

Arm structures of the ophiomyxid brittlestars (Echinodermata: Ophiuroidea: Ophiomyxidae)

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ABSTRACT: The arms of Ophiomyxidae are ensheathed in two strata of connective tissue that obscure the underlying skeleton. The arm integument of *Ophiomyxa flaccida*, *O. tumida* and *Ophiobyrssa serpens* is composed of a thin layer of feltwork connective tissue and a thick layer of dense fibrillar connective tissue. The arm of *Ophiogeron supinus* is largely feltwork connective tissue fibers with a predominance of interfibrillar matrix. Comparative study of the arms of these four ophiomyxid species reveals that there is an inverse relationship between the thickness of the connective tissue and the size of skeletal elements. In Ophiomyxidae, connective tissue plays a supportive role that in other brittlestars is fulfilled by calcite. Behavioral observations indicate that the connective tissue exhibits variable tensility, a feature that may contribute to the skeletal properties of the integument. The functional and systematic significance of the arm structure of ophiomyxid brittlestars is discussed, and analogous specializations of Paleozoic ophiuroids are re-interpreted based on ophiomyxid adaptations.

1 INTRODUCTION

The ophiuroid body wall consists of an outer epidermis overlain by the cuticle, and an inner dermis chiefly composed of calcite stereom and connective tissue (Hyman 1955; Fontaine 1964). Until recently, histologists considered the epidermis to be syncytial (see Hyman 1955), but ultrastructural examination reveals that it is a distinct cellular tissue, separated from the dermis by a basal lamina (Märkel and Roser 1985; Hendler and Byrne 1987). Brittlestars are generally depicted as having a heavily calcified integument with a dermis composed of prominent skeletal plates and an underlying connective tissue sheath (Hyman 1955; Fontaine 1964; Wilkie 1978a; Märkel and Roser 1985; Hendler and Byrne 1987). Although this is typical of members of the order Ophiurida, the integument of the order Phrynophiurida is often poorly calcified (Matsumoto 1917). The phrynophiurid family Ophiomyxidae has a body wall with a reduced skeleton that is usually obscured by thick integument (Matsumoto 1917).

As a result of their fleshy integument, Ophiomyxidae are soft to the touch and, as their name suggests (myxa = mucus), they

often have a slimy coat. Although the secretory cells of the epidermis have been described (Reichensperger 1908; Pentreath 1970), histology of the ophiomyxid integument has not been examined. In this study, a comparative examination of the arm structure of shallow water and bathyal ophiomyxids was undertaken, to examine the functional, systematic and paleontological significance of their distinctive integument. The morphology of fleshy integument of the two ophiomyxid subfamilies is compared, and is contrasted with the structures of Ophiurida. Because connective tissue in the ophiomyxid integument appears to replace the calcite in the integument of Ophiurida we consider the roles of soft tissue and calcite in skeletal support of the arms. Finally, the behavior and arm morphology of living ophiomyxids are used to evaluate the specializations of Paleozoic ophiuroids.

2 MATERIALS AND METHODS

Specimens of *Ophiomyxa flaccida* (Say), *O. tumida* Lyman and *Ophiogeron supinus* Lyman, from the subfamily Ophiomyxinae, and *Ophiobyrssa serpens* Lyman from the subfamily Ophiobyrssinae were observed and collected

in several Caribbean locations. *Ophiomyxa flaccida* was found using SCUBA in Belize, Panama and the Bahama Islands between approximately 5-25 m. *Ophiobyrsa serpens* was sampled at 24 m on the Belize Barrier Reef (Hendler and Peck, these proceedings). *Ophiomyxa tumida* and *Ophiogeron supinus* were collected with the Johnson-Sea-Link submersible in the Bahama Islands, between about 300-600 m depth.

Brittlestars for scanning electron microscopy (SEM) and light microscopy (LM) were relaxed by adding magnesium sulfate crystals to the seawater in which they were held. For LM, the arms were fixed and decalcified in Bouin's solution. Following decalcification, the tissues were dehydrated with ethanol, cleared in xylene, embedded in paraffin and sectioned at 7 μ m. The sections were stained with haematoxylin and eosin or with alcian blue/periodic acid Schiff's (AB/PAS) method.

