

The Archaeogastropod Family Addisoniidae Dall, 1882: Life Habit and Review of Species

by

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Abstract. The family Addisoniidae is reported for the first time in the eastern Pacific with the description of *Addisonia brophyi* spec. nov., which lives within spent egg cases of two species of cat sharks (family Scyliorhinidae). The thin shell and the characteristic radular morphology are adaptations to this habitat. Illustrations of the gill structure, hermaphroditic gonad, and the open seminal groove are given. The other two species in the family are reviewed: *A. lateralis* (Requien, 1848), from the Mediterranean and eastern Atlantic, and *A. paradoxa* Dall, 1882, type species of the genus, from the western Atlantic.

INTRODUCTION

Addisonia in the eastern Pacific was first collected off southern California by Pat Brophy, of Pacific Bio-Marine Laboratories, who obtained it on four separate occasions during the summer months of 1968 and 1972 while salvaging biological specimens as a guest on trawling vessels. Based on this material, HICKMAN (1983) included a radular illustration of the new species in her discussion of radular morphology in deep-sea limpets. The new species *A. brophyi* is validated here.

Prior to the discovery of the new species, *Addisonia* had been considered to include only the western Atlantic type species, *A. paradoxa*, and the European species, *A. lateralis*. These two taxa have been variously recognized, synonymized, or related as "varieties" by different authors. Here they are redefined and recognized as distinct.

Notes on external anatomy in *Addisonia paradoxa* were given by DALL (1882a, 1889a), VERRILL (1884), and THIELE (1908), the latter under the name *A. lateralis*. I include here notes on anatomy in the new species and discuss the significance of the association of the genus with spent egg cases of sharks.

MATERIALS

I have been able to locate shells of the east Atlantic *Addisonia lateralis* in the collections of the Paris Museum and the Brussels Museum. Shells with dried animals of the western Atlantic *A. paradoxa* were located in the U.S. National Museum of Natural History. Preserved specimens of *A. brophyi* have been used for radular prepara-

tions and histologic sectioning. Light microscope preparations of radulae of *A. brophyi* and *A. paradoxa* were made; preparations of the same two species were examined by C. S. Hickman, using scanning electron microscopy (SEM). Transverse and sagittal sections of *A. brophyi* were made, but the initial fixation in alcohol was not adequate for histological work and the sections of the internal organs were shattered. However, the sections suffice to demonstrate the condition of the gill and the hermaphroditic gonad. The shark egg cases were identified by comparison with illustrations of COX (1963).

Abbreviations for museum collections cited here are: CAS, California Academy of Sciences, San Francisco; IRSNB, Institut Royal des Sciences Naturelles de Belgique; LACM, Los Angeles County Museum of Natural History, Los Angeles; MNHNP, Museum of National d'Histoire Naturelle, Paris; USNM, United States National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Order ARCHAEOGASTROPODA

Suborder LEPTELLINA

Superfamily LEPETELLACEA

Families: Addisoniidae Dall, 1882; Bathypeltidae Moskalev, 1971; Bathyphytophilidae Moskalev, 1978; Bathysciadiidae Dautzenberg & Fischer, 1900; Cocculinellidae Moskalev, 1971; Cocculinidae Dall, 1882; Lepetellidae Dall, 1882; Pseudococculinidae Hickman, 1983. Each family has a characteristic radula.

The Lepetellacea (sole superfamily here recognized in the suborder Lepetellina) occupy a position intermediate between that of archaeogastropods and mesogastropods. Gill characters suggest neither archaeogastropods nor mesogastropods, as the gill (if present) is secondary. As in archaeogastropods, the radula is rhipidoglossate (or degeneratively rhipidoglossate). As in lower mesogastropods, the heart is monotocardian and the right kidney is lacking. However, a true pallial gonoduct, which replaces the right kidney of archaeogastropods in the lower mesogastropods, has not developed. All members are simultaneously hermaphroditic and have a seminal receptacle; in some, the right tentacle bears a sperm groove and functions in copulation.

Anatomy in these families has been treated only by THIELE (1903, 1908), who illustrated serial sections of three genera, reporting first on *Cocculina* (1903) and subsequently on *Lepetella* and *Bathysciadium* (1908). External features of *Addisonia* were compared in the second paper. He concluded (THIELE, 1908) that these four genera are closely related anatomically, despite major differences in radular configuration.

Two families, the Cocculinidae and Pseudococculinidae, have rhipidoglossate radulae in which lateral teeth are generally like those of adjacent laterals in size and shape. The remaining families have lateral teeth that are not similar to adjacent laterals and, except for the Bathyphytophilidae, lack marginals. THIELE (1929) interpreted these radulae to be degeneratively rhipidoglossate. Support for this interpretation is provided by the recently named Bathyphytophilidae, a transitional group in which there are 6–20 pairs of marginal teeth and non-repeating “lateral” elements that most closely resemble those of the Lepetellidae.

Systematic papers treating these families are those of THIELE (1909), MOSKALEV (1971, 1973, 1976, 1978), WARÉN (1972), and MARSHALL (1983). HICKMAN (1983) gave SEM radular illustrations for many of these groups; only the radula of the Bathyphytophilidae remains to be illustrated with SEM.

