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A NEW MONOPLACOPHORAN LIMPET  
FROM THE CONTINENTAL SHELF OFF SOUTHERN CALIFORNIA

*By James H. McLean*



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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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# A NEW MONOPLACOPHORAN LIMPET FROM THE CONTINENTAL SHELF OFF SOUTHERN CALIFORNIA<sup>1</sup>

By James H. McLean<sup>2</sup>

**ABSTRACT:** A new subgenus and species of monoplacophoran, *Vema (Laevipilina) hyalina*, is described from specimens with a maximum length of 2.3 mm taken on rocks from depths between 174–388 m on the Santa Rosa-Cortes Ridge of the southern California continental borderland. The shell differs from other living neopilinids in being nearly transparent and lacking clathrate sculpture. As in the genus *Vema*, there are six pairs of gills and distinct postoral tentacles. *Vema*, on the basis of six pairs of gills is here regarded as generically distinct from *Neopilina*, which has five. On shell characters the new subgenus *Laevipilina* differs from *Vema* in lacking concentric sculpture and in having its structural prisms of a depth equal to their diameter rather than twice the diameter. Radular comparisons among neopilinids are here made for the first time; the radula of the new species differs from that of three other neopilinids in having a more prominent first lateral tooth. *Vema (Laevipilina) hyalina* is the first monoplacophoran to be verified as living on a rocky substratum and the first to be found at continental shelf depths. Living specimens are accessible, suggesting that much will soon be learned about its anatomy and life history.

## INTRODUCTION

Until 1952 the monoplacophoran limpets were known only from the Paleozoic fossils. On shell characters they differ from modern gastropod limpets in having the muscle scar divided metamERICALLY. Paleontologists had regarded the fossil genera as early patellaceans. No advance was made until 1938, when Wenz (1938: 59) suggested that the symmetrically paired muscle scars of the Silurian genus *Tryblidium* might correspond to the arrangement of muscles in chitons. At that point he separated them from the Patellacea and established the superfamily Tryblidiacea for the group. Two years later he developed his idea further by considering them to represent untorted gastropods and distinguished them from prosobranch gastropods at the subclass level (Wenz 1940). He was the first to mention the name Monoplacophora but did not use it in a formal sense, stating that N. H. Odhner had suggested the name to him (see Knight, Lemche, and Yochelson, 1958). Knight (1952) enlarged upon Wenz's theory and used Monoplacophora with ordinal rank equivalent to Polyplacophora, the chitons.

Dramatic proof that monoplacophorans were untorted limpets became available in 1952 when a living species was discovered by the Danish Galathea Expedition at abyssal depths in the eastern Pacific off Costa Rica. The announcement of the discovery took place five years later when the species was described by Lemche (1957) as *Neopilina galathea*. Its anatomy was thoroughly monographed by Lemche and Wingstrand (1959). Additional anecdotes about the original discovery were given later (Lemche 1972).

*Neopilina* is an untorted limpet with a posterior anus and seri-

ally repeated muscles, gills, and other organs. *Neopilina* was the most exciting malacological discovery of the century, a living fossil — a relict of a once diverse group of mollusks. An additional living class of mollusks was recognized, now apparently surviving only in the deep sea.

Further finds of *Neopilina* since the original discovery proved that living monoplacophorans are more widely distributed than was originally assumed. In recent years five more species of *Neopilina* have been described and other records of unidentified species have been published, all found at abyssal or hadal depths. The second described species, *Neopilina ewingi* Clarke and Menzies 1959, from the Peru-Chile Trench, differed from *N. galathea* in having six pairs of gills instead of the five pairs of *N. galathea*. Because of this difference it was made the type species of the subgenus *Vema* Clarke and Menzies 1959. Further discoveries brought the number of described species of *Neopilina* to a total of five and those of *Vema* to two.

My involvement in the study of monoplacophorans began in 1966, when, in connection with my interest in gastropod limpets, I was given the opportunity to work upon two small specimens in the S. Stillman Berry Collection. The specimens, not exceeding 2.3 mm in length, had been taken on rocks snagged on hook and

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line by a fisherman, Louis Zermatten, in the vicinity of the Cortes Bank, due west of San Diego, California, in 1965. One was from a depth of 95 fathoms (174 meters) and the other from 125 fathoms (229 meters). The rocks bearing the limpets were saved for John E. Fitch of the California Department of Fish and Game. He removed the associated mollusks and gave them to S. Stillman Berry of Redlands, California.

The dried animal of the first specimen was sacrificed for a radula preparation. Initial study of the radula (Figs. 20, 21) suggested a new group in the Patellidae, with a radula characterized by a narrow rachidian, three pairs of laterals and two pairs of flaring marginals. A minute, deep water representative of the Patellidae, otherwise known from robust intertidal forms, was unexpected, but it seemed clearly to be the case, based on the radular evidence. In the hope that more specimens would eventually be found, I delayed further work on this remarkable find. Nine years passed but no additional material came to light.

In 1975 I again turned my attention to the specimens on hand. Only then did I closely examine the specimen that still contained the dried animal. Through the dorsal surface of the nearly transparent shell I noted the circularly coiled intestine that is one of the hallmarks of the described species of *Neopilina* (Fig. 1). Then other monoplacophoran features such as metamericly paired shell muscles and a posterior anus were observed. Upon rehydrating the animal and examining it in fluid, the shell

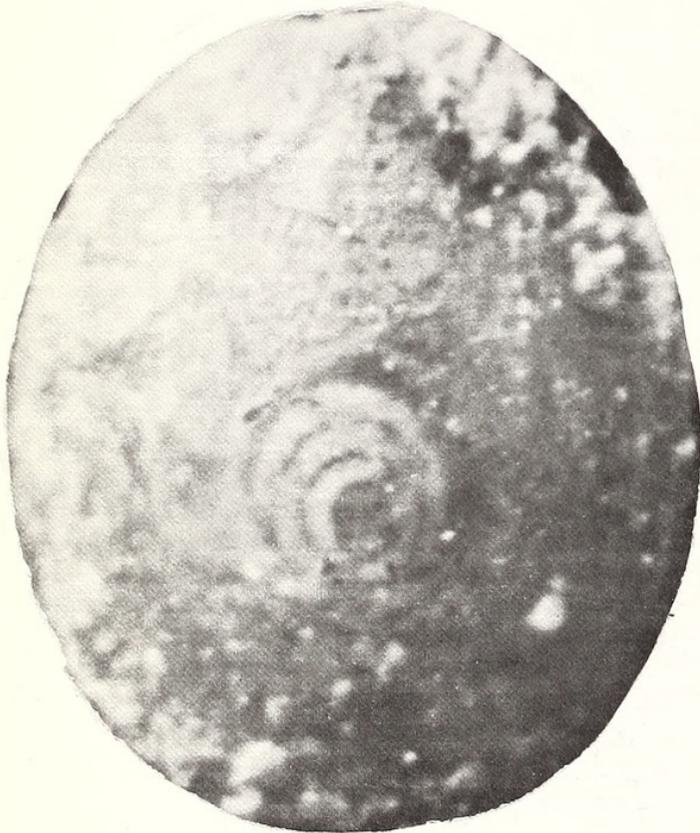


FIGURE 1. *Vema (Laevipilina) hyalina* new species. LACM 19149, 2.16 mm in length, dorsal view prior to rehydration of the soft parts and prior to removal of encrustations from the shell surface. The anterior apex is visible near the top and the intestine with four coils is seen through the nearly transparent shell slightly posterior to the midpoint. Photograph by Solis.

became more transparent and its structural prisms visible (Figs. 2, 3). It thereupon became clear to me that this was a monoplacophoran limpet. Contrary to all previous expectations for the group, it had come from a rocky substratum in relatively shallow water.

The rehydration of the specimen containing the dried animal did not fully restore the features of the ventral surface. Structures recognized were the head, mouth, velum extending laterally and posteriorly to the head, radiating pedal retractor muscles, and the posterior anus. There seemed to be no sign of gills or of postoral tentacles that also characterize the group. Moreover, the true shape of the foot could not be discerned. It seemed that it was partially missing with nothing remaining but a stump in the central area. An S-shaped structure that was clearly visible was interpreted as the radular sac, considering that the radula extracted from the other specimen was more than half the length of the shell. The shell appeared completely smooth, devoid of all traces of clathrate sculpture seen in the described species of *Neopilina*. The radula also seemed to differ considerably from that of *N. galathea*, the only species for which a radula had been illustrated.

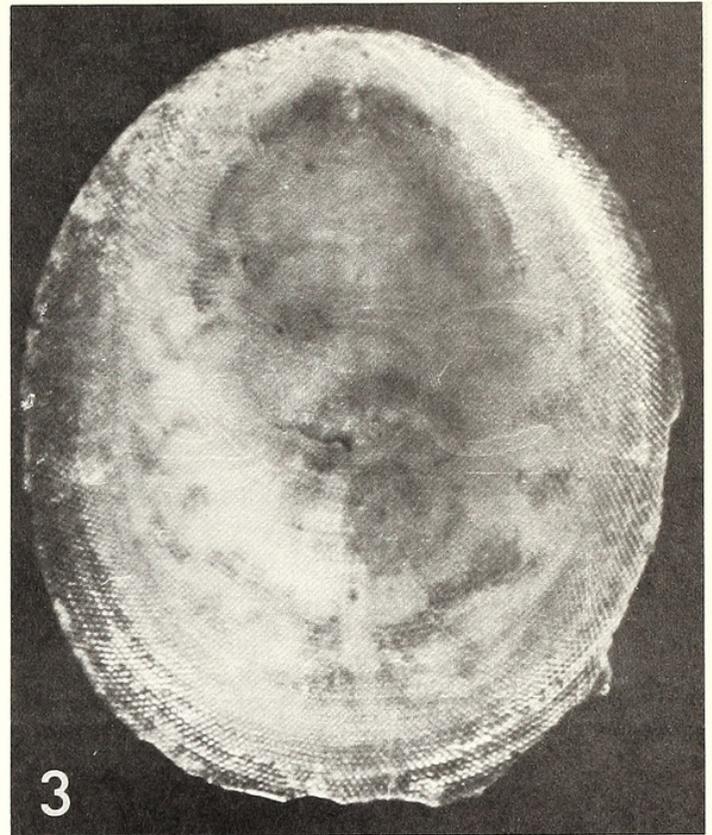
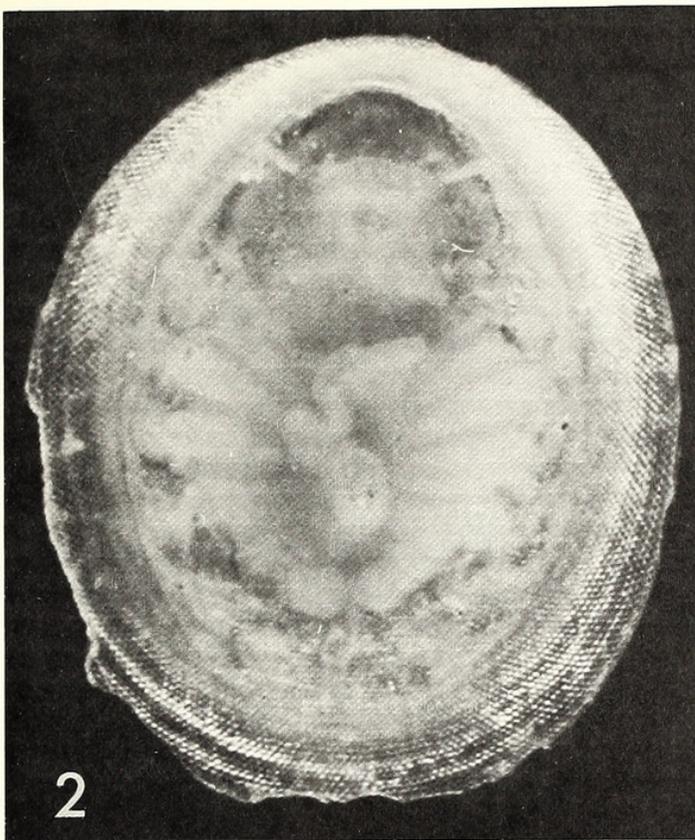
At that point in my studies I presented the preliminary findings to the American Malacological Union — Western Society of Malacologists joint meeting in San Diego, June 1975. Based on the smooth shell, radular differences, and apparent absence of gills, I considered that a new genus was indicated for the newly discovered species, and so announced an intention to propose one. The abstract resulting from my presentation was published 30 January 1976 (McLean 1976).

