

A Review of the Genus *Agaronia* (Olividae) in the Panamic Province and the Description of Two New Species from Nicaragua

by

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Abstract. Three previously recognized Panamic species, *Agaronia testacea* (Lamarck, 1811), *A. propatula* (Conrad, 1849), and *A. griseoalba* (von Martens, 1897) (senior synonym here replacing *A. murrha* Berry, 1953), are reviewed and their occurrences reported for the Panamic province. Two new species, *A. nica* and *A. jesuitarum*, are described, primarily from records in Nicaragua. Species are defined using parameters of protoconch type, spire height, aperture width, pillar lirae count, and shell length. Two distinct kinds of protoconch—acuminate and mammillate—are distinguished: species with acuminate protoconchs are *A. testacea*, *A. propatula*, and *A. jesuitarum*; those with mammillate protoconchs are *A. griseoalba* and *A. nica*.

INTRODUCTION

Two species, *Agaronia testacea* (Lamarck, 1811), and *A. propatula* (Conrad, 1849), have been regarded as broadly distributed in the Panamic province (see KEEN, 1958, 1971). A third species, *A. murrha* Berry, 1953, has been cited by Keen as known only from Corinto, Nicaragua. Previous authors have not realized that the latter species is broadly distributed in the southern Panamic province and has an older name. The extent to which the same patterns of color variation are shared by co-occurring species has not been understood. Here we demonstrate, based on meristic characters, that there are five Panamic species, two of which are new.

MATERIALS AND METHODS

The identity of previously described taxa presented a problem only for one of the names introduced by VON MARTENS, 1897: *Oliva* (*Agaronia*) *testacea* var. *griseoalba*. The type specimen was received on loan from the Zoologisches Museum of Humboldt-Universität in Berlin (ZMB) by Dr. McLean at the Los Angeles County Museum of Natural History, where it was photographed for inclusion here.

Von Martens also proposed *Oliva* (*Agaronia*) *testacea* mut. *candida*, but that name is preoccupied by *Oliva candida* Lamarck, 1811, and need not be considered.

Specimens were collected by us at low tide and by wading and snorkling at a number of localities in Nicaragua and Costa Rica (Table 1). Information provided by Dr. McLean about the occurrences of these species elsewhere in the Panamic province is also included. We have also examined specimens received on loan from Carol Skoglund of Phoenix, Arizona, and David G. Robinson of Tulane University, New Orleans, Louisiana. Voucher specimens of previously described species and type specimens of the new species have been placed in the following institutional collections: CAS—California Academy of Sciences, San Francisco, California; LACM—Los Angeles County Museum of Natural History, Los Angeles, California; LSM—La Salle Museum of Natural History, San José, Costa Rica; UCA—Central America University, Managua, Nicaragua; UCRZ—Zoology Museum of University of Costa Rica, San José.

The meristics are based on 38 specimens of each of the five species. Measurements were made with vernier calipers, with an accuracy of 0.05 mm. Abbreviations for the physical parameters (Figures 1, 2, and text) are as follows: *a*, lateral spire height from tip of callus above aperture to protoconch tip; *b*, width, maximum distance from labrum

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to opposite side; *c*, crest on fasciolar band; *d*₁, distance along labrum from suture to fasciolar band; *d*₂, same distance (suture to fasciolar band) on side opposite from lip; *e*, edge of pillar pleats; *f*, spire factor, *a/w*, a measure of spire acuteness; *g*, breadth factor, *o/l*, a measure of aperture width; *h*, maximum height; *k*, dorsal color band; *l*, length of shell from protoconch to tip of columella; *n*, number of specimens examined; *o*, maximum aperture width from tip of penult pillar pleat to edge of labrum; *p*, pillar pleats; *r*, relative growth factor *d*₁/*d*₂, a measure of relative growth of shell length; SD, standard deviation; *s*₁, posterior pillar lirae; *s*₂, anterior pillar lirae; *t*, terminal pleat; *w*, width of diameter of spire base measured from tip of callus above aperture to opposite point on suture.

SYSTEMATIC TREATMENT

Family OLIVIDAE Latreille, 1825

Subfamily AGARONIINAE Olsson, 1956

Genus *Agaronia* Gray, 1839

Type species (monotypy): *Voluta hiatula* Gmelin, 1791. Recent, west Africa.

The shell is medium thick, ovate-fusiform, with a truncate flaring aperture extending about 0.7 of shell length. One strong terminal pleat (*t*) extends internally from the pillar through the spire whorls. Separated from it by a sulcus are 8 to 20 lirae on the inner surface of the pillar and the anterior parietal callus. The count of lirae provides a useful specific character. Some of these lirae are engraved and prolonged into the fasciole as strong pleats (*p*) over the pillar. The highest of these usually marks the posterior limit of the anterior pillar lirae (*s*₂), but more posteriorly there are a few posterior pillar lirae (*s*₁), particularly on *Agaronia griseoalba*. The average number of lirae, including the terminal pleat, varies from a minimum of 9.1 for *A. propatula* to a maximum of 16.7 for *A. griseoalba*. The slightly raised callus pad on the pillar and fasciole is microscopically wrinkled, white, sometimes suffused with purple. There is wide fasciolar band, covered with callus, that forms the base of the shell. The morphology of the fasciolar band is similar to that seen in the genus *Ancilla* Lamarck, 1799, which has an "ancillid" band and a fasciolar band separated by the "posterior fasciolar groove" (KILBURN, 1981). In *Agaronia* the two bands are fused together, but a very slight crest (*c*) corresponding to the posterior fasciolar groove of *Ancilla* is present. The callus of the fasciolar band is the same color as the spiral band callus, and both often have a slightly uneven surface, variegated with streaks of a different color. A short distance above the fasciolar band there is a dorsal color band (*k*), white or light purple, most easily seen on dark shells. Its background color is made up of a closely knit web of microscopic zigzag lines overset with larger, thin irregular streaks that are visible without magnification. These streaks are contained within the limits of the dorsal color band, but in large shells they sometimes occur on other parts of

