

Review of *Muricanthus* Swainson, 1840 and some Recent species assigned to *Hexaplex* s.s. Perry, 1810, *Hexaplex (Trunculariopsis)* Cossmann, 1921 and *Phyllonotus* Swainson, 1833

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ABSTRACT. A systematic revision of species based on shell morphology and ontogeny is here proposed for some *Hexaplex* Perry, 1810, *Phyllonotus* Swainson, 1833 and all known *Muricanthus* Swainson, 1840. Modifications are indicated in the classification of *Hexaplex* and *Phyllonotus*. Five species are reassigned to *Muricanthus*: *M. ambiguus* (Reeve, 1845), *M. callidinus* Berry, 1958, *M. nigrinus* (Philippi, 1845), *M. radix* (Gmelin, 1791) and the elusive *M. strausi* (A.H. Verrill, 1950). All these species are described, commented on and illustrated. More than twenty other taxa are here assigned or reassigned to *Hexaplex* s.s., *Hexaplex (Trunculariopsis)* Cossmann, 1921 and *Phyllonotus* Swainson, 1833.

RÉSUMÉ. Une révision systématique basée sur la morphologie et l'ontogénie des coquilles est proposée ici pour certaines espèces de *Hexaplex* Perry, 1810 et de *Phyllonotus* Swainson, 1833 et pour toutes les espèces de *Muricanthus* Swainson, 1840. Des modifications sont signalées dans la classification de *Hexaplex* et de *Phyllonotus*. Cinq espèces sont réassignées à *Muricanthus* : *M. ambiguus* (Reeve, 1845), *M. callidinus* Berry, 1958, *M. nigrinus* (Philippi, 1845), *M. radix* (Gmelin, 1791) et le mystérieux *M. strausi* (A.H. Verrill, 1950). Toutes ces espèces sont décrites, commentées et illustrées.

Plus de vingt autres taxons sont ici assignés ou réassignés à *Hexaplex* s.s., *Hexaplex (Trunculariopsis)* Cossmann, 1921 et *Phyllonotus* Swainson, 1833.

INTRODUCTION

The following article was initially intended to separate the species of *Muricanthus* Swainson, 1840, but as the project progressed, the complexity in the classification of *Hexaplex* Perry, 1810 and *Phyllonotus* Swainson, 1833 also became apparent.

The generic and subgeneric usage of *Hexaplex*, *Muricanthus*, *Phyllonotus* and *Trunculariopsis* has been a topic of debate since the original descriptions, but more so in recent years. The following synopsis is a brief account of the recent history and usage of *Muricanthus* and some of those allied groups. Keen (1971) assigned the four Eastern Pacific species, *Muricanthus ambiguus* (Reeve, 1845), *M. callidinus* Berry, 1958, *M. nigrinus* (Philippi, 1845) and *M. radix* (Gmelin, 1791) to *Muricanthus*, in addition to, *Murex*

princeps Broderip, 1833. Vokes (1971, 1988, 1990) assigned the five *Muricanthus* species, here reviewed, in *Hexaplex* Perry, 1810. Kaicher (1973: cards 159 and 186) illustrated two species, *H. nigrinus* and *H. ambiguus* in *Hexaplex*, and *M. radix* in *Muricanthus* (Kaicher, 1980: card 2540). Fair (1976) followed Vokes (1971) and in a short review, Houart (1976) illustrated drawings of the four Eastern Pacific species that were then also assigned to *Hexaplex*, regarding *H. callidinus* (Berry, 1958) as valid. The same year, Radwin & D'Attilio (1976) assigned several species to *Muricanthus*, including *M. radix*, of which, *M. ambiguus*, *M. callidinus* and *M. nigrinus* were considered junior synonyms of that species (Ibid., 1976: 77). The other species assigned to *Muricanthus* were *M. angularis* (Lamarck, 1822), *M. fulvescens* (G.B. Sowerby II, 1834), *M. kuesterianus* (Tapparone

Canefri, 1875), *M. megacerus* (G.B. Sowerby II, 1834), *M. princeps*, *M. saharicus* (Locard, 1897) and *M. varius* (G.B. Sowerby II, 1834), all of which are here assigned to *Hexaplex* s.l. Vermeij (2001: 500) separated *Muricanthus* based on the different labral tooth morphology, specifically, this tooth being the central member of a group of three crenulations on the edge of the outer lip, a characteristic also observed the same year by Houart (2001). The three species assigned to *Muricanthus* by Vermeij (2001) were *M. ambiguus*, *M. nigrinus*, and *M. radix* and later confirmed by Houart (2003). In a review of European Muricidae, Houart (2001: 27) also assigned these three species to *Muricanthus* and neglected to mention *M. callidinus* and *M. strausi* (Verrill, 1950). All other species were then assigned by him to *Hexaplex* s.s., *Hexaplex (Trunculariopsis)* and a doubtful group of West African species. Merle et al. (2011) considered *Muricanthus* a subgenus of *Hexaplex*, with *H. (M.) ambiguus*, *H. (M.) nigrinus*, *H. (M.) radix* and *H. (M.) strausi* as valid, and *Muricanthus callidinus* as a junior synonym of *H. (M.) ambiguus*.

Material

Material examined

All specimens listed and illustrated here are deposited in the first author's collection, unless otherwise cited.

Abbreviations

Terminology used to describe the spiral cords and the apertural denticles after Merle (2001; 2005) and Merle & Houart (2003):

Ab: abapical: away from shell apex toward base along axis or slightly oblique to it; abapertural: away from shell aperture; Ad: adapical: toward shell apex along axis or slightly oblique to it; adapertural: toward shell aperture; P: primary spiral cord; s: secondary spiral cord; t: tertiary spiral cord.

Subsutural area (between the suture and the P1 shoulder cord)

abis: abapical infrasutural secondary cord; IP: infrasutural primary cord; adis: adapical infrasutural secondary cord.

Convex part of teleoconch whorl

P1: shoulder cord; P2–P6: other abapical primary cords; s1–s6: secondary cords (example: s1 - secondary cord between P1 and P2; s2 - secondary cord between P2 and P3, etc.); t: tertiary cord (example t1 - tertiary cord between P1 and s1 or between s1 and P2); t2 - tertiary cord between P2 and s2 or s2 and P3, etc.).

Siphonal canal

ADP: adapertural primary cord on the siphonal canal; ads: adapertural secondary cord on the siphonal canal (between ADP and MP); MP: median primary cord on the siphonal canal; ms: median secondary cord on the

siphonal canal (between MP and ADP); ABP: abapertural primary cord on the siphonal canal; abs: abapertural secondary cord on the siphonal canal.

Repositories

CASIZ: California Academy of Sciences, Invertebrate Zoology, San Francisco, California, U.S.A.

RH: collection of Roland Houart

SYSTEMATICS

Family **Muricidae** Rafinesque, 1815

Subfamily **Muricinae** Rafinesque, 1815

Genus **Hexaplex** Perry, 1810. Type species by subsequent designation (Iredale, 1915: 469): *Hexaplex foliacea* Perry, 1811 (= *Murex cichoreum* Gmelin, 1791), Philippines.

Subgenus **Hexaplex** s.s.

Diagnosis

The species of *Hexaplex* s.s. have a small P2 spiral cord as illustrated by Merle et al. (2011: 79, fig. A; 82, figs A–D and 86, fig. A). The P2 spiral cord starts from the first teleoconch whorl and is of the same strength as the P1 and P3 cords. It is only from the third whorl onwards that this cord starts to usually and gradually decrease in size and becomes similar in strength to a secondary or even tertiary cord on the last whorl, between the normal sized P1 and P3 cords. A small or strong labral tooth is present in *Hexaplex* s.s. and this labral tooth appears at the end of the groove between the P4 and P5 spiral cords, more particularly between s4 and P5 (Fig. 13H & J).

Discussion

Hexaplex bozzadamii (Franchi, 1990), *H. cichoreum* (Gmelin, 1791), *H. conatus* (McMichael, 1964), *H. kuesterianus*, *H. rileyi* D'Attilio & Myers, 1984, *H. stainforthi* (Reeve, 1843) and the West African *H. angularis*, are here assigned to *Hexaplex* s.s.

Subgenus **Trunculariopsis** Cossmann, 1921. Type species by original designation: *Murex trunculus* Linnaeus, 1758, Mediterranean.

Discussion

The labral tooth is absent in *Hexaplex (Trunculariopsis)* compared to the presence of this tooth in both *Hexaplex* s.s. and *Muricanthus*.