In the fall of 1975 an intensive offshore sampling program was initiated by the U.S. Bureau of Land Management (BLM) on the continental shelf of southern California, coinciding with the leasing of offshore tracts for oil exploitation. A group of biologists headed by Gilbert F. Jones of the University of Southern California contracted to do the biological portion of the work. Although most of the stations were made on soft bottoms, there were some box core stations from rocky areas. Sorters and technicians were alerted to watch for the new microscopic monoplacophoran, but after six months of sampling none were found.

Meanwhile, early in 1976 I decided to publish my preliminary description of the species in the hope that this notice would stimulate efforts to find other specimens. After more closely scrutinizing the rehydrated specimen with improved optics I noted swellings on the mantle margin in the position where gills could be expected. Contrary to my earlier observations, six pairs of gills seemed to be present, although no clear configuration could be seen.

No radular descriptions had been published on any monoplacophoran species since the initial monograph of Lemche and Wingstrand (1959). I was able to obtain specimens of two other neopilinid species for radular comparisons. The results, discussed herein, indicated that the two other species bridged the gap between the radula of the new form and that of *N. galathea*.

Although many questions remained unanswered, a draft of the manuscript was completed and circulated for review. As I was preparing to submit the paper for publication, two freshly collected specimens were found in sediment from one of the BLM stations. One had been picked from the residue by the sorters and subsequently recognized by Patrick I. LaFollette, a member of the BLM project. He reexamined the residue and found another. This was the breakthrough I had hoped would occur, for I now



FIGURES 2, 3. *Vema (Laevipilina) hyalina* new species. LACM 19149, 2.16 mm in length, rehydrated and photographed in alcohol. FIGURE 2, ventral view; FIGURE 3, dorsal view. Shell prisms show at the margin, arranged in curved rows; lighter and darker concentric rings represent growth lines. Head with mouth near top center. Below the head is the S-shaped radular sac and foot stump. Tubular rectum at bottom center. Seven pairs of pedal retractor muscles radiate from the center; the first pair is narrow, the second, third, fourth and fifth pairs are long and broad, the sixth and seventh pairs are short. Beyond the lateral terminations of all but the first pair of retractor muscles are 6 pairs of gills visible as swellings that blur the shell prisms. The dorsal view shows four dark coils to the intestine in lower center. In the dorsal view, the light areas encircling the central visceral area are the terminations of the broad bands of the pedal retractor muscles. Gills represented by the blurred lighter areas between the edge of the shell and the pedal muscle terminations. Photographs by Draper.

had preserved specimens showing the true condition of the foot and the clear presence of gills (Figs. 4, 5).

The two fresh specimens were somewhat smaller than the original two, with a maximum length of 1.75 mm. They came from a box core station on the Santa Rosa-Cortes Ridge between San Nicolas and Tanner Basins, at a depth of 388 m. Efforts to find more specimens in sediment residues from other unprocessed BLM stations from rock bottoms were unsuccessful.

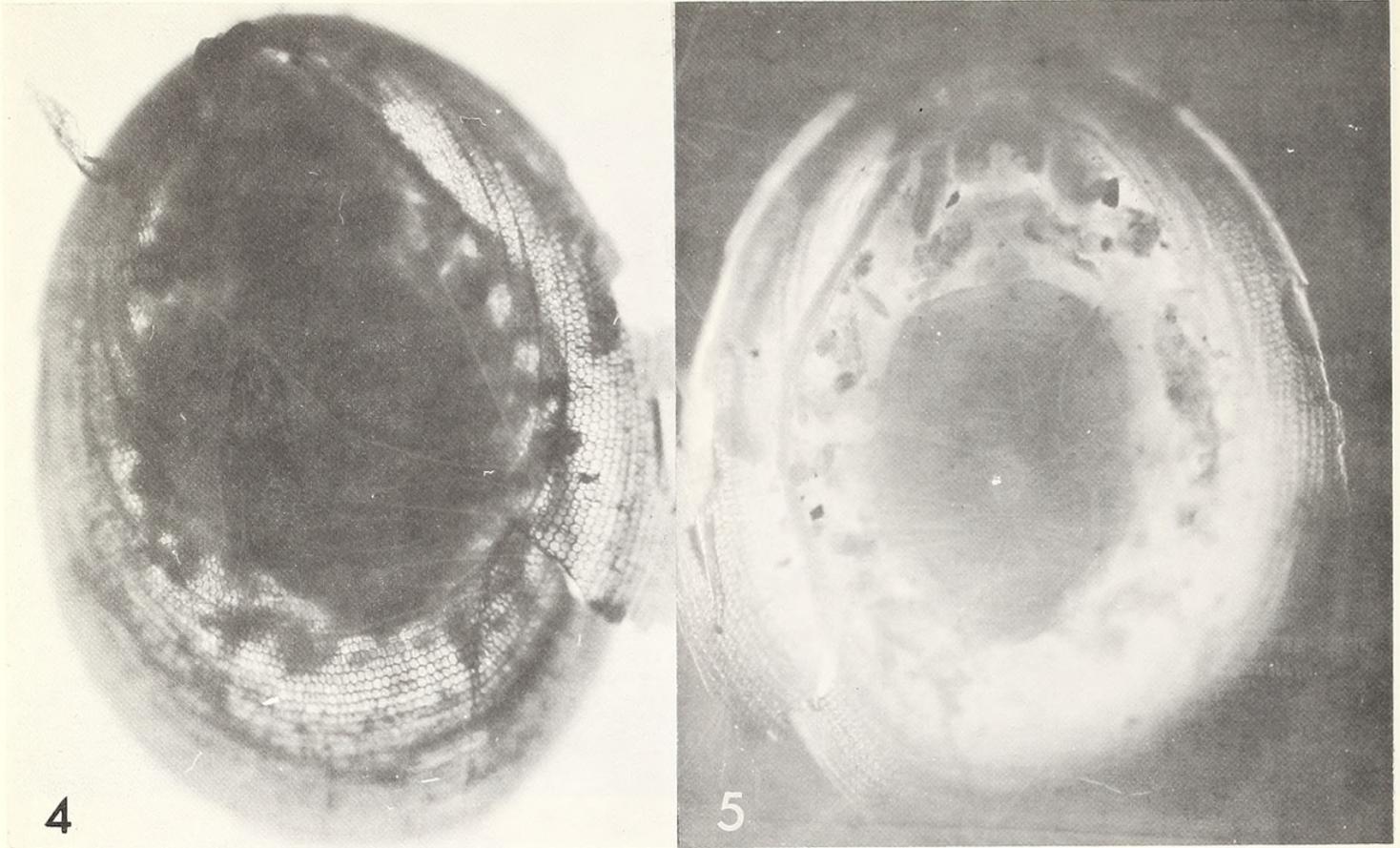
Publication of the paper was withheld until I could learn more about the anatomy of the species. Although the specimens had not been fixed for histologic sectioning, it was hoped that sectioning would be possible. I asked the help of M. Patricia Morse at Northeastern University in Nahant, Massachusetts, who along with her associate, Nathan W. Riser, had work already underway on *Neopilina ewingi*.

Once again the material had limitations due to the lack of proper fixation. Many sections made by Morse and Riser from the smaller of the two specimens did not hold together and the results were disappointing. However, they prepared the larger specimen (Figs. 4, 5) by critical-point drying for viewing with a scanning electron microscope (SEM). That effort produced some

highly satisfactory pictures on 11 February 1977, which are reproduced here (Figs. 6–8, 11).

In February 1977 further specimens were collected on a three day cruise of the *VELERO* led by Heinz A. Lowenstam of the California Institute of Technology, and assisted by LaFollette, now a member of the Malacology Section of the Museum. Efforts to recover the species with rock dredges and box cores were successful at the same locality as the earlier BLM station. Six living specimens attached to their rock substratum were obtained. The animals survived for several weeks at ambient water temperatures (Lowenstam 1977, abstract). A report on the behavior, ecology, and shell ultrastructure will be published elsewhere by Lowenstam. One of the living specimens was fixed for histologic sectioning to be done by Morse and Riser, who will also report separately on their results.

The rocks obtained on the cruise were examined aboard ship for living specimens and then preserved in 70% ethanol. Further examination of the rocks by LaFollette produced four more specimens that became the type lot. One of these specimens (Fig. 9), designated the holotype, is in excellent condition and shows most of the features now attributed to the species.



FIGURES 4, 5. *Vema (Laevipilina) hyalina* new species. LACM 19150, 1.75 mm in length. FIGURE 4, dorsal view, showing the regularity of the shell prisms, gills darkly outlined. FIGURE 5, ventral view, showing the 6 pairs of gills, U-shaped anterior lip of the mouth, the postoral tentacles clearly visible between the mouth and the foot. Photographs by Morse and Riser, light microscope, 4 X objective.

### SUPRASPECIFIC CLASSIFICATION OF LIVING MONOPLACOPHORANS

The Monoplacophora have been recognized as a separate class of mollusks for a relatively short period. A revised classification of the Paleozoic fossil representatives was given by Knight and Yochelson (1958). Starobogatov (1970), and more recently, Runnegar and Jell (1976), have offered other versions.<sup>3</sup>

These classifications have been based largely upon shell form and the count and configuration of muscle attachment scars on the shell. The modern monoplacophorans have thin shells that lack readily visible muscle scars. Unfortunately, details of the musculature are known only for *Neopilina galathea* as given by Lemche and Wingstrand (1959). There is therefore a poor basis upon which to compare diversity in the living species with the considerable diversity indicated in the fossil record.

When Lemche (1957) proposed *Neopilina galathea* he placed it in the family Tryblidiidae, a group otherwise unknown since the Devonian. Knight and Yochelson (1958) established the subfamily Neopilinae for the species. Subsequent authors followed this scheme until Starobogatov (1970) disassociated the group from the Tryblidiacea altogether by recognizing both a separate family Neopilinidae and superfamily Neopilinoidea. However, Runnegar and Jell (1976) retained *Neopilina* in the Tryblidiidae.

A consideration of the overall classification of Monoplacophora is not within the scope of this paper; there are evidently some controversial aspects that will not readily be settled. Certainly a Recent family Neopilinidae may be justified on grounds in addition to the great disparity in age. The shells of neopilinids are thin and lack the massive development of the nacreous layer of the Devonian Tribliidiidae (Erben, Flajs and Siehl 1968).

Generic criteria within the Neopilinidae are also lacking a sound basis for comparison. *Vema* Clarke and Menzies 1959, type species *Neopilina (Vema) ewingi* Clarke and Menzies 1959, was proposed as a subgenus of *Neopilina* chiefly on the presence of six pairs of gills, rather than five of *Neopilina*.