Table 1

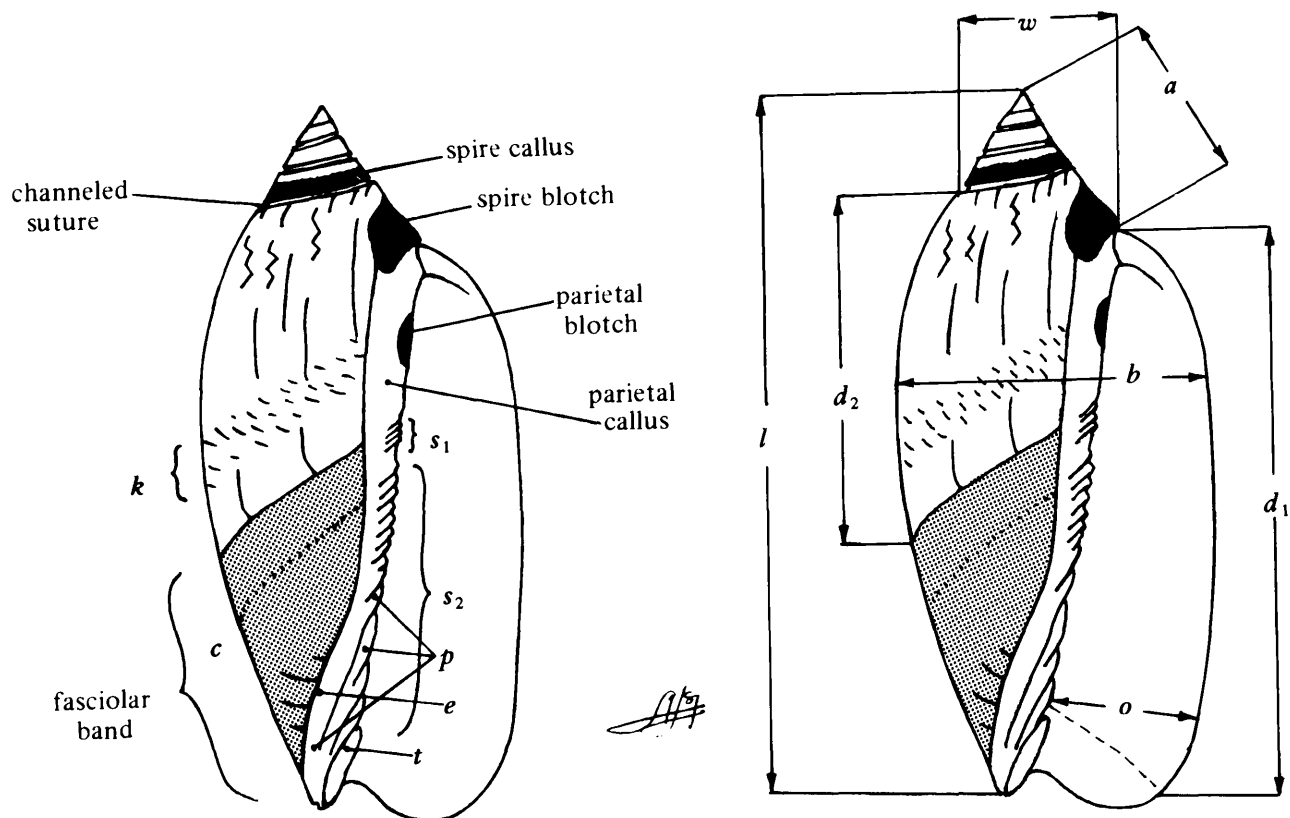
Latitude and longitude of collecting localities.

