THE ANATOMY AND VENOM-EMITTING MECHANISM OF THE GLOBIFEROUS PEDICELLARIAE OF THE URCHIN *PARECHINUS ANGULOSUS* (LESKE) WITH NOTES ON THEIR BEHAVIOUR

A. J. CANNONE

Zoology Department, University of Cape Town

INTRODUCTION

Pedicellariae are appendages of the test peculiar to the echinoderm classes Echinoidea (sea-urchins) and Asteroidea (star-fish), and are best developed and always present in the former. In echinoids they are present in large numbers between the spines and on the peristome. There are four kinds of echinoid pedicellariae, although variations of these basic types also occur. They are the tridentate or tridactyle, the triphyllous or trifoliate, the ophiocephalous, and the globiferous (sometimes also called gemmiform or glandular).

Sladen (1880) was the first investigator to describe the morphology of pedicellariae, in this case the globiferous pedicellariae of *Sphaerechinus granularis*. He recognised the secretory ability of these organs but not the toxic nature of the secretion. Subsequent contributors to our knowledge of the structure and function of pedicellariae include Foettinger (1881); Romanes and Ewart (1882); Koehler (1883); Hamann (1887); Prouho (1890), who was the first to suggest a function of defence; Von Uexküll (1899), who studied the behaviour of pedicellariae and established the toxic nature of the secretion of the globiferous type; Fujiwara (1935) who described the morphology of globiferous pedicellariae of *Toxopneustes pileolus*; and Pérès (1950), who gave a detailed account of the structure of globiferous pedicellariae of *Sphaerechinus granularis*.

Pedicellariae have not only proved to be fascinating organs to study in themselves, but are also important taxonomically in species discrimination. In fact it is mainly the structure of the skeletal elements of the globiferous pedicellariae of *Parechinus* which distinguishes this genus from the genera *Pseudechinus* and *Notechinus* (Mortensen 1943).

The present work on the globiferous pedicellariae of *Parechinus angulosus* was undertaken with a view to developing a comprehensive picture of their anatomy, since the detailed structure of these pedicellariae appears to differ considerably from one genus to another. In particular, the literature tends to be vague as regards the nervous elements of these organs. However, a great deal is known of the histology of the various tissues concerned (Foettinger 1881; Koehler 1883; Hamann 1887; Pérès 1950), and consequently will not be dealt with here.

MATERIALS AND METHODS

Parechinus angulosus occurs abundantly in Cape waters and is in fact the only echinoid found in intertidal pools. A number of pedicellariae were removed with forceps and placed immediately in Bouin's fixative. They were then decalcified by treating for 24 hours in a 3% solution of nitric acid made up in 70% alcohol. Due to the extremely small size of the

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pedicellariae (0·2 – 0·45 mm diameter), "bulk staining" was used to facilitate orientation in the wax. Heidenhain's azan stain was employed (Gurr 1952, p. 46) in which bulk-staining with borax carmine was substituted for azocarmine. After this the procedure was unaltered, and it was found that 15 to 20 minutes in aniline blue – orange G, acetic, gave the best results, with muscles orange, connective tissue blue, nuclei red (borax – carmine), and nerve tracts blue – purple. The glandular secretion of the pedicellariae also stained blue.

Pedicellariae were sectioned at 10 μ, both longitudinally and transversely, and in the latter case with the jaws both open and closed. The mounting medium used was Kirkpatrick and Lendrum's D.P.X.

Skeletal elements were prepared by boiling pedicellariae in a 20% aqueous solution of potassium hydroxide. This dissolves the surrounding tissues, leaving the valves and the rod of the stalk intact.

Technical difficulties precluded a serial reconstruction programme. However, it is felt that a considerable degree of accuracy was nevertheless attained by comparison of longitudinal and transverse sections.

In addition to a morphological study, observations on the behaviour of both intact and isolated pedicellariae were made in order to form a basis for discussion of the neuro-sensory relationships of these organs.

