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Ecsenius markalleni, a new species of coral blenny (Teleostei: Blenniidae) from the eastern Indo-west Pacific Ocean

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Abstract

Ecsenius markalleni, n. sp. is described from 28 specimens, 19.7–64.7 mm SL, collected from northwestern Australia, Taiwan, and Japan. It is also reported on the basis of underwater photographs, non-type specimens, and previously authenticated records from the Andaman Islands, Indonesia, Malaysia, and Vietnam. The new coral blenny is a member of the Lineatus Group of *Ecsenius*, which until now contained only the single species, *E. lineatus*. The group is distinguished by the color pattern consisting of either a solid, dark, upper mid-lateral band across the upper body, sometimes broken into a series of dark segments, extending as a dark postorbital band onto the head; a deeply notched dorsal fin; 16–18 segmented dorsal-fin rays; 18–20 segmented anal-fin rays; and 34–36 vertebrae. The new species differs from its sister species *E. lineatus*, found in the central and southwestern Indian Ocean, by color patterns of both adults and juveniles. The adult of *E. markalleni* is best distinguished from *E. lineatus* by the having the dark lateral band typically uninterrupted vs. the band broken into distinct segments in *E. lineatus*. Juveniles of *E. markalleni* show the adult color pattern while juvenile *E. lineatus* are mostly similar to adults but have a greyish anterior half of the body and a yellowish rear body. The two allopatric species also diverge by 4.1% in the mtDNA COI barcode sequence.

Key words: taxonomy, ichthyology, coral-reef fishes, cryptic species, Australia, Indonesia, Malaysia, Vietnam,Taiwan, Japan

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Introduction

The genus *Ecsenius* McCulloch, 1923 contains small, colorful blenniid fishes that are common inhabitants of coral reefs throughout the Indo-west and central Pacific region from East Africa to the Marquesas. The widespread use of scuba-diving equipment by researchers and concomitant underwater photography has played a major part in the discovery of a plethora of new species. Consequently, the genus is now the largest in the family, containing 55 valid species (Fricke et al. 2026). The majority (39 species) were described by the late Smithsonian researcher Victor Springer, including 24 species that were described in major revisions (Springer 1971, 1988). An additional 14 species were described from 1972–2024, frequently with various co-authors (Springer 1972, McKinney & Springer 1976, Springer 1991, Springer & Randall 1999, Springer & Allen 2001, Springer 2002, Springer & Allen 2004). With 35 documented species (Allen & Erdmann 2024), the East Indian region, extending from the Andaman Sea to the Solomon Islands northward to the Philippines, is home to more *Ecsenius* species than any other region.

Ecsenius lineatus Klausewitz, 1962 was described from a single specimen collected at Fadiffulu Atoll, Maldives, western Indian Ocean. It was subsequently reported by Springer (1971, 1988) from a wide geographic range, including Sri Lanka, Mauritius, Reunion, Western Australia, Malaysia, Vietnam, Philippines, South China Sea, Taiwan, and Okinawa. However, during a visit to Laamu Atoll, Maldives in February 2018, we (GRA & MVE) noted pronounced color differences between this species and individuals of "*E. lineatus*" previously encountered and photographed at Western Australia and eastern Indonesia (Aru Islands and West Papua). Subsequent investigations, including analyses of mtDNA CO1 sequences, reveal that true *E. lineatus* is restricted to the central and southwestern portions of the tropical Indian Ocean and populations from Western Australia, the Andaman Sea, and the western rim of the Pacific represent a new species described herein.

Materials and Methods

The relatively brief description follows the methodology and format of Springer's (1988) review of this genus. Standard length (SL) was taken from the midtip of the upper lip to the midlateral posterior margin of the hypural fan, indicated externally by a crease at the caudal-flexure point. The last dorsal-fin spine, situated below the notch between the spinous and soft (segmented ray) portions of the dorsal fin is usually much reduced and difficult to detect, unless with an x-ray. Springer (1988) explained how morphometric measurements are generally of little use for differentiating species and therefore are not part of this description. They vary greatly within species and are difficult to obtain due to the vagaries of preservation and handling damage. Also many morphometrics, unlike meristic features, vary allometrically and by sex and location. Consequently, after studying hundreds of specimens, Springer concluded that all species of *Ecsenius* can be distinguished by color-pattern differences and several key meristic features such as counts of fin-rays, vertebrae, and dentary incisor teeth. Dentary incisor teeth include the total on both dentaries, excluding posterior canines (Fig. 2 in Springer 1988). Segmented dorsal and anal-fin rays and vertebral elements were counted from digital x-rays

Counts for the paratypes are in parentheses if different from the holotype. Fish collections include BPBM- Bishop Museum, Honolulu; CAS- California Academy of Sciences, San Francisco; KAUM- Kagoshima University Museum, Kagoshima, Japan; NTM- Museums and Art Galleries of the Northern Territory, Darwin; SMF- Senckenberg Research Institute and Natural History Museum, Frankfurt; USNM- Smithsonian Institution National Museum of Natural History, Washington, D.C.; and WAM- Western Australian Museum, Perth (WAM)..

We have utilized the published data of Springer (1988) for the holotype of *E. lineatus* (SMF 5532), collected at Fadiffulu Atoll, Maldives. We have also examined two specimens (WAM P.34839–001) of *E. lineatus*, 38.1 & 51.2 mm SL, from Laamu Atoll, Maldives. Counts of segmented dorsal and anal-fin rays, dentary incisor teeth, and vertebrae (Tables 2 & 3) were taken from Springer's (Table 15; 1988) account of *Ecsenius lineatus*, supplemented with additional data for 8 type specimens of the new species from Western Australia, two paratypes from Okinawa, and two non-type specimens from West Papua, Indonesia. We also utilized a series of excellent high-definition photographs provided by KAUM to obtain additional counts of segmented dorsal and anal-fin rays from 20 specimens of the new species, which were subsequently designated as KAUM paratypes. We also utilized x-rays available on the USNM fish-collection website for fin-ray and vertebral counts of 32 additional specimens of *E. lineatus* from Mauritius. In addition, we obtained additional distribution records for the new species based on photographs adjudged reliable posted on the iNaturalist website (https://www.inaturalist.org/).

DNA isolation, extraction, and sequencing followed Allen, Erdmann & Liu (2019). Phylogenetic analyses used Maximum Likelihood (ML) and Neighbor-Joining (NJ) methods generated by MEGA12 (Kumar et al. 2024). Prior to phylogenetic reconstruction, the most appropriate nucleotide substitution model was determined using MEGA version 12 with Akaike Information Criterion (AICc), and Bayesian Information Criterion (BIC) methods. The HKY+G model (Hasegawa-Kishino-Yano 1985 & Gamma distribution) model was chosen by MEGA 7. Supporting values on the branch were evaluated by non-parametric bootstrapping with 1000 replicates performed for ML and by repeated resampling for 1000 replicates (NJ). Our voucher sequences of *E. lineatus* from Maldives were compared with reference sequences from GenBank (Appendix Table) to evaluate interspecific K2P distances.

Figure 1. *Ecsenius markalleni*, n. sp., about 50 mm SL, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen).

Ecsenius markalleni, n. sp.