In the 18 years that have passed since the first two species were proposed, four more species of *Neopilina (Neopilina)* have been described, along with one more species of *Vema*. The number of gill pairs has proven to be a consistent character in species of each group regardless of size or growth stage. The supplementary criteria for *Vema*, thinner shell and thinner periostracum,

<sup>3</sup>While this paper was in its final stage of preparation, I received a useful review paper on the Recent monoplacophorans (Cesari and Guidastri 1976). The article, in Italian, contains an extensive bibliography that includes many titles omitted here. Also, an obituary of the late Henning Lemche (Knudsen 1977) includes references to other papers by Lemche on *Neopilina* and its affinities.

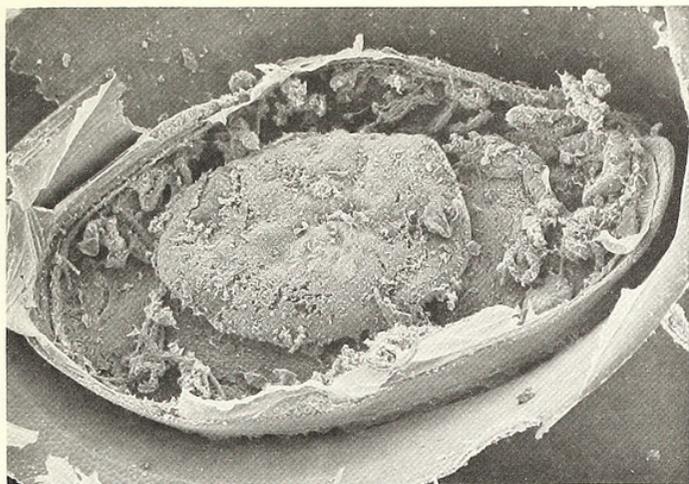


FIGURE 6. *Vema (Laevipilina) hyalina* new species. LACM 19150, 1.75 mm in length, critical-point dried, SEM micrograph. Lateral view of ventral surface, showing the 6 pairs of gills, the anterior lip of mouth, the velar ridge extending laterally around the mouth, the ridge between the mouth and foot bearing the postoral tentacles. Shrinkage of the body has revealed the pallial line midway in the exposed portion of the shell, the nacreous layer on the innermost portion thick enough to obscure the pattern of hexagonal prisms. X 80.

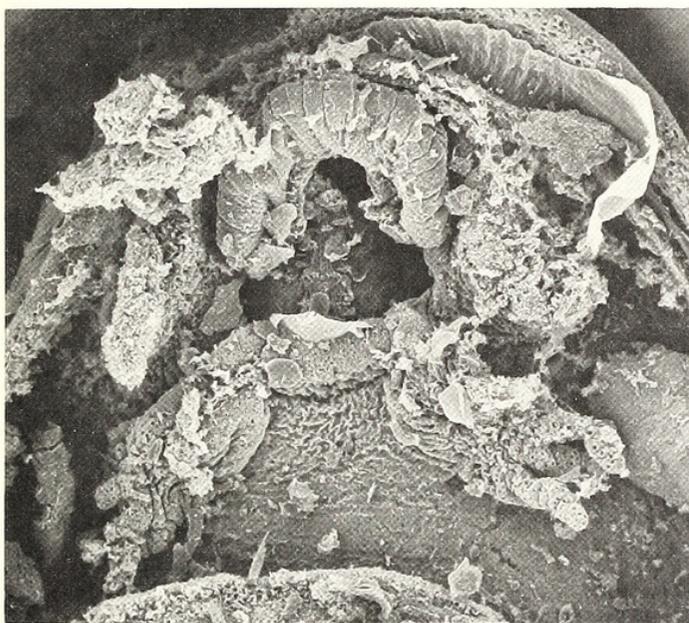


FIGURE 7. *Vema (Laevipilina) hyalina* new species. LACM 19150, length 1.75 mm, critical-point dried, SEM micrograph. Ventral aspect, enlargement of head area, showing the U-shaped anterior lip of the mouth, the radula exposed on the odontophore within. Postoral tentacles visible on the ridge below the mouth. The velum is a narrow ridge anterior to the mouth and extending laterally on both sides. X 190.

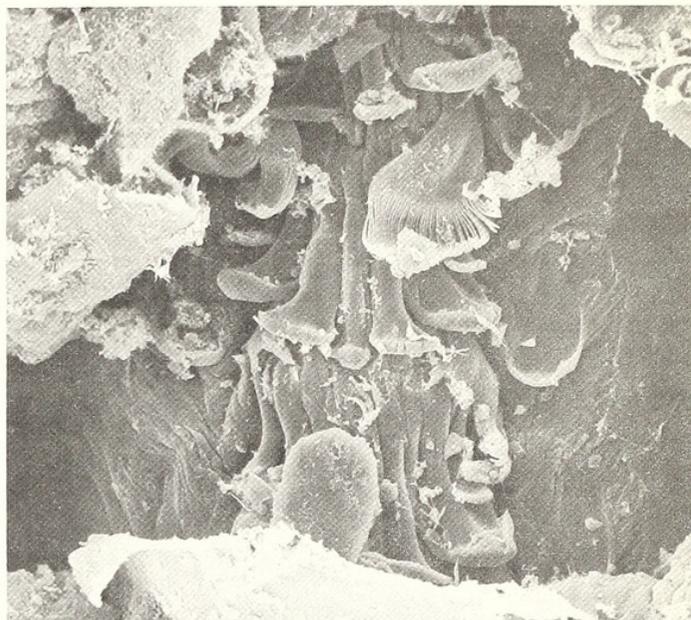


FIGURE 8. *Vema (Laevipilina) hyalina* new species. LACM 19150, critical-point dried, SEM micrograph. Radular ribbon exposed on the odontophore within the mouth cavity. This is an enlargement of the area visible in Figure 7, oriented with the anterior at the top as in the other figures. Rachidian and lateral teeth as drawn in Figure 22. One of the fringed first marginals is fully exposed, showing depth to the comblike surface. X 900.

have been maintained in the second reported *Vema*, *N. (Vema) bacescui* Menzies 1968. The two species of *Vema* are known only from the southern hemisphere in the eastern Pacific, whereas the species of *Neopilina* have been shown to have a broader distribution in abyssal depths at the base of the continental slope in the eastern Pacific in both hemispheres and in the Indian Ocean and mid-Pacific.

Inasmuch as the anatomy of *Vema ewingi* has not been described in detail, there is no sound basis upon which to decide whether the separation of the two groups should be at the subgeneric, generic or familial level. Starobogatov (1970:301) stated: "*Vema* can hardly be regarded as a subgenus of *Neopilina*. Moreover it cannot be stated with confidence that *Vema* is a member of the same family . . . it is in any case appropriate to await publication of detailed data on the anatomy of *Vema*." Nevertheless, for a group in which serial repetition of key structures is fundamental, other internal organs in *Vema* can be expected to have an arrangement differing from that of *Neopilina*. Once the results of comparative anatomical studies are available, there will, in my opinion, be ample reasons to consider

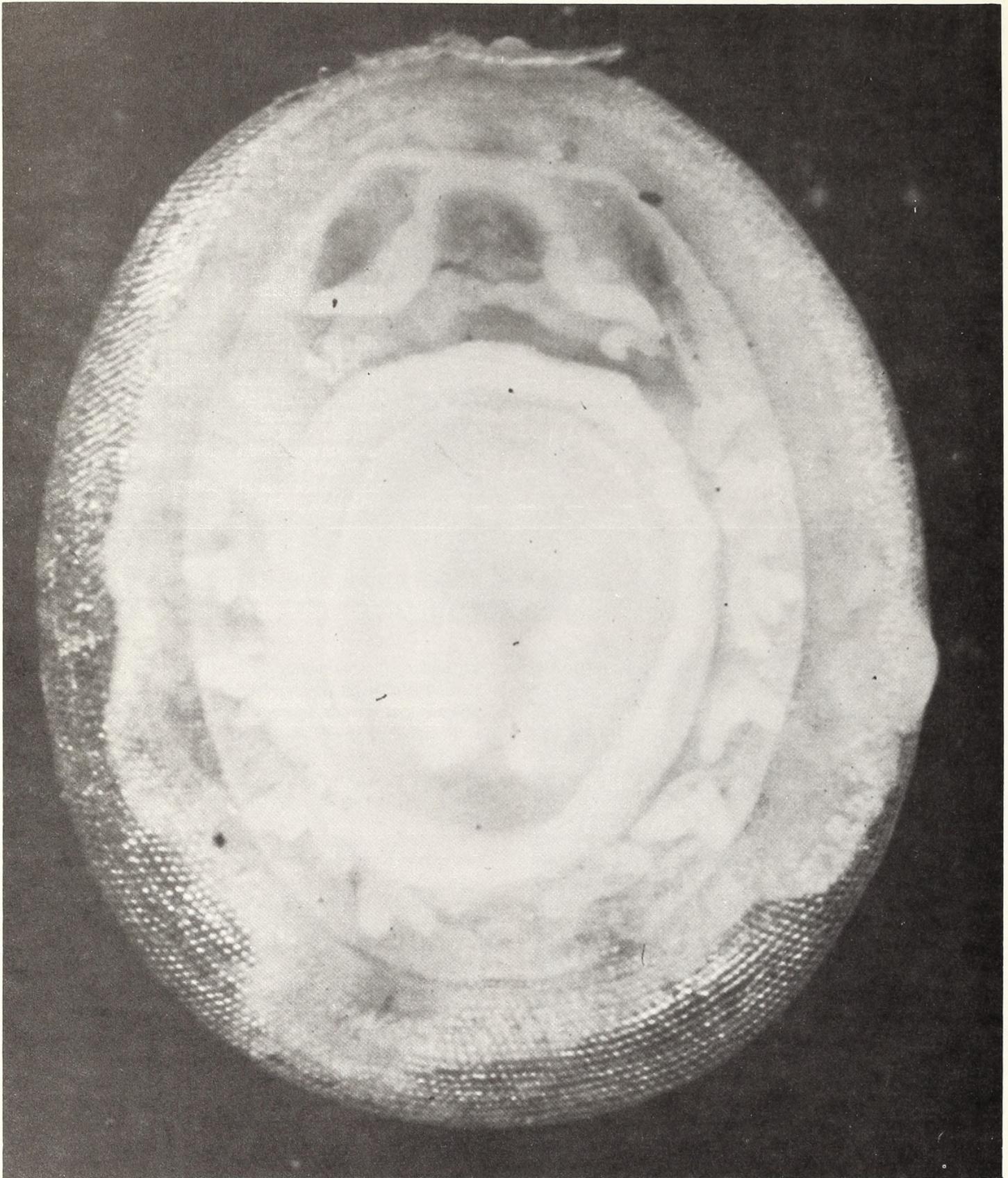


FIGURE 9. *Vema (Laevipilina) hyalina* new species. Holotype, LACM 1787, 1.94 mm in length, preserved and photographed in alcohol. Shell prisms show at the margin on the left side where the pallium is lifted away. The pallial fold encircles the head area and borders the outer side of the pallial cavity, in which six pairs of gills are visible. The anterior lip of the mouth is surrounded by the velum, which extends laterally into the pallial cavity. Between the velum and the foot is the ridge bearing the postoral tentacles. Foot with thickened margin, the two posterior lobes of the gonad visible through the transparent sole. The opaque area at the lower left is due to an encrusting foraminiferan on the outer surface of the shell. Photograph by Draper.

the two groups to be generically distinct. Although some might argue that it is premature to make this distinction, it is necessary to do so in order to recognize a subgenus within the six-gilled *Vema* lineage. There is a major dichotomy between the abyssally occurring species with sculptured shells and the small, smooth shelled, more shallowly occurring new species. I believe it prudent to recognize this distinction now at the subgeneric level.