EXTERNAL FEATURES

A globiferous pedicellaria consists of a "head" of three separate jaws merging with each other at their bases. This head is supported on, and articulates with a rigid stalk varying in length from 1·5 to 2·25 mm. The base of the stalk articulates with the test by means of a ball-and-socket joint (Hyman 1955). Each jaw has a swollen appearance due to the presence of a venom gland. At the tip of each jaw is a sharp tooth projecting through the epidermal layer. Other teeth, sub-terminal and lateral in position, may or may not project through the epidermis. On the inner surface of each jaw a conspicuous swelling is apparent which Von Uexküll (1899) has termed a neurodermal organ. Another less well-defined neurodermal organ may be seen near the jaw tip beneath the terminal tooth (Fig. 2). The head of a pedicellaria is slightly longer than broad, varying in diameter from 0·2 to 0·45 mm.

THE ENDOSKELETON

The internal supporting structures of both head and stalk of the pedicellaria form a true endoskeleton, for as Hyman (1955) points out, they are embedded in the dermis and are derived from it. Each jaw possesses a valve of characteristic shape, and the stalk has a central rod which extends to the head of the pedicellaria, in the base of which it terminates as an enlarged structure with a circular convex surface forming a platform. The valves (Fig. 1) are shaped somewhat like an acute triangle, with a variable number of inwardly-projecting teeth (a maximum of four on any one side) present in the distal third portion. In addition there is always a single large terminal tooth at the tip of the valve, and this has a groove

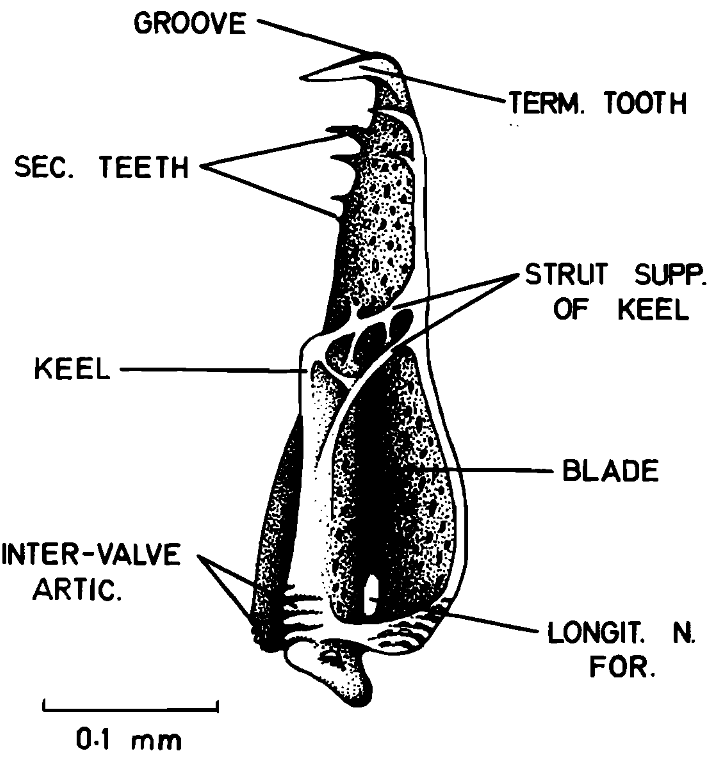

FIGURE 1

The valve of a globiferous pedicellaria of *Parechinus angulosus*. *Inter-valve artic.*, inter-valve articulation; *longit. n. for.*, longitudinal nerve foramen; *sec. teeth*, secondary teeth; *strut supp. of keel*, strut supports of keel; *term. tooth*, terminal tooth.

extending along its upper surface for the first two-thirds of its length. The secondary teeth are seldom paired.

In the proximal half of the valve a median keel projects inwards at a right angle to the blade. The distal part of this keel is strengthened by struts. The inner proximal edge of the keel is thickened and thrown into folds, as are also the lateral edges of the base of the valve. These folds form the articulation between valves. A lateral view of the keel indicates that the inner proximal edge is slightly convex. This is important when considering the opening of the jaws. Projecting from the base of a valve is a thickened process serving to support the valve on top of the skeletal rod of the stalk, and to allow the jaws to open and close freely. At the base of a valve is a medial vertical slit serving as a nerve foramen. In addition, the whole valve is perforated.

THE MUSCULATURE

The three sets of muscles responsible for:

(*a*) opening the jaws (abductors),
(*b*) closing the jaws (adductors),
(*c*) flexure of the head of the pedicellaria on the stalk (flexors),

are shown in Fig. 2. Of these, the three adductor muscles are the largest and most powerful. Each adductor muscle stretches from the inner surface of the proximal half of a valve to that of an adjacent valve. Both the blade and keel of a valve are involved in the insertion, hence the need for the elaborate strut supports of the latter.