Hexaplex bifasciatus (A. Adams, 1853), *H. brassica* (Lamarck, 1822), *H. duplex* (Röding, 1798), *H. fulvescens*, *H. pecchiolianus* (d'Ancona, 1871), *H. princeps* (Broderip, 1833), *H. rosarium* (Röding, 1798), *H. trunculus* (Linnaeus, 1758) and *H. varius* are here regarded as *Hexaplex (Trunculariopsis)*.

Chicoreus clausii (Dunker, 1879) is also assigned to *Hexaplex (Trunculariopsis)* as a three varical form of *H. (T.) varius*. Additionally, two species and one subspecies from West Africa, assigned to *Hexaplex* s.s. in MolluscaBase (2021), remain quite doubtful in any of these genera. These three taxa, *H. megacerus*, *H. saharicus saharicus* and *H. saharicus ryalli* Houart, 1993 are here tentatively assigned to *Hexaplex (Trunculariopsis)* until further phylogenetic studies can be conducted.

Houart (2001) recognized some striking resemblances, such as the number of varices, the morphology of the varical fronds and of the aperture, between these west African species and two fossil taxa included in *Chicoreus* by Vokes (1963, 1965, 1990): *Chicoreus lepidotus* (Vokes, 1963) from the lower Miocene of Florida, and *C. bourgeoisi* (Tournouër, 1875) from the Miocene of France. As suggested by Houart (2001: 26), *H. megacerus* and *H. saharicus* s.l. are presumed to be descendants of those Miocene species.

Genus *Muricanthus* Swainson, 1840, n.n. for *Centronotus* Swainson, 1833 (not *Centronotus* Schneider, 1801). Type species by subsequent designation (ICZN, 1970): *Murex radix* Gmelin, 1791, Gulf of California to southern Ecuador.

Aaronia A.H. Verrill, 1950. Type species by monotypy: *Murex (Aaronia) strausi* Verrill, 1950, Dominica and Martinique, Lesser Antilles.

Diagnosis

Shell large, up to 197 mm in length, spire low to moderately high, last teleoconch whorl broad, with seven to ten varices. Spiral cords with short, frondose or acute spines at intersection of axial ribs. Aperture large, broad, outer apertural lip weakly convex in shape, more prominent between P3 and P4, with a weak or strong labral tooth extending from the groove between the secondary s3 and tertiary t3 spiral cords. Columellar lip almost entirely adherent to shell, low parietal callus at adapical extremity. Siphonal canal broad, open abaxially, short or moderately long. Spiral cord coloration black or brown, white between cords.

Discussion

The species of *Muricanthus* also have a small P2 spiral cord as illustrated by Merle et al. (2011: 79, fig. A; 82, figs A–D and 86, fig. A) and here (Fig. 2E). Similarly, as with *Hexaplex* s.s., the P2 spiral cord starts from the first teleoconch whorl and is of the same strength as the P1 and P3 cord, as can be seen here (Fig. 2E). The cord also gradually decreases in size beginning on the third whorl and is similar in strength to secondary or tertiary cords on the final whorl, also between the larger P1 and P3 cords.

A small or strong labral tooth is also present in *Muricanthus* and appears at the end of the groove between P3 and P4, more particularly between s3 and

t3, which are the secondary and tertiary cords between P3 and P4 (Figs 2B; 4E; 7O; 8B, G). Vermeij (2001: 500) separated *Muricanthus* based on the different labral tooth morphology, this tooth being the central member of a group of three more expanded crenulations on the edge of the outer lip, as was also observed the same year by Houart (2001).

Muricanthus is primarily known as an intertidal genus with few records of subtidal specimens.

In the chresonymy proposed below, specimens were determined based on published imagery, most references without illustrations were not taken into account. Most juvenile specimens figured by Tryon (1880) and Merle et al. (2011) are here omitted due to their questionable status.

Muricanthus ambiguus (Reeve, 1845)

Figs 1; 2A–B; 4A–L

Murex ambiguus Reeve, 1845a: 86–87; Reeve, 1845b: pl. 13, fig. 51.

Murex melanoleuca Mörch, 1852: 96.

Murex nitidus (non Broderip, 1833) — Reeve, 1845b: pl. 17, fig. 70a–b.

Murex (Phyllonotus) nitidus (non Broderip, 1833) — Tryon, 1880: fig. 242.

Phyllonotus nitidus (non Broderip, 1833) — Smith, 1944: 24, fig. 294.

Muricanthus ambiguus — Keen, 1958: 354, fig. 343 (left); Keen, 1971: 521–523, fig. 999 (right).

Hexaplex ambiguus — Vokes, 1971: 15; Fair, 1976: 20, pl. 12, fig. 149; Houart, 1976: figured.

Muricanthus callidinus (non Berry, 1958) — Keen, 1971: fig. 1000 (lower right); Dance, 1974: 126, figured.

Muricanthus radix (non Gmelin, 1791) — Radwin & D'Attilio, 1976: pl. 12, fig. 1.

Murex (Muricanthus) ambiguus — Eisenberg, 1981: 92, fig. 11.

Hexaplex (Muricanthus) ambiguus — Merle et al., 2011: 83, text fig. 34A, pl. 34, fig. 7–11.

Hexaplex (Muricanthus) radix (non Gmelin, 1791) — Merle et al., 2011: pl. 34, fig. 13.

Type material. Not located.

Type locality. Unknown.

Material examined. West Mexico, Sonora, Guaymas (1); West Mexico, Colima, Manzanillo (1); West Mexico, Guerrero, Acapulco (1); Western Mexico (no other data) (2); Costa Rica, Puntarenas Province, Palo Seco (1 juv.); West Panama, Panama Oeste Province, Taboga Island (1 juv.); West Panama, Panama Province, Pearl Islands (3).

Distribution. Central and southern Gulf of California (Hendrickx et al., 2005; Houart & Hendrickx, 2020) to the Pearl Islands, Panama Province, Panama (herein), known as an intertidal species (Fig. 1).

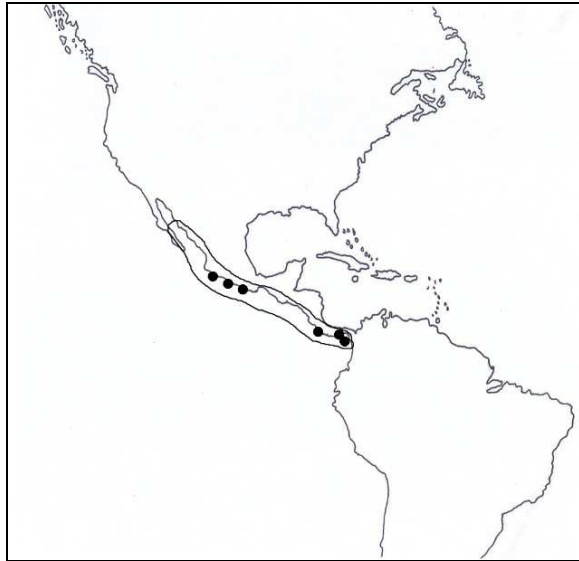


Figure 1. Distribution of *Muricanthus ambiguus* (black circles: material examined)

Description. Shell up to 197 mm in length (Pisor, 2008: 100), average size 80–100 mm at maturity. Shell large, profile rounded, weakly shouldered, final whorl broad and globose. Spire low or moderately high, protoconch features unknown.

Axial sculpture of last teleoconch whorl usually with 7 or 8 broad, low laying spinose varices, each with 6 moderately long, narrow, frondose and weakly abaperturally recurved IP, P1, P3, P4, P5, MP spines, extending from primary cords and shorter, narrower spines extending from P2 primary and secondary cords. Spiral sculpture of weak, yet broad, low profile primary cords, narrower P2 and P6 cords of same approximate strength as in secondary cords.

Aperture broadly ovate, columellar lip smooth, completely adherent to shell except on small abapical portion, outer lip strongly denticulate, strong labral tooth abapically, extending from groove between s3 and t3. Siphonal canal moderately long, spines abapically bent, broad, open abaxially, dorsally curved in a subtle fashion. ADP spine long and broad,

followed by moderately long MP, occasional short ads spine present.

Shell white with black spiral cords and spines, siphonal canal similar, occasionally marked entirely with black coloration.

Remarks. The spiral sculpture is similar in nearly all specimens examined in this study, except one, where the longest subsutural spine extends from the secondary adis cord and not from the primary IP cord. Comparisons to *Muricanthus callidinus* and *M. radix* can be reviewed under the profiles provided below. This species is syntopic with *M. radix* in the Pearl Islands, West Panama.

