

Systematics of Indo-Pacific *Philippia* (*Psilaxis*), Architectonicid Gastropods with Eggs and Young in the Umbilicus¹

ROBERT ROBERTSON²

ABSTRACT: The subgenus *Psilaxis* Woodring is distinguished from *Philippia* Gray, s.s., on the basis of differences in the shells, jaws, opercula, and doubtfully radulae. Only two species of *Psilaxis*, differing mainly in three protoconch characters, are recognized in the Indo-Pacific. *Philippia* (*Psilaxis*) *radiata* (Röding), with the generally smaller protoconch, is the most abundant and widespread species, ranging from South Africa and the Red Sea east to the Marquesas and the Hawaiian Islands; it is thus both tropical and subtropical. *Philippia* (*Psilaxis*) *oxytropis* A. Adams has a larger protoconch and a disjunct range, being known only from the subtropical western and central Pacific Ocean—including Japan, the Hawaiian Islands, and New Zealand but excluding latitudes between 20° N and 20° S. Young postlarval *P. oxytropis* live in the umbilicus of the adult shells, and in *P. radiata* one egg mass has been found in an umbilicus. Nevertheless it is concluded from the small egg size of *P. radiata* (average diameter 63 μ) that both species have a long pelagic larval stage. *Philippia hybrida* (Linn.) is a Mediterranean species in the subgenus *Philippia*, s.s., and *P. layardi* A. Adams is a synonym of *P. radiata*. In Marquesan *P. radiata* there is a noteworthy increase and bimodality in protoconch size that are attributed tentatively (with no chromosomal evidence) to polyploidy. Polyploidy perhaps also is involved in the origin of species of *Philippia* and in the origin of *Psilaxis* from *Philippia*, s.s. By the Miocene, *Psilaxis* seems to have displaced *Philippia*, s.s., from most areas except peripherally in the subtropics. The pyramidellid-like egg capsules of architectonicids are described for the first time, and the larvae are also opisthobranch-like. *Philippia* has a cuticularized esophageal tube and radular teeth similar (analogous?) to those in the Epitoniidae.

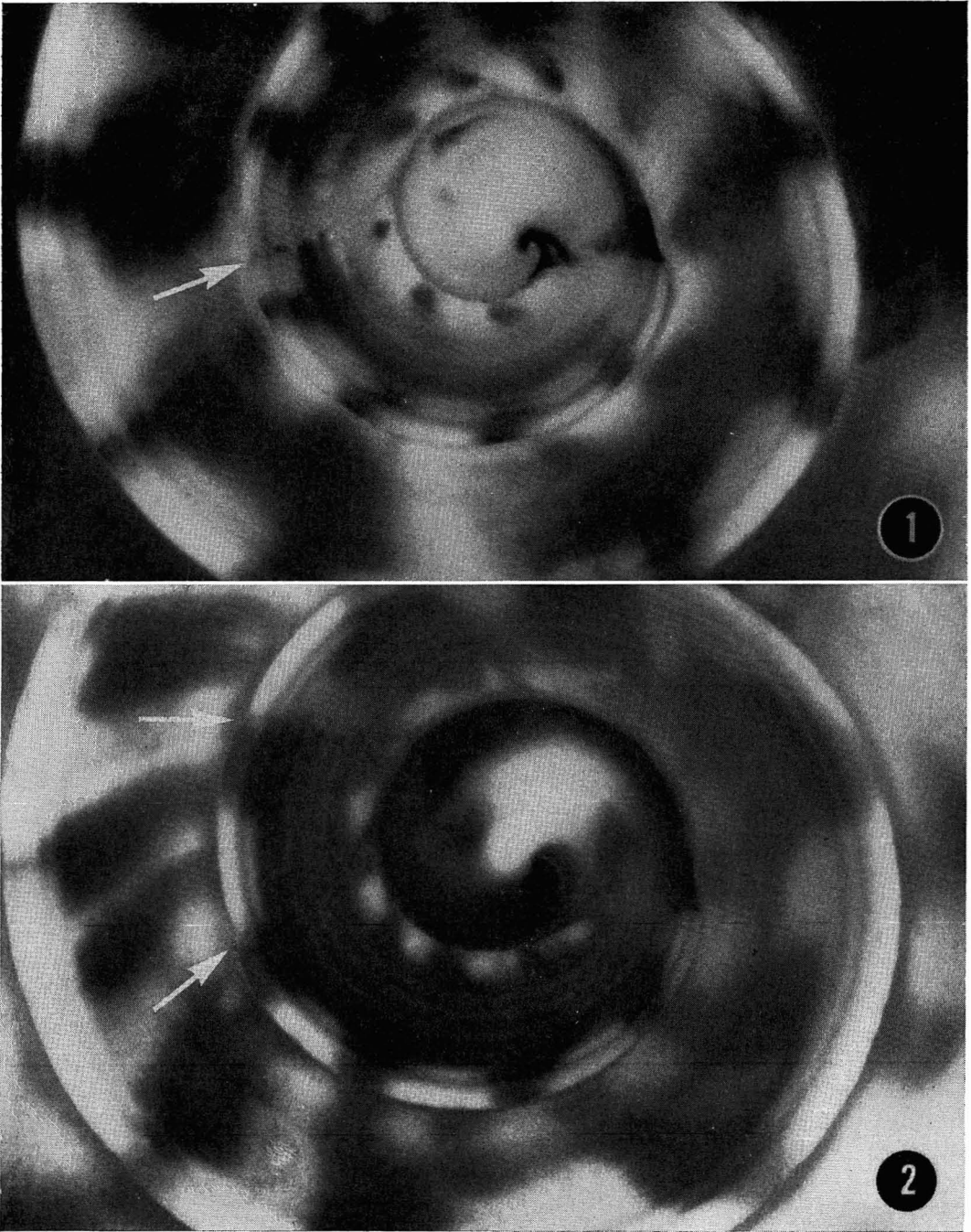
IN CONNECTION with the preceding paper (Robertson, Scheltema, and Adams, 1970) a review of the systematics of the architectonicid genus *Philippia* in the Indo-Pacific was found necessary. Charles Bayer (1942) has published a useful summary of the taxonomic literature on the Recent species in the genus. He included some new information on interspecific differences and geographic ranges, and he also made some nomenclatural innovations. *Philippia radiata* (Röding), the most common Indo-Pacific species, has been widely referred to as *P. hybrida* (Linn.). Bayer gave compelling

reasons for restricting the latter name to a Mediterranean species.

Most *Philippia* species were known to Bayer only from the literature. He distinguished *P. radiata* and *P. layardi* A. Adams mainly on the basis of the color patterns of their shells. However, Bayer also believed that *P. layardi* differs from *P. radiata* "by the more convex whorls, the more rounded carina [peripheral spiral cord] and the convex basis [base]" (p. 15). Bayer had available for study only 5 shells that he identified as *P. radiata* (from the "Indian Ocean" and from two localities in the East Indies), and 16 that he identified as *P. layardi* (mainly from the East Indies, but also from the "Indian Ocean," Australia, and unknown localities). Using almost the same cri-

¹ Manuscript received May 9, 1969.

² Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania 19103.



FIGS. 1 and 2. Apical views of the protoconchs and early teleoconch whorls of the two Indo-Pacific species of *Philippia* (*Psilaxis*), both at the same scale ($\times 30$). Fig. 1, *Philippia* (*Psilaxis*) *radiata* (Röding), Hawaiian Islands (same shell as Figs. 2 and 3 in the preceding paper). Fig. 2, *Philippia* (*Psilaxis*) *oxytropis* A. Adams, Rarotonga, Cook Islands (ANSP 278835). The three arrows show the growth lines invariably present on the first teleoconch whorls of all architectonicid shells.

teria with few shells, von Martens (1875, pp. 107–110, 116), in a paper overlooked by Bayer, also distinguished two Indo-Pacific species. More recently this has again been done (anonymously) in Hawaiian Shell News (vol. 16, no. 12, p. 7; December 1968). Without specifying differences (he lacked specimens), Bayer also recognized as distinct two other Indo-Pacific species here classified in the subgenus *Psilaxis* (diagnosed later): *P. manifesta* Iredale and *P. oxytropis* A. Adams.