Blackband Coral Blenny

urn:lsid:zoobank.org:act:7304C5AE-91D0-4288-80C1-07A532242B90

Figures 1–5 & 7–8A

Ecsenius lineatus (*non* Klausewitz) Springer 1971: 30, in part (Fig. 23 from Taiwan and specimens from Vietnam, Pratas Reef & Okinawa); Springer & McKinney 1976: 7, in part (Western Australia); Masuda et al. 1984: 300 & Plate 269N (Japan); Springer 1988: 50, in part (Fig. 30 from Taiwan & Fig 31 from Cuyo Islands, Philippines & specimens from Okinawa, Taiwan, Pratas Reef, Vietnam, Malaysia, Philippines & Western Australia); Allen & Swainston 1988: 130 (Western Australia); Shen et al. 1993: 501 (Taiwan); Kuiter & Tonozuka 2001: 601 (unnumbered photographs from Bali and Flores, Indonesia); Allen 2009: 208 (Western Australia, Indonesia & Philippines); Allen & Erdmann 2012: 813, in part (unnumbered photograph from West Papua, Indonesia & records from Sabah, Brunei, Indonesia, Philippines & Western Australia).

Ecsenius sp. Allen & Erdmann 2024: 896 (unnumbered photograph from West Papua, Indonesia & records from Andaman Sea, Western Australia, Malaysia, Indonesia, Philippines, Vietnam, Taiwan & Japan).

Holotype. WAM P. 34747-006, male, 46.5 mm SL, Western Australia, Dampier Archipelago, Enderby Island, -20.61798°, 116.4642°, 15–16 m, G.I. Moore & M.G. Allen, 27 March 2017.

Paratypes. Western Australia: WAM P.25371-006, 2 specimens, female 45.0 & male 53.2 mm SL, North West Cape, outer reef off Tantabiddi Creek, -21.9019°, 113.9323°, 15–18 m, spear, G.R. Allen, 30 June 1975; WAM P. 25373-004, male, 56.6 mm SL, North West Cape, off Mildura shipwreck, -21.7841°, 114.1681°, 14–16 m, spear, G.R. Allen, 1 July 1975; WAM P.25376-001, female, 50.4 mm SL, North West Cape, outer reef off Tantabiddi Creek, -21.9019°, 113.9323°, 15–18 m, spear, G.R. Allen, 1 July 1975; WAM P.34441-009, 2 specimens, male 26.7 & female 35.8 mm SL, Monte Bello Islands, 5.2 km northeast of Ah Chong Island, -20.4992°, 115.5898°, 18 m, G.I. Moore & S.M. Morrison, 16 April 2015; WAM P.34742-008, female, 39.1 mm SL, Dampier Archipelago, north side of Nelson Rocks, -20.4420°, 116.6697°S, 10–18 m, G. I. Moore & M.G. Allen, 25 March 2017. Taiwan (Dongsha Atoll, also known as Pratas Reef): KAUM I.-111260, 64.0 mm SL, off Dongsha Island, 20.6678°, 116.7668°, 8–10 m, K. Koeda et al., handnet, 4 December 2017. Japan: (Kagoshima Prefecture unless stated otherwise): KAUM I.-29588, 48.7 mm SL, Osumi Islands, off west coast of Iwo-Jima Island, 30.784°, 130.257°, 5–20 m, KAUM Fish Team, hand net, 28 May 2010; KAUM I.-31635, 31.5 mm SL, Osumi Islands, off west coast of Iwo-Jima Island, 30.784°, 130.257°, 5–10 m, KAUM Fish Team, hand net, 13 August, 2010; KAUM I.-71572, 64.7 mm SL, Uji-jima Island, 31.2°, 129.4667°, 10–16m, H. Motomura et al., hand net, 22 April 2015; KAUM I.-74605, 21.7 mm SL, Tokyo Prefecture, Ogasawara Islands, Chichi-jima Island, 30.784°, 130.257°, 5–45 m, S. Chiba et al., hand net, 3 July 2015;): KAUM I.-83933, 55.6 mm SL, Ohto Port, 31.4198°, 130.1695°, 3 m, M. Itou, hand net, 14 November 2015; KAUM I.-88962, 37.4 mm SL, Okinawa Prefecture, Yaeyama Islands, Yonaguni-jima Island, 24.4593°, 122.9507°, 15 m, K. Koeda, hand net, 23 September 2015; KAUM I.-122029, 49.9 mm SL, Amami Islands, Okinoerabu-jima Island, 27.3835°, 128.5183°, 10–30 m, D. Uyeno et al., hand net, 22 October 2015; KAUM I.-124315, 26.4 mm SL, Miniami-satsuma, 31.434°, 130.1528°, 10–16 m, M. Yamada et al., hand net, 16 December 2018; KAUM I.-124416, 64.0 mm SL, south of Kome-jima Island, 31.4258°, 130.1198°, 6–14 m, M. Yamada et al., hand net, 16 December 2018; KAUM I.-145124, 46.1 mm SL, Amami Islands, Okinoerabu-jima Island, 27.4028°, 128.5367°, 20-30 m, K. Fujiwara et al., hand net, 31 July 2020; KAUM I.-145135, 29.3 mm SL, same data as previous specimen; KAUM I.-145136, 48.4 mm SL, same data as previous specimen; KAUM I.-145137, 60.9 mm SL, same data as previous specimen; KAUM I.-147444, 34.0 mm SL, Shimokoshiki-shima Island, 31.8418°, 129.9207°, 10-15 m, T. Fujii et al., hand net, 17 October 2020; KAUM I.-145137, 60.9 mm SL, same data as previous specimen; KAUM I.-159703, 19.7 mm SL, Amami Islands, Okinoerabu-jima Island, 27.40287°, 128.5367°, 10–25 m, K. Fujiwara et al., hand net, 20 August 2021; KAUM I.-159731, 38.1 mm SL, Amami Islands, Okinoerabu-jima Island, 27.3878°, 128.52°, 5–10 m, K. Fujiwara et al., hand net, 21 August 2021; KAUM I.-169581, 48.6 mm SL, Kusagaki Islands, north of Shimono-shima Island, 30.842°, 129.4265°, 10–30 m, M. Yamada et al., hand net, 16 June 2022; KAUM I.-179359, 37.1 mm SL, Osumi Islands, Iwo-Jima Island, 30.7878°, 130.274 °, 15–25 m, S. Dewa et al., hand net, 9 January 2023; KAUM I.-217686, 55.1 mm SL, north side of Oto Port, 31.4208°, 130.1692°, 16 m, Y. Dewa, hand net, 16 June 2025; KAUM I.-222938, female 41.3 mm SL, Japan, Ryukyu Islands, Okinawa Prefecture, Kumejima, 26.2951°, 126.8252°, Japan, 20 m, M.V. Erdmann, 8 September 2025; KAUM I.-222939, male 43.7 mm SL, same data as previous KAUM specimen.

