

Systematic Revision of *Allochroa* Ancey, 1887 (Pulmonata: Ellobiidae), with an Account of the Anatomy of *Allochroa layardi* (H. & A. Adams, 1855) and the Description of Two New Species

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ABSTRACT

Of the nominal species of *Allochroa* Ancey, 1887 described to date, only two are recognized: *A. bronni* (Philippi, 1846), endemic to the Hawaiian Islands, and *A. layardi* (H. & A. Adams, 1855), distributed throughout the Indo-Pacific. Examination of the USNM collection revealed two additional species, *A. nana* Martins, n. sp. and *A. tenuis* Martins, n. sp., herein described. The anatomy of *A. layardi* is described and serves as the basis for determining the relationships of this genus within the Ellobiidae. *Allochroa* has a monaulic, entirely glandular pallial gonoduct and a wide visceral nerve ring with a long right parieto-visceral connective, confirming placement in the Pythiinae. Its close relationship to the Mediterranean and Eastern North Atlantic genus *Ovatella* Bivona, 1832 is indicated by similar apertural dentition, protoconch morphology of *A. tenuis*, and by the internal structure of the penial complex, where the penis appears as the development of one of the pilasters.

Key Words: Ellobiidae, Pythiinae, *Allochroa*, systematics, anatomy.

INTRODUCTION

The Ellobiidae are a group of primitive, mostly halophilic pulmonate mollusks, commonly found near and above the high tide limit of mangroves, salt marshes, and boulder and cobble beaches. Morphologically very diverse and ranging in length from barely 1 mm (*Leuconopsis*) to about 100 mm (*Ellobium*), they nevertheless share basic shell characters and body features that allow them to be considered within a single family. Pfeiffer (1853) was the first to attempt a subfamilial organization, based on shell characters alone. He assigned those species with a thick, reflected outer lip to the Auriculae [=Ellobiinae], while he included the species with sharp outer lip in the Melampea [=Melampodinae]. Utilizing radular and also some anatomical characters, Odhner (1925) recognized a more complex subfamilial arrangement and redistributed the ellobiid genera among four additional

subfamilies: Carychiinae, Pedipedinae, Pythiinae and Cassidulinae. Odhner's outline was supported on conchological features by Zilch (1959). The first detailed use of anatomical characters, in a review that included species belonging to 11 genera, was by Morton (1955). His study supported Odhner's classification, but the Cassidulinae were included in the Pythiinae, on the basis of similarities of the reproductive system. In a study of species belonging to 17 of the 23 genera currently recognized in the Ellobiidae, Martins (in press a) clarified Morton's (1955) findings by redefining the subfamilial morphological patterns of the reproductive and nervous systems.

Preserved specimens of *Allochroa layardi* (H. & A. Adams, 1855) are used here as the basis for detailed anatomical investigations of the family extending the preliminary findings reported in Martins (in press b). Insight on the anatomy of *A. layardi* provided information needed to define the phylogenetic relationships of *Allochroa* Ancey, 1887 within the Pythiinae. The present work reviews the taxonomy of the species of *Allochroa* and describes the anatomy of *A. layardi*. Examination of the Mollusk collection at the National Museum of Natural History, Smithsonian Institution, consisting of only dry material, revealed the existence of two new species, herein described.

MATERIALS AND METHODS

This taxonomic revision is based primarily on dry specimens of *Allochroa* in the USNM collection. Four specimens of *A. layardi*, collected on Henderson Island in 1991, were provided for anatomical work. The fully retracted animals were preserved in alcohol and, except for the eyes and the tip of the tentacles, appear to have lost all other pigmentation. Two specimens were dissected under a binocular microscope and drawn using a camera lucida.

Shells with protoconchs were mounted using double-

coated tape. Radulae were stretched across a cover slip after cleaning with KOH solution. Both structures were mounted on stubs and examined and photographed using a Cambridge Stereoscan 250 Mk2 Scanning Electron Microscope.

Acronyms for specimen repositories are as follows:

ANSP:	The Academy of Natural Sciences, Philadelphia
BMNH:	The Natural History Museum, London
MCZ:	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN:	Muséum National d'Histoire Naturelle de Paris
USNM:	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

KEY TO THE SPECIES OF *ALLOCHROA* ANCEY, 1887:

1. Shell thick 2
Shell thin 3
2. Aperture oval elongated (base narrow) ... *A. bronni*
Aperture auriculate (base expanded) ... *A. layardi*
3. Shell length at least 4 mm 4
Shell length less than 4 mm 5
4. Protoconch width less than .5 mm *A. layardi*
Protoconch width at least .6 mm 5
5. Protoconch without umbilicus and with apertural lip not reflected *A. nana*
Protoconch with umbilicus and with apertural lip slightly reflected *A. tenuis*

SYSTEMATICS

Class GASTROPODA Cuvier, 1797
Subclass PULMONATA Cuvier, 1817
Order Archaeopulmonata Morton, 1955
Family Ellobiidae H. & A. Adams in Pfeiffer, 1854
Subfamily Pythiinae Odhner, 1925
Genus *Allochroa* Ancey, 1887

Allochroa Ancey, 1887:288. Type species by original designation: *Auricula bronni* Philippi, 1846.

Description: Shell length to 12 mm, oval-conic, fragile to somewhat solid, sometimes hirsute. Umbilicus absent. Spire with up to 7.4 flat to slightly convex whorls, sculptured with more or less marked spiral lines; body whorl 55 to 80% of shell length, usually with three chestnut spiral bands over a whitish to light-brown background, the band just above the aperture consistently strongest, the one near the suture sometimes faint, the one near the columella largest, sometimes coalescing with the median band. Aperture about 50 to 60% of shell length, oval-elongated to semi-circular, angled posteriorly, rounded anteriorly; inner lip slightly reflected over the columella, with three more or less equidistant teeth: one oblique columellar tooth, a more or less horizontal anterior parietal tooth, and a sometimes strongest, oblique

posterior parietal tooth; outer lip sharp, usually with one prominent fold entering the aperture at about the level of the parietal teeth, forming a somewhat marked anal canal. Protoconch bulbous, smooth, with up to 1.3 whorls visible.

Radula: Central tooth narrow, base deeply emarginate, with two median flaring arms, unicuspid; lateral teeth with elongated, sinuous base with two projecting asymmetric arms, inner arm lower, crown large and long, subquadrangular; marginal teeth with sharp endocone gradually becoming as long as mesocone as row progresses outward, developing a sometimes conspicuous basal ectocone.

Anatomy: Reproductive system monaulic, pallial gonoducts entirely glandular, pallial gland present. Central nervous system with wide visceral ring; right parieto-visceral connective as long as left.

Remarks: The name *Allochroa* was proposed by Ancey (1887) to replace the supposedly preoccupied "*Laimodonta* des auteurs [H. & A. Adams, 1853] (non Nuttall)" (type species *Auricula bronni* Philippi, 1846). "*Laimodonta* Nuttall", wrongly taken as an emendation of *Laemodonta* Philippi, 1846, was restricted to a different assemblage (type species *Auricula striata* Philippi, 1846), following Nevill (1878). A more detailed account of the synonymy of *Laemodonta* and *Laimodonta* is presented elsewhere (Martins, in press a).

Ancey (1887) also made clear that *Marinula* King, 1832, very similar to *Pedipes* Scopoli, 1777, was not an eligible group for his new assemblage, and that *Monica* H. & A. Adams, 1855 [= *Ovatella* Bivona, 1832], although decidedly conchologically closely related, is restricted to Mediterranean and West Atlantic species.