MOSKALEV (1971, 1973, 1976, 1978), in papers published in Russian (translations available, see Acknowledgments), has proposed three of these families. His family definitions are accepted because each family has radular characters that are different enough to warrant recognition. However, he inflated the classification to contain four superfamilies. I do not follow Moskalev in this action because he did not offer sufficient justifications and he made no original contributions of his own to an understanding of anatomy. Moreover, his classification (see translation of 1978, summary section) did not properly take Thiele's work into account. He did not cite THIELE'S (1903) paper on the Cocculinidae, claiming that anatomy in that family had not been investigated; and, although he cited THIELE (1908), he followed PELSENER (1900) in relating the Bathysciadiidae to the docoglossate patella-ceans, despite the fact that THIELE (1908) amply dem-

onstrated that Pelseener's conclusions were wrong. Thus, MOSKALEV (1978) erroneously placed the families Bathysciadiidae and Bathypeltidae in the order Docoglossa.

Until major anatomical differences among the families under discussion can be demonstrated, I accept THIELE'S (1908) conclusion that all members are closely related anatomically, and following MARSHALL (1983), recognize only the superfamily Lepetellacea (which has priority over Cocculinacea). I do not relate the suborder Lepetellina to other archaeogastropods or to lower mesogastropods, but arbitrarily retain the suborder in the order Archaeogastropoda on the strength of the rhipidoglossate radula.

Family ADDISONIIDAE Dall, 1882

Addisonia Dall, 1882

Addisonia DALL, 1882a:404. Type species (original designation): *A. paradoxa* Dall, 1882. Recent, northwestern Atlantic.

The single genus *Addisonia*, with three species, comprises the family Addisoniidae. Radular characters are unique. Although BOSS (1982), following THIELE (1908), placed *Addisonia* in the Lepetellidae, genera in that family differ in having a symmetrical shell and an entirely different radula.

Dall's generic name honored his contemporary, Addison E. Verrill.

Shell (Figures 1–6): Cap-shaped, thin, non-nacreous; periostracum thin, smooth. Margin sharp and fragile, ends slightly raised relative to sides. Outline asymmetrical, anterior either broader or narrower than posterior. Apex of young shells (to 6 mm in length) near mid-dorsal line, $\frac{1}{4}$ shell length from posterior margin; apex in larger shells offset toward left, curved backward and downward. Protoconch deciduous, apical tip sealed over. Radial sculpture of fine striae; concentric sculpture of microscopic growth lines. Muscle scar horseshoe-shaped, narrow throughout, not broken into discrete bundles, anterior terminations curved inward and directed posteriorly; termination of right side with broader inward curve than that of left. A narrow pallial line extends in broad arch from anterior limitation of muscle scar.

The shell edge is so thin that all specimens tend to have broken and chipped margins.

Radula (based on *Addisonia brophyi* and *A. paradoxa*, Figures 15, 16): The following description is based upon the SEM illustration of HICKMAN (1983), one of which is reproduced here (Figure 15), and partially paraphrases her description: Rachidian subcylindrical, uncusped, fitting with rachidian elements anterior and posterior to it to form continuous, jointed cylindrical column along central longitudinal axis; rachidian flanked by two pairs of uncusped, solid rhomboidal plates in a V-shaped alignment; these plates flanked by two pairs of narrow sigmoid elements; outermost 3 plates complexly interlocked; first

of these triangular and bicuspid; second large and bicuspid, overlapping the first; third a narrow element separating the large bicuspid plate from the corresponding plate anterior and posterior to it.

Hickman's description of this radula was the first clear understanding of it, as earlier interpretations of light microscope preparations (see Figure 16) were incorrect.

As Hickman noted, this radula is neither rhipidoglossate nor docoglossate, nor has it any features to suggest relationships with other families in the superfamily with which it shares anatomical characters. The other families in the superfamily also have odd and essentially unique radulae.

Addisonia brophyi and *A. paradoxa* differ in the morphology of the rachidian element as discussed in the species accounts; no intact specimens of *A. lateralis* were available.

Anatomy (based on Thiele's description of *Addisonia paradoxa* and my examination of *A. brophyi*, Figures 7–10, 12): Foot oval, thin at center, where it reveals darker digestive gland tissue within; edge of foot thin, projecting; epipodial processes lacking. Mantle edge simple, thickened. Secondary gill in right mantle groove, extending on right side adjacent to right cephalic tentacle to adjacent to foot tip; leaflets produced by folding of mantle skirt, each leaflet with a thin extension at tip (Figure 10). Eyes lacking, snout expanded at tip, mouth opening triangular, lacking oral lappets. Cephalic tentacles bent ventralward, nearly equal in size; right tentacle with sperm groove on lateral side; sperm groove leading to right tentacle clearly visible on neck and outer body wall (Figures 9, 17).

According to THIELE's description of *Addisonia paradoxa* (1908): "The dorsal side contains the gonad in the center, the duct of which runs anteriorly and on the right. Next to it lies the hindgut, while more to the left the heart is visible." These organs are readily apparent on the intact specimen illustrated here (Figure 8), in which the developing eggs are visible in the central gonad. The gonad is simultaneously hermaphroditic; male and female cells are closely associated, as can be seen in sections (Figure 12).