The outline that follows includes all of the taxa proposed to date in the Neopilinidae<sup>4</sup>. As more continues to be learned about the anatomy of the living species, the diagnoses can be enlarged. Uncertainties now exist concerning the musculature and repetition of internal structures; discussion of these characters is therefore omitted.

## SYSTEMATIC ACCOUNT

### NEOPILINIDAE Knight and Yochelson 1958

NEOPILININAE Knight and Yochelson 1958:39; Starobogatov 1970:301 (familial rank).

DIAGNOSIS: Shell thin, cap shaped, apex anterior; shell layers consisting of a thin periostracum, a dominant prismatic layer, and a thin internal nacreous layer. Eyes lacking, mouth bordered anteriorly by a velum, posteriorly by postoral tentacles; foot sole thin, weakly muscularized; anus posterior to foot; gills 5 to 6 pairs, with simple lamellae. Radula with a narrow rachidian, three pairs of laterals and two marginals, edge of first marginal fringed.

The family is limited to the known Recent monoplacophorans. It differs from the Paleozoic families in having an extremely thin internal nacreous layer of the shell.

### *Neopilina* Lemche 1957

*Neopilina* Lemche 1957:414. Type species: *N. galathea* Lemche 1957.

DIAGNOSIS: Shell with radial and concentric ridges at least in early stages, periostracum moderately prominent; gill pairs 5.

SPECIES: *N. galathea* Lemche 1957 (Costa Rica); *N. veleronis* Menzies and Layton 1963 (Baja California, Mexico); *N. adenensis* Tebble 1967 (Indian Ocean); *N. bruuni* Menzies 1968 (Peru); *N. oligotropa* Rokop 1972 (mid-Pacific).

OTHER RECORDS: *N. galathea*, Parker 1962 (off Cape San Lucas, Baja California); unidentified, Menzies 1968 (Costa Rica); unidentified, Rosewater 1970 (South Atlantic east of Falkland Islands); unidentified, Filatova, Vinogradova and Moskalev 1974 (Atlantic-Antarctic); same record identified as *N. galathea*, Filatova, Vinogradova, and Moskalev 1975.

DISTRIBUTION: Abyssal, Eastern Pacific: Baja California, Costa Rica, Peru; east of southern tip of South America; mid-Pacific; Indian Ocean.

REMARKS: Of the four species described, *N. galathea* is the only one known from material from other than the type locality. *Neopilina veleronis* was described prior to the availability of scanning electron microscopy. No intact shells of *N. veleronis* are extant; shells of the remaining paratypes have been altered by the preservative (Figs. 14, 15). Shells of the two original specimens of *N. oligotropa* were thought to have been altered by the initial preservative (Rokop 1972). *Neopilina veleronis* and *N. oligotropa* were described from specimens not exceeding 3 mm in length; *N. veleronis* was considered mature because ripe ova were recognized by Menzies and Layton (1962); *N. oligotropa*

was presumed mature, having come from an oligotrophic or food-poor environment. *Neopilina adenensis* and *N. bruuni* were described from single specimens, the latter species briefly diagnosed but not described in detail.

### *Vema* Clarke and Menzies 1959

*Vema* Clarke and Menzies 1959:1027. Type species: *Neopilina (Vema) ewingi* Clarke and Menzies 1959.

DIAGNOSIS: Shell thinner, periostracum thinner, sculpture weaker than that of *Neopilina*: gill pairs 6.

### Subgenus *Vema s. str.*

DIAGNOSIS: Moderate in size, sculptured with fine radial ribs and raised concentric ridges especially strong in early stages; depth of structural prisms twice that of surface diameter. Gill pairs 6, gill lamellae 5–7.

SPECIES: *V. ewingi* (Clarke and Menzies 1959) (Peru); *V. bacescui* (Menzies 1968) (Peru).

DISTRIBUTION: Abyssal, Peru-Chile Trench.

REMARKS: *Vema ewingi* (Figures 12, 13) has been collected at a number of stations (Menzies 1968; Meenakshi et al. 1970) off Peru, but *V. bacescui* is known from a single station, the original number of specimens not mentioned. The latter species was said to have a distinctive reticulate pattern on the shell surface and a greater abundance of postoral tentacles. Further comparative details were not given.

### Subgenus *Laevipilina* NEW SUBGENUS

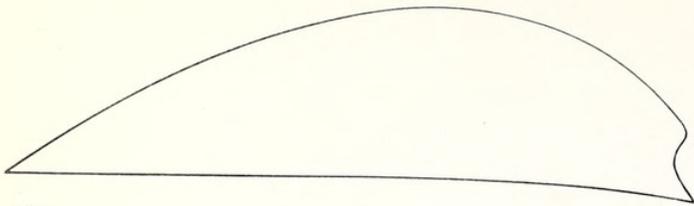
Type species: *Vema (Laevipilina) hyalina* new species.

DIAGNOSIS: Small (under 3 mm in length), lacking concentric and radial sculpture; structural prisms hexagonal, uniform in size, their depth equal to their surface diameter. Gill pairs 6, gill lamellae 2–3.

DISTRIBUTION: Continental Shelf, southern California.

ETYMOLOGY: The subgeneric name, like that of *Neopilina*, is based on *Pilina*, a fossil (Silurian) monoplacophoran of the family Tryblidiidae. The prefix *laevi* (from *laevis*, the Latin adjective for smooth) emphasizes the unsculptured surface of the shell in the new taxon.

<sup>4</sup>One published record may now be removed. Filatova, Sokolova and Levenstein (1968) and Filatova and Zenkevich (1969) reported finding a monoplacophoran at a mid-Pacific seamount northwest of Hawaii. The apex was said to be close to the center of the shell rather than near its anterior margin as in the known species. It was therefore considered to represent a new genus in the Tryblidiidae. In response to my inquiry about the current status of this specimen, she stated (Filatova, personal communication, 12 July 1976): "As to our small specimen of *Neopilina* (?) from Hawaii region it was very young one and it was difficult to decide about its true systematic position, especially for it had the central umbo, and it was only a single specimen."



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FIGURE 10. *Vema (Laevipilina) hyalina* new species. LACM 19149, length 2.16 mm. Lateral profile, the anterior apex at the right.

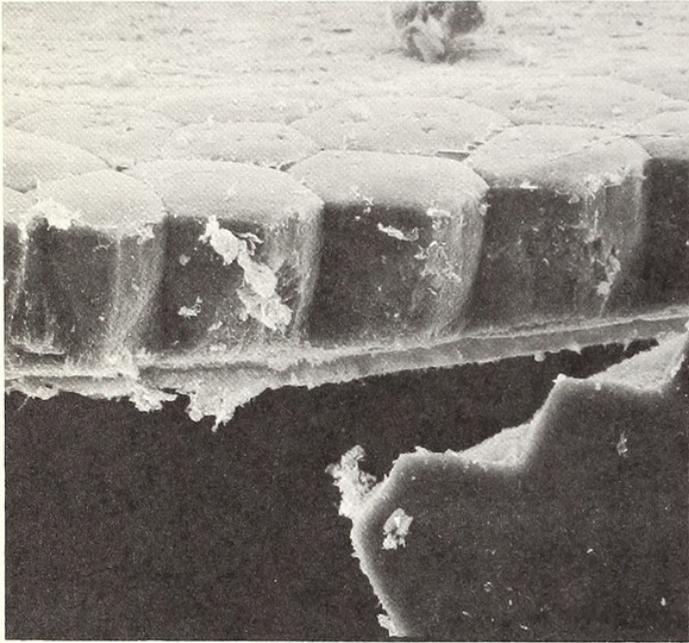
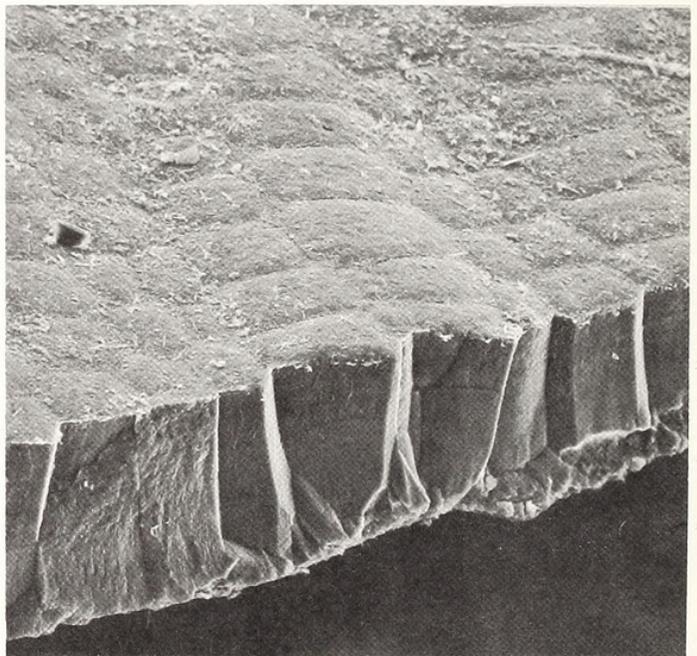


FIGURE 11. *Vema (Laevipilina) hyalina* new species. LACM 19150, SEM micrograph, fractured edge of shell. The narrow band below represents the periostracum. From an area outside the pallial line and therefore lacking the internal nacreous layer. This shows the hexagonal surface outline of the prisms and the depth approximately equivalent to the diameter. X 1100.

FIGURE 13. *Vema (Vema) ewingi*. SEM micrograph, fractured edge of shell near the outer margin. Some of the prisms have a hexagonal surface, while others are more irregular and elongate. Depth of prisms approximately twice the diameter of those with hexagonal surface. Compare with same view of *N. hyalina* in Figure 11, noting differences in magnifications. X 240.



FIGURE 12. *Vema (Vema) ewingi* (Clarke and Menzies 1959). Anterior face of broken shell showing the bulbous apex at the left; strong concentric and weaker radial sculpture is visible in early growth stages. LACM 65-11, 6200 m, 110 mi. W of Callao, Peru, R/V ANTON BRUUN, 24 November 1965. Photograph by Draper. X 45.



*Vema (Laevipilina) hyalina*

## NEW SPECIES

Figures 1–11, 20–22

McLean 1976:60 (abstract, not named); Cesari and Guidastrì 1976:235 (review, McLean 1976); Lowenstam 1977:1076 (abstract, reporting collection of living specimens of "a new monoplacophoran species").

**DIAGNOSIS:** *Vema hyalina* differs from other 6-gilled neopilinids in its smaller size at maturity, lack of concentric and radial shell sculpture, shallow depth of the structural prisms and reduced number of gill lamellae.

**SHELL:** Small (largest known specimen 2.3 mm in length), thin, transparent, iridescent; surface smooth, clathrate sculpture lacking. Periostracum thin, visible as a yellow sheen; prismatic layer thick; internal nacreous layer thin. Pallial line visible at one-fourth the distance from the margin to the center, inside of which the thicker nacreous layer obscures the pattern of prisms. Muscle scars not apparent. Structural prisms visible under magnification, irregular in shape, usually hexagonal, some pentagonal, not elongate on surface; depth of prisms approximately equal to their diameter; prisms arranged in concentric rows corresponding to growth lines at the shell margin and also showing a pattern of curved lines radiating from the mid-dorsal region. Base of shell in one plane, outline evenly elliptical, length 1.2 times that of width; maximum shell height anterior to mid-point. Apex smoothly papillate, positioned slightly behind anterior margin at half the shell height, projecting and rendering anterior face slightly concave. Apical area completely transparent, not showing defined structural prisms, clear area extending for approximately 10% of shell length.