Allochroa is conchologically characterized by the presence of an outer lip internal lamella which, in conjunction with the anterior parietal tooth, divides the aperture into two roughly equal halves: a posterior portion, where the shell is thinner; an anterior, thickened half, sometimes with an additional internal fold on the outer lip. The inner lip of the aperture is typically pythiine, i.e., roughly equidistantly tridentate, with one small columellar tooth and two parietal teeth. The lamellar, outer lip tooth readily separates this genus from the closely related *Laemodonta*, which usually has two round tubercles on the outer lip, and also from *Ovatella*, where the outer lip lamellae are much shorter. The single columellar tooth sets *Allochroa* apart from *Pedipes* which, as in *P. mirabilis* (Mühlfeld, 1816) and *P. pedipes* (Bruguière, 1789), has a strong, crest-like outer lip fold penetrating inside the aperture. In *Pedipes*, the single parietal tooth is very strongly pronounced.

The six species assigned by authors to *Allochroa* are here synonymized into two: the Hawaiian *Allochroa bronni* (Philippi, 1846) and the Indo-Pacific *Allochroa layardi* (H. & A. Adams, 1855). Two additional new species are described herein.

Kuroda and Habe (1952) listed *Pedipes affinis* Férussac, 1821, under *Allochroa*, owing probably to the presence of a strong lamella inside the outer lip. Férussac

(1821), however, had mentioned a bidentate columella as characteristic of *Pedipes*, and Ancey (1887) also used this feature of *P. affinis* to separate it from *Laemodonta*, where Jickeli (1874) had erroneously placed it. Following the above reasoning, I concur with Ancey (1887) in considering Férussac's species a *Pedipes*.

Similarly, the New Caledonian *Pedipes forestieri* Souverbie and Montrouzier, 1864, has been erroneously assigned to *Allochroa* (Franc, 1954; Smith, 1992). In the original description Souverbie and Montrouzier (1864a) mentioned the presence of two columellar teeth, stating that their observations were based on a single, probably juvenile specimen. In a later paper (1864b) the same authors, reacting to the epistolary comment of L. Pfeiffer on that subject "*Spec. nov., sed Marinula*", changed the taxonomic combination to "*Marinula* (an *Pedipes*?)", cautiously justifying, however, their original generic choice by pointing out features such as "1) shell positively striated transversely; 2) two positively columellar folds; 3) external border of the columellar lip contouring behind the upper columellar fold as in *Pedipes mirabilis*, Mühlf., which we possess." The accompanying figure (Souverbie & Montrouzier, 1864a: pl. X, fig. 1) appropriately illustrated their reasoning. Franc (1954) claimed to have found an adult specimen of Souverbie and Montrouzier's species in the Jousseume collection at the MNHN, and assigned it to *Allochroa*. The redescription of *Pedipes forestieri* provided by Franc (1954), mentions the presence of a spiral fold inside the outer lip characteristic of *Allochroa*, but corroborates the presence of "two columellar folds closer to each other than to the parietal", a feature diagnostic of some pedipedine genera, namely *Pedipes* and *Marinula*. Taking into account Souverbie and Montrouzier's (1864a, b) insistence on the pedipedine characteristics of the apertural dentition, a feature confirmed by Franc (1954), and in my inability to examine the type material, I consider the assignment of *Pedipes forestieri* to *Allochroa* to be unwarranted.

The similarity of the basic patterns of shell morphology and color throughout the genus creates some difficulties in separating species. Larger specimens of the highly variable, widely distributed *A. layardi* overlap in shape and color with smaller specimens of the Hawaiian *A. bronni* (compare Figs. 1 and 5). At the other extreme, thin, less distinctly banded forms of *A. layardi* could be confused with lighter specimens of *A. tenuis*, n. sp. (compare Figs. 10 and 19). However, species can be readily separated on the basis of other conchological characters such as the ratio number of whorls/shell length or using protoconch features.

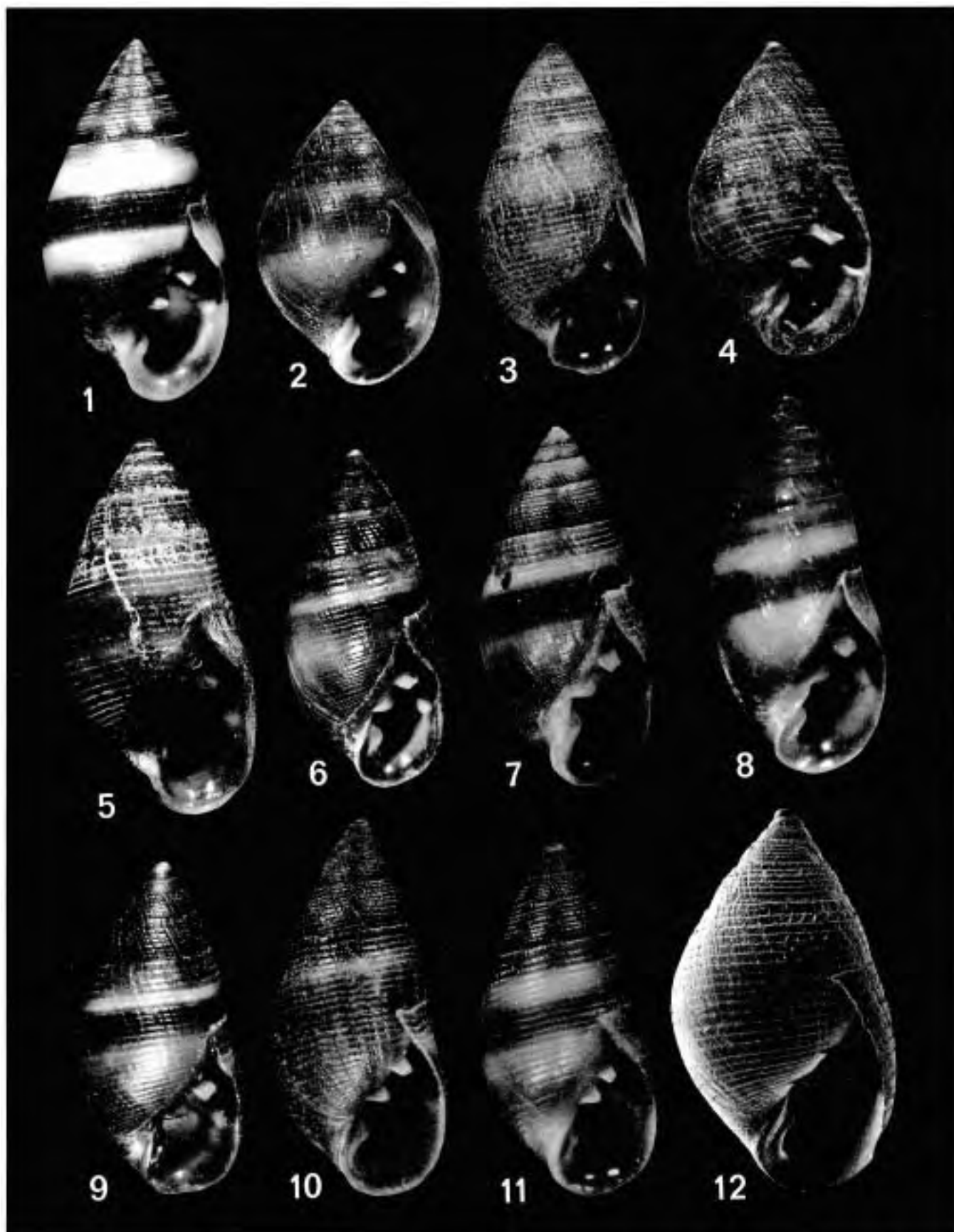
Allochroa bronni (Philippi, 1846)
Figures 1–2, 21, 31–32

