

Comparative Morphology and Function  
of Dermal Structures in  
Oceanic Squids (Cephalopoda)

CLYDE F.E. ROPER  
and  
C.C. LU

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 493

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SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1990

## ABSTRACT

Roper, Clyde F.E., and C.C. Lu. Comparative Morphology and Function of Dermal Structures in Oceanic Squids (Cephalopoda). *Smithsonian Contributions to Zoology*, number 493, 40 pages, 81 figures, 1 table, 1990.—A survey was conducted on the histology and functional morphology of dermal structures (dermal cushions or “scales” and tubercles) of 10 species in 6 families of oceanic squids using SEM and light microscopy. Specific differences in connective tissue and cartilaginous tissue types were noted. Cartilages reminiscent of elastic cartilage and fibrocartilage of vertebrates are reported in cephalopods, one of the few such reports in invertebrates. Hyaline cartilaginous tubercles also are present. Functions hypothesized for dermal structures based on structural analysis and biology of the species include two dermal buoyancy mechanisms, like buoyancy vests, and a locomotory mechanism suggested for reducing hydrodynamic drag. Comparative morphology of dermal structures permitted reassessment of systematic relationships in *Lepidoteuthis*, *Pholidoteuthis*, and *Tetronycho-teuthis*.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

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Library of Congress Cataloging in Publication Data

Roper, Clyde F.E., 1937—

Comparative morphology and function of dermal structures in oceanic squids (Cephalopoda) / Clyde F.E. Roper and C.C.

Lu.

p. cm.—(Smithsonian contributions to zoology ; no. 493)

Includes bibliographical references.

1. Cephalopoda—Anatomy. 2. Cephalopoda—Classification. 3. Dermis. I. Lu, C.C. II. Title. III. Series. QL1.S54 no. 493 [QL430.2] 591 s—dc20 [594'.58] 89-600344

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# Comparative Morphology and Function of Dermal Structures in Oceanic Squids (Cephalopoda)

*Clyde F.E. Roper and C.C. Lu*

## Introduction

Cephalopods, perhaps more than any other group of animals, use their skins as an integral part of their daily lives, short-term (individual) and long-term (species) survival, and evolution. Not merely a protective envelope, the skin of cephalopods is a reflection of the life-style, habitus, well-being, and milieu of the animal, for it contains numerous elements that constitute an integrated biological system. In fact, Packard (1988:37) considers coleoid skin as having evolved "psychological dimensions," as an organ of expression and concealment. Basic elements of epidermal and dermal structures may incorporate the following: pigmentation (ground coloration), chromatophores, iridophores, leucophores, photophores, cilia, Koelliker's tufts, papillae, cirri, ridges, flaps, scales, tubercles, and various secretory and sensory structures. This array of structures supports numerous functions, e.g., osmotic shield, protection from disease, background matching (camouflage) by color (chromatophores, etc.) and light (photophores), tactile roles, chemoreception, behavioral roles in predation, defense, courtship, and intraspecific and interspecific communication.

While the structure and function of some of these dermal elements have been determined to varying degrees, mainly in coastal species, scales and tubercles have received such scant attention that their structure, composition, and especially function are virtually unknown.

This study explores the histology and morphology of several of these poorly understood structures in the skin of 10 species of oceanic squids. It further presents hypotheses concerning the function of these structures: buoyancy maintenance and locomotory efficiency through reduction of hydrodynamic drag.

Although invertebrate cartilage tissue was described early in

the nineteenth century (Schultze, 1818; Koelliker, 1844; Gegenbaur, 1858), considerable doubt was expressed at the turn of the century about it being "true cartilage" (Schaffer, 1930; Lubosch, 1938). Even Hyman (1940:281) stated that "true cartilage and bone are absent in invertebrates." Schaffer (1930) and Pritchard (1956) (fide Person and Philpott, 1969) also stated that cartilage is a uniquely vertebrate tissue. Person and Philpott (1969) in comprehensive reviews concluded that true cartilage does indeed occur in invertebrates. They studied the cartilages in several invertebrate phyla; they concluded that in cephalopods the tissues of the dermal scales of *Cranchia scabra* and the head cartilage of *Loligo pealeii* strongly resemble vertebrate hyaline cartilage in both their chemistry and histology (Person and Philpott, 1967, 1969). Person (1983) reviewed invertebrate cartilages and once again demonstrated that the cartilage that occurs in several invertebrate phyla is true cartilage. It need not be referred to as "hyaline-like" cartilage.

Person and Philpott (1969) did not suggest that an evolutionary or taxonomic significance exists between invertebrate and vertebrate cartilages, but they did suggest that cartilage would have originated in invertebrates rather than vertebrates, and they remarked about the interesting evolutionary aspects of the chemical constituents of cartilaginous tissues, e.g., the mucopolysaccharides, collagens, etc., as well as the histology. Mathews (1975) discussed the occurrence of cartilage in invertebrates and cephalopods and Bairati (1985) reviewed collagens and cartilages in mollusks, including cephalopods. Our study reveals that hyaline cartilage also occurs in dermal structures of families of squids other than the Cranchiidae. Furthermore, tissues reminiscent of elastic and fibrocartilages of vertebrates also occur in invertebrates. In the case of cephalopod cartilaginous tubercles, their significance in the evolution of cephalopods remains unclear. Person (1969) pointed out that the evolutionary development of homologous organs in vertebrates and cephalopods, e.g., eyes and brain, deserve further study; to these we now can add cartilages, as well.

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The majority of squids commonly are considered to have smooth skin, unadorned with permanent structures such as scales, tubercles, or papillae. The few exceptions generally have been regarded as oddities, little more than quirks of evolution on "rare" deep-sea species. The first such record was that of Leach (1817), who characterized *Cranchia scabra* as having rough, hard tubercles over the entire surface of the mantle. Subsequently several genera and species of cranchiid squids, for example, *Leachia cyclura* Lesueur, 1821, *Liocranchia reinhardti* (Steenstrup, 1856), and *Pyrgopsis pacificus* (Issel, 1908), were described as possessing some form of tubercles on the body, but limited to one or two rows associated with the mantle-funnel locking apparatus, which is fused in the Cranchiidae.

Joubin (1895) described *Lepidoteuthis grimaldii* from a specimen regurgitated by a sperm whale taken in the Azores, in the eastern North Atlantic Ocean. Joubin characterized the species by its overlapping rhomboidal scales that cover the surface of the mantle. According to Joubin (1900:71) the scales are of a "cartilaginous consistency." Pfeffer (1900:161) erected the genus *Tetronychoteuthis* to accommodate *Onychoteuthis dussumieri* Orbnigny, 1839, the mantle of which is covered with many small roundish, non-overlapping, juxtaposed scales on the surface. Adam (1950) proposed the family Pholidoteuthidae for the new genus and species, *Pholidoteuthis boschmai*, which possesses many round scales on the surface of the mantle. Voss (1956:132) described a second species, also scaled, *Pholidoteuthis adami*, from the Gulf of Mexico. These three "scaled" genera had been placed in the family Lepidoteuthidae for convenience by some authors on the ground that they all possess scalation, but they conceded that the grouping is unnatural based on other characters (Roper et al., 1969; Voss, 1977). Clarke (1980) has maintained separate familial rank for *Lepidoteuthis*. Elsewhere we present a summary and clarification of a systematic scheme, as we understand it, for this group based on analysis of dermal structures and other characters (Roper and Lu, 1989).

In addition to the above-mentioned species, several other species in various families have been reported to possess some form of tubercle-like or scale-like structures on the surface of the mantle or arms. Such structures are present in these species: *Ocythoe tuberculata* Rafinesque, 1814, the tubercles implied in the name of this epipelagic octopod; *Histioteuthis meleagroteuthis* (Chun, 1910), described with "cartilaginous tubercles" by Pfeffer (1900:170); *Galiteuthis glacialis* (Chun, 1906) redescribed with "cartilaginous tubercles" over the mantle (McSweeney, 1978:5); *Mastigoteuthis cordiformis* Chun, 1908, described with "modified subcutaneous connective tissue" tubercles; *Tetronychoteuthis massyae* Pfeffer (1912:102), with "chitinous tubercles" reported in the original description; *Histioteuthis miranda* (Berry, 1918:226) with "cartilaginous, tubercle-like spines" reported in the original description; *Echinoteuthis danae* Joubin, 1933:13, originally described with papillae of a "cartilaginous nature"; *Chiroteuthis acan-*

*thoderma* Lu, 1977, originally described with "cartilaginous tubercles"; and all the species of the subfamily Cranchiinae, which by definition possess rows of cartilaginous tubercles on the mantle in various locations.

Despite the long history of the discoveries of scales or tubercles, few detailed studies on their structure have been undertaken until recently. Two early exceptions were Joubin's (1900) work on *Lepidoteuthis grimaldii* and Chun's (1910) description of the structure of the mantle and the scales of *Lepidoteuthis grimaldii* and *Mastigoteuthis cordiformis*. More recently a series of articles dealing with some aspects of the scales of *Lepidoteuthis grimaldii* was published (Clarke, 1960, 1964; Clarke and Maul, 1962). The designation of the tubercles of *Cranchia scabra* as cartilaginous in structure was confirmed by Person (1969), who referred to them as "dermal scales." Dilly and Nixon (1976) described the structure of the tubercles in *C. scabra* and suggested possible functions: (1) the scabrous surface could retard the sinking rate, or (2) could form a "prickly ball" to discourage predators. McSweeney (1978) described the numerous cartilaginous tubercles on the surface of the mantle in *Galiteuthis glacialis*, including histological details.

Although the occurrence of dermal structures is well described in the literature, few authors have studied the internal composition of these structures. They have been referred to as cartilaginous, chitinous, modified connective tissue, elastic, etc., with little or no verification of the actual class of tissue, with the few exceptions mentioned in the previous paragraph which were mostly in cranchiids. The structures themselves have been termed scales, plates, tubercles, papillae, humps, spots, spines, warts, etc.

The use of the terms "scale" and the others listed above needs clarification at this point. Clarke (1960:955) accepted the term introduced by Joubin (1895), because the slightly overlapping structures in *Lepidoteuthis grimaldii* "resemble ganoid scales [of fishes] in general appearance." The research reported in this paper shows these structures to be myxoid, highly vacuolated, fluid-filled, loose connective tissue, unrelated to cartilage. Further, the corresponding structures in *Pholidoteuthis adami* are of identical structure, but they do not overlap and they do not "look-like" scales grossly. Therefore, the terms "scales" or "cartilaginous scales" are now deemed inaccurate and inappropriate. As they convey an incorrect concept, these terms should no longer be used to refer to the dermal structures of cephalopods discussed in this paper. We introduce the new terminology, "dermal cushions," which conveys both structurally and functionally the concept of these structures, especially as they refer to those of *L. grimaldii* and *P. adami*. The term "tubercle(s)" is appropriate for the dermal structures of cartilaginous or cartilage-like projections that occur in *Tetronychoteuthis massyae* and *Cranchia scabra*, formerly referred to as scales, as well as in the other species studied in this project.

This study has the following objectives: (1) to survey the



squids in the Order Teuthoidea to determine the occurrence of dermal structures called dermal cushions (formerly "scales") and tubercles;<sup>1</sup> (2) to determine whether the occurrence of dermal structures and their distribution within taxa bear systematic or phylogenetic relevance; (3) to describe the morphology and histology of dermal cushions and tubercles in squids; (4) to hypothesize functions that may be applicable to these dermal structures.<sup>2</sup>

#### MATERIALS AND METHODS

Tissue samples were obtained from cephalopod specimens in the USNM collections of the National Museum of Natural History, Smithsonian Institution, with the exception of *Chiroteuthis acanthoderma*. The information on these specimens is listed below in the following order: species name, USNM catalog number, sex of specimen (F = female, M = male, I = immature), mantle length (ML) in mm, locality of capture, ship and station number, date of capture.

*Lepidoteuthis grimaldii*, USNM 730180, M, 180 mm ML, South Atlantic Ocean, 39°53'S, 21°33'W, *Walther Herwig* sta 380-III-71, 12 Mar 1971.

*Pholidoteuthis adami*, 300 mm ML, Norfolk Canyon, 37°09'N, 74°54'W, *Gillis* sta 74-O4-10, 14 Nov 1974.

*Tetronychoteuthis massyae*, USNM 728888, I, 100 mm ML, Bermuda, 32°22'N, 64°04'W, *Delaware II* [Ocean Acre] sta 12-70-N, 22 Aug 1971.

*Histioteuthis meleagroteuthis*, USNM 728893, F, 38 mm ML, Bermuda, 32°11'N, 64°00'W, *Delaware II* [Ocean Acre] sta 12-63-N, 22 Aug 1971.

*Chiroteuthis acanthoderma*, Zoological Museum, Copenhagen, I, 144 mm ML, paratype, New Guinea, 3°18'N, 129°02'E, *Dana* sta 3745(I), 8 Jul 1929.

*Mastigoteuthis cordiformis*, USNM 574891, F, 87 mm ML, Philippines, Sombbrero Is., 13°36'N, 120°45'E, *Albatross* sta 5114, 20 Jan 1908.

*Mastigoteuthis hjorti*, USNM 815484, F, 93 mm ML, South Africa, 80°07'S, 05°24'E, *Walther Herwig* sta 431-II-71, 31 Mar 1971.

*Cranchia scabra*, USNM 727214, F, 94 mm ML, Bermuda, 32°10'N, 63°30'W, *Albatross IV* [Ocean Acre] sta 7-2-N, 6 Sep 1969.

*Liocranchia reinhardti*, USNM 727211, F, 29 mm ML, Bermuda, 32°15'N, 63°35'W, *Trident* [Ocean Acre] sta

8-5-N, 25 Nov 1969.

*Leachia cyclura*, USNM 727250, M, 55 mm ML, Bermuda, 32°13'N, 63°40'W, *USNS Sands* [Ocean Acre] sta 6-24-N, 30 Apr 1969.

Tissues prepared for SEM examinations were freeze dried, mounted on stubs, and gold-coated. For light microscopy, tissues were prepared following standard histological procedures. Tissue blocks were embedded in paraffin and sectioned at 6 micrometers. Sections were treated with the following stains: Mayer's haematoxylin and eosin, PAS (periodic acid leucofuchsin), PAS with light green, PTAH (phosphotungstic acid haematoxylin), Toluidine blue O, and Masson's trichrome. These stains provided information about general histology of the structures or were specific for cartilage, collagen, and other connective tissue differentiation.

We emphasize that all the specimens from which we obtained tissue samples are museum specimens that were not initially fixed for histological purposes. They were fixed in buffered or seawater formalin and preserved in 50% isopropyl alcohol for permanent storage. Most specimens had been in the museum collection for a number of years before they were selected for this study. Consequently, some tissue deterioration may have occurred since the time specimens were captured and fixed.

The work of Bone et al. (1981) illustrates squid mantle in section from species without dermal structures and should be helpful in interpreting our results.

#### ABBREVIATIONS

Abbreviations used in line drawings are as follows:

|      |                                  |
|------|----------------------------------|
| CCT  | Chondrofibrous connective tissue |
| CH   | Chamber                          |
| CM   | Circular muscle                  |
| CO   | Chondrocytes                     |
| CP   | Chromatophores                   |
| CT   | Connective tissue                |
| CU   | Cuticle                          |
| D    | Dermal tissue                    |
| DCT  | Dense connective tissue          |
| E    | Epidermis                        |
| EC   | Elastic cartilage                |
| FCT  | Fibrous connective tissue        |
| IME  | Inferior mantle epithelium       |
| LCT  | Longitudinal connective tissue   |
| LFCT | Loose fibrous connective tissue  |
| LM   | Longitudinal muscle              |
| LOCT | Loose ordinary connective tissue |
| M    | Mantle                           |
| MF   | Muscle fibers                    |
| OM   | Oblique muscle                   |
| P    | Perichondrium                    |
| PS   | Pigment sac                      |
| RM   | Radial muscle                    |
| T    | Tubercle                         |
| VL   | Vacuolate layer                  |
| VT   | Vacuolate connective tissue      |

<sup>1</sup>Other species are known to have peculiar dermal structures, but we did not have material available for sectioning and study. These are *Moroteuthis* spp. (Onychoteuthidae) and *Brachioteuthis* spp. (Brachioteuthidae), and there may be others, as well.

<sup>2</sup>We emphasize that hypothesized functions are based on analyses of structures and deduction from preserved specimens, as well as on knowledge about the biology and life-style of the species. Most of the deep-sea species reported on here have never been seen alive, so to date the functions are proposed from an empirical rather than an experimental basis.

## ACKNOWLEDGMENTS

We gratefully acknowledge the people and organizations who contributed to this study. Linda Cullen, from the Registry of Tumors in Lower Animals, Smithsonian Institution, skillfully prepared the histological slides and provided valuable information; John Harshbarger, Director, Registry of Tumors in Lower Animals, kindly made the Registry's resources available to us. Mary-Jacque Mann, Susann Braden, and Walter Brown of the Scanning Electron Microscope Laboratory, National Museum of Natural History (NMNH) assisted immeasurably with the SEM work and photographs. Initial photography of histological sections was done by Roy Ficken, Biology Department, Memorial University of Newfoundland. Frank Coffa, John Augier, and Rodney Start, Photography Department, Museum of Victoria, provided valuable support. Molly Ryan, Department of Invertebrate Zoology, NMNH, skillfully prepared the line drawings of the micrographs. Michael J. Sweeney, Department of Invertebrate Zoology, Division of Mollusks, NMNH, provided invaluable technical assistance throughout the study. Ann Oliver, Division of Mollusks, NMNH, assisted with a very thorough search of the literature. Tim Stranks, Department of Invertebrate Zoology, Museum of Victoria kindly proof-read the text. Ingrid Roper typed the original draft of the manuscript and Lisa Giuliani, Division of Natural History, Museum of Victoria and Michael J. Sweeney skillfully and patiently typed the final drafts. The manuscript benefitted greatly from discussions, correspondence, and reviews from John Harshbarger, Registry of Tumors in Lower Animals, Smithsonian Institution; W. Duane Hope, Department of Invertebrate Zoology, NMNH; William Kier, Department of Biology, University of North Carolina; Marion Nixon, Wellcome Institute, United Kingdom; Ester Peterson, Registry of Tumors in Lower Animals, Smithsonian Institution; and Richard E. Young, Department of Oceanography, University of Hawaii.

Funding for support of various phases of this study was provided by grants from the Secretary's Fluid Research Fund and Research Opportunities Fund and a private Mollusk Research Fund, Smithsonian Institution. Use of the facilities and resources of the Museum of Victoria, Melbourne, and the National Museum of Natural History, Washington, D.C., are gratefully acknowledged.

## Structure

## Family LEPIDOTEUTHIDAE Naef, 1912

*Lepidoteuthis grimaldii* Joubin, 1895

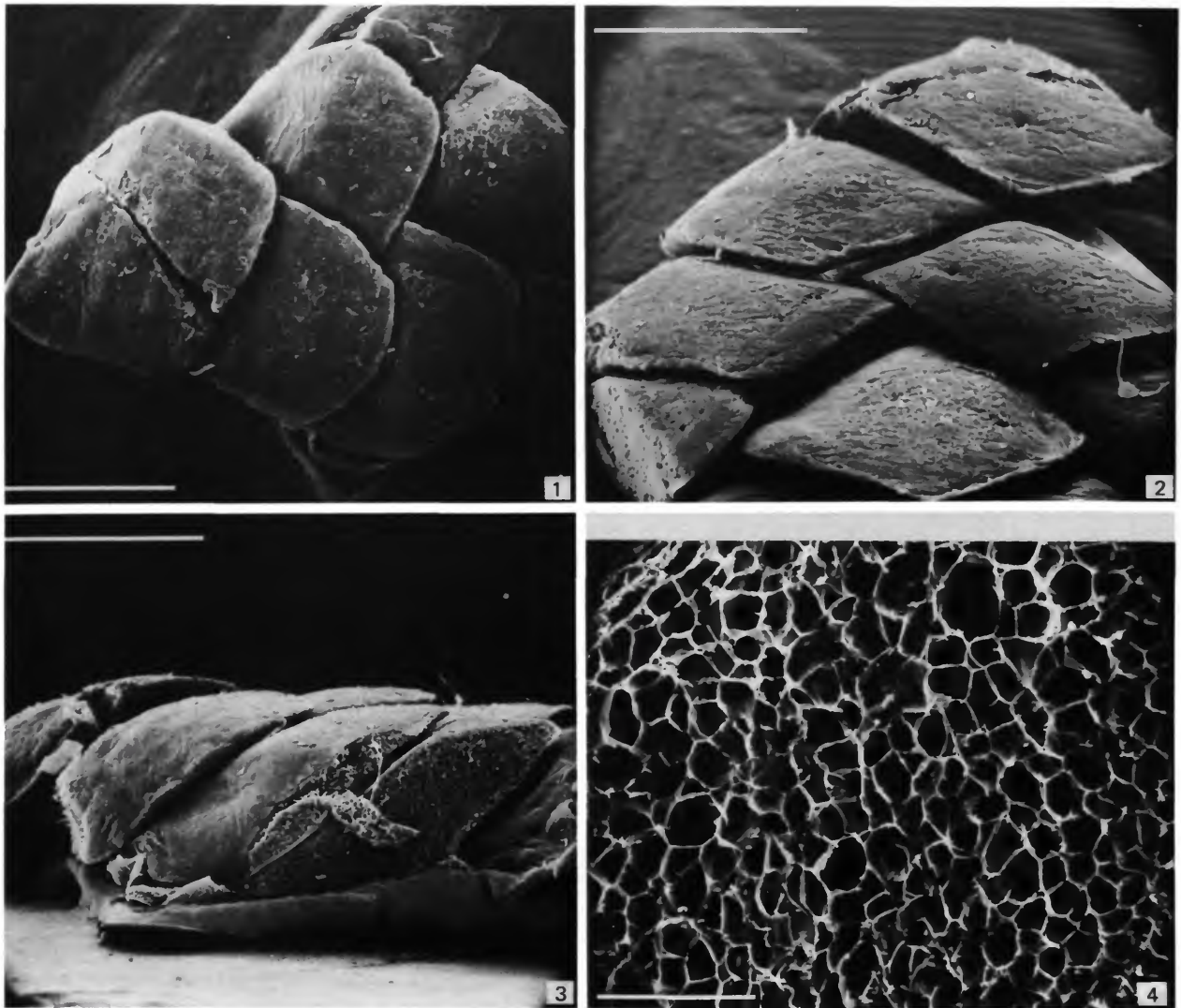
## FIGURES 1-7

Detailed descriptions and illustrations of this species are given in Joubin (1895, 1900), Clarke (1964, 1966), Clarke and Maul (1962), and Clarke et al. (1979). The most striking feature

of *L. grimaldii* is the presence of many relatively large, diamond- to hexagonal-shape dermal cushions, formerly called "scales," that cover the mantle except on the posteroventral part under the posterior half of the fins. These structures resemble some fish scales in outline and overlapping arrangement (Figures 1-3), but they lack the solid boney structure. The diagonally arranged dermal cushions overlap and fit closely together like roofing tiles, with the fixed edge attached posteriorly and the free edges overlapping the one dermal cushion directly anteriorly and two dermal cushions anterovertrally (cf. Joubin, 1900, pls. 6, 7; Clarke and Maul, 1962, pl. 3). Dermal cushions from a young specimen of 180 mm ML (mantle length) are about 1.5 mm wide, 2.0 mm long, and 0.5 mm high. Dermal cushions from a specimen of 755 mm ML measure up to 10 mm wide and 12 mm long. In specimens preserved in alcohol the dermal cushions have a fleshy to semigelatinous consistency; they are easily compressed, but soon rebound to their original form after pressure is discontinued. Further, dermal cushions in preserved animals are rather easily dislodged and removed from the mantle.

