

The Feeding, Larval Dispersal, and Metamorphosis of *Philippia* (Gastropoda: Architectonicidae)¹

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ABSTRACT: In the Hawaiian Islands, *Philippia* (*Psilaxis*) *radiata* (Röding) lives in sand or rubble near the hermatypic stony coral *Porites lobata* Dana, and emerges to feed at night on the polyps. Other species of *Philippia* (*Psilaxis*) probably have the same mode of life with corals. *Philippia* (*Psilaxis*) veliger larvae are abundant in tropical and subtropical oceanic plankton distant from any potential shallow-water hosts, and are dispersed great distances by near-surface currents. Duration of the pelagic larval stage is between several weeks and 6 months or longer. Metamorphosis, involving loss of the 4-lobed velum, initial growth of the teleoconch, and other changes, can precede contact with a host and is induced by capture from the plankton. Newly settled *Philippia* quickly attain a stage of arrested growth and can remain alive without feeding for several months. At this stage the postlarvae presumably crawl in search of hosts, and failure to find hosts doubtless causes the high mortality observed.

Experiments at Woods Hole, Massachusetts, with newly metamorphosed *P.* (*Psilaxis*) *krebsii* (Mörch), obtained as larvae from plankton in the Sargasso Sea, together with the ahermatypic coral *Astrangia danae* Agassiz, reveal physical problems for *Philippia* in assuming the adult mode of life with other corals. Young *Philippia* showed no ability to detect *Astrangia* except by touch. Young *Philippia* lacked immunity to *Astrangia* nematocysts but were not seriously injured by them. The young gastropods are, however, subject to predation by this coral. Most contacts with the living tissues of *Astrangia* caused a *Philippia* to be promptly drawn through the mouth and ultimately digested. The large protoconchs of *Psilaxis* would preclude their being swallowed by hermatypic corals such as *Porites*, with polyps smaller than those of *Astrangia*. Proboscis eversion and feeding were not observed in young *P. krebsii*.

IN A PAPER reporting that the genus *Heliacus* comprises obligate symbionts that feed on colonial zoanthinarian sea anemones, Robertson (1967) mentioned that nothing was known of the feeding habits of the two other major genera in the Architectonicidae, *Philippia* and *Architectonica*. Subsequently, Nordsieck (1968, p. 65) has mentioned the Mediterranean and Lusitanian species *Philippia* (*Philippia*) *hybrida* (Linn.) "auf Korallen" at about 40 me-

ters. However, Nordsieck has informed us (*in litt.*) that he has no more specific data than that *P. hybrida* lives in a coral and coralline habitat. Taylor (1968, p. 187) mentioned that *Architectonica perspectiva* (Linn.) "probably feeds upon zoanthids" at 15 to 25 meters in the Seychelles, but Taylor has informed us (*in litt.*) that he dredged *A. perspectiva* together with zoanthids, and extrapolated from Robertson's (1967) conclusions on *Heliacus*. Shuto (1969, p. 25, footnote) states that *A. perspectiva* is "strictly speaking . . . synbiotic [sic] with sand-dwelling sea anemones"; no supporting data were given. Abbott (1968, p. 86) mentioned *Architectonica nobilis* Röding "in shallow water among sea pansies." *Architectonica nobilis* commonly is washed ashore on