Brittlestars for SEM were preserved in ethanol. Arm pieces were cleaned in dilute sodium hypochlorite solution until sufficient soft tissue was dissolved to reveal the skeleton. The samples were washed in ethanol, air-dried, and mounted on stubs using toluene-soluble Bakelite glue. Samples were coated with carbon, gold-palladium sputter coated, and examined with a Cambridge Stereoscan 100 microscope.

3 RESULTS

3.1 External features and behavior

Ophiomyxa flaccida is one of the commonest shallow-water Caribbean ophiuroids, and its bathyal counterpart, *O. tumida* is similarly abundant and widespread (Clark 1941; Hendler in prep.). The disc integument of both species is particularly soft because it is not reinforced by large scales. The arms are slimy, and the arm spines are rough to the touch, even though integument covers the thorny skeleton of the spine. Sediment often adheres to the spines of *O. tumida*, presumably entrapped in mucus.

Ophiomyxa flaccida inhabits crevices in living coral and in coral rubble and is cryptic during the daytime, but emerges to open areas of the reef at night. *Ophiomyxa tumida* was observed in crevices and exposed on hard substrata covered by a thin veneer of sand. *Ophiomyxa* spp. move with an arm "rowing" motion that is generated by muscular arm flexion characteristic of epifaunal brittlestars. First, a propulsive arm bends and the raised proximal portion of the arm extends in the direction of travel, then the arm is set on the bottom,

straightens, and propels the disc forward. *Ophiomyxa flaccida* and *O. tumida* also coil their arms and bend them beneath the disc to transport food to the mouth. *Ophiomyxa flaccida* stiffens when it is handled, and a rigid arm will support the weight of the rest of the body when an individual is lifted from the water. Attempts to collect *O. tumida* were hampered because their rigidity, in response to disturbance, prevented them from passing through the tube of the suction device on the submersible manipulator.

Ophiobyrsa serpens was collected at 24 m in Belize for this study and is reported from 126-210 m elsewhere in the Caribbean (Clark 1915). The body surface of *O. serpens* is slimy. As yet, the modes of locomotion and feeding have not been observed for *Ophiobyrsa* species.

Ophiogeron supinus has been found between 323-627 m depth (Clark 1915, 1941; Hendler unpub. obs.). It is strikingly different from the other species due to its translucent, fleshy arm integument which has a consistency of stiff gelatin (see below). Its arms are smooth, but not slimy, and the disc is extremely soft and fragile. It was observed in open areas on steep hard bottoms covered with sand. The tube feet of *O. supinus* support the disc and arms above the substratum. They range between 350-500 μ m diameter, and are much larger than the maximum tube foot diameter of other species in this study (250 μ m). *Ophiogeron supinus* moves on the surface of the sediment at a rate of about 1 m/min, propelled solely by the tube feet bending in metachronal waves. It advances with its arms extended and the thin tips of several arms raised above the bottom. This brittlestar does not generate propulsion by arm flexion and the arms do not stiffen in response to disturbance or damage.

3.2 Histology

The arm structure of *Ophiomyxa flaccida* (Figs. 1-5, 14-16) provides a basis to compare the arms of the other three species. A cross section of the arm of *O. flaccida* shows an integument dominated by dermal connective tissue that is overlain by the cuticle and epidermis (Figs. 1-5; Table 1). Connective tissue dominates the dorsal surface as well as being prominent on the ventral surface and in the region between the arm segments. The dermal covering over the lateral arm plate (LAP) and spines is thinner.

The dermis consists of an outer feltwork of loosely arrayed fibers with an overall

longitudinal orientation, and an internal dense layer of regularly arranged, longitudinally oriented fibers (Figs. 1,5; Table 1). The skeletal plates are surrounded by and embedded in a dense connective tissue layer (Figs. 1,4,5), which binds the arm plates of adjacent segments (Figs. 14-16). A dorsal arm plate (DAP) is occasionally seen in LM sections, where its position is marked by the lattice-like appearance of the stromal tissue remaining after decalcification (Figs. 2,5). The LAPs and ventral arm plates (VAPs) are the major skeletal elements of the integument. Internally, the vertebral ossicles and the arm muscles are prominent features taking up to 40% of the cross-sectional area of the arm (Fig. 1).