THIELE (1908) observed a swelling at the base of the right tentacle, which reminded him of the sperm groove of the copulatory organ of *Bathysciadium*. Here I confirm that there is a sperm groove in *Addisonia*, visible in illustrations of two species—on the preserved specimen *A. brophyi* (Figure 9), and a dried specimen of *A. paradoxa* (Figure 17). This had been missed by DALL (1882a, 1889a) and VERRILL (1884). VERRILL's statement (1884) that males and females differ in appearance is incorrect, as the species is hermaphroditic.

DALL's drawing of the animal of *Addisonia paradoxa* (1889a, b), which has been the principal cited figure—copied by PILSBRY (1890) and ABBOTT (1974)—is incorrect in showing a ventral axis connecting the gill filaments. The first figure of the species, that of VERRILL (1884), correctly showed the gill, but this figure has been ignored by most subsequent authors.

The pronounced asymmetry of the mature shell is a result of asymmetry in the animal: the enormous secondary gill on the right side requires extra space, forcing this side of the shell to become inflated and the shell apex to be diverted to the left.

Three broadly allopatric species are known in the genus *Addisonia*. Specific characters include relative size and differences in proportions of the rachidian element in two of the three species. However, the radula of one species is not available. These differences are admittedly few. Unfortunately, sufficient specimens are not available to allow rigorous study. It may well be that the differences among the three are purely quantitative, but in the absence of sympatry the question is moot. A pragmatic approach is taken here in accepting three species, although it is recognized that equal justification could be offered for the recognition of three subspecies of a single, widely distributed species.

Addisonia paradoxa Dall, 1882

(Figures 1, 2, 16, 17)

Addisonia paradoxa DALL, 1882a:405; 1882b:737; VERRILL, 1882:533; VERRILL, 1884:256, pl. 29, figs. 10, 11, 11a, 11b; DALL, 1889b:158, pl. 25, figs. 1a–e, pl. 44, figs. 10, 11–11b, pl. 63, fig. 100; THIELE, 1909:25, pl. 4, figs. 20–23; ABBOTT, 1974:35, fig. 206 [copy Dall figs.]; HICKMAN, 1983:81, fig. 10 [radula].

Addisonia lateralis var. *paradoxa*: DALL, 1889a:344, pl. 25, figs. 1a–e; PILSBRY, 1890:139, pl. 25, figs. 1–3 [copy Dall figs.].

Addisonia lateralis paradoxa: JOHNSON, 1934:66.