	N latitude	W longitude
Nicaragua		
Cosiguina, Chinandega	13°03'00"	87°34'00"
Jiquillo, Chinandega	12°45'00"	87°31'30"
Aposentillo, Chinandega	12°37'52"	87°21'55"
Aserradores, Chinandega	12°36'27"	87°20'37"
Corinto, Chinandega	12°30'00"	87°10'00"
Poneloya, León	12°22'55"	87°02'49"
Los Playones, León	12°07'02"	86°44'42"
Masachapa, Managua	11°47'13"	86°31'01"
Pochomil, Managua	11°47'00"	86°30'30"
La Boquita, Carazo	11°40'40"	86°22'30"
Huehueté, Carazo	11°36'59"	86°19'34"
Chococente, Carazo	11°32'06"	86°11'15"
Rio Escalante, Rivas	11°31'04"	86°10'13"
Boca de Brito, Rivas	11°20'33"	85°58'37"
Majagual, Rivas	11°17'52"	85°55'00"
Marsella, Rivas	11°17'06"	85°54'14"
El Toro, Rivas	11°16'30"	85°53'59"
San Juan del Sur, Rivas	11°15'34"	85°52'49"
La Flor, Rivas	11°08'05"	85°47'38"
Ostional, Rivas	11°06'30"	85°46'00"
Costa Rica		
Playa del Coco, Guanacaste	10°33'32"	85°42'08"
Tamarindo, Guanacaste	10°18'07"	85°50'29"
Puntarenas, Puntarenas	9°58'52"	84°49'11"
Tivives, Puntarenas	9°52'10"	84°42'04"
Tárcoles, Puntarenas	9°45'49"	84°37'53"
Montezuma, Puntarenas	9°39'28"	85°04'17"
Jacó, Puntarenas	9°36'31"	84°37'30"
Esterillos, Puntarenas	9°31'31"	84°30'26"
Manuel Antonio, Puntarenas	9°23'42"	84°09'13"
Dominical, Puntarenas	9°13'22"	83°50'57"

the dorsum. The surface of *Agaronia* is smooth and shiny, but not highly glazed except where covered with callus. The interior is dark purple in some shells and light purple, yellow, or white in other specimens, often with two well-marked purple bands. The edge of the lip reveals the color of the dorsum along its length.

The height and shape of the spire is important as a specific character. The spire has a channeled suture and three moderately callused whorls. There is a strongly marked spiral callus and blotch of darker color that often dips into the aperture. It is deep purple or brown on dark shells, light purple or yellow on light shells. Sometimes a light purple parietal blotch is apparent on fresh shells, but this may fade with time.

The protoconch is translucent or opaque, of 2 to 2.5 whorls, generally darker than the ground color of the spire. The protoconch is entirely devoid of sculpture, with the almost imperceptible suture developing into a channel on the last nepionic whorl. The contrast between the protoconch and the first whorl of the teleoconch is what determines a mammillate (Figure 3) or an acuminate (Figure 4) form of the protoconch. In the acuminate form, the



Explanation of Figures 1 and 2

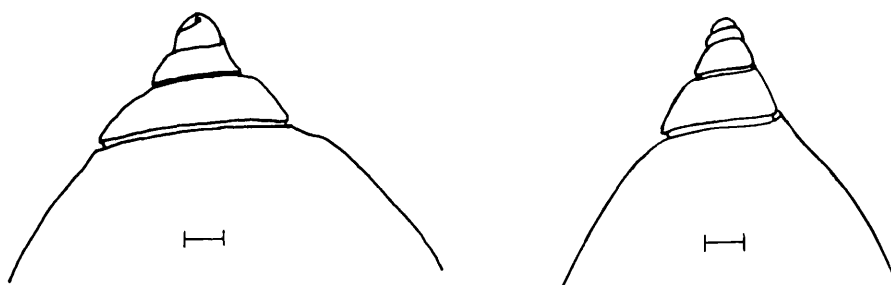
Figure 1. Shell features of *Agaronia*: *c*, crest on fasciolar band; *e*, edge of pillar pleats; *k*, dorsal band; *p*, pillar folds; *s*₁, posterior pillar lirae, *s*₂, anterior pillar lirae; *t*, terminal fold.

Figure 2. *Agaronia*: measurements taken for statistical analysis. See list in text.

increase in diameter of the whorls is gradual, so that protoconch and teleoconch fuse into a smooth, continuous cone with an angle of about 32 degrees. In the mammillate form, the first whorl of the teleoconch is about twice the diameter of the protoconch, which stands out nipple-like, and the cone forms an angle of about 50 degrees in *Agaronia griseoalba* and about 62 degrees in *A. nica*. An additional

difference between the two forms is that the diameter of the embryonic whorl varies from 0.45 to 0.7 mm in the three acuminate forms, *A. jesuitarum*, *A. testacea*, and *A. propatula* respectively, and from 0.6 to 1.2 mm in *A. nica* and *A. griseoalba*, the two mammillate forms.

In order to quantify the height of the spire, we define a spire factor ($f = a/w$), where (*a*) is the lateral length of



Explanation of Figures 3 and 4

Figure 3. Protoconch, mammillate form of *Agaronia nica* sp. nov. Scale bar = 1 mm.

Figure 4. Protoconch, acuminate form of *Agaronia jesuitarum* sp. nov. Scale bar = 1 mm.



Figure 5

SEM view of radula of *Agaronia griseoalba*, showing tricuspid rachidian with closely adjacent secondary cusps, and single pair of hook-shaped lateral teeth. Scale bar = 20 μm .

the spire and (w) is the diameter of the spire base, both measured from the tip of the callus just above the aperture. The very sharp outline of the channeled suture makes it possible to duplicate the measurements. Average values for the spire factor for the Panamic species vary from 1.35 (SD, ± 0.07) for *Agaronia testacea* to 1.01 (SD, ± 0.04) for *A. nica*. The latter has a convex spire, in contrast to the others, which have spires with straight or concave profiles.

