numerous undescribed cryptic species within the genus. Variations in eye-color patterns within nominal species from different parts of their ranges suggests that the genetics of these populations should be examined in the future. An example is *E. sigillata*, originally described from the Cargados Carajos Shoals near Mauritius in the southeast Indian Ocean, but also recorded from various areas in the Pacific Ocean. The eyes of specimens thought to be *E. sigillata* based on body coloration, but from different areas, are compared in Figure 8 and show some major differences. Supporting the distinction is the fact that Jewett & Lachner (1983) included



**Figure 8.** Eyes from underwater photographs of fish thought to be *E. sigillata* based on body coloration from various areas (J.E. Randall, except Surin Id. by G.R. Allen).

Pacific Ocean specimens in the description of *E. sigillata* only as non-type specimens, noting that those from the Great Barrier Reef and Indonesia have a dorsal/anal fin-ray formula of 8/7, whereas those from the Indian Ocean have a formula of 9/8 (DNA analyses have yet to be conducted). It is becoming apparent that most of the widespread nominal species of *Eviota* described mainly on morphological and meristic characters are likely to be complexes of more geographically restricted species.

## Speciation

The present geographical distributions of species of *Eviota* suggest that several modes of speciation have occurred, including long-distance dispersal with subsequent isolation, allopatric speciation, and sympatric speciation. Island endemics at peripheral locations in the Indo-Pacific would fit the long-distance dispersal with subsequent isolation mode well, and the three species in the Hawaiian Islands are likely candidates. *Eviota epiphanes* occurs in the Hawaiian Island chain and also at Johnston Atoll, 1,513 km to the west, and at Kiribati Atoll in the Line Islands, 2,957 km to the south. The species has a mean larval duration of 26.5 days (Reagan 2013). Although Johnston and the Line islands are closest geographically to the Hawaiian Island chain, Randall (2007, p. 8) suggested that they most likely came from an even greater distance, along the North Pacific current from the Ryukyu or Izu Islands. Nevertheless, with a larval duration of 26.5 days, arrival of a larval *Eviota* would be a rare event; then, once isolated, natural selection and genetic drift could operate rapidly because of their short life span and high turnover rate. This type of scenario also could apply to other relatively isolated species such as *E. sodwanaensis* in South Africa.

Allopatric speciation has been suggested for at least two species complexes (*E. nigriventris* & *E. bifasciata*) as a result of sea-level fluctuations and subsequent isolation of water bodies in the Coral Triangle during the late Pliocene through the Pleistocene (Tornabene *et al.* 2015). Tornabene *et al.* (2016) estimated a Pliocene split for the species *E. sebreei* and *E. punyit*, suggesting that they were separated by the Indo-Pacific Barrier between the Pacific and Indian Oceans. At a finer spatial scale, Farnsworth *et al.* (2010) found a genetically distinct population of *E. queenslandica* at an island in the reef lagoon near other inter-shelf reefs of the Great Barrier Reef in Australia, indicating that genetic isolation can occur over relatively short distances in these gobies, perhaps due to self-recruitment facilitated by larval behavior and subsequent habitat selection.

Sympatric speciation is a somewhat controversial mechanism (see discussion in Rocha *et al.* 2005), but has been proposed when sibling species share geographic ranges, occupy different microhabitats, and no vicariant event can be identified. An example may be *E. dorsopurpurea* and *E. brahmi* (as “*E. nigriventris*”), which can be collected from the same area at Milne Bay, Papua New Guinea, but in separate aggregations above different coral species (Greenfield & Randall 2011), suggesting a case of sympatric speciation as a result of microhabitat partitioning and assortative mating (Tornabene *et al.* 2015). Two of the three Hawaiian species, *E. susanae* and *E. rubra*, may be another example. They share a unique rugose urogenital papilla, have elongate delicate pelvic fins with a fifth ray present, and lack the IT pore, suggesting that they are closely related (Greenfield & Randall 1999). Nevertheless, they have quite different preferred habitats: *E. susanae* is found in shallow (<4.6 m), protected fouling communities, whereas *E. rubra* prefers deeper, spur-and-groove and ledge habitats from 12.2–28.7 m and is the only *Eviota* species in water greater than 18 m depth in Kan‘eohe Bay, O‘ahu (*E. epiphanes*, the remaining species, occurs between the other two species, in higher-energy, shallow spur-and-groove habitat not used by the other species). Tornabene *et al.* (2015) suggested that *E. susanae* and *E. rubra* might represent a case of sympatric speciation because the two closely related species co-occur at this very isolated region.

### Future research directions

The large number of species in the genus *Eviota* are excellent candidates for future studies in many areas, including taxonomy, life history, and ecological interrelationships. The systematics of the genus is far from resolved, and many undescribed species remain, especially in poorly collected regions. Indeed, when these gobies are specifically targeted, more species are likely to be collected even in well-sampled locations. As discussed above, it is likely that many wide-ranging nominal species will be split up into allopatric species complexes. A combination of underwater photography to document live color patterns, detailed morphological examination, and DNA analyses will be required to resolve the species boundaries within complexes, and a focus on collecting at the type localities for nominal species is imperative. At present, the majority of species have not been sampled for DNA extraction and many have no record of the live-color patterns.

Aspects of the life history of these gobies, including age, growth, trophic ecology, and reproduction, has been studied for only a few species, and those studies have yielded intriguing and useful results, indicating a need for future studies in these areas. Furthermore, the fact that at least some of these species can be easily maintained and bred in the laboratory provides opportunities for experimental investigations into their life histories and reproductive biology. Finally, the role that these small fishes play in the coral-reef food web has yet to be investigated thoroughly and, given their abundance on coral reefs, they may comprise an especially important component of the reef community.

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