Gland cells are abundant on the dorsal and lateral surfaces, including the spines, and are less abundant on the ventral surface (Figs. 3-5). They are fibrillar-type cells which are particularly long in the spines (range: 10-44 μm X 22-54 μm), and contain elongated strands of secretory material. The fibrillar cells are nested in the connective tissue and their apical portions traverse the epidermis forming one or several secretory ducts. The fibrillar material is intensely PAS+, and basophilic with haematoxylin. Some AB+ material is also present in the cells. In the epidermis there is a less common type of secretory cell (about 8-24 X 6-8 μm) which contains an eosinophilic and AB+ product. In addition, there are small granular cells approximately 13 μm in diameter that contain PAS+ spherules (4-5 μm diameter).

As in *Ophiomyxa flaccida*, the integuments of *O. tumida* and *Ophiobyrsa serpens* are composed of feltwork and dense connective tissue layers (Figs. 6,8,9,10; Table 1). Cell processes filled with pigment granules (1 μm diameter) are abundant in the feltwork region of *O. serpens* and confer a black color on this tissue layer (Fig. 10). A DAP was not seen in LM sections of either species although the structure of the DAP is revealed by SEM of *O. tumida* (Figs. 18, 20) and *O. serpens* (Figs. 22,24). The VAPs and LAPs are the major skeletal plates of the integument, and the vertebrae and muscles are prominent features of the arm (Figs. 6,8,18-25; Table 1).

Fibrillar cells are abundant on the lateral surface of *O. tumida* and *O. serpens*, and completely cover the spines where they are located in large pores in the stereom (Figs. 6,7,8,10). For *O. tumida* and *O. serpens* the fibrillar cells are approximately 10 X 50 μm , and 20 X 40 μm . Unlike *O. flaccida*, there are few fibrillar cells on the dorsal arm surfaces of these brittlestars. The fibrillar cells of *O.*