The foot and body of *Agaronia* species are white to buff, more or less intensely speckled with purple; some animals appear to be entirely of this color except for a white, narrow edge around the foot. The siphon is ribbonlike but tubular, also buff and speckled with purple, but with an orange tip. The posterior lobe of the foot is easily broken off at a "tear" line. The gut is dark gray with a granular white or yellow digestive gland ventrally.

The animals live in the sand in the tidal zone. When active, the shells are nearly completely covered by the propodium and the parapodia. We have often seen them feeding on *Olivella semistriata* (Gray, 1839), which is abundant in Nicaragua and Costa Rica, and rarely on small Donacidae and Tellinidae. The prey is enveloped by the foot and then the *Agaronia* burrows into the sand while feeding (LÓPEZ, 1978). Dissection has also revealed remains of other small invertebrates in the stomach.

Contrary to previous descriptions (KEEN, 1971:625; ABBOTT, 1974:238), Panamic *Agaronia* do not have an operculum. However, *A. travassosi* Morretes, 1938, which is endemic to Brazil, does have an operculum (RIOS, 1975).

Radulae for all species except *Agaronia testacea* were examined; that of *A. griseoalba* is illustrated (Figure 5). As in all Olividae, the radula is rachiglossan with a tricuspid rachidian tooth, the central cusp being slightly smaller than the other two. Lateral to the two large cusps are small secondary cusps; in this detail, *Agaronia* and *Olivancillaria* d'Orbigny, 1840, differ from the rest of the

Olividae, which do not have these denticles (BURCH & BURCH, 1964). Radulae of different *Agaronia* species show no detectable differences in the shape and spacing of cusps. In *A. propatula*, the external sides of the outer cusps are aligned, giving the ribbon a more regular appearance. In fresh specimens of *A. jesuitarum*, the tips of the laterals have a marked golden hue not seen in the other species.

Only three fossil species of the Olividae have been reported to date from Central America. OLSSON (1922) described *Oliwa testacea* var. *costaricensis* from the Rio Banano Formation, now dated as being Pliocene in age, and *O. mancinella* from the Pleistocene Moín Formation, both from the Limón Province of Costa Rica. Later, WOODRING (1964) reassigned these two taxa to the genus *Agaronia* and treated both as subspecies of *A. testacea*. He also described a new subspecies, *A. testacea hadra* from the Pliocene Gatún Formation of Panama. These fossil taxa need to be reviewed, taking into account their probable descendants in the Caribbean and Panamic biogeographic provinces.

KEY TO LIVING PANAMIC SPECIES OF *Agaronia* (data from meristics under each species)

- (1) Protoconch acuminate
 - (a) Spire very high, $f = 1.4$ *A. testacea*
(lirae 10; length 34.5 mm)
 - (b) Spire high, $f = 1.2$ *A. jesuitarum*
(lirae 15; length 21.5 mm)
 - (c) Spire medium, $f = 1.1$ *A. propatula*
(lirae 9; length 42.0 mm)
- (2) Protoconch mammillate
 - (a) Spire medium, $f = 1.1$ *A. griseoalba*
(lirae 18; length 32.0 mm)
 - (b) Spire low, $f = 1.0$ *A. nica*
(lirae 12; length 24.5 mm)

Agaronia testacea (Lamarck, 1811)

(Figures 6–9)

Oliva testacea LAMARCK, 1811:324; REEVE, 1850:pl. 18, fig. 36; MARRAT, 1871:26, pl. 348, figs. 334, 335.*Oliva (Agaronia) testacea*: VON MARTENS, 1897:163, pl. 16, figs. 7, 12.*Agaronia testacea*: BERRY, 1953:418, text fig. 6; HERTLEIN & STRONG, 1955:239; KEEN, 1958:422, fig. 629; BURCH & BURCH, 1964:111, pl. 6, fig. 2; KEEN, 1971:625, fig. 1370; ABBOTT, 1974:233, pl. 13, fig. 2548; ABBOTT & DANCE, 1982:196 [color fig.].*Agaronia reevei* MÖRCH, 1860:87 [designated fig. 36 of REEVE, 1850].*Oliva (Agaronia) testacea* var. *philippi* VON MARTENS, 1897:165, pl. 15, figs. 13, 14.

Description: Spire straight-sided and highest among Panamic agaronias; protoconch acuminate, light colored; shell height 31–50 mm, profile subfusiform. The body color is usually grayish brown, with axial, brown irregular lines. The aperture is bluish white or gray, the edge of labrum white, often stained with brown; pillar is white. The spire callus band reaches only halfway across from suture to suture. The callus band and the fasciolar band callus are light brown, variegated with whitish streaks. The protoconch is acuminate and light colored. Spiral blotch weak to obsolete.

Meristics ($n = 38$): Spire factor 1.35 (SD, ± 0.07); length 34.55 mm (SD, ± 8.56); breadth factor 0.18 (SD, ± 0.02); relative growth factor 1.37 (SD, ± 0.07); lirae count 9.76 (SD, ± 2.59).

Distribution: Empty shells were found in fair to good condition at nearly all sandy beaches in Nicaragua, but always in small numbers. Most of our specimens were collected from the northern beaches, from the Gulf of Fonseca to Aserradores. No live specimens were found. However, McLean reports (personal communication) that there are numerous live-collected records from the Gulf of California and southern Mexico, as well as Panama, in the LACM collection.