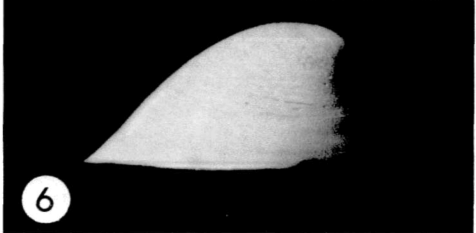
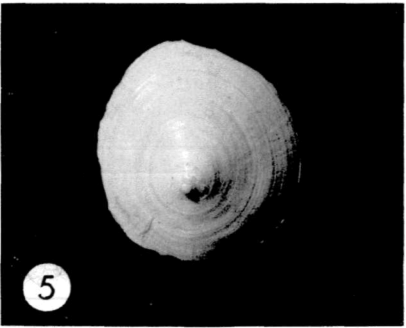
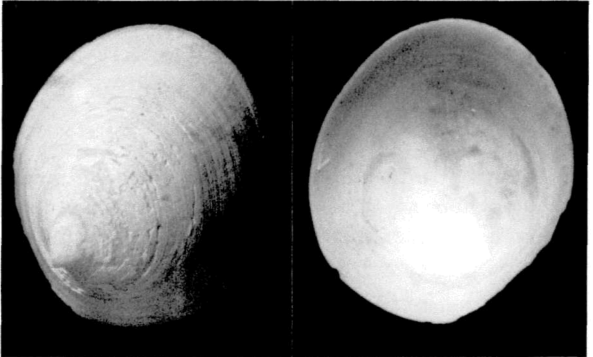
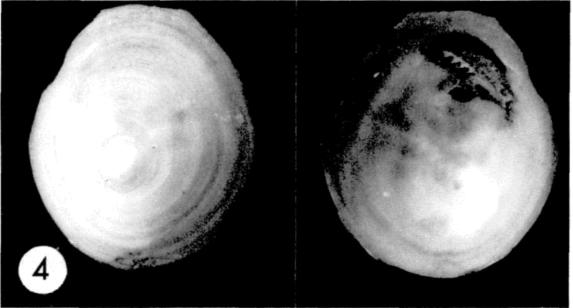
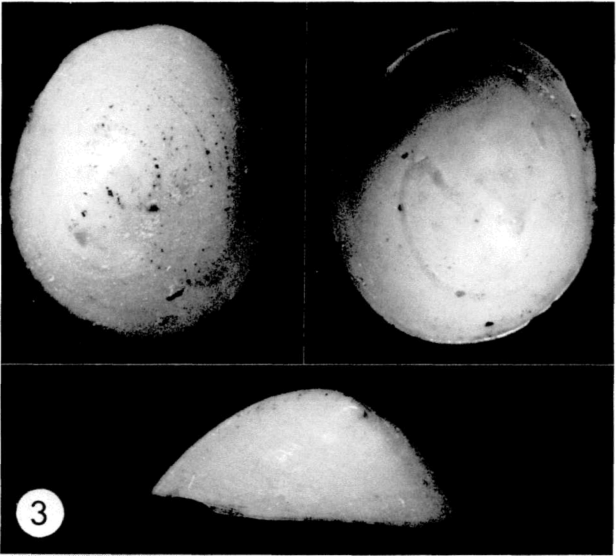
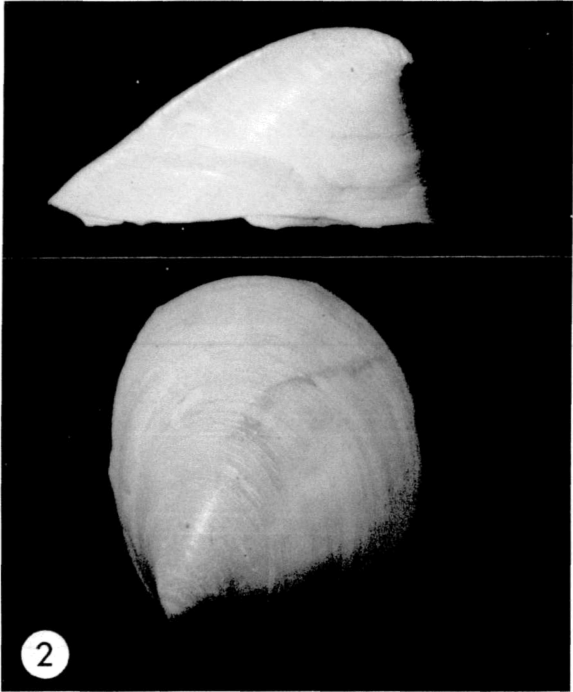
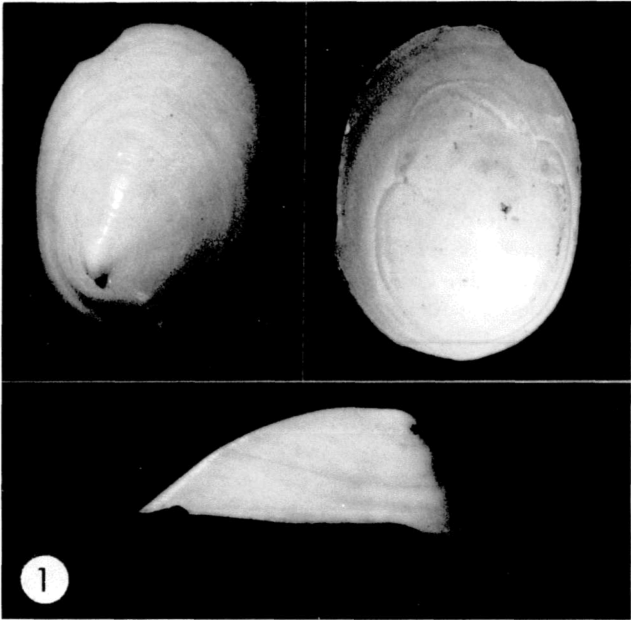
Diagnosis: Differing from both *Addisonia lateralis* and *A. brophyi* in its much larger size and having only a trace of the interior radial sculpture that is so pronounced in *A. lateralis*. The subcylindrical rachidian element differs from that of *A. brophyi* in having convex rather than parallel sides (compare Figures 15 and 16).

Dimensions: Lectotype: length 10.8, width 8.0, height 4.0 (Figure 1). Largest specimen: length 20.3, width 16.0, height 10.5 mm (Figure 2, USNM 50404, off North Carolina).

Type material: Original specimens of *Addisonia paradoxa* were collected in 1881 from three U.S. Fish Commission stations (923, 940, 950) off Martha's Vineyard Island, Massachusetts, 126–238 m. A lectotype, USNM 43741 (Figure 1), from station 950 is here designated; two paralectotypes USNM 333747, same station; 3 paralectotypes USNM 33748, sta. 923. The material from sta. 940 has not been located.

Distribution: Grand Banks, Nova Scotia, to Kingston, Jamaica, in depths of 119–1170 m.

Material examined: All USNM: USNM 226271, "Grand Banks, USFC"; 7 lots off Martha's Vineyard; 1 lot off St. Augustine, Florida; 3 lots off Virginia and North Caro-



lina; 3 lots off Florida Keys; 1 lot (USNM 811797) off Kingston, Jamaica (R/V *Oregon* sta. 3560). Depth range 115–878 m.

USNM 43743 (Martha's Vineyard) contained two dried animals, one of which is illustrated (Figure 17), the other was prepared for the radular mount (Figure 16). USNM 47345 (Martha's Vineyard) has an original label that reads "from skate egg." This was overlooked in all the published accounts, but confirms the association of this species with elasmobranch egg cases.