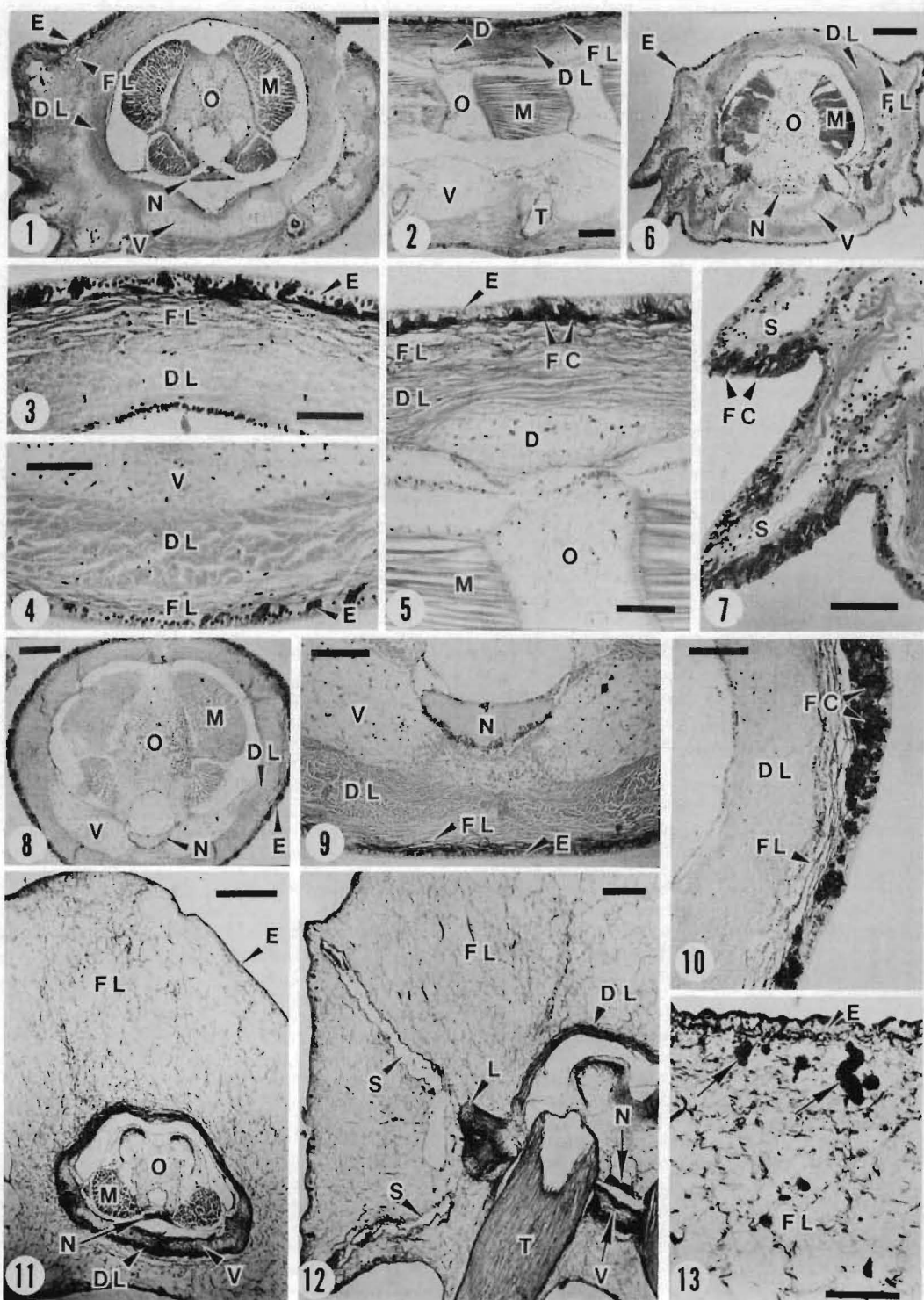
tumida are PAS+ and/or AB+. Most of the fibrillar cells of *O. serpens* are intensely PAS+, however they may contain AB+ material. As noted for *O. flaccida*, the fibrillar cells of *O. tumida* are basophilic with haematoxylin, whereas those of *O. serpens* are not. Eosinophilic secretory cells (approximately 6 X 10 μm) occur in the epidermis of *O. serpens*.

Table 1. Dimensions of ophiomyxid arm structures measured from LM sections.

Species	Thickness (minimum-maximum) μm			
	Total arm	Connective tissue layer: spine feltwork	Connective tissue layer: dense	
<i>Ophiomyxa flaccida</i>	150-450	50-90	30-150	100-370
<i>Ophiomyxa tumida</i>	200-750	50-100	30-300	150-350
<i>Ophiobyrsa serpens</i>	150-350	50-100	30-100	100-270
<i>Ophiogeron supinus</i>	950-2000	*	900-1900	30-150

* spines are embedded in arm integument

The integument of *Ophiogeron supinus* is strikingly different from that of the other species due to its thickness and the fragility of the calcite skeleton (Figs. 11-13; Table 1). The arm skeleton is reduced to a thin rod enveloped by a 1.0-2.0 mm thick layer of connective tissue. The vertebral ossicles and intervertebral muscles comprise only 21-26% of the cross sectional area of the arms (Fig. 11), contrasting with the enhanced development of the integument and tube feet (Fig. 12). The integument is largely a feltwork of fibrils with a predominance of interfibrillar matrix. Just below the epidermis there is a thin layer with a higher density of fibrils (Fig. 13). A thin layer of dense connective tissue lies along the internal margin of the integument, forming a tube in which the ossicles are embedded and surrounding the vertebral ossicles. In LM sections, the DAPs are not visible, the VAP is a small structure and LAP-arm spine articulations are readily apparent (Fig. 12). The arm spines are spoke-like supports surrounded by feltwork connective tissue. Secretory cells (6-20 X 20-45 μm) with an AB+ product are scattered beneath the surface and appear to be fibrillar cells (Fig. 13).