***Muricanthus callidinus* Berry, 1958**

Figs 2E; 3; 5A–D; 7A–E, G–O

Muricanthus callidinus Berry, 1958: 84; Keen, 1958: 355, fig. 343a; Keen, 1971: 523, fig. 1000 (upper left); Hertz, 1984: 14, fig. 23.

Murex nitidus Broderip, 1833: 176; G.B. Sowerby II, 1834: pl. 58, fig. 4 (not *Murex nitidus* Pilkington, 1804).

Hexaplex callidinus — Vokes, 1971: 28; Fair, 1976: 29, pl. 11, fig. 136; Houart, 1976: figured.

Type material. Holotype, CASIZ 043992, height 80.9 mm, width 69.1 mm (Fig. 7A–E).

Type locality. Culebra Bay, Guanacaste Province, Costa Rica, Eastern Pacific Ocean.

Material examined. Costa Rica, Gulf of Nicoya, Puntarenas Province, Cedros Island (1 juv.); West Panama, Panama Province, Pearl Islands, Bayoneta Island (6 juv.); West Panama (no other data) (1 juv.); Peru, Tumbes Province, off Puerto Pizarro (2 subadults); locality unknown (1 juv.).

Distribution. Guatemala to Costa Rica (Keen, 1971: 523) to off Puerto Pizarro, Tumbes Province, Peru (herein), to 6 m depth (DuShane & Poorman, 1967: 428) (Fig. 3).

Figure 2

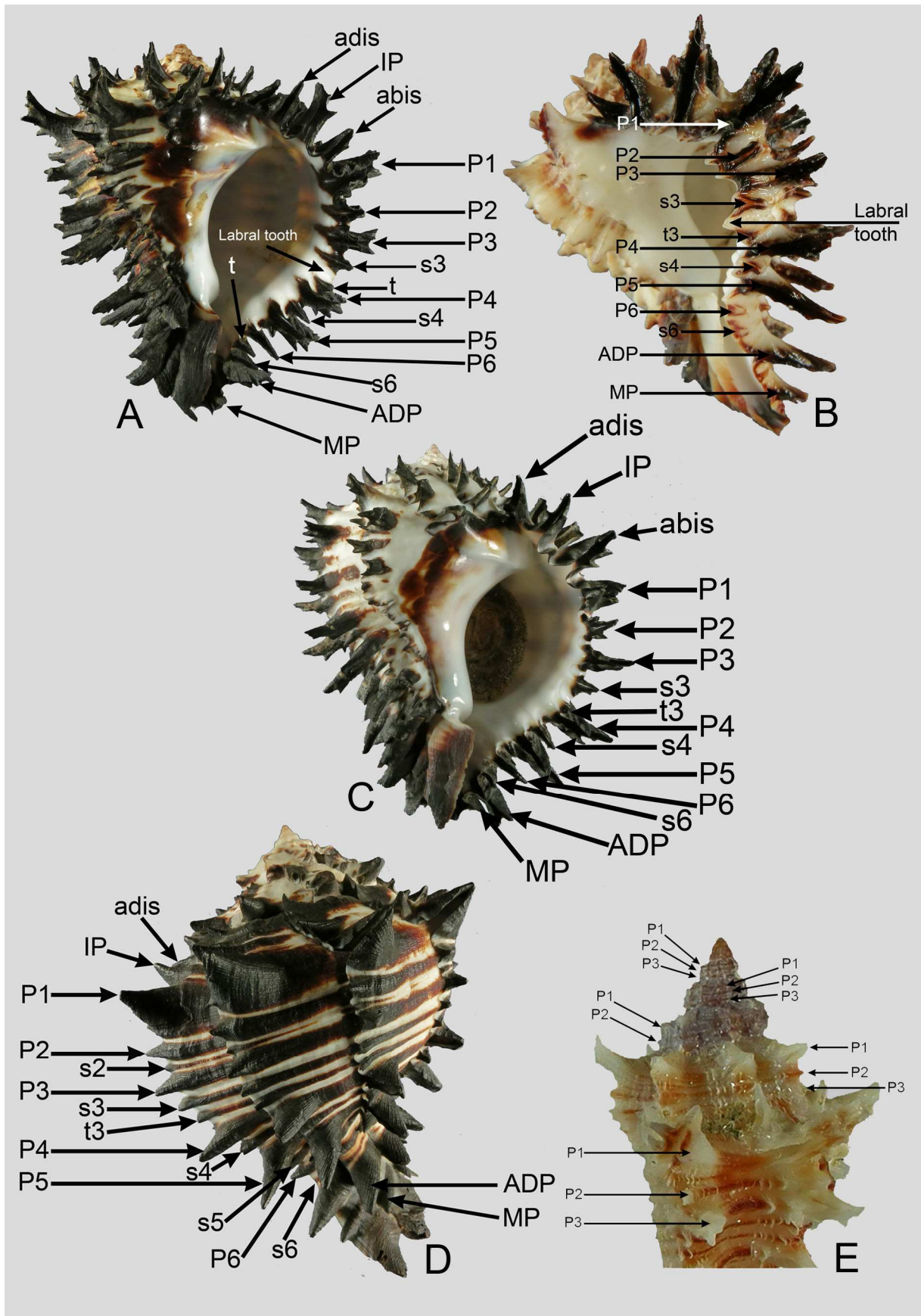
A–E. Spiral cords morphology of Panamic *Muricanthus* species.

A–B. *Muricanthus ambiguus* (Reeve, 1845). A. West Mexico, 93.2 mm; B. Taboga Island, Panama Oeste Province, Panama, 38.8 mm.

C. *Muricanthus radix* (Gmelin, 1791), Pearl Islands, Panama Province, Panama, 88.4 mm.

D. *Muricanthus nigrinus* (Philippi, 1845), Guaymas, Sonora, Mexico, 131.0 mm.

E. *Muricanthus callidinus* Berry, 1958, Cedros Island, Gulf of Nicoya, Puntarenas Province, Costa Rica, 24.4 mm.



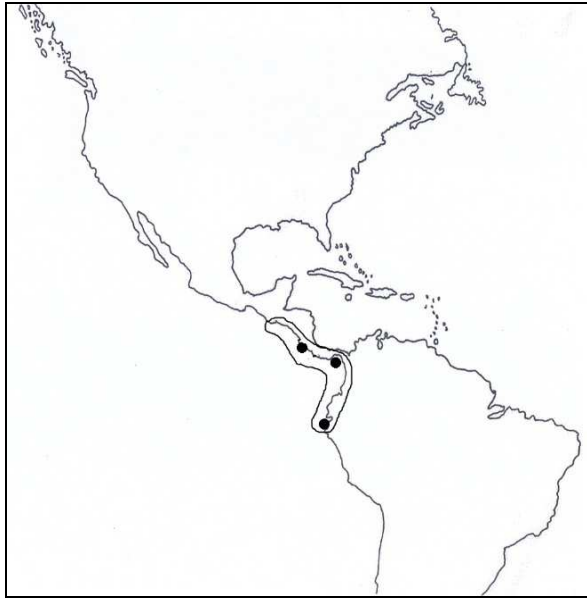


Figure 3. Distribution of *Muricanthus callidinus* (black circles: material examined)

Description. Shell up to 99.4 mm in length at maturity (Berry, 1958), large sized, broad, strongly shouldered, last whorl broadly triangular. Spire moderately high, protoconch conical, of 3 or more whorls with sinusigeral notch (Fig. 7M).

Axial sculpture of last teleoconch whorl usually consisting of 6 or 7 broad, low profile, spinose varices, each with 6 moderately long, narrow, frondose, weakly abaperturally recurved adis, P1, P3, P4, P5, MP spines extending from secondary and primary cords and with shorter, narrower spines extending from P2 primary cord and other secondary cords. Spiral sculpture of weak, broadly spaced, primary cords, except narrower P2 and P6 cords of approximately same strength as secondary cords.

Aperture broadly ovate, columellar lip smooth, completely adherent to shell except on small abapical portion, outer lip strongly denticulate, distinct labral tooth abapically, extending from groove between s3 and t3. Siphonal canal moderately long with abapically bent spines, moderately broad, open abaxially, dorsally curved and weak. ADP spine long

and broad followed by MP spine of moderate length, occasional short ads present.

Shell white with brown spiral cords and spines. Siphonal canal lighter colored, darker brown on anterior tip.

Remarks. The holotype illustrated by Fair (1976: pl. 11, fig. 136) and Hertz (1984: 14, fig. 23) is here figured in color (Fig. 7A–E). The P2 spiral cord is quite wide in the holotype as seen in other species such as *M. ambiguus*, an unusual but not exceptional circumstance. The longest spine that extends from the subsutural spiral cords originates from the secondary adis cord, and not from the primary IP cord as in other species, while the adis spiral cord is present in young specimens, which becomes obsolete in shell development. The holotype has a split IP cord on the last teleoconch whorl.