Auricula bronni Philippi, 1846:98 [Hawaiian Islands; location of type unknown]. *Auricula sandwichiensis* Souleyet, 1852: 524, pl. 29, figs. 29–32 [Hawaiian Islands; type not found, supposedly at BMNH (Gray, 1855)]. *Ophicardelus (Laemodonta) sandwichiensis* (Eydoux & Souleyet). H. & A. Adams, 1855a: 34 [misspelling of *sandwichiensis*]. *Melam-*

pus bronni (Philippi). Pfeiffer 1854:147. *Ellobium brownii* (Philippi). H. & A. Adams, 1855b:237 [misspelling of *bronni*]. *Laimodonta sandwichiensis* (Eydoux & Souleyet). H. & A. Adams, 1855b:246, pl. 83, figs 1, 1a [misspelling of *sandwichiensis*]. *Melampus sandwichiensis* (Souleyet). Pfeiffer, 1856:50. *Ophicardelus sandwichiensis* (Eydoux). J. E. Gray in M. E. Gray, 1859:(3), pl. 304, fig. 2; (4):118. *Laemodonta bronni* (Philippi). Martens & Langkavel, 1871: 57. *Marinula (Laemodonta) bronni* (Philippi). Nevill, 1878: 220. *Allochroa bronni* (Philippi). Ancey, 1887:288. *Tralia (Laemodonta) bronni* (Philippi). Crosse, 1894:321. *Melampus (Laimodonta) bronni* (Philippi). Kobelt, 1898: 200, pl. 23, figs. 1, 2. *Laimodonta bronni* (Philippi). Dautzenberg & Fischer, 1905: 107.

Description: Shell (Figs. 1–2, 21) length to 12 mm, ovate-conical, somewhat solid; violet-brown to light-brown, banded. Spire moderately high with up to 7.4 flattened whorls, with marked spiral striae crossed by irregular growth lines that give the surface a matte appearance; one light-brown subsutural band, a median white band followed by a dark-brown band. Body whorl averaging 60% of shell length, sculptured as spire; coloration pattern showing a subsutural light-brown band followed by a marked, white, narrow band halfway between the suture and the aperture, a wide, dark-brown band extending just below the posterior apertural angle, a whitish to brownish band as wide as the previous one gradually merging with the dark-brown, anteriormost band that extends to the anterior tip of the aperture. Aperture oval-elongated, rounded anteriorly, acute posteriorly; inner lip with three subequidistant teeth: one oblique columellar tooth faintly continuous with a callus that runs along the anterior border of the aperture and connects to the tip of the outer lip tooth; two parietal teeth, the anterior one half the length of the aperture, perpendicular to the columellar axis and continuing inward; the posterior one usually strongest, not continuing inward; outer lip sharp, with a ridge-like tooth about opposite the anterior parietal tooth, penetrating inside the aperture for about half a whorl; a wide callus develops anterior to the outer lip tooth. Protoconch 235x155 μ m, whitish, smooth, somewhat inflated, barely over one whorl, with elongated, narrowing lip (Fig. 21).

Radula: (Figs. 31–32) Formula [31+24+1+24+31] $\times 100+$. Central tooth slightly above the plane of the lateral teeth; base narrow, subquadrangular, deeply emarginate with medial lateral projections flaring out; crown less than half the length of the lateral teeth, narrow, unicuspid: mesocone somewhat sharp. Lateral teeth 24, base elongated, slightly bent medially, with lateral projections flaring out asymmetrically, the inner projection smaller, at about the first third of the base, the outer one at about mid-length of the base; crown covering three quarters of base, quadrangular, with a longitudinal depression in the middle. Marginal teeth 31; basis barely longer than crown, diminishing gradually to completely disappear under crown, developing a basal ectocone; crown bicuspid, endocone sharp, short on first teeth, gradually elongating towards the end of the row, mesocone long and narrow, blunt at tip.



Remarks: The Hawaiian *Allochroa bronnii* is the largest species of the genus, sometimes reaching 12 mm in length (Souleyet, 1852; USNM 131288). It has been confused with larger forms of the highly variable *Allochroa layardi*, an Indo-Pacific species (Dautzenberg & Fischer, 1905). They can be set apart by the narrower base of the aperture in *A. bronnii*, whereas shells of identical size of *A. layardi* have a wider apertural base (see Figs. 1 and 5). In Hawaii, where both species overlap, they are morphologically very distinct (see Figs. 1, 2, 4). Although size alone seems to be sufficiently diagnostic to separate these two species, *A. bronnii* shows also a proportionally smaller number of whorls for the length of the shell. However, anatomical studies are needed to ascertain better the differences between these two closely related species.

Habitat Notes: "Found seaward of *Melampus*, *Pedipes*, and *Laemodonta*, often buried in gravel in high tide pools and along rocky shores" (Kay, 1979).

Range: *Allochroa bronnii* is endemic to the Hawaiian Islands.

Material Examined: (Sample size in parenthesis). HAWAIIAN ISLANDS: [USNM 20795 (5), 31582 (4), 98175 (6), 98176 (9), 98178 (3), 131288 (1), 319528 (4), 346615 (11)]; HAWAII ISLAND: Keei, near Napoopoo, Kona Coast [USNM 767596 (1)]; OAHU ISLAND: Honolulu [USNM 159574 (1)]; Pearl City, Honolulu [MCZ 55989 (1)]; 1935 dredgings, Hickham Air Force Base, Pearl Harbor [USNM 484416 (3)]; Kaneohe Bay [USNM 887316 (8)].

Allochroa layardi (H. & A. Adams, 1855)

Figures 3–14, 22–27, 30, 33–35, 39–45

Melampus layardi 'Ads.' Pfeiffer, 1854:147. *Nomen nudum*.

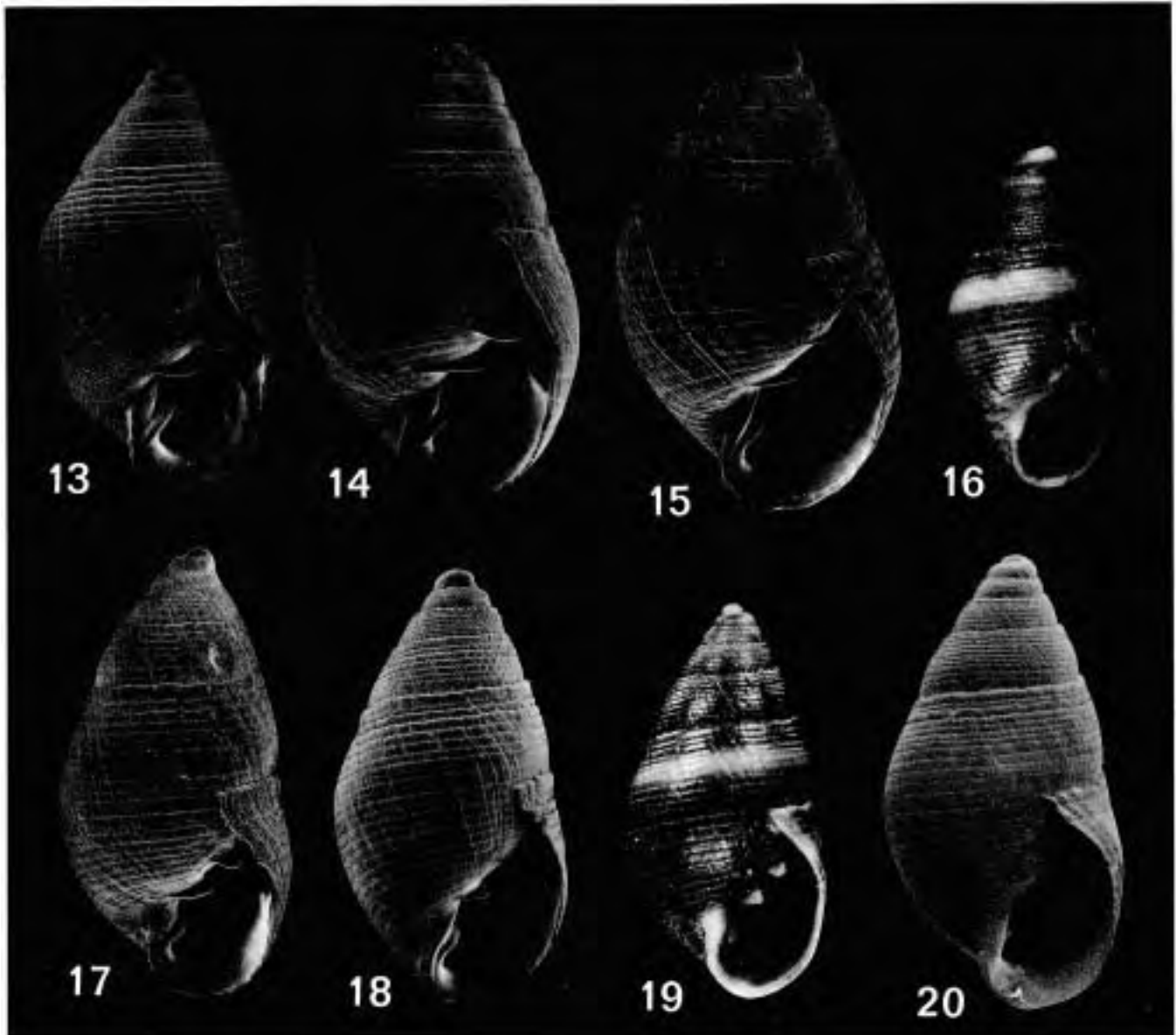
Ophicardelus (Laimodonta) layardi H. & A. Adams, 1855a: 35 [Ceylon; lectotype herein selected BMNH 196980/1 (Fig. 3); two paralectotypes BMNH 196980/2–3]. *Laimodonta layardi* (H. & A. Adams). H. & A. Adams, 1855b: 246. *Laimodonta pfeifferi* Dunker in Pfeiffer 1860: 201 [Japan; location of type unknown]; Dunker, 1861:25, pl. 2, fig. 19. *Laimodonta conica* Pease 1863: 242 [Pacific Islands; lectotype selected by Kay (1965) BMNH 1964292 (Fig. 4); five paralectotypes BMNH 1964293]. *Laimodonta conica* Pease. Pease, 1868:101, pl. 12, fig. 15 (misspelling of *Laimodonta*). *Laimodonta anaensis* Mousson, 1869: 63 [Anaa Island, Paumotu group; location of type un-