Remarks: When first proposed, DALL believed *Addisonia* to be monotypic; however, he shortly thereafter (1882b: 737) allocated *Gadina excentrica* Tiberi, 1857, to the genus. A year later JEFFREYS (1883) placed Dall's species in the synonymy of *A. excentrica* (Tiberi). DALL subsequently wavered; in (1889b) he recognized his own species but in (1889a) he considered it a "variety" of the European species. DALL (1889a) noted that the "figures, descriptions, and specimens I have seen of European origin all indicated the shell as very much smaller than our American specimens . . ." Recent authors (ABBOTT, 1974; HICKMAN, 1983) have used the name *A. paradoxa*, without mentioning the unresolved taxonomic question. I consider the size difference to be sufficiently important to warrant the recognition of separate species.

Addisonia lateralis (Requien, 1848)

(Figures 3, 4)

- Gadina lateralis* REQUIEN, 1848:39; PETIT, 1869:92, 264.
Addisonia lateralis: DAUTZENBERG, 1886:1; PILSBRY, 1890: 139, pl. 25, figs. 26, 27 [copy Tiberi figs.]; THIELE, 1909:25, pl. 4, figs. 18, 19 [copy Tiberi figs.]; HUBENDICK, 1946:77; NORDSIECK, 1968:35, fig. 21.10.
Gadina excentrica TIBERI, 1857:27, pl. 2, fig. 6; PETIT, 1869: 92, 264; WEINKAUFF, 1870:90; LOCARD, 1898:93.
Addisonia excentrica: DALL, 1882b:737; WATSON, 1886:32.
Addisonia excentrica: JEFFREYS, 1883:673 [emendation of *excentrica* Tiberi].

Diagnosis: Differing from both *Addisonia paradoxa* and *A. brophyi* in having a less deflected apex; smaller than *A. paradoxa*.

Dimensions: Length 10.5, width 8.9, height 4.2 mm (Figure 3, holotype *Addisonia excentrica*).

Type material: *Gadina lateralis* Requien, 1848, was never figured, and, according to DANCE (1966:299), the Requien Collection was neglected and abandoned. Philippe Bouchet of the Paris Museum reports (personal communication) that he had searched unsuccessfully for Requien's type material in Avignon and Toulouse. The description was included in Requien's catalogue of mollusks of the French Mediterranean island Corsica. Although short, the description is adequate and subsequent authors have accepted the synonymy.

A specimen marked "type" of the junior synonym *Gadina excentrica* Tiberi, 1857, has been examined (Figure 3). The published locality is the Italian Mediterranean island Sardinia, from the "coral fishery." PILSBRY (1890) copied the illustrations and translated the Latin description to English. The above cited measurements are less than the published dimensions of 17 × 14 × 11 mm.

Distribution: Mediterranean Sea: Sicily to Corsica; Eastern Atlantic: Bay of Biscay to Morocco.

Material examined: MNHNP: Single specimens of LOCARD (1898:93): sta. 26 off Portugal; sta. 35, off Atlantic Morocco (Figure 4); 5 specimens from Atlantic Morocco (33°59'N, 07°50'W), *N. O. Vanneau* sta. 37, 1923–1929. IRSNB: 4 lots: Sciacca, Sicily; South of Sicily (*Princesse Alice*); Ile Yeu, Bay of Biscay (cited by Dautzenberg, 1886); *N. O. Vanneau* sta. 46, Atlantic Morocco.

Remarks: DAUTZENBERG (1886) accepted JEFFREYS' (1883) conclusion that Dall's genus *Addisonia* was represented in the eastern Atlantic, but used the oldest name, *Gadina lateralis* Requien, 1848, for the Atlantic species.

None of the published accounts has mentioned an association with elasmobranch egg cases. According to P. Bouchet, there are no recent collecting records of *Addisonia lateralis* in European waters and no accounts in recent literature. The synonymy given by DAUTZENBERG (1886) includes several references not mentioned here.

The radula of this species has not been illustrated.

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Explanation of Figures 1 to 6

Exterior, interior (anterior at top), and lateral (left side) views of shells of *Addisonia* species. Shell edges of all specimens are chipped; shell apex is posterior and deflected to left in mature specimens (Figures 1 to 3, 6), posterior and near mid-dorsal line in immature specimens (Figures 4, 5). Interior views show the narrow muscle scar and anterior pallial line. Dimensions are given as length, width, and height.

Figure 1. *A. paradoxa* Dall, lectotype, USNM 43741. USFC sta. 950, 130 m off Martha's Vineyard Island, Massachusetts. 10.8 × 8.0 × 4.0 mm.