Muricanthus callidinus differs from *M. ambiguus* in having brown colored spiral cords instead of black, and in having more strongly shouldered teleoconch whorls. The shell is more triangular and has a weaker subsutural slope.

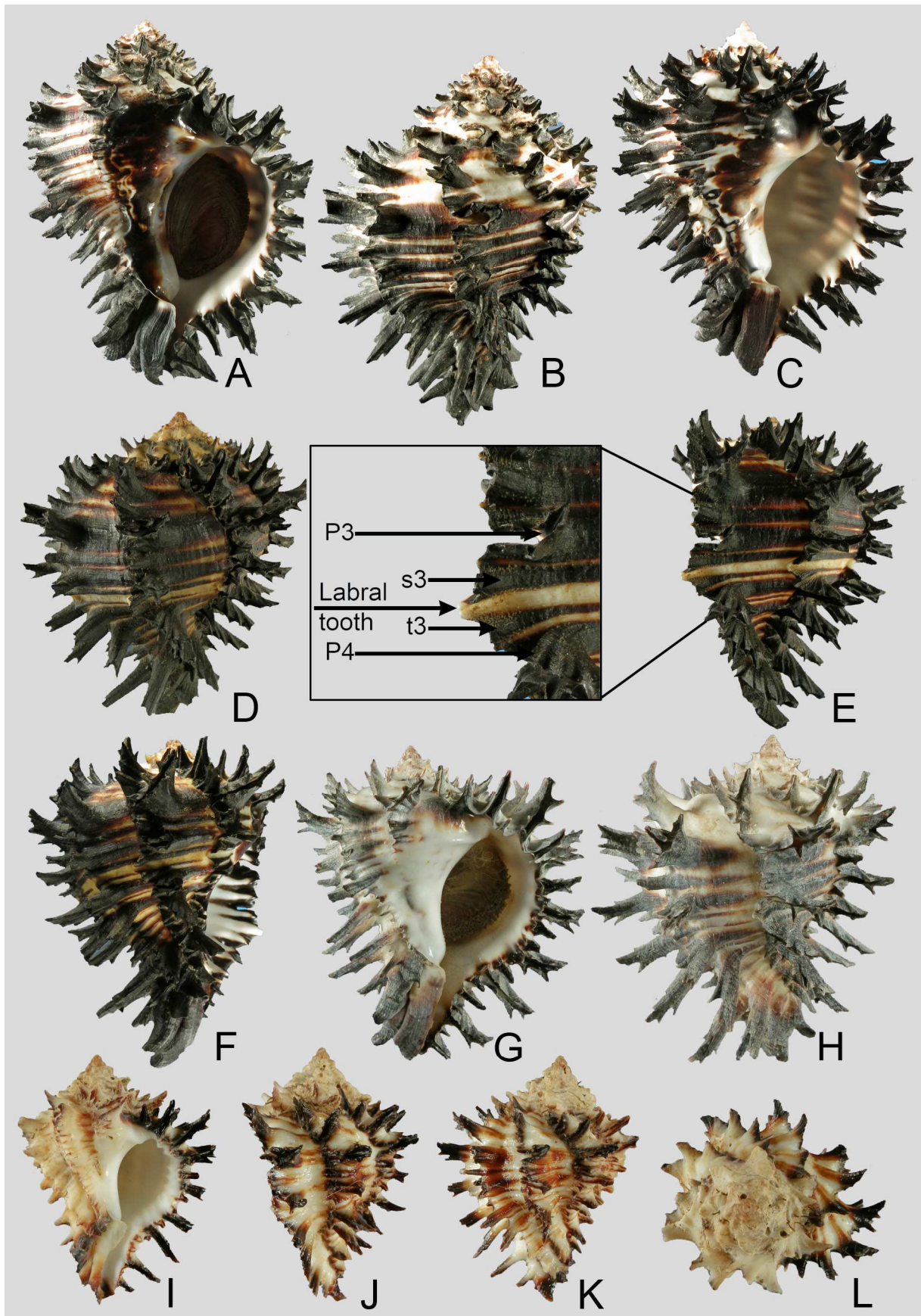
Muricanthus callidinus is also similar to *Hexaplex princeps* (Figs 7F; 13A–F), which has approximately the same outline and coloration. However, even in young specimens of *M. callidinus*, it differs in having the outer apertural margin ornamented with a strong labral tooth extending from a groove between s3 and t3 (Fig. 7B, H, O), while *H. princeps* has an outer apertural lip with small denticles but no labral tooth (Figs 7F; 13C). The axial ribs in *M. callidinus* are lower, narrower and the shell is slightly less shouldered, more globose in appearance than in *H. princeps*.

The name *Murex nitidus* Broderip, 1833 is here considered invalid and a synonym of *Muricanthus callidinus* based on the original description of a 28 mm shell and the figure illustrated by Sowerby (1834: pl. 58, fig. 4), both matching young specimens of *M. callidinus* figured herein (Fig. 5A–D).

This species was listed by DuShane & Poorman (1967: 428) from Guaymas, Sonora, Mexico which is questionable and needs verification.

Figure 4

A–L. *Muricanthus ambiguus* (Reeve, 1845). A–B. near Manzanillo, Colima, Mexico, 148.3 mm; C. West Mexico, 128.4 mm; D–F. West Mexico, 93.2 mm; G–H. Pearl Islands, Panama Province, Panama, 63.0 mm; I–L. Taboga Island, Panama Oeste Province, Panama, 38.8 mm.



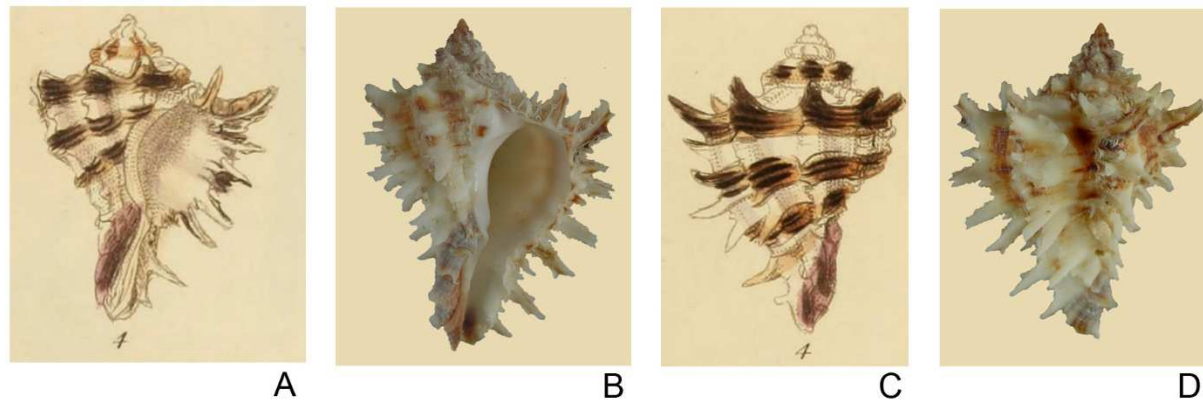


Figure 5 A–D. *Muricanthus callidinus* Berry, 1958 (juvenile). A, C. *Murex nitidus* Broderip, 1833, reproduced from G.B. Sowerby, 1834: pl. 58, figs 4 (Image from Biodiversity Heritage Library, www.biodiversitylibrary.org); B, D. Cedros Island, Gulf of Nicoya, Costa Rica, 24.4 mm, RH.

Muricanthus nigrinus (Philippi, 1845)
Figs 2D; 6; 8A–J

Murex nigrinus Philippi, 1845: 191, pl. 1, fig. 1; Reeve, 1845b: pl. 12, fig. 47; G.B. Sowerby II, 1879: pl. 397 (*Murex* pl. 18), fig. 169; Sorenson, 1943: 4, pl. 4.

Muricanthus nigrinus — Keen, 1958: 356, fig. 344; Keen, 1971: 523, fig. 1001; Dance, 1974: 126, figured; Farmer, 1987: 42, fig. 1; Vokes, 1971: 74.

Hexaplex nigrinus — Fair, 1976: pl. 12, fig. 148; Houart, 1976: figured; Abbott & Dance, 1982: 138, figured; Wye, 1991: 132, figured; Trego, 1996: 46–47, figs 1–2; Bertsch & Rosas, 2016: 215, fig. 467.