Material examined: MEXICO (Skoglund collection): Bahía Cholla, Sonora, 9 specimens; Playa Novillero, Nayarit, 7 specimens. NICARAGUA (UCA): Aserradores sea beach and estero beach: 5 lots, 24 specimens. Single shells and fragments from Cosiguina, Aserradores, Corinto, Huehete, San Juan del Sur, La Flor. COSTA RICA: Tamarindo (LSM); Montezuma (UCRZ). PANAMA: Kobbe Beach, 2 specimens (Skoglund collection). Specimens from Aserradores had intact protoconchs and were used for spire measurements. This is the only species of *Agaronia* that we have not collected alive in Nicaragua.

Remarks: *Agaronia testacea* may readily be distinguished from the other species by its medium to large size, high spire, and acuminate protoconch.

Specimens from the Atlantic coast of Central America identified as this species have been reported by FLUCK (1905:18), HOUBRICK (1968:16), OLSSON & MCGINTY

(1958:17), and WOODRING (1964:281). Those that we have collected at Moín, Puerto Limón, Atlantic coast of Costa Rica, do not agree with *A. testacea*, in having lower spires, broader apertures, and a lower count of lirae, and remain unidentified.

The holotype of *Oliva (Agaronia) testacea* var. *philippi* von Martens (Figure 9) is a small shell similar to those from Panama in the LACM collection. The locality Cobija, in northern Chile, quoted by VON MARTENS (1897), is obviously erroneous, as the species has not been recorded south of Panama.

Agaronia propatula (Conrad, 1849)

(Figures 10, 11)

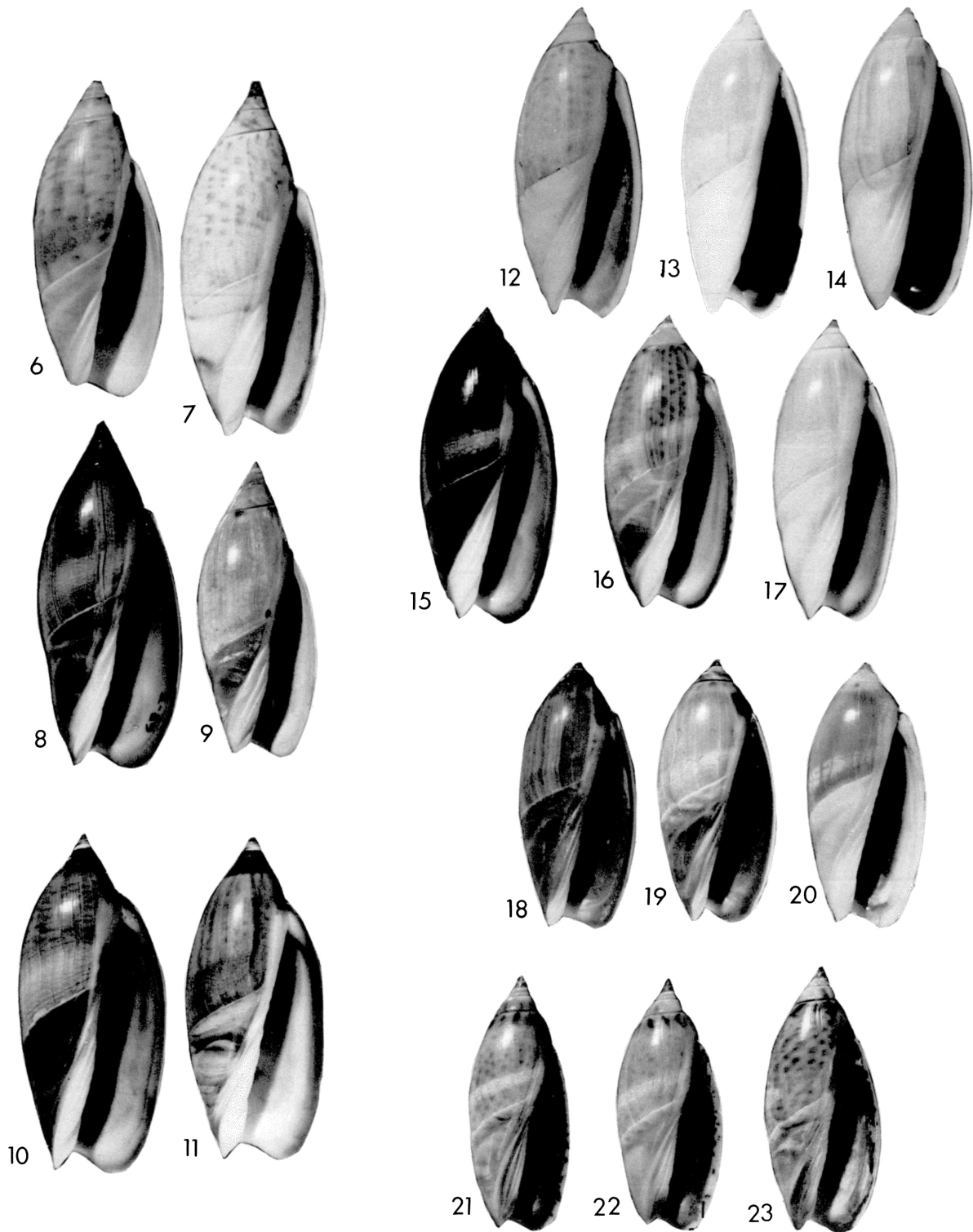
Oliva propatula CONRAD, 1849:280, pl. 39, fig. 7.*Agaronia propatula*: KEEN, 1958:422, fig. 629; KEEN, 1971:625, fig. 1369 [copy Conrad fig.].Not *A. propatula* of HEMMEN, 1981:128, pl. 27 [color fig.]; of ABBOTT & DANCE, 1982:196 [color fig.]. [= *A. gri-seoalba*].