Non-type specimens. (data from Springer [1988] except WAM specimens) Taiwan (northern): USNM 203129, 4 specimens, 42–48 mm SL; USNM 203130, 2 specimens, 49 & 55 mm SL; USNM 203131, 55 mm SL; USNM 203132, 2 specimens, 45 & 50 mm SL; USNM 204477, 60 mm SL; BPBM 23078, 3 specimens, 45–64 mm SL. Okinawa: BPBM 22281, 2 specimens, 27& 33 mm SL. Viet Nam (Nha Trang Bay): CAS 24489, 47 mm SL; South China Sea (Pratas Reef): CAS 24477, 20 mm SL. Philippines (Cuyo Islands): USNM 219315, 2 specimens, 54 & 56 mm SL. Malaysia, Pulau Tulai: BPBM 21940, 3 specimens, 34–45 mm SL, Pulau Chebeh; BPBM 21956, 44 mm SL. Indonesia (West Papua Province): WAM P.34973-001, 41 mm SL, WAM P.32789-006, 47 mm SL.

Diagnosis. A species of *Ecsenius* with general morphometrics for genus; dorsal-fin elements XII,16–18, total 28–30, with a deep notch between spinous and segmented-ray portions; anal-fin elements II,18–21 (usually 19 or 20); pectoral-fin rays 13; segmented caudal-fin rays 13; dentary incisor teeth (total) 45–50; lateral line without vertically paired pores, extending back to below base of dorsal-fin spine 10 (from 9–11); elongate cirrus (usually unbranched, rarely with single branch) on posterior rim of anterior naris; diagnostic color pattern a prominent, broad, dark-brown or blackish band from behind eye along upper mid-lateral body to mid-caudal-fin base, infrequently partially coalesced segments or rarely separated segments mostly on rear half of body; fins mainly translucent without markings.

Description. Dorsal-fin elements XII,16 (XII,16–18); a deep notch between spinous and segmented-ray portions; anal-fin elements II,18–21 (usually 19 or 20); pectoral-fin rays 13; segmented caudal-fin rays 13; vertebrae 10+24 =34 (10+24–26 =34–36); dentary incisor teeth (including anterior canines) 47 (45–50); lateral line without vertically paired pores, extending back to below base of dorsal-fin spine 9 (10 or 11); posterior rim of anterior nostril with an elongate, usually unbranched, cirrus 25% (19–38%) of head length.

Color in life. (Figs. 1–4A, 5 & 8A) A broad, dark-brown to blackish band extending from just behind eye across upper mid-lateral body to middle of basal caudal-fin rays, gradually increasing in width to mid-body, gradually decreasing posteriorly and terminating in a pointed extension onto caudal-fin base; some specimens with scalloped margins becoming partially coalesced segments (Fig. 2B) or, rarely with separated segments primarily on rear half of body; body above dark band light brown or greyish to dark brown or to reddish brown, bisected by a narrow yellow stripe from above upper rim of eye rearwards, transitioning at mid-dorsal fin level

Figure 2. *Ecsenius markalleni*, n. sp., about 50 mm SL: A) Havelock Island, Andaman Islands (G.R. Allen); B) Okinawa, Japan (M.V. Erdmann).

Figure 3. *Ecsenius markalleni*, n. sp., Triton Bay, West Papua, Indonesia; A) about 45 mm SL, banded pattern; B) about 45 mm SL, partially coalesced segments; C) juvenile, about 20 mm SL (G.R. Allen).

to a more greyish or pale stripe continuing to caudal peduncle; a second short, narrow, yellow stripe immediately behind middle of eye, adjacent to upper edge of postocular portion of dark lateral band, also occasionally a diffuse yellowish area extending along dorsal edge of dark band on anterior half of body; a third yellow stripe just below ventral margin of dark band, extending from behind eye to posterior lateral body, increasing in width and becoming less intense posteriorly; remainder of head and body (lower two-thirds of head and lower half of body) white, except yellowish on lower jaw, chin, and adjacent isthmus; iris of eye with a dark band continuous with dark lateral band, below iris band a whitish or yellowish area, above iris band a narrow yellow stripe continuous with second head stripe; fins mostly translucent with pale-grey fin rays; nasal cirri white.

Freshly collected specimens from Japan (Fig. 5) are similar to described live coloration, but generally darker and lateral band less well-contrasted and narrow yellow stripes bordering postocular dark band either absent or significantly faded.

Color in alcohol. (Fig. 4B) Head and body tan with a broad blackish lateral band from just behind eye to middle of basal caudal-fin rays, gradually increasing in width to middle of body, then decreasing in width terminating in a pointed extension on caudal-fin base; lateral band infrequently partially coalesced segments or rarely separate segments, primarily on rear half of body; head and body above dark band brownish, cheek greyish and lips abruptly pale tan; fins semitranslucent without markings; nasal cirri covered with numerous pepper-like melanophores.

Sexual dimorphism. There are no obvious color differences between males and females, but Springer (1971) discussed several gemder-related morphological features that are typical for *Ecsenius* and other blenniid genera.

Figure 4. *Ecsenius markalleni*, n. sp., Western Australia, A) adult about 50 mm SL, North West Cape (A. Hoschke); B) preserved male holotype (WAM P.34747-006), 46.5 mm SL, Dampier Archipelago (G.R. Allen).