Muricanthus radix (non Gmelin, 1791) — Radwin & D’Attilio, 1976: pl. 12, fig. 2.

Murex (Muricanthus) nigrinus — Eisenberg, 1981: 92, fig. 12.

Hexaplex (Muricanthus) nigrinus — Merle et al., 2011: 84, pl. 34, figs. 1–6.

Hexaplex (Muricanthus) radix (non Gmelin, 1791) — Merle et al., 2011: pl. 34, fig. 12.

Type material. Not located.

Type locality. Mexico, Pacific coast.

Material examined. Mexico, Baja California, south of San Felipe, Percebu Lagoon (1); Mexico, Baja California, San Felipe (1); Mexico, Baja California Sur, Mulege (3); Mexico, Sonora, Guaymas (2); Mexico, Baja California (no other data) (1).

Distribution. Two suspect records of live specimens from Bird Rock, San Diego, California (Farmer, 1987; Trego, 1996), Bahia Magdalena, Baja California (Skoglund, 2002: 105) throughout the Gulf of California (Hendrickx et al., 2005; Houart & Hendrickx, 2020) to off Manzanillo, Colima, Mexico (Skoglund, 2002: 105), common in the intertidal, uncommonly dredged to 31 m (DuShane & Poorman, 1967: 428). One specimen from Guatemala was illustrated by Merle et al. (2011: pl. 34, fig. 4) and the locality is questionable and needs confirmation (Fig. 6).

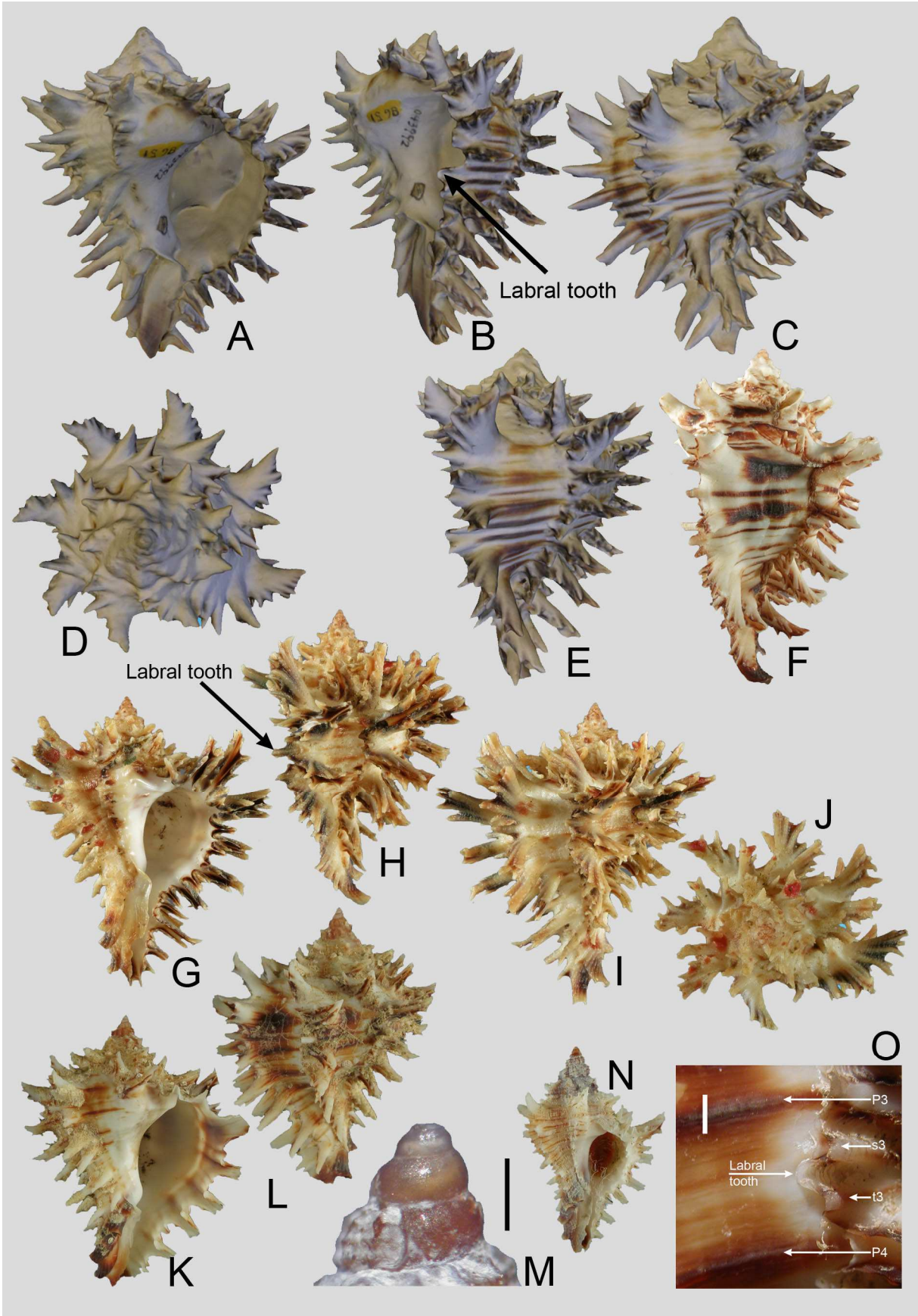


Figure 6. Distribution of *Muricanthus nigrinus* (black circles: material examined)

Figure 7 (scale bars: N: 500 μ m; O: 1 mm)

A–E, G–O. *Muricanthus callidinus* Berry, 1958. A–E. Culebra Bay, Guanacaste Province, Costa Rica, Holotype CASIZ 043992, 82.45 mm (photo: California Academy of Sciences); G–J. off Puerto Pizarro, Tumbes Province, Peru, 50.2 mm; K–L, O. West Panama, 34.8 mm; M–N. Bayoneta Island, Pearl Islands, Panama Province, Panama, 16.6 mm.

F. *Hexaplex (Trunculariopsis) princeps* (Broderip, 1833). Mazatlan, Sinaloa, Mexico, 91.6 mm.



Description. Shell up to 160 mm, average size 100–120 mm at maturity, and probably reaching 200 mm (Pisor, 2008: 109), large sized, profile rounded, strongly shouldered on final whorl, broadly triangular and globose. Spire low to moderately high, protoconch unknown.

Axial sculpture of last teleoconch whorl usually consisting of 6–8 broad, low profile, spinose varices, each with 6 moderately long, broad, straight, triangularly shaped IP, P1, P3, P4, P5, MP primary spines extending from primary cords with shorter, narrower spines extending from adis, abis, P2 and other secondary cords, longest and broadest spines originating from P1, P4, P5 and MP. Spiral sculpture of weak but broad, low primary cords, P1, P4, P5 and IP spiral cords broadest.

Aperture broad, ovate, columellar lip smooth, completely adherent to shell except on small abapical portion, outer lip strongly denticulate, labral tooth weak abapically, extending from groove between s3 and t3 cords. Siphonal canal broad, open abaxially, moderately long or long with abapically bent spines, dorsal end weakly curved, ADP spine short, followed by broad and long MP spine, occasional short ads.

Shell white with black spiral cords and spines, occasionally black in entirety (Fig. 8D–E).

Remarks. *Muricanthus nigrinus* differs from other species in having a more triangular shape with short, non-foliose varical spines, of which the most impressive extends from cords P1 and P5, a labral tooth less obvious than other species, and a comparatively longer siphonal canal. Spiral cord P1 broadest, P2 and P3 similar in size, a rare circumstance in other *Muricanthus* species.

Muricanthus radix (Gmelin, 1791)

Figs 2C; 9; 10A–K

Murex radix Gmelin, 1791: 3527; Reeve, 1845b: pl. 17, fig. 69; Chenu, 1859: 133–134, figs. 570, 572; G.B. Sowerby II, 1879: 33, pl. 397 (*Murex* pl. 18), fig. 170.

Murex (Phyllonotus) radix — Tryon, 1880: 105–106, pl. 27, figs. 244.

Phyllonotus radix — Smith, 1944: 24, fig. 290.

Hexaplex (Muricanthus) radix — Wenz, 1941: 1088, fig. 3091; Merle et al., 2011: 84, text fig. 34, pl. 34, fig. 15.

Phyllonotus nigrinus (non Philippi, 1845) — Smith, 1944: 24, fig. 291 (left & right).

Murex (Muricanthus) radix — Eisenberg, 1981: 92, figs. 9 & 9A; Monfils, 2000: 24, pl. 2, fig. 90.