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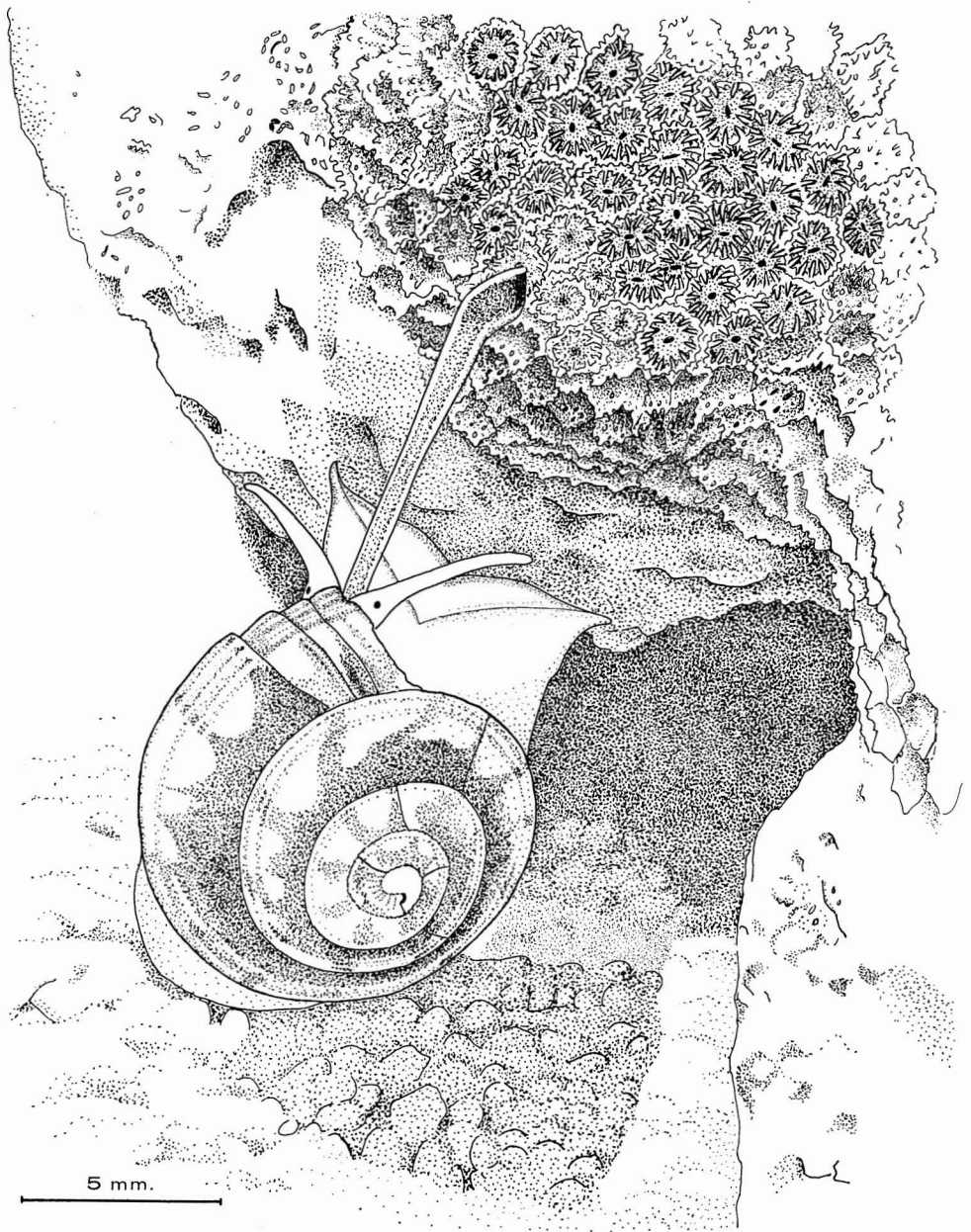


FIG. 1. Postlarval *Philippia* (*Psilaxis*) *radiata* (Röding) feeding on the polyps of the hermatypic stony coral *Porites lobata* Dana. Composite drawing by Mary Fuges from photographs of a Hawaiian animal feeding, from other photographs of extended *Philippia* animals, and from specimens of the shell and coral. The *Philippia* lives in the coarse sand near the coral and crawls out to feed at night.

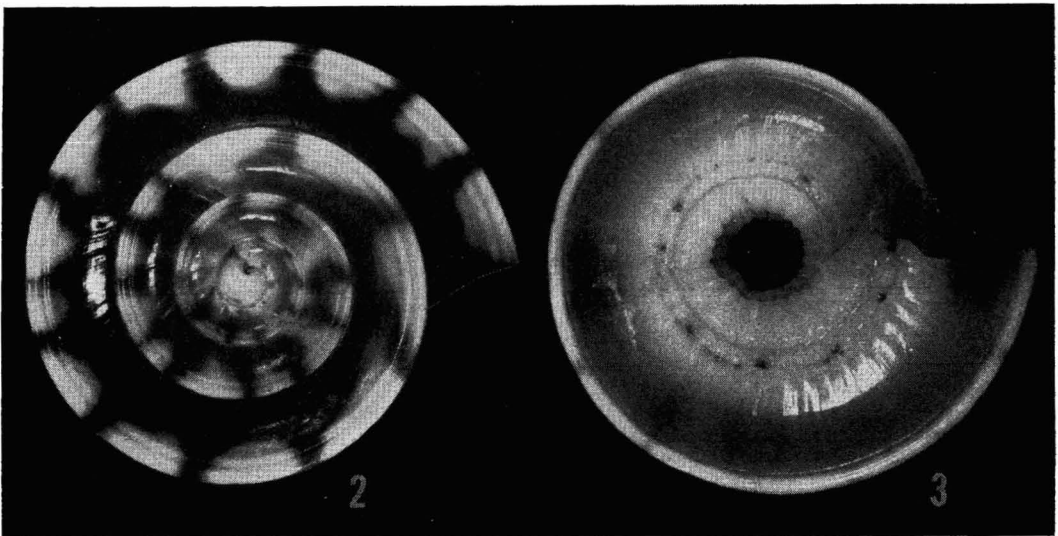
Texas beaches together with pennatulids (*Renilla muelleri* Kölliker; teste R. T. Abbott). Most recently, *A. nobilis* has several times been seen with its proboscis everted, presumably while feeding on something (Futch, 1969). Thus, all five of these tantalizing reports provide no definite information. There are similarly vague hints that *Gyriscus*, a fourth architectonicid genus, may live with gorgonians (Tiberi, 1868) and sponges (Powell, 1965, pp. 161–162).