Description: This is the largest and most massive of the Panamic agaronias. The spire is medium high, concave over the aperture owing to overhang of heavy callus, protoconch acuminate. Shell length about 42 mm, profile inflated, most globose of the five species. Lirae count lowest, about 9. The body color is often gray with dark gray zigzags, but it can also be light brown or terracotta marked by gray or brown axials that score the growth lines, giving the shell a woodlike appearance. These growth lines are somewhat sinusoid, as is the edge of the lip, especially in large specimens. The fasciolar band and the spire callus are dark purple-brown and highly glazed, this callus not reaching all the way from suture to suture on the spire and being variegated with whitish streaks. The aperture is bluish white or gray, the inner edge of the labrum whitish brown. The dorsal color band is white or purple, often with a blend of both. The protoconch is dark brown, contrasting with the first teleoconch whorl, which is usually white. The spiral blotch is dark brown, strongly marked, dipping well into the aperture, and extending along the spire callus.

Meristics ($n = 38$): Spire factor 1.11 (SD, ± 0.08); shell length 42.31 mm (SD, ± 10.66); breadth factor 0.22 (SD, ± 0.01); relative growth factor 1.56 (SD, ± 0.07); lirae count 9.1 (SD, ± 1.66).

Distribution: Only a few live shells were taken at San Juan del Sur, La Flor, Chococente, and Poneloya in relatively coarse sand. Empty shells were found at many sandy beaches, especially at Aserradores. KEEN (1971) gave the range as southern Mexico to Ecuador. McLean reports (personal communication) that the LACM collection contains 9 lots of dead-collected specimens ranging from Guatemala to Panama.

Material examined: MEXICO: Bahía de Los Angeles, Baja California, 5 specimens (Skoglund collection); GUATE-



Explanation of Figures 6 to 23

Figures 6–9. *Agaronia testacea* (Lamarck, 1811). Figure 6: LACM 127342; Aserradores, Nicaragua; length 39.6 mm. Figure 7: LACM 127343; Bahía de Adair, Sonora, Mexico; length 50.8 mm. Figure 8: LACM 68-3; Novillero, Nayarit, Mexico; length

48.7 mm. Figure 9: Holotype, ZMB, *Oliva (Agaronia) testacea* var. *philippi* von Martens, 1897; length 31.2 mm.

Figures 10, 11. *Agaronia propatula* (Conrad, 1849). Figure 10:

MALA: San José, Escuintla, 2 specimens (D. G. Robinson collection); NICARAGUA (UCA): Living specimens from San Juan del Sur (2 lots); Chococente, 2 single lots; single lots from Poneloya and La Flor. Dead shells to 65 mm in length from Aserradores, Aposentillo, Corinto, Poneloya, Huehuete, La Boquita, Chococente, and El Toro. No specimens were found by us in Costa Rica.

Remarks: At Poneloya the living specimens occurred with *Agaronia jesuitarum*. At Chococente they occurred with *A. jesuitarum*, *A. nica*, and *A. griseoalba*. We found this species to be only slightly less scarce than *A. testacea*.

Agaronia griseoalba (von Martens, 1897)

(Figures 12–17)

Oliua (*Agaronia*) *testacea* var. *griseoalba* VON MARTENS, 1897: 64, pl. 15, figs. 18, 19.

Agaronia murrha BERRY, 1953:417, pl. 29, fig. 1, text fig. 5; HERTLEIN & STRONG, 1955:240; BURCH & BURCH, 1964: 112 [not pl. 6, fig. 4]; KEEN, 1958:422, fig. 628; KEEN, 1971:725, fig. 1368.

“*A. propatula*” of HEMMEN, 1981:128, pl. 27 [color fig.]; of ABBOTT & DANCE, 1982:196 [color fig.]. Not *A. propatula* (Conrad).

Description: Spire straight or slightly concave, medium high, shell length about 32 mm, whorls somewhat inflated. Protoconch mammillate, lirae count highest of the five species, average 17, maximum 27. As noted by BERRY (1953), the typical form is “slightly grayish porcelain-white,” with a white, yellow, or light brown callus on fasciole and spire, where it usually covers spire whorls from suture to suture. The aperture is dark purple or brown; the labrum has a white inner edge. Rarely the shell is pink with an orange aperture, with or without two purple bands. Variants from Costa Rica, Panama, and Ecuador include olive-brown shells with zigzag lines and some black shells (later turning gray) with an amorphous white dorsal band.