Muricanthus radix — Keen, 1958: 356, fig. 347; Keen, 1971: 523, fig. 1003; Dance, 1974: 127, figured; Radwin & D'Attilio, 1976: 77–78, pl. 12, fig. 9; Myers & D'Attilio, 1986: 64, protoconch figured; Kaicher, 1980: card 2540.

Hexaplex radix — Vokes, 1964: 11–12, pl. 1, fig. 16; Vokes, 1971: 89; Fair, 1976: 71, pl. 12, fig. 150; Houart, 1976: figured; Abbott & Dance, 1982: 138, figured; Wye, 1991: 132, figured; Coltro, 2000: 8, figured; Wall, 2016: 31–32, 34, figured.

Muricanthus ambiguus (non Reeve, 1845) — Keen, 1971: fig. 999 (left).

Murex (Hexaplex) nigrinus (non Philippi, 1845) — Abbott, 1974: 174, fig. 1835a.

Murex (Hexaplex) radix — Abbott, 1974: 174, color pl. 8, fig. 1836.

Murex (Muricanthus) callidinus (non Berry, 1958) — Eisenberg, 1981: 92, fig. 10.

Type material. Not located.

Type locality. Unknown.

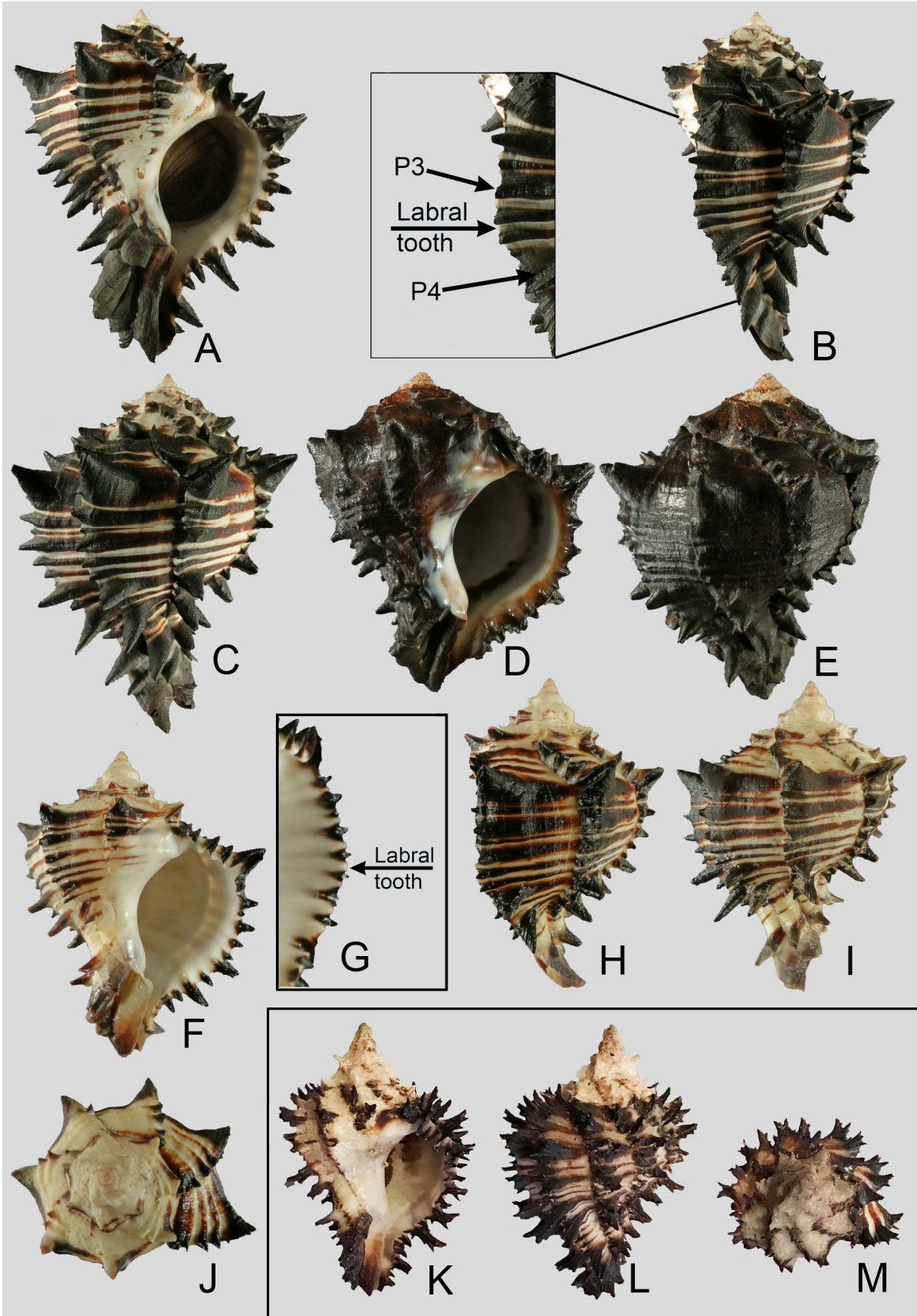
Material examined. West Mexico, Colima, Manzanillo (1); El Salvador (1); Costa Rica, Puntarena Province, Venado Island (1 juv.); West Panama, Panama Province, Pearl Islands, Pedro Gonzales Island, (2); West Panama, Panama Province, Kobbe Beach (1 juv.); West Panama, Panama Province, Pearl Islands (4); West Panama (no other data) (2); Ecuador, Guayas Province, near Guayaquil (1).

Distribution. Bahia Magdalena, Baja California Sur (Strong & Hanna, 1930: 12) to the southern Gulf of California (Hendrickx et al. 2005; Houart & Hendrickx, 2020) to Paita, Piura Region, Peru (Hertlein & Strong, 1955: 257), known as an intertidal species (Fig. 9).

Figure 8

A–J. *Muricanthus nigrinus* (Philippi, 1845). A–C. Guaymas, Sonora, Mexico, 131 mm; D–E. Gulf of California, 98.3 mm; F–J. San Felipe, Baja California, Mexico, 80.4 mm.

K–M. *Muricanthus strausi* (A.H. Verrill, 1950), Dominica, Lesser Antilles, 46.5 mm (coll. V. Attolino).



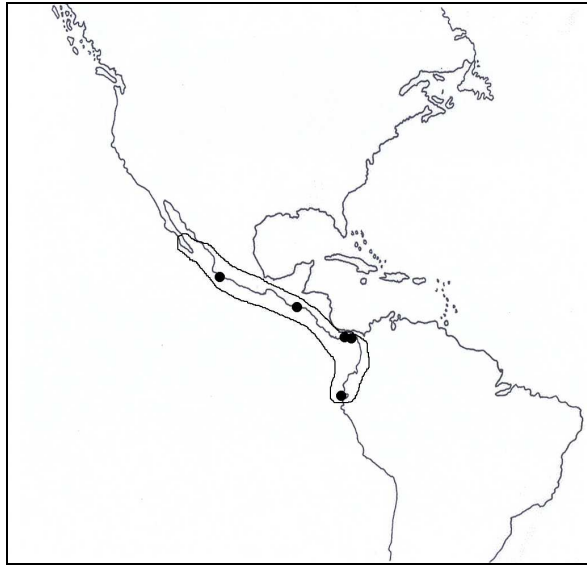


Figure 9. Distribution of *Muricanthus radix* (black circles: material examined)

Description. Shell up to 180 mm in length, average size 80–90 mm at maturity, large sized, heavy, profile rounded, shoulder weak, final whorl broad and globose in shape. Spire low or moderately high, protoconch conical, of 2.75 whorls (Myers & D'Attilio, 1986: 64).

Axial sculpture of last teleoconch whorl primarily consisting of 8–10 broad, low laying, but spinose varices, each with 7 short or moderately long, narrow, weakly frondose, very weak abaperturally recurved adis, IP, P1, P3, P4, P5, MP spines and shorter, narrower spines extending from P2 primary cord and secondary cords. Spiral sculpture of weak, broad, low primary cords except narrower P2 and P6 cords of approximately same strength as secondary cords.

Aperture broad, ovate, columellar lip smooth, completely adherent to shell except on small abapical portion, outer lip strongly denticulate, labral tooth strong abapically, extending from groove between s3 and t3. Siphonal canal short or moderately long with broad spines bent abapically, open abaxially, weakly curved near dorsal end. ADP spine long, broad, followed by moderately long or short MP spine.

Shell color white with black spiral cords and spines, siphonal canal occasionally all black.