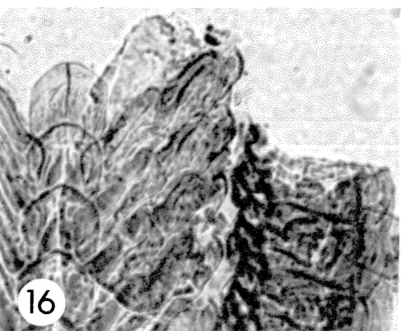
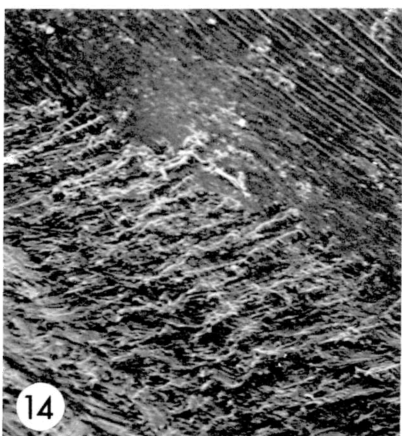
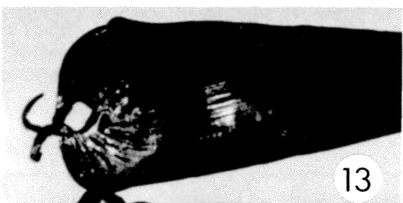
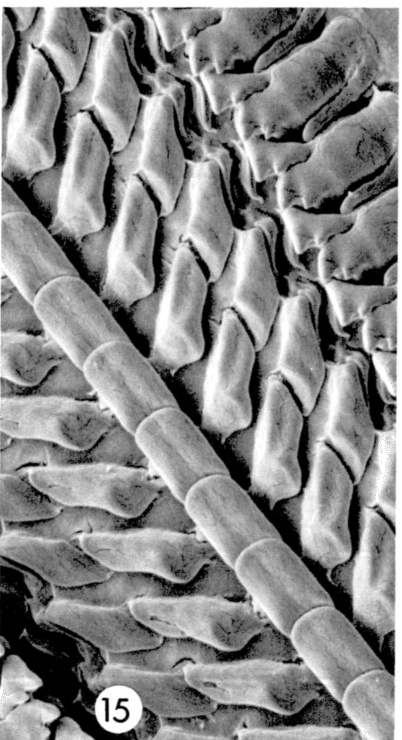
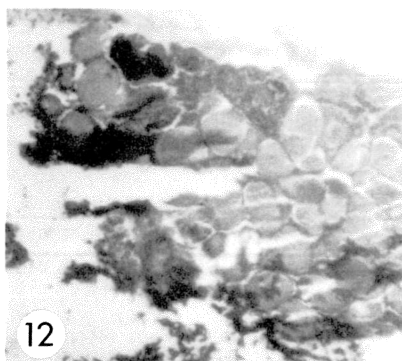
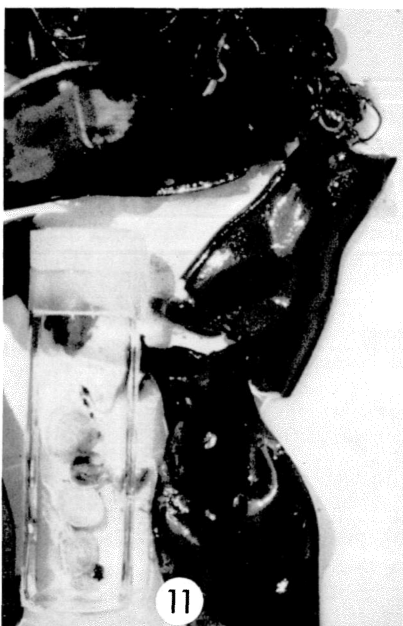
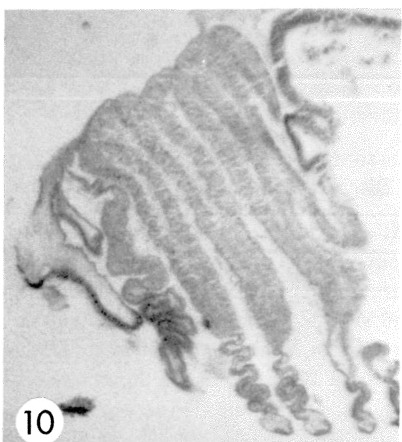
Figure 2. *A. paradoxa* Dall, USNM 50404. USFC sta. 2425, 218 m off North Carolina. 23.3 × 16.0 × 10.5 mm.

Figure 3. *A. lateralis* (Requien), MNHNP, uncatalogued. Holotype of *Gadina excentrica* Tiberi. Off Sardinia, Mediterranean Sea. 10.5 × 8.9 × 4.2 mm.

Figure 4. *A. lateralis* (Requien), MNHNP uncatalogued. LOCARD (1898) sta. 35, off Atlantic Morocco. 7.3 × 6.4 × 2.8 mm.

Figure 5. *A. brophyi*, spec. nov., LACM 111551. 91 m off Catalina Isthmus, California. 6.0 × 5.3 × 1.9 mm.

Figure 6. *A. brophyi* spec. nov., holotype, LACM 2082, 155–174 m off Gaviota, California. 10.1 × 8.5 × 4.8 mm.



MOSKALEV (1978) erred in stating that HUBENDICK (1946) "convincingly showed that *G. excentrica* Tiberi is an independent species" [of *Gadinia*]. In actuality, HUBENDICK (1946:77) merely listed it in a catalog of names and referred it to *Addisonia lateralis*.

Addisonia brophyi McLean, spec. nov.

(Figures 5–12, 15)

Addisonia n. sp., HICKMAN, 1983:81, figs. 38a, 38b (radula).

Diagnosis: Smaller than *Addisonia paradoxa* and with apex more displaced than that of *A. lateralis*.

Although half the size of large specimens of *Addisonia paradoxa*, the apex is fully displaced to the left; on specimens of *A. paradoxa* of comparable size (for example, the lectotype, Figure 1), the apex is only partially offset to the left. The subcylindrical rachidian differs (Figure 15) from that of *A. paradoxa* (Figure 16; HICKMAN, 1983, fig. 10) in having parallel rather than convex sides.