The abductor muscles, also three in number, are much smaller than the adductors. Each abductor muscle stretches from the outer basal part of the blade of a valve to that of the adjacent valve. The proximal part of the keel of each valve being convex, acts as a fulcrum, so that contraction of the abductors results in the opening of the jaws.

There are six flexor muscles which have their origin on the skeletal rod of the stalk, immediately beneath the head of this rod. The rod at this point has a rough pitted texture to receive these muscles. From their common point of origin, pairs of flexor muscles extend around the head of the skeletal rod to insert on the outer surface of the base of a valve, the insertion being more distal in position than that of the abductors. The presence of six discrete flexor muscles imparts a considerable degree of flexure of the head of a pedicellaria on the stalk.

THE VENOM GLAND

Each jaw of a globiferous pedicellaria bears a glandular venom sac on the outside of the valve, extending from the base of the valve to the tip of the jaw where it opens to the exterior by means of a duct lying above the terminal tooth. The glandular epithelium of this venom gland is enclosed by a muscular sheath composed mainly of longitudinal muscle fibres. The proximal part of the venom sac, however, has, in addition, variously-orientated fibres which for convenience may be regarded as forming a circular layer between the longitudinal muscle layer and the glandular epithelium. This "circular" muscle layer in fact consists of criss-crossed fibres forming a meshwork encircling the lower part of the gland. The muscle sheath has its origin on the outer surface of the proximal part of the valve, the surface of the valve in this region being thrown into small folds (Fig. 4). This origin of the venom gland muscle-sheath is important when considering the venom ejection mechanism and will be dealt with after consideration of the structure of the secretory duct. Distal to the point of origin, the muscle sheath consists entirely of longitudinal fibres.

It was not within the scope of the present study to investigate the nature of the glandular epithelium. Pérès (1950) gave a detailed account of this epithelium in *Sphaerechinus granularis*. In *Parechinus angulosus* it consists of a single layer of cells lining a large lumen containing the secreted fluid. It is of interest to note that Alender (Ph.D. Thesis, 1964) failed to find any evidence of a glandular epithelium in globiferous pedicellariae of *Tripneustes gratilla*, a species known to produce venom of a toxic nature.