Remarks. *Muricanthus radix* differs from *M. ambiguus* in having a more globose, thicker, and heavier shell. Similar sized specimens of *M. ambiguus* are always 33–70% lighter in weight than *M. radix*. The more convex subsutural ramp on final teleoconch whorl, more acute apex, shorter and less frondose axial spines and a comparatively shorter siphonal canal also separate *M. radix* from *M. ambiguus*. This species appears to be syntopic with *M. ambiguus* in the Pearl Islands, West Panama.

Muricanthus strausi (A.H. Verrill, 1950)
(new comb.)
Figs 8K–M; 11; 12

Murex (*Aaronia*) *strausi* A.H. Verrill, 1950: 4, text figs.

Hexaplex strausi — Vokes, 1964: 11, pl. 1, fig. 18; Vokes, 1971: 101; Fair, 1976: 79, fig. 59; Sully, 1986: 57, fig. 57; Lamy & Pointier, 2018: 347, pl. 117, fig. 1a–b.

Hexaplex (*Muricanthus*) *strausi* — Merle et al., 2011: 84, pl. 34, figs. 16a–b.

Type material. The type material was not located by Vokes (1968: 105).

Type locality. Soufriere Bay, Dominica, Lesser Antilles, Caribbean Sea, 75–100 fms (137–183 m) (from Verrill, 1950: 50).

Material examined. One specimen from Dominica, Lesser Antilles, from the collection of Vittorio Attolino (Roma, Italy) (Fig. 8K–M).

Distribution. Dominica (Verrill, 1950: 5; Lamy & Pointier, 2018: 347, here confirmed) and Martinique (Sully, 1986: 57; Lamy & Pointier, 2018: 347), Lesser Antilles, at depths between 6–135 m (Lamy & Pointier, 2018: 347) and 137–183 m (Verrill, 1950: 5) (Fig. 11).

Figure 10

A–K. *Muricanthus radix* (Gmelin, 1791). A. Near Guayaquil, Guayas Province, Ecuador, 139.9 mm; B–D. Gulf of Panama, 88.5 mm, E. Pearl Islands, Panama Province, Panama, 107 mm; F–H. Pearl Islands, Panama Province, Panama, 88.4 mm; I–K. Pearl Islands, Panama Province, Panama, 69.2 mm.

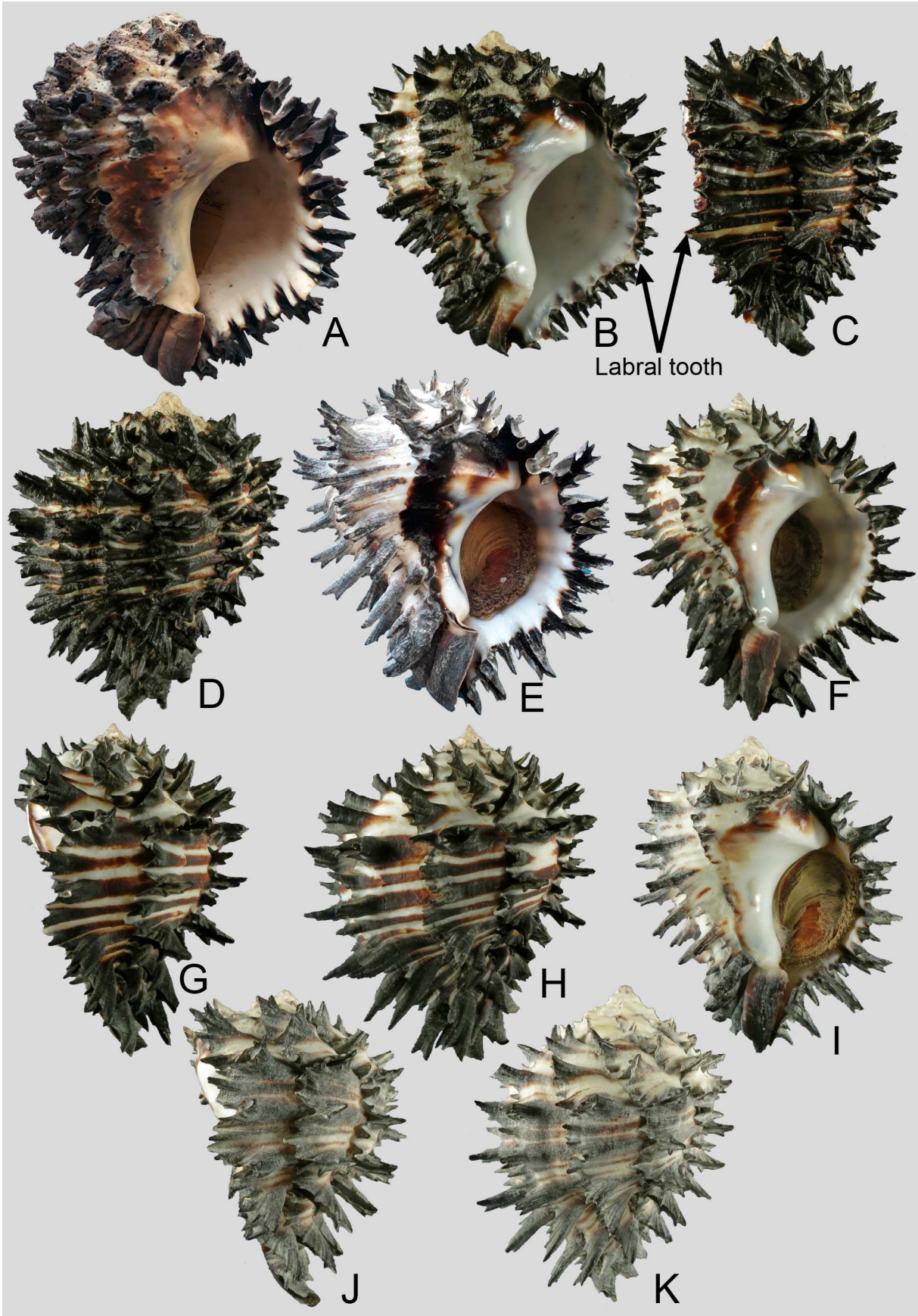




Figure 11. Distribution of *Muricanthus strausi* (black circle: material examined)

Original description. First three whorls with no spines but with strong varices and conspicuous concentric ribs. Fourth whorl with low spines on the last four or five varices, these increasing in size and number on the fifth whorl. Last whorl with ten low varices extending from the shoulder to the extremity of the canal and placed at an angle to the axis of the shell, the upper extremity of each varice being in line with the posterior end of the varice preceeding it. Each varice with eight almost straight spines 4 to 6 mm in length, broadened or fan-shaped at the tips and with their bases forming strong elevated concentric ribs. Each spine and the spaces between them with numerous raised ridges extending from one varice to another between the larger ribs. Canal short, broad, inclined to the left and with the extremity sharply upturned and bearing four blunt spines. A conspicuous groove or channel at the upper angle of aperture. Young specimens have no spines but the varices bear

prominent nodules with interconnecting ribs and small ridges as in the adults. In these young shells the notch in the aperture is more pronounced than in the adults. Color, both adults and young, rich cinnamon-brown with spines and ribs seal-brown, the tips of spines almost black. Canal ochraceous. Interior of aperture and lip white. Operculum horny, thickened at center and with a thin membraneous edge. Surface with numerous concentric lines.
Length, adults: 50–59 mm. Greatest breadth 36–40mm.
Length of young: 12–16 mm
Three adult and two young shells taken in trap in 75 to 100 fathoms, Soufriere Bay, Dominica, B.W. I.

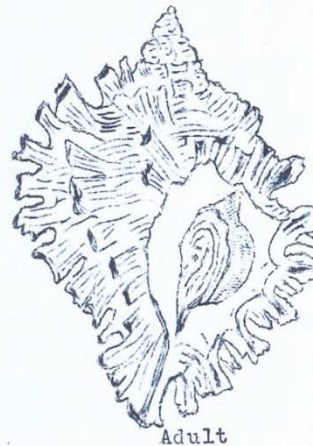


Figure 12. Illustration of *Murex (Aaronia) strausi*, from A.H. Verrill (1950) (image from Biodiversity Heritage Library, www.biodiversitylibrary.org).

Remarks. The original, poorly illustrated specimen by Verrill, 1950 (Fig. 12) suggests a juvenile specimen of *M. radix* or *M. ambiguus*. A figure by Sutty (1984; 1986: fig. 57) illustrates a specimen collected alive at 6.4 m from Martinique, with an additional live record in the same publication. This same specimen, 32.5 mm in length, was later figured by Merle et al. (2011: pl. 34, fig. 16a–b) and Lamy & Pointier (2018: pl. 117, fig. 1a–b).