A longitudinal section of a dermal cushion reveals that the internal structure is highly vacuolated and consists of numerous, small, irregularly sized and shaped chambers partitioned by thin membranous walls (Figures 4, 5). The membranous walls appear non-cellular and consist of PAS positive collagenous material. Sections of the dermal cushions and mantle wall show an epidermal layer that envelops the dermal cushion and continues as the outer epithelium of the mantle. (This epithelium is too delicate and fragile to show on many sections and hence is not seen in the published figures.) Figures 6, 7 show the internal structure of the dermal cushion to be a highly vacuolated area of loose ordinary connective tissue. This loose ordinary connective tissue consists of collagenic, elastic, and probably reticular fibers, and of a non-staining amorphous area, interpreted as "ground substance," that gives the appearance of vacuoles or empty spaces. Possibly the large intermembranous chambers are comprised of the acid mucopolysaccharide, hyaluronic acid. However, the possibility also exists that these are filled with tissue fluid containing light weight ammonium ions or simply water. The few nuclei present belong to widely scattered muscle fibers as differentiated by PTAH, particularly in the peripheral zone. The base of the dermal cushion is considerably smaller than the diameter of the body of the dermal cushion (Figures 6, 7). The base is relatively large in small specimens but becomes proportionally much smaller, almost stem-like, in adults. Internally the dermal cushions are continuous with the connective tissue of the mantle, and they are covered by the fine epidermis of the mantle. In the dermis on the superior side of the dermal cushions are elongate pigment sacs that contain melanin granules. The vacuolated area of the dermal cushion is nearly devoid of any other material except an occasional muscle fiber.

The mantle *sensu stricto* (Figures 6, 7) consists of the

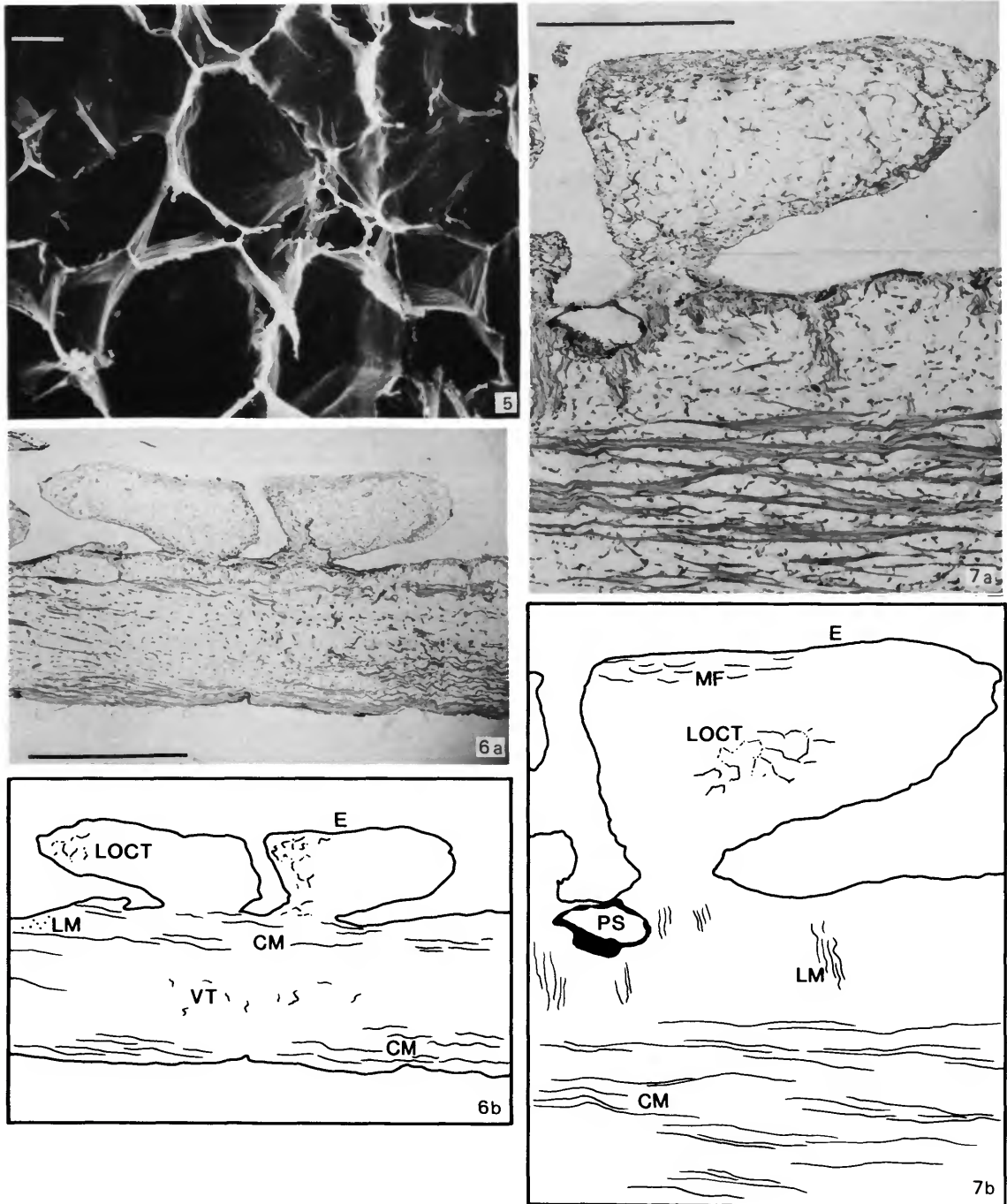


FIGURES 1-4.—*Lepidoteuthis grimaldii*: 1, dermal cushions in situ on mantle,  $\times 21$ , SEM, scale 1 mm; 2, anterior-directed view of dermal cushions on mantle,  $\times 34$ , SEM, scale 1 mm; 3, dermal cushions in situ on mantle, lateral view, section through middle of one scale and edge of another (note the numerous chambers),  $\times 26$ , SEM, scale 1 mm; 4, highly vacuolated area of loose connective tissue in dermal cushions,  $\times 210$ , SEM, scale 0.1 mm.

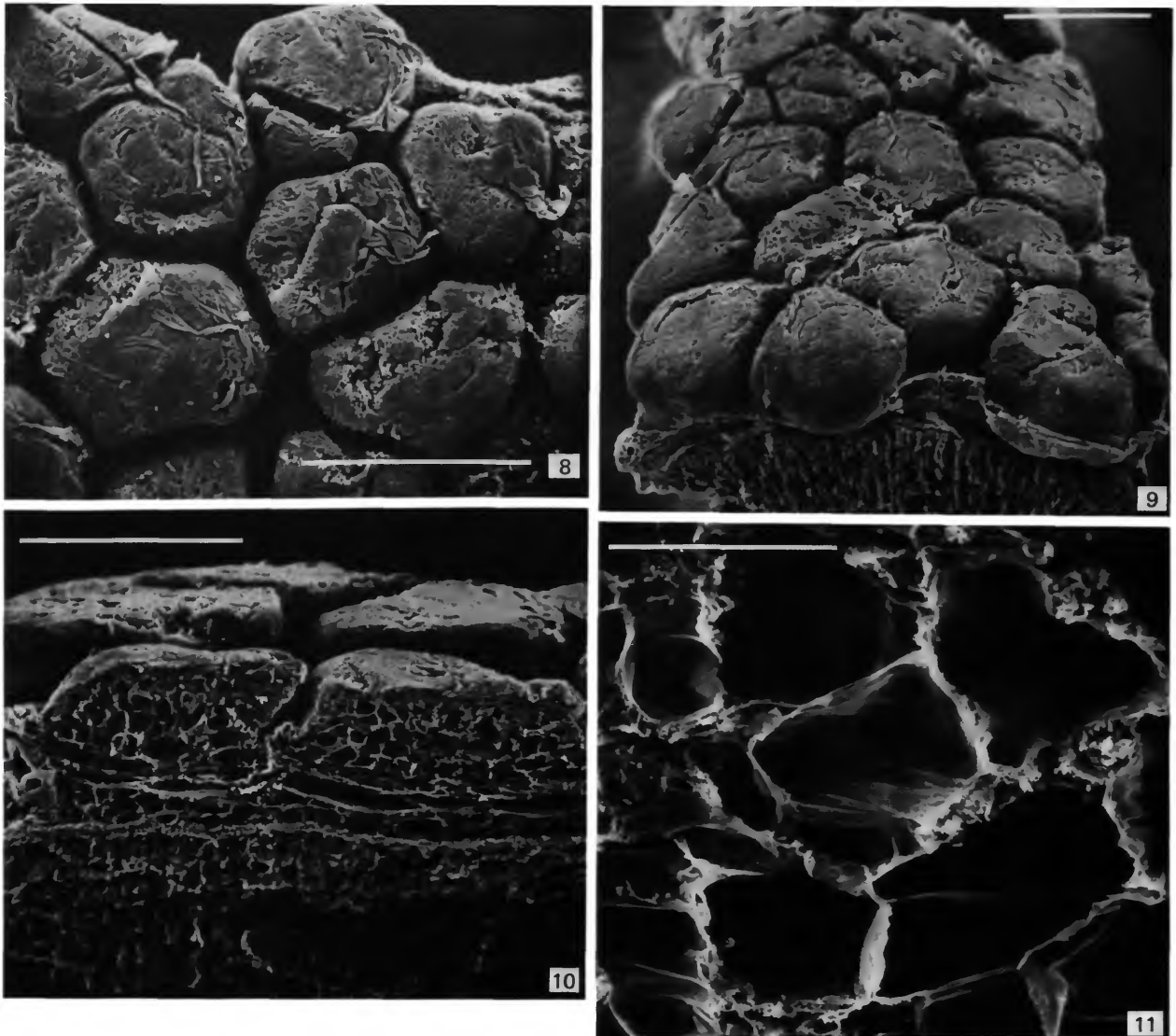
epidermis with basement membrane, the dermis with pigment cells, a thin layer of longitudinal muscle, a thin vacuolated intercellular area, a band of circular muscle, a thick layer of

vacuolated tissue interspersed with widely scattered longitudinal and circular muscle fibers, a thick inferior layer of circular muscle, and the internal mantle epithelium with pigment cells.





FIGURES 5-7.—*Lepidoteuthis grimaldii*: 5, further enlargement of a portion of Figure 4 (note thin membranes of chambers),  $\times 825$ , SEM, scale 0.01 mm; 6a, cross section of mantle and two dermal cushions,  $\times 16$ , light microscopy, stain H & E, scale 1 mm; 6b, diagram of Figure 6a identifying tissue types; 7a, cross section of mantle and a dermal cushion,  $\times 40$ , light microscopy, stain H & E, scale 0.5 mm; 7b, diagram of Figure 7a identifying tissue types.



FIGURES 8-11.—*Pholidoteuthis adami*: 8, dermal cushions in situ on mantle,  $\times 54$ , SEM, scale 0.5 mm; 9, anteriorly directed view of dermal cushions on mantle,  $\times 43$ , SEM, scale 0.5 mm; 10, section through two dermal cushions and mantle showing highly vacuolate nature of loose connective tissue,  $\times 80$ , SEM, scale 0.5 mm; 11, close-up of chambers in dermal cushion (note thin membranous walls of connective tissue),  $\times 825$ , SEM, scale 0.05 mm.

*Pholidoteuthis adami* Voss, 1956

FIGURES 8-13

The mantle of this species is covered with a layer of closely set, small, soft dermal cushions, formerly called "scales," that are irregularly rounded to crudely pentagonal in outline

(Figures 8, 9). They do not overlap and are about 0.5 mm in diameter and 0.3 mm in height on a specimen of 300 mm ML. Sections of the dermal cushions indicate that they are almost entirely vacuolate, consisting of continuous thin-walled, irregularly shaped chambers (Figures 10-13).

The base of each dermal cushion is nearly equal in diameter



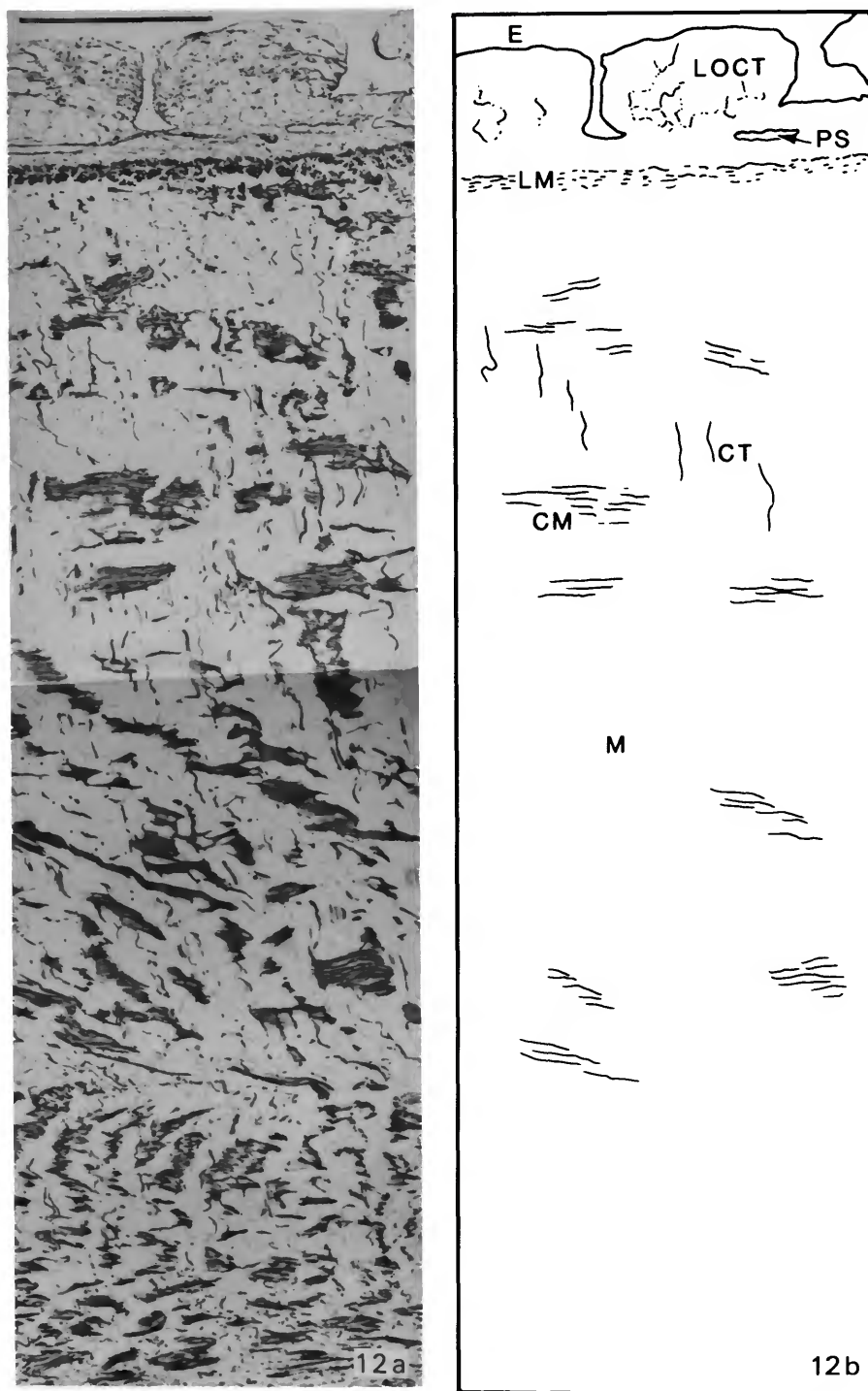


FIGURE 12.—*Pholidoteuthis adami*: 12a, cross section through dermal cushion and mantle,  $\times 16$ , light microscopy, stain H & E, scale 0.5 mm; 12b, diagram of Figure 12a identifying tissue types.

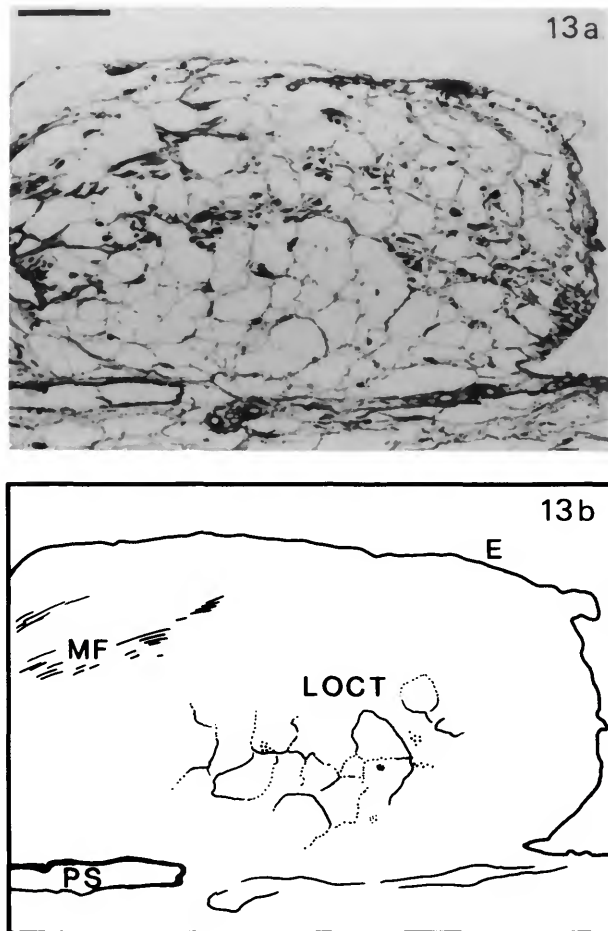


FIGURE 13.—*Pholidoteuthis adami*: 13a, close-up of cross section through a dermal cushion showing vacuolate connective tissue chambers,  $\times 160$ , light microscopy, stain H & E, scale 0.1 mm; 13b, diagram of Figure 13a identifying tissue types.

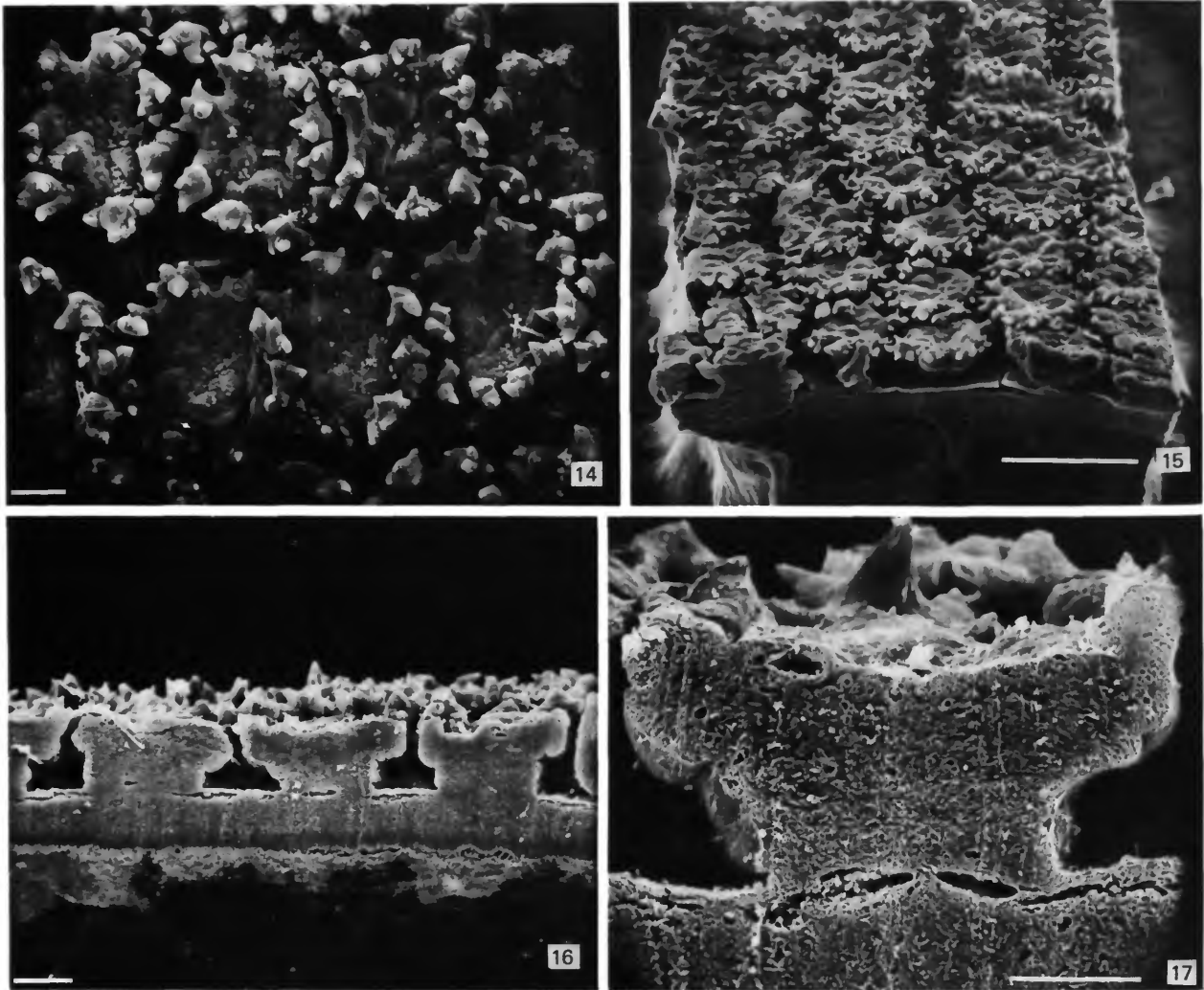
to the dermal cushion itself. The vacuolated tissue of the dermal cushion is a continuation of similar tissue from the dermal layer of the mantle (Figures 10, 12, 13). The surface epidermis is very thin and continuous over the dermal cushions and mantle, making the dermal cushions an integral part of the surface of the mantle (Figures 12, 13). However, in preserved specimens, at least, the dermal cushions are relatively easily dislodged from the mantle.

The internal structure of the dermal cushion is largely vacuolate, loose ordinary connective tissue. The irregular, thin-walled, empty-looking vacuoles may represent the locale of the amorphous ground substance of connective tissue, hyaluronic acid, that does not fix and stain satisfactorily. However, we suspect it is more likely that the vacuoles contained fluid enriched with ammonium ions, an interpretation consistent with the suggested function of a buoyancy mechanism (Clarke et al., 1979). The membranous walls consist of collagenic and elastic fibers and the vacuolated area is interspersed with scattered muscle fibers and nuclei of loose connective tissue (Figure 13). There seems to be no obvious pattern of arrangement of fibers. In the subcutaneous (dermal) area beneath and between the bases of the dermal cushions and superficial to the longitudinal muscle layer lie elongate, flattened chambers with dark walls. These structures are the pigment sacs that provide the background coloration of the squid.