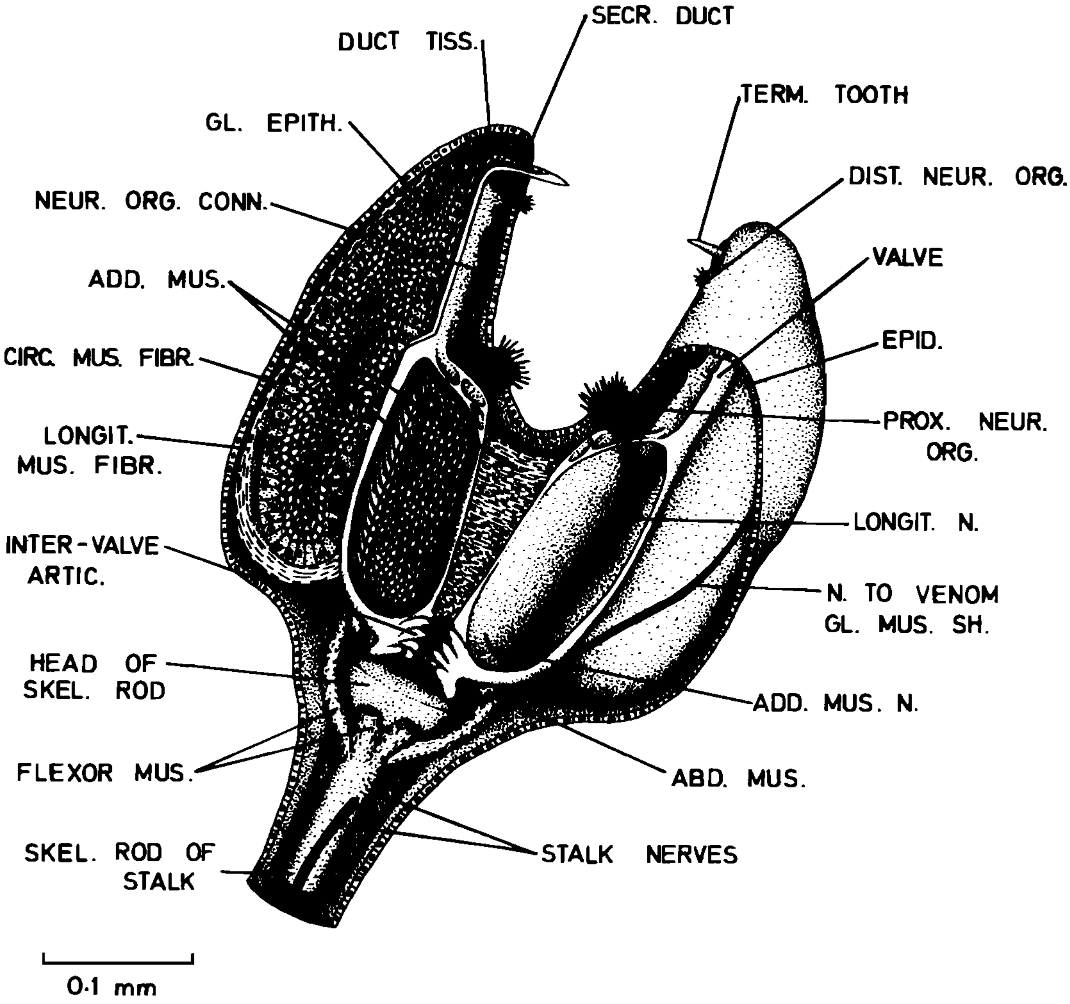

FIGURE 2

Diagrammatic stereogram of a globiferous pedicellaria of *P. angulosus* after removal of one jaw. *Abd. mus.*, abductor muscle; *Add. mus.*, adductor muscle; *Add. mus. n.*, adductor muscle nerve; *Circ. mus. fibr.*, circular muscle fibres; *Dist. neur. org.*, distal neurodermal organ; *Duct. tiss.*, duct tissue; *Epid.*, epidermis; *Flexor mus.*, flexor muscles; *Gl. epith.*, glandular epithelium; *Head of skel. rod*, head of skeletal rod; *Inter-valve artic.*, inter-valve articulation; *Longit. mus. fibr.*, longitudinal muscle fibres; *Longit. n.*, longitudinal nerve; *N. to venom gl. mus. sh.*, nerve to venom gland muscle sheath; *Neur. org. conn.*, neurodermal organ connective; *Prox. neur. org.*, proximal neurodermal organ; *Secr. duct.*, secretory duct; *Skel. rod of stalk*, skeletal rod of stalk; *Term. tooth*, terminal tooth.

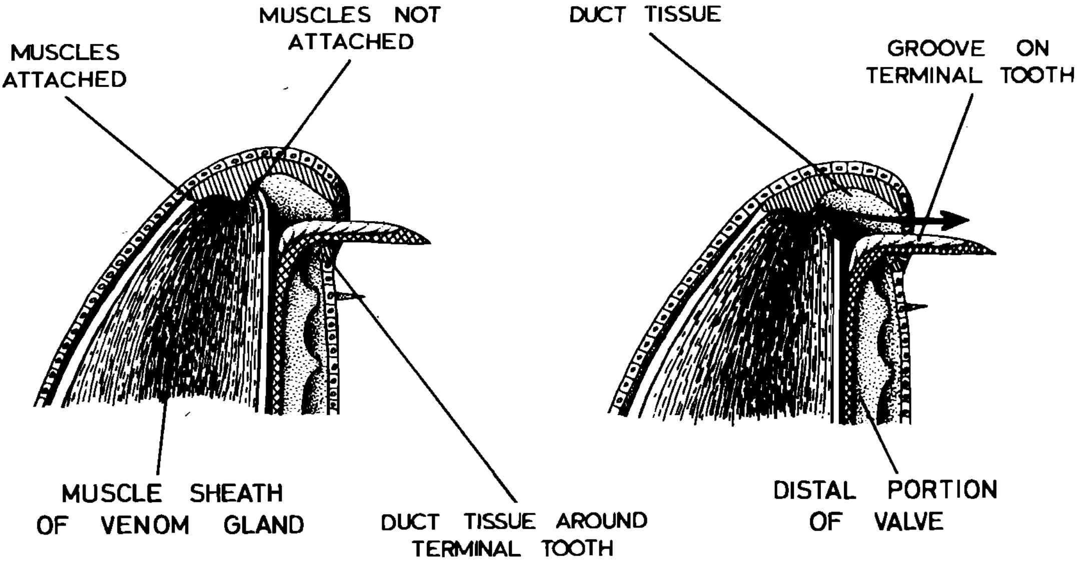

FIGURE 3

Stereograms of the duct region of a globiferous pedicellaria of *P. angulosus* illustrating conditions before (left) and after (right) contraction of the muscle sheath. Arrow indicates the course of venom flow. The glandular epithelium is not included.