New observations (by Adams) are here reported on *Philippia* (*Psilaxis*) *radiata* (Röding) which in the Hawaiian Islands lives near and feeds on the soft tissues of the hermatypic stony coral *Porites lobata* Dana (Fig. 1). (This discovery was briefly mentioned in Hawaiian Shell News, vol. 15, no. 10, p. 4; October 1967). The Architectonicidae become the fifth family of prosobranch gastropods definitely known to include predators or parasites on stony (scleractinian) corals (Robertson, 1970a). The habitat and feeding data are preceded here by a review of the structure of the proboscis, jaws, and radula of *Philippia*. Their specialization and uniformity lead us to believe that food and mode of feeding are uniform throughout the genus.

Our information on larval dispersal and the metamorphosis of *Philippia* enhance the interest of the nutritional dependence of the postlarvae on coelenterates. All three species in the subgenus *Psilaxis* have planktotrophic veligers that remain for long periods in the plankton (Robertson, 1964; Scheltema, 1968; Robertson, 1970b). We have but scanty data on the two Indo-Pacific species, and therefore we summarize here some of our data on the larvae of the Atlantic Ocean species *Philippia* (*Psilaxis*) *krebsii* (Mörch), on its metamorphosis in the laboratory at Woods Hole, and on the interaction between the young postlarvae and the ahermatypic coral *Astrangia danae* Agassiz. Information on the systematics, zoogeography, and bathymetry of Indo-Pacific *Philippia* (*Psilaxis*), and on eggs and young postlarvae in the umbilicus of adults, is given in the following paper (Robertson, 1970b).

PROBOSCIS STRUCTURE

Like other architectonicids, *Philippia* has a remarkably long, acrembolic proboscis. When this is fully everted, the true mouth and the small buccal mass containing the radula are at the tip. Thus the animal can feed only when



FIGS. 2 and 3. Shell of the *Philippia radiata* specimen seen to have fed on *Porites lobata* (45 feet off Makua, western Oahu, Hawaiian Islands; shell in the collection of Frank W. Adams). Apical and basal views, respectively (both $\times 6$).

the proboscis is fully everted. The lining of the buccal cavity and esophagus is cuticularized as in epitoniids, and this prevents injury from nematocysts in both groups (Robertson, 1970*b*). The laterally paired jaws of *Philippia* are elongate, are comprised of scalelike elements, and are the distal part of the buccal cavity wall. Upon complete proboscis eversion, the jaws are near the mouth edge. The radula, uniform throughout the genus, is narrow and comprised of elongate teeth bent distally and with one to six points. As observed long ago by Troschel (1875, p. 155), these architectonicid radular teeth resemble those of epitoniids. The resemblance was attributed by Troschel to phylo-

genetic relationship and by Thiele (1928, pp. 87-88) to convergence. Epitoniids are now known to feed on coelenterates exclusively and we are inclined to agree with Thiele.