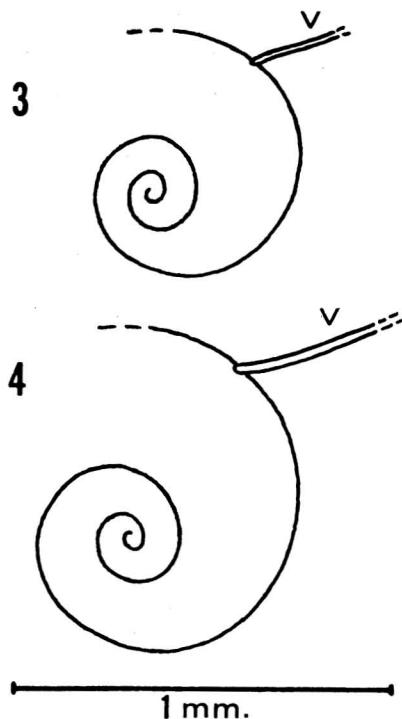
Study of the several hundred *Philippia* shells available from the Indo-Pacific at the Academy of Natural Sciences of Philadelphia (ANSP), at the Museum of Comparative Zoology (MCZ), and at the United States National Museum (USNM) has led to the conclusion that the four species cannot all be distinguished. A frequent color form has on the apical side of the shell a brown subsutural band with fairly regularly spaced extensions radiating to the periphery (see Fig. 2 in the preceding paper). Bayer restricted the name *P. radiata* to this color form, which, however, intergrades with shells of other patterns. Some have brown subsutural bands lacking the radial extensions, others have nearly uniform brown on the apical side (except for regularly spaced white spots at the periphery), and still others have patchy and irregular radiations with no subsutural band. The darker coloration varies in intensity and is yellowish or reddish brown. The basal side ranges from white to fairly dark brown, darkening away from the umbilicus. The outer periumbilical cord generally is white with brown spots. On both the apical and basal sides, the more darkly colored shells sporadically have regularly spaced spiral stripes (three to five on each side) that are pale buff to almost white.

There also is variation in shell morphology. The convexity of the whorls shows slight and continuous variation (acknowledged by Bayer), as do also the roundness of the prominent peripheral cord and the convexity of the base. The height of the spire varies considerably, even among large shells (Fig. 13 shows a fairly high-spined shell). The width of the umbilicus also varies greatly.

Rather unexpectedly, study of the protoconchs has revealed that there are two distinct

kinds, involving differences in size, structure, and coloration (Figs. 1 and 2). The detailed differences are described and discussed near the end of this paper. I must emphasize that I have detected only one character of the teleoconch (postlarval shell) that consistently correlates with the protoconch differences: all the shells with brown subsutural bands and radial extensions are the form with the smaller protoconch. Shells with other patterns have either kind of protoconch. The umbilicus of the form with the larger protoconch averages wider, but the teleoconchs of the two forms attain similar sizes. From some localities, shells with the two kinds of protoconchs thus have essentially identical teleoconchs.

The form with the generally smaller protoconch is both tropical and subtropical and ranges from South Africa and the Red Sea east to the Marquesas and Hawaiian islands



FIGS. 3 and 4. Whorl outlines of the protoconchs of the two species as seen through the umbilicus of postlarval shells, showing the false spire and the varix (V). Both figures are at the same scale. Fig. 3, Average-sized non-Marquesan *Philippia radiata*. Fig. 4, Average-sized *P. oxytropis*.

(Fig. 5, *spots*), while the form with the larger protoconch has a disjunct range in the subtropical western and central Pacific Ocean (Fig. 5, *circles*). The two forms are sympatric in the Ryukyu Islands, southern Japan, the Hawaiian Islands, New Caledonia, northern New Zealand, the Cook Islands, and probably also in New South Wales and at Lord Howe Island. Thus the form with the larger protoconch coexists with the more widespread form and is entirely absent from the Indian Ocean and from the Pacific Ocean between latitudes 20° N and 20° S. In both forms, eggs and/or young occur (consistently?) in the umbilicus of adult shells, but the veligers are nevertheless pelagic.

Among marine gastropods, protoconch size and morphology are usually good species characters. The few cases of supposed intraspecific differences in protoconch size have been attributed either to variations in the number of nurse eggs (Thorson, 1952, pp. 283–285) and/or to differing salinities affecting estuarine species (Rehfeldt, 1968).³ Architectonicids do not have nurse eggs and are not estuarine, so such intraspecific differences are out of the question in Indo-Pacific *Philippia*. There are also some as yet undocumented data showing that depth differences can affect the protoconch morphology of some eurybathic gastropods. Living at nearly the same depths and being sympatric, the two protoconch forms of *Philippia* cannot be bathymetrically or climatically induced. As shown later, both forms have long-lived planktonic larvae like those of the Atlantic Ocean species *P. krebsii* (Mörch); thus they do not reflect direct and planktonic larval development within one species. Even though I am reluctant to distinguish species mainly on protoconch differences, I do so here because the differences involved are clearcut and (except for size) consistent. The zoogeographic evidence also seems to support the conclusion that there are two species, even though the range of one is widely disjunct.

I have been unable to identify a few Indo-

Pacific *Philippia* shells with broken apices. However, I have found a way to identify shells with protoconchs that are abraded or broken on the apical side only. Using the vertical illumination prism on a Wild dissecting microscope, one can readily see the false spire of the protoconch through the umbilicus (Robertson, 1964, p. 5, figs. 5–6). With the camera lucida, comparisons of whorl outlines and varix positions clearly reveal which shells have the larger protoconchs (Figs. 3 and 4).

Not all the names for Indo-Pacific species listed by Bayer (1942) are accounted for here. Some do not pertain to species of *Philippia* (for example, *Solarium abyssorum* Melvill and Standen is a juvenile *Architectonica*). *Trochus perspectiviunculus* Meuschen (Bayer, 1942, pp. 8–9), a probable but not specifically identifiable *Philippia*, is a rejected name (International Commission on Zoological Nomenclature, Opinion 261, 1954). I have not had access to any of the relevant type-specimens, but these are likely to affect the dispositions of only the junior synonyms of *P. oxytropis*.

ARCHITECTONICID RELATIONSHIPS

While studying the intrageneric relationships of the Indo-Pacific species and the distinctness of two subgenera of *Philippia*, I discovered that *Philippia* has an *Epitonium*-like cuticularized esophageal tube (grossly, *Philippia* radular teeth are also *Epitonium*-like). This raised new questions as to the higher category relationships of the Architectonicidae. Despite their hyperstrophic protoconchs (Robertson, 1963), architectonicids still generally are classified as prosobranchs but as long ago as 1928 were transferred (without stated reasons) by Kuroda (1928, pp. 78–82) to the opisthobranchs. The Epitoniidae lack hyperstrophic protoconchs and are also generally classified as prosobranchs, but they too have been transferred to the opisthobranchs (Knight et al., 1954, p. 174, as Scalacea; Sohl, 1964, p. 313). Thorson (1957) observed that epitoniid (“scalid”) veligers have darkly colored excretory organs closely resembling those in larval opisthobranchs. Larval architectonicids have black excretory organs, and ar-

³ An alternative explanation for the differences in the estuarine rissoids and pyramidellids is that there are pairs or series of sibling species with contrasting salinity tolerances, egg sizes, and modes of larval development.