The mantle tissue per se is thick and spongy, and it consists of the following layers as seen in histological sections (Figures 12, 13): the outermost epidermis with basement membrane; a vacuolated area with interspersed elongate, dark-walled pigment sacs; a thin layer of longitudinal muscle; an extremely thick layer of circular muscle with scattered, longitudinal fibers (the muscles in this layer are loosely distributed throughout a non-cellular, vacuolated matrix of connective tissue, similar in appearance to the vacuolate tissue in the dermal cushions and subcutaneous layer); and finally, the thin epithelium lining of the inferior surface of the mantle.

#### Family Unresolved

The familial status of *Tetronyctoteuthis* and its relationship to *Lepidoteuthis* and *Pholidoteuthis* has long been a matter of debate. The comparative morphology of dermal structures from this study has permitted a reassessment of their systematic relationships. This problem is addressed in Roper and Lu, 1989.



FIGURES 14-17.—*Tetranychoteuthis massyae*: 14, plan view of papillose tubercles on surface of mantle,  $\times 110$ , SEM, scale 0.1 mm; 15, anteriorly directed view of longitudinally arranged rows of papillose tubercles on mantle,  $\times 55$ , SEM, scale 0.5 mm; 16, longitudinal section of papillose tubercles showing intertubercular channels and pores opening to surface,  $\times 115$ , SEM, scale 0.1 mm; 17, enlargement of tubercle from Figure 16,  $\times 370$ , SEM, scale 0.1 mm.

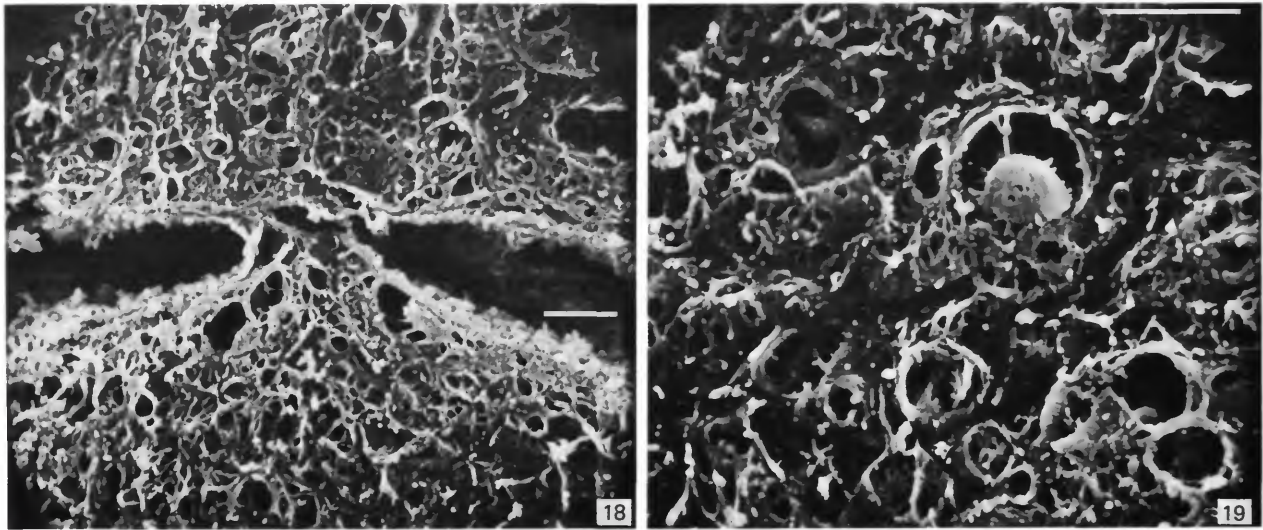
***Tetranychoteuthis massyae* Pfeffer, 1912**

FIGURES 14-22

The mantle of this species is covered with many solid, stellate, minute, tightly-packed, papillose tubercles (Figures 14, 15). Each tubercle is roughly mushroom-shape in profile with

a slightly concave central disc and a thick base. The periphery of the tubercle contains several (mostly 7 to 10) 2-, 3-, or 4-prong, conical papillae (Figures 14-16). The discs on a specimen of 100 mm ML are about 0.3 mm in diameter and 0.15 mm in height. The tubercles consist of very densely packed material with chondrocytes, reminiscent of elastic





FIGURES 18, 19.—*Tetranychoteuthis massyae*: 18, enlargement of a portion of tubercle from Figure 17,  $\times 2000$ , SEM, scale 0.01 mm; 19, further enlargement of a portion of tubercle from Figure 17,  $\times 3700$ , SEM, scale 0.01 mm.

cartilage, regularly distributed throughout the dense connective tissue matrix of the disc and the base (Figures 17–22). SEM examination shows that the dense tissue is interspersed throughout with small vacuoles of varied sizes and shapes (Figures 18, 19). The walls of the vacuoles and the matrix are relatively thick and fibrous. The small vacuoles are mixed with large tubule-like spaces that give an overall dense spongy structure.

Histologically the following features occur through the tubercles and mantle (Figures 20–22). A delicate acellular cuticle envelops the surface of the tubercles and the papillae. The surface of the mantle between the tubercles is covered with normal epidermis that is fused with the bases of the tubercles. The base of each tubercle is continuous with and has the same chondrofibrous composition as the outer layer of the dermis, the foundation layer that envelops the mantle superior to the muscle layers. Pigment sacs (chromatophores) that provide the background coloration occur in the boundary zone between epidermis and dermis. Along the inferior boundary of the foundation layer occurs a layer of large, closely packed chondrocytes that immediately overlie the dense, thin layer of longitudinal dense connective tissue fibers of the mantle (Figure 20). Inferior to the connective tissue fibers is another

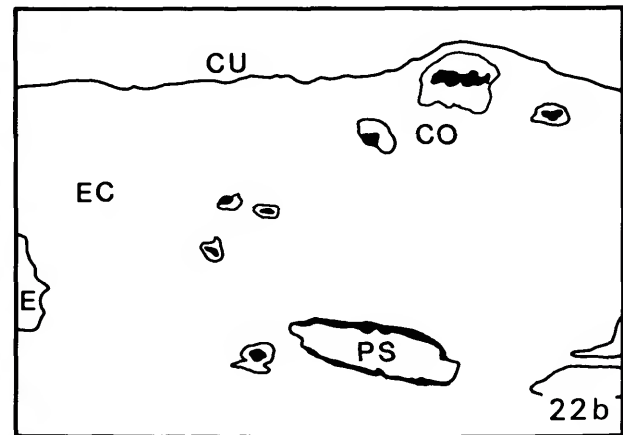
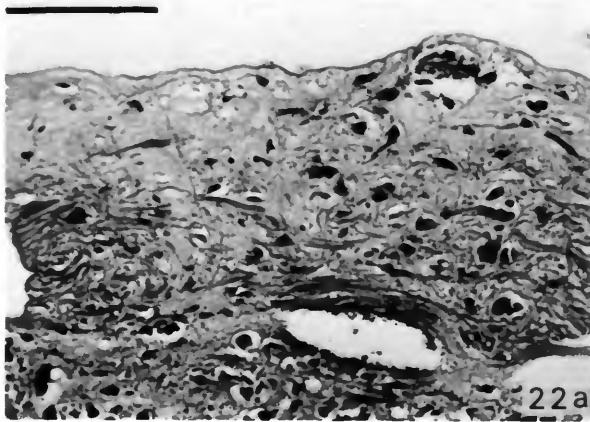
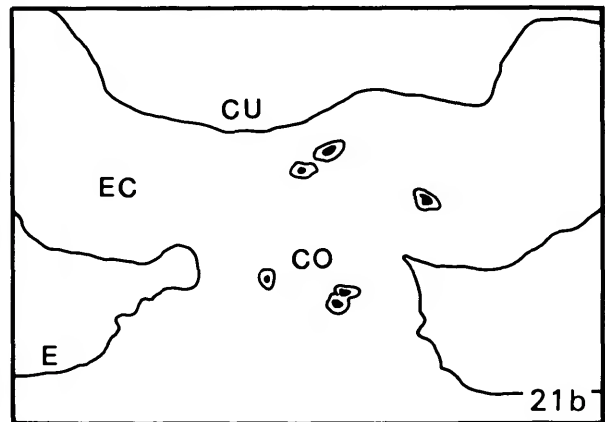
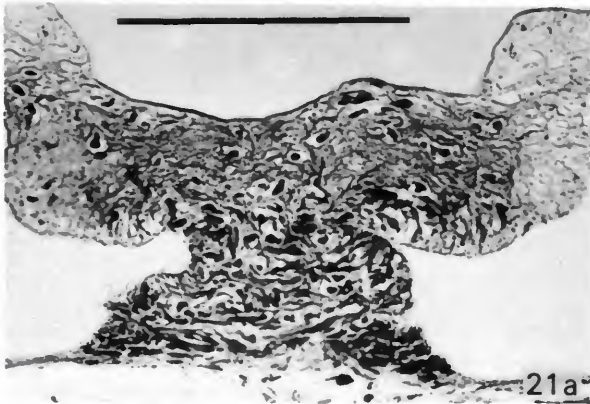
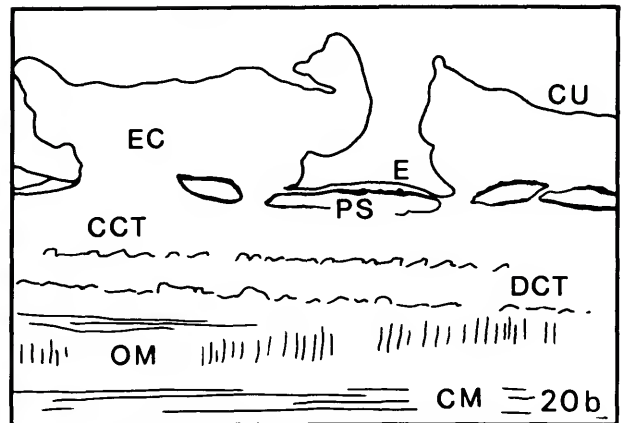
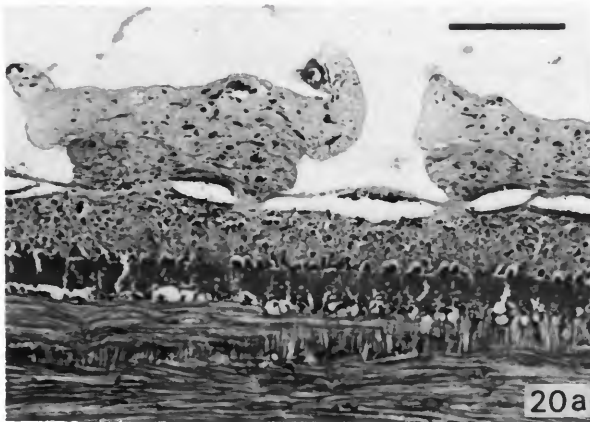
thin layer of connective tissue regularly penetrated by oblique and circular muscle fibers that extend from the underlying mantle musculature. Inferior to this boundary zone lie several alternating layers of compact circular and oblique muscles that comprise most of the thick wall of the mantle (not shown in figure sections). The inferior-most layer of the mantle musculature consists of interspersed circular and oblique muscles which insert into the inferior mantle epithelium. No inferior layer of longitudinal muscle exists.

#### Family HISTIOTEUTHIDAE Verrill, 1881

#### *Histioteuthis meleagroteuthis* (Chun, 1910)

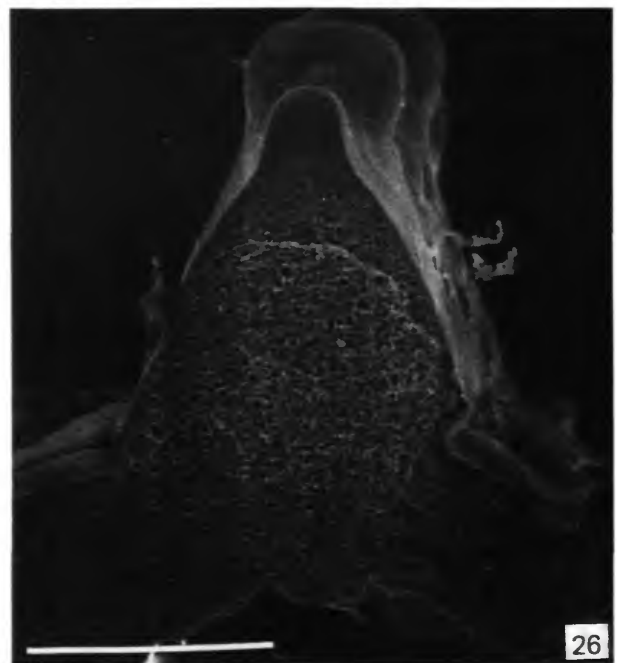
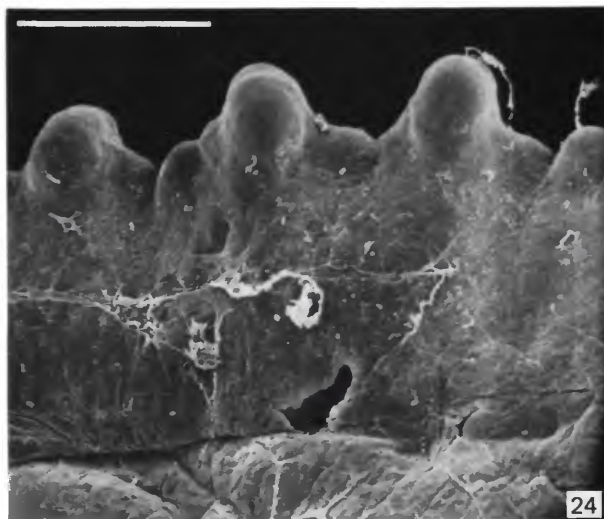
FIGURES 23–46

*Histioteuthis meleagroteuthis* is characterized by the possession of a prominent ridge of strong, knob-like tubercles along the anterior  $2/3$  of the dorsal midline of the mantle, as well as along the proximal half of the median aboral surfaces of arms I, II, and III (Figures 23–26, 35, 36; Voss, 1969, fig. 26d). These ridges and tubercles are very hard and rigid in live animals as well as in fixed specimens and have been termed “cartilaginous” (Pfeffer, 1900:170; Chun, 1910:170; Voss, 1969:805). The tubercles appear on the mantle in the juvenile



FIGURES 20-22.—*Tetronychoteuthis masryae*: 20a, section of outer portion of mantle with tubercles (note chondrofibrous outer layer of dermis),  $\times 160$ , light microscopy, stain H & E, scale 0.1 mm; 20b, diagram of Figure 20a identifying tissue types; 21a, section of a tubercle showing elastic cartilage tissue,  $\times 400$ , light microscopy, stain Masson's trichrome, scale 0.1 mm; 21b, diagram of Figure 21a identifying tissue types; 22a, section of a tubercle showing dense elastic cartilage tissue,  $\times 400$ , light microscopy, stain Masson's trichrome, scale 0.05 mm; 22b, diagram of Figure 22a identifying tissue types.





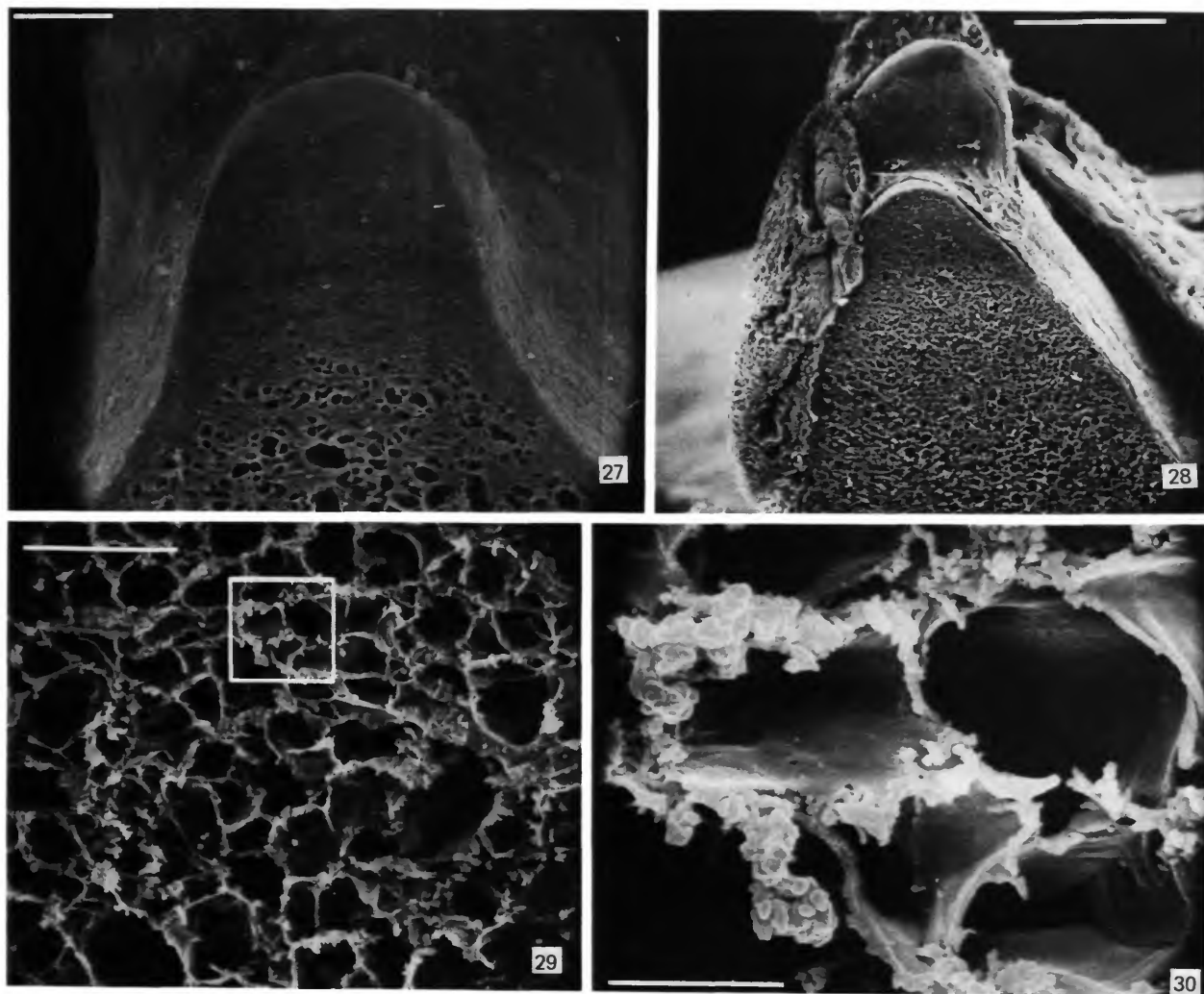
FIGURES 23, 24.—*Histioteuthis meleagroteuthis*: 23, plan view of dorsal midline mantle tubercles and ridge,  $\times 22$ , SEM, scale 1 mm; 24, side view of dorsal midline mantle tubercles and ridge,  $\times 35$ , SEM, scale 1 mm.

FIGURES 25, 26.—*Histioteuthis meleagroteuthis*: 25, dorsal midline mantle tubercles protruding through epidermis,  $\times 34$ , SEM, scale 1 mm; 26, cross section through dorsal midline mantle tubercle and ridge,  $\times 37$ , SEM, scale 1 mm.

stage of development at a mantle length of about 15 mm and are recognizable as a row of small, separate protuberances or knobs. With growth, additional tubercles appear, and finally the ridge emerges on which the tubercles lie (Figures 23, 24). The tubercles along the arms remain somewhat more distinct with only the bases coalesced (Figure 35) and the ridges are less developed. The tubercles and subsequently the entire ridge appear to protrude through the epidermis (Figures 25, 28) in SEM preparations, but extensive examination of serial sections and whole specimens reveals a delicate layer of epidermis

covers the tubercles (Figure 45). The absence of epidermis in many preparations is due to abrasion and damage during capture.

The internal structure of the tubercles on the mantle under SEM shows an extremely dense, uniform zone that grades inferiorly to a more vacuolated area along the base of the ridge and into the wall of the mantle (Figures 26, 27). The vacuolated tissue varies from very thin, almost membranous vacuole walls in the interior section of the ridge (Figures 29, 30) to a more thick-walled fibrous matrix near the periphery (Figures



FIGURES 27-30.—*Histiototeuthis meleagroteuthis*: 27, enlargement of tubercle portion of Figure 26 showing dense elastic cartilaginous tip,  $\times 185$ , SEM, scale 0.1 mm; 28, cut end of dorsal midline mantle ridge,  $\times 55$ , SEM, scale 0.5 mm; 29, enlargement of a portion of Figure 28 showing small chambers in tubercle ridge tissue,  $\times 550$ , SEM, scale 0.05 mm; 30, further enlargement of a portion of Figure 29 showing thin connective tissue walls of chambers,  $\times 3235$ , SEM, scale 0.01 mm.

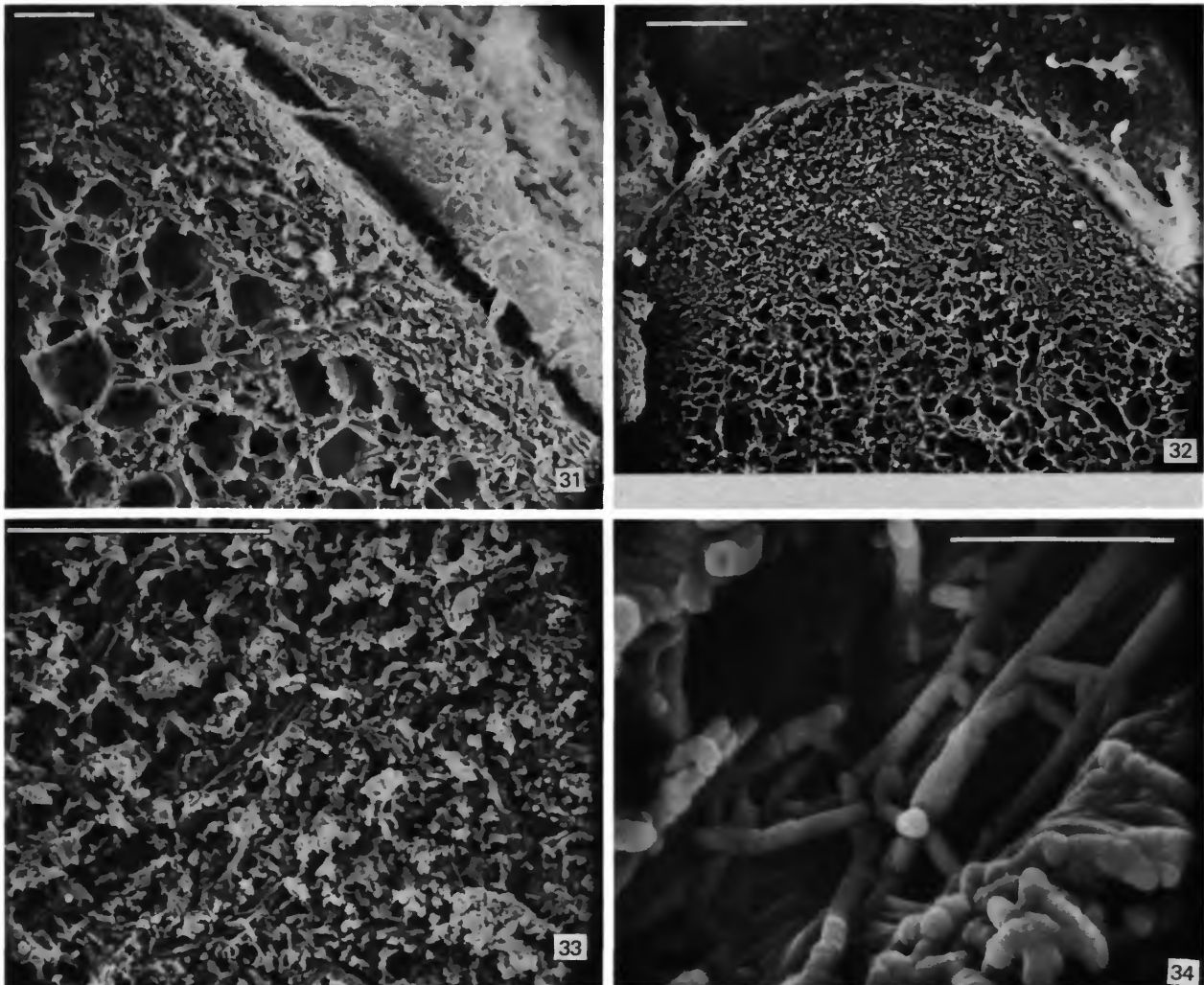


31–34). The vacuolated tissue extends inferiorly and blends in laterally with the wall of the mantle, the tissue of which appears similar to that of the ridge (Figure 26).