Description: Cap-shaped, thin, non-nacreous; periostracum thin, smooth. Margin sharp and fragile, ends slightly raised relative to sides. Outline asymmetrical, anterior either broader or narrower than posterior. Apex near midline, $\frac{1}{4}$ shell length from posterior margin in young shells (to 6 mm in length); apex in larger shells offset toward left, curved backward and downward. Protoconch lost, apical tip sealed over. Radial sculpture of fine striae; concentric sculpture of microscopic growth lines. Muscle scar horseshoe-shaped, narrow throughout, not broken into discrete bundles, anterior terminations curved inward and

directed posteriorly; termination of right side with broader inward curve than that of left side. A narrow pallial line extends in broad arc from anterior limitation of muscle scar.

Dimensions: Holotype: Length 10.1, width 8.5, height 4.8 mm. Largest specimen: length 10.2, width 9.5, height 4.4 mm (CAS 056077).

Type locality: 85–95 fm (155–174 m) off Gaviota, Santa Barbara County, California (approx. 34°12'N, 120°12'W).

Type material (all collected by Pat Brophy on trawling vessels working at or near the type locality): 10 specimens extracted from 7 egg cases (Figure 11) identified by McLean as brown cat shark *Apristurus brunneus* (Gilbert), 28 August 1968, distributed as follows: Holotype LACM 2082, 7 paratypes (with egg cases) LACM 2083, 2 paratypes USNM 784754. Additional paratypes: LACM 2084, 3 specimens, 17 July 1968, "in shark egg cases." CAS 056076, 1 specimen with egg case (Figure 13) identified by McLean as swell shark *Cephaloscyllium uter* (Jordan & Gilbert), 17 July 1968. CAS 056077, 5 specimens, 25 July 1968, "in shark egg case."

Referred material: LACM 111551 (Figure 5), 3 immature specimens, not with egg case, but with original label reading "in swell shark egg case," 91 m (50 fm) off Catalina Isthmus, Catalina Island, California, June 1972. As in other juveniles, the apex in these specimens is near the mid-dorsal line.

Distribution: Gaviota, Santa Barbara County, to Cata-

Explanation of Figures 7 to 17

Figure 7. *Addisonia brophyi* spec. nov., paratype. Ventral view of preserved animal, showing mantle cavity gill on right side, foot with digestive gland (dark patch) showing through, head with large oral disc and cephalic tentacles bent down. Length of preserved specimen 6.5 mm.

Figure 8. Same specimen as Figure 7. Dorsal view, showing gill extending to right, large light colored heart near anterior termination of gill; gonad with light colored eggs, dark digestive gland bordered by narrow shell muscle.

Figure 9. Same specimen as Figure 7. Right lateral view showing structures noted above and the sperm groove (light colored with dark channel) leading from base of right tentacle toward 7:00 o'clock position.

Figure 10. *Addisonia brophyi*, histologic section through 5 filaments of gill on right side, showing that each filament is an outpocket of epithelium. Smooth mantle edge at left edge of frame, mantle cavity space at right. Horizontal dimension of field 1.5 mm.

Figure 11. Egg capsules of brown cat shark *Apristurus brunneus* shown with paratypes of *Addisonia brophyi* in vial, LACM 2083. Actual size, horizontal dimension of field 54 mm.

Figure 12. *Addisonia brophyi*, histologic section through her-

maphroditic gonad, showing large eggs and dark staining testes cells interspersed. Horizontal dimension of field 1.5 mm.

Figure 13. Egg case of swell shark *Cephaloscyllium uter* from which a paratype specimen of *Addisonia brophyi* was collected, CAS 056076. Actual size, horizontal width of field 53 mm.

Figure 14. SEM view of inside wall of egg case illustrated in Figure 13. Undamaged interior of egg case in upper right, grooves identified as radular scraping marks made by *Addisonia brophyi* present at lower left. 100×.

Figure 15. SEM view of radular ribbon of paratype of *Addisonia brophyi*, showing columnar rachidian elements running diagonally, two rhomboidal plates in V-shaped alignment, and the outer bicuspid plates (see text for more detailed description). Horizontal dimension of field 200 μm.

Figure 16. *Addisonia paradoxa*, light microscope preparation of radula, to show the rachidian elements with convex sides and to illustrate the difficulty of interpretation of such radular preparations. Horizontal dimension of field 200 μm.

Figure 17. *Addisonia paradoxa*, specimen with dried animal, sperm groove clearly visible on body wall (the dark groove in lighter area extending from base of right tentacle), USNM 43743. Shell length 11.0 mm.

lina Island, Los Angeles County, California (records above).

Remarks: All collecting records of *Addisonia brophyi* have been associated with the spent egg cases of the cat shark family Scyliorhinidae, as discussed below.

DISCUSSION

Other deep-sea limpet families in the suborder Lepetelina are associated with, and feed upon, various kinds of organic debris that have a frequent but scattered occurrence in the deep sea (HICKMAN, 1983). Cocculinids and pseudococculinids are usually associated with wood, although some have adapted to cephalopod beaks (MOSKALEV, 1976); bathysciadiids and bathypeltids are associated with cephalopod beaks (MOSKALEV, 1973); bathyphytophilids are associated with turtle grass debris (MOSKALEV, 1978); lepetellids reside within polychaete tubes (MOSKALEV, 1978); cocculinellids derive their nutrition from fish bone (MARSHALL, 1983). Therefore, it comes as no surprise to learn that *Addisonia* has an obligate association with shark egg cases.