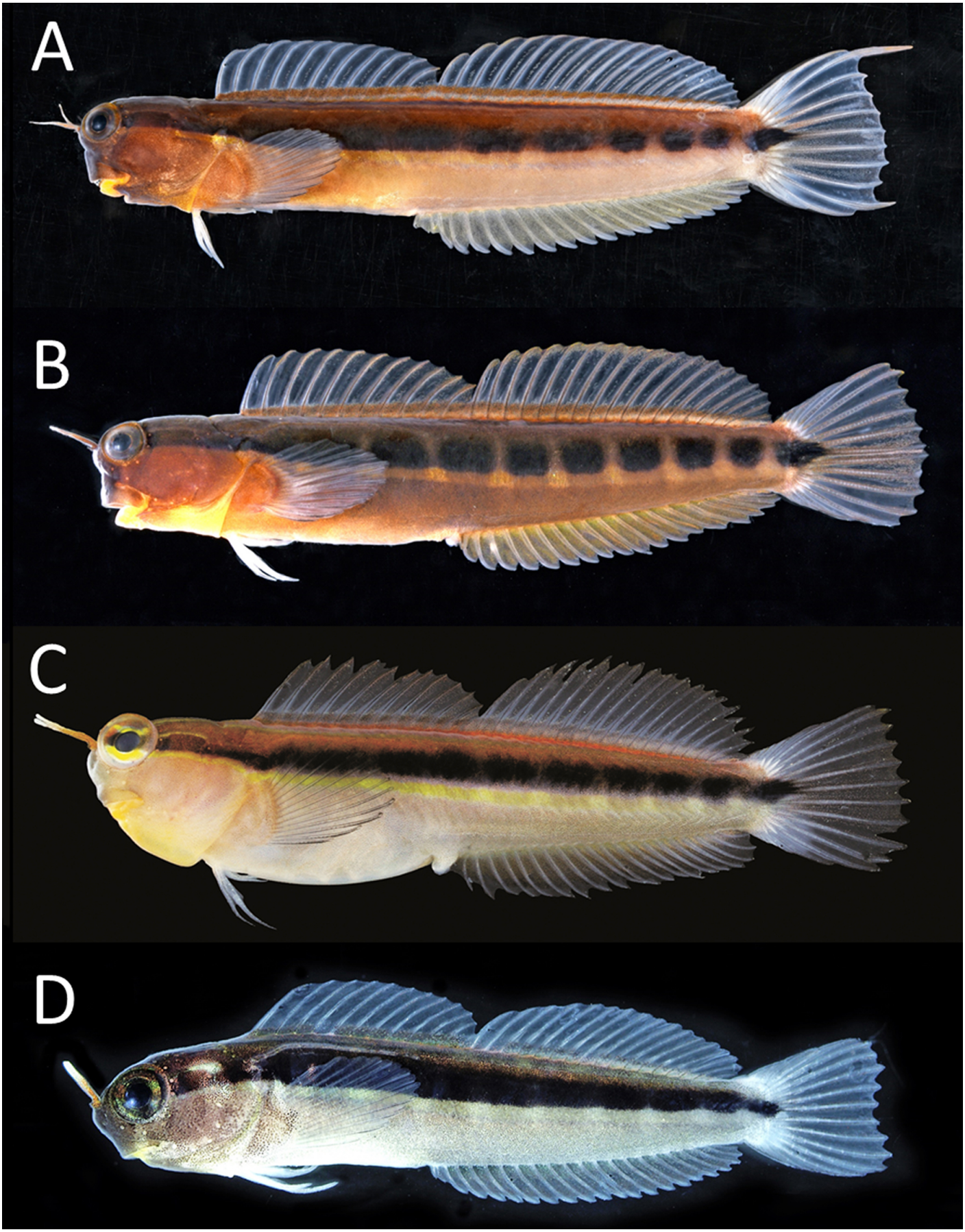

Figure 5. *Ecsenius markalleni*, n. sp., freshly collected paratypes from Japan: A) male, 60.9 mm SL (KAUM I.-145137), Amami Islands; B) female, 48.6 mm SL (KAUM I.-169581), Kusagaki Islands; C) female, 31.5 mm SL (KAUM I.-31635), Osumi Islands; D) juvenile, 21.7 mm SL, Ogasawara Islands (KAUM photographs).

These include a difference in urogenital structures, characterized by the first anal-fin spine in females greatly reduced and not visible externally, but enveloped in a fleshy lobe (Fig. 5C) that contains a large urogenital opening and a papilla. In contrast, both anal-fin spines of the male are distinct (Fig. 5A) and the urogenital opening is a tiny orifice at the tip of a short, slender tube. In addition, mature adult males tend to develop thick, fleshy tips on most of the anal-fin rays, a feature that is absent in females. Lastly, the upper and lower caudal-fin lobes of males generally become increasingly longer with increased size and maturity (Fig. 5A).

Etymology. The new species is named in honor of the first author's son, Dr. Mark Gregory Allen, in recognition of his invaluable assistance on many expeditions and his unflagging enthusiasm and commitment to fish biology and conservation. He was also the co-collector of the holotype..

Distribution and habitat. *Ecsenius markalleni*, n. sp. is widely distributed along the western margin of the Pacific Ocean and the eastern Indian Ocean, ranging from the Andaman Islands and Gulf of Thailand eastward to West Papua Province of Indonesia, and from Western Australia northward to Japan. The current distribution (Fig. 6) includes the Andaman Islands; northwestern Australia; Indonesia (Anambas Islands, Bali, Flores, Alor, West Papua, and Aru Islands); Malaysia (eastern Sabah and islands on the east coast of the main peninsula); Vietnam (Nha Trang Bay); Philippines (Luzon, Calamianes Islands, Cuyo Islands, and northern Palawan); northern Taiwan;

Figure 6. Map of eastern Indo-west Pacific region showing distribution records for *Ecsenius markalleni*, n. sp.; yellow star is type locality; solid yellow circles are specimens and photographs from this study; yellow circles with a black center are specimens reported by Springer (1988); yellow rectangles are locations of photographs from iNaturalist.

the South China Sea (Pratas Reef); and Japan (Ryukyu Islands to the Izu Peninsula and Ogasawara Islands). The southernmost population, which inhabits coastal reefs (vicinity of North West Cape) and nearshore islands (Monte Bello Islands and Dampier Archipelago) of Western Australia, represents an isolated outlier. Detailed investigations over the past 50 years by author GRA and other staff of the Western Australian Museum and the Museum and Art Gallery of the Northern Territory failed to record *E. markalleni* from any other locations along the northern Australian coast, including the Kimberley region (between 122° and 129° E longitude) and adjacent seas of the Northern Territory. It is also apparently absent or rare from the coral-rich reefs and shoals lying on the edge of the northwestern Australian continental shelf, including the Rowley Shoals, Scott Reef, Seringapatam Reef, Cartier Reef, and Hibernia Reef, except for a single specimen known from Ashmore Reef (NTM S.11980-013), which lies 135 km south of the Indonesian island of Rote. Although its Australian distribution is highly restricted, it follows the general pattern of the majority of reef fishes from this region, which exhibit a strong affinity to the Pacific rather than the Indian Ocean faunal province.

The habitat occupied by the new species generally consists of rocky shorelines at depths between about 3 and 30 m. Among the locations we have observed this species, it was most common in the vicinity of Triton Bay, West Papua, where we encountered about 10–20 individuals in 3–6 m depth on each dive. Individuals were observed perching on a variety of substrates, including algae, tunicates, sponges, and hard corals. They retreated to abandoned worm tubes when disturbed (Fig. 7).

Comparisons. The new species is a member of the Lineatus Group of *Ecsenius* as defined by Springer (1988), which previously contained only the single species, *E. lineatus*. The group is distinguished by a dark postorbital band and a deeply incised dorsal fin. Springer (1988) reviewed this species in detail, including a meristic analysis

Figure 7. *Ecsenius markalleni*, n. sp. occupying a worm-tube refuge, about 45 mm SL, Triton Bay, West Papua, Indonesia (G.R. Allen).

of 41 specimens from Okinawa, Taiwan, Pratas Reef (South China Sea), Vietnam, Malaysia, Philippines, Western Australia, Sri Lanka, Maldives, Mauritius, and Réunion. In spite of small differences in meristic data and preserved color patterns, he concluded only a single species was represented.

We had the opportunity to observe and collect specimens from the Maldive Islands, the type location of *E. lineatus*. The collections were made at Laamu Atoll during February 2018. It was immediately apparent that the species previously referred to as *E. lineatus* from Western Australia, Indonesia, and other Pacific locations differed consistently in both juvenile and adult color pattern from the Maldive Island population, and deserved description as a new species.

Springer (1988) emphasized the importance of color pattern in differentiating *Ecsenius* species, concluding that "Most species of *Ecsenius* can be identified on color pattern alone, and I believe relationships are reflected to a great extent by color-pattern similarities". He further stated that "there is even a reasonable possibility that some of the *Ecsenius* species I recognize will warrant subdivision when more complete geographical samples are available (e.g. *E. opsifrontalis* and *E. lineatus*), or when more is known about their genetics". His 1988 revision included 46 species, 20 of which he described as new. Subsequent work on the genus by Springer (1991, 2002), Springer & Randall (1999), Springer & Allen (2001, 2004), Allen et al. (2019), and Allen & Erdmann (2024) added 9 new species, and, to a large extent, species were diagnosed by distinctively different color-patterns.