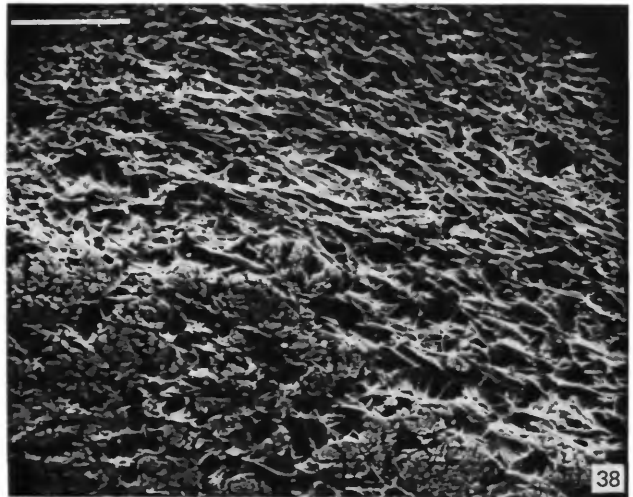
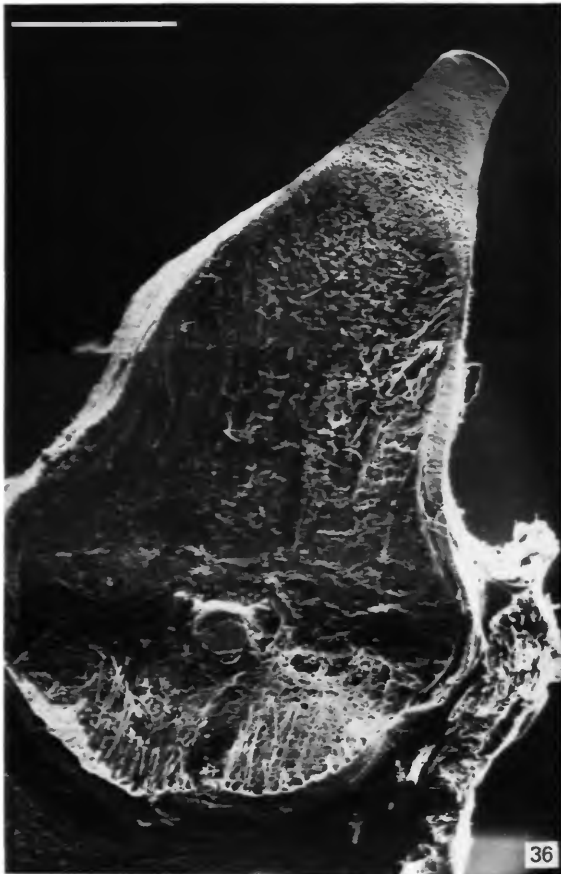
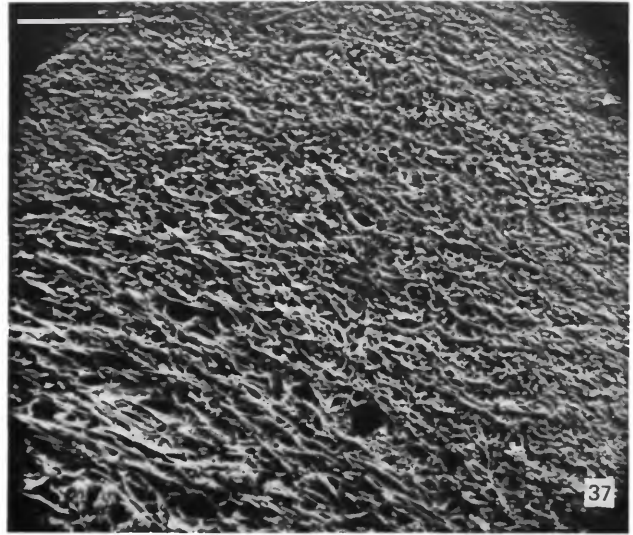
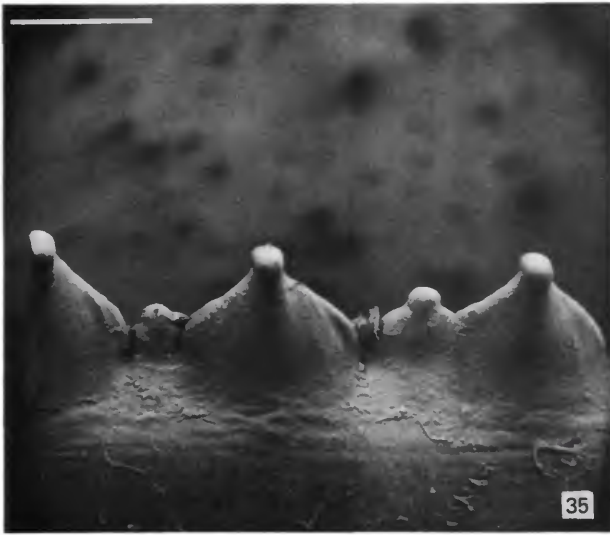
The tip of the mantle tubercle (Figures 26, 27) is extremely dense tissue that consists of a heavy fibrous matrix punctuated by numerous chondrocytes (Figures 26, 27, 44). This tissue in histological sections has the appearance of elastic cartilage, very similar to that of vertebrates. In the core of the tubercle and inferiorly through the base of the ridge, the tissue becomes less dense, more vacuolated, and the chondrocytes become more

widely scattered (Figure 43). The inferior-most zone of the base of the tubercular ridge is sheathed by a thin layer of connective tissue, then, finally, the epithelium of the dorsal side of the shell sac with its densely packed cells.

A transition zone of vacuolated, loose connective tissue interspersed with scattered bundles of circular and radial muscle of the mantle lies lateral to the base of the tubercular ridge. Lateral to this the regular mantle tissue occurs with the following constituents: the epidermal layer consisting of a thin epithelium; a thick, vacuolated, gelatinous dermal layer



FIGURES 31–34.—*Histiotteuthis meleagroteuthis*: 31, enlargement of a portion of Figure 28 showing boundary between the dorsal midline mantle ridge and epidermis,  $\times 600$ , SEM, scale 0.01 mm; 32, enlargement of a portion of Figure 28 showing densely packed fibers which form elastic cartilage of dorsal midline mantle tubercular ridge,  $\times 230$ , SEM, scale 0.1 mm; 33, enlargement of Figure 32 showing elastic cartilage fibers,  $\times 1200$ , SEM, scale 0.05 mm; 34, enlargement of a portion of Figure 33 showing fibers of tubercle,  $\times 10500$ , SEM, scale 0.005 mm.



FIGURES 35-38.—*Histioteuthis meleagroteuthis*: 35, side view of tubercles and ridge on arm III,  $\times 22$ , SEM, scale 1 mm; 36, cross section of entire arm III and cartilagenous tubercle,  $\times 25$ , SEM, scale 1 mm; 37, enlargement of a portion of Figure 36 showing densely packed fibers on base of tubercle,  $\times 180$ , SEM, scale 0.1 mm; 38, enlargement of a portion of Figure 36 at the base of tubercle showing interwoven tubercle fibers (top  $\frac{2}{3}$  of photograph) and longitudinal muscle fibers (bottom  $\frac{1}{3}$ ),  $\times 180$ , SEM, scale 0.1 mm.

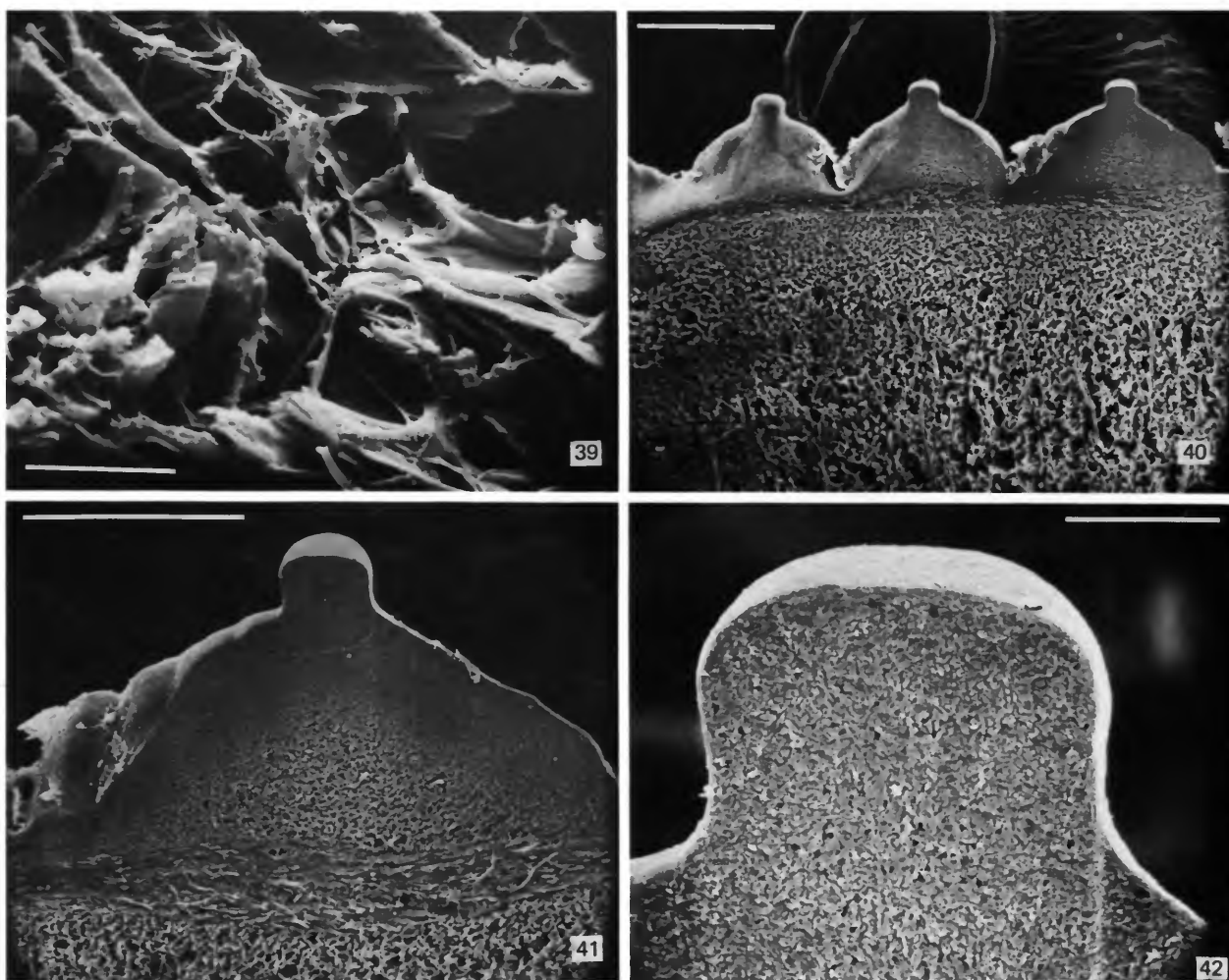


supported by connective tissue; a thin sheath of longitudinal muscle; a thick zone of circular muscle compartmented by radial muscle walls that extend the whole thickness of the muscular portion of the mantle; a moderately thick layer of thin-walled, probably gelatinous, vacuolate, loose connective tissue sandwiched between the superior and inferior layers of circular muscle; a few scattered strands of longitudinal muscle; and the thin inner epithelial layer of the mantle wall.

The tubercles on the arms are distinctive and nipple-like (Figure 35). In cross section, viewed with SEM, the tips of the tubercles are extremely dense and fibrous (Figures 36, 40–42). Toward the center of the tubercle the tissue becomes less dense, more vacuolated (Figure 36), and the matrix consists of

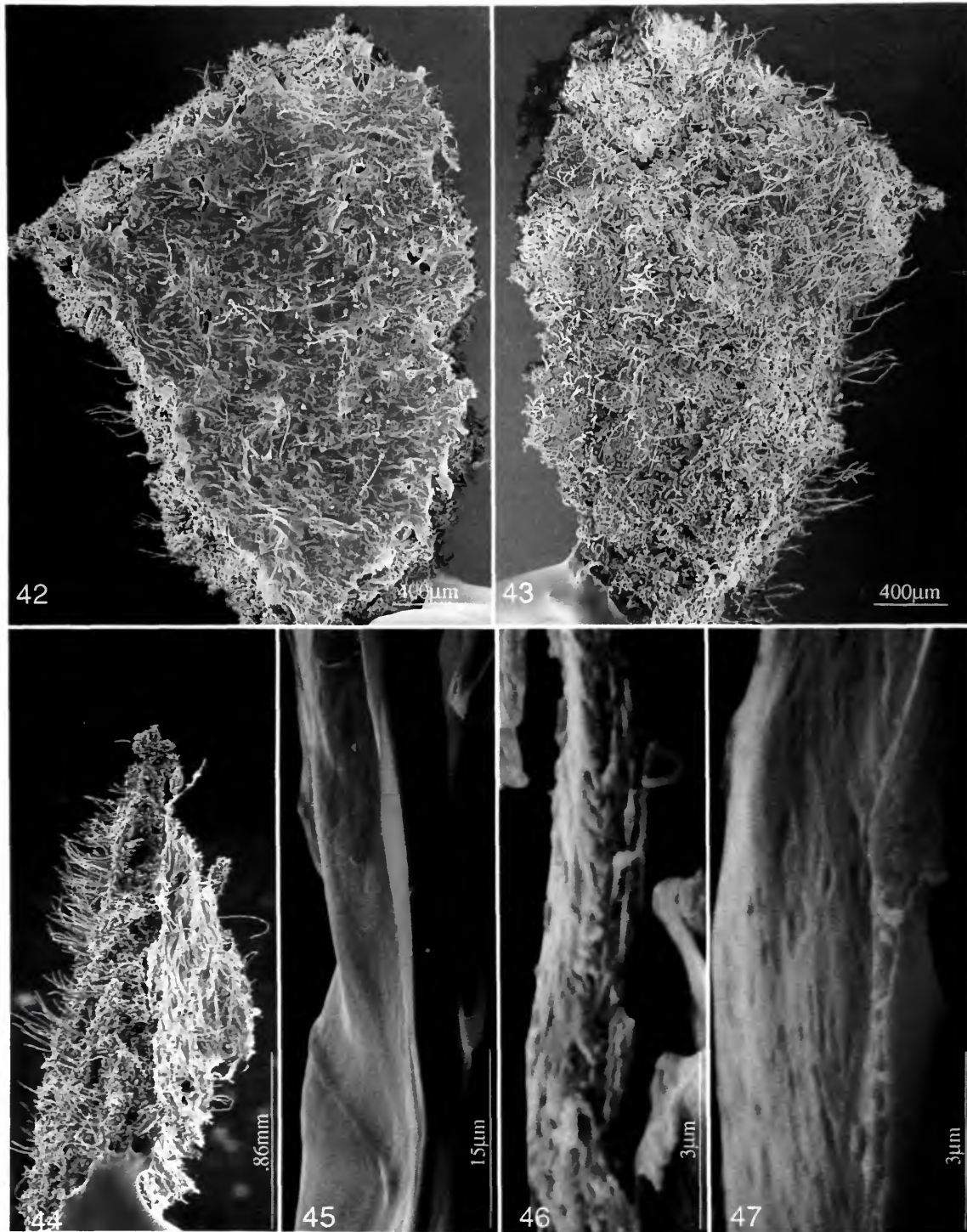
membranous walls and fibrous rods (Figure 37). Inferior to this lies the aboral longitudinal musculature of the arm arranged in loose bundles interspersed with the vacuolated connective tissue (Figures 36, 38–41). The internal structure of the arm consists of loosely arranged, spongy-looking, vacuolated connective (gelatinous) tissue containing scattered radial (transverse) muscle bundles (Figures 45, 46).

The tips of the mantle and arm tubercles under light microscopy are heavily invested with chondrocytes in a dense fibrous matrix (Figures 45, 46). In its staining characteristics this tissue resembles elastic cartilage of vertebrates. A strand of fibrous connective tissue originates on the tubercle and continues to the base of the tubercle where it lies in immediate



FIGURES 39–42.—*Histiot euthis meleagroteuthis*: 39, enlargement of a portion of Figure 38 showing connective tissue fibers (top) and muscle fibers (bottom left),  $\times 1200$ , SEM, scale 0.02 mm; 40, longitudinal section of arm III showing tubercles, arm musculature, and loose connective tissue,  $\times 22$ , SEM, scale 1 mm; 41, enlargement of a tubercle from Figure 40,  $\times 70$ , SEM, scale 0.5 mm; 42, enlargement of a portion of Figure 41 showing dense elastic cartilaginous tip of tubercle,  $\times 300$ , SEM, scale 0.1 mm.





FIGURES 42-47.—Cocoons, *Eustenogaster eximia* (Bingham), Kanneliya: 42, inner surface of section of pupal cell with glistening cocoon fabric covering strands of *Fusarium* hyphae; 43, outer surface of same section covered by hyphae; 44, edge of same cell section, outer surface at left; 45-47, edge of cocoon showing varying degrees of thickness as denoted by scale lines.