Meristics ($n = 38$): Spire factor 1.14 (SD, ± 0.05); height 31.94 mm (SD, ± 6.99); breadth 0.19 (SD, ± 0.01); relative growth factor 1.47 (SD, ± 0.06); lirae count 16.76 (SD, ± 3.98).

Distribution: San José, Escuintla, Guatemala, to Canoa, Manabí, Ecuador. These represent new northern and southern distributional records beyond those reported in KEEN (1971).

Material examined: GUATEMALA: 1 large specimen from San José, Escuintla (D. G. Robinson collection). NICARAGUA (UCA): Jiquilillo, Aserradores, Corinto, Poneloya, Huehuete, Pochomil, Chococente, Rio Escalante, Maja-gual, Marsella, San Juan, La Flor. COSTA RICA: Playas del Coco, Puntarenas, Tivives, Tárcoles, Jacó, Esterillos, Dominical (UCA). PANAMA: Las Lajas, Playa Jobo (LACM). ECUADOR: Atacames, Esmeraldas (D. G. Robinson collection). This is the most abundant *Agaronia* in Costa Rica.

Remarks: BERRY (1953) proposed *Agaronia murrha* (Figure 13, holotype), from Corinto, Nicaragua, but overlooked the prior name *A. griseoalba* of VON MARTENS, 1897, from “Mexico,” which we here reinstate, based on our examination of the type specimen (Figure 12). The species has not been frequently cited enough to warrant an effort to conserve Berry’s name. Berry did not have material to demonstrate the color variation possible in this species, owing in part to the prevalence of the gray-white color form at his type locality and most localities throughout Nicaragua. Although he remarked in a footnote that a dark phase seemed to be present at San Juan del Sur, Nicaragua, these specimens prove to be *A. nica*, described herein. Dark specimens of *A. griseoalba* (Figures 15, 16) have the size range, the lirae count, and the mammillate protoconch to match that of typical *A. griseoalba*, so there is no possible doubt as to their identity.

Agaronia nica A. López, Montoya
& J. López, sp. nov.

(Figures 18–20)

“*Agaronia murrha*,” in part, of BERRY, 1953:419 [footnote only]; in part of BURCH & BURCH, 1964 [fig. 4 only].

Description: Shell solid, small, length about 25 mm, spire low, convex, body whorl inflated, lirae count medium, about 12. The light brown, mammillate protoconch of two

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LACM 65-88; Mata de Limón, Costa Rica; length 46.8 mm. Figure 11: LACM 127344; Aserradores, Nicaragua; length 40.9 mm.

Figures 12–17. *Agaronia griseoalba* (von Martens, 1897). Figure 12: Holotype, ZMB, *Oliua* (*Agaronia*) *griseoalba* von Martens, 1897, “Mexico”; length 38.4 mm. Figure 13: Holotype, CAS, *Agaronia murrha* Berry, 1953; Corinto, Nicaragua; length 36.3 mm. Figure 14: LACM 127345; Huehuete, Nicaragua; length 37.2 mm. Figure 15: LACM 127346; Tivives, Costa Rica; length 39.4 mm. Figure 16: LACM 127346; Tivives, Costa Rica; length 34.7 mm. Figure 17: LACM 127346; Tivives, Costa Rica; length 35.8 mm.

Figures 18–20. *Agaronia nica* López, Montoya & López, sp. nov. Figure 18: Holotype, LACM 2269; San Juan del Sur, Nicaragua; length 24.7 mm. Figure 19: LACM 127347; San Juan del Sur, Nicaragua, collected by H. N. Lowe; length 25.5 mm. Figure 20: LACM 127348; Marsella, Nicaragua; length 23.5 mm.

Figures 21–23. *Agaronia jesuitarum* López, Montoya & López, sp. nov. Figure 21: Holotype, LACM 2271; Poneloya, Nicaragua; length 21.2 mm. Figure 22: Paratype, LACM 2272; Poneloya, Nicaragua; length 22.6 mm. Figure 23: Paratype, LACM 2272; Poneloya, Nicaragua; length 24.5 mm.

whorls is similar, and of about the same size as that of *Agaronia griseoalba*, although shells of *A. nica* are smaller. This is the most variable of the agaronias in color. We have seen uniform white shells and others that are black, as well as yellow, orange, brown, gray, and intermediate shades. Some are devoid of maculations, whereas others are partially or entirely covered with lines, dots, or zigzags. The aperture is dark purple in dark shells and lighter in others. The most common color combination (represented in the holotype) is dark gray with darker zigzags, dark brown spiral and columellar band callus, brown protoconch, bluish pillar, and dark aperture. The spire whorls are covered by callus from suture to suture.

Dimensions of holotype: length 24.7 mm, height 8.0 mm, width 11.1 mm, spire lateral height 5.7 mm, spire base diameter 5.8 mm; spire factor 1.017, lirae count 9.

Meristics ($n = 38$): Spire factor 1.01 (SD, ± 0.04); length 24.41 (SD, ± 2.82); breadth factor 0.22 (SD, ± 0.01); relative growth factor 1.49 (SD, ± 0.07); lirae count 12.21 (SD, ± 1.80).

Type locality: San Juan del Sur, Rivas, Nicaragua.

Type material: Holotype, LACM 2269. Paratypes, LACM 2270; paratypes, CAS 050208 through 050212. Paratypes from all listed localities in Nicaragua (UCA).