**EXTERNAL ANATOMY:** Foot large, thin, oval, nearly transparent, its base outlined by a thickened ridge. Gills six pairs; in mature specimens the first two pairs bilobate, next four with three fleshy fingerlike lobes; located in pallial groove between foot and pallial fold. Pallial fold a well-defined ridge in front of head and extending on sides halfway between foot and shell edge, its position corresponding to pallial line on shell interior. Pallium of thin mantle tissue extending to shell margin outside of pallial fold. Mouth surrounded on front and sides by thick U-shaped anterior lip. Velum a narrow ridge in front of anterior lip, extending laterally on either side, terminating in large triangular flaps that extend into pallial groove. Postoral tentacles located on both ends of a ridge extending laterally between mouth and foot; tentacles prominent and finely branched into at least six branches. Anus posterior to foot, close to mantle margin.

**INTERNAL ANATOMY:** Gut coils four, visible through transparent shell, coils filling space between midpoint and half the distance to posterior edge of shell, final coil extending to anus. Gonad visible through semi-transparent foot sole, divided posteriorly into two broad lobes. Radula sac S-shaped, prominent. Pedal retractor muscles tentatively seven pairs; first pair narrow; second, third, fourth, and fifth relatively broad and long; sixth and seventh pairs broad and short. Gills positioned just outside terminations of retractor muscles on shell, terminations of first pair of muscles without corresponding gills.

**RADULA:** Ribbon of original specimen 1.6 mm long, about 70% of shell length, with 25 rows of fully developed teeth and 17 rows in developmental stages. Each inverted V-shaped row approximately .08 mm wide, containing a rachidian, 3 pairs of

lateral teeth, and 2 pairs of marginal teeth. Rachidian tooth long and slender, four times longer than wide, with a slightly swollen and overhanging tip. Shaft of first lateral tooth of similar diameter, its tip more than twice the width and with a smooth overhanging edge. Second lateral similar to the first, its free end nearly three times width of the shaft. Third lateral smaller, free end about twice its width, positioned below the second lateral. First marginal large, positioned well below the lateral teeth, broadly triangular, basal outline faintly visible, free edge broadly curved and finely fringed; extending past midpoint of ribbon and overlapping with opposite tooth, extending on outside well beyond basal membrane. Second marginal small, free edge smooth, extending beyond edge of basal membrane.

**TYPE MATERIAL:** Holotype, Los Angeles County Museum of Natural History (LACM) 1787, 2 paratypes LACM 1788, 1 paratype National Museum of Natural History (USNM) 758556. Other specimens from the vicinity of the type locality retained by Heintz A. Lowenstam, California Institute of Technology.

**TYPE LOCALITY:** Santa Rosa-Cortes Ridge (32°59.0' N, 119°32.8' W), depth 373–384 m. Collected by Heinz A. Lowenstam and Patrick I. LaFollette, R/V Velero IV sta. 25765, 14 February 1977.

**ADDITIONAL RECORDS:**

1) LACM 19148, radula slide (Figs. 20–22) and shell fragments on SEM stub. One specimen, 95 fm (174 m), between Cortes and Tanner Banks, California (32°41' N, 119°17.3' W), February 1965, collected by Louis Zermatten, ex S. S. Berry Collection, no. 33351. Shell used for SEM analysis by Lowenstam.

2) LACM 19149, rehydrated specimen (Figs. 1–3). One specimen, 125 fm (229 m), Cortes Bank, California (32°25.8' N, 119°13.5' W), April 1965, collected by Zermatten, ex Berry Collection no. 33333. Specimens from these two localities were attached to rocks brought up by hook and line; the hooks had been snagged in bore holes made by pholad bivalves. The dried specimens were removed by John E. Fitch and given to Berry. Coordinates were supplied by Fitch in 1976 after consulting with Zermatten. Both localities were productive fishing sites for the red rock cod *Sebastes miniatus* and were regularly fished by Zermatten.

3) LACM 19150, scanned specimen (Figs. 4–8, 11). Two specimens, 388 m, Santa Rosa-Cortes Ridge, California (32°58.85' N, 119°33.05' W), 1 May 1976, R/V VELERO IV sta. 24904, BLM sta. 569 (Figure 16, bottom photograph). This was the first record of the species at the type locality. The specimens were found in the alcohol-preserved rock and gravel residue by LaFollette. One specimen was used in an attempt at sectioning by Morse and Riser, the other remaining specimen was critical-point dried and examined with SEM.

**DIMENSIONS:**

	length	width	height
LACM 1787 (holotype)	1.94	1.62	0.55
LACM 1788a (paratype)	1.54	1.22	0.41
LACM 1788b (paratype)	0.81	0.66	0.26
USNM 758556 (paratype)	1.94	1.62	0.59
LACM 19148 (radula)	2.16	1.70	0.70
LACM 19149 (rehydrated)	2.28	1.93	0.64
LACM 19150 (scanned)	1.75		

**ETYMOLOGY:** The specific name is an adjective based on the Greek noun *hyalos* (glass), to denote the glassy, transparent nature of the shell.

## DISCUSSION

The discovery of a monoplacophoran living at a depth considered to be the approximate boundary between the continental shelf and the continental slope is remarkable and unanticipated on the basis of previous knowledge of living monoplacophorans.

Prior to the discovery of this species, there had been none of the abyssal species recovered alive, nor had it been possible to obtain specimens without the use of an oceanographic vessel capable of trawling in great depths. Now, 20 years following the announcement that a group of mollusks supposed extinct in the early Paleozoic survives today, it is possible to obtain living specimens and observe them under laboratory conditions.

*Vema hyalina* is small and therefore is not an ideal laboratory animal. Nevertheless, interest in the species should enable future investigators to surmount the inherent difficulties.

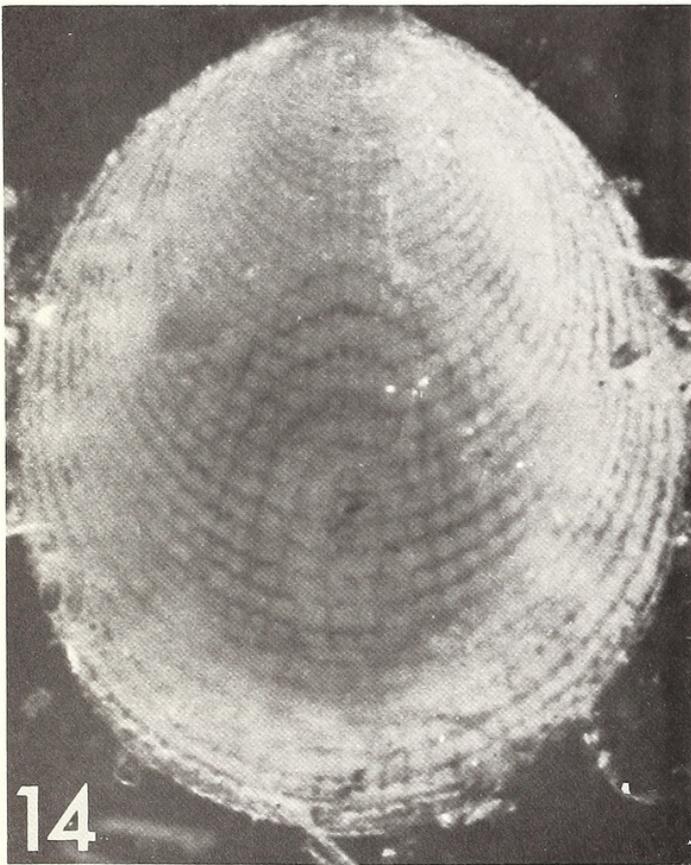
## SIZE AND STRUCTURE

The maximum length known for the species is 2.3 mm. A sufficient number of specimens are known of less than that size, so that it now seems unlikely that larger ones will be found. The sectioned specimen, which measured 1.6 mm in length, showed mature sperm and was therefore considered sexually mature.

Shells of *Vema hyalina* have a mature look; they do not have a disproportionately large apical area as would be the case with immature specimens. The shell structure is so fragile that larger specimens would be unlikely.

*Vema hyalina*, the third species of *Vema* to be described, is the smallest of the genus, being about one-tenth the size of the others. Two small-shelled species of *Neopilina* s. str. are known: *N. veleronis* and *N. oligotropa*. That *N. veleronis* (Figs. 14, 15) was described from mature specimens is reasonably certain from the fact that mature ova were observed in histologic sections, as noted in the original account of the species. *Neopilina oligotropa* was considered likely to be mature because it came from a mid-ocean environment with limited food sources. The other associated fauna was represented by similarly small forms. Size differences of this magnitude within genera are somewhat unusual in mollusks, but are not unknown.

The lack of surface shell sculpture distinguishes *Vema* (*Laevipilina*) *hyalina* from other described neopilinids. The shells of all the other species are reinforced, at least in their young stages, by concentric and radial sculpture, which strengthens without greatly increasing weight or bulk. Although all neopilinid shells are thin and fragile, they apparently provide sufficient support for the moderately large species (*N. galathea* reaches 37 mm in length) living at abyssal depths where the physical conditions are rela-



FIGURES 14, 15. *Neopilina veleronis* Menzies and Layton, length 2.1 mm. Recent photographs of holotype in alcohol. FIGURE 14, dorsal view. FIGURE 15, ventral view. The anterior apex is at the top. Five coils of the intestine are visible through the translucent shell. The shell is now considerably decalcified; the visible nodular structures that remain are the intersections of the radial and concentric sculpture. Photographs by Draper.

tively stable. A shallow water counterpart would be expected to have a stronger shell, one better suited to an environment in which physical stresses are greater. The habitat of *V. hyalina* at the edge of the continental shelf is more variable than that of the deep sea but is far less rigorous than that of intertidal or sublittoral zones. *Vema hyalina* has, however, the most fragile shell of any of the species. Its existence in a somewhat more variable environment seems to be at the cost of a major reduction in size.

Shell structure of *Vema hyalina* follows the basic neopilinid plan, summarized most recently by Meenakshi et al. (1970). Present are the periostracum, prismatic, and nacreous layers. The periostracum is extremely thin. The prismatic layer forms the major component of the shell, with the diameter and depth of the prisms nearly equal. In *Vema ewingi* (Figs. 12, 13) there are hexagonal prisms and also some prisms with a more elongate surface. The depth of the prisms in *V. ewingi* seems to be about twice the diameter at the surface of the regular hexagonal prisms. In *V. ewingi* there are also some prisms with surface area smaller than in the regular hexagons. Small prisms are not found in *V. hyalina*. These differences are regarded as more than specific differences between the two species of *Vema*; the differences are regarded as supraspecifically diagnostic of the subgenera *Vema* and *Laevipilina*.

The internal nacreous layer of neopilinids is very thin (Meenakshi et al. 1970:211) and this is also true for *V. hyalina*. Shells of *V. hyalina* show a pallial line corresponding to the position of the pallial fold of the mantle, inside of which the nacreous layer is thick enough to slightly obscure the pattern of prisms when viewed from within.

The early developmental stages in neopilinid monoplacophorans are largely unknown. Lemche and Wingstrand (1959:16, 64, figs. 34, 49) described and illustrated a coiled protoconch for *Neopilina galathea*. No subsequent author has reported a coiled protoconch in other specimens of *N. galathea* or any other species. Menzies (1968:7, figs. 8a-d) illustrated an unidentified juvenile *Neopilina* shell, showing a bulbous, transparent protoconch with an abrupt transition to the adjacent shell area, which is structured with prisms that are elongate on the surface. As discussed by Menzies, the loss of such a protoconch and subsequent repair to the area would produce a circular scar like that originally reported by Clarke and Menzies (1959: fig. 1d) at the apex of *V. ewingi*. The apical profile of *V. hyalina* (Fig. 10) is similar to that of the unidentified species illustrated by Menzies (1968: fig. 8c), and it is possible that the protoconch is missing and the area sealed over. However, in *V. hyalina* there is no sharp transition line between the apical tip and the area where prismatic structure begins; the prismatic structure becomes apparent, faintly at first, some distance away from the apex. It is to be hoped that future workers will investigate the early development of the species.