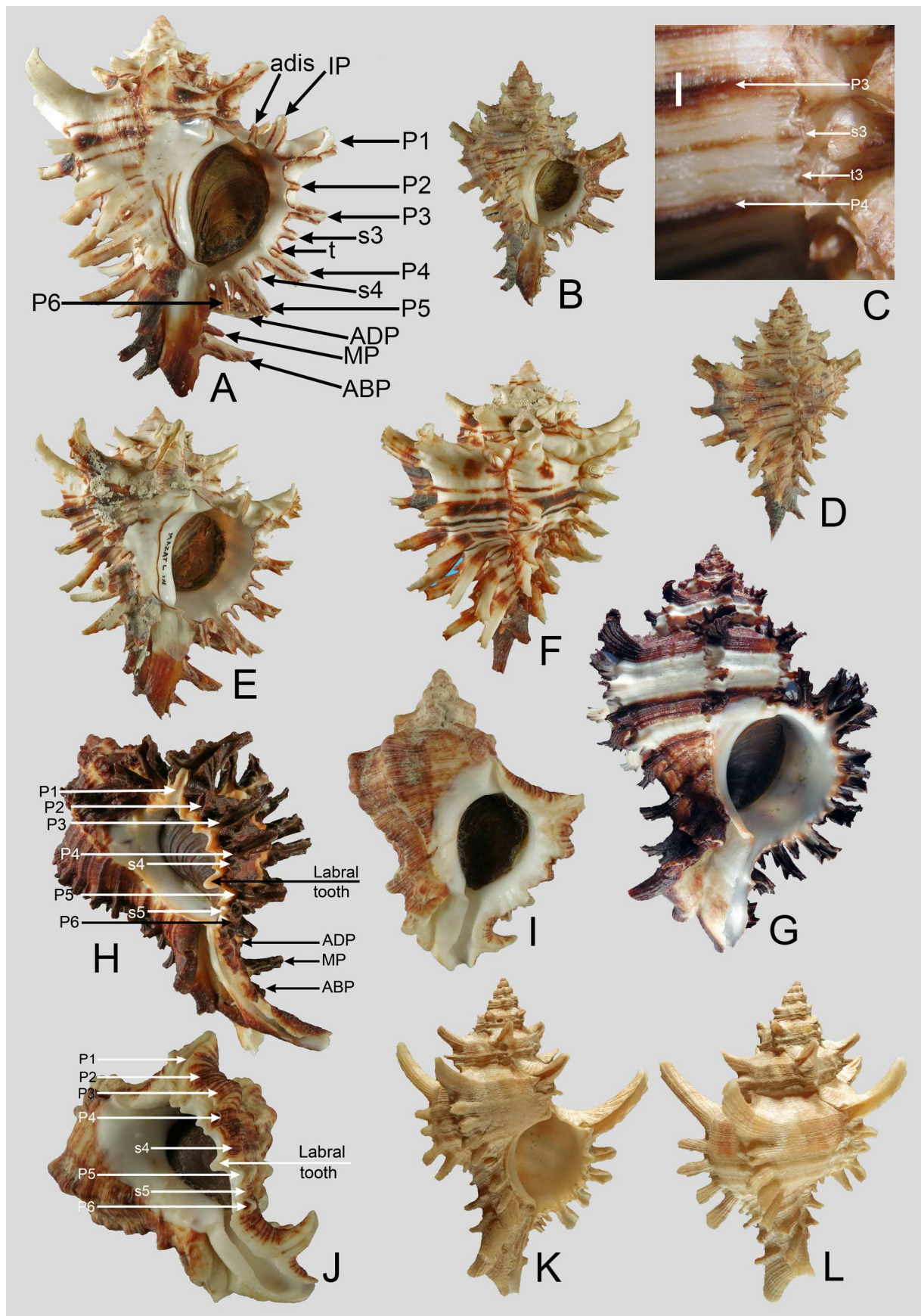
Figure 13

A–F. *Hexaplex (Trunculariopsis) princeps* (Broderip, 1833). A. Mazatlan, Sinaloa, Mexico, 91.6 mm; B–D. Taboga Island, Panama Oeste Province, Panama, 49.5 mm; E–F. Mazatlan, Sinaloa, Mexico, 72.8 mm.

G–H. *Hexaplex (Hexaplex) cichoreum* (Gmelin, 1791). G. Masbate, Masbate Province, Philippines, 122.5 mm; H. Punta Engaño, Mactan Island, Cebu Province, Philippines, 84.6 mm.

I–J. *Hexaplex (H.) kuesterianus* (Tapparone Canefri, 1875), Masirah Island, Ash Sharqiyah Governorates, Oman, 60.9 mm.

K–L. ?*Hexaplex (?Trunculariopsis) saharicus saharicus* (Locard, 1897), Port of St. Louis, Senegal, 68.2 mm.



Photos of a specimen from Dominica were recently examined from the collection of Vittorio Attolino (Roma, Italy). The specimen in question was among a lot of about 300 shells, some with data tags dating back to the 1970's, other specimens were without data. Along with this shell, other specimens of the *Conus cedonulli* Linnaeus, 1767 group were present. One label titled, "*Murex callidinus* Dominica Island on rock at low tide" (see Fig. 14), was detected, and morphological affinities to this species suggest this is an example of *M. strausi*. It is possible this specimen could be a juvenile specimen of *M. ambiguus*, as seen with specimens from West Panama (Fig. 4I–L), although the Dominica specimen has a higher spire which is more consistent with the Caribbean species. Reports of eight specimens [Verrill, 1950 (5); Sully, 1986 (2) and Vittorio Attolino (1)] suggest that this species is rare and known only from the Lesser Antilles. This species is here considered valid and the hope of the authors is that additional specimens will come to light for further analysis of this fascinating and elusive species.

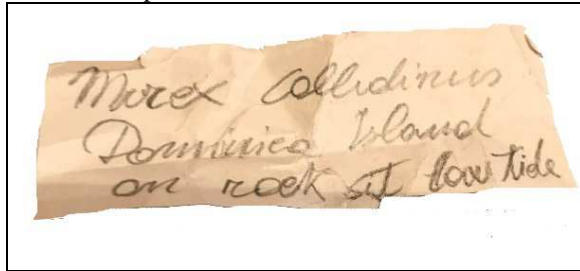


Figure 14. Original label of *Muricanthus strausi* in coll. Vittorio Attolino.

Genus *Phyllonotus* Swainson, 1833. Type species by subsequent designation (Swainson, 1833: pl. 109): *Murex imperialis* Swainson, 1833 (= *Murex margaritensis* Abbott, 1958), Margarita Island, Venezuela.

Diagnosis

Shell medium-sized to large, up to 200 mm in length, spire high. Last teleoconch whorl fusiform or broadly fusiform, bearing 3–6 rounded and spinose varices. Other axial sculpture consisting of 1–5 rows of nodes. Spiral sculpture of last teleoconch whorl with P1 to P6 primary cords similar in size and narrower secondary s1 to s6 cords.

Aperture broadly ovate, outer lip strongly crenulated with prominent lirae within. Columellar lip often broadly expanded apically. Siphonal canal short or moderately long.

Phyllonotus is also characterized by the lack of a labral tooth.

Discussion

Hexaplex (Muricanthus) erythrostomus (Swainson, 1831) and *H. (M.) regius* (Swainson, 1821) assigned

by Merle et al. (2011: 84) fit the criteria presented in the diagnosis above and are therefore here transferred to *Phyllonotus*.

Summary

Muricanthus ambiguus, *M. callidinus*, *M. nigritus*, *M. radix* and *M. strausi* are considered valid and assigned to the genus *Muricanthus*.

Hexaplex bozzadamii, *H. cichoreum*, *H. conatus*, *H. kuesterianus*, *H. rileyi*, *H. stainforthi* and the West African *H. angularis*, are assigned to *Hexaplex* s.s.

Hexaplex bifasciatus, *H. brassica*, *H. duplex*, *H. fulvescens*, *H. pecchiolianus*, *H. princeps*, *H. rosarium*, *H. trunculus* and *H. varius* are assigned to *Hexaplex (Trunculariopsis)*. *Chicoreus clausii* is also assigned to *Hexaplex (Trunculariopsis)* as a three varical form of *H. (T.) varius*.

The three West African taxa *H. megacerus*, *H. saharicus saharicus* and *H. saharicus ryalli* are tentatively assigned to *Hexaplex (Trunculariopsis)*.

Hexaplex (M.) erythrostomus and *H. (M.) regius* (in Merle et al., 2011) are transferred to *Phyllonotus*.

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