THE SECRETORY DUCT

The lumen of the venom gland opens to the exterior via a single duct which passes over the terminal tooth, the groove on the terminal tooth forming the floor of this duct (Fig. 2). Sections through this duct region revealed the presence of a type of tissue not found anywhere else in the globiferous pedicellaria. It consists of a single layer or at most a double layer of darkly-staining cells bounded on the outer side by a relatively thick connective tissue layer which stains blue in azan. Longitudinal sections show that at the opening of the duct to the exterior there is a complete ring of duct tissue surrounding the terminal tooth and duct, this being the only point at which duct tissue encloses the secretory duct completely (Fig. 3). Aside from this ring of tissue, duct tissue is only present above the secretory duct itself. Fig. 3 also shows clearly that there is a mass of duct tissue at the proximal end of the duct which projects into the secretory duct from above. Between this projection and the base of the terminal tooth, the venom gland muscle-sheath terminates without inserting onto any structure. The muscle fibres of the outer part of the venom gland, however, enter the duct to insert between the duct tissue and the connective tissue layer. The muscle sheath thus forms a sac, the neck of which is partly attached to the duct tissue and partly free-ending, with the latter part extending around the projecting mass of duct tissue, thus effectively closing off the lumen of the venom gland from the exterior.

MECHANISM OF POISON EMISSION

Foettinger (1881) had noted a rather different type of glandular epithelium in the region of the secretory duct in *Sphaerechinus*. Pérès (1950) described the histology of this duct region in detail but it is apparent that this tissue is not the same as the duct tissue here described. The duct tissue in *Parechinus* is of a structural rather than a glandular nature, whereas Pérès believes that in *Sphaerechinus* the tissue is secretory, though the secretion differs from that of the remainder of the gland and probably serves the function of facilitating emission of the venom. Other investigators have also recognised the need for a controlling mechanism of venom emission. Fujiwara (1935) considered that in *Toxopneustes pileolus*, ejaculation of the gland contents is brought about by a contraction of the muscle sheath and by pressure of the valve, initiated by the closing of the jaws. However, Hyman (1955) points out that ejection of the venom is relatively independent of jaw closure, occurring only if the jaws close upon a source of chemical stimulation such as the podia of a starfish. The fact that the venom gland muscle-sheath is innervated (Fig. 2) supports this view.

Emission of the gland contents in *Parechinus* is probably brought about by a twofold effect of the contraction of the sheath fibres. Firstly, due to the fact that the outer part of the muscle sheath, from its point of origin on the valve, is curved around the gland and attached to the duct tissue, the net result of contraction would be compression of the gland lumen. The "circular" muscle fibres would contribute a more direct compressing effect. The duct itself remains firmly in position owing to the complete ring of duct tissue encircling the terminal tooth. Secondly, contraction (shortening) of the inner part of the muscle sheath would result in the secretory duct being opened (Fig. 3). Compression of the gland lumen, and the opening of the secretory duct would therefore be simultaneous (Fig. 4), the contents of the gland being ejected under pressure into the puncture created by the terminal tooth.

THE INNERVATION

The major nerve tracts are shown in Fig. 2. Three nerve fibres originate from the subepidermal nerve plexus and ascend the stalk of a pedicellaria. Each of the three jaws is innervated by one such stalk nerve, which passes between members of a pair of flexor muscles. Each stalk nerve passes through the foramen at the base of its respective valve to continue along the angle subtended by keel and blade as the longitudinal nerve. Prior to passing through the foramen, the stalk nerve gives off a stout branch to the muscle sheath of the venom gland. At the level of the foramen, the stalk nerve also gives off two branches to the adductor muscles, one on each side of the keel. Each adductor muscle, therefore, receives two nerves, each arising from different stalk nerves. The innervation of the abductor and flexor muscles could not be distinguished.