Philippia radiata:

HAWAIIAN HABITAT AND FEEDING DATA

Philippia (Psilaxis) radiata is one of two closely related species in the Hawaiian Islands (Robertson, 1970*b*). The postlarvae, rarely collected alive, are known from shallow water to about 150 feet. During daylight, the animals are usually buried 1 to 4 inches in silty sand or loose, algal-covered rubble, the sand

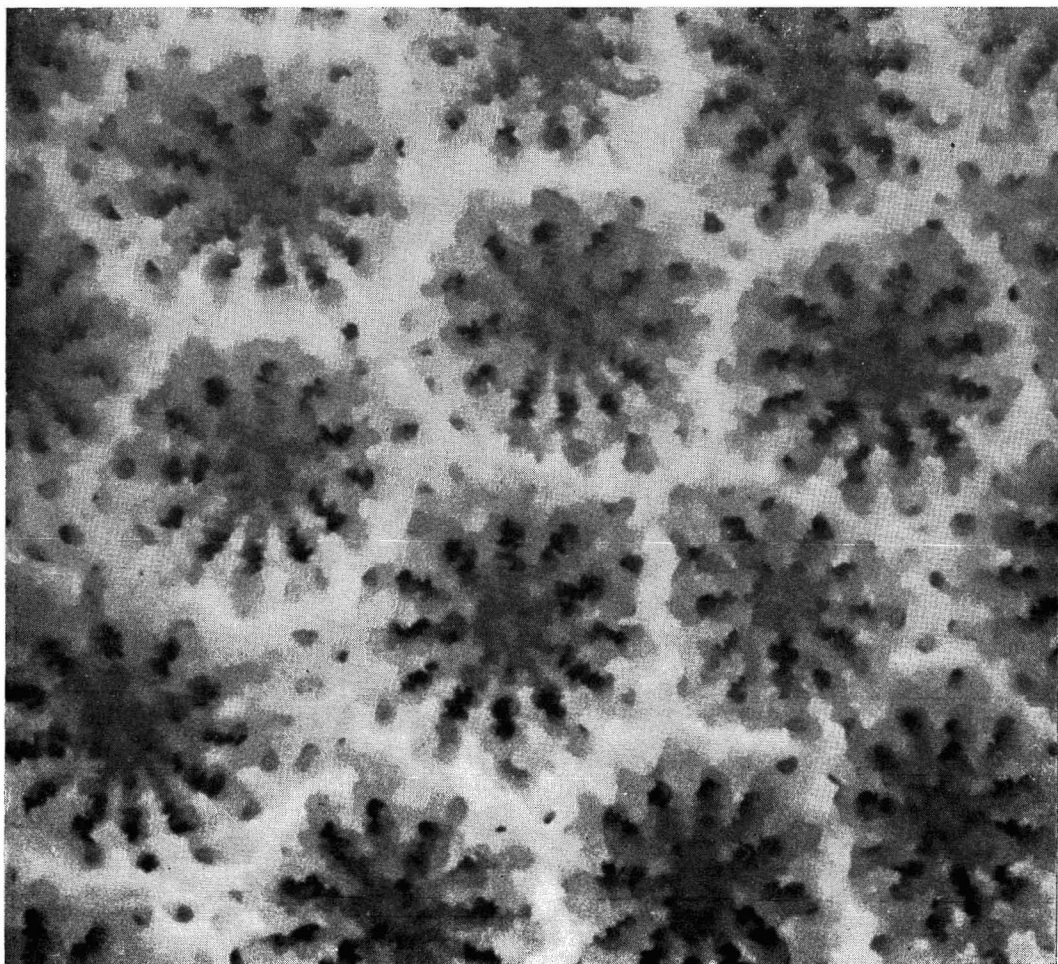


FIG. 4. *Porites lobata*. Some of the calices of the cleaned skeleton of the coral seen to have been fed on by *Philippia radiata*. $\times 30$.

and rubble shallowly overlying basalt (Hawaiian Shell News, vol. 16, no. 12, p. 7; December 1968). In every case known to us, the living animals were near massive or incrusting colonies of *Porites lobata*.

One living *Philippia radiata* with a fairly small shell (Figs. 2 and 3) was collected by Adams while scuba diving at a depth of 45 feet off Makua, western Oahu, in April or May 1967. It was taken from a patch of sand near a small living colony of *Porites lobata* on a mainly dead skeleton resting on the sand. Both the gastropod and the coral were kept alive in an aquarium. The *Philippia* remained alive for about two months and was secretive, retracting into its shell whenever ordinary light was shone on it. Infrared light was found not to disturb the animal. Late one evening, under infrared, the *Philippia* was seen with its pro-

boscis fully everted adjacent to the *Porites* colony as it fed delicately on the still partly expanded polyps. Under bright photoflood lights, two color photographs were taken before the *Philippia* inverted its proboscis and retracted into its shell. The drawing (Fig. 1), based in part on these photographs, probably does not show the full length of the extended proboscis.