True *E. lineatus* is restricted to the western Indian Ocean, reported to date from Maldives, Mauritius, and Réunion. Adults are distinguished from *E. markalleni* by having the lateral band broken into distinctly separated squared-off segments, in some cases only on the posterior half of the body (Fig. 8B & 9). Populations of *E. markalleni* are easily recognized by having an unbroken lateral black band, with, at most, some scalloping of the margins of the band (Fig. 8A). A few exceptions are found in some specimens from Taiwan and Japan, notably far distant from the native range of *E. lineatus* in the western Indian Ocean, where the band can be incompletely segmented with coalesced blotches, or, in one case in Japan, where the band is completely broken into segments. The significance of an isolated distant population with the broken lateral band is uncertain. An additional distinction is apparent in juveniles, where juvenile *E. lineatus* have distinct blocks and a bicolor appearance with a more greyish anterior body and a yellowish posterior (Fig. 9B) vs. *E. markalleni* juveniles where the lateral

Figure 8. Preserved specimens: A) *Ecsenius markalleni*, n. sp., female, 40.8 mm SL, WAM P. 24973-001, Western Australia; B) *Ecsenius lineatus*, male, 51.2 mm SL, WAM P.34839-001, Laamu Atoll, Maldives (G.R. Allen).

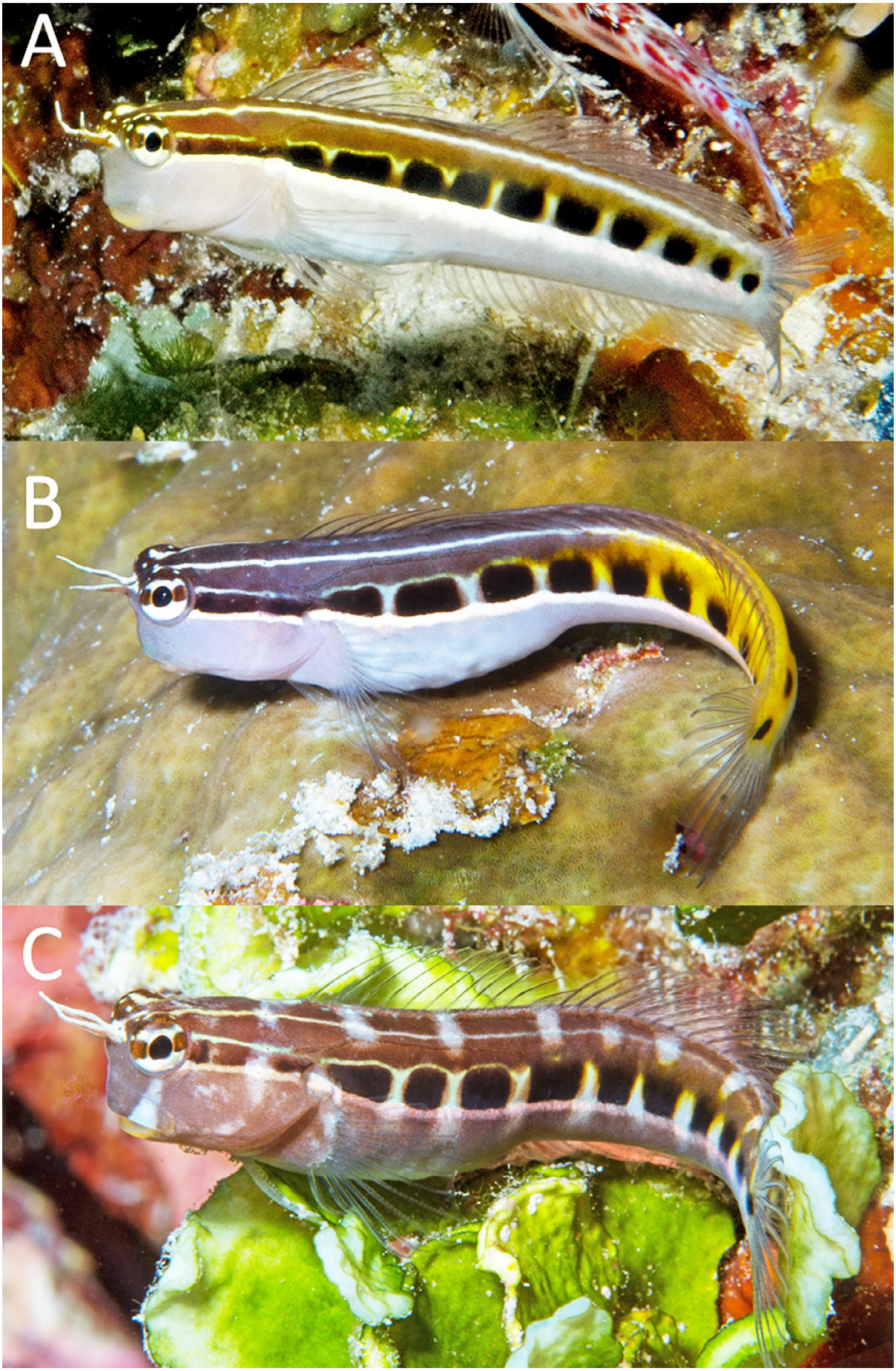

Figure 9. *Ecsenius lineatus* at Laamu Atoll, Maldives: A) about 55 mm SL; B) juvenile, about 20 mm SL; C) adult, about 55 mm SL, transient nocturnal coloration (G.R. Allen, B & C by M.V. Erdmann).

Figure 10. *Ecsenius lineatus*, southwest Indian Ocean:: A, B & C) about 35-55 mm SL, Réunion; D) freshly collected, 56 mm SL, BPBM 15943, Wolmar, Mauritius (F. Libert except D by J.E. Randall)).

band is wide and unbroken and divides the head and body into a brownish dorsal and a white ventrum without a yellowish tail.

The status of the Mauritius and Réunion population remains uncertain; the appearance of the lateral band is somewhat different (Fig. 10). The consistency of markings and the potential genetic divergence in that region needs to be evaluated. Springer (1988) evaluated the meristic values he found useful in distinguishing some *Ecsenius* species, i.e., segmented dorsal and anal fin-rays, vertebrae, and dentary incisor teeth. His counts from the