The longitudinal nerve of each jaw passes between the strut supports of the keel and enters a proximal neurodermal organ situated on the inner surface of the jaw. A short neurodermal organ connective leaves the proximal neurodermal organ and terminates in a smaller distal neurodermal organ situated immediately beneath the terminal tooth. Epidermal tissue does not cover these organs as they are made up of large numbers of neural cells including

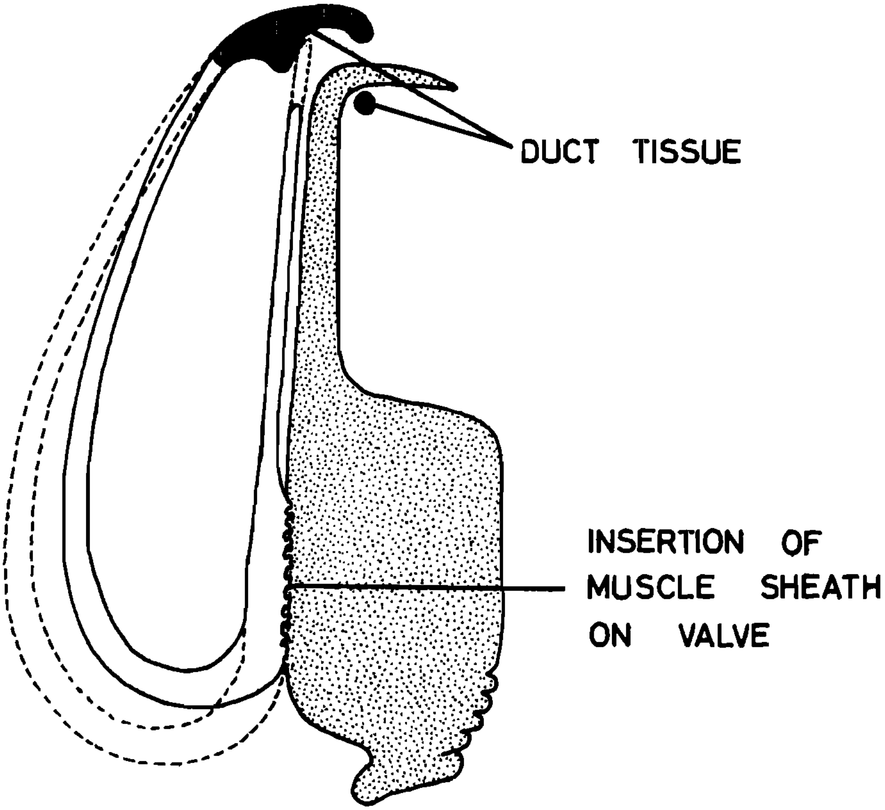

FIGURE 4
Diagrammatic sagittal section of one jaw of a globiferous pedicellaria of *P. angulosus* to show the muscle sheath of the venom gland before (broken lines) and after (unbroken lines) contraction. Skeletal valve stippled.

sensory-receptor cells equipped with sensory hairs. These sensory hairs were not evident in the sections, having been destroyed most probably during fixation or decalcification of the pedicellariae. They are readily seen on fresh pedicellariae using the phase contrast technique.

DISCUSSION

Globiferous pedicellariae of echinoids are known to be able to function normally when removed from the test, even to the extent of venom emission. Hyman (1955) in her excellent review of the Echinodermata, points out that they respond readily to both mechanical and chemical stimulation. However, although a certain amount of reflex control can be effected within an isolated pedicellaria, it will become apparent that in *Parechinus angulosus* overall co-ordination is vested elsewhere. Although Hyman (1955) concludes that pedicellariae are morphologically equivalent to spines, the work of Von Uexküll (1900) and Bolin(1926) indicates that the nervous control of spines and pedicellariae differs somewhat. Whereas normal reactions of pedicellariae are wholly unaffected by destruction of the circum-oral nerve ring, the spines become un-coordinated in their movements and the animal is in general immobilised and inactive. In the case of pedicellariae it seems probable that it is the sub-epidermal nerve plexus, which includes ganglion cells in local reflex centres at the base of the spines and pedicellariae, that exerts an overall control via the stalk nerves which arise from such centres.