## HABITAT AND ECOLOGY

The localities known for *Vema hyalina* are on the western edge of the "southern California continental borderland" (see Emery 1960). Unlike continental shelves in most other areas of the world, the submarine topography is complex, with high and low areas, and ridges and troughs running roughly parallel to the adjacent land mass and its mountain ranges. Some of the topographic highs form islands, others form shallow banks, and the lows form a number of deep, closed basins. Patterns of currents

at the surface and at intermediate depths are complex. The localities known for *V. hyalina* are on the Santa Rosa-Cortes Ridge, a submarine range that includes Santa Rosa Island, Begg Rock, San Nicolas Island, Tanner Bank and Cortes Bank. East of the area is the San Nicolas Basin, to the south are the East and West Cortes Basins and to the west the Tanner Basin. Further to the west is another ridge of lesser elevation and beyond that is the Patton Escarpment, a steep mud slope that drops to abyssal depths.

Bottom temperatures at continental shelf depths in southern California vary but little throughout the year. Joseph L. Reid of the Scripps Institution of Oceanography informs me that at a depth of 400 m at positions near the type locality the estimated range of temperatures is 6.4° to 7.5° C, based on data of the California Cooperative Oceanic Fisheries Investigations, summarized in data reports from Scripps Institution. The shallowest of the original records for the species was 174 m. Temperatures at 200 m in southern California are in the vicinity of 8° to 9° C (Emery 1969: 98). The known bathymetric range for *Vema hyalina* is 174 to 388 m; bottom temperatures correspondingly range from a maximum of 9° to a low of 6.4° C.

It is unlikely that the species will be found at shallower depths, considering the extent to which sampling at shallow depths has been done in southern California. However, the lower limit of the bathymetric range is unknown; we may have sampled only the upper limits of the species' bathymetric range. The scarcity of rocky substrata at greater depths may well be the limiting factor.

There is considerable information available on the bottom conditions at the type locality. When the first two specimens from the type locality were collected on 1 May 1976 the station was sampled with a box core and the bottom was photographed just before the sample was taken (Fig. 16). Bottom conditions were recorded as follows: "Smooth bottom with pebbles and small rocks, sparse shell debris." The photograph shows small rocks somewhat obscured by fine sediment and some moderately large invertebrates, including the seastar *Rathbunaster californicus*, another seastar, the echinoid *Allocentrotus fragilis*, a gorgonian, a massive sponge, and brittle stars. Rocks from the station are of moderately hard shale and were partially encrusted with several different species of bryozoans. The chiton *Hanleyella oldroydi* was common.

The species composition is therefore diverse and includes molluscan predators such as seastars and muricid gastropods (*Boreotrophon* spp.) that bore through shells. *Vema hyalina* must have some methods enabling defense against predators, whether it be a rapid escape response as used by many shallowly occurring limpets, or seclusion in deep crevices. Study of living animals should answer these questions.

The histologic sectioning by Morse and Riser of one of the specimens showed the presence of diatom frustules and sponge spicules in the gut, suggesting that the species browses upon the detrital material that accumulates in crevices. For neopilinids from abyssal depths, Menzies et al. (1959:179) reported that: "A fecal pellet removed from the hindgut of a specimen of *Neopilina (Vema)* showed the presence of diatom frustules, radiolarian skeletons, pelagic foraminiferal tests and innumerable bacteria-size particles as well as sponge spicules. This evidence suggests that *Neopilina* is a mud-ingesting animal or at least an unselective detritus feeder." Thus the feeding habits of all modern neopilinids are probably similar. This is also suggested by the similarity of radular structure among the neopilinids, as discussed in

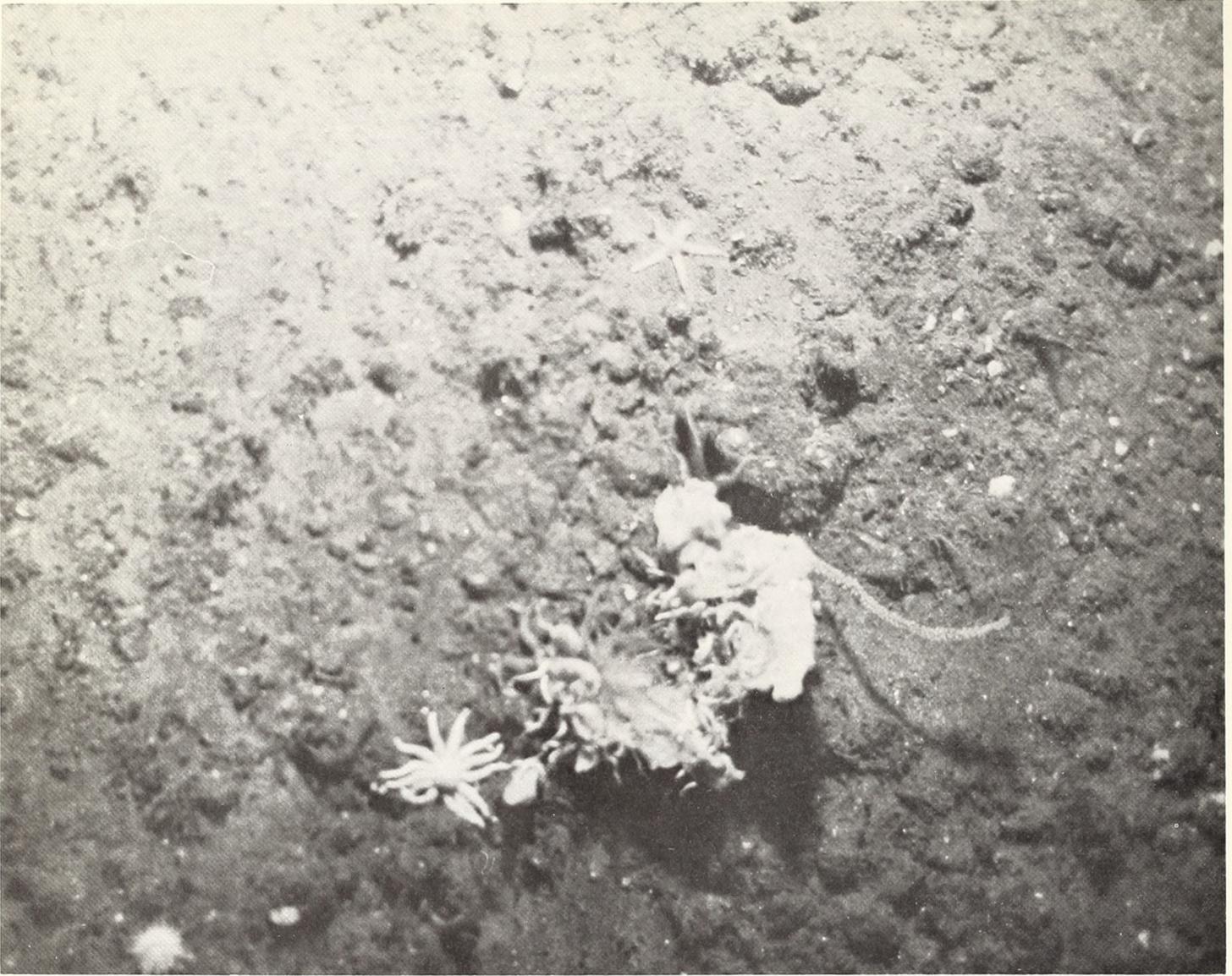


FIGURE 16. Bottom photograph near type locality taken just before sampling with box core. Depth 388 m, Santa Rosa-Cortes Ridge, California ( $32^{\circ} 58.85' N$ ,  $119^{\circ} 33.05' W$ ), 1 May 1976, R/V VELERO IV sta. 24904, BLM sta. 569. Bottom consists of small rocks obscured by sediment. See text for description of the invertebrates pictured. Photograph courtesy of Gilbert F. Jones, BLM project.

detail below. The neopilinid radula has a feathery appearance, and is not sufficiently robust to enable feeding by rasping or piercing of prey organisms.

*Vema hyalina* is the first neopilinid definitely known to be associated with a hard substratum. The first described species of *Neopilina* and *Vema* were assumed to be free living on soft bottoms of ooze on the abyssal sea floor. No rocks or hard-surfaced objects were reported in dredge hauls. Menzies, Ewing, Worzel, and Clarke (1959) included bottom photographs of tracks presumed made by *Neopilina*, but this observation was later questioned by Wolff (1961), who suggested that the tracks were made by a bivalve. No photographs are yet available that actually reveal the life mode of any of the abyssal species of *Neopilina* or *Vema*.

Not until 1972 with the description of *N. oligotropa* was the availability of hard substratum documented along with the taking of a neopilinid. Rokop (1972) reported the presence of manganese nodules in the vicinity of *N. oligotropa* but had no evi-

dence to suggest that the species was attached to the nodules. In 1974 Filatova et al. reported that their unidentified *Neopilina* from the Atlantic sector of the Antarctic came from a bottom of mud with sand and pebbles. They considered it a foregone conclusion that all *Neopilina* require a hard substratum: "The hard substratum to which *Neopilina* adheres (stones, manganese nodules or pebbles) is dispersed in good quantity in the Antarctic region by the action of floating ice."

Doubts about the habitat of the abyssally occurring species of *Neopilina* will persist until some way is found to photograph or observe living specimens. In view of the apparent absence of hard surfaces in the abyssal depths off Costa Rica (type locality of *N. galathea*), in the Peru-Chile Trench (type localities of *V. ewingi*, *V. bacescui*, and *N. bruuni*) and in the Cedros Trench off Baja California, Mexico (type locality of *N. veleronis*), it seems to me that the weight of evidence would associate the abyssal species with soft bottoms.

Yet this remains an anomaly because all other limpets (gastro-

pods of several families) are, without exception, attached to hard surfaces. However, the foot of *Neopilina* is somewhat unusual compared to that of gastropod limpets. Lemche and Wingstrand (1959:31) prefaced their detailed description of the foot of *N. galathea* as follows:

“The circular foot occupies the central parts of the ventral side of the animal. Being strongly contracted in the preserved specimens, its diameter is about half that of the shell. For descriptive purposes the foot is here regarded as the central body wall underlying the large peri-intestinal blood sinus. Its central part forms a circular membranous disc, which, at places, is little more than 0.1 mm thick and therefore somewhat transparent even in the preserved material. The periphery of the foot is developed as a prominent muscular foot margin all round the organ.”

Thus the foot of *Neopilina* is characterized by its small diameter, extremely thin sole, and highly muscularized margin. Lemche (1957) had originally postulated that *N. galathea* lived upside down, but that idea was immediately challenged by Yonge (1957), who considered it possible that the foot could indeed be too weakly muscularized for creeping on a hard surface, but that it could prevent the animal from sinking into the bottom ooze. Clarke and Menzies (1959) reported that the original specimens of *V. ewingi* were coated with mucus on the ventral surface and this was considered to function as an aid to locomotion on soft bottoms.

Perhaps the forthcoming histological work with *V. hyalina* will yield some insight. If the foot of *V. hyalina* proves to be more highly muscularized than that of the other species, it will suggest that the other species are adapted for existence on soft bottoms, whereas *V. hyalina* is better adapted to adhere to rocks.