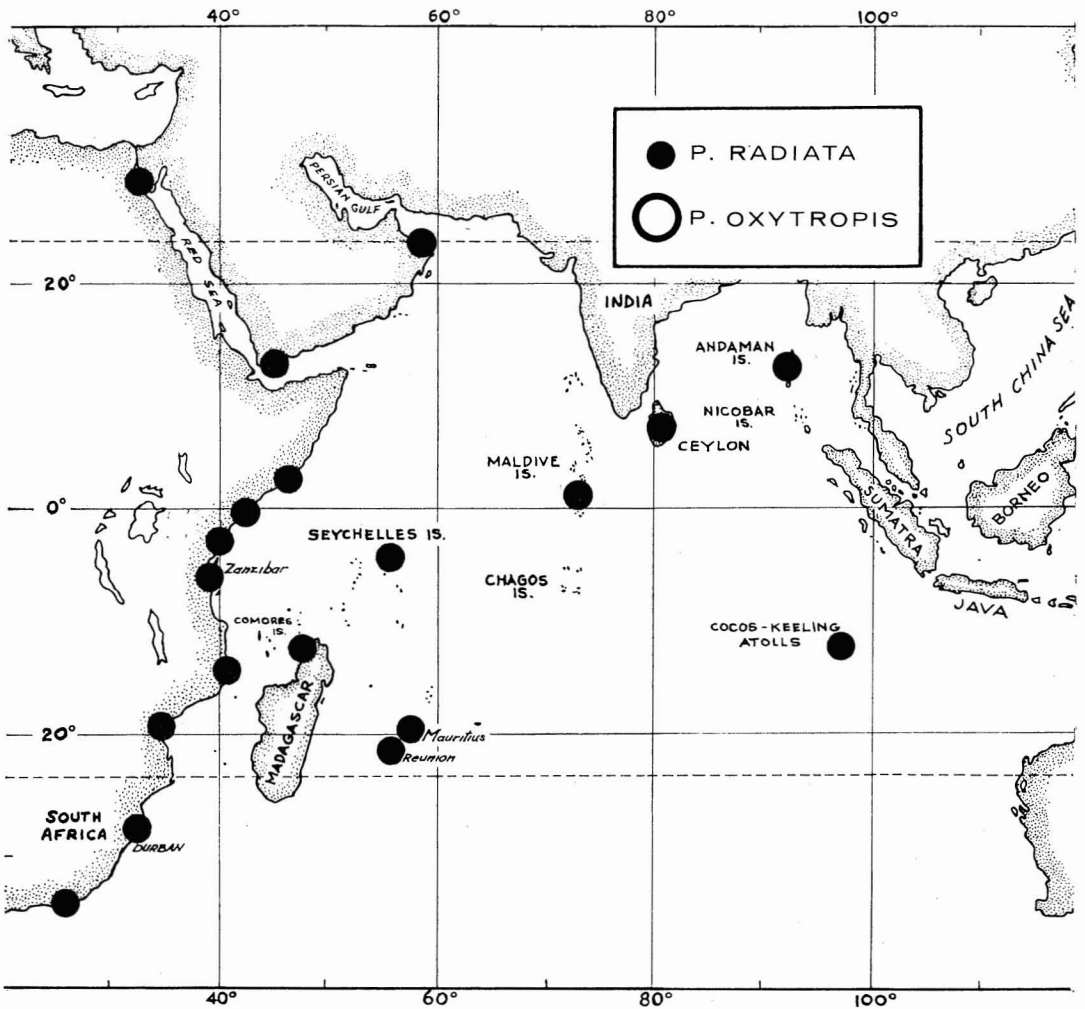


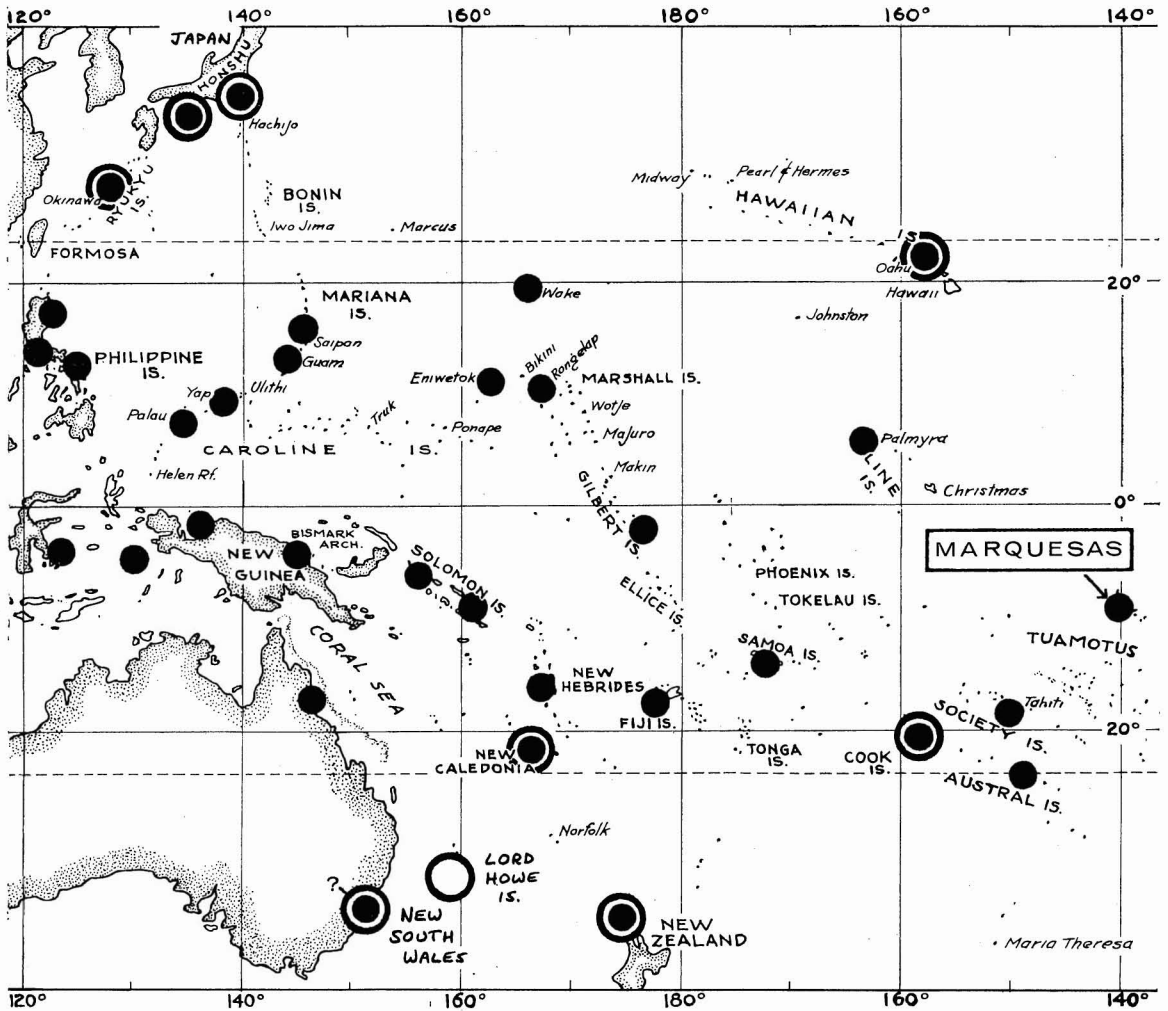
FIG. 5. Geographic records of *Philippia radiata* and *P. oxytropis*, based on museum specimens and literature records listed in the text. *Philippia oxytropis*, the species with the larger protoconch, is restricted to the subtropical western and central Pacific Ocean, being unknown between latitudes 20° N and 20° S and in the entire Indian Ocean. A disjunct population of *P. oxytropis* has recently been discovered at the head of the Red Sea (see Addendum).

chitonic egg capsules are here shown also to be opisthobranch-like. Further discussion of gastropods combining prosobranch (mesogastropod) and opisthobranch traits is deferred for another paper.

ESOPHAGEAL TUBES, JAWS, RADULAE, AND OPERCULA

Philippia jaws and radulae have been studied previously only by Troschel (1861, pp. 93, 97–

98, figs. 10–12; 1875, p. 156, pl. 15, figs. 5a–5c) and Thiele (1925, p. 113[79], pl. 46[34], figs. 18–19; 1928, p. 87, fig. 8; 1929, p. 184, fig. 169). Thiele's descriptions and illustrations differ considerably from those of Troschel. Before studying the jaws and radulae myself, I wrongly attributed the differences to Thiele's having studied a species in the subgenus *Psilaxis* (diagnosed below), whereas Troschel studied a *Philippia*, s.s. Troschel identified the species he studied as *P. lutea* (Lamarck), but it is evident



that he had true *P. hybrida* (*Philippia*, s.s.) from the Mediterranean. Thiele did not identify the species he described and figured in 1925, but in 1928 and 1929 he identified the newly studied species as "*P. hybrida*." At that time, this species name was still being misapplied to *P. radiata* (subgenus *Psilaxis*).

My study of the radulae of species in both subgenera has shown that they are difficult to interpret, that the previously published information is inaccurate, and that there are no definite subgeneric radular differences. I succeeded in extracting radulae from four species (Table 1). Only one of the specimens (ANSP 213257) had been kept in alcohol; the remain-

ing five were dried. Unfortunately, none of the six could be sexed.

In all of the specimens the acrembolic proboscis was fully inverted, and therefore I found the radula deep in the body. In each case the radula was inside a cuticularized tube connecting a pleated esophageal tube with the wrinkled wall of the buccal cavity, both likewise cuticularized. In all four species studied these structures are as shown in Figure 6. Figure 6 also shows the inferred changes in position upon complete proboscis eversion, and the inferred path of the ingested food. The esophageal tube must turn inside out through the buccal cavity and must then comprise the inner

TABLE 1
MEASUREMENTS OF SPECIMENS FROM WHICH RADULAE WERE EXTRACTED

<i>Philippia</i> SPECIES	LOCALITY	ANSP	SHELL (mm)		RADULA (mm)		"ROWS" OF TEETH
			DIAMETER	HEIGHT	LENGTH	HEIGHT	
<i>P. hybrida</i>	Sicily	38792	11.4	6.9	0.72	0.09	48
<i>P. krebsii</i>	S.E. Florida	195932	4.6	2.3	0.33	0.05	29
<i>P. oxytropis</i>	New Caledonia	271729	8.9	4.3	0.43	0.08	34
<i>P. radiata</i>	Zanzibar	213257	16.4	11.9	1.4	0.14	59
<i>P. radiata</i>	New Caledonia	247663	12.5	7.0	0.87	0.12	52
<i>P. radiata</i>	Yap, Carolines	250040	9.3	5.5	0.42	0.09	39

wall of the esophagus. Remarkably, these structures resemble the (everted) esophageal tubes of *Epitonium* described and illustrated by

Clench and Turner (1952, pp. 352-353, pl. 175). I suggest that there has been convergence resulting from the same food, the cuticularized lining of architectonicid and epitoniid esophagus preventing injury from nematocysts.