Hyman (1955), reviewing the physiology of echinoids, states that "isolated globiferous pedicellariae usually remain open or can be caused to open by lightly stroking the tip or the outer surface. Any touch on the sensory hillocks (neurodermal organs) evokes wider opening, but if chemical stimulation is simultaneously applied, as a grain of salt or a starfish podium, closure occurs. Following such chemical stimulation of the test surface, the globiferous pedicellariae bite at mechanical objects of stimulation but do not eject their poison. The ejection of the poison is relatively independent of jaw closure, but follows if the jaws close upon a source of chemical stimulation as the podia of a starfish. The emission of the toxin can be evoked without jaw closure by laying a bit of chemical on the opened jaws" (parenthesis by author). These responses have on the whole been verified by the author for *P. angulosus*. One may conclude, therefore, that firstly globiferous pedicellariae must be sensitised by a chemical stimulus before they will respond by jaw closure to a mechanical stimulus, and secondly, that emission of venom depends on a "direct" chemical sensitivity after jaw closure. The distinction between a "direct" and what may be called an "indirect" chemical sensitivity becomes apparent when one considers the following series of observations that were made.

A homogenate of the podia of the asteroid *Marthasterias glacialis*, a known predator of *P. angulosus*, was obtained by grinding large numbers of podia and centrifuging the resultant slurry to remove cellular debris. The tissue-free supernatant was then poured into sea-water bathing a number of *P. angulosus* in a basin. The globiferous pedicellariae of these, which prior to this treatment were tightly shut, immediately became "sensitised", i.e., the jaws opened to their fullest extent, and the pedicellariae became fully extended at right angles to the test surface. This response, however, could not always be repeated, indicating possibly that other factors, such as concentration of homogenate, decreasing sensitivity, etc., need be taken into account. On the other hand this sensitising effect was invariably obtained by placing an intact *M. glacialis* onto the surface of *P. angulosus*, but in this case, in addition the spines flattened out, allowing the pedicellariae free access to the starfish, onto the podia, tubercles and papulae of which they closed and clung tenaciously, becoming detached from the sea-urchin test in the process. In this "sensitised" condition, isolated pedicellariae often responded by jaw closure to contact by such objects as brush bristles and pieces of algae, but opened immediately without emission of venom. On the other hand, closure on an isolated starfish podium was always permanent and venom could usually be seen to be emitted as a light-red coloured fluid, which perfuses into the tissue of the podium.

These and other observations carried out indicate at least two roles of the sub-epidermal nerve plexus in the co-ordination and control of pedicellarial behaviour. Two urchins and a starfish (*M. glacialis*) were placed some distance apart in a container of sea water. The presence of the starfish close to *P. angulosus* had no effect on the pedicellariae. One would not, in fact, expect sensitisation of pedicellariae to occur under these circumstances as both echinoderms are found together in inter-tidal pools, and to suppose that the majority of *P. angulosus* in their natural environment are in a constant state of "alarm" is not justified, nor is it in keeping with the facts. Placing an arm of the starfish in contact with an urchin, however, has an immediate effect, i.e., globiferous pedicellariae *over the whole of the test* become sensitised. This co-ordination can only be effected by the sub-epidermal plexus. A number of more discriminating tests led to the conclusion that it is a combination of simultaneous chemical and tactile stimuli on a podium or a spine of *P. angulosus* that evokes the response. In fact Hyman (1955) notes that "the same stimulus successively brings into play withdrawal of the spines, action of the globiferous pedicellariae and extension of the podia away from the source of stimulation" (flight). It is even more remarkable that such a high degree of response and co-ordination can be evoked by contact of a single starfish podium with a single spine or podium of *P. angulosus*.

A second role of the sub-epidermal plexus in pedicellarial activity is perhaps more difficult to analyse. Isolated globiferous pedicellariae of *P. angulosus* could not normally be induced to close on podia of the same individual nor on those of other urchins, even after they had been "sensitised" by contact with *M. glacialis*. Occasionally, however, isolated pedicellariae did bite at urchin podia but would then open immediately with no venom emission. These observations indicate that the chemo-sensitivity of isolated pedicellariae, while not being specific to starfish alone – a variety of substances evokes a response – at least excludes an intra-specific response. However, placing an urchin on top of another results in an immediate venom attack by the urchin underneath. This attack, however, is not maintained for longer than 5–10 seconds, and rarely more than 12 pedicellariae have been found attached to the podia of the urchin that sustained the attack. Neither could the attacker be induced to attack the same urchin a second time. Furthermore a side-by-side contact of urchins does not induce such an attack. Since isolated pedicellariae do not respond to urchin podia by venom emission, but under certain circumstances intact pedicellariae do, this suggests that the sub-epidermal plexus can influence the chemosensitive response of intact pedicellariae to some extent. While it is emphasised that more rigorous and more numerous tests would be required to establish this influence of the sub-epidermal plexus beyond doubt, such a control of chemo-sensitive response of pedicellariae by the sub-epidermal plexus would be of obvious value to *P. angulosus* in their natural habitat, where in fact one often sees extremely dense populations inhabiting pools and rock crevices, but never individuals lying on top of one another.