known]. *Laemodonta conica* (Pease). Martens & Langkavel, 1871:57. *Plecotrema anaensis* (Mousson). Paetel, 1873:114. *Laimodonta bronni* var. *conica* (Pease). Jickeli, 1874:178, pl. 7, fig. 3. *Melampus pfeifferi* (Dunker). Pfeiffer, 1876:319. *Melampus conicus* (Pease). Pfeiffer, 1876:319. ?*Melampus anaensis* (Mousson). Pfeiffer, 1876:320. *Marinula (Laimodonta) conica* (Pease). Nevill, 1878:220. *Marinula (Laemodonta) conica* (Pease). Martens, 1880: 208. *Laimodonta conica* var. *conicoides* Tapparone Canefri, 1883:240 [Aru Island, New Guinea; location of type unknown]. *Laemodonta (Tralia) layardi* (H. & A. Adams). Crosse, 1894:321. *Melampus (Laimodonta) conicus* (Pease). Kobelt, 1898:224, pl. 26, fig. 14. *Melampus (Laimodonta) anaensis* (Mousson). Kobelt, 1898:228, pl. 27, figs. 10–11. *Laimodonta bronni* var. *producta* Dautzenberg & H. Fischer, 1905:108, pl. IV, figs. 20, 21 [Anse du Crâne, Bahie d'Along, Tonkin; syntypes MNHN (Fig. 5)]. *Enterodonta conica* (Pease). Germain, 1921:264. *Allochroa conica* (Pease). van Benthem Jutting, 1941:283. *Allochroa pfeifferi* (Dunker). Kuroda & Habe, 1952:38. *Allochroa layardi* (H. & A. Adams). Franc, 1954:365.

Description: Shell (Figs. 3–14, 22–27) length to 8 mm, ovate-conical, fragile to somewhat solid; chestnut-brown to pale-yellow, banded. Spire moderately high, whorls 6.0 to 6.5, plano-convex, with spiral striae crossed by irregularly marked longitudinal growth lines which give the surface a faint granulose appearance. Body whorl about 70% shell length, sculptured as the previous whorls; color pattern showing a faint subsutural light band, a marked whitish band halfway between the suture and the aperture, also visible on the two previous whorls, sometimes with a third, wider pale-yellow band gradually becoming dark-brown anteriorly. Aperture auriculate; inner lip tridentate; one oblique columellar tooth not reaching the border of the lip; two parietal teeth, anterior lamellar, transverse, continuing inwards, posterior largest, thick and bifid in larger individuals, slightly elongated but not continuing inwards; outer lip sharp, with a ridge-like tooth about halfway along the length of the aperture, penetrating deep inside the aperture; a wide callus may develop anteriorly, as a continuation of the outer lip tooth, also penetrating inwards; a second outer lip tooth is sometimes present over the callus, located at a level between the anterior parietal tooth and the columellar tooth. Juveniles pilose, the hairs distributed along the spiral striae (Fig. 12). Protoconch 210–235 x 150–175 μ m whitish, smooth, somewhat inflated, a little over one whorl, with rounded peristome (Figs. 22–27).

Figures 1–2. *Allochroa bronnii* (Philippi); 1. Hawaii, USNM 98175, sl = 8.2 mm; 2. Pearl City, Honolulu, Hawaii, MCZ 55989, sl = 3.5 mm.

Figures 3–12. *Allochroa layardi* (H. & A. Adams); 3. Lectotype, Ceylon, BMNH 196980.a, sl = 7.0 mm; 4. Lectotype of *Laimodonta conica* Pease, Pacific Islands [Hawaii], BMNH 1964292, sl = 4.2 mm; 5. Holotype of *Laimodonta bronni* var. *producta* Dautzenberg & Fischer, Bahie d'Along, Anse du Crâne, Tonkin, China, MNHN (not numbered), sl = 8.0 mm; 6. Paumotu [Tuamotu] Islands, specimen illustrated in Pease (1868, pl. 12, fig. 15), ANSP 22610 [type written in label], sl = 7.0 mm; 7. Mataira Island, Raroia, Tuamotu Islands, USNM 698771, sl = 5.8 mm; 8. North Beach, Henderson Island, Pitcairn Islands, R. C. Preece coll., sl = 6.1 mm; 9. Lijeron Island, Jaluit Atoll, Marshall Islands, USNM 660035, sl = 4.6 mm; 10. Lugbon Island, Philippines, USNM 201147, sl = 5.5 mm; 11. Riu Kiu Islands, Japan, USNM 345877, sl = 5.0 mm; 12. Hirado, Hizen, Japan, USNM 345878, sl = 4.1 mm. sl = shell length.



Figures 13–14. *Allochroa layardi* (H. & A. Adams), Mataira Island, Raroia, Tuamotu Islands, USNM 698771, sl = 3.5, and 2.5 mm.

Figures 15–18. *Allochroa nana* Martins, n. sp., Eninman Island, Bikini, Marshall Islands; **15, 17–18.** paratypes, USNM 585963, sl = 2.2, 3.7, and 3.0 mm; **16.** holotype, USNM 585963.a, sl = 3.2 mm. **Figures 19–20.** *Allochroa tenuis* Martins, n. sp., Noumea, New Caledonia; **19.** holotype, USNM 724374.a, sl = 4.1 mm; **20.** paratype, USNM 724374, sl = 3.5 mm. sl = shell length.