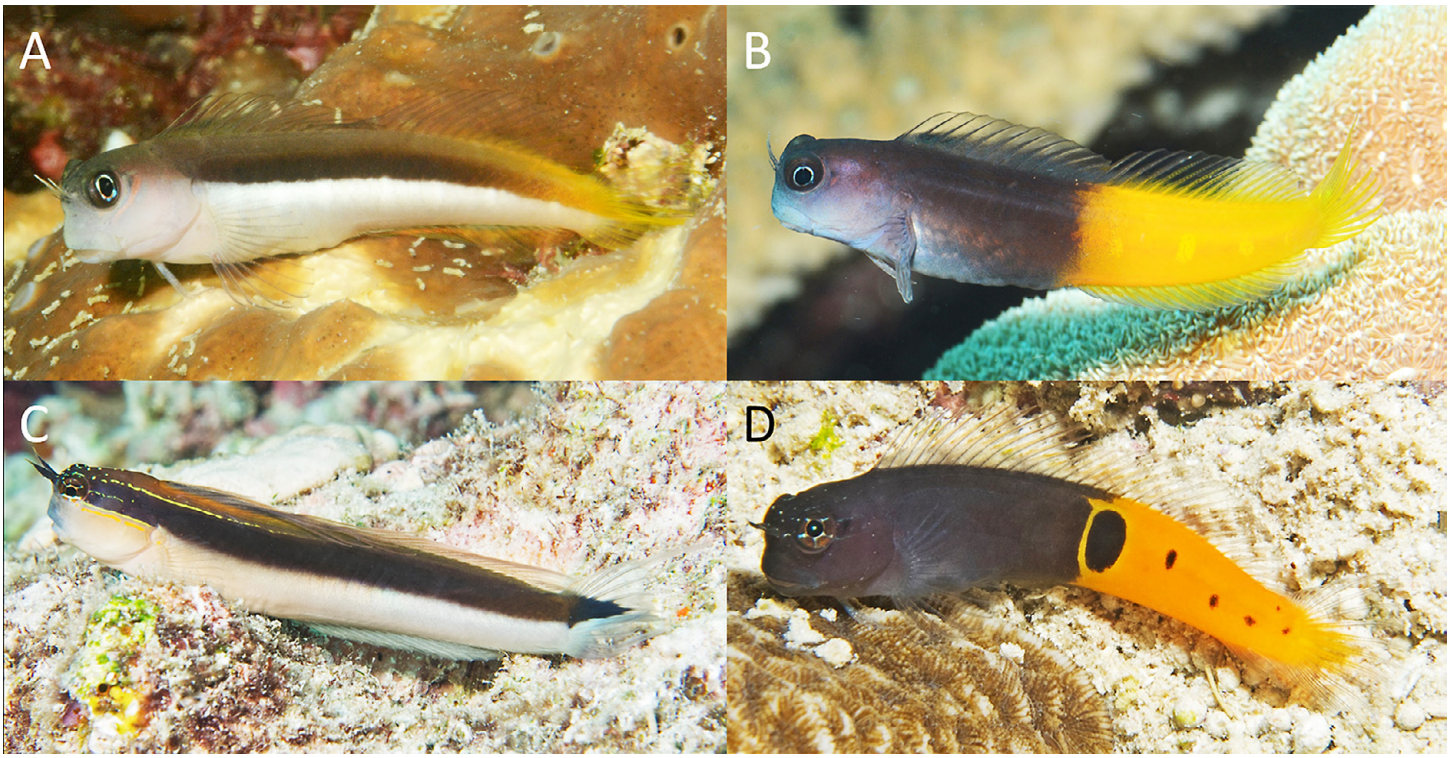

Figure 11. *Ecsenius* spp. similar to *E. markalleni*: *E. bicolor*, West Papua, Indonesia A) banded phase; B) bicolor phase; C) *Ecsenius* sp., Socotra Archipelago C) banded phase; D) bicolor phase(A & B by G.R. Allen; C & D by S.V. Bogorodsky).

TABLE 1

Frequency distributions for selected characters in populations of *Ecsenius markalleni*

Data from Springer (1988) supplemented with 22 specimens from Japan, 6 from W. Australia, 2 from West Papua

	Segmented dorsal-fin rays				Segmented anal-fin rays					Dentary Incisor Teeth						
Location	16	17	18	mean	18	19	20	21	mean	45	46	47	48	49	50	mean
Japan		7	17	17.7		5	18	1	19.8		2	1	1			46.8
Taiwan		11	2	17.2		4	9		19.7	3	2	2	3	3		47.1
Pratas Reef		1	1	17.5			2		20			1				-
Viet Nam			1	--		1			-	1						-
Malaysia	1	3		16.8		4			19		1	1				47.5
Philippines	1	1		16.5	1	1			18.5			1	1	1		46
West Papua	1	1		16.5		1	1		19.5	1	1					45.5
W. Australia	1	5	2	17.1	1	2	5		19.5	2		4			1	46.9
Totals	4	21	10	17.2	2	13	20		19.5	7	6	10	5	4	1	46.9

	Precaudal Vertebrae		Caudal Vertebrae				Total Vertebrae			
Location	10	mean	24	25	26	mean	34	35	36	mean
Japan	4	10		2	2	25.5		2	2	35.5
Taiwan	13	10	2	11		24.8	2	11		34.8
Pratas Reef	1	-			1	-			1	-
Viet Nam	1	-		1		-		1		-
Malaysia	4	10	3	1		24.2	3	1		34.2
Philippines	2	10	2			24	2			34
West Papua	2	10		2		25		2		35
W. Australia	8	10	2	5	1	24.9	2	5	1	34.9
Totals	35	10	9	22	4	24.9	9	22	4	34.9

TABLE 2

Frequency distributions for selected characters in populations of *Ecsenius lineatus*

Data from Springer (1988) supplemented with 32 specimens from Mauritius (except teeth) & two from the Maldives

	Segmented dorsal-fin rays					Segmented anal-fin rays				Dentary Incisor Teeth						
Location	16	17	18	19	mean	18	19	20	mean	45	46	47	48	49	51	mean
Sri Lanka	3		1		17.3	1		3	19.8	1		1	1	1		47.3
Maldives	2	2			16.5	1	1	2	19.3		1	1	2			47.3
Mauritius		12	28	1	17.7	1	9	31	19.7			2	2	1	1	48.3
Reunion			1		-			1	-							-
Totals	5	14	30	1	17.5	3	10	37	19.7	1	1	4	5	2	1	47.7

	Precaudal Vertebrae			Caudal Vertebrae				Total Vertebrae			
Location	10	11	mean	24	25	26	mean	34	35	36	mean
Sri Lanka	4		10			4	25		4		35
Maldives	4		10			4	25		4		35
Mauritius	7	34	10.8	17	19	5	24.7	2	16	23	35.5
Reunion	1		-			1	-		1		-
Totals	16	34	10.7	17	27	6	24.8	2	24	24	35.4

Mauritius population (and only a single specimen for Réunion) compared to Maldives specimens and *E. markalleni* from both our data and Springer's reveals mostly overlapping counts, except for a modal count of 11 precaudal vertebrae at Mauritius vs. uniformly 10 in all other populations, leading to about equal frequencies of 35 and 36 total vertebrae vs. a strong mode of 35 elsewhere (Tables 1 & 2). However, Springer noted an overall tendency in the genus for higher-latitude (>20°) populations to have increased numbers for some meristic characters (also true for many other marine fishes). The addition of genetic data would help evaluate the taxonomic status of that population, it may represent an undescribed species.

Two other species, the widespread *Ecsenius bicolor* (Day, 1888) from the Indo-west Pacific (Fig. 11A & B) and an undescribed *Ecsenius* sp. from Oman and the Socotra Archipelago in the northwestern Indian Ocean (Fig. 11C & D), possess a banded morph that could be mistaken for *E. lineatus* and *E. markalleni*. Those two other species have phases that can be seen on the same reef and intergrade among individuals, including bicolor phases and a banded phase that can fade to uniform. The undescribed northwestern species does not share its range with either *E. lineatus* and *E. markalleni*, By both color-pattern similarity and genetic affinity it is a sister species to *E. pulcher* from adjacent areas and into the Arabian Gulf (S.V. Bogorodsky, pers. comm.).