The laterally paired jaws of *Philippia* are continuous with the radula-containing tube and with the buccal cavity wall (Fig. 6). They are narrow and parallel to the mouth edge. There is a subgeneric difference in the shape of the jaw elements, those of the three species of *Psilaxis* being elongate (Fig. 7) and those of *Philippia hybrida* being subcircular (Fig. 8). Also the single *P. hybrida* jaw that I studied was arcuate and much smaller relative to shell size than in *Psilaxis*. In *Philippia hybrida*, Troschel observed wider jaws (each about four times as long as wide) and with four to six longitudinal rows of irregularly positioned, round-tipped imbricate scales. In *Psilaxis*, Thiele observed scales with pointed tips.

In preserved specimens, the radula is curved as shown laterally in Figure 6. Its size relative to shell size is nearly constant (Table 1). The basal ribbon to which the long, curved teeth are attached is narrow, and the transverse rows of teeth are ill defined. The narrow and bilaterally symmetrical teeth are densely packed together (the whole radula is therefore remarkably high and narrow), and their longitudinally elongate bases are positioned in an irregularly diagonal pattern across the ribbon. On the under side of the ribbon there are from 29 to 59 sinuities, and these reflect the number of serially repeated teeth or transverse "rows." The number of "rows" gradually increases with increasing radula size (Table 1). There appear to be about five teeth per "row." Thiele believed there were

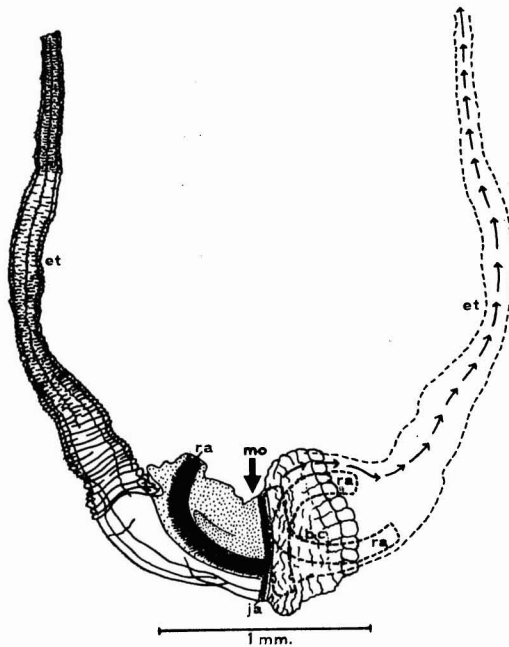


FIG. 6. Left side of the cuticularized esophageal tube (et) and buccal cavity wall (bc) of *Philippia radiata* (New Caledonia, ANSP 247663), showing the positions of the laterally paired jaws (ja) and the narrow radula (ra). The esophageal tube is shown inverted, and the inferred positions of this and the radula when the acrembolic proboscis is fully everted are shown with dashed lines. The esophageal tube turns inside out through the buccal cavity and the jaws are then near the open mouth (mo). The radula is shown at the beginning and the end of an effective stroke within the buccal cavity, and the thin arrows show the inferred path of the food toward the stomach.

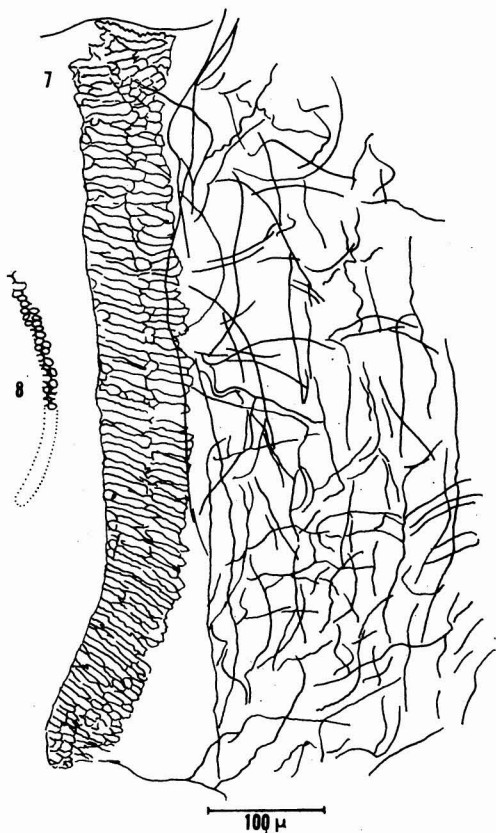


FIG. 7. Left jaw of *Philippia* (*Psilaxis*) *radiata* (Zanzibar, ANSP 213257) attached to the wrinkled and cuticularized wall of the buccal cavity (same orientation as Fig. 6).

FIG. 8. Part of jaw of *Philippia* (*Philippia*) *hybrida* (Linn.) (Sicily, ANSP 38792), the completed outline shown by the dotted line. This is at the same scale as Figure 7 but is from a smaller specimen (Table 1).

this many per transverse row in *Psilaxis*, and Troschel was wrong in believing that *Philippia hybrida* has about as many teeth per row as *Architectonica* (i.e., about 28).

On account of their curvature, it is difficult to place individual teeth in other than lateral positions under a cover slip. There are three main kinds of teeth, and I have been unable to discern whether their arrangement is consistent (possibly it is variable or even asymmetric). Troschel believed that the innermost teeth were the largest. I think it more likely that the innermost teeth are the ones that are smallest, nar-

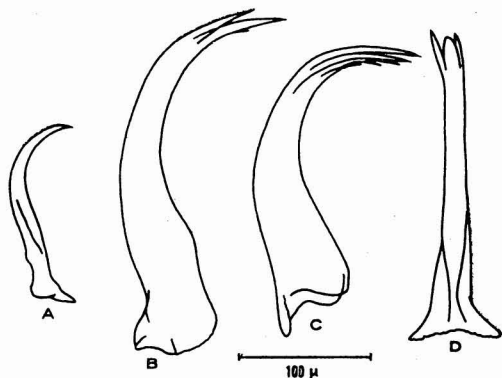


FIG. 9. Radular teeth of *Philippia radiata*, all from one specimen (Zanzibar, ANSP 213257). A, B, and C show left lateral views of the three main kinds of teeth, and D the same kind of tooth as C but in frontal view.

rowest, and singly pointed (Fig. 9A). The other two kinds of teeth differ in length, thickness, curvature, and the number of distal spines. The longer ones (Fig. 9B) have two or three spines, while the shorter ones are laterally thicker and more curved and have three to six spines (Fig. 9C). One of the latter teeth, definitely not from the center of the radula, in frontal view (Fig. 9D) resembles Thiele's figure (1928, p. 87) of a *Psilaxis* "central." I have detected no definite difference between the teeth of *Philippia hybrida* and of the three species of *Psilaxis*, although *Philippia*, s.s., may have slightly more slender teeth and longer distal spines.

Philippia opercula have been studied previously only by Thiele (1928, pp. 86-87, fig. 7a; 1929, p. 184, fig. 168) and Odhner (1932, pp. 12-13, fig. 1 [*P. krebsii* misidentified as *P. hybrida*]). Thiele and Odhner each studied one species. I have studied the opercula of all four species from which I also obtained radulae (Table 1), mostly from the same specimens. There were six opercula from *P. radiata* but only one from each of the other three species.