Radula: (Figs. 33–35) formula [26+23+1+23+26] × 115. Central tooth slightly above the plane of the lateral teeth; base deeply emarginate, with lateral projections flaring out at mid-length, gradually tapering to neck region; crown half-length of that of lateral teeth, narrow, unicuspid; mesocone somewhat sharp. Lateral teeth 23; base elongated, slightly bent medially; a rounded inner prominence arises on the lower third, an outer projection flares out at mid-length and tapers towards neck; crown covering two thirds of base and as wide as the latter, unicuspid; cusp rounded. Marginal teeth 26; bases of first teeth barely longer than crown, gradually diminishing

to completely disappear underneath crown, developing a conspicuous lateral basal cusp on the last 13 teeth; crown bicuspid; endocone, sharp, short on first teeth, gradually elongating to about three quarters of mesocone; mesocone as long as that of last lateral teeth, rounded at tip.

Visceral mass: Conical, not following external winding of shell, with whorl impressions weakly insinuated, indicating the extensive resorption of the inner whorls of the shell.

Digestive system: Mandible (Fig. 39) with fibrous appearance, tripartite; median portion roughly quadran-

gular with extremities abruptly tapering posteriorly, lateral portions of sparse, loose fibers, tapering on both extremities. Salivary glands long, cylindrical. Stomach (Fig. 40) tripartite; cardiac region dilated, thin, receiving at its base the duct of anterior diverticulum; mid-portion comprising most of the stomach's volume, muscularized; gastric caecum thin, pouch-like, receiving posterior diverticulum; pyloric region small, thin.

Reproductive system: (Fig. 30, 41–44) Ovary long, inverted claviform acini embedded in the conical posterior lobe of the digestive gland, connecting with a collecting duct by their thinner ends, the broader, dark-red dotted extremities appearing at the surface of the digestive gland as an irregular, winding band; proximal half of the hermaphroditic duct thin, relatively straight, distal half forming a greatly convoluted and somewhat dilated seminal vesicle; pallial gonoduct hermaphroditic to the vaginal aperture; albumen gland beneath the anterior lobe of digestive gland and intestinal convolutions; posterior mucus gland tightly convoluted; anterior mucus gland and prostate gland covering entire length of pallial spermoviduct; bursa spherical, fitting under posterior mucus gland; bursa duct nearly equal in length to spermoviduct, emptying near vaginal opening. Pallial gland long, sharply bent about midlength, anterior portion more dilated and slightly longer than posterior one, emptying at the female genital opening. Penial complex relatively short, proximal third dilated; vas deferens adhering to penial sheath, entering penial structure at the distal end of the proximal quarter; penis oval-oblong, blunt, constituted of a thickened, sharply bent, compactly folded muscular pilaster, lodged in the thin, membranous dilation of the penial sheath; internal wall of the penial sheath with fine, radiating grooves at the site of the dilation, with two irregularly grooved longitudinal folds running forward to the aperture, one of them connecting distally to the penis, the other originating at the level of the tip of the penial papilla; penial retractor about as long as the penial complex, relatively thick.

Nervous system: (Fig. 45) Cerebral commissure short, about half the width of a cerebral ganglion; left cerebropleural connective twice the length of the right one; right cerebro-pedal connective somewhat longer than the left one; pleural ganglia small; right pleuro-parietal connective very short, about one-third of the left one; left parietal ganglion as small as pleural ganglia, right one three times larger, with a thick pneumostomal nerve from where a rudimentary osphradial ganglion buds off; parieto-visceral connectives relatively long, the left one somewhat longer.

Remarks: *Allochroa layardi* was described by H. & A. Adams (1855a) from specimens from Ceylon [Sri Lanka], in the Cuming collection. H. & A. Adams' manuscript, although submitted for publication in 1854, was not published until January 1855 (see Duncan, 1937; Trew, 1992). Pfeiffer, who had access to the manuscript of the Adams brothers, listed their new species in his Synopsis (1854), giving credit to the original author(s) and placing the species under the genus *Melampus*. Pfeiffer, however,

did not add any descriptive notes; for this reason, the name "*Melampus layardi* 'Ad.' Pfeiffer" should be treated as *nomen nudum*. The Adams brothers' name was apparently ignored in the various subsequent descriptions of taxa here considered as synonyms of *A. layardi*, and comparisons referred rather to *A. bronni*. Such was the case of *Laimodonta pfeifferi*, from Japan, and of *Laimodonta bronni* var. *producta* from China (see Fig. 5). *Allochroa layardi*, however, has a more slender overall shape and is smaller than *A. bronni*, mainly in Hawaii where both species coexist. Pease (1863) described *Laimodonta conica* from the Hawaiian Islands (Fig. 4); five years later, however, Pease (1868) figured his Hawaiian species using a specimen from Paumotu [Tuamotu Islands], almost twice the size and more elongated than the type specimens (Fig. 6). Mousson (1869) described and figured the larger Tuamotu shells from Anaa Island as *Laemodonta anaaensis*, commenting on their clear relationship with *A. bronni*, but at the same time calling attention to the smaller size of his species relative to the latter; his measurements (8 mm), however, are the largest known for *A. layardi*.

Very variable across the Indo-Pacific, *A. layardi* is usually markedly striated, although some specimens can be extremely smooth (Fig. 8). It also varies in shell thickness, the thick specimens sometimes showing an additional internal lamella on the outer lip (Figs. 7, 9, 13), which Tapparone Canefri (1883) considered to be the variety *conicoides* of *Laimodonta conica* [= *A. layardi*]. The color pattern remains basically the same throughout; however, the banding delimitation may sometimes lack sharpness (Fig. 10). The shape and size of the protoconch are consistently homogeneous throughout the distributional range of the species (Figs. 22–27). *Allochroa bronni* (Fig. 21) possesses a protoconch similar to that of *A. layardi*, also stressing the close affinities of the two species. However, as pointed out before, the size and ratio between the number of whorls and the length of the shell justify their taxonomic separation.

Only one radula of each species was studied. It appears that the base of the central tooth of *A. layardi* is decidedly triangular (Fig. 33), whereas that of *A. bronni* is narrowly quadrangular (Fig. 31). The crown of the lateral teeth of *A. bronni* seems to be narrower and longer than that of *A. layardi*.

Habitat Notes: Gassies (1863) stated that this animal appears to be completely marine, and that Montrouzier found it under stones near the shore, together with columbellids, ranellids and tritons. Preece (personal communication) found them in crevices of exposed rocks at about high tide level.

Range: *Allochroa layardi* is widely distributed throughout the Indo-Pacific; it has been reported from Mauritius (Morelet, 1882), Sri Lanka, India (Nevill, 1878), China, Japan, Philippines, New Guinea, Australia, New Caledonia, Marshall Islands, Tuamotu Islands, Hawaii.

Material Examined: (Sample size in parenthesis) CEYLON [SRI LANKA] [BMNH 196980/1 (lectotype),