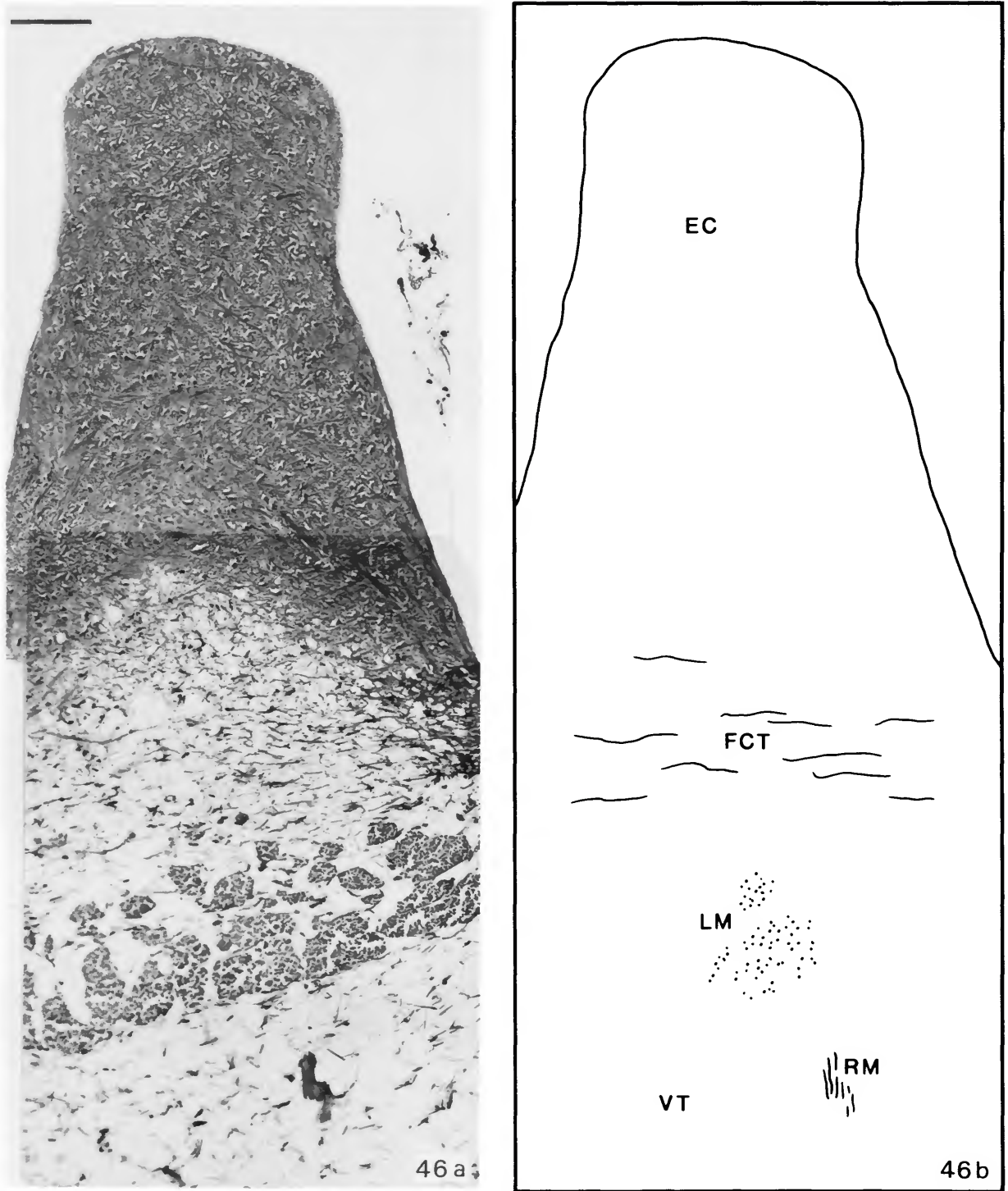
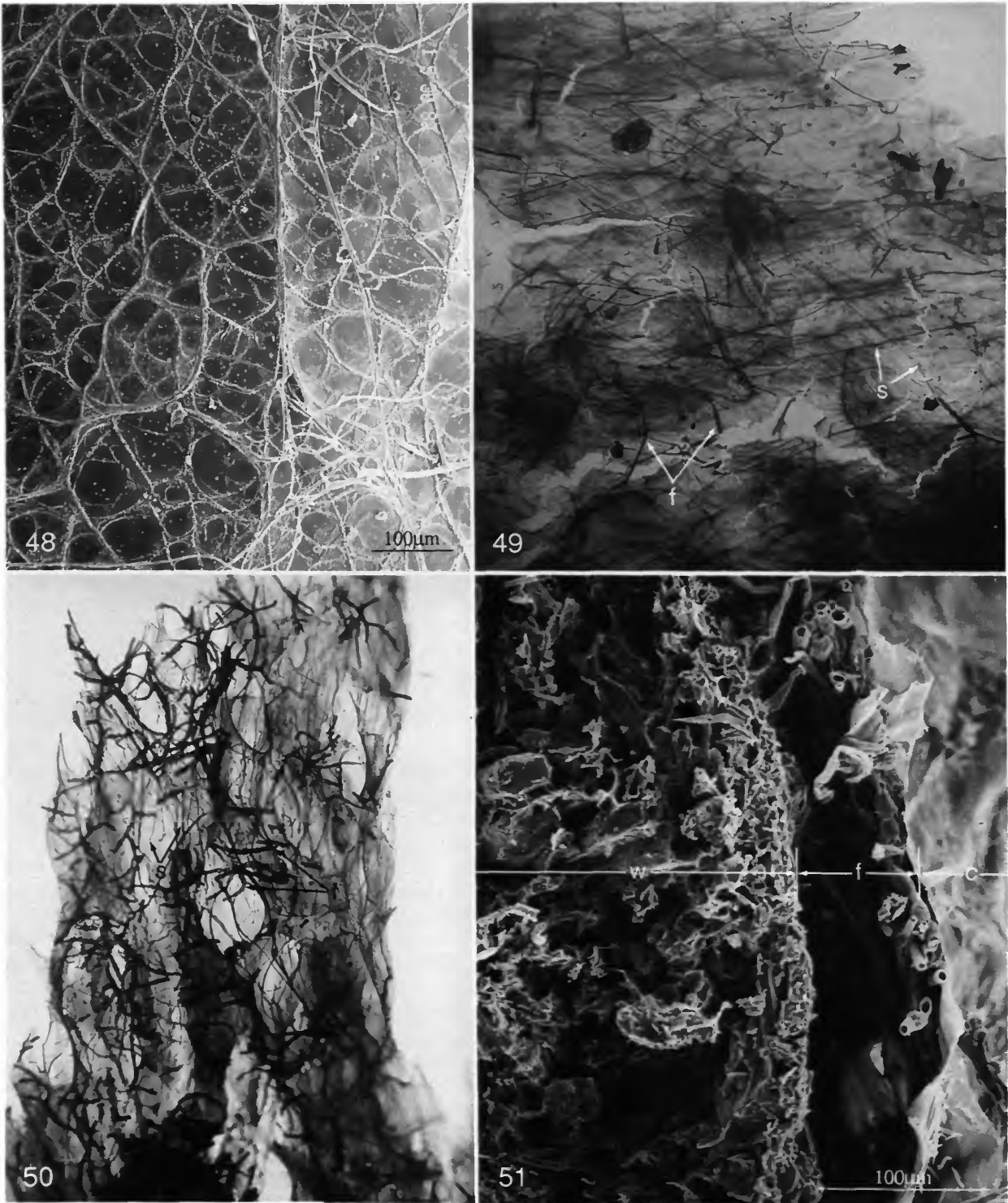
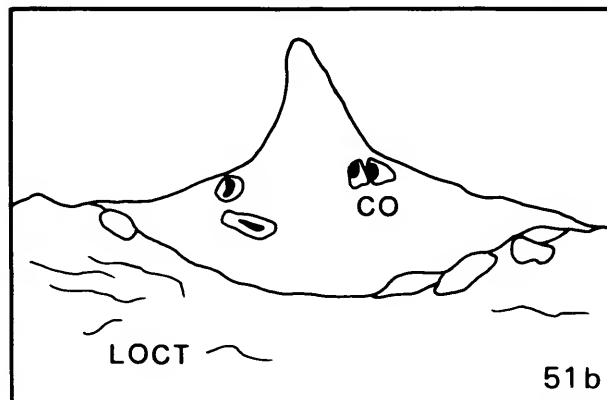
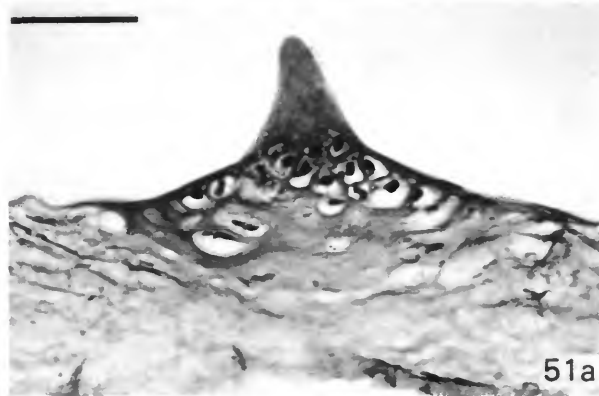
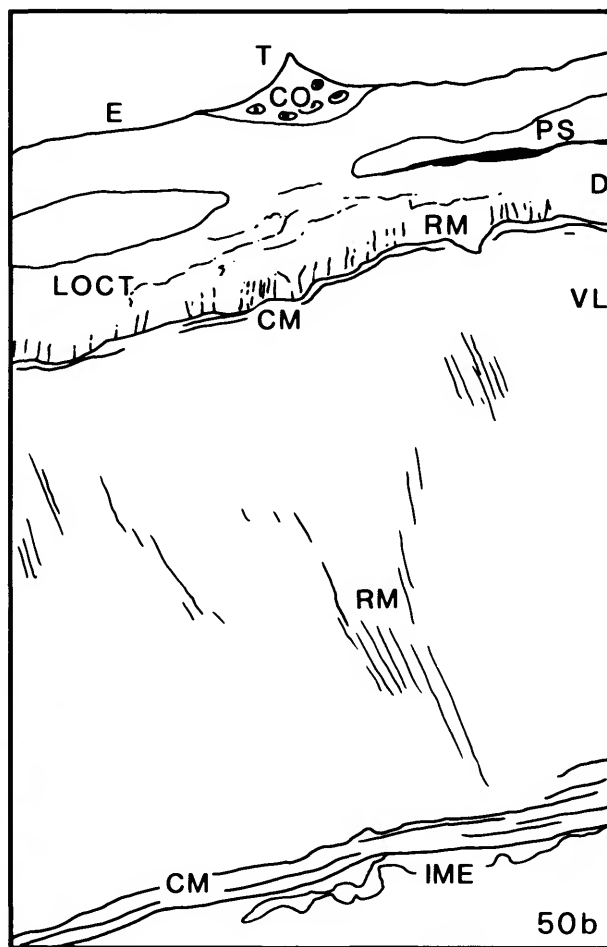
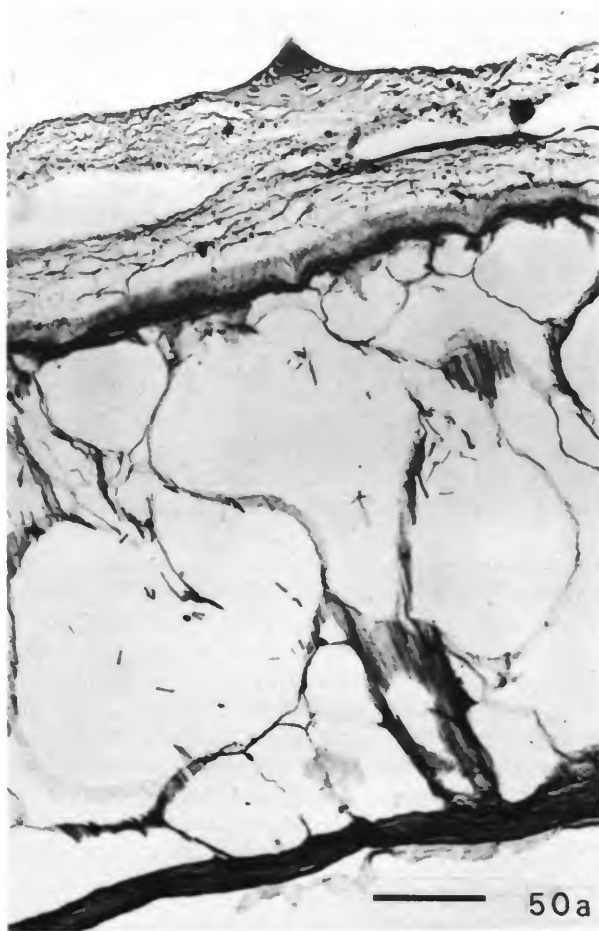


FIGURE 46.—*Histoteuthis meleagroteuthis*: 46a, cross section of arm III showing elastic cartilage tubercle and adjacent muscles and connective tissues,  $\times 40$ , light microscopy, stain H & E, scale 0.1 mm; 46b, diagram of Figure 46a identifying tissue types.





FIGURES 48-51.—Cocoon fabric and fungi: 48, *Crossocerus (Blepharipus) stictochilos* Pate, Plummers Island, Maryland, section of cocoon wall with silken strands overlying glistening film; 49-51, *Eustenogaster eximia* (Bingham), Kanneliya; 49-50, sections of cocoon fabric from alcohol stained with acid fuchsin, darker, thicker, curved, and/or beaded filaments are *Fusarium* hyphae, finer, lighter filaments are silken strands,  $\times 80$ ; 51, section of pupal cell from alcohol, part of cell wall (w) at left, mass of *Fusarium* hyphae (f) in center, and thin cocoon (c), oblique aspect, at right.



FIGURES 50, 51.—*Chiroteuthis acanthoderma*: 50a, cross section of mantle through a tubercle (from Lu, 1977, fig. 14B),  $\times 160$ , light microscopy, stain H & E, scale 1 mm; 50b, diagram of Figure 50 identifying tissue types; 51a, close-up of a hyaline cartilage tubercle showing chondrocytes,  $\times 400$ , light microscopy, stain H & E, scale 0.05 mm; 51b, diagram of Figure 51 identifying tissue types.



The *C. acanthoderma* tubercle does not appear to be true hyaline cartilage, as in the Cranchiidae, for example, because the basal matrix especially is so heavily invested with fibrous material.

The tissues of the mantle consist of the following layers from superior to inferior (Figure 50): a thin epidermis; a relatively thick, vacuolated dermal layer of loose connective tissue containing pigment sacs; a thin layer of a few scattered longitudinal muscle fibers in a connective tissue sheath; a layer of fine radial muscles that interconnect through a thin layer of dense circular muscle; a very thick vacuolate layer of loose connective (gelatinous) tissue with extremely large, thin-wall vacuoles, and this entire layer is interspersed with radial muscle; an inferior layer of circular muscle, about triple the thickness of the superior circular muscle layer; and finally, the inferior epithelium.

#### Family MASTIGOTEUTHIDAE Verrill, 1881

##### *Mastigoteuthis cordiformis* Chun, 1908

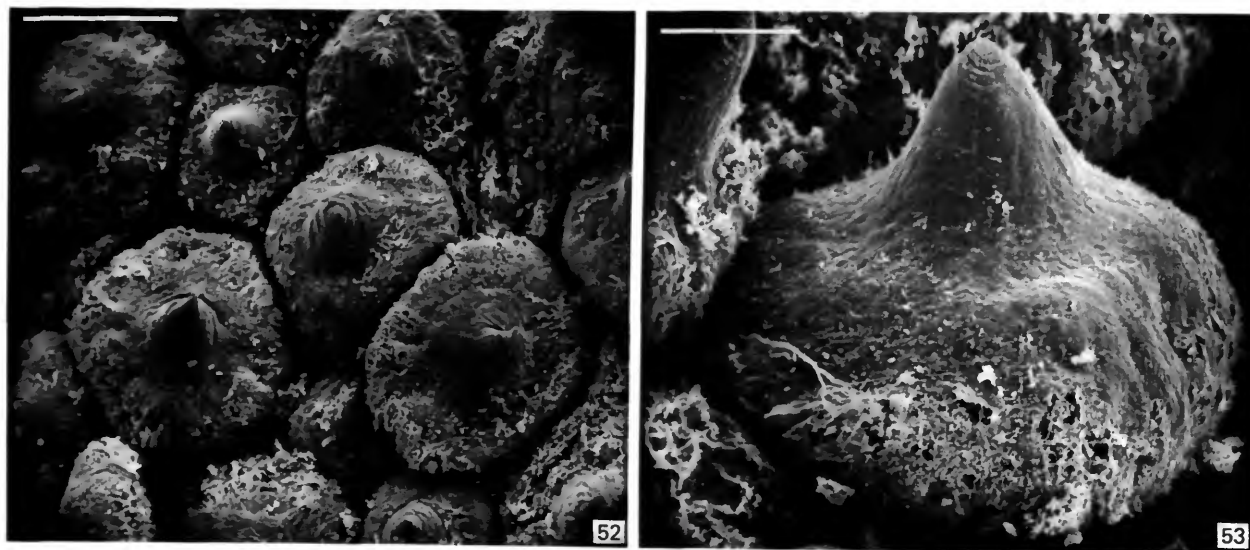
###### FIGURES 52-56

This species is characterized by having the surface of the mantle, head, and arms covered with minute, closely-packed, conical tubercles with blunt to sharply pointed apices (Figures 52, 53). On a specimen of 87 mm ML the tubercles are 0.2 mm in diameter and 0.2-0.3 mm high. The tubercles are covered with a fine epidermis in life, but this epidermal layer generally is rubbed off in preserved specimens, as is the case with the material figured. The internal structure consists of dense

connective tissue which has staining properties and appearance reminiscent of elastic cartilage or fibrocartilage of vertebrates. The fibers are arranged in an orderly pattern (Figures 54-56).

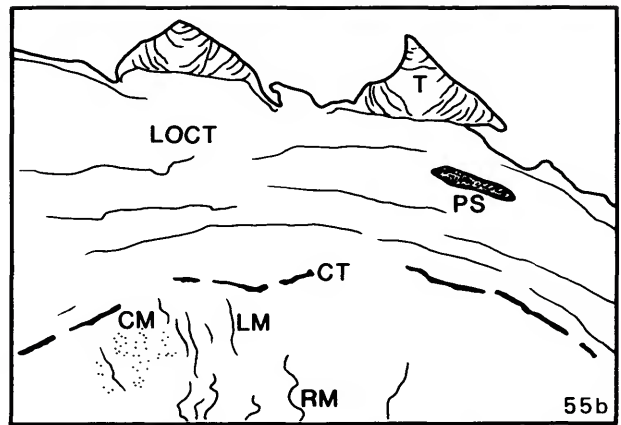
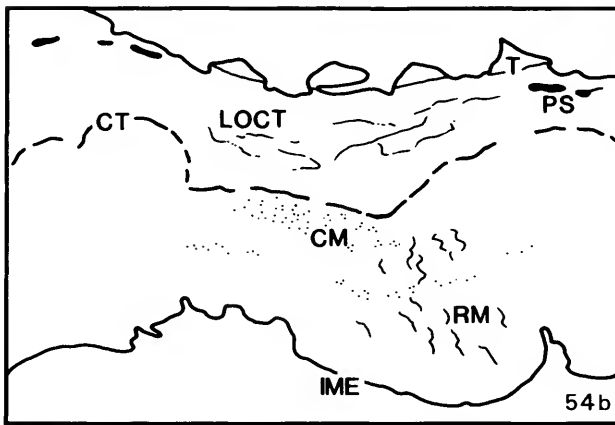
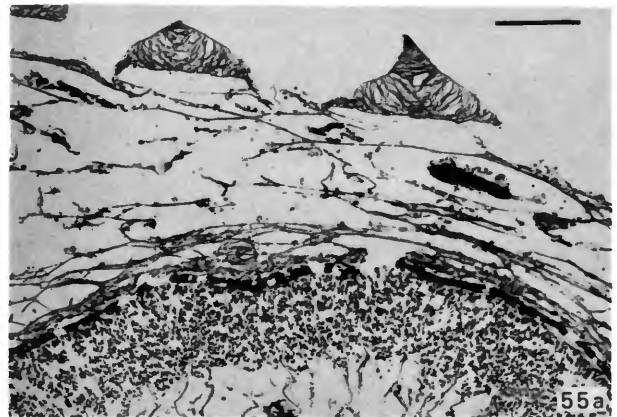
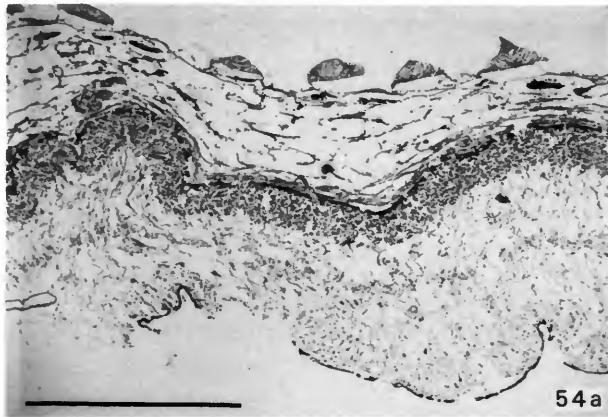
The tubercles consist of a matrix with numerous, elongate vacuoles that are arranged in an orderly pattern; those in the basal portion (in longitudinal section) radiate diagonally in layers from the center of the tubercle to the periphery, while those nearer the tip are somewhat concave and arranged in layers parallel with the surface of the mantle (Figures 55, 56). The walls of the vacuoles are moderately thick and fibrous. A zone of nuclei of epithelial cells is conspicuous around the basal periphery of the tubercles and along the basal discs that lie against the surface of the mantle.

The tissues in histological section (longitudinal sections, Figures 54-56) from superior to inferior through the mantle consist of the following layers: a thin epidermis (frequently rubbed off in preparations); the tubercles; a thick layer of loose ordinary connective tissue, with large, elongate vacuoles, the walls of which have large, dense nuclei; a pigment/chromatophore layer at the superior-most boundary of this vacuolated area; a thin, dense sheath of connective tissue; a thick muscular layer that consists primarily of circular muscle, interspersed with bundles of longitudinal muscle, and penetrated by radial muscle fibers from the inferior thick layer of radial muscle in which is sandwiched a narrow band of circular muscle (the radial muscle is loosely arranged with large spaces between fiber bundles); an inferior-most sub-layer of very loosely scattered circular muscle bundles and other randomly oriented muscle fibers; and the thin, dense inferior mantle epithelium. It should be noted that this tissue sample comes



FIGURES 52, 53.—*Mastigoteuthis cordiformis*: 52, plan view of surface of mantle showing tubercles,  $\times 200$ , SEM, scale 0.1 mm; 53, side view of a tubercle,  $\times 500$ , SEM, scale 0.05 mm.





FIGURES 54, 55.—*Mastigoteuthis cordiformis*: 54a, longitudinal section of a portion of mantle through several tubercles,  $\times 16$ , light microscopy, stain H & E, scale 0.5 mm; 54b, diagram of Figure 54a identifying tissue types; 55a, enlargement of a portion of Figure 54a with two elastic/fibrocartilage tubercles,  $\times 40$ , light microscopy, stain H & E, scale 0.1 mm; 55b, diagram of Figure 55a identifying tissue types.

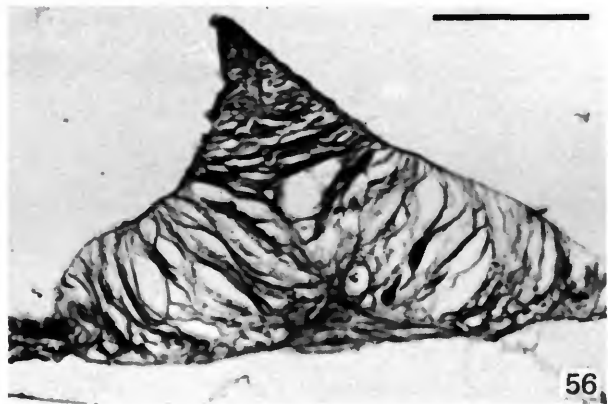


FIGURE 56.—*Mastigoteuthis cordiformis*: enlargement of a tubercle from Figure 54a showing elastic/fibrocartilage tissue,  $\times 400$ , light microscopy, stain H & E, scale 0.05 mm.

from a long-preserved specimen in which the initial fixation was not uniform, and the inferior tissue has deteriorated to a certain extent. Subsequent examination of well-fixed specimens shows that the inferior layer of circular muscle actually is as well developed and extensive as the superior circular muscle.

***Mastigoteuthis hjorti* Chun, 1913**

FIGURES 57-61

*Mastigoteuthis hjorti* has extremely minute, disc-like, closely packed tubercles, each with a central conical papilla or spire, that cover the surface of the mantle, head, and arms (Figures 57, 58). The tubercles on a specimen of 93 mm ML measure 0.1-0.2 mm in diameter and 0.05-0.1 mm high. These tubercles and the epidermal layer in which they are embedded frequently are lost during capture. The tubercles (Figures 60, 61) consist of a relatively densely-staining

Kandy District: Hasalaka, Thawalammenne, and Kandy, Udawattakele Sanctuary

Colombo District: Labugama Reservoir and Mirigama Scout Camp

Ratnapura District: Weddagala, Gilimale, and Belihul Oya

Badulla District: Ella

Monaragala District: Angunakolapelessa

Galle District: Kanneliya

Matara District: Deniyaya

NESTING BEHAVIOR.—I observed this only once in Udawattakele Sanctuary, at 1512 on 22 September 1980. The wasp, 22 mm long, was finishing the closure of her nest, which was placed on a slight slope in dense jungle against a tree root. She tugged at several large leaves, apparently trying to obtain small fragments to conceal the nest entrance. I captured her in a few minutes, and found that her nest was in the tunnel of the prey spider. The tunnel extended 6.4 cm from the entrance to the terminal cell of the spider. The wasp had filled the tunnel loosely with soil. The cell was 2.5 cm long, 2.0 cm high, and 1.5 cm wide. The bulky spider, 21.5 mm long, was thoroughly paralyzed and had been placed on its back with the cephalothorax toward the inner end of the cell. The slightly curved egg, 2.9 mm long and 0.9 mm in diameter, was placed transversely toward the anterior end of the abdominal venter of the spider.

P.B. Karunaratne told me that this spider constructs its nest near the soil surface, lines the tunnel and terminal cell with silk, and makes a funnel-shaped entrance that is camouflaged with pieces of leaf or bark. The wasp must have removed the silk lining the entrance and tunnel before making the closure, for I found a silken lining only at the inner end of the cell.

PREY.—The prey specimens that we collected with the wasps were large, bulky, typical tarantulas belonging to the families Idiopidae and Barychelidae.

The prey at Udawattakele was an adult female idiopid, possibly a species of *Scalidognathus* Karsch. The other three prey specimens, two from Angunakolapelessa and one from Induruwa Jungle, Gilimale, were immatures of the barychelid spider, *Plagiobothrus semilunaris* Karsch. I kept one of the prey from Angunakolapelessa alive for some hours. In 6½ hours it recovered enough from thorough paralysis, so that it could flex its legs but was incapable of walking.

PREY TRANSPORT.—I saw a small *convexa*, 14 mm long, crawling rapidly and excitedly over an almost vertical bank of a dry streambed at Angunakolapelessa at 0943, 27 March 1981. After about five minutes she visited her thoroughly paralyzed prey, 13.5 mm long, that was lying venter up on a small flat ledge near the top of the bank. The wasp then disappeared in the leaf litter next to the bank, and returned at 0954. She started to drag off the prey, was frightened by my proximity, and I captured her when she returned 10 minutes later.

At 1415 on this same date T. Wijesinhe saw a small *convexa*, 12 mm long, walking on the leaf litter in the same dry streambed. She pulled a paralyzed spider, 15.5 mm long, from beneath the leaves, turned it venter down, and, walking backward, dragged the prey while grasping it at the head end.