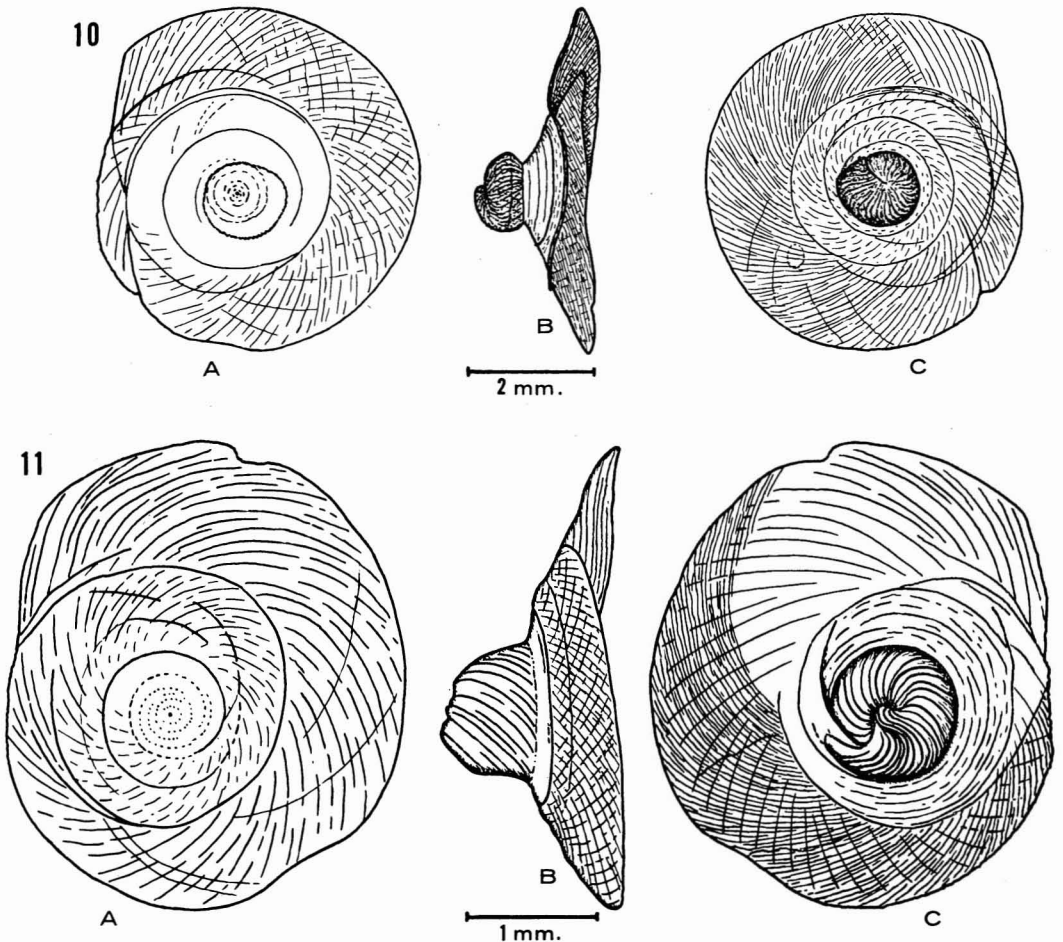
Externally, the operculum is concave and multispirally coiled counterclockwise. Internally, there is an opaque central knob that extends into the tissues of the foot. Detached and dried, the knob shrivels. The knob is pale yellow-brown while the remainder of the operculum is amber colored, semitransparent, and flexible.

Both surfaces are mostly smooth and shiny but can be irregularly wrinkled, pitted, and blistered. Growth lines are mainly external and minutely beaded, while threads at right angles to these are internal and absent from the last part of the last whorl.

There are subgeneric opercular differences. The three species of *Psilaxis* have relatively small central knobs that are always constricted basally and have fine sculpture radiating counter-clockwise (Fig. 10). The central knob of *P. hybrida* is larger and more solid (less pervious), is not basally constricted, and has coarse grooves radiating clockwise (Fig. 11). The outer part of the operculum of *P. hybrida* is

paucispiral; the last whorl is attached to the outer edge of the penultimate whorl (even slightly overlapping it). Large *Psilaxis* opercula differ in that the outer whorls underlap and are attached near the middle of each preceding whorl; the suture therefore is flanged externally. The last whorl of extra large *Psilaxis* opercula is partly detached from the penultimate whorl, and a thin callus spreads widely under all the preceding whorls. The operculum of *P. hybrida* is thicker around the central knob, and the external growth lines are coarser.

Because of the radular and opercular differences between *Architectonica* and *Heliacus*, some malacologists have followed Troschel (1875,



FIGS. 10 and 11. Opercula of the two subgenera, viewed externally (A), laterally (B), and internally (C). Fig. 10, *Philippia (Psilaxis) radiata* (Zanzibar, ANSP 213257). Fig. 11, *Philippia (Philippia) hybrida* (Sicily, ANSP 38792). The pervious central knobs are both shown inflated with water.

p. 158) in segregating a family Heliacidae (or "Toriniacea" = Toriniidae) from the Architectonicidae, s.s. Thiele (1928) believed wrongly that *Philippia radulae* are transitional. However, their opercula are structurally transitional between those of *Architectonica* (paucispiral) and *Heliacus* (multispiral, with a hypertrophied sutural flange). Larval shells also provide evidence for the cohesiveness of the Architectonicidae, s.l. (Robertson, 1963).

SYSTEMATICS

Family ARCHITECTONICIDAE
["SOLARIIDAE" + HELIACIDAE]

Genus *Philippia* Gray, 1847

Proc. Zool. Soc. London 15, p. 146. Type-species (original designation): *Solarium luteum* Lamarck.

Subgenus *Philippia*, s.s.

This group is not represented in the tropical Indo-Pacific. It comprises such species as *P. hybrida* (Linn.) of the Mediterranean and nearby eastern Atlantic, *P. lutea* (Lamarck) of southern Australia and northern New Zealand, and *P. japonica* (Pilsbry and Stearns)⁴ of south-central Japan. These all have small, relatively high-spined shells, small protoconchs (less than 0.9 mm in diameter), two subequal spiral cords at the periphery, and only one periumbilical sulcus.

The jaw is arcuate, smaller than in *Psilaxis*, and with subcircular elements (Fig. 8). The radula is like that of *Psilaxis* but the teeth possibly are slightly more slender and have longer distal spines. The operculum (Fig. 11) has a large internal central knob that is not constricted basally; the last whorl is attached to the outer edge of the penultimate whorl (no sutural flange).

⁴ This is one of the few species overlooked by Bayer (1942). It was named as a variety of *Solarium conulum* [conulus] Weinkauff [= *P. hybrida* (Linn.)] by Pilsbry and Stearns (in Pilsbry, 1895, p. 65). Even though widely separated geographically, these three species have closely similar shells.

Subgenus *Psilaxis* Woodring, 1928

Miocene Mollusks, Bowden, Jamaica 2 [Carnegie Inst. Washington Publ. 385], pp. 7, 355. Type-species (original designation): *Architectonica (Philippia) krebsii* Mörch.

Hitherto, *Psilaxis* has usually been classified as a subgenus or "section" of *Architectonica*. The less sculptured shells much more closely resemble those of *Philippia*, s.s. *Psilaxis* comprises three predominantly tropical species: *Philippia krebsii* (Mörch) of the Atlantic Ocean (Robertson, 1964), and the two Indo-Pacific species treated herein. Judging by protoconch characters, *P. krebsii* is the Atlantic Ocean homologue of *P. oxytropis* of the subtropical Pacific Ocean. *Psilaxis* and *Philippia*, s.s., are not quite allopatric, species in both groups being sympatric in south-central Japan, New South Wales, northern New Zealand, and the Canary Islands. This zoogeographic evidence suggests that *Philippia*, s.s., originally was widespread even in the tropics, that there has been intersubgeneric competitive exclusion, and that *Psilaxis* has replaced *Philippia*, s.s., in most areas except peripherally in the subtropics. Meager paleontological evidence (not here documented) suggests that this happened by or during the Miocene, by which time the present distributions were approximated. Morphologically, some of the species have changed little or not at all since that time, and the resulting disjunct distributions of identical or closely similar forms are remarkable.

Compared with *Philippia*, s.s., the species of *Psilaxis* have larger shells that are lower-spined. They also have larger protoconchs (more than 1.2 mm in diameter), one prominent peripheral spiral cord accompanied by two others (one above and one below), and two periumbilical sulci with a differently patterned cord between them (Fig. 14 and, in the preceding paper, Fig. 3). The groove in the columella opposite the inner periumbilical cord is deeper.

The jaw is nearly straight, is larger than in *Philippia*, s.s., and has elongate elements (Fig. 7). The operculum (Fig. 10) has an internal central knob that is smaller than in *Philippia*, s.s., and is constricted basally; the outer whorls underlap and are attached near the middle of

each preceding whorl (externally, the suture is therefore flanged).

Philippia (Psilaxis) radiata (Röding)

Figs. 1 and 12–14 (in the preceding paper, Figs. 1–3)

Architectonica radiata Röding, 1798, Mus. Boltenianum, p. 79 (no locality). Based in part on Chemnitz, 1781, Neues syst. Conch.-Cab. 5, pl. 173, figs. 1704–1705.

Solarium cingulum Kiener, 1838–39, Spécies . . . Iconogr. Coquilles Vivantes 10, Genre Cadran (*Solarium* Lam.), pp. 6–7, pl. 3, figs. 6, 6a (mer des Indes).