SPECIFICITY OF *Philippia* TO CORAL HOSTS

Extrapolating from the Hawaiian habitat data, from the single feeding observation, from the fact that the proboscis is adapted for feeding on coelenterates, and from the much more thorough knowledge of the mode of life of *Heliacus*, it seems probable that *Philippia* is host-specific to stony corals. The world distri-

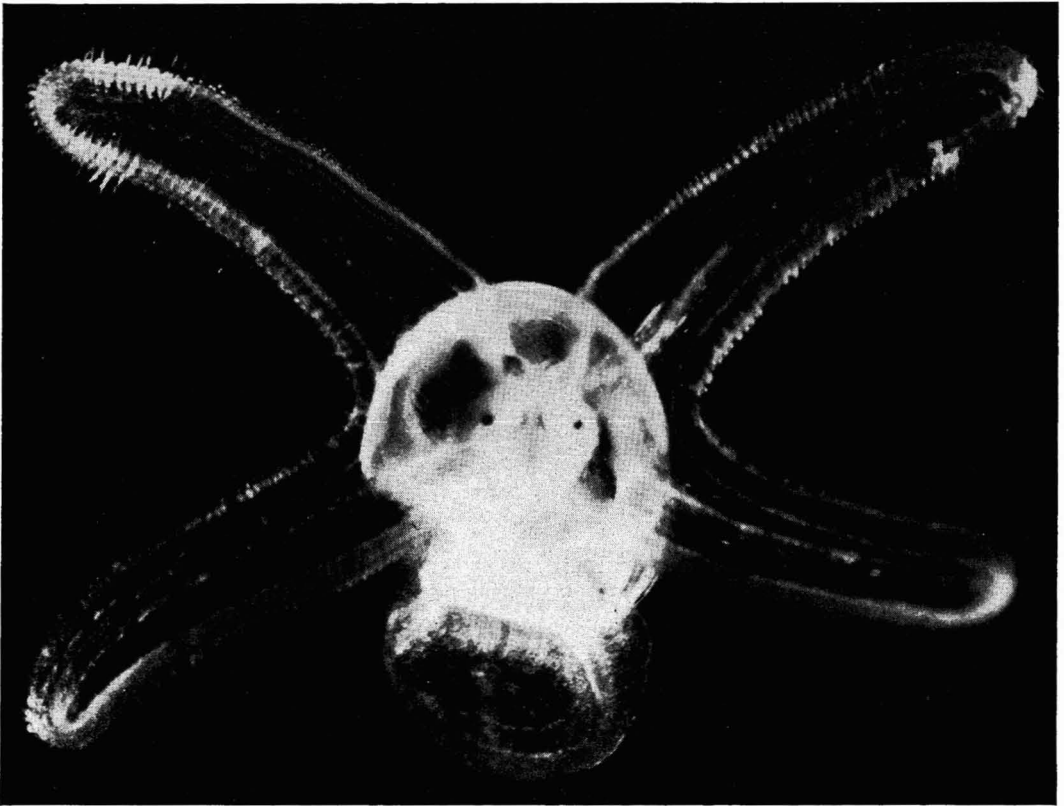


FIG. 5. Incompletely developed veliger larva of *Philippia (Psilaxis) krebsii* (Mörch) with the 4-lobed velum fully extended, showing also the operculum and non-tentaculate eyes. From 38°08' N, 69°55' W. $\times 50$. The fully developed larva has longer velar lobes.

bution of *Psilaxis* coincides closely with areas where there are more than two to five genera of hermatypic corals (Stehli, 1968, p. 209, fig. 45). We infer that postlarval *Philippia* (*Psilaxis*) is obligately associated (symbiotic) with hermatypic corals, and that the soft tissues and mucus of corals are its exclusive food.