Genetic analysis. The maximum-likelihood tree based on 551 bp of the mtDNA COI gene sequence from 8 *Ecsenius* species shows divergent lineages for the named species (Fig. 12, Table 3). The new species *E. markalleni* forms a well-supported monophyletic group, containing samples from Kumejima (Okinawa), Yehliu (Northern Taiwan), Western Australia (Dampier Archipelago), and West Papua (Triton Bay). The clade is sister to *E. lineatus* from Maldives, which is also a tight monophyletic clade. The node uniting *E. markalleni* and *E. lineatus* is strongly supported, confirming a close phylogenetic relationship. A nearby cluster contains lineages of *E. gravieri*, *E. pulcher*, and *E. frontalis*. Although Springer's 1(988) review of *Ecsenius* was in the pre-genetic era, he included both *E. gravieri* and *E. pulcher* in the Pulcher Group with *E. frontalis*. Springer's inclusion of both *E. stictus* and *E. yaeyamaensis* in the Yaeyamaensis Group) is also supported since they are recovered as sister species (each monophyletic) and they are sister to *E. dentex* which is also a member of the group. The K2P pairwise genetic

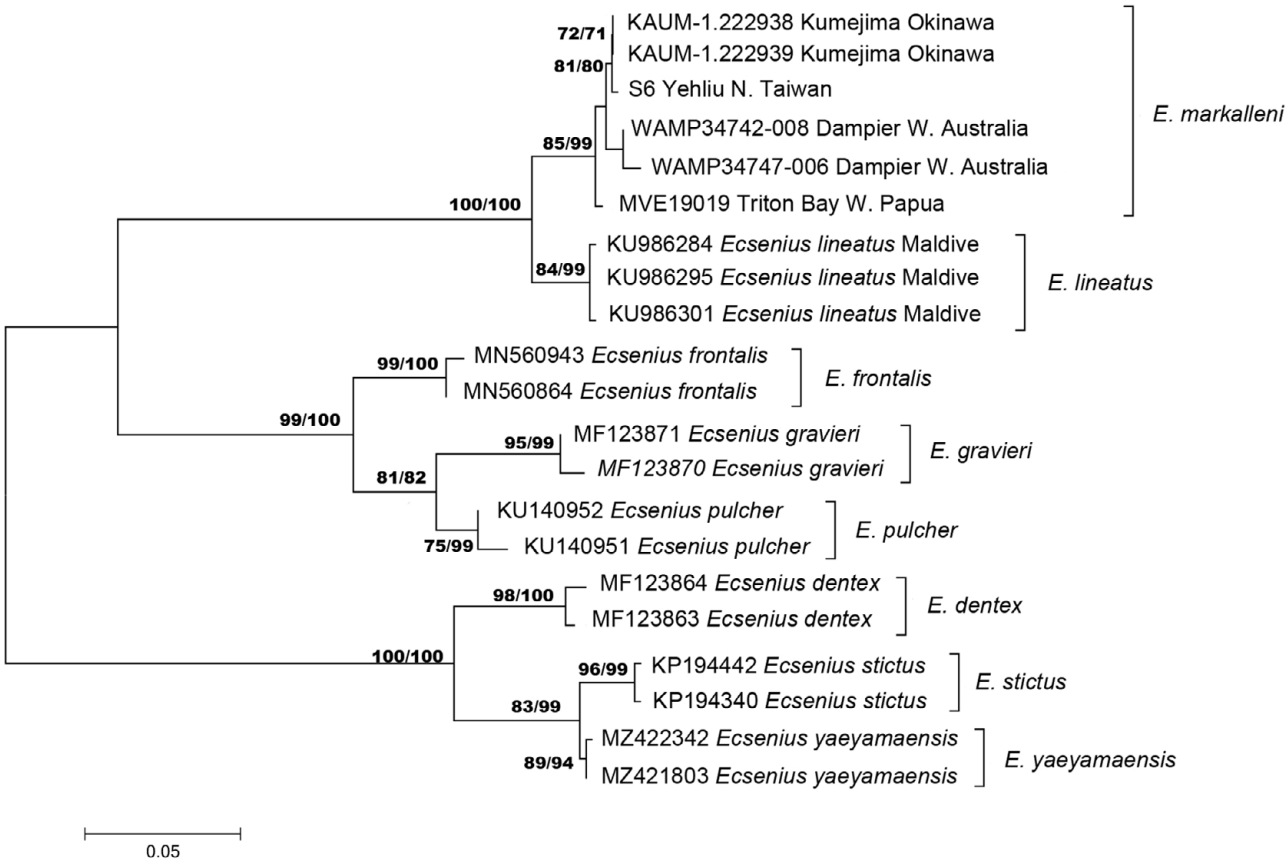

Figure 12. The maximum-likelihood tree based on COI sequences for 8 *Ecsenius* species, including *E. markalleni* n. sp. Bootstrap values from the Maximum Likelihood and Neighbor-Joining methods which were higher than 70% are shown on the branch (ML/NJ).

TABLE 3

Estimates of K2P genetic distance between species pairs among 8 *Ecsenius* species

	Species	1	2	3	4	5	6	7	8
1	*E. gravieri*	—							
2	*E. dentax*	0.177	—						
3	*E. frontalis*	0.077	0.163	—					
4	*E. pulcher*	0.051	0.159	0.065	—				
5	*E. stictus*	0.194	0.078	0.186	0.176	—			
6	*E. yaeyamaensis*	0.198	0.069	0.180	0.169	0.021	—		
7	*E. lineatus*	0.157	0.183	0.149	0.156	0.191	0.193	—	
8	*E. markalleni* n.sp.	0.160	0.182	0.161	0.168	0.195	0.193	0.041	—

distances between the 8 species calculated here shows the greatest interspecific genetic distance is 19.8% between *E. yaeyamaensis* and *E. gravieri*, and the closest interspecific distance is 2.1% between *E. yaeyamaensis* and *E. stictus* (Table 3). The pairwise distance of 4.1% between *E. lineatus* and *E. markalleni* is comparable to other interspecific distances between species.

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References

Allen, G.R. (2009) *Field guide to marine fishes of tropical Australia and south-east Asia*. Western Australian Museum, Perth, Western Australia, 287 pp.

Allen, G.R. & Erdmann, M.V. (2012) *Reef fishes of the East Indies. Volume 2*. Tropical Reef Research, Perth, Western Australia, pp. 424–856.

Allen, G.R. & Erdmann, M.V. (2024) *Reef Fishes of the East Indies. revised second edition. Volume II*. Tropical Reef Research, Perth, Australia, pp. 470–945.

Allen, G.R., Erdmann, M.V. & Liu, S-Y.V. (2019) *Ecsenius springeri*, a new microendemic species of blenny (Teleostei: Blennidae) from the Fakfak Peninsula, West Papua, Indonesia. *Journal of the Ocean Science Foundation*, 32, 68–78. https://doi.org/10.5281/zenodo.2634454

Allen, G.R. & Swainston, R. (1988) *The marine fishes of north-western Australia*. Western Australian Museum, Perth, Western Australia, 201 pp.