Egg cases are produced by three shark families: the cat sharks (family Scyliorhinidae), of which there are more than 85 species in the world (ESCHMEYER *et al.*, 1983), the bullhead or horn sharks (family Heterodontidae), and the skates (family Rajidae). COX (1963) and ESCHMEYER *et al.* (1983) illustrated the egg cases of the Californian species in these families. *Addisonia* is now known to live within old egg cases of two species of cat sharks; it should also be expected to inhabit the spent egg cases of skates and horn sharks, although the single Californian species in the latter group occurs in shallower water than known for *Addisonia*.

WOURMS (1977) reviewed the literature on shark egg case structure and formation. Egg cases are composed primarily of layers of the structural protein collagen, that of the egg cases having unique chemical and physical properties. The egg cases protect the shark embryos for up to nine months, after which there is little evidence of deterioration. Data are not available, but the spent egg cases probably endure for a number of years in the marine environment. This is, therefore, a persistent and reliable food source, but one that must require enzymes capable of digesting collagen. One other prosobranch gastropod, the North Atlantic *Choristella tenera* (Verrill, 1882), is known to be associated with elasmobranch egg cases (VERRILL, 1882; HICKMAN, 1983:86), upon which it presumably feeds (for current taxonomy of *Choristella*, see BOUCHET & WARÉN, 1979:225).

The wall thickness in preserved egg cases of the brown cat shark (LACM 2083) is 0.1 to 0.2 mm. Specimens preserved in alcohol and viewed with transmitted light show thinner areas on the inner surface and some holes. Grooves presumed to be tooth scraping marks made by *Addisonia* on the inner surface of a dried specimen of swell shark egg case (CAS 056076) are illustrated here in an

SEM micrograph (Figure 14). It is apparent that *Addisonia* feeds upon inner layers of the egg case. The low relief of the functional teeth (the bicuspidate outer elements) can penetrate the complex layering of the inner lining of the egg case without rupturing the egg case and thereby exposing the limpet to predators.

Bone-feeding *Cocculinella* have not the same constraint, as the bone itself provides no containment. Thus the teeth of *Cocculinella*, illustrated by MARSHALL (1983), have comparatively high relief for feeding upon bone softened by bacterial activity.

Partially digested collagen within the hindgut of the preserved specimens of *Addisonia brophyi* may account for the dark-brown coloration of the digestive gland, which matches that of the egg cases. The hardness of the collagen particles may also have been a contributing factor in the shattering of the digestive organs in the serial sections of the present material.

Although early development is unknown, the veliger stage must be brief, owing to the small protoconch. Demersal veligers probably enter the spent cases and grow to maturity within. The egg cases provide shelter and protection from predators for the thin-shelled limpets. The shell margin with raised ends enables the limpet to have a good fit on the concave surface within the confines of the egg cases.

The largest specimen of *Addisonia brophyi* reported here is 10.2 mm in length, much smaller than the largest specimen of *A. paradoxa* (20.3 mm in length). The egg cases supporting *A. brophyi* were too small to support larger limpets. Therefore, the egg cases that support *A. paradoxa* must be larger.

It is surprising that only one of the records of *Addisonia paradoxa* noted the association of the limpets with shark egg cases. Collection by trawling usually produces immense masses of bottom debris; large limpets could have been clinging to partially disintegrated remains of the cases, so that the association could easily have been missed. Shark egg cases are sufficiently common in the accumulations of debris brought up by trawlers to suggest that more records of *Addisonia* will come to light when an effort is made to examine old egg cases, particularly in the summer months, the time at which the specimens of *A. brophyi* were collected.

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provided the SEM radular illustration. Copies of Moskalev's papers, translated by George Shkurkin, were provided by Hickman. THIELE (1903) was translated by David R. Lindberg and THIELE (1908) by Silvard Kool. Specimens of *A. lateralis* were loaned by Philippe Bouchet of the Paris Museum and J. van Gothem of the Brussels Museum; those of *A. paradoxa* were loaned by R. Houbriek and J. Rosewater of the U.S. National Museum. J. P. Wourms sent additional information about shark egg cases. I am grateful to Eugene Coan, David R. Lindberg, and Bruce A. Marshall for reading the manuscript and offering helpful suggestions.

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NOTE ADDED IN PROOF:

Too late for inclusion in the text, P. Bouchet has sent me a copy of a paper published in an Italian journal in which the same habitat for *Addisonia* is described:

Villa, R. 1985. Note su habitat ed ecologia di *Addisonia lateralis* (Réquien, 1848). Notiz. CISMA, "1983," 5(1-2):9-12.

Villa reported the collection of *A. lateralis* within the egg cases of the elasmobranchs *Scyliorhinus canicula* and *Raja* sp. from Fiumicino on the Mediterranean coast near Rome. "The specimens of *Addisonia* were found inside the egg case and there is no opening that would permit the mollusk to enter. I suppose the mollusk penetrates the egg case at an early stage." [translation]