My last prey record was in the Induruwa Jungle, Gilimale, at

1240, 16 April 1981. A female *convexa*, 22 mm long, was dragging her thoroughly paralyzed spider, 16.5 mm long, venter up, at the edge of a trail through the dense rain forest.

Williams (1956) noted that the egg of *H. ustulata ochroptera* was 4.25 mm long, slightly curved, and was attached at one side of the ventral line and at midlength of the spider's abdomen. He also stated that the cocoon was 35 mm long, and was spun of brown silk with a single wall that was varnished on the inner surface.

### *Hemipepsis indiana* Wahis

This rather uncommon species occurs in Sri Lanka and southern India (Bengal, Tranquebar in Tamil Nadu, and Coimbatore in Kerala). Within Sri Lanka it has been collected only in the Dry Zone at altitudes from near sea level to 30 m and with an average annual rainfall ranging from 920 to 1000 mm. Our few records of its occurrence in Sri Lanka are as follows.

Mannar District: 0.8 km NE of Kokmotte Bungalow, Wilpattu National Park

Anuradhapura District: Padaviya

Hambantota District: Palatupana Tank

PREY HUNTING.—I saw one female, 20 mm long, hunting for a prey in the leaf litter beneath a small malith tree, *Woodfordia fruticosa* (Lythraceae) in an open field at Palatupana Tank at 0810, 28 September 1977. During her search she flicked her wings rapidly from a position of being folded flat over her abdomen, and antennated the ground incessantly. She paused briefly at a silken burrow entrance, 10 mm in diameter, next to a tree root, antennated the entrance, and then moved on. She returned 10 minutes later and entered the burrow. A minute later I saw a large spider run rapidly down a slight slope from a second entrance on the other side of the root. The wasp lost sight of the spider scurrying away, but picked up its trail five minutes later. I captured the wasp at 0838, after she had clearly lost the spider's trail.

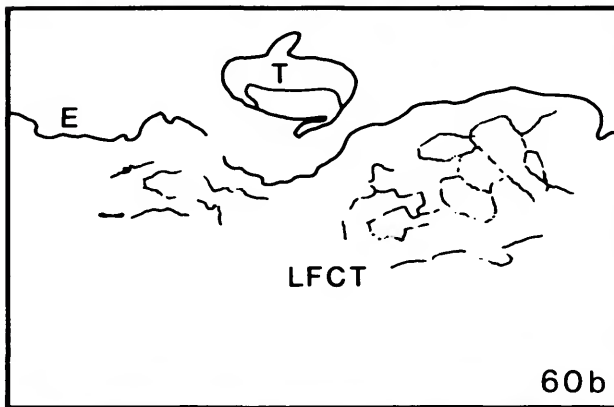
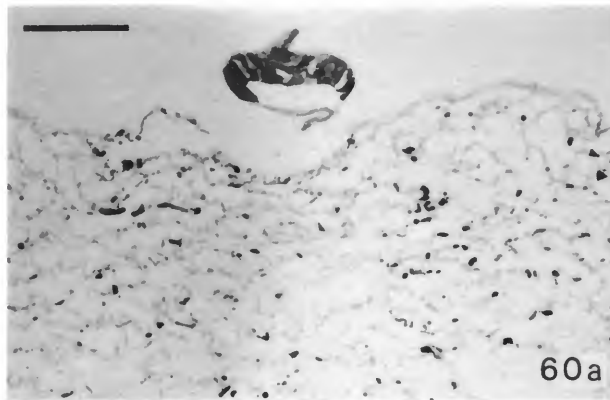
### *Dipogon kandiensis* (Turner)

This species is endemic to Sri Lanka where we collected it in the Wet Zone at altitudes of 610–1050 m with an average annual rainfall of 3000 mm as follows.

Kandy District: Thawalammenne and Kandy, Udawattakele Sanctuary

Both of my behavioral records are from Udawattakele, the area in which Turner's holotype specimen was probably captured by O.S. Wickwar.

NEST.—I found a female, 8.7 mm long, sealing the nest entrance in a cavity in a standing dead tree in mid-morning, 22 March 1981. Her abdomen was curved beneath her, and she was using the tip to compact the debris that formed the closing plug. The nest was in an abandoned boring, presumably of a beetle, in sound dead wood with an entrance diameter of about 7 mm. The plug, which came to within 3 mm of the surface when I captured the wasp, consisted of small bits of bark and



FIGURES 60, 61.—*Mastigoteuthis hjorti*: 60a, cross section of mantle and elastic/fibrocartilage tubercles,  $\times 160$ , light microscopy, stain H & E, scale 0.1 mm; 60b, diagram of Figure 60a identifying tissue types; 61, close-up of tubercle from Figure 60a,  $\times 400$ , light microscopy, stain H & E, scale 0.05 mm.

tubercles have round, triangular, or rectangular bases from which arise 2, 3, 4, or 5 projections (Figures 62–64) which in turn have 2–5 sharp to bluntly rounded cone-shaped papillae at the tip of each projection (Dilly and Nixon, 1976, pl. 1a). From a specimen of 94 mm ML the 4-armed tubercles, which resemble Maltese crosses, and the 5-armed tubercles are the largest with a diameter of about 0.5 mm and a height of 0.4 mm. The 2-armed tubercles are about 0.8 mm in diameter and 0.2 mm high, while the 3-armed tubercles are about 0.4 mm in diameter and 0.3 mm high.

The histological structure of the tubercles resembles vertebrate hyaline cartilage in appearance under light microscopy (Figures 66, 67). The tubercles contain many single and double-chambered chondrocytes suspended in a homogeneous matrix. A dimly visible reticulation of fine dark lines or fibers is disbursed throughout the matrix and may be comparable with the fibers in vertebrate hyaline cartilage. The growing site is at the tips of the papillae where the chondrocytes are new cells that are flat, elongate, and densely packed, versus the single, round chondrocytes, widely distributed through the matrix of the tubercle. The epidermis adheres to the tip of the tubercle.

The mantle tissue (Figure 66) consists of the following histological layers: the epidermal layer; a wide, subepidermal connective tissue layer of chambers that occupy the same level with the tubercles; a dense layer of circular muscle from which the bases of the tubercles arise; a thick layer of longitudinal muscle interwoven with a very thick layer of radial muscle; and a relatively thin layer of circular muscle immediately adjacent to the large-celled, epithelial lining of the mantle cavity.

#### *Liocranchia reinhardtii* (Steenstrup, 1856)

FIGURES 68–74

*Liocranchia reinhardtii* is characterized by a pair of V-shape rows of conical, cartilaginous tubercles on the anterior ventral surface of the mantle and by a single row of conical cartilaginous tubercles along the dorsal midline of the mantle nearly to the anterior level of the fins (Figures 68, 69). The ventral V-shape rows of tubercles diverge posteriorly, arising from the subcutaneous, cartilaginous bases that originate at the cartilaginous fusion of the mantle-funnel locking mechanism. Tubercles are an integral outgrowth from the bases and do not occur as individual tubercles isolated from the bases (see *Leachia cyclura*). The dorsal row of tubercles arises from a thin, narrow, subcutaneous, cartilaginous band that lies immediately dorsal to the gladius and shell sac and extends the length of the mantle. Each tubercle is a single, conical structure covered by the epidermis. Tubercles are 0.15–0.2 mm high and 0.2–0.3 mm in diameter on a specimen of 29 mm ML.

The composition of the tubercles and basal bands is cartilaginous, similar in appearance to hyaline cartilage in vertebrates (Figures 71–74). The chondrocytes appear typical



Singapore, Sarawak, Sumatra, Java, and possibly Sulawesi. Within Sri Lanka it occurs in all three ecological zones at localities with an altitude from near sea level to 610 m and an average annual rainfall of 1000–5000 mm. We collected it in Sri Lanka as follows.

Mannar District: 0.8 km NE of Kokmotte Bungalow, Wilpattu National Park

Anuradhapura District: Hunuwilagama

Polonnaruwa District: Pimburettawa

Trincomalee District: Trincomalee, China Bay

Amparai District: Ekgal Aru Reservoir

Kandy District: Gannoruwa, Hasalaka, and Kandy, Udawattakele Sanctuary

Ratnapura District: Gilimale

PREY.—P.B. Karunaratne caught a female of *blandus*, 12.5 mm long, with her prey on a plant leaf along a trail through the Induruwa Jungle, Gilimale on 10 October 1980. She had amputated all legs from her spider prey, and was feeding on the blood exuding from the stumps. The prey, 12 mm long, was an immature giant crab spider, a species of Sparassidae.

ADULT BEHAVIOR.—P.B. Karunaratne noted an unusual behavioral characteristic on 13 September 1977. This occurred during the dark overcast preceding a mid-afternoon shower in Ekgal Aru Reservoir jungle. A number of both females and males had congregated in the deep crevices between the buttress roots of a large *Ficus* species.

#### *Auplopus cyanellus* Wahis

This uncommon species is endemic to Sri Lanka, where we collected the type series in the Wet Zone at altitudes of 90–610 m with an average annual rainfall of 2032–5000 mm. The Sri Lankan records are as follows.

Kandy District: Kandy, Udawattakele Sanctuary

Ratnapura District: Gilimale

PREY.—P.B. Karunaratne collected a female, 6.5 mm long, with prey at 1130 on 9 September 1977, in Udawattakele. The wasp was on the leaf of a plant a meter above the ground, with a paralyzed, green running or sac spider, a species of *Clubiona* Latreille (Clubionidae), 7.5 mm long. The wasp had amputated all of the spider's legs.

#### *Auplopus funerator* Wahis

This species is known only from the holotype from Kegalla District, Bandarakele Jungle, Kitulgala, in the Wet Zone at about 200 m with an average annual rainfall about 5000 mm.

PREY.—I captured this female, 7.0 mm long, on a leaf at 1240 on 15 April 1981. She held beneath her a thoroughly paralyzed spider, 7.5 mm long, from which she had amputated all legs beyond the coxae. The prey was an immature of a species of *Psechrus* Thorell (Psechridae), a cribellate spider.

#### *Auplopus gomus* (Cameron)

This species is known from Sri Lanka, southern India,

Assam, Singapore, and Penang. Within Sri Lanka it occurs in all three ecological zones in localities with altitudes from near sea level to 610 m and average annual rainfall of 1500–3900 mm. We collected it as follows.

Anuradhapura District: Padaviya

Amparai District: Ekgal Aru Reservoir and Lahugala Sanctuary

Matale District: Kibissa near Sigiriya

Kandy District: Gannoruwa, Thawalammenne, Hasalaka, and Kandy, Udawattakele Sanctuary

Colombo District: Gampaha, Labugama Reservoir, and Handapangoda

Ratnapura District: Ratnapura and Rajawaka

Badulla District: Ulhitiya Oya 24 km NNE of Mahiyangana

Monaragala District: Angunakolapelessa

PREY CAPTURE AND TRANSPORT.—P.B. Karunaratne made two observations of this wasp with her wolf spider prey. The first was at Lahugala Reservoir on 15 June 1976. The wasp, 11 mm long, walked forward, carrying the paralyzed prey by its mouthparts, and raising the spider off the ground during transport. She paused briefly to feed on blood exuding from the severed stumps of the legs, all of which she had amputated at the coxae. The lycosid spider, 9.0 mm long, was a species of *Pardosa* Koch.

The second observation was made along a vehicular road outside of Hasalaka at noon on 17 February 1977. The wasp, 12 mm long, was dragging her prey, 10 mm long, up a roadside bank by a front leg. She walked forward with her head turned sideways. The spider got caught in a crevice, and she fed on blood exuding from the severed stumps of several legs. She had already amputated the two posterior legs on one side, and three posterior legs on the other. The spider moved a little, and the wasp stung it again, inserted her mandibles in the mouthparts of the prey, and then fed again on blood from the severed leg stumps. The lycosid spider, 10.0 mm long, was a species of *Trochosa* Koch.

#### *Auplopus himalayensis* (Cameron)

This common species has a wide distribution in the Oriental Region, ranging from the Indian subcontinent eastward to Thailand, North Borneo, Sarawak, Sumba, and the Philippines. Within Sri Lanka it occurs at localities in all three ecological zones in localities with altitudes from near sea level to 610 m and an average annual rainfall of 1200–5000 mm. We collected it as follows.

Mannar District: 0.8 km NE of Kokmotte Bungalow, Wilpattu National Park

Vavuniya District: Paralanalankiyulam

Polonnaruwa District: Polonnaruwa

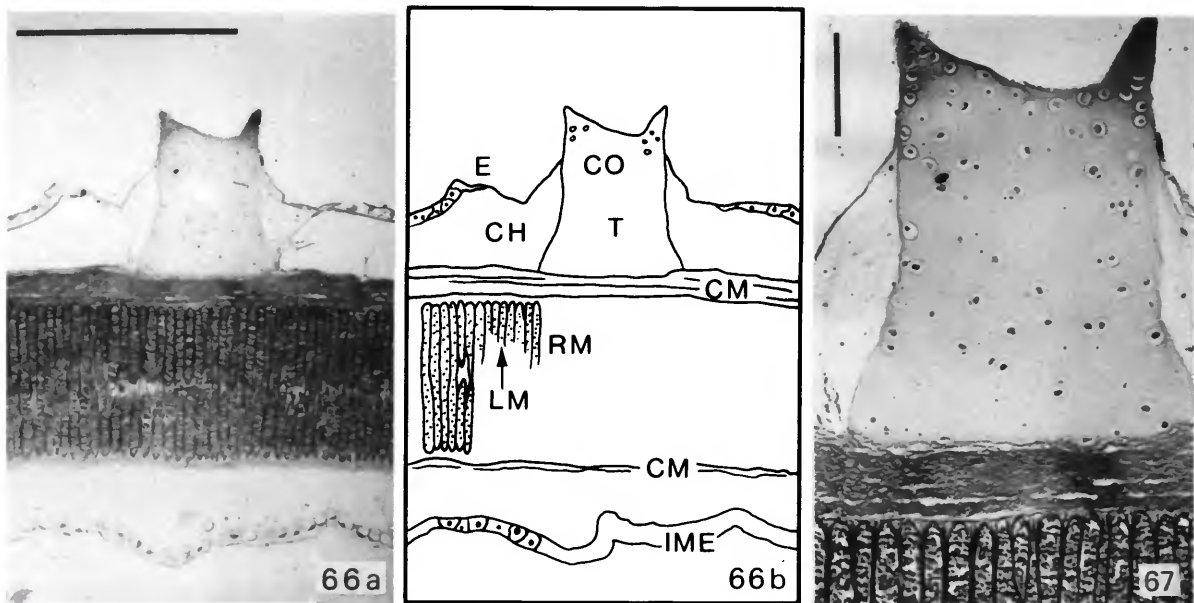
Trincomalee District: Trincomalee, China Bay

Amparai District: Ekgal Aru Reservoir

Matale District: Kibissa near Sigiriya

Kandy District: Hasalaka and Kandy, Udawattakele Sanctuary

Kalutara District: Agalawatte



FIGURES 66, 67.—*Cranchia scabra*: 66a, cross section of mantle through a hyaline cartilage tubercle,  $\times 63$ , light microscopy, stain H & E, scale 0.5 mm; 66b, diagram of Figure 66a identifying tissue types; 67, close-up of tubercle from Figure 66a showing details of hyaline cartilage structure,  $\times 160$ , light microscopy, stain H & E, scale 0.1 mm.

musculature as a thick admixture of circular and radial muscle bundles with a band of longitudinal muscles sandwiched in the center; a thin sheath of connective tissue; and a fine epithelial inner lining of the mantle.

### *Leachia cyclura* Lesueur, 1821

FIGURES 75–81

*Leachia cyclura* is characterized by a single row of cartilaginous tubercles that extends posteriorly on a cartilaginous band from each of the ventral mantle-funnel fusion points (Figure 75). The tubercles continue in a line posteriorly from the termination of the cartilaginous band. They are isolated from each other and arise from slightly enlarged bases that are embedded in the entire cross-sectional extent of the mantle musculature (i.e., they do not arise from the outer tunic of connective tissue on the superior surface of the mantle wall). The tubercles vary in shape from small, simple, conical papillae to large, complex structures with numerous conical projections. Normally, these tubercles exhibit an alternating pattern with a large, complex tubercle situated at the mantle-funnel fusion followed posteriorly by a few small conical papillae, then a large complex tubercle, etc. Tubercles from a specimen 55 mm ML range from 0.1–0.2 mm in height and 0.3–0.4 mm in diameter. No tubercles are present in the dorsal midline superior to the gladius.

In sections observed with the SEM the tubercles show a very

dense uniform matrix interspersed with a few large vacuoles (Figures 76, 77). Histological sections examined with light microscopy show a collagen-rich structure of hyaline cartilage with very densely distributed chondrocytes (Figures 78–81). The chondrocytes are in all stages of development including large concentrations of nest cells particularly in the cartilaginous band (Figure 81). A series of numerous, irregular, collagenous fibers are disbursed through the matrix of chondroid tissue; the fibers appear to interconnect the chondrocytes (Figure 81). The collagenous fibers that radiate from the chondrocytes in the peripheral zone of the band appear to extend only toward the interior of the band, while none arise on the sides facing the boundary of the band along the mantle (Figure 80).

A delicately thin layer of perichondrium is associated with the cartilaginous band, particularly along its inferior edge (Figure 80). It is difficult to distinguish along the lateral borders where the muscles of the mantle insert with the cartilage. Remnants of perichondrium appear on the superior surface of the band and on the tubercles, where most of the epidermal tissue is rubbed off during capture and fixation.

Growth of the tubercle seems to occur primarily from the perichondrium along the periphery of the supporting band. Chondrocytes are well developed, mature, and nested in the tubercles and tips. Young chondrocytes occur on the superior surface of the band and around the periphery of the base of the tubercles.

level to 610 m and with an average annual rainfall of 1000–2032 mm. We collected it as follows.

Mannar District: Ma Villu, Kondachchi, and 0.8 km NE of

Kokmotte Bungalow, Wilpattu National Park

Anuradhapura District: Padaviya

Trincomalee District: Trincomalee, China Bay

Kandy District: Kandy, Udawattakele Sanctuary

Puttalam District: Panikka Villu

Colombo District: Katunayaka

Kalutara District: Agalawatte

PREY CAPTURE AND TRANSPORT.—P.B. Karunaratne and I spent two hours watching a female of *smithii*, 14 mm long, capture and transport her prey at Panikka Villu. The wasp entered a burrow in sandy soil near the shore of the villu at 1545 on 1 November 1977. While the wasp was inside, a large wolf spider ran toward the villu from another burrow entrance. The wasp soon emerged, searched the sand on foot for five minutes, and then flew toward the spider which was now running about five meters from the burrow. She followed the spider for nearly two meters, landed on its body, and probably stung it, for the spider turned on its back and tried to bite the wasp. The latter preened herself for half a minute, during which time the spider righted itself and crawled slowly toward another burrow. Before it could enter, the wasp landed on its abdomen, and stung it three more times. Then she went to the front of the spider, and stung it again on the venter near the juncture of the cephalothorax and abdomen. She remained at the front, and appeared to be feeding at the spider's mouthparts for half a minute. Then she groomed herself for a minute, malaxated the prey near the base of the first two legs on the right side of the spider, and fed for another minute. Then, grasping one of the front legs, she dragged the spider into the hoofprint of a deer, and stayed there for an hour, alternately feeding on the spider's hemolymph, or grooming herself. She remained in the hoofprint with her prey until 1650, when she grasped the spider by the second leg on the right side, and, walking backward, dragged it about two meters toward the spider's burrow. She remained in that spot for 45 minutes, alternately feeding at the base of the spider's legs and grooming herself, moving the spider no more than two centimeters during this time. We captured the wasp at 1745. The spider was a species of *Lycosa* Latreille (Lycosidae), 15 mm long.

#### *Pompilus mirandus* (Saussure)

This species was recorded by Day (1981) from Pakistan to Sri Lanka, Burma, Malaya, and Java. He listed Sri Lankan localities as follows.

Jaffna District: Mandaitivu Island, Mankuppana on Leiden Island, and 16 km S of Pooneryn

Mannar District: 0.8 km NE of Kokmotte Bungalow in Wilpattu National Park, Olaittoduvai, Silavatturai, and Kondachchi, Mullikkulam across Moderagam Aru from Wilpattu National Park

Anuradhapura District: Padaviya and Hunuwilagama

Trincomalee District: Tennamaravadi and Trincomalee, China Bay

Amparai District: Panama, Radella Tank

Kandy District: Aruppola, Teldeniya, Hasalaka, and Kandy, Udawattakele Sanctuary

Puttalam District: Panikka Villu and Tala Wila

Colombo District: Katunayaka, Colombo Museum Garden, Kohuwala, Nugegoda, Papiliyana, and Ratmalana

Ratnapura District: Uggalkaltota

Monaragala District: Angunakolapelessa and Mau Aru

Hambantota District: Hambantota and Palutapana

The species occurs usually on rather sandy soil in all three ecological areas, although it is most abundant in the Dry Zone. It is found from sea level to 510 m in localities where the average annual rainfall is 920–2032 mm.

PREY.—P.B. Karunaratne caught a female, 7 mm long, with her prey at 1120 on 14 June 1976, on the bund of Radella Tank at Panama. The spider was an immature wolf spider, 4.5 mm long, a species of Lycosidae.

#### *Aporinellus hecate* (Cameron)

This widespread pompilid is found in all three ecological areas but, like the preceding species, it is most abundant in the Dry Zone, usually nesting in rather sandy soil. It occurs from sea level to 510 m in localities where the average annual rainfall is 920–4900 mm. We collected it as follows.