Globiferous pedicellariae of *P. angulosus*, therefore, are seen to be remarkably complex organs with regard to both structure and physiological behaviour, capable of reciprocal excitation and inhibition of antagonistic muscles, superimposed on which is a sensory perception of both chemical and tactile stimuli, these activities being effected entirely by local neural circuits. Superimposed on this again is the role of the sub-epidermal nerve plexus which to some extent at least effects ultimate control and co-ordination. However, as

Smith (1966) points out, phenomena such as these have not as yet been adequately analysed; the present study being but a start in that direction.

One of the interesting points which requires elucidation is the function of having two neurodermal organs per jaw in *P. angulosus*. It is of interest to note that in a number of urchins, as for example *Toxopneustes pileolus* (Fujiwara 1935) and *Strongylocentrotus lividus*, only one neurodermal organ per jaw has been reported; whereas Ludwig and Hamann (1902) consider *Echinus acutus* to have three per jaw, the third being represented by numerous sense cells in the epidermis between the distal and proximal organs. It seems unlikely that two separate sensory centres would be equally sensitive to both mechanical and chemical stimulation. A separation of functions would be more likely, with the position and relatively smaller size of the distal neurodermal organ in *P. angulosus* suggesting that it has a chemosensitive function. Situated as it is at the base of the terminal tooth, it could in fact be the determinant of venom emission, since globiferous pedicellariae once sensitised, will bite at objects providing a mechanical stimulus, but will not emit venom unless the object at the same time provides a chemical stimulus. Whereas both a starfish podium and an algal particle would be penetrated by the terminal tooth and both would come into contact with the distal neurodermal organ, only the starfish podium would provide the chemical stimulus necessary for venom emission. Selective destruction of the distal neurodermal organs, together with appropriate tests and controls, would perhaps yield a more valid conclusion than would pure speculation alone.

In conclusion, the globiferous pedicellariae of *Parechinus angulosus* are seen to be compact organs of defense with a particularly complex structure when it is considered that they are thought to have evolved from spines (Hyman 1955). Their value in defense, in terms of the toxicity of the venom, has yet to be determined for *P. angulosus*. Preliminary investigations indicate that the venom produced is not nearly as toxic as that produced by some species, notably *Toxopneustes pileolus* (Fujiwara 1935) and *Tripneustes gratilla* (Mortensen 1943, Alender 1964), stingings from the globiferous pedicellariae of which are known to produce both local and systemic effects in humans. The toxic nature of extracts of globiferous pedicellariae of a number of other echinoids has also been established (see summary by Alender and Russell, 1966).

The globiferous pedicellariae of *P. angulosus* illustrate the degree of specialisation attained by pedicellariae in general. The simplest pedicellariae known are characteristic of the asteroid order Phanerozonia, and are simply groups of two or more movable spines attached directly by muscle and connective fibres to one or more skeletal ossicles (Hyman 1955). On the other hand, globiferous pedicellariae of echinoids have well-developed venom glands, musculature, endoskeleton, sensory-nervous system, and last, but not least, in *P. angulosus* there is evidence of a remarkable mechanism of control of venom emission.

SUMMARY

An anatomical investigation, using chiefly serial sections, has been undertaken on the globiferous pedicellariae of *Parechinus angulosus*. The endoskeleton, musculature, sensory-nervous system and venom apparatus have been described. Evidence is presented which indicates

that the venom apparatus includes a remarkable system of control of venom emission regulated by the sensory-nervous system and dependent on a unique "duct tissue" for its efficacy.

The complexity and degree of autonomy of the sensory-nervous system is reflected in the responses of both intact and isolated pedicellariae to stimuli. Preliminary observations suggest that the sub-epidermal nerve plexus plays a role in the control of chemosensitive responses of globiferous pedicellariae.

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