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The cruciform muscle complex in Egeria radiata L. (Bivalvia, Tellinacea, Donacidae)

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INTRODUCTION

Characters of systematic interest in the bivalve molluscs of the order Tellinacea include mobile and separate siphons, highly developed siphonal retractor muscles and a cruciform muscle complex. The latter consists of a pair of special muscle strands originating in the mantle edge close to the bases of the inhalant siphons. The strands cross each other diagonally in the mantle cavity as they become inserted in the posteroventral mantle margin of the opposite side. A sense organ, responding to chemical stimuli (Odiete, 1978), is always associated with the posterior ends of the cruciform muscle. In *Gari, Tellina, Solecurtus, Macoma* (Graham, 1934) and *Scrobicularia* (Graham, 1934; Odiete, 1978) the sense organ opens to the exterior at the siphonal space, while in *Donax* (Graham, 1934; Moueza & Frenkiel, 1974), *Tagelus* (Hoffmann, 1914; Frenkiel, 1979) and *Sanguinolaria* (Frenkiel, 1979) the organ is closed.

The cruciform muscle has long been considered one of the important taxonomic characters for classifying bivalve molluscs possessing this structure. Graham (1934) divided the Solenacea into the Solenidae, possessing no cruciform muscle, and the Solecurtidae possessing it. The latter family was incorporated into the Tellinacea in the family Psammobiidae (= Asaphidae Winckworth, 1932) by Thiele (1934) thus emphasizing that the Tellinacea contain exclusively all lamellibranchs possessing a cruciform muscle. Yonge (1949) retained this system of classification and recently, Frenkiel (1979) suggested the separation of species in the Psammobiidae with open sense organ from those with the closed type.

Earlier studies on the cruciform muscle complex were mainly, if not only, on European species. Frenkiel (1979) has now added studies on North American species which, like the European species, were either marine or estuarine. Only two of the 38 genera constituting the Tellinacea are freshwater inhabitants, namely, *Egeria* and *Iphigenia* (Thiele, 1934). Both are tropical genera in the family Donacidae.

Since the cruciform muscle complex is of taxonomic importance and since no investigation has been reported on African nor on freshwater species, a study of the complex in the West African freshwater bivalve, *Egeria radiata* (Lam.), has been undertaken. The results constitute this presentation.

MATERIAL AND METHODS

Egeria radiata is abundant in sandy beds in the lower reaches of the Cross River in

Nigeria, the Volta River in Ghana and the Sanaga River in Cameroon. The species is thus exclusively West African.

Specimens were collected from Itu on the Cross River and kept for months in a sandy pond in the Biological Garden of the University of Lagos until required for study. The structures of the cruciform muscle and its sense organ in *Egeria* were studied by means of dissections and by making serial sections of specimens fixed in alcoholic Bouin (Duboscq-Brasil). Paraffin sections were stained in Mallory triple stain.

RESULTS

As in other species of the Tellinacea that have been investigated (Von Ihering, 1900; Hoffmann, 1914; Graham, 1934; Yonge, 1949; Moueza & Frenkiel, 1974; Odiete, 1978), except in *Tagelus divisus* (Spengler) (Ghosh, 1920) which has one strand, the cruciform muscle in *Egeria* consists of two silvery-white strands situated near the bases of the siphons in the posteroventral margins of the mantle. Several small groups of longitudinally-running muscle bands in the mantle edge join in forming the anterior attachments of the cruciform muscle. The strands course diagonally and posteroventrally to the opposite mantle edge. Where they cross each other (chiasma or cross, fig. 1) each strand divides into three flat strips which interlock in the manner