## RADULAR COMPARISONS

The neopilinid radula has not been discussed since the original treatment by Lemche and Wingstrand (1959:27, fig. 88) of *Neopilina galathea*. Subsequent authors have apparently been hesitant to sacrifice part of their material for whole-mount radular studies. The radula of *V. hyalina* differs considerably from that of *N. galathea*, although the basic plan is similar. In order to make further comparisons I prepared slides from a single specimen of *V. ewingi* in the LACM collection and a paratype of *N. veleronis* from the Hancock Collection. Because of the scarcity of material of all species, I had had to base my observations on single specimens of each, using standard whole mounting methods. Future studies should use SEM with its much finer resolution and depth of field.

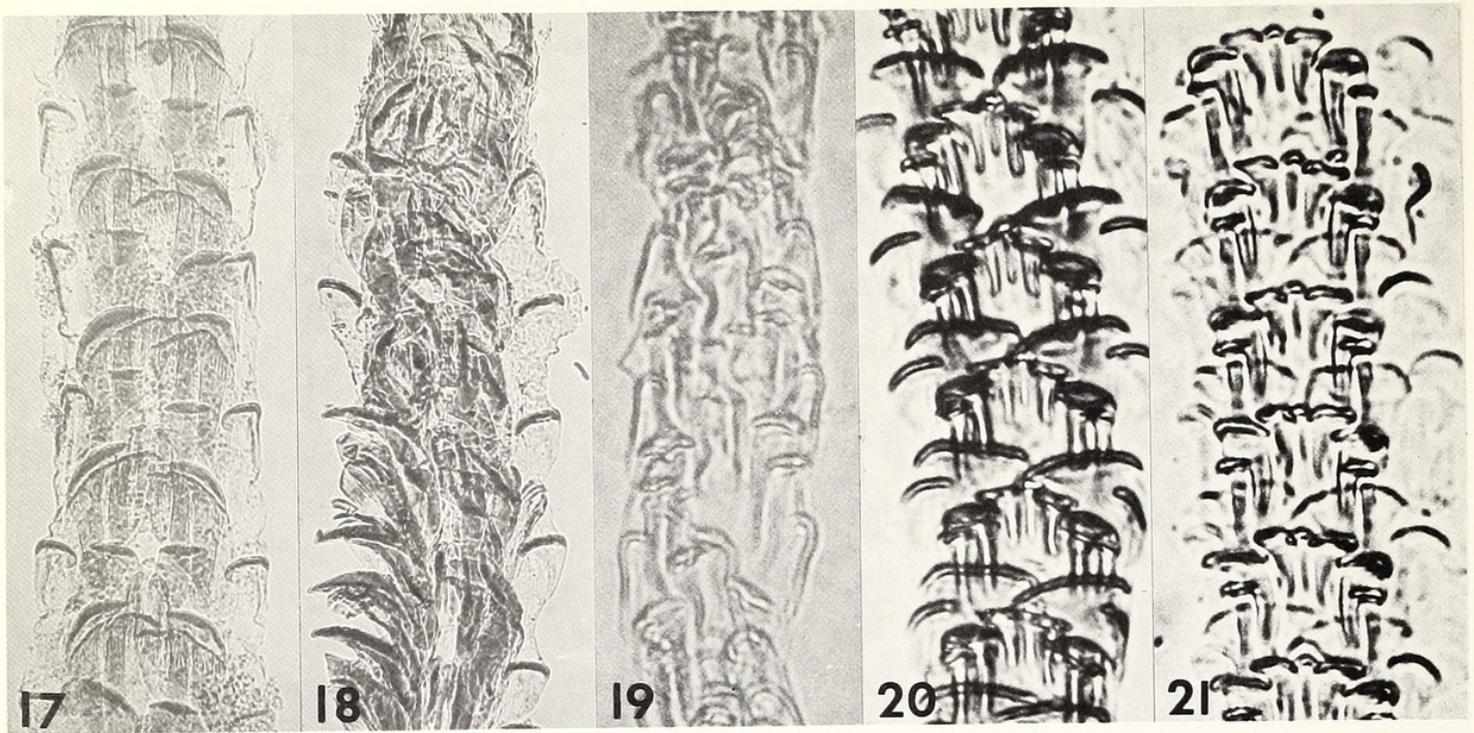
The neopilinid radula consists of a narrow rachidian and five pairs of additional teeth arranged in an inverted V-shaped row across the ribbon. Lemche and Wingstrand called all five pairs lateral teeth but gave no reasons for doing so. I regard the innermost three pairs as lateral teeth and the outer two pairs as marginal teeth for two reasons: (1) the fourth tooth, here called the first marginal, has a fringed edge unlike that of the preceding laterals; (2) the marginals did not stain as darkly as the laterals in my preparations using stained, non-resinous mounting medium, suggesting that the marginals differ from the laterals in thickness and composition.

Figure 25 herein is redrawn from Lemche and Wingstrand's illustration of the radula of *Neopilina galathea*. The rachidian tooth is slender, with no overhanging cusp, resembling the reduced, vestigial central tooth of some Patellidae. The first lateral tooth is only slightly larger, and has a blunt, overhanging edge. The second lateral is longer and broader, with a broad overhanging edge; and the third is similar but placed considerably below the first. The next tooth, here called the first marginal, was described as a “membranous tooth” or “comb tooth,” with its overhanging edge “slit up into some 40 long and curved denticles pointing aborally.” The final tooth, here called the second marginal, is triangular and projects beyond the edge of the ribbon. It has a narrow, overhanging edge.

The radula of *Vema ewingi* (Figs. 17, 18, 23) differs from that of *N. galathea* in minor ways. One portion of the ribbon (Fig. 17) was stained and mounted in non-resinous medium after slight treatment with NaOH in an effort to clean it. The teeth remained aligned as in figure 17. Further cleaning was attempted on another portion of the ribbon, but the teeth folded over in the resulting mount (Fig. 18), suggesting that the teeth are more delicate than those of various gastropod radular ribbons with which I am familiar. However, the latter preparation does show the teeth in side view. In *V. ewingi*, as in *N. galathea*, the first lateral is small, although somewhat larger than the central tooth. The most significant difference is that the second lateral of *V. ewingi* extends well above the position of the first lateral, rather than to approximately the same level. The second and third laterals seem to be longer than those of *N. galathea*, and show an overhanging tip when viewed in the aligned position, whereas in side view they are shown to be long and evenly curved (Fig. 18). It is possible that Lemche and Wingstrand missed the overhanging tip in their drawing of *N. galathea*; the second and third lateral teeth might therefore be larger than they indicated. The fringed first marginal of *V. ewingi* resembles that of *N. galathea* and the second marginal is similar, except that its outer edge is thicker.

I had difficulty interpreting the radula of the only small-sized species of *Neopilina* available, *N. veleronis*, because I was unable to mount in an aligned position any of five separate pieces of the ribbon. Here again, this may indicate that neopilinid radulae are more fragile than gastropod radulae of similar size. However, all of the teeth may be recognized in the portion photographed (Fig. 19), even though the rachidian and the fringed first marginal are not clearly shown. In *N. veleronis* (Fig. 24) the first lateral is more prominent than in either *N. galathea* or *V. ewingi*, and extends slightly above the position of the rachidian. In addition, the fringed first marginal is broader than in either *N. galathea* or *V. ewingi*. These differences place the radula of *N. veleronis* closer to that of *V. hyalina* than to that of the two relatively large-sized neopilinids. However, the second marginal is more than twice as long as that in any of the other species. *Neopilina veleronis* is unique among the species studied in the length of the second marginal.

A detailed description of the radula of *V. hyalina* is included in the species description above. The whole-mounted ribbon of the original specimen is shown in figure 20, focused on the shaft of the lateral teeth, and in figure 21, focused on the fringed edge of the first marginal. The teeth are drawn in figure 22. After the drawings were finished I received an SEM view of the radula in place within the mouth cavity (Fig. 8). The radula differs from that of both *N. galathea* and *V. ewingi* in having the first lateral fully developed and about equal in size to the second lateral,



FIGURES 17–21. Neopilinid radular ribbons, magnifications adjusted to show a similar number of teeth rows. FIGURE 17, *Vema (Vema) ewingi*, intact ribbon with teeth aligned (LACM 65–11, 6200 m, 110 mi. W of Callao, Peru, R/V ANTON BRUUN, 24 November 1965). FIGURE 18, *Vema (Vema) ewingi*, another portion of same ribbon with lateral teeth turned to the side. FIGURE 19, *Neopilina veleronis*, intact ribbon of paratype, teeth not aligned (AHF 603, 2730–2769 m, 30 mi. W of Natividad Island, Baja California, Mexico). FIGURE 20, *Vema (Laevipilina) hyalina* new species, intact ribbon with teeth aligned, focused on shafts of lateral teeth (LACM 19148). FIGURE 21, *Vema (Laevipilina) hyalina*, same ribbon, focused on fringe of first marginal teeth.

instead of the highly reduced condition in these two species. Although the first lateral of *N. veleronis* is somewhat larger than it is in the other two species, that of *V. hyalina* is still the larger. The fringed first marginal of *V. hyalina* is much broader than in *N. veleronis*. Only in *V. hyalina* is the fringed tooth so broad that it overlaps the opposite member in the central part of the ribbon. The second and third laterals of *V. hyalina* are not significantly different from those of the other three species, whereas the second marginal is similar to those of *N. galathea* and *V. ewingi*, but not the exceptionally long second marginal of *N. veleronis*.

To summarize the radular differences noted among the four species: *Vema hyalina* exhibits major differences in two of the five teeth compared to the two rather similar species *N. galathea* and *V. ewingi*, whereas the condition of these two teeth in *N. veleronis* is intermediate between these two species and *V. hyalina*. The radula of *N. veleronis* is unique in the extreme elongation of the second marginal.

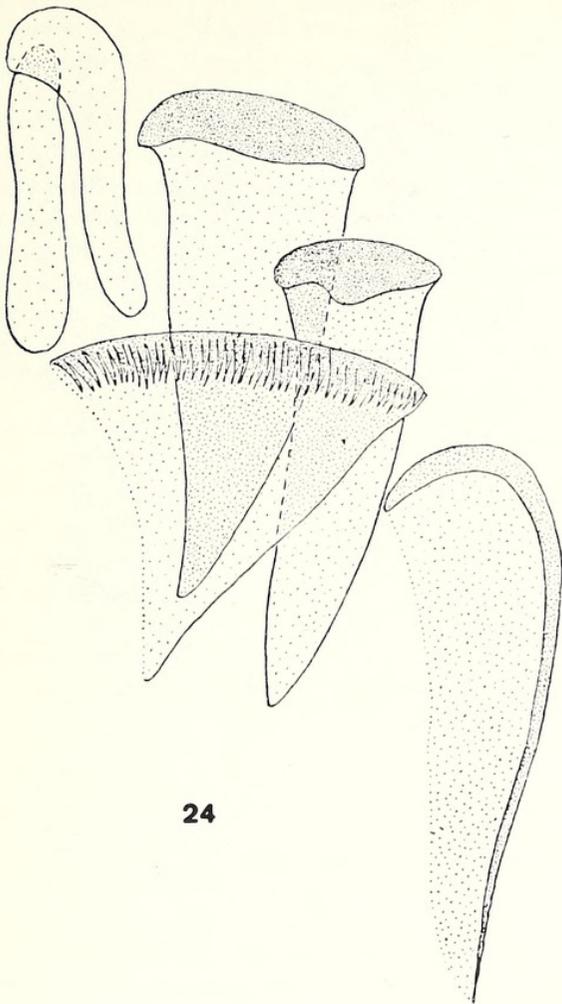
The radular differences noted in the four species do not correlate with the existing generic division based on number of gill pairs, five in *Neopilina* and six in *Vema*. The only correlation is in size. Both large-sized species have similar teeth and the two

small-sized species have similar teeth. Radular differences among the species examined are quantitative rather than qualitative, supporting placement of the four species in the same family. A study of the radulae of the other three living species of neopilinids should reveal further specific differences.