Atta, C.J., Coker, D.J., Sinclair-Taylor, T.H., DiBattista, J.D., Kattan, A., Monroe, A.A. & Berumen, M.L. (2019) Conspicuous and cryptic reef fishes from a unique and economically important region in the northern Red Sea. *PLoS One*, 14 (10), e0223365. https://doi.org/10.1371/journal.pone.0223365

Attaran-Farimani, G., Estekani, S., Springer, V.G., Crimmen, O., Johnson, G.D. & Baldwin, C.C. (2016) Validation of the synonymy of the teleost blenniid fish species *Salarias phantasticus* Boulenger 1897 and *Salarias anomalus* Regan 1905 with *Ecsenius pulcher* (Murray 1887) based on DNA barcoding and morphology. *Zootaxa*, 4072 (2), 171–184. https://doi.org/10.11646/zootaxa.4072.2.2

Fricke, R., Eschmeyer, W.N. & van der Laan, R. (Eds.) (2026) *Eschmeyer's catalog of fishes: Genera, Species, References*. San Francisco (California Academy of Sciences). Electronic version accessed 29 April 2026 at http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Kimmerling, N., Zuqert, O., Amitai, G., Gurevich, T., Armoza-Zvuloni, R., Kolesnikov, I., ... & Sorek, R. (2018) Quantitative species-level ecology of reef fish larvae via metabarcoding. *Nature Ecology & Evolution*, 2 (2), 306–316. https://doi.org/10.1038/s41559-017-0413-2

Klausewitz, W. (1962) *Ecsenius lineatus* n. sp. von den Malediven (Pisces, Blenniidae). *Senckenbergiana Biologica*,43 (2), 145–147.

Kuiter, R.H. & Tonozuka, T. (2001) *Pictoral guide to: Indonesian Reef Fishes. Part 2, Caesionidae to Callionymidae*. Zoonetics, Seaford, Australia, 304–622.

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S. & Tamura, K. (2024) MEGA12: Molecular Evolutionary Genetics Analysis version 12 for adaptive and green computing. *Molecular Biology and Evolution*, 41 (12), msae263. https://doi.org/10.1093/molbev/msae263

Masuda, H., Amaoka, K., Araga C., Uyeno, T. & Yoshino, T. (1984) *The fishes of the Japanese Archipelago*. Tokai University Press, Tokyo, 437 pp. & 370 pp.

McKinney, J.F. & Springer, V.G. (1976) Four new species of the fish genus *Ecsenius* with notes on other species of the genus (Blenniidae: Salariini). *Smithsonian Contributions to Zoology*, 236, 1–27.

Pham, M.H., Hoang, D.H., Panfili, J., Ponton, D. & Durand, J.D. (2022) Diversity of fishes collected with light traps in the oldest marine protected area in Vietnam revealed by DNA barcoding. *Marine Biodiversity*, 52 (3), 30. https://doi.org/10.1007/s12526-022-01266-4

Shen, S.-C., Shao, K..-T., Lee, S.-C., Mok, H.-K., Chen, C.-T., Chen, C.-H (1993) *Fishes of Taiwan*. National Taiwan University, Taipei, Taiwan, 956 pp.

Springer, V.G. (1971) Revision of the fish genus *Ecsenius* (Blenniidae, Blenniinae, Salariini). *Smithsonian Contributions to Zoology*, 72, 1–74.

Springer, V.G. (1972) Additions to revisions of the blenniid fish genera *Ecsenius* and *Entomacrodus*, with descriptions of three new species of *Ecsenius*. *Smithsonian Contributions to Zoology*, 134, 1–13.

Springer, V.G. (1988) The Indo-Pacific blenniid fish genus *Ecsenius*. *Smithsonian Contributions to Zoology*, 465, 1–134.

Springer, V.G. (1991) *Ecsenius randalli*, a new species of blenniid fish from Indonesia, with notes on other species of *Ecsenius*. *Tropical Fish Hobbyist*, 39 (12), 100–113.

Springer, V.G. (2002) *Ecsenius niue*, new species of blenniid fish, and new distribution records for other species in the Opsifrontalis species group. *Zootaxa*, 72, 1–6. https://doi.org/10.11646/zootaxa.72.1

Springer, V.G. & Allen, G.R. (2001) *Ecsenius ops*, from Indonesia, and *E. tricolor* from western Philippines and northwestern Kalimantan, new species of blenniid fishes in the stigmatura species group. *Aqua, Journal of Ichthyology and Aquatic Biology*, 4 (4), 151–160.

Springer, V.G. & Allen, G.R. (2004) *Ecsenius caeruliventris* and E. *shirleyae*, two new species of blenniid fishes from Indonesia, and new distribution records for other species of *Ecsenius*. *Zootaxa*, 791, 1–12. https://doi.org/10.11646/zootaxa.791.1.1

Springer, V.G. & Randall, J.E. (1999) *Ecsenius polystictus*, new species of blenniid fish from Mentawai Islands, Indonesia, with notes on other species of *Ecsenius*. *Revue française d'Aquariologie Herpétologie*, 26 (1–2), 39–48.

Steinke, D., deWaard, J., Gomon, M.F., Johnson, J.W., Larson, H.K., Lucanus, O., Moore, G., Reader, S. & Ward, R.D. (2017) DNA barcoding the fishes of Lizard Island (Great Barrier Reef). *Biodiversity Data Journal*, 5, e12409. https://doi.org/10.3897/BDJ.5.e12409

Ward, R.D, Zemlak, T.S., Innes, B.H., Last, P.R. & Hebert, P.D.N. (2005) DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society, B*, 360,1847–1857. https://doi.org/10.1098/rstb.2005.1716

Appendix Table

List of *Ecsenius* specimens and sequences used in this study

Species	GenBank	Source
Ecsenius markalleni		
KAUM – I.222938	PX959550	Kumejima Okinawa, Japan (present study)
KAUM – I.222939	PX959551	Kumejima Okinawa, Japan (present study)
S6	PX959553	Yehliu, N. Taiwan (present study)
WAMP34742008	PX959548	Dampier, W. Australia (present study)
WAMP34747006	PX959549	Dampier, W. Australia (present study)
MVE19019	PX959552	Triton Bay, W. Paupua, Indonesia (present study)
Ecsenius lineatus		
mal15el3	KU986284	Maldives, aquarium trade, Benjamin Victor, via BOLD
mal15el1	KU986295	Maldives, aquarium trade, Benjamin Victor, via BOLD
mal15el2	KU986301	Maldives, aquarium trade, Benjamin Victor, via BOLD
Ecsenius frontalis		
AWCF808	MN560943	Red Sea, Atta et al. 2019
AWCF410	MN560864	Red Sea, Atta et al. 2020
Ecsenius gravieri		
RH1131	MF123871	Eilat, IUI reef, Israel, Kimmerling et al. 2018
RH1094	MF123870	Eilat, IUI reef, Israel, Kimmerling et al. 2018
Ecsenius pulcher		
IRAN 2	KU140952	Iran, Attaran-Farimani et al. 2016
IRAN 1	KU140951	Iran, Attaran-Farimani et al. 2017
Ecsenius dentex		
RH1056	MF123864	Eilat, IUI reef, Israel, Kimmerling et al. 2018
RH1071	MF123863	Eilat, IUI reef, Israel, Kimmerling et al. 2018
Ecsenius stictus		
UG0298	KP194442	Lizard Island, Australia, Steinke et al. 2017
UG0378	KP194340	Lizard Island, Australia, Steinke et al. 2017
Ecsenius yaeyamaensis		
R1A-250417-117A	MZ422342	Viet Nam, Pham et al. 2022
R1A-250417-80A	MZ421803	Viet Nam, Pham et al. 2023