The coral on which our feeding observations were made (Fig. 4) was identified for us by Professor John W. Wells as *Porites lobata* Dana. Among the other symbionts with corals, host-specificity to particular genera or families is uncommon (Robertson, 1970a). There is no reason to suppose that *Philippia radiata* is specific to *Porites lobata*. Nevertheless, *Porites lobata* is potentially a major host for *Philippia radiata* in the tropical west and central Pacific because it is abundant in the Hawaiian Islands (Vaughan, 1907, pp. 196–207) and widespread elsewhere, being known also from the Marshall, Line, Samoa, and Fiji islands, and from the Great Barrier Reef, Australia (Crossland, 1952, p. 242; Wells, 1954, p. 452). *Porites lobata* is not known from the Indian Ocean, and so *Philippia radiata* must have different hosts in this ocean.

LARVAL AND POSTLARVAL *Philippia krebsii*

Larval Dispersal

As has been reported elsewhere (Robertson, 1964; Scheltema, 1968, p. 1160, fig. 1), the pelagic veliger larvae of *Philippia* (*Psilaxis*) *krebsii* are remarkably abundant in near-surface waters of the tropical and subtropical Atlantic Ocean. So far, the benthic adults (fairly scarce in museums) are known only from the western Atlantic (Barbados, Curaçao and Yucatan north to Bermuda and off Cape Hatteras) and from two areas in the eastern Atlantic (Canary and Cape Verde Islands). The known bathymetric range is 4 to 112 fathoms (7 to 205 meters), the living animals being mostly in the shallower depths.

Plankton collections made from various research vessels during the past several years have revealed that larval *P. krebsii* occurs the entire distance across the Atlantic, offshore over deep water as well as in coastal regions. (For methods and other results from earlier

stages in the collecting program, see Scheltema, 1966 and 1968). The larvae live in the same depth range as the adults but frequently are distant from any potential hosts. The known stations of occurrence range from latitudes 44°N (east of Nova Scotia) to 18°S (east of Brazil) and from longitudes 85°W (western Caribbean) to 8°W (south of Liberia). This area includes 9.1 million square nautical miles (27 million square kilometers) of ocean. Out of a total of 502 plankton samples from different stations within the area of occurrence, larval *P. krebsii* were found in 113 (22 percent of the total). Sea surface temperatures ranged from 29°C down to 19°C, but most of the larvae probably were at depths below the warmest water.

Duration of the Pelagic Larval Stage

The maximum duration of the pelagic larval stage, deduced from the localities of occurrence and the maximum current velocities from the nearest potential spawning areas, is in the order of six months or longer. Trans-Atlantic transport by ocean currents must be frequent, although neither larvae nor adults are yet known from the West African continental shelf.³

The minimum duration of the pelagic stage is of interest because this probably is critical in maintaining local populations. Incompletely grown veligers of *Philippia krebsii* occur no farther from spawning areas than ocean currents could transport them within several weeks. Thus, growth of the veliger is rapid, full size is quickly attained, and settlement would seem possible within several weeks after hatching. With hydrographic conditions such as those at Bikini (Johnson, 1949) and Bermuda (Boden, 1952; Boden and Kampa, 1953), larval *Philippia* (*Psilaxis*) could sometimes settle near their parents. The geographic variations in protoconch size (Robertson, 1970b) are an indication that some of the populations are truly semi-isolated.

³ In a paper on coral-inhabiting crabs in the eastern Pacific, Garth and Hopkins (1968, pp. 45–46), quoting W. K. Patton, argue that highly adapted "commensals" with corals are more likely than are free-living species to establish populations after trans-oceanic transport.

Living Larvae

The new observations here reported on larval and young postlarval *Philippia krebsii* are based on living animals from plankton in the Gulf Stream and in the western Sargasso Sea. Repeatedly, these were brought for study to Woods Hole. Here they frequently survived for several months in small containers of Massachusetts sea water changed daily or weekly, and with or without added food (unialgal culture). A detailed description of the morphology and coloration of the veliger is beyond the scope of this paper, and will be included in another study in progress on the larvae of all Atlantic Ocean achitectonicids.

The hyperstrophically coiled larval shell is smooth and lustrous, and before metamorphosis it is transparent and mainly colorless (pale

amber at the sutures, on the anal keel, and on the left side near the varix). The four velar lobes (Fig. 5) lengthen as the larva grows. There are paired eyes but no tentacles until metamorphosis. Probably on account of the green pigmentation of the unicellular algal food, the pale brown digestive gland has a greenish cast. Seen in transparency through the shell on the right side of the body is a conspicuous (opisthobranch-like) black larval excretory organ that is irregularly oval in outline.