Philippia layardi A. Adams, 1855, Proc. Zool. Soc. London "1854," p. 317 (Ceylon). This has never been illustrated.

Solarium (Philippia) cingulum var. *subconcolor* Martens, 1880, Beitr. Meeresfauna Mauritius u. Seychellen, Moll., p. 290 (Mauritius).

Philippia stipator Iredale, 1931, Rec. Australian Mus. 18, pp. 229, 235, pl. 25, figs. 17–18 (locality not stated [Sydney Harbour, New South Wales, *vide* Iredale and McMichael, 1962, p. 68]).

Solarium kowiensis W. H. Turton, 1932, Marine Shells Port Alfred S. Africa, pp. 134–135, pl. 29, figs. 971 (Port Alfred, South Africa).

Of the above names, the following are based on shells with color patterns similar to Figure 2 in the preceding paper: *Architectonica radiata*, *Solarium cingulum*, and *Philippia stipator*. Teleconchs having this color pattern with brown radiations occur only in the species with the smaller protoconchs. These three names, therefore, all pertain to this species; *P. radiata*, the oldest and hence valid name, is apt only for shells with the brown radiations. *Philippia layardi* is included in this synonymy on account of its Indian Ocean type-locality; the description is not diagnostic.

LOCALITY RECORDS (Fig. 5 [map]; unless otherwise indicated, all ANSP and MCZ): Port Elizabeth to Natal, South Africa; Mozambique; northern Madagascar; La Réunion; Mauritius; Seychelles; Tanganyika (Spry, 1961, p. 9, as *P. hybrida* and *P. radiata*); Zanzibar; Kenya;

Somali Republic; Aden (E. A. Smith, 1891, p. 415, as *Solarium (Philippia) hybridum*); Gulf of Suez (Cooke, 1885, p. 265, as *Solarium cingulum*; Odhner, 1932, p. 12, as *Philippia hybrida*); Masqat, Gulf of Oman (Melvill, 1928, p. 100, as *P. hybrida* and "Muscat"); Maldive Is. (E. A. Smith, 1903, p. 615, as *P. cingulum*); Ceylon (type-locality of *P. layardi* A. Adams); Andaman Is. (Melvill and Sykes, 1899, p. 226, as *Solarium (Philippia) cingulum*; E. A. Smith, 1903, p. 595, as *P. cingulum*); Cocos-Keeling Is.; southern Japan; Ryukyu Is.; Philippines; Celebes; Moluccas; Palau Is.; Yap Is.; New Guinea; Mariana Is.; Solomon Is.; Queensland; near Sydney, New South Wales (see below); northern New Zealand [Takou Bay, between Kaeo and Bay of Islands, MCZ 271264]; New Caledonia; New Hebrides; Fiji Is.; Gilbert Is.; Marshall Is.; Wake Is.; Hawaiian Is.; Line Is.; Samoa Is.; Cook Is.; Austral Is.; Society Is.; Marquesas Is.

I have seen no *Philippia* specimens from New South Wales, but there are six different literature records, at least some of which pertain to *P. radiata* (others presumably are *P. oxytropis*): Angas (1871, p. 92), *P. hybrida* and *P. layardi*; Odhner (1932, p. 12), *P. hybrida*; Bayer (1942, p. 10), *P. layardi*; Iredale and McMichael (1962, p. 68), *P. stipator* and *P. manifesta*.

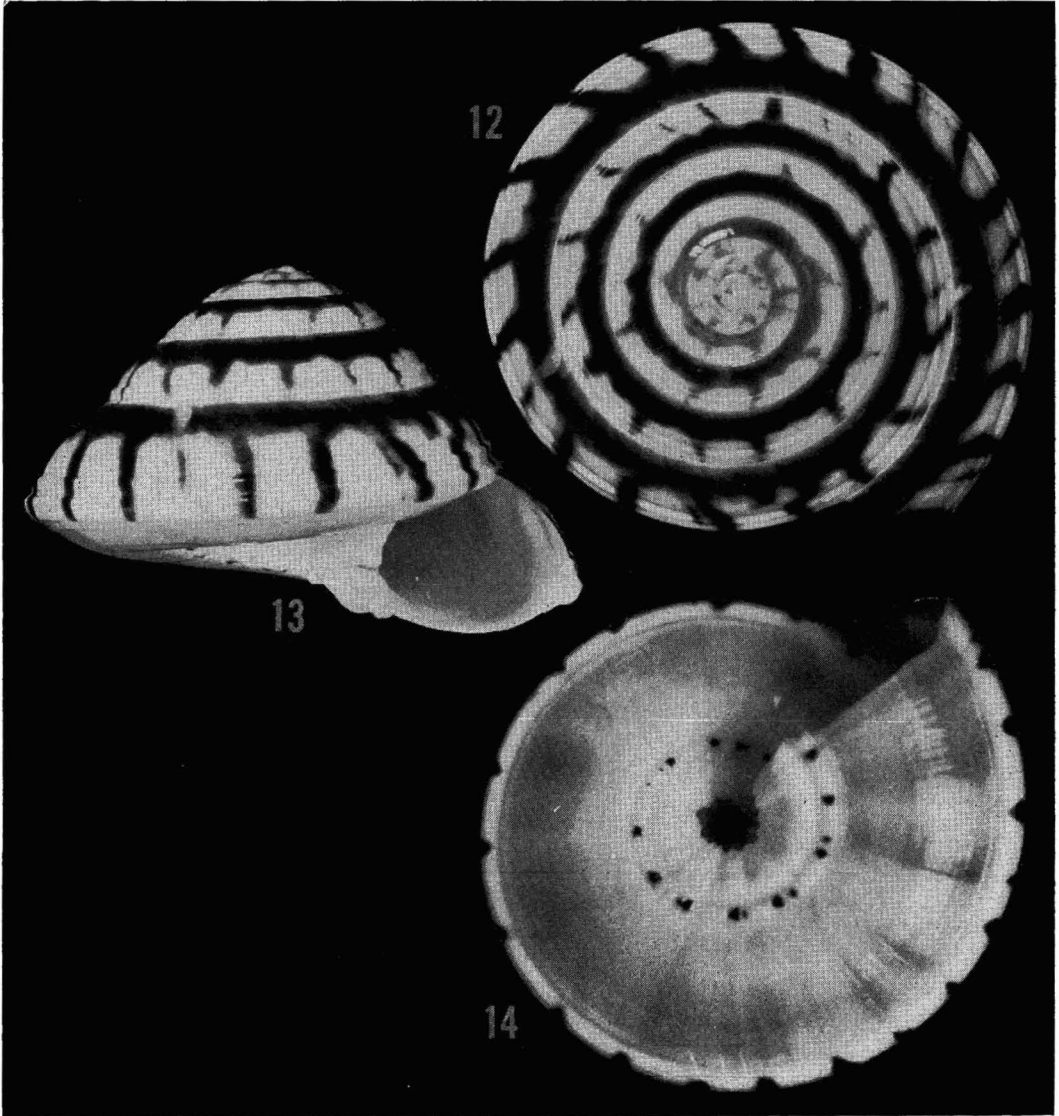
Under various names, there are numerous additional literature records of *Philippia* in the East Indies and the central and western tropical Pacific. Most of these records undoubtedly are based on *P. radiata*, but they are not documented or mapped here because of the slight possibility that some pertain to *P. oxytropis*. *Philippia radiata* seems to be absent from the silty coasts of the Persian Gulf and India. *Philippia oxytropis* is known from only one locality where *P. radiata* is not also known: Lord Howe Island (a record based on a single shell); *P. radiata* can be expected at Lord Howe. Barnard's (1963, p. 158) discussion of *P. layardi* in South Africa pertains to *P. radiata*, the only *Philippia* so far known there. Bayer (1942, pp. 8, 10) reidentified Odhner's (1932, p. 12) Canary Island record of *P. hybrida* as *P. layardi*, but this was based on *P. krebsii* [Robertson, 1964, p. 20].

In the Hawaiian Islands, *P. radiata* has been seen to feed on the polyps of *Porites lobata* Dana (Robertson, Scheltema, and Adams, 1970). The few available live-collected specimens with bathymetric data suggest that in the Hawaiian Islands *P. radiata* lives in deeper water than elsewhere (as deep as 150 feet, versus 2 to 40 feet elsewhere). Also, the Hawaiian specimens from the greatest depths

are the largest known (Figs. 12–14). These observations parallel Kay's (1967, p. 100) on some other Hawaiian marine mollusks.