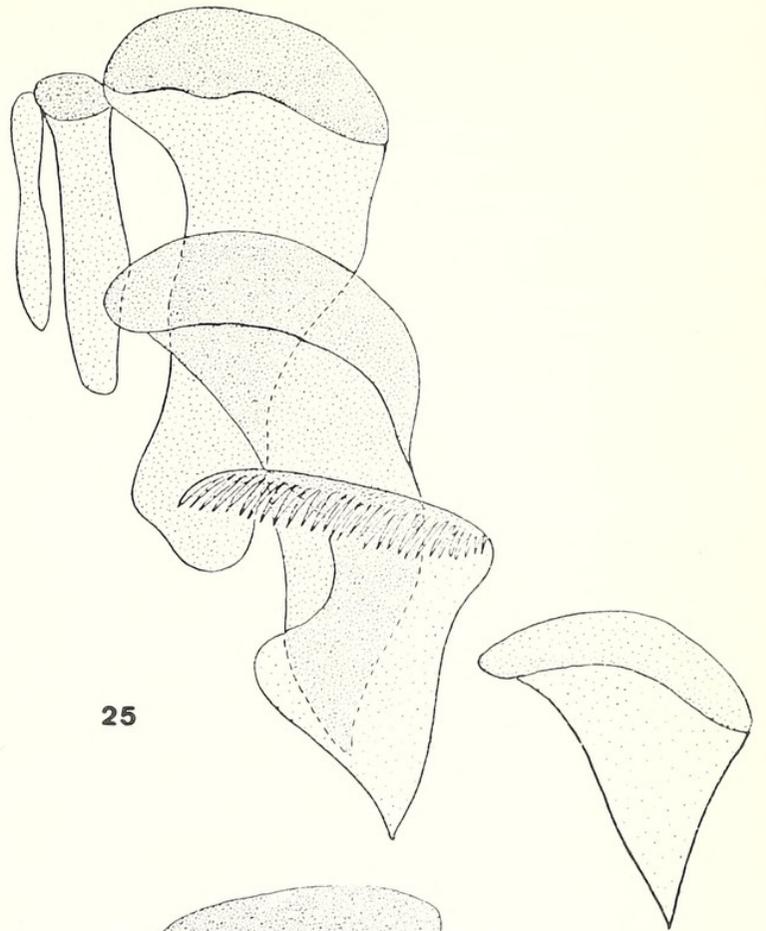
The radula of neopilinid monoplacophorans is very similar to that of chitons and patellacean limpets having the docoglossate radula. In the three groups the radula has in common: a reduced or absent rachidian; strong, hook-shaped lateral teeth; and few, weakly developed marginal teeth. Lemche and Wingstrand (1959) found major similarities in the radular supportive mechanism in *Neopilina* and chitons. Golikov and Starobogatov (1975) discussed the similarities in form and function of the docoglossate radula with that of chitons and neopilinids.

The docoglossate radula has long been known to function in a way that differs from that of other gastropods. Fretter and Graham (1962:200) gave a detailed comparison of radular function in the two kinds of radulas. In the docoglossate radula there is no longitudinal bending; the entire ribbon works as a rasp with numerous rows functioning at once. In the rhipidoglossate and other non-docoglossate radulae, rows of teeth bend longitudinally

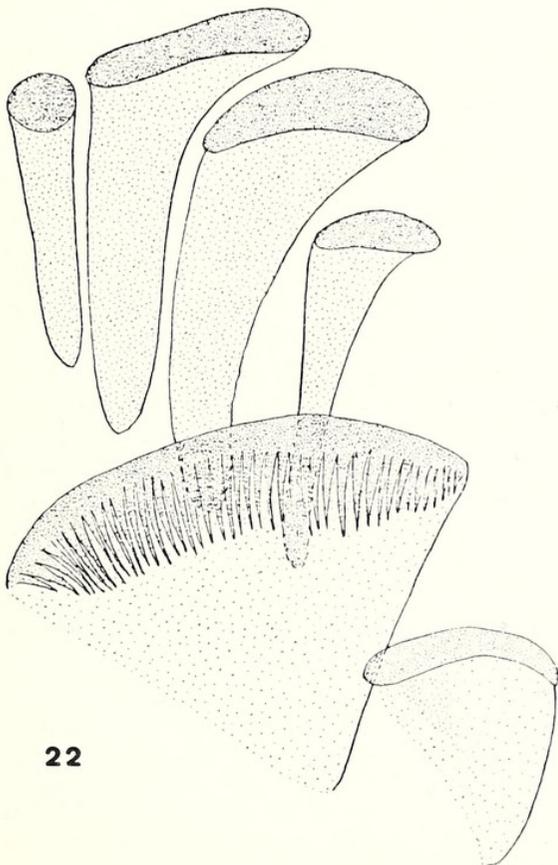
FIGURES 22–25. Radular dentition of neopilinids, drawn from slides photographed in figures 17–21. FIGURE 22, *Vema (Laevipilina) hyalina* new species. FIGURE 23, *V. (Vema) ewingi*. FIGURE 24, *Neopilina veleronis*. FIGURE 25, *N. galathea*, after Lemche and Wingstrand, 1959. Teeth from left to right are the rachidian; first, second, and third laterals; fringed first marginal; and the outermost, second marginal. Drawings by Mary Butler.



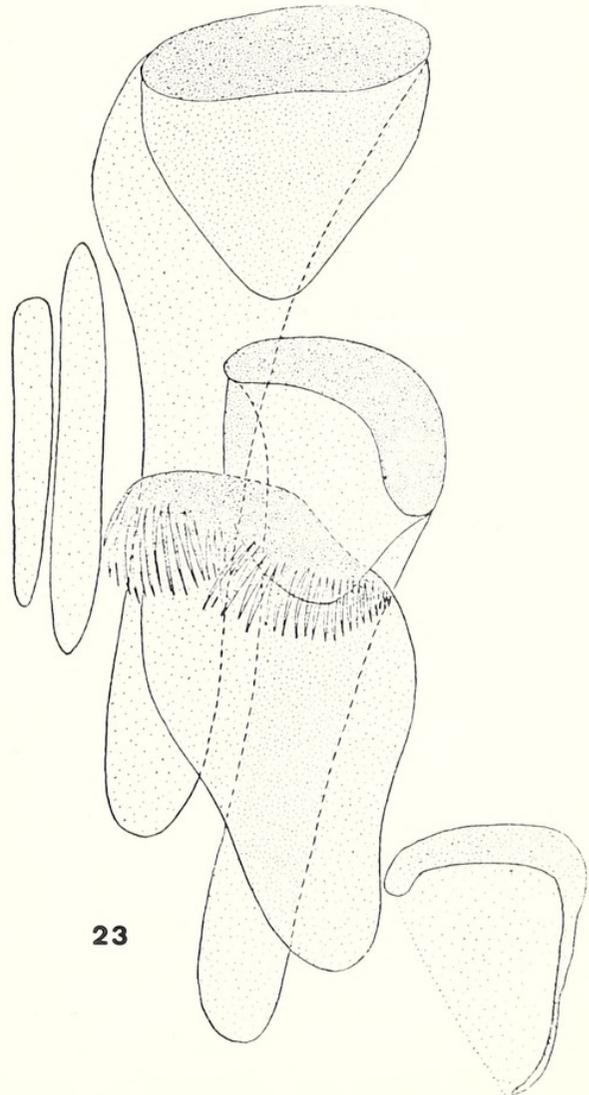
24



25



22



23

and the teeth are most effective at the 'bending plane.'

Golikov and Starobogatov consider the rasp type of radula — for which a more technical term has not been proposed — as the most archaic in the Mollusca. Most other authors, such as Fretter and Graham (1962), consider the rhipidoglossate radula as the most primitive and the docoglossate radula derived from it in an as yet unexplained way. The matter remains controversial because there is no apparent affinity between these two kinds of gastropod radulae.

A comblike fringe, similar to that on the neopilinid first marginal tooth, occurs on the marginal teeth of some genera of the docoglossan limpet family Lepetidae. In the Neopilinidae the fringe is found only on the first marginal tooth, but in the Lepetidae the very similar appearing fringe is found on both pairs of marginal teeth. The origin and significance of these comblike teeth remains to be explained. Could the fringe be a clue to a more direct affinity between the Monoplacophora and the Docoglossa?

The Paleozoic monoplacophorans are found in shallow water deposits. They were probably grazing animals like modern patellean limpets and chitons. The large and robust radular teeth in modern limpets and chitons are opaque and mineralized (Lowenstam 1967, 1971). The neopilinid radula is probably less robust than that of its fossil predecessors, but is probably similar to what was present in the extinct families of Monoplacophora. As in the chitons and docoglossan limpets, the neopilinid radula is large in proportion to body size. Its mineral content should be investigated.

The radula of the Polyplacophora, the chitons, is not especially diverse from family to family. I would expect Monoplacophora as a whole, to have had a diversity similar to that of the Polyplacophora, in which the level of organization is primitive, the family distinctions are not profound, and the species are relatively few in number.

## ORIGINS

When the discovery of *Neopilina galathea* was announced, who could have predicted that it represented but one of a small number of species of this relict group? Can it be that the *Laevipilina* branch in the Neopilinidae is represented elsewhere in the world? The possibility should be considered by those who have opportunity to dredge rocks at the edge of the continental shelf. The offshore fauna of southern California is one of the most often sampled and best known in the world. This discovery comes at a time when there are rather few new species being discovered in the area. Experienced collectors have no doubt had it on hand before, but have missed it. Many years may pass before the faunas of rocky bottoms on the outer continental shelves will be sufficiently known to answer the question.

Unfortunately, a fossil record of the abyssal fauna is not accessible. Many families of modern mollusks seem to have centers of origin in which extensive speciation has taken place. One might consider the eastern Pacific as the place of origin of the neopilinid stock, since most of the species and records are from that region. This might seem to be a foregone conclusion were it not for those species described from single records in the Indian Ocean and the mid-Pacific. The most likely explanation seems to be that accepted by most authors (e.g. Parker 1962) that the neo-

pilinid line is a monoplacophoran offshoot that happened to invade the deep sea and has existed there in the absence of severe competition and predation since the Paleozoic. The shallow occurrence of *Vema* (*Laevipilina*) would thereby represent a reinvasion of the shallow water habitat from an abyssal stock.

Yet there is now an alternative theory: there is a possibility that the monoplacophorans have continued to survive at intermediate depths since the Paleozoic and that the deep-sea invasion is of relatively recent occurrence. The discovery of other monoplacophorans from intermediate depths would support this idea. However, the lack of eyes in *Vema* (*Laevipilina*) *hyalina*, a species that lives at a depth where considerable light is available, suggests that it is a derivative from forms existing in deep, lightless environments.

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Photographs are largely the work of Bertram C. Draper, Museum Associate, with several others by Armando Solis, Museum Photographer. Radular slides were prepared and photographed by Jo-Carol Ramsaran, Museum Volunteer, and drawn by Mary Butler, Museum Illustrator.

NOTES ADDED IN PROOF: 1) An account of the role of N.H. Odhner in introducing the name Monoplacophora was provided by that author (Odhner 1961). 2) In a paper just received Lowenstam (1978) has described the behavior and illustrated a living specimen of *Vema hyalina*, which he referred to as "McLean's *Vema* sp." 3) Recent efforts to find rocky bottom at the two positions mentioned for the original specimens from the Berry Collection have not been successful.

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