Distribution: Sayulita, Nayarit, Mexico, to Puntarenas, Costa Rica.

Referred material: MEXICO: Sayulita, Nayarit (Skoglund collection); Playa Encantada, Acapulco (Skoglund collection); Acapulco (LACM 127386), 2 specimens from Earl Huffman collection, matching the "hypotype from Acapulco" figured by BURCH & BURCH (1964:fig. 4) and evidently from the same lot (J. McLean, personal communication). NICARAGUA (UCA): Jiquillo, Poneloya, Los Playones, Masachapa, Pochomil, La Boquita, Huehuete, Chococente, Boca de Brito, Marsella, San Juan del Sur, La Flor, Ostional (UCA). Numerous specimens from San Juan del Sur, Nicaragua, collected by H. N. Lowe in 1931 (Figure 19), now in LACM, San Diego Natural History Museum, and other collections. COSTA RICA: Puntarenas, a single specimen collected with *Agaronia griseoalba* by D. Shasky, Redlands, California.

Remarks: *Agaronia nica* is half the size of the three larger species (*A. testacea*, *A. propatula*, and *A. griseoalba*). Its mammillate protoconch separates it from *A. testacea*, *A. propatula*, and *A. jesuitarum*, as well as its low, usually convex spire, even when the first two species are only half grown and about the same size as fully grown *A. nica*. When comparing mature *A. nica* with juvenile *A. griseoalba* of the same color and length, the distinction lies in the low convex spire of *A. nica*, its more inflated body, and its lower lirae count. Color differences are not reliable criteria for discrimination.

The footnote to BERRY's (1953) description of *Agaronia murrha* noted "a large series of small dark *Agaronia* in the

San Diego Museum taken in 1931 by H. N. Lowe at San Juan del Sur, Nicaragua. These shells are mostly of purplish-gray coloring with deep brown (rarely light yellowish-brown) apex and fasciole, and appear to represent a dark phase of the species here described." The above mentioned specimens are typical *A. nica*. A true dark phase of *A. griseoalba* is also now known to exist (Figures 15, 16).

This is the most common *Agaronia* in Nicaragua but has not previously been recognized as a distinct species, having been mistaken for juvenile *A. testacea* or *A. propatula*. As it is common in Nicaragua, we have named it *nica*, the familiar name by which persons and objects from Nicaragua are known throughout Central America.

Agaronia jesuitarum A. López, Montoya
& J. López, sp. nov.

(Figures 21–23)

Description: Shell small, thin, subfusiform; spire high, straight sided, length about 22 mm, body whorl not inflated, lirae count relatively high, about 15. Protoconch acuminate, caramel colored. The body whorl is grayish or yellowish olive, profusely marked with broken zigzags or triangles. We have also seen several specimens with an orange ground color. The aperture is deep purple and the inner labrum edge matches the ground color or is mottled with purple. There is a subsutural band of slanted dashes, similar to those of *Agaronia testacea*. The spire and columellar band callus is yellowish brown and covers the whorls from suture to suture. The pillar callus pad is slightly more raised than in other agaronias, bluish white.

Dimensions of holotype: length 21.2 mm, height 6.5 mm, width 8.8 mm, spire lateral height 6.5 mm, spire base diameter 5.3 mm; spire factor 1.226, lirae count 15.

Meristics ($n = 38$): Spire factor 1.21 (SD, ± 0.04), length 21.48 mm (SD, ± 4.68); breadth factor 0.19 (SD, ± 0.009); relative growth factor 1.46 (SD, ± 0.06); lirae count 15.05 (SD, ± 1.81).

Type locality: Poneloya Beach, at river mouth, León, Nicaragua.

Type material: Holotype, LACM 2271, 5 paratypes LACM 2272, 1 paratype CAS 050213. Twenty paratypes UCA.

Distribution: Poneloya to Boca de Brito, Nicaragua. About 40 specimens were found over the course of one year at Poneloya in coarse sand at low tide. The first six specimens were taken by Al and Julio López in December 1982. Four more specimens were collected at the same site a year later, where 30 additional specimens were also found by A. Fernandez, R. Meabe, and F. Zarrabe. Three were found in 1984 by Michel Montoya 6 km south of Poneloya and one at Boca de Brito, 100 km farther south. Some 20 additional specimens were found in 1985 at La Boquita and Huehuete, and four specimens at Chococente in 1986.

Remarks: *Agaronia jesuitarum* is the smallest of the Panamic agaronias and also the most distinct. It is easily separated from the others based on its small size and characteristic yellow or gray-olive ground color profusely covered with small aligned spots or zigzags. Because of its high spire and acute protoconch, it could be mistaken for a very small, immature *A. testacea*; but the color, high count of lirae, and subfusiform outline are distinctive.

This species is difficult to find. We are unable to explain why no dead specimens have been seen. The living specimens remain buried in the sand, rather than foraging on the surface, as observed in the other species. Feeding has not been observed. Other olivid species present at the type locality included *Agaronia griseoalba*, *A. nica*, *A. propatula*, *Oliva undatella*, and the ubiquitous *Olivella semistriata*. The specimens of *A. jesuitarum* were collected by Jesuits from the Central American University, and the name given to the species honors their dedication.

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