Philippia (*Psilaxis*) *oxytropis* A. Adams
Fig. 2

Philippia oxytropis A. Adams, 1855, Proc. Zool. Soc. London "1854," p. 317 (New Caledonia). Presumed type figured by



FIGS. 12–14. Apical, apertural, and basal views (all $\times 3$) of the largest observed shell of *Philippia radiata*, 25 mm in diameter and with 5.7 teleoconch whorls. Hawaiian Islands (empty shell from 130 feet off Makua, western Oahu; in the collection of Frank W. Adams).

Hanley (1863, Sowerby, Thesaurus Conchyliorum 3, pl. 253, figs. 46–47).

?*Solarium hybridum* (Linn.) var. *undata*
Hanley, 1863, *ibid.*, p. 236, pl. 253, figs. 42–43 (no locality).

?*Solarium hybridum* (Linn.) var. *australis*
Hanley, 1863, *ibid.*, p. 236 (no figure; no locality). Not *Solarium australe* Philippi, 1849.

?*Philippia manifesta* Iredale, 1931, Rec. Australian Mus. 18, p. 229, 235, pl. 25, figs. 9–10 [not "19, 20" as given on p. 229] (locality not stated [Sydney Harbour, New South Wales, *vide* Iredale and McMichael, 1962, p. 68]).

Philippia oxytropis has the consistently largest protoconch of any species in the Architectonicidae (1.55 to 1.75 mm in diameter). A. Adams' description of *P. oxytropis* mentions "a large smooth glassy nucleus" (i.e., protoconch). This and the type-locality (whence shells with the larger protoconchs are available) seem reasonably diagnostic for the species. The species name *oxytropis* alludes to a sharp peripheral keel, which is no sharper in this species than in *P. radiata*. The descriptions and illustrations of the three junior synonyms are not diagnostic, and so any of these could also belong in the synonymy of *P. radiata*.

LOCALITY RECORDS (Fig. 5 [map]; all ANSP and MCZ): southern Japan; Ryukyu Is.; Lord Howe Is. [H. L. Clark, April 1932, MCZ 271265]; northern New Zealand [Takou Bay, between Kaeo and Bay of Islands: Powell, 1938, p. 168, as *P. manifesta*, and MCZ 235153]; New Caledonia; Cook Is.; Hawaiian Is. Regarding doubtful New South Wales literature records of this species, see under *P. radiata*. My allusions to *P. layardi* [Robertson, 1964, pp. 20–21] pertain to *P. oxytropis*.

Even where the two closely related species are sympatric, *P. oxytropis* is collected less frequently than *P. radiata*. The peculiar disjunct distribution of *P. oxytropis* suggests that it can compete with *P. radiata* only in the subtropics. It would be interesting to know if the pelagic larvae of *P. oxytropis* occur across the equatorial Pacific. *Philippia oxytropis* may consistently live slightly deeper than *P. radiata*. However, the

only bathymetric data available for live-collected *P. oxytropis* are: 50 feet (New Caledonia) and 150–200 feet (Hawaiian Islands).

EGGS AND YOUNG IN THE UMBILICUS

I have found one egg mass in the wide umbilicus of an adult *Philippia radiata*, and there also is information that young postlarval *P. oxytropis* live in the umbilicus of adult shells. *Philippia* eggs have not been observed hitherto, and therefore it is uncertain whether they consistently are laid in the umbilicus. Likewise, it is uncertain whether the postlarvae consistently are brooded in the umbilicus, or whether they merely are gregarious and live in any dark cranny. Reasons are given below for inferring that the veligers of *P. radiata* and *P. oxytropis* cannot be brooded and must have a long pelagic stage, despite the unusual placement of the eggs and postlarvae.

The *P. radiata* with the egg mass (Fig. 15) was collected alive by R. W. Foster, M. A. Miller, or R. E. M. Osteimer in 0 to 2 feet of water at Rarotonga, Cook Islands, between January and March 1962, and preserved in 70 percent ethyl alcohol. The gelatinous egg mass was in the outer part of the umbilicus between the periostracal fringe and the suture, and contained 361 encapsulated, pyramidellid-like eggs (Fig. 16). Unquestionably these had been laid by the *Philippia* because I have observed virtually identical eggs laid by another architectonicid, *Heliacus cylindricus* (Gmelin) [Robertson, unpublished]. The eggs were mostly uncleaved (a few were 2-celled) and ranged in diameter from 61 to 67 μ (average 63 μ ; 20 measured), and thus are small enough to prove that the veligers must be pelagic and planktotrophic, there being too little yolk for direct development (Thorson, 1952, p. 281–283). (Gastropod eggs shrink hardly at all in alcohol.) The ovoid capsules (more distorted than the preserved eggs), each containing a single egg, ranged in maximum length from 79 to 90 μ (average 84 μ ; 20 measured) and contained various-sized granules around the egg. The capsule wall was thickened at each end and had a long chalaza. The chalazae (observed with difficulty) connect all the capsules in the mass

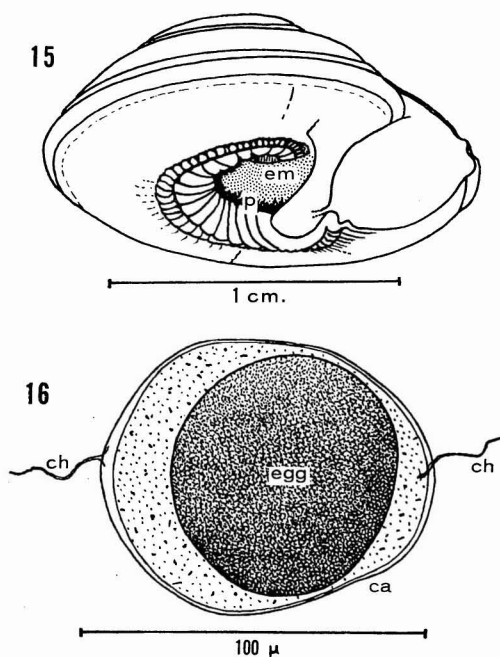


FIG. 15. Tilted apertural view of a shell of *Philippia radiata* from the Cook Islands (ANSP 279284), showing the position of an egg mass (em, stippled) in the outer part of the wide umbilicus and edged outwardly by a fringe of periostracum (p, shown black).

FIG. 16. One of 361 eggs from the above mass, contained in its capsule (ca) and with a chalaza (ch) at each end.

like beads on a string. Even allowing for some swelling of the capsule during development, its maximum length (90μ) is so much smaller than the minimum diameter of the full-grown larval shell (1200μ) that the larva must hatch in the very early veliger stage.

An adult specimen of *Philippia oxytropis* now in the collection of Mr. and Mrs. Crawford N. Cate (no. 655), dredged alive by Mr. Clifton S. Weaver at a depth of 150 feet at the entrance of Keehi Lagoon, 2.5 miles west of Honolulu, Hawaiian Islands, in April 1959, had in its umbilicus two juveniles, both at the stage of early postlarval arrested growth (one has about one-quarter of a teleoconch whorl, the other about half a teleoconch whorl). These specimens, and presumably others, were the basis for a paragraph on "*Architectonica*" in Hawaiian Shell News (vol. 10, no. 10, p. 7; August 1962) mentioning "sometimes five or

six" juveniles per adult, "living deep in the umbilicus." Judging by the first whorl diameters of the protoconchs (Figs. 3 and 4), the eggs of *Philippia oxytropis* must be about the same size as those of *P. radiata*. Thus I conclude that the veligers of *P. oxytropis* are similarly pelagic and planktotrophic (just as in *P. krebsii*, the most closely related congener), and that direct development and larval brood protection are out of the question.

The only other gastropods known to me in which young live in the umbilicus of the adults are the trochacean *Arene socorroensis* (Strong) [Turbinidae: Liotiinae], observed by Shasky (1968), and the Pacific island land snail family Endodontidae, discussed in a fascinating paper by Solem (1968). In the *Arene* there probably is direct development comparable to that in *Clanculus bertheloti* (Orbigny) [Trochidae] (Thorson, 1967). Thus, *Philippia* (*Psilaxis*) seems unique in having a long pelagic and planktotrophic larval stage that is both preceded and followed by (obligate?) umbilical brood protection.

PROTOCONCH DIFFERENCES AND GEOGRAPHIC SIZE VARIATION

The main differences between the shells of *Philippia radiata* and *P. oxytropis* involve the sizes, structure, and coloration of their protoconchs (Figs. 1 and 2). General information on architectonicid protoconchs, an assessment of their taxonomic utility, and definitions of terminology have already been published (Robertson, 1963; 1964, pp. 4-8) and are not repeated here.