196980/2–3 (paralectotypes of *Ophicardelus (Laimodonta) layardi*). CHINA: Bahie d'Along, Anse du Crâne, Tonquin [MNHN, not numbered, holotype and paratype of *Laimodonta bronni* var. *producta*]. JAPAN: Hirado, Hizen [USNM 345878 (30)]; Riu Kiu Islands [USNM 345877 (56)]; Loo Choo Islands [USNM 30811 (12), 161507 (2)]; Nago, Okinawa Island, Loo Choo Islands [USNM 363720 (1)]. PHILIPPINE ISLANDS: Bohol Island [USNM 302973 (4)]; off Point Origon, Tablas [USNM 281503 (1)]; Lugbon Island [USNM 201147 (7)]; Point Hinayangan, Leyte [USNM 887317 ex Chicago Academy of Sciences (3)]; Sogod Bay, Leyte [USNM 283799 (1)]; off Point Dumurug, Masbate [USNM 274834 (1)]; off Adyagan Island, E Masbate [USNM 281808(1)]; Ragay Gulf, off Arena Point, Luzon [USNM 284250 (1)]; off Matabot Point, W Louzon [USNM 259939 (1)]; off Pescador Island, Tanon Station [USNM 281169 (1)]; off Capitancillo Island, N Cebu [USNM 287800 (1)]; off Lanis Point, E Cebu [USNM 290562 (2)]; Pujada Bay, E Mindanao [USNM 255647 (1), 276398 (2)]; Tilig, Lubang Island [USNM 229914 (1)]. NEW CALEDONIA: Lifu [USNM 422639 (1), 422640 (1), 423167 (4)]. AUSTRALIA: [USNM 887318 (1)]; mouth of Bigota Creek, Barrow Island [USNM 691788 (1)]. COOK ISLANDS: Tupapa, E of Avarua, Rarotonga [USNM 721509 (1)]. MARSHALL ISLANDS: N end of Lijeron Island, Jaluit Atoll [USNM 660035 (8)]. TUAMOTU ISLANDS: [USNM 98177 (3), 711465 (6)]; RAROIA ISLANDS: Ngarumaoa Island [USNM 697524 (1), 697767 (1), 698079 (2), 720349 (17)]; S end of Ngarumaoa Island [USNM 697593 (3)]; Mataira Island [USNM 698771 (8), 711673 (1)]; Kumekumo Island [USNM 698492 (5)]; Teteu Island [USNM 722685 (1), 722687 (1)]; S end of Teteu Island [USNM 722756 (50)]; Havana Island [USNM (1 fragment)]; Okaea Island [USNM 722834 (1)]; S end of Opaquea Island [USNM 722554 (79), 723548 (1)]; Oneroa Island [USNM 720768 (2)]; Ohava Island [USNM 720503 (19)]; Otikaheru Island [USNM 720684 (1)]; Vahi Tahī [USNM 613207 (1)]; Te-mao Harbor, Makatea [USNM 629788 (1)]; NE side of Tepukamaruia Island, Takumo [USNM 723724 (1)]; Motu Taraururoa, Mangareva Island [USNM 638224 (4)]. PITCAIRN ISLANDS: E end of North Beach, Henderson Island [R. C. Preece collection (4)]. HAWAIIAN ISLANDS: [BMNH 1964292 (lectotype), 1964293 (5 paralectotypes)]; USNM 15157 (2), 20796 (3), 20797 (12), 887319 (4)].

Allochroa nana Martins, new species
Figures 15–18, 28

Description: Shell (Figs. 15–18, 28) length to 3.7 mm, ovato-conical, fragile, spirally striated, dark-brown to golden-brown, banded. Spire moderately high, 5 plano-convex, dark-brown to brown whorls, sometimes with a faint equatorial lighter band; spiral striae undulated due to crossing by marked growth lines which are predominant on the early whorls of teleoconch. Body whorl about 70% of shell length, sculptured as previous whorls; banded color pattern as follows: a light-brown, fine band from

the suture to the first spiral stria, a darker band on the next two striae, a wider, white band covering the next 3–4 striae, a dark-brown band extending to the posterior end of the aperture, frequently continuing to the anterior tip of the shell, sometimes broken up by a diffuse, lighter band extending from the posterior end of the aperture to about the level of the anterior parietal tooth. Aperture semicircular, oblique; inner lip equidistantly tridentate: one small, oblique columellar tooth, two parietal teeth, the anterior strongest and perpendicular to the columellar axis. The posterior about as strong as columellar tooth; outer lip sharp, very rarely with an elongated thickening opposite the anterior parietal tooth and weakly projecting inside the aperture (Fig. 17). Juveniles pilose (Fig. 15). Protoconch 285x210 μm , bulbous, light-brown, with growth lines showing as faint narrow bands, with elongated, somewhat widening lip (Fig. 28).

Type Locality: Eninman Island, Bikini, Marshall Islands. From drift line along tide pool at N end of island, outer reef side.

Material Examined: (Sample size in parenthesis) MARSHALL ISLANDS: Eninman Island, Bikini [USNM 585963 (holotype), 887320 (64 paratypes)]; Rojoa Island, Enewetak [USNM 587120 (1)]; Pujiyuru Island, Enewetak [USNM 587101 (1)]; N end of Bock Island, Rongerik [USNM 594920 (2)].

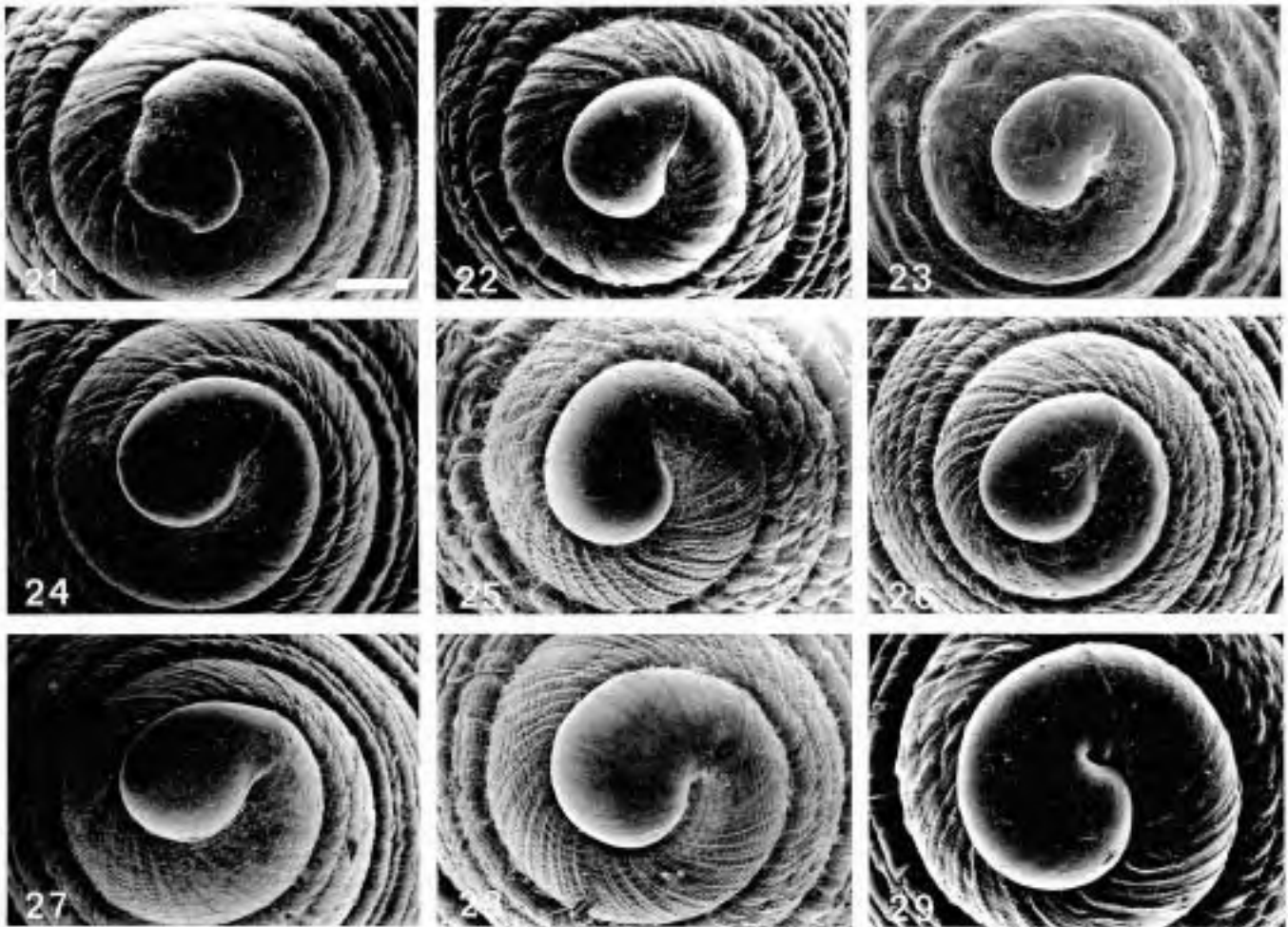
Etymology: *nanus*, *i* = dwarf.