Metamorphosis in the Laboratory

Upon capture from the plankton, the larvae invariably lack any growth of the teleoconch (postlarval shell). If they are fully developed (i.e., if the peritreme is thickened into a varix), the larvae lose their velums within a

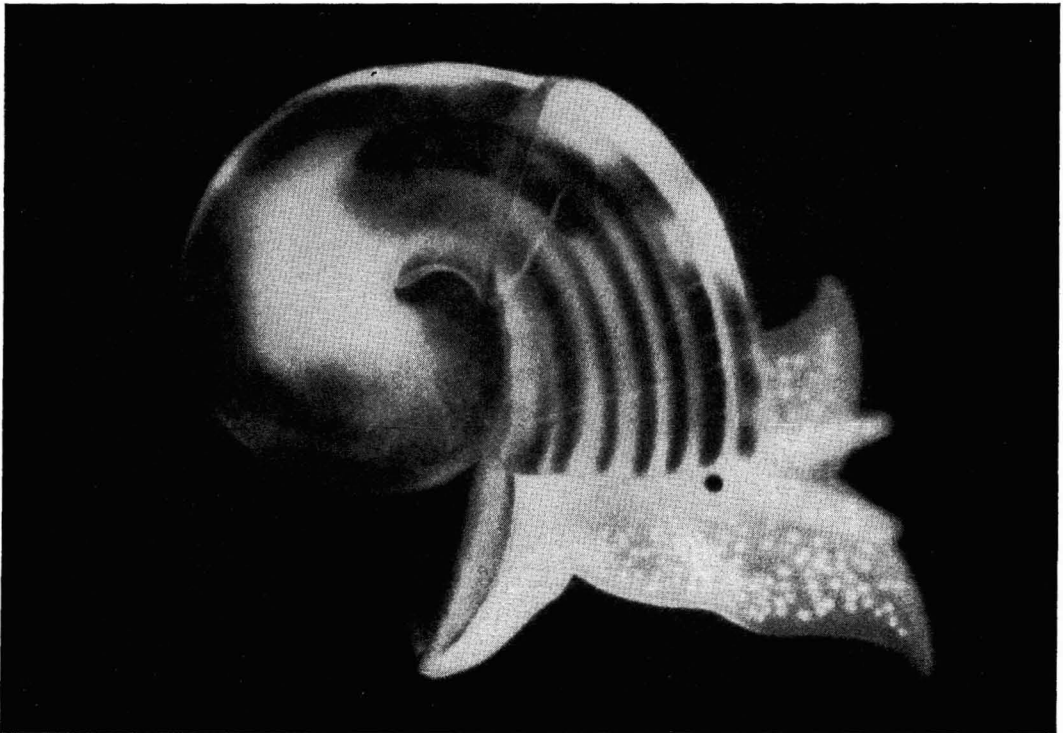


FIG. 6. Young postlarval *Philippia krebsii* in the stage of arrested growth, showing the smooth and lustrous protoconch (larval shell) with its consistent color pattern that develops during metamorphosis, the teleoconch (postlarval shell) with its brown spiral cords crested with periostracum, the opaque white pigment spots on the translucent white body, the broad foot with its median anterior cleft, the pair of tentacles, the right eye positioned on the lateral base of the tentacle, the round operculum on the hind end of the foot (seen in an oblique view), and (in transparency through the shell) the elongate, vesicular, black larval excretory organ. Larva from 35°27' N, 66°53' W. X 50.

few days. Settlement in the laboratory occurs in the absence of corals, and apparently is induced by contact with any solid surface.

At metamorphosis, the velum disappears first; the ciliated edges drop off in fragments and the remainder is resorbed. Subsequently, the digestive gland loses its greenish cast, and slowly becomes more granular exteriorly. The protoconch darkens—especially on the right side, where the consistent brown and white pattern appears. Then the black larval excretory organ slowly lengthens and becomes vesicular. Next, tentacles appear and the body assumes its postlarval coloration (translucent white, with opaque white spots on the tentacles and upper side of the foot). About a week after capture, the teleoconch suddenly begins to grow, and the animal then actively crawls

about on its broad foot (Fig. 6). After developing from between one-sixth to about one-half a whorl in one or two days, growth of the teleoconch stops. Animals remained alive in this state of arrested growth without further changes for several months. The minimum temperature in the laboratory was 20.5°C.