Jaffna District: Kilinochchi

Mannar District: Kondachchi, Ma Villu, Silavatturai, 16 and 21 km S of Pooneryn, and 0.8 km NE of Kokmotte Bungalow in Wilpattu National Park

Vavuniya District: Parayanalankulam

Anuradhapura District: Hunuwilagama, Medawachchiya, Padaviya, and Ritigala Natural Reserve

Trincomalee District: Trincomalee, Port Frederick, China Bay, Kanniyai, and Tennamaravadi

Amparai District: Ekgal Aru Reservoir, Inginiyagala, Lahu-gala Sanctuary, and Mannampitiya

Matale District: Kibissa 0.8 km W of Sigiriya

Kandy District: Hasalaka, Thawalammenne, and Kandy, Udawattakele Sanctuary

Puttalam District: Panikka Villu

Kurunegala District: Kurunegala, Badegamuwa Jungle

Colombo District: Colombo Museum Garden, Gampaha Botanical Garden, Labugama, Ratmalana, and Handapangoda

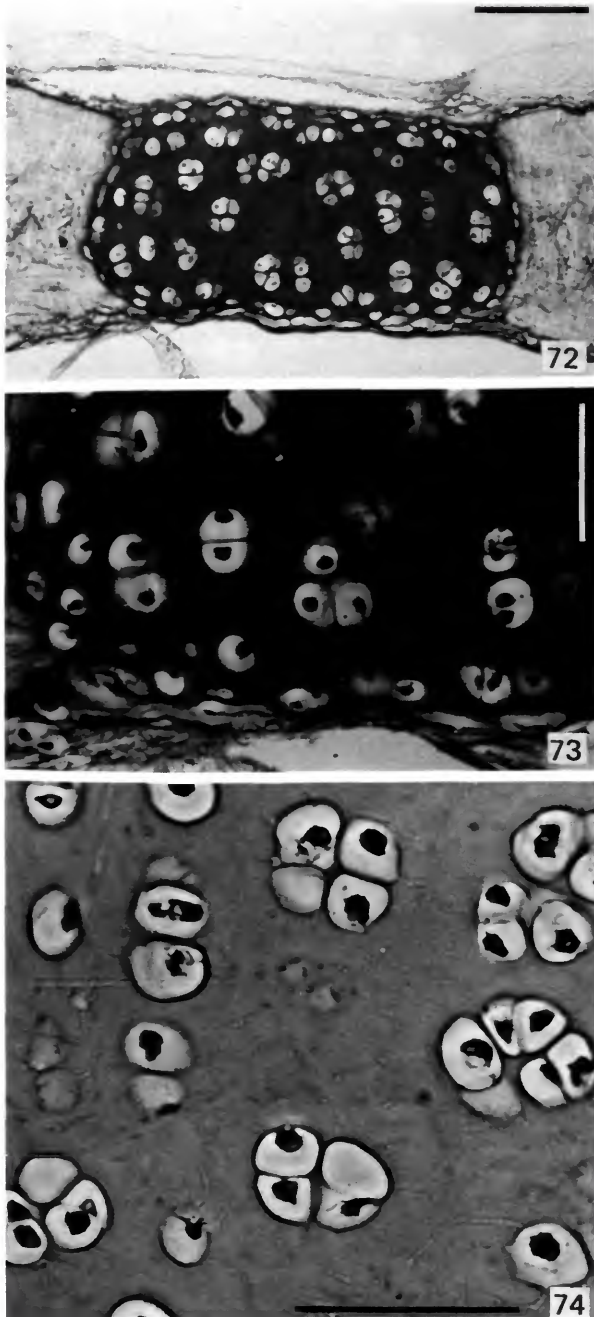
Ratnapura District: Ratnapura, Rajawaka, Uggalkaltota, and Weddagala

Badulla District: Ella and Ulhitiya Oya 24 km NNE of Mahiyangana

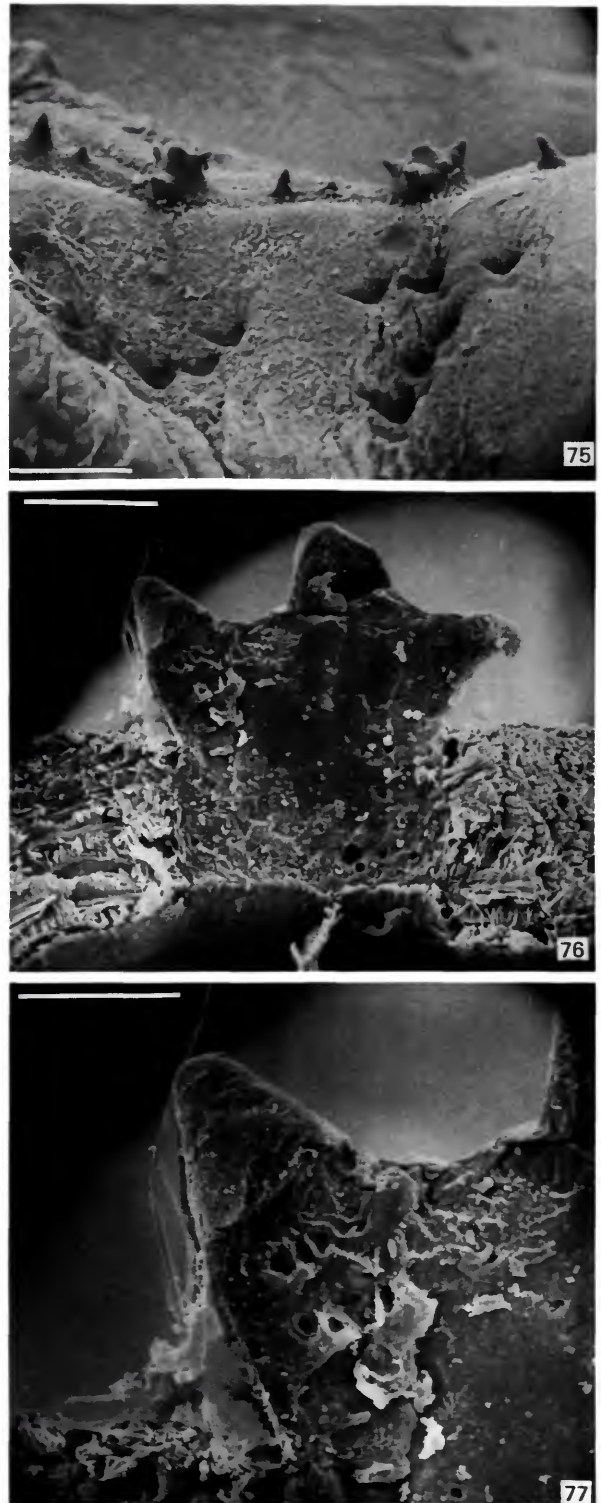
Monaragala District: Mau Aru, Angunakolapelessa, and Wellawaya

Matara District: Deniyaya

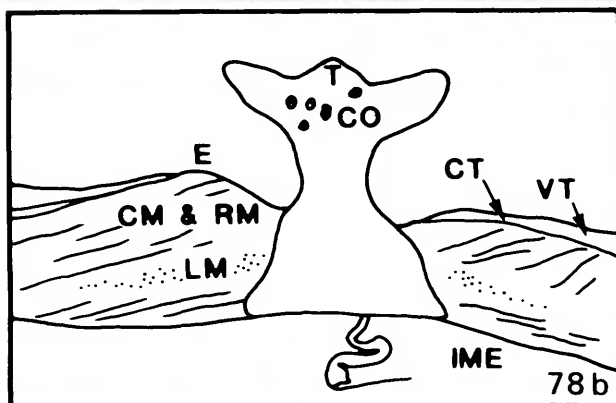
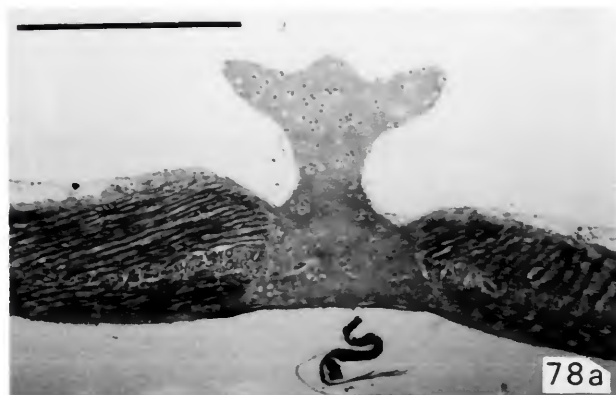




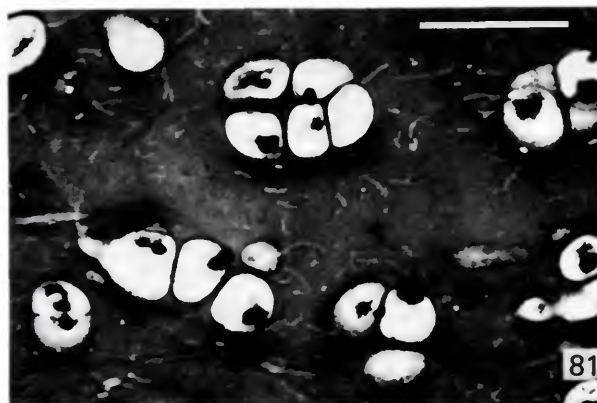
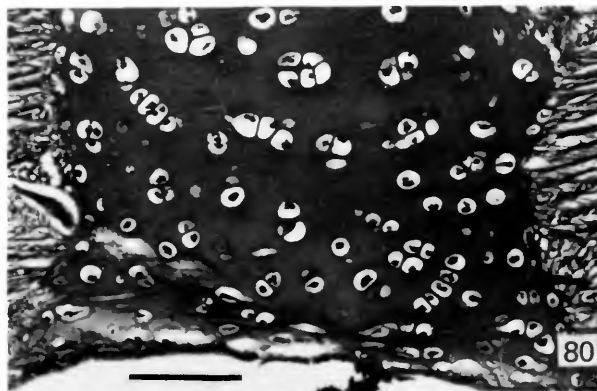
FIGURES 72-74.—*Liocranchia reinhardi*: 72, cross section of mantle through ventral cartilaginous band,  $\times 160$ , light microscopy, stain PAS with light green, scale 0.1 mm; 73, cross section of mantle through a tubercle showing junction between hyaline cartilage of tubercle, perichondrium, and surrounding mantle tissue,  $\times 400$ , light microscopy, stain Toluidine blue, scale 0.05 mm; 74, close-up of a section of a tubercle showing chondrocytes of hyaline cartilage,  $\times 160$ , light microscopy, stain H & E, scale 0.05 mm.



FIGURES 75-77.—*Leachia cyclura*: 75, side view of tubercles of funnel-mantle fusion on mantle surface,  $\times 50$ , SEM, scale 0.5 mm; 76, cross section of mantle through a hyaline cartilage tubercle,  $\times 190$ , SEM, scale 0.1 mm; 77, enlargement of tubercle projection from Figure 76,  $\times 225$ , SEM, scale 0.1 mm.



FIGURES 78, 79.—*Leachia cyclura*: 78a, cross section of mantle through a hyaline cartilage tubercle,  $\times 63$ , light microscopy, stain Masson's trichrome, scale 0.5 mm; 78b, diagram of Figure 78a identifying tissue types; 79, close-up of hyaline cartilage tubercle from Figure 78,  $\times 160$ , light microscopy, stain Masson's trichrome, scale 0.1 mm.



FIGURES 80, 81.—*Leachia cyclura*: 80, cross section of mantle through ventral cartilaginous band showing perichondrium along bottom,  $\times 160$ , light microscopy, stain Toluidine blue, scale 0.1 mm; 81, close-up of a tubercle showing chondrocytes and collagenous fibers of hyaline cartilage,  $\times 400$ , light microscopy, stain Toluidine blue, scale 0.05 mm.

The tissue layers in histological section are as follows (Figures 78-79): a thin epidermis; a moderately thick, vacuolated layer of connective tissue (VT); a thin layer of fibrous connective tissue (CT); a thick layer of completely intermixed circular and radial muscle; a thin layer of longitudinal muscle; a second, inferior layer of intermixed circular and radial muscle; a thin layer of fibrous connective tissue; and the thin inferior mantle epithelium.

#### SUMMARY

Table 1 summarizes the morphological features of various dermal structures of the 10 species of oceanic squids we have studied.

TABLE 1.—Summary of morphological features of dermal structures in oceanic squids.

| Species                              | Structure             | Tissue  | Shape  | Size, mm<br>(Dia. × Ht.)                 | ML<br>mm | Epidermis over<br>structure |
|--------------------------------------|-----------------------|---|--|--|----------|-----------------------------|
| <i>Lepidoteuthis grimaldii</i>       | Dermal cushion        | Connective tissue in honeycomb arrangement            | Rhomboid to hexagonal  | 2.0 × 0.5                                | 180      | Yes                         |
| <i>Pholidoteuthis adami</i>          | Dermal cushion        | Connective tissue in honeycomb arrangement            | Round to pentagonal  | 0.5 × 0.3                                | 300      | Yes                         |
| <i>Tetronychoteuthis massyae</i>     | Tubercle and papillae | Dense connective with chondrocytes; elastic cartilage | Roundish   | 0.3 × 0.15                               | 100      | No; acellular cuticle       |
| <i>Histioteuthis meleagroteuthis</i> | Tubercle              | Elastic cartilage                                     | Ridge of knob-like tubercles                                     | 0.4–0.8 × 1.3–1.9*<br>0.6–2.2 × 0.7–2.3† | 38       | Yes                         |
| <i>Chiroteuthis acanthoderma</i>     | Tubercle              | Hyaline-like cartilage                                | Conical  | 1.0 × 0.4                                | 144      | Yes                         |
| <i>Mastigoteuthis cordiformis</i>    | Tubercle              | Elastic or fibrocartilage                             | Conical  | 0.2 × 0.3                                | 87       | Yes                         |
| <i>Mastigoteuthis hjorti</i>         | Tubercle              | Elastic or fibrocartilage                             | Conical  | 0.1–0.2 × 0.05–0.1                       | 93       | Yes                         |
| <i>Cranchia scabra</i>               | Tubercle              | Hyaline cartilage                                     | Round, triangular, or rectangular bases with 2–5 projections     | 0.4–0.8 × 0.2–0.4                        | 94       | Yes                         |
| <i>Liocranchia reinhardti</i>        | Tubercle              | Hyaline cartilage                                     | Conical  | 0.2–0.3 × 0.15–0.2                       | 29       | Yes                         |
| <i>Leachia cyclura</i>               | Tubercle              | Hyaline cartilage                                     | Small conical to large complex with numerous conical projections | 0.3–0.4 × 0.1–0.2                        | 55       | Yes                         |

\* Tubercle from mantle ridge; length = 24 mm.

† Tubercle from arm ridge; length = 40 mm.

### Function

The form and composition of the dermal structures of the species of squid we investigated apparently represent several different origins. Consequently, we can anticipate several different functions for these structures.

### HYALINE CARTILAGE

The type of cartilage commonly known to zoologists is hyaline cartilage of vertebrates. Among oceanic squid hyaline cartilaginous dermal structures occur primarily, but not exclusively, in the Cranchiidae. These cartilaginous tubercles are either an outgrowth from the cartilaginous bands that extend posteriorly in the mantle from sites of origin at the

mantle-funnel and mantle-nuchal fusion points (e.g., *Leachia*, *Liocranchia*), or they emerge from the entire surface of the mantle (*Cranchia*). Sections through both kinds of tubercles show the tissue to be a homogeneous matrix in which chondrocytes are embedded, and which, in its staining characteristics, closely resembles hyaline cartilage of vertebrates and invertebrates (Person and Philpott, 1969; Person, 1969; Philpott and Person, 1970; Dilly and Nixon, 1976; McSweeney, 1978). The tubercles continue to grow as the animal grows, as evidenced by the concentration of chondrocytes at the tips of the conical papillae on the already-developed tubercles, as well as on the emerging tubercles in *Cranchia* and in the perichondrium that surrounds the cartilaginous bands in *Leachia* and *Liocranchia*.



The function of the tubercles in cranchiids is unknown. Certainly the bands, directly associated with the fused mantle-funnel and mantle-nuchal locking sites, serve as strengthening or supporting rods during the muscular contractions for swimming (see below). Dilly and Nixon (1976) suggested that the tubercles of *C. scabra*, which cover the entire surface of the mantle, may serve to reduce sinking rate and/or deter predators. However, the tubercles are extremely small relative to the body size and they project only slightly through the thin epidermal sheath that covers the mantle and the tubercles to the tips. Projections that aid marine organisms in reducing sinking rates normally are very long in relation to the body size, as found in foraminiferans, radiolarians, copepods, sergestid and other crustacean larvae, pteropods (*Clio*), etc. Whether the large number of tiny tubercles plus the globular shape that the mantle normally assumes compensate for lack of tubercular length is uncertain. It does seem certain, however, that any contribution to a reduced sinking rate from the tubercles would be minor in comparison with the primary buoyancy mechanism, the ammonium chloride-filled coelom that provides sufficient lift to make the animal nearly, though not completely, neutrally buoyant (Denton et al., 1969; Denton and Gilpin-Brown, 1973; Clarke et al., 1979).

The "prickly ball" theory as a deterrent to predation against small predators (Dilly and Nixon, 1976) may have merit to the extent that the "balling-up response" increases the cross-sectional diameter of the potential prey and makes it too large to capture. However, most of the known predators on midwater squids, primarily fishes, are the same size or larger than their prey, and their feeding mechanisms involve swallowing the prey whole; long sharp teeth in large mouths would not be deterred by the small tubercles of *C. scabra*. The contention that the tubercles give the impression of a greater size is unsupported for two reasons. First, the tubercles are at most 1 mm high and any illusion of increased size (diameter) probably would not be discriminated by a potential predator in an overall ball diameter of 100 mm or more. Second, in the sea the tubercles would not be seen easily as they are covered by the thin epidermal sheath that envelops the mantle, so they would not serve well to break up the background; this sheath normally is ruptured and rubbed off in captured animals which gives the false impression of a prickly surface.

The occurrence of cartilaginous tubercles over the surface of the mantle of *C. scabra*, as well as of *Galiteuthis glacialis*, appears to be functionally related to the thin, epidermal sheath that envelops the mantle (Figure 66). The sheath lies external to the superior surface of the mantle connective tissue and circular muscle and is attached to and supported like a canopy by the tubercles, leaving an "empty space" in histological sections, but which must be filled with fluid in the live animal. This space may be filled with a buoyant fluid, probably light weight ions of ammonium chloride, that functions as a buoyancy vest, an adjunct to the buoyancy function of the coelom. The tough tubercles probably serve as columns to hold the epidermal

sheath in position and to maintain shape and conformity of the buoyancy vest in conjunction with the flexible mantle. The identical structural relationship was described and illustrated by McSweeney (1978, figs. 1, 2) for the Antarctic Ocean tuberculate cranchiid *Galiteuthis glacialis*, that attains a mantle length up to 500 mm. This dermal buoyancy mechanism could provide a basic, passive level of buoyancy, while the internal coelomic chamber provides the primary source of buoyancy. In fact, the addition of the dermal flotation vest might be sufficient to bring the animal to neutral buoyancy, because the coelomic chamber alone provides lift to make the animals "nearly neutral," as observed and calculated by Denton et al. (1969). Denton and Gilpin-Brown (1973:204) calculated that the specific gravity of the ammoniacal coelomic fluid is 1.010, lighter than that of sea water (1.021-1.028) and considerably lighter than the animals with their coelomic fluid removed (1.046). Their measurements on captured animals would not have given a completely accurate result, because, in all probability, the fragile epidermal sheath would have been ruptured during capture and the buoyant fluid lost. Even though the space between the surface of the mantle and the epidermal sheath is narrow, when the entire surface area of the mantle is included, the volume of buoyant fluid is significant. For example, we calculate that in a 100 mm ML squid the volume of the buoyant fluid would be increased by about 4%. We believe this is sufficient to provide a beneficial contribution toward achieving neutral buoyancy in the animals.

The function of the cartilaginous tubercles on the cartilaginous bands of *Leachia cyclura* and *Liocranchia reinhardtii* is unknown. They occur only along the bands, or in line with the bands posteriorly in *Leachia*, and nowhere else on the mantle. Therefore, it seems unlikely that they function in a similar manner as that suggested for the tubercles in *Cranchia scabra* and *Galiteuthis glacialis*. Tubercles extend along the dorsal midline superior to the gladius nearly to the anterior level of the fins in *Liocranchia* (except in *L. valdiviae*), while they are entirely absent in the dorsal midline of *Leachia*. The posterior free tubercles in *Leachia* arise from slightly swollen bases that pass through the entire thickness of the mantle musculature, whereas the tubercles in *Cranchia scabra* and *Galiteuthis glacialis* arise from the tunic of connective tissue on the superior surface of the mantle. In *Liocranchia* the tubercles are limited to the V-bands as an integral part of that cartilaginous structure.

The function of the bands per se may be related in *Leachia* and *Liocranchia* to a pseudoskeletal role of providing solid insertion for the mantle muscles, strong support during swimming contractions, or internal attachment for some visceral tissue (e.g., the septum covering the coelom). Indirect evidence of a supportive function of the cartilaginous bands is seen in preserved specimens of *Leachia*. The mantle posterior to the ends of the bands frequently is strongly contracted in a series of accordion-like folds, while the anterior part of the mantle, through which the cartilaginous bands extend, exhibits

no such contractions and remains undistorted. This would prevent the coelom from being compressed with resultant loss of buoyancy fluid and damage to vital organs.

The structure of the tissue of the tubercles of *Chiroteuthis acanthoderma* is hyaline-like cartilage, somewhat similar to that of the tubercles of *Cranchia*. Otherwise, the tubercles of *C. acanthoderma* are quite dissimilar to those of *Cranchia*. They are very small and widely spaced, and their bases are set in little depressions in the fibrous, vacuolate tissue of the mantle; but they are structurally distinct from the underlying tissue. While the epidermis is absent in most of the preparations, sufficient patches exist to indicate that the tubercles and mantle are covered with epidermis. *Chiroteuthis* species and closely allied species are known to be neutrally buoyant as a result of the ammonium chloride contained in the highly vacuolate tissues of the mantle and arms. We are unable to suggest a function for the tubercles of *C. acanthoderma*. Because of their minute size and very widely-spaced distribution on the mantle, it seems unlikely that they function in buoyancy or locomotion as hypothesized for other species.

#### DERMAL CUSHIONS

The dermal structures of oegopsid squids we have studied other than those of cranchiids and the unusual tubercles of *Chiroteuthis acanthoderma*, do not consist of hyaline cartilage. Instead, the structures generally are highly fibrous tissues that are other types of cartilage and/or connective tissue. Most of them yield strongly positive staining reactions indicative of the presence of collagen and mucopolysaccharides. Staining characteristics of some make them comparable with elastic and fibrous cartilage, some with loose connective tissue, and some with dense connective tissue.

Joubin (1900:72) described the "scales" of *Lepidoteuthis grimaldii* as having a "cartilaginous consistency" and a "fibrous structure"; this has led most subsequent authors to refer to cartilaginous scales. Our work has shown that the staining properties of the dermal cushions are not cartilaginous at all, but rather they consist of vacuolate loose connective tissue interspersed with collagenic, elastic, and reticular fibers, and a few muscle fibers.

The dermal cushions of *Lepidoteuthis grimaldii* and *Pholidoteuthis adami* are relatively large and are continuous with the subepidermal, highly vacuolated, loose connective tissue on the surface of the mantle. While the bases of the dermal cushions are smaller in diameter than the dermal cushions themselves, they do provide a broad connection between dermal cushions and mantle. The appearance and composition of the tissue in the dermal cushions is identical to that of the vacuolated layer in the mantle (Figures 6, 7, 12). In histological sections and in SEM preparations the spaces in the vacuolated tissue are "empty," but in live animals they must be filled with fluid. Clarke et al. (1979:272) suggested that the reticular tissue or "spongy layer" in the mantle of *L. grimaldii* contains a solution

of ammonium chloride that is responsible for the buoyancy. Lipinski and Turoboyski (1983) confirmed the presence of ammonium ion ( $\text{NH}_4^+$ ) in the mantle of *L. grimaldii* at a concentration of 172 mM.

We suggest that the dermal cushions also function primarily as a buoyancy mechanism that, in conjunction with the vacuolate layer in the mantle, envelops the muscular mantles of *Lepidoteuthis grimaldii* and *Pholidoteuthis adami*. In live animals the vacuoles, which constitute a large proportion of the volume of the tissue, contain ions of light weight ammonium chloride solution, a commonly occurring substance that provides buoyancy for squids and other marine invertebrates (Denton et al., 1969; Clarke et al., 1969; Clarke et al., 1979; Lipinski and Turoboyski, 1983). The dermal cushions and associated subepidermal vacuolate tissue, therefore, provide the species of these genera with a stable dermal buoyancy device.