Range: Known from Bikini, Enewetak and Rongerik, in the Marshall Islands.

Remarks: *Allochroa nana* is the smallest species of the genus, and size alone will easily distinguish it from the previously described species. It is, however, best characterized by its large protoconch with faint colabral bands marking the growth lines and with a somewhat widening lip (Fig. 28).

Allochroa tenuis Martins, new species
Figures 19–20, 29, 36–38

Description: Shell (Figs. 19–20, 29) length to 4.6 mm, ovato-conical, fragile, spirally striated, purple-brown to brown, banded. Spire moderately high, 5.5 plano-convex, spirally striated, dark-brown whorls, the last one darkest, usually purple-brown. Body whorl about 70% of shell length, sculptured as previous whorls; banded color pattern as follows: a gradually darkening brown band extending from the suture to the third stria, a marked white band over the next three striae, and a more or less homogeneous brown region extending to the tip of the shell, sometimes broken up by a diffuse, lighter band between the end of the aperture and the posterior parietal tooth. Aperture ovate; inner lip equidistantly tridentate; one columellar tooth, oblique, not reaching the border of the aperture lip, two parietal teeth, the anterior strongest and perpendicular to the columellar axis, the posterior about as strong as columellar tooth; outer lip sharp, rarely with an elongated thickening opposite the anterior pa-



Figures 21–29. Protoconchs of *Allochroa* species. **21.** *Allochroa bronniei* (Philippi), Hawaii, USNM 98175. **22–27.** *A. layardi* (H. & A. Adams); **22.** Hawaii, USNM 20797; **23.** paralectotype, Ceylon, BMNH 196980; **24.** Henderson Island, Pitcairn Islands (R. C. Preece); **25.** Lugbon Island, Philippines, USNM 201147; **26.** Riu Kiu, Japan, USNM 345877; **27.** Mataira Island, Raroia, Tuamotu Islands, USNM 698771 (specimen shown in fig. 14). **28.** *A. nana* Martins, n. sp., Eninman Island, Bikini, Marshall Islands, lectotype, USNM 585963. **29.** *A. tenuis* Martins, n. sp., Noumea, New Caledonia, lectotype, USNM 724347. Scale bar = 100 μ m.

rietal tooth and weakly projecting inside the aperture (Figs. 19–20). Protoconch $385 \times 240 \mu\text{m}$, bulbous, light-brown, showing 1.3 whorls, with somewhat reflected lip creating an umbilical slit (Fig. 29).

Radula: (Figs. 36–38) Formula [17+14+1+14+17] $\times 100+$. Central tooth barely above the plane of the lateral teeth; base deeply emarginate, with lateral projections flaring out at mid length; crown small, with narrow, pointed mesocone. Lateral teeth 14, base elongated with lateral projections asymmetrical, the inner lower and serving as “point d’apui” for the articulation with the outer basal projection of the next tooth in the row (see Fig. 36); crown subquadrangular, long, with rounded mesocone. Marginal teeth 17, with one sharp endocone becoming longer towards the end of the row; mesocone becoming sharper towards the end of the row.

Type Locality: Lighthouse island opposite Noumea, New Caledonia. From crevices on undersides of coral slabs, outer reef.

Material Examined: (Sample size in parenthesis) NEW CALEDONIA: Lighthouse island opposite Noumea [USNM 724374 (holotype), 887321 (117 paratypes)]; N side of N’Go Bay [USNM 725042 (1)]; Touaourou [USNM 724628 (1), 724722 (1)]. PHILIPPINES: Pujada Bay, E Mindanao [USNM 887322 (1)].

Etymology: *tenuis*, *e* = thin.

Range: Known from New Caledonia and Mindanao, Philippines.

Remarks: *Allochroa tenuis* is readily distinguished from all other species in the genus on the basis of its thinner, darker shell and its large protoconch with flaring lip (see Fig. 29). The smaller, lighter but equally thin *Allochroa nana*, described above, also has a large protoconch, but without a flaring lip. The shape of the protoconch of *A. tenuis*, although unique among the known *Allochroa*, strongly resembles that of *Ovatella aequalis* (Lowe, 1832).

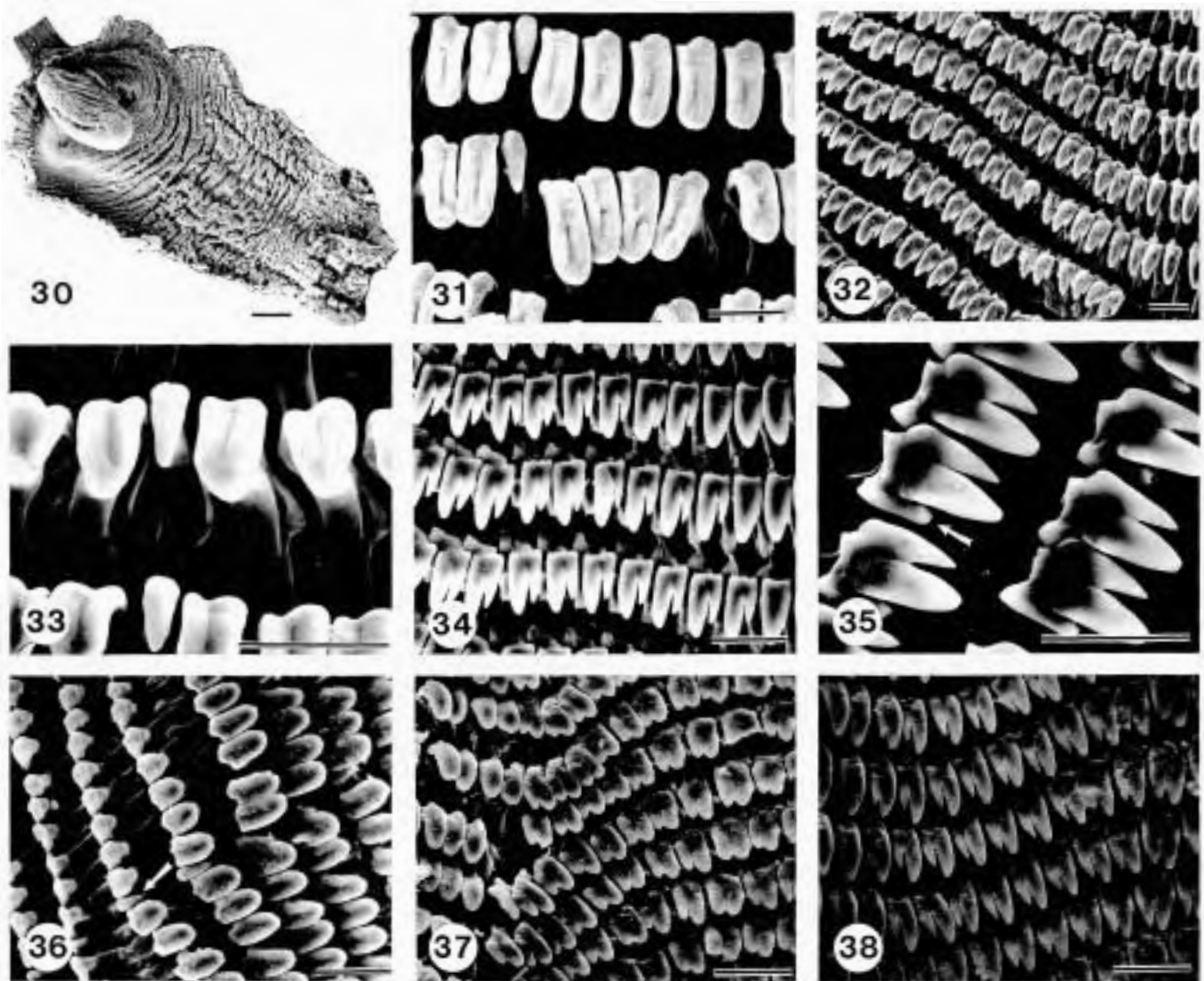


Figure 30. Internal structure of the penial complex of *Allochroa layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands. **Figures 31–38.** Radulae of *Allochroa* species. **31–32.** *A. brononii* (Philippi), Hawaii; **31.** central tooth and first lateral teeth; **32.** last lateral teeth and marginal teeth. **33–35.** *A. layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands; **33.** central tooth and first lateral teeth; **34.** last lateral teeth and marginal teeth; **35.** marginal teeth showing basal cusp (arrow). **36–38.** *A. tenuis* Martins, n. sp., Noumea, New Caledonia; **36.** central tooth (arrow) and lateral teeth; **37.** last lateral teeth and marginal teeth in a worn region; **38.** last lateral teeth and marginal teeth in a fresh region. Scale bar = 100 μm for Fig. 30, 10 μm for all others.