Except at one locality, the protoconchs of *P. radiata* invariably are smaller than those of *P. oxytropis*, those of *P. radiata* ranging in (immersed) diameter from 1.20 to 1.45 mm and those of *P. oxytropis* from 1.55 to 1.75 mm (all protoconch measurements in this paper are rounded to the nearest 0.05 mm). The exceptional locality is the Marquesas Islands, where *P. oxytropis* is unknown and where *P. radiata* is at the easternmost limit of its known range. Here the interspecific size difference disappears, and *P. radiata* can have a protoconch as large as that of *P. oxytropis* (Fig. 17). Protoconchs of Marquesan *P. radiata* range in

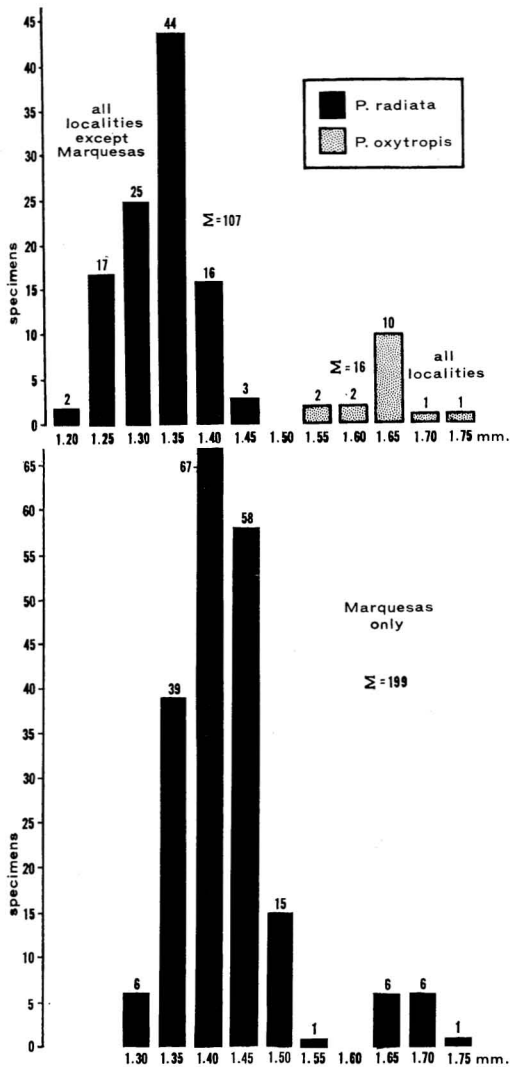


FIG. 17. Histograms showing that the immersed protoconch diameters of *Philippia radiata* are consistently smaller than those of *P. oxytropis* at all localities except the Marquesas, where the sizes overlap and the size distribution is bimodal. *P. oxytropis* is unknown from the Marquesas. The data are based on all shells with measurable protoconchs at ANSP, supplemented by others at MCZ and USNM from additional localities.

diameter from 1.30 to 1.75 mm, and, peculiarly, the size distribution is bimodal, approximating the interspecific bimodality elsewhere.

Most of the Marquesan shells are unusually darkly colored—a normal occurrence for species

around these basaltic islands, where all of the sand is black. Rehder has mentioned *P. radiata* (1968, p. 30, as *P. hybrida*) as being unusually "common" in the Marquesas. This is borne out by the numbers of specimens available with measurable protoconchs: nearly twice as many from the Marquesas as from all other localities combined (Fig. 17). One lot of 181 specimens was collected by R. L. Sixberry between December 1966 and mid-February 1967 at the head of Taiohae Bay, Nuku Hiva, on algae at night in tide pools in volcanic rock (USNM 679535; duplicates ANSP 316199). Out of the total of 199 Marquesan shells, 13 (6.5 percent) have enlarged protoconchs (1.65 to 1.75 mm in diameter). The teleoconchs of these 13 specimens differ from the others in having much stronger axial wrinkles on the inner side of the first whorl, a growth line marking the stage of arrested growth farther from the protoconch (more than half a whorl, instead of about one-quarter or one-third of a whorl). Additionally, the shells with large protoconchs have lower spires and more prominently keeled peripheries, and the brown coloration is pale and less intricately interrupted with white. These teleoconch differences are within the range of variation at non-Marquesan localities, and the divergent Marquesan shells appear to have grown faster than the others.

All presently available shells from all other Indo-Pacific localities, including the Hawaiian Islands, show no protoconch size overlap between *P. radiata* and *P. oxytropis*. Character displacement is out of the question because there is not the slightest protoconch size increase in *P. radiata* at the many places besides the Marquesas where *P. oxytropis* is also absent. I have wondered if the Marquesan populations are isolated by ocean currents. In southeastern Polynesia, the westward-flowing South Equatorial Current might hinder larval recruitment from the west. However, the Marquesas are at about the latitude of the eastward-flowing South Equatorial Countercurrent.⁵

⁵ *Philippia krebsii* also has enlarged protoconchs at the easternmost limit of its range in the eastern Atlantic (Robertson, 1964, pp. 19–20, and unpublished data). Two other Indo-Pacific architectonicids, *Helicacis variegatus* (Gmelin) and *Architectonica*

The anal keels of the two species consistently differ. Even in the Marquesas, *P. radiata* has a short, sharply crested keel that nearly always is colored brown. *Philippia oxytropis* has a differently positioned, longer, and more rounded keel that is not differently colored (Figs. 1 and 2).

The protoconch of *P. radiata* commonly is white, with brown next to the varix and the nearby suture. *P. oxytropis* always has a fairly sharply differentiated, centrally placed white mark surrounded by brown; commonly, there is a darkened brown spot at each end and indenting the white mark (Figs. 1 and 2). *Philippia radiata* can have its protoconch partly or wholly suffused with brown, and palest at the center but never with a demarcated white area. These differences in coloration are remarkably constant, and the Marquesan shells show clearly the characters of *P. radiata*.

CONCLUSION: HYPOTHETICAL POLYPLOIDY

To explain the protoconch size bimodality of *Philippia radiata* in the Marquesas and the size similarity with *P. oxytropis*, I suggest that the large protoconch form is a polyploid and has the same number of genomes as *P. oxytropis* and *P. krebsii*, both of which, I suggest, arose by polyploidy from ancestral *P. radiata*. Despite the total lack of chromosomal evidence and the few well-documented cases of polyploidy in mollusks (Burch, 1965; Burch and Huber, 1966; Patterson, 1967), I suggest further that *P. radiata* with normal-sized protoconchs is itself a polyploid, that protoconch size in *Philippia* reflects the level of polyploidy, and that the base chromosome number therefore should be found in the subgenus *Philippia*, s.s. If these things are so, the large protoconch form of *P. krebsii* should have the highest chromosome number in the genus. Polyploid vigor should account at least initially for the protoconch size increases, and these size increases (which have occurred three times) would have

perspectiva (Linn.), also show geographic variation in protoconch size but without size increases at the easternmost limits of their ranges (Robertson, unpublished). The protoconchs of *Philippia oxytropis* from Japan average slightly smaller (1.55 mm in diameter) than those from elsewhere (1.65 mm).

progressively better adapted *Philippia* for young postlarval life with corals (preventing their being swallowed by corals). Polyploid vigor would also account for the evidently more rapid teleoconch growth of the Marquesan shells with enlarged protoconchs. A possible cause of polyploidy in the Marquesas and Canaries would be the adverse habitats, hermatypic corals being scarce and well-developed reefs being absent at both places.

A few (0.5 to 1 percent) of the spermatozoa of the limpet *Patella caerulea* Linn. are diploid and have longer heads containing twice as much deoxyribonucleic acid (DNA) as the haploids (Indelicato and Streiff, 1969). Like *Patella*, *Philippia* could have both haploid and diploid spermatozoa, and fertilization of a haploid ovum with a diploid spermatozoon would yield a triploid zygote. Alternatively, polyploid *Philippia* might have an even number of genomes. Chromosome counts are greatly needed for *Philippia*.

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ADDENDUM (ADDED IN PRESS) *Philippia oxytropis* at the Head of the Red Sea

Since this paper was accepted for publication, I have discovered that a remarkably disjunct population of *Philippia oxytropis* occurs at the head of the Red Sea north of 20° north latitude. This is an extension of known range of 6,300 statute miles westward. Two empty shells from Elat (Eilat), Israel (Gulf of Aqaba), collected by the late Aryeh Hadar (USNM 671277), have the protoconch morphology and coloration of *P. oxytropis*. How-

ever, the protoconchs are only 1.25 and 1.30 mm in diameter (versus 1.55 to 1.75 in the Pacific). This protoconch size reduction at the northwestern end of the range of *P. oxytropis* is reminiscent of the protoconch size increase in *P. radiata* at the eastern end of its range. At each place one species assumes the protoconch size diagnostic of the other species elsewhere.

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