Observations on a live juvenile of *Lepidoteuthis grimaldii* by Clarke (1964:77), indicate that the animal uses its fins for locomotion and that mantle pumping maintains respiration but "did not propel the animal at all." The "slightly negative" buoyancy was attributed to the efforts of the animal to swim downward, implying that the animal is neutrally buoyant at rest. It should be pointed out that Clarke's use of the term "slightly negatively buoyant" is confusing because he referred to a condition in which the squid attempted to swim "downward," implying that the animal was lighter than neutral buoyancy, or, in fact, was positively buoyant. Negative buoyancy refers to an object that is heavier than neutral buoyancy and therefore tends to sink. These observations by Clarke on a live animal support the suggestion that a buoyancy mechanism exists, and the physical evidence presented here indicates that the mechanism consists of the vacuolate tissue of the dermal cushions and the mantle in which buoyant ammonium chloride is stored.

Clarke and Maul (1962) and Clarke (1964) gave detailed descriptions of the "scales" of *Lepidoteuthis*. Following the argument of Clarke (1960), they accept as appropriate the term "scale" as applied to the dermal structure of *Lepidoteuthis*, but we are unable to support this terminology (see "Introduction"). Clarke and Maul (1962) on the basis of the weakly-muscled mantle and very well developed muscular fins, conclude that *Lepidoteuthis* is a weak swimmer; its primary locomotion provided by the fins rather than jet action. Whatever the mode of propulsion, the dermal cushions are configured to permit the smooth passage of the body tail first through the water, because they are fixed posteriorly and overlap laterally and anteriorly along the length of the mantle like fish scales (which overlap anterior to posterior) or roofing tiles. The dermal cushions are arranged in a diagonal pattern of overlapping rows rather than in rows parallel or perpendicular to the longitudinal axis of the mantle. Even if the squid were not a powerful swimmer, the overlapping and linear arrangement should help to reduce hydrodynamic resistance by allowing an efficient flow of water



across the surface of the mantle, thereby providing an energy-conserving function. A similar function has been demonstrated in sharks and fishes (Reif, 1978; Burdak, 1969, 1981). Webb (1975) suggests that various drag-reducing mechanisms apply during normal swimming speeds, rather than during the less frequent bursts of maximum speed.

Bone (1972) described a complex system of projecting ctenoid scales, pores, and subdermal spaces in the integument of the gempylid fish *Ruvettus pretiosus* and attributed to it a hydrodynamic function. The system functions to generate vortices that are directed posteriorly and out, allowing replacement of energy to the boundary layer and preventing separation of the attached boundary layer. Bone (1972) suggested that the dermal cushions of *Lepidoteuthis grimaldii* might also function as vortex generators to delay or prevent the separation of the boundary layer. While the dermal cushions are different from the integument in gempylids, we can not rule out the possibility of their functioning as a vortex generating system.

Finally, we can not overlook the possibility that the dermal cushions also may function as spongy, resilient cushions to protect the mantle from mechanical damage.

So, we suggest the possibility of multiple functions for the dermal cushions of *Lepidoteuthis grimaldii*: primarily a dermal buoyancy mechanism and a drag reduction system for efficient swimming, and, secondarily, a protective mechanism to cushion the mantle from physical damage. The same functions probably apply to *Pholidoteuthis adami*, as well, especially that of the dermal buoyancy mechanism. The dermal cushions of the two species are very similar in structure, the primary difference being that those in *P. adami* do not overlap as they do in *L. grimaldii*.

The genus *Pholidoteuthis* was erected by Adam (1950) for the new species *P. boschmai*, which, among other distinguishing characters, has "scales" that Adam likened to those of *Lepidoteuthis* which are larger in size. They are extensively figured in Adam (1950, pl. II). The systematic status of *Lepidoteuthis* and *Pholidoteuthis* has been examined and is published elsewhere (Roper and Lu, 1989).

Utilization of tissue fluids that are lighter than sea water as a buoyancy mechanism is a common occurrence among the oegopsid families. Clarke, Denton, and Gilpin-Brown, through several investigations, established the existence of this strategy for 14 of the 26 teuthoid families: Octopoteuthidae, Architeuthidae, Histioteuthidae, Bathyteuthidae, Lepidoteuthidae, Pholidoteuthidae, Cycloteuthidae, Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Grimalditeuthidae, Cranchiidae, and the genus *Ancistrocheirus* of Enoploteuthidae (Clarke, et al., 1979). Lepidoteuthidae subsequently was reported as being ammoniacal (Lipinski and Turoboyski, 1983). Based on examination of material available to us, and comparing it with families known to be ammoniacal, we now believe that the Promachoteuthidae, the Batoteuthidae, possibly *Alluroteuthis* of the Neoteuthidae, and *Enoploteuthis* of the Enoploteuthidae also employ this method of buoyancy.

## ELASTIC CARTILAGE

The dermal structures on *Tetronychoteuthis massyae* are unique in form and structure in comparison with those of other squids examined. The tubercles are very small, very closely set against each other, and regularly arranged; they have rounded caps or discs with papillose projections, narrow bases, and a network of interconnecting channels between the bases of the tubercles; their bases are contiguous with the subepidermal foundation layer of fibrous connective tissue. The epidermis of the mantle does not cover the tubercles but attaches only to their bases immediately superior to the foundation layer. The composition of the tissue of the tubercles and the underlying foundation layer appears identical, consisting of a very dense fibrous connective tissue interspersed with chondrocytes and minute vacuoles. This material stains positively for collagen, mucopolysaccharides, and cartilage with PAS/green, PTAH, and Masson's trichrome stains. With these characteristics we consider it to be a type of elastic cartilage.

The structure and arrangement of the dermal tubercles of *Tetronychoteuthis massyae* seem to preclude functions concerned with buoyancy. For example, subepidermal chambers occur as in *Cranchia*, but while vacuoles do occur, they are exceedingly small so that the vacuolar volume is proportionally very low in comparison with the dense nonvacuolate tissue. Further, these structures do not appear to function as supportive pillars because the epidermis adheres only to the surface of the mantle and the bases of the tubercles but does not cover the tubercles.

The uniform arrangement of the tubercles, their size, shape, and configuration suggest a function related to locomotion. *Tetronychoteuthis massyae* is a very streamlined squid with thick, dense mantle musculature, indicative of a strong, fast swimmer. Tokaty (1971) suggested that no fluid flows are free of turbulence. Therefore, even considering their streamlined shapes, many squids swim fast enough to exceed simple laminar flow of water over their bodies so that energy-consuming drag is created. Thus, it would be advantageous for the squid to exert some type of boundary layer control for reduction of hydrodynamic drag.

Trueman (1983) reviewed locomotion in cephalopods and presented an extensive list of references. Most research on cephalopod locomotion has concentrated on the nature of the jet propulsion system in swimming and the physiology and morphology of the engine that drives it, the mantle. Some work deals with the role of the fins in squid locomotion. However, we are aware of very little work specifically on hydrodynamics of squid swimming, other than that of Zuev (1966) concerning observations of turbulent flow around *Todarodes sagittatus*.

When we began to consider the functional aspects of the tubercles in squids we suspected that they might play a role in locomotion, as similar structures had been shown to do in other fast swimming nektonic marine animals. Since so little research seems to have been done on hydrodynamics of cephalopods, we have had to rely on work in other groups; most



hydrodynamic research that seems applicable to cephalopods has been done on vertebrates. Webb (1975) reviewed hydrodynamics and energetics of fish propulsion and provided an analysis of various hypothesized drag-reduction mechanisms that can be used to prevent separation of the boundary layer during laminar and transitional flow and thus to reduce frictional drag on an object moving in a fluid. Some of these mechanisms seem applicable to squids.

1. Streamline or laminar profile. Fast-swimming animals have evolved streamlined shapes that make it possible to keep the flow laminar close to the surface of the body for much of its length. No single best shape exists to which evolution should trend, because optimal laminar profiles differ for each species, depending on their length, body configuration, "design" speed, etc. Hertel (1966, 1969) presented laminar profiles for several fast-swimming fishes and cetaceans and they all differ in outline. According to Kramer (1960) the theoretical optimal laminar profile has its maximum thickness at about the posterior two-thirds of its length. Many fishes and cetaceans have their maximum thickness in the anterior third, at the "shoulders." But in the fast swimming fishes of the Scombridae, Thunnidae, and Katsuwonidae the "shoulder" is located about two-thirds of the length posteriorly, matching highly efficient man-made bodies. This configuration extends the favorable pressure gradient posteriorly and maintains the laminar boundary layer flow along most of the body. During fast swimming by means of jet propulsion, squids move tail first with fins wrapped tightly around the tail, and the head and arms form a tightly held, streamlined cone extending backward. The maximum thickness of the body is around the region of the mantle opening and head, approximately two-thirds of the total length from the functionally anterior, morphologically posterior, tip of the body. This configuration would allow laminar flow to remain in effect for much of the length of the body, then give way to transitional flow toward the end of the arm cone and preventing turbulence and boundary layer separation. There seems little doubt that in the fast swimming squids like *Tetronychoteuthis massyae* laminar profile plays an important role in reduction of hydrodynamic drag.

2. Surface roughness. Several authors have hypothesized that rough surfaces created by denticles or modified scales on fishes and sharks are designed to induce transition, delay separation of the boundary layer, and reduce pressure drag (Walters, 1962; Hertel, 1966, 1969; Ovchinnikov, 1966; Bone and Howarth, 1967; Burdak, 1969, 1981; Reif, 1978, 1983). This method of boundary layer control has been achieved in several ways, but essentially it requires some form of rough surface with an arrangement of small protuberances that convey the laminar boundary layer posteriorly and prevent the separation that marks the onset of turbulence and drag. Two types of roughness mechanisms may exist. One is a band of modified scales around the "shoulders" of some scombrid fishes that might act as a hydrodynamic tripping wire (Walters, 1962). The second is distributed roughness wherein the

elements cover the entire surface of the body, as in sharks (Bone and Howarth, 1967; Reif, 1978, 1983).

The tubercles of *T. massyae* cover most of the mantle and may present sufficient distributed roughness to function like that in sharks. In the juvenile specimens we have, the tubercles are small and we do not know if they are large enough to penetrate the boundary layer sufficiently to be effective. However, the tubercles do increase in size with growth, as follows: 45 mm ML, 0.117 mm; 50 mm ML, 0.175 mm; 60 mm ML, 0.188 mm; and 105 mm ML, 0.35 mm. While we do not know the maximum size attained by *Tetronychoteuthis*, presumably the tubercles would continue to be proportionally larger. Even on the specimen of 105 mm ML the tubercles are easily seen and felt.

3. Walters (1963) described a system of cartilaginous tubercles, pores, and canals in the trachipterid fish *Desmodema polysticta*. He hypothesized that they function to impart boundary layer control of laminar flow, decreasing hydrodynamic drag by 60% to 75%. Called distributed dynamic damping, the proposed mechanism works as follows. As swimming occurs, water pressure against parts of the skin increases as the boundary layer disturbance increases. The layer pushes through the pores into the canals, flows to regions of lower pressure, and re-enters the unperturbed (laminar) boundary layer through the pores. This simultaneous redistribution of pressure dynamically dampens the disturbance.

The orderly arrangement of the tubercles on the mantle surface, the small openings between tubercles, and the basal channels or ducts in between closely packed tubercles lead us to suggest that distributed dynamic damping also may be involved in drag reduction in *T. massyae*. The tubercles cover the anterior  $\frac{3}{4}$  of the mantle surface from the mantle opening to about the point where the mantle tapers posteriorly. The basal channels between tubercles are unobstructed so that water under pressure can enter at any pore, flow freely along channels, and exit through any pore, including out the edge of the mantle opening over a thin flange on the inferior edge of the opening that seals it against the posterior surface of the head. In addition to the primary pressures created by the propulsion of the squid through water, the rapid changes in mantle configuration during strong muscular contractions also create areas of pressure differential across the mantle. Dynamic distributed damping might be a mechanism to help maintain boundary layer control and drag reduction.

Bone (1972) described the vortex generating system that prevents boundary layer separation in gempylid fishes and suggested that the mechanism might be applicable to other fishes and even to *Lepidoteuthis grimaldii*. We are uncertain if this mechanism can be attributed to the system of tubercles, canals, and pores of *T. massyae*, but the morphologies look very different.

Finally, we point out that no matter which drag-reduction mechanism is proven to be employed by *Tetronychoteuthis*, we consider it to be an extremely fast swimmer. Its morphology,

body shape, and musculature indicate this. The rough surface and tubercular/canal system imply drag reduction for fast swimming. Its extreme rarity in collections infers fast swimming as well. This species is rare in collections in spite of the fact that in the past three decades extensive midwater trawling programs have been carried out using a great variety of fast, efficient, and large nets. *Tetronychoteuthis* appears to be powerful enough and fast enough most of the time to avoid even the meganets with mouth openings ~100 m, nets that have succeeded in capturing otherwise fast, elusive species.

We acknowledge the speculative nature of these hypotheses and encourage that additional theoretical and observational research be done to help understand the nature of hydrodynamics in squids. Not the least of the problems, for example, are the hydrodynamic effects and complexities introduced by a flexible, relatively soft body that continuously changes shape during rapid locomotion.

The tubercles and ridges of *Histioteuthis meleagroteuthis* look (to the unaided eye) and feel similar to the hyaline cartilaginous structures of the cranchiids, but histological sections confirm that they consist of an extremely dense fibrous tissue that stains positive for collagen and mucopolysaccharides, especially at the distal tips where they are virtually a solid mass (Figures 43, 46). The tissue however, is not hyaline cartilage but resembles in staining characteristics elastic cartilage in vertebrates. The internal structure of the arms and mantle consists almost entirely of vacuolate tissue interspersed with small bundles of muscle fibers. These vacuolate tissues have been shown to contain ammonium chloride that provides buoyancy for *Histioteuthis* (Clarke et al., 1969; 1979).

The structure of the tubercles of *Histioteuthis meleagroteuthis* is very different from the dermal cushions of *Lepidoteuthis* and *Pholidoteuthis* and from the tubercles of the other species examined in this study. The function appears to be different as well. The tuberculate ridges surely are not used in buoyancy as they are too dense. The tuberculate ridges along the arms and on the dorsal mantle may serve as strong, rigid keels for insertion of arm and dorsal mantle muscles to provide support during the sudden muscular contractions required when strong locomotion occurs, e.g., an escape reaction or an attack on prey. Young animals, especially, may have to compensate for the absence of strong arm and mantle muscles, which have been modified for buoyancy, with rigid structures in the form of a pseudoskeleton against which the remaining muscles could contract. The arms on the few live juvenile *H. meleagroteuthis* we have observed are more rigid and less flexible in the basal regions than are those of live animals of non-tubercular species of *Histioteuthis*.

The tuberculate ridges on the arms and mantle of adult *H. miranda*, which attains a mantle length of 250 mm, are proportionally much smaller and less conspicuous than in juveniles. The tubercles are hardly visible above the level of the skin, and often can be detected only by running a probe along

the area where the ridges clearly occur in smaller animals. The tubercles and underlying bases seem to stop growing at a certain stage; we can not determine with the material available whether the tubercular tissue degenerates as well, or merely stops growing. Further, the musculature in adults is more dense and more extensively developed than in juveniles. This may explain the proportional reduction of the tubercular ridges; with increased muscular development and density in adults the pseudoskeletal function in juveniles would no longer be necessary. Based on extensive sampling in southern Australian waters it may be significant that adult *H. miranda* have been captured only near the bottom in depths of 400–600 m, while juveniles have been captured only in midwater (C.C. Lu, unpublished data). Therefore, the ontogenetic reduction in tuberculate ridges might be associated with habitat and morphological changes as well. We have not seen specimens of *H. meleagroteuthis* that are of maximum size, so we do not know whether a similar proportional reduction occurs in that species.

A question persists concerning this suggested function. Why do only three of the 15 species of *Histioteuthis*, *H. meleagroteuthis*, *H. miranda*, and *H. bruuni*, possess the tubercular ridges? The genus generally is quite homogeneous morphologically, so the occurrence of the pseudoskeletal ridges may be indicative of a different, more active mode of life in the midwater habitats, possibly at earlier stages of life history.

#### ELASTIC/FIBROCARILAGE

The minute, papilla-like, conical tubercles of the two species of *Mastigoteuthis* we have studied are similar to each other. They consist of dense connective tissue that closely resembles elastic cartilage or fibrocartilage of vertebrates. The thick, underlying, subepidermal connective tissue is highly vacuolate and stains positive for collagens and mucopolysaccharides. This connective tissue is a site of concentration of buoyancy fluid, as is much of the relatively weakly-muscle, vacuolate mantle. The function of the tubercles appears to be related neither to buoyancy nor to support. The tubercles of *M. cordiformis* appear to be attached to the mantle around their bases by the epidermis that adheres to the subepidermal layer and does not leave a space as in the tubercular cranchiids. Chun (1910) described the tubercles as being covered with epidermis, but always rubbed off. However, we have examined scores of specimens of *M. cordiformis* throughout its size range and have found no evidence of epidermis covering the tubercles. Further, all our histological sections indicate that the papillate or conical tips of the tubercles are free of epidermis. Possibly these exposed tubercles perform a function similar to that suggested for *Tetronychoteuthis*; that is, they may be a mechanism for reducing hydrodynamic drag along the boundary layer to ensure that laminar flow is maintained. This seems more likely in the case of *M. cordiformis* in which the tubercles, although



minute, are numerous and thickly distributed, and they adhere firmly to the mantle.

As far as we know, *M. cordiformis* is the largest *Mastigoteuthis*, reaching mantle length in excess of 700 mm (and not yet mature). Furthermore, the mantle musculature of *M. cordiformis* is much more strongly developed than in other species of *Mastigoteuthis* at the same mantle length. These factors indicate that *M. cordiformis* might be a stronger swimmer than its congeners, and it would benefit from a drag-reduction mechanism.

The tubercles of *M. hjorti*, while thickly distributed, rub off easily in preserved specimens, but it seems unlikely that they would be easily lost in live animals in the deep sea. The aid to locomotion imparted by the maintenance of laminar flow seems a reasonable function to suggest for these tubercles, but their minute size may preclude such a function.

Chun (1910:226, 227, pl. 37: fig. 5) noted that the entire body of *M. cordiformis* was covered with small tubercles that at first he thought were light organs. However, after examining their "fine structure" he refuted that notion and considered them to be humps of "modified subcutaneous connective tissue," an interpretation that is essentially correct even today. Sasaki (1929:312) referred to the tubercles as "fine warts" and Voss (1963:140) to "small round tubercles." Perhaps misinterpreting Chun's statement or the misleading legend to the figure (pl. 37: fig. 5) of the "...conical tubercle (luminous organ?)..." Young (1972:67) mentioned that the "whole body is covered with small light organs." We have examined a large number of specimens that range from 40 to 600 mm ML and no photophores have been found. The results of our study show that the tubercles consist of elastic/fibrocartilage, similar to that of vertebrates.

The nature of the material available for this study precluded a more detailed analysis of tissues. In the future, specimens should be specifically fixed for various biochemical, histological, and histochemical analyses so that a more precise determination can be made of the composition and morphology of the dermal structures of oceanic squids. Fresh and well-fixed material could lead to a better understanding of the functions of these structures, as well. The hypothesized function of increased swimming efficiency through reduced hydrodynamic drag should be tested using models in flow tanks as well as mathematically.

This study has described several kinds of structures in the integument of some oceanic squids and has led to the suggestion of possible functions of these structures. Additional research needs to be done, and the problems are confusing and complicated by several factors. For example, a wide variety of morphological and structural integumental elements have been described and surely others exist, yet to be recognized. Their distribution and patterns on the body are different. These structures occur on different types of squids of different form and behavior and from different habitats. All these factors need to be considered in future research.

## Summary

This survey has revealed the morphological and histological features of the dermal structures of 10 species in 6 families of oceanic squids, and it has resulted in hypotheses about functions for these varied structures.

1. The tubercles and dermal cushions consist of loose fibrous connective tissue (*Lepidoteuthis grimaldii*, *Pholidoteuthis adami*), elastic cartilage (*Tetronychoteuthis massyae*, *Histioteuthis meleagroteuthis*), elastic/fibrocartilage (*Mastigoteuthis cordiformis*, *M. hjorti*), hyaline-like cartilage (*Chiroteuthis acanthoderma*), and hyaline cartilage (*Cranchia scabra*, *Liocranchia reinhardi*, *Leachia cyclura*).

2. The existence of elastic cartilage and fibrocartilage in invertebrates is reported; these tissues heretofore had been regarded to occur almost exclusively in vertebrates,<sup>4</sup> just as hyaline cartilage had until the definitive work of Person and Philpott (1969). The occurrence of hyaline cartilage tubercles is demonstrated here for additional species of Cranchiidae and in the Chiroteuthidae (hyaline-like).

3. This study has shown that "cartilaginous scales" do not exist in any cephalopods currently known. All cartilaginous (hyaline, elastic, fibro-) dermal structures are tubercles. The so-called "scales" consist of loose connective tissue, not cartilage. The term "dermal cushions" is introduced to replace the terms "scales" and "cartilaginous scales," terms which are inappropriate to cephalopods, and their use should be discontinued. Thus, the dermal structures in *L. grimaldii* and *P. adami* are dermal cushions, and the structures in *T. massyae* and *C. scabra*, formerly referred to as "scales," are tubercles.

4. One of the objectives of this study was to determine if the occurrence of dermal structures bears systematic or phylogenetic relevance. Certainly within family groups the type of dermal structure and the composition of tissue of that structure show definite relationships, e.g., in the Cranchiidae, Mastigoteuthidae, and Histioteuthidae. Further, the dermal cushions of *Lepidoteuthis grimaldii* and *Pholidoteuthis adami* are virtually identical in tissue composition and provide additional evidence of the close relationship of these two taxa. At the same time, their dermal cushions are so different in composition and structure from the tubercles and papillae of *Tetronychoteuthis massyae* as to preclude a relationship of these genera with *T. massyae*. These differences were sufficient to enable us to begin a reassessment of the systematic relationships of these three troublesome taxa (Roper and Lu, 1989).

5. The hypothesized functions for dermal structures are derived from our analysis of their structure, as well as knowledge about the gross morphology, locomotion, and

<sup>4</sup>Tissue that resembles fibrocartilage in vertebrates has been reported in the endosternite of the horseshoe crab, *Limulus polyphemus*, by Packard (1880) and in scorpions, spiders, and mites (Schimkewitsch, 1893, 1895; Nalepa, 1892) (fide Person, 1983).



habitus of the animals. They include (a) a buoyancy mechanism involving the highly vacuolate, ammonium chloride fluid-filled dermal cushions that envelop the mantle (*Lepidoteuthis grimaldii* and *Pholidoteuthis adami*); (b) a buoyancy mechanism that involves the epidermis supported by the cartilaginous tubercles that envelops the mantle and may contain ammonium chloride fluid as a dermal buoyancy vest (*Cranchia scabra* and

*Galiteuthis glacialis*); (c) a pseudoskeletal mechanism for insertion and support of muscles in aid of locomotion (*Histioteuthis meleagroteuthis*, *H. miranda*, *Liocranchia reinhardti*, and *Leachia cyclura*); (d) a locomotory mechanism for maintaining laminar flow along the boundary layer by reducing hydrodynamic drag (*Tetronychoteuthis massyae*, possibly *Mastigoteuthis cordiformis* and *M. hjorti*).

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