3.3 Skeleton

In *O. flaccida* the major skeletal elements external to the vertebrae are DAPs, LAPs bearing arm spines, and VAPs (Figs. 14-17). As is typical for the genus (Matsumoto 1917), the DAPs are a series of separate scales forming an arch over the top and sides of the arm, and the LAPs are subventral. Notably, the arm plates of successive segments do not overlap, and the gaps between the plates are filled with connective tissue. Also characteristic of the genus, the arm spine skeleton is thorny. The arm plates of *O. tumida* are relatively thin, but their positions are very similar to those of *O. flaccida* (Figs. 18-21). Minor differences between the species include the dominance of the two medial DAP ossicles, and the more slender, smoother arm spines of *O. tumida*.

Important similarities between the arm skeleton of *Ophiobyrsa serpens* and *Ophiomyxa* species include: fragmented DAPs, subventral LAPs, and gaps between the arm plates of successive segments that are filled with connective tissue (Figs. 22-25). Differences include: DAPs composed of only two symmetrical pieces, LAPs with large lateral projections nearly perpendicular to the axis of the arm, and VAPs composed of a regular mosaic of four scales. The arm spines are smoother and more slender than in *O. tumida*.

Ophiogeron supinus also has fragmented DAPs and gaps between the arm plates of successive segments, but there are striking differences between *O. supinus* and its congenerials (Figs. 26-29). The DAPs are represented by a number of thin, perforate scales on the dorsal and lateral surface of the vertebra. Most of the LAP is restricted

to the ventral surface of the arm. The spine articular-ridge and its fossae are reduced, the ventral portion is enlarged, and proximal and distal extensions of adjacent VAPs nearly touch. The VAP is very small and it bears two relatively large, tab-shaped tentacle scales. Podial pores between the LAPs and VAPs are quite large. The arm spines are very long, with only a few minute spinulose projections near the tip.