The relationships of *Allochroa* with this European genus are therefore strengthened.

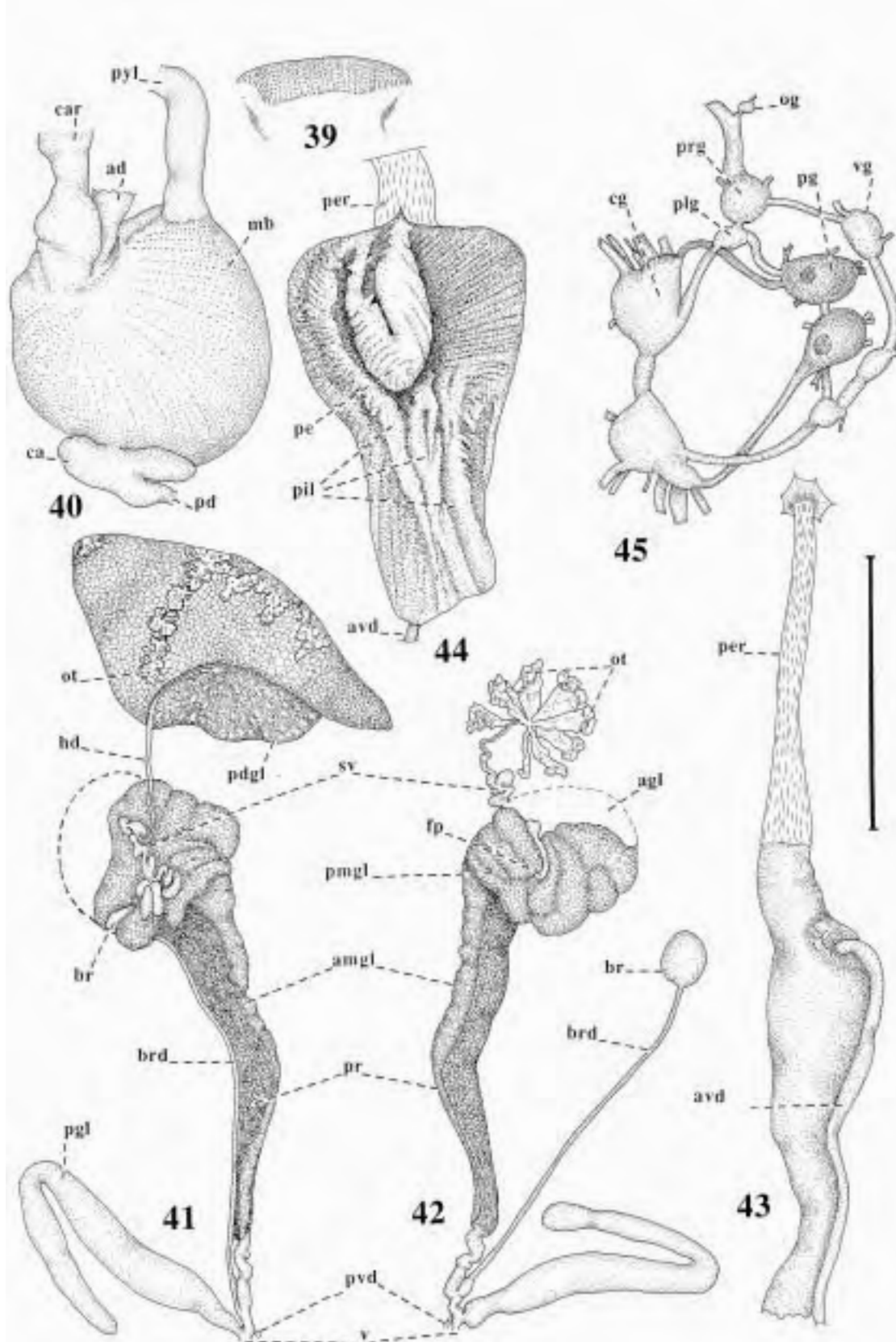
RELATIONSHIPS WITHIN THE ELLOBIIDAE

Since the studies of Odhner (1925) and Morton (1955) the subfamilial division of the Ellobiidae has been based

on anatomical characters, mainly on those of the reproductive system. Martins (in press a, b), studying the characteristics of the central nervous system, concurred with Morton's (1955) conclusions and provided a more complete subfamilial characterization. The Pythiinae, the most primitive subfamily, have a monaulic, entirely glandular, pallial gonoduct and a wide visceral nerve ring

Figures 39–45. Anatomy of *Allochroa layardi* (H. & A. Adams), Henderson Island, Pitcairn Islands; **39.** mandible; **40.** stomach; **41, 42.** reproductive system; **43.** penial complex; **44.** internal structure of penial complex; **45.** central nervous system. Scale bar = 2 mm for Figs. 41–42, 1 mm for all others.

ad, anterior diverticulum; agl, albumen gland; amgl, anterior mucus gland; avd, anterior vas deferens; br, bursa; brd, bursa duct; ca, stomachal caecum; car, cardiac region of stomach; cg, cerebral ganglion; fp, fertilization pouch; hd, hermaphroditic duct; mb,



muscular band; og, osphradial ganglion; ot, ovotestis; pd, posterior diverticulum; pdgl, posterior lobe of digestive gland; pe, penis; per, penial retractor muscle; pg, pedal ganglion; pgl, pallial gland; pil, penial pilasters; plg, pleural ganglion; pmgl, posterior mucus gland; pr, prostate gland/spermiduct; prg, parietal ganglion; pvd, posterior vas deferens; pyl, pyloric region of stomach; sv, seminal vesicle; v, vagina; vg, visceral ganglion.

with a long right parieto-visceral connective. The Ellobiinae have a diaulic reproductive system with entirely glandular pallial gonoducts; the visceral nerve ring is wide and has a short right parieto-visceral connective. The Carychiinae have a monaulic reproductive system with the prostate concentrated distally on the gonoduct and a central nervous system of the ellobiine type. The Pedipedinae possess a monaulic or incipient semi-diaulic pallial gonoduct where only the proximal half is glandular and a concentrated visceral nerve ring. The Melampodinae are characterized by an advanced semi-diaulic reproductive system with non-glandular pallial gonoducts and by concentration of the visceral nerve ring.

Taking into account the preceding arrangement, *Allochroa* must remain within the Pythiinae in view of its monaulic, entirely glandular pallial gonoducts and the wide visceral nerve ring with a long right parieto-visceral connective.

Within the Pythiinae, *Allochroa* shows strongest affinities with the Mediterranean and Eastern North Atlantic *Ovatella*, based primarily on the presence of an internal lamella inside the outer lip, the protoconch of *A. tenuis* which, although different from all others in the genus, is very similar to that of *Ovatella*, and the configuration of the internal structure of the penial complex, where the penis appears as the development of one of the pilasters (Martins, in press b).

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