Postlarvae with Astrangia danae

Knowledge that postlarval *Philippia* feeds on the polyps of stony corals prompted experiments at Woods Hole with young postlarval *P. krebsii* to see if they would feed on *Astrangia danae*, the only local stony coral. Unlike *Porites*, *Astrangia* is a nontropical, ahermatypic coral with large polyps. The results were negative in that young *Philippia krebsii* was not seen even to evert its proboscis.



FIG. 7. Young postlarval *Philippia krebsii* being drawn through the large mouth of a polyp of the ahermatypic stony coral *Astrangia danae* Agassiz. $\times 30$.

The observations reveal problems for *Philippia* inherent in assuming an adult mode of life with corals.

When a young *Philippia* was placed on the broad oral disc of *Astrangia*, a feeding response was elicited not in the gastropod but in the coral, which clasped the shell with the adhesive nematocysts on its tentacles and quickly drew the gastropod through its mouth into the gastrovascular cavity (Fig. 7). One *Philippia* survived several hours in an *Astrangia* gastrovascular cavity without apparent injury, but another was completely digested in less than 18 hours (the empty shell and operculum were expelled afterwards).

The behavior of *Philippia* near *Astrangia* was best seen at night; as with *Philippia radiata*, *P. krebsii* is most active then. Young *P. krebsii* showed no ability to detect *Astrangia* polyps except by contact. Whenever the tentacles or anterior end of the foot of a *Philippia* touched any part of the living tissues of *Astrangia*, the gastropod reacted by quickly withdrawing into its shell and expelling mucus. The coral usually reacted by swallowing the *Philippia*. The gastropod lacked immunity to *Astrangia* nematocysts but seemed not to be seriously injured by them, recovering within several hours from extensive contact.

The corals normally fed upon by *Philippia* (*Psilaxis*) probably cannot swallow the young postlarval gastropods. The calices, polyps, and mouths of *Astrangia* are larger than those of *Porites* (Figs. 4 and 7, at the same scale). The maximum diameter of the elastic mouth of *Astrangia* is about 2 mm. This is barely large enough to allow passage, and a *Porites* mouth would be too small.

EARLY POSTLARVAL ARRESTED GROWTH

The stage of early postlarval arrested growth is not confined to *Philippia* but is recorded on well-preserved shells of all postlarval architectonicids. Invariably there is one (rarely two or more) distinct growth lines in the first or second quadrant of the first teleoconch whorl (Woodring, 1959, pp. 168–170, pl. 30, fig. 7; Robertson, 1964, fig. 4; Jung, 1969, p. 455, pl. 46, fig. 4; Robertson, 1970*b*, figs. 1–2). This uniformity suggests that throughout the

family there is the same sequence of structural and behavioral changes at settlement, and that the stage of arrested growth seen in the laboratory is normal. At this stage the animals presumably crawl in search of their hosts. Many architectonicids die at this stage: the Recent and fossil shells are common in museum collections.⁴ We suggest that this high mortality is caused mainly by the spatial problems in finding hosts at this critical stage in the life cycle.

CONCLUSIONS

The life cycle of *Philippia* (*Psilaxis*) is remarkable because the larvae and young postlarvae have to overcome major spatial and physical problems in order to maintain the populations of adults. The long-lived larvae are spawned in prodigious numbers and are dispersed over enormous areas and distances by near-surface ocean currents. To grow and attain sexual maturity, the postlarvae must first find, and then live near, shallow subtidal coral polyps—presumably their exclusive food. The larvae frequently are distant from any potential hosts, over deep water and in shallow water where corals are sparse or absent. Larval mortality is extensive. However, the minimum duration of the pelagic stage may enable some of the larvae to settle near their parents.

Settlement can precede contact with a host, and in metamorphosis the velum is lost first. This suggests that the swimming-crawling (pediveliger) stage is very short, and that the young postlarvae (in a state of arrested growth) crawl in search of hosts. Mortality is extensive at this stage also. The young appear to have no means of detecting coral polyps except by touch, and they lack immunity to nematocysts. In the laboratory they are also subject to predation by large coral polyps, but probably not by their normal hermatypic hosts.

⁴ Such shells are figured by Robertson (1964, figs. 12–17 [*Philippia*]), Hedley (1903, pp. 349–350, fig. 73 [*Architectonica*]), and Janssen (1967, p. 133, pl. 7, figs. 1–2, 4 [various fossil architectonicids]). Janssen studied a collection from a Miocene fauna in Germany; there were six species and 149 specimens, 24 (16 percent) of which were juveniles.

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