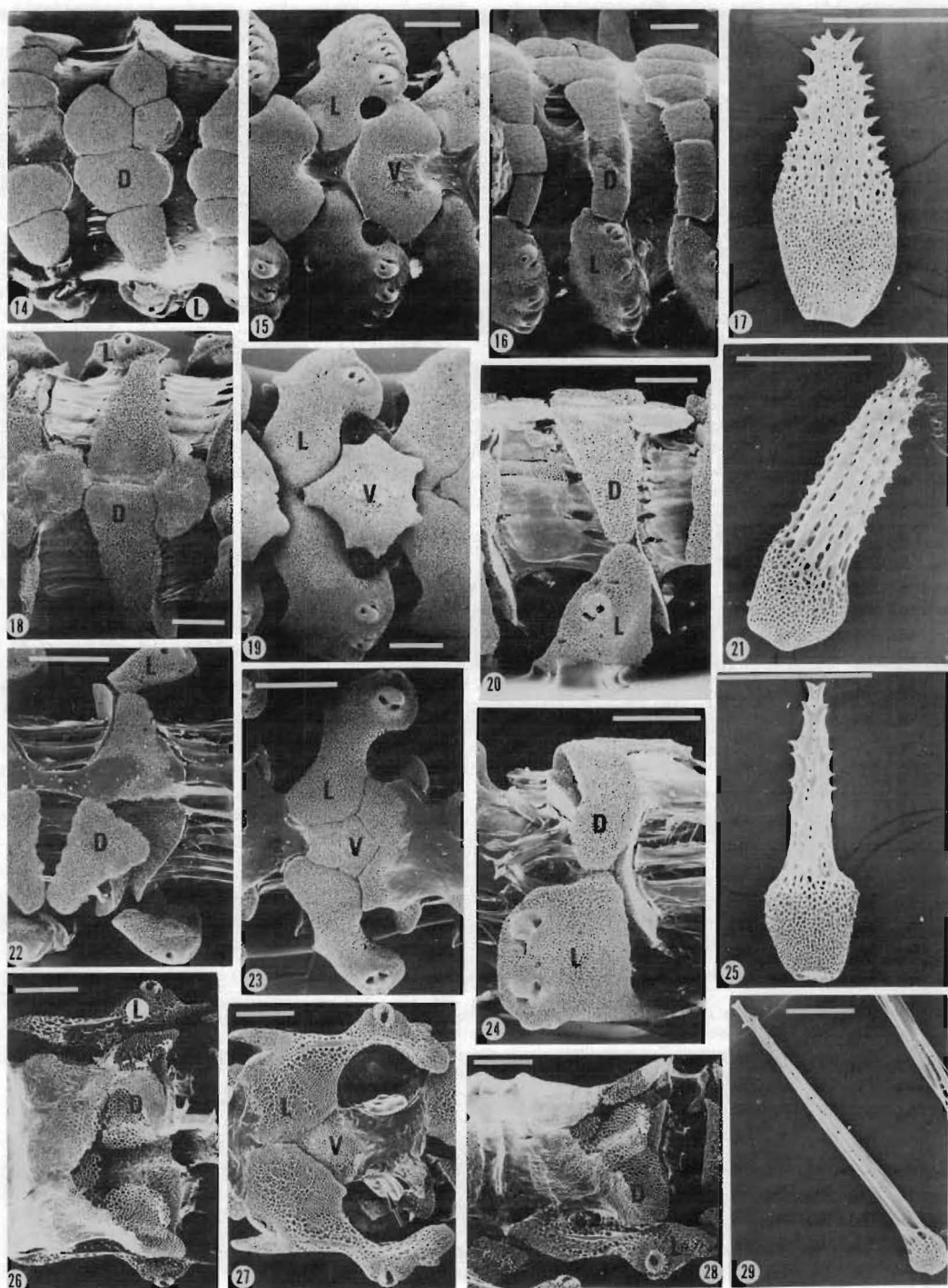
4 DISCUSSION

The soft integument of ophiomyxid ophiuroids contrasts with the calcareous cover of most ophiuroids. The arm plates that connect the arm segments of most heavily armored Ophiurida are reduced in the Ophiomyxidae. In the Ophiomyxidae there is an inverse relationship between the proportions of connective tissue and calcified elements in the integument. A continuum in this relationship is seen among *Ophiomyxa*, *Ophiobyrsa* and *Ophiogeron* species with an increasingly thicker envelope of connective tissue and a decreasing amount of skeletal material.

The ophiomyxid integument is composed of feltwork and dense connective tissue strata, presumably containing low and high densities of collagen fibrils. The calcite skeleton is bound together by the dense layer and this tissue appears to be homologous to the fibrillar sheath in the integument of the Ophiurida. However, a feltwork layer appears to be absent in the Ophiurida (Fontaine 1965; Märkel & Roser 1985; Hendler and Byrne 1987).

For *Ophiomyxa* spp. and *Ophiobyrsa serpens*, dense fibrillar connective tissue

Figures 1-13. Histological sections of: *Ophiomyxa flaccida* arm - (Fig. 1) cross section showing glandular epidermis (E), outer feltwork layer (FL) and inner dense layer (DL) of connective tissue; (Fig. 2) longitudinal section showing small dorsal arm plates (D) and large ventral arm plates (V); (Fig. 3) cross section, dorsal surface; (Fig. 4) cross section, ventral surface; (Fig. 5) longitudinal section of dorsal surface showing longitudinally oriented fibers of dense layer (DL) [see Fig. 2]. *Ophiomyxa tumida* arm - (Fig. 6) cross section; (Fig. 7) arm spines, H/E stain, showing the abundant basophilic fibrillar cells (FC) [see Fig. 6]. *Ophiobyrsa serpens* arm - (Fig. 8) cross section; (Fig. 9) cross section, ventral surface. (Fig. 10) cross section, lateral surface, AB/PAS stain, showing abundant PAS+ fibrillar cells (FC) and dark pigment granules in feltwork layer (FL). *Ophiogeron supinus* arm - (Fig. 11) cross section showing thick feltwork connective tissue layer (FL), and reduced skeleton embedded in dense connective tissue layer (DL); (Fig. 12) lateral and ventral surface showing a large tube foot (T); (Fig. 13) dorsal surface, AB/PAS stain, showing AB+ secretory cells (arrows). Abbreviations: D, dorsal arm plate; DL, dense layer of connective tissue; E, epidermis; FC, fibrillar cells; FL, feltwork layer of connective tissue; L, lateral arm plate; M, intervertebral muscle; N, radial nerve; O, vertebral ossicle; S, arm spine; T, tube foot; V, ventral arm plate. Scale bar = 250 μ m in Figs. 1,2,6,8,11,12; 100 μ m in Figs. 3-5, 7,9,10,13.



dominates the integument, while in *O. supinus*, feltwork connective tissue predominates. This difference may be reflected in the behavioral responses of their arms to disturbance. *Ophiomyxa* spp. stiffen their arms when disturbed, whereas *O. supinus* does not. It appears that the dense layer of longitudinally oriented fibrils conveys a rigidity to the arms of *Ophiomyxa* spp., whereas compact connective tissue is essentially lacking in *O. supinus*. In *Ophiomyxa* spp. the compact connective tissue may serve as a ligament traversing from the disc to the tips of the arms. The skeletal properties of the gelatin-like integument of *O. supinus* with its fragile ossicles are weak in comparison.

The arm stiffening reaction exhibited by *Ophiomyxa* spp. when disturbed by predators and collectors, is a defensive response (Sides 1987) and is reminiscent of the catch state observed in the connective tissue of several echinoderms (Motokawa 1984; Wilkie 1984). We suggest that integument catch acts in concert with catch of the intervertebral ligament to effect the stiffening defense by strengthening connections between adjacent arm segments. On the other hand, the integument of *Ophiomyxa* must be compliant enough to allow arm-coiling during feeding. In addition, arm autotomy occurs in *Ophiomyxa* at an intersegmental breakage plane, suggesting that the dermal connective tissue may also have the mutable properties demonstrated for the intervertebral ligament (Wilkie 1978b). The tensile state of the integument ranges from stiff to compliant, suggesting that the dermal connective tissue may have the variable tensility properties characteristic of echinoderm connective tissue (Motokawa 1984; Wilkie 1984).

Connective tissue and calcite are the two integral elements of the integumental support system of ophiomyxids. The connective tissue of ophiomyxids plays a supportive role that is fulfilled by calcite in other ophiuroids, in addition to its ligamental and tendonous functions. The integrity of the integument may depend on the variable tensility of the connective tissue, with

the ossicles serving as stiffeners to reinforce the soft tissue. The fleshy integument of *Ophiomyxa* spp. does not appear to be a weak structure, although the putative catch properties of their distinctive ophiomyxid integument requires verification through physiological investigation.

A glandular epidermis is characteristic of the Ophiomyxidae (Reichensperger 1908; Pentreath 1970) and the release of the fibrillar material presumably accounts for the slimy coating of these brittlestars. Reichensperger (1908) and Pentreath (1970) suggest that the slimy coating repels predators or acts as an "anti-fouling" agent. Notably, Ophiogeron arms lack both a heavily glandular epidermis and a slimy surface. Fibrillar cells occur in the Ophiurida (Fontaine 1965; Pentreath 1970; Hendlar and Byrne 1987), but not with the abundance seen in some ophiomyxids.

The histological results of this investigation bear on certain aspects of Matsumoto's (1917) classification of the Ophiuroidea. More conservative systematists, such as Mortensen (1927), recognized a division of Ophiuroidea into the orders Ophiurales and Euryales, and did not accept Matsumoto's (1917) notion of uniting the ophiuroid family Ophiomyxidae with the euryalous taxa in a new order Phrynophiurida. Emson and Wilkie (pers. comm.) have observed connective tissue strata in *Asteroschema* and *Astroporpa* species that resemble the histological features we have described in the Ophiomyxidae. This evidence for homologous soft tissue structures among the Ophiomyxidae and other euryalous taxa further corroborates Matsumoto's hypothesis.

Matsumoto (1917) separated ophiomyxid genera into two subfamilies, Ophiobyrinae and Ophiomyxinae, and regarded the latter as the most "archetypal" group of living Ophiuroidea based on the similarities between the skeleton structures of ophiomyxines and certain Paleozoic ophiuroids. The two-stratum morphology of the soft integument of *Ophiobyrsa serpens* (Ophiobyrinae) and *Ophiomyxa* spp. (Ophiomyxinae), seen here, is consistent

Figures 14 - 29. SEM micrographs of: *Ophiomyxa flaccida* arm in dorsal (Fig. 14), ventral (Fig. 15), lateral (Fig. 16) views, and arm spine (Fig. 17) - note connective tissue between arm plates of successive arm segments. *Ophiomyxa tumida* arm in dorsal (Fig. 18), ventral (Fig. 19), lateral (Fig. 20) views, and arm spine (Fig. 21). *Ophiobyrsa serpens* arm in dorsal (Fig. 22), ventral (Fig. 23), lateral (Fig. 24) views, and arm spine (Fig. 25). *Ophiogeron supinus* arm in dorsal (Fig. 26), ventral (Fig. 27), lateral (Fig. 28) views (arrow indicates tentacle scale), and arm spine (Fig. 29). Abbreviations: D, dorsal arm plate; L, lateral arm plate; V, ventral arm plate. Scale bar = 500 μ m.

with other synapomorphies described for Ophiomyxidae (Matsumoto, 1917). However, Matsumoto's assignment of Ophiogeron supinus and Ophiomyxa spp. to one subfamily (Ophiomyxinae), is arguable in light of the morphological contrasts between those genera. On the other hand, if he was correct, the atypical histological features of *O. supinus* can be regarded as specializations.

Several findings in this study point to the need for revisionary systematic analysis of ophiomyxid morphological structures. The histology of the integument has been overlooked, but our results show that it is of potential systematic importance. Moreover, descriptions of the skeletal features of many ophiomyxids are based on incomplete and inaccurate observations of specimens covered with integument. For example, in Lyman's (1883) descriptions of the species, the DAPs and tentacle scales of *O. supinus* are considered to be completely lacking, the DAPs of *O. tumida* are characterized as "nearly wanting", and the unusual mosaic VAP of *O. serpens* is not mentioned. Therefore, classifications based on published information on skeletal structures could be misleading.

To consider the paleontological implications of this study we refer to the Stenurida Spencer and the Oegophiurida Matsumoto as Paleozoic brittlestars, and to the Phrynophiurida and Ophiurida as recent brittlestars. The skeletal features distinguishing the four orders are clues to their functional morphology and natural history. Based on the articulation and putative musculature of the ambulacral plates, it is thought that many Paleozoic brittlestars have arms that are capable of limited movement, whereas arms of recent brittlestars are generally flexible and capable of rapid movement (Spencer 1951). Moreover, many Paleozoic brittlestars have been characterized as sedentary burrowers, and as selective deposit feeders or suspension feeders with an amphiurid-like life style (Spencer 1950, 1951; Spencer and Wright 1966).

The thick integument and enlarged tube feet of *O. supinus* are structural features related to the distinctive mode of locomotion of the species. Having relatively large tube feet, *O. supinus* may have a counterpart in the Paleozoic taxa, since the capacious podial basins of Paleozoic ophiuroids probably housed large tube-feet (Spencer 1951). Some fossils of Paleozoic brittlestars have well preserved skin surrounding the skeletal elements (Hammann and Schmincke 1986), but the biomechanical properties of this integument are not clear, and its similarity to the tissue of *O. supinus* is uncertain. However, limited

arm mobility, rather than integumentary structure, is evidence of functional similarity between *O. supinus* and some Paleozoic brittlestars.

Our observations on the morphology and locomotion of *O. supinus*, argue against the sedentary nature of Paleozoic ophiuroids. By analogy with *O. supinus*, Paleozoic ophiuroids may have been epifaunal forms with a pattern of locomotion more similar to some recent astropectinid asteroids than to amphiurid ophiuroids. We do not suggest that the behavior of Ophiomyxidae is "primitive". Rather, we propose that the locomotion of some Paleozoic ophiuroids with restricted arm mobility and large tube feet may have resembled the perambulation of *O. supinus*, combining a limited range of arm movement and effective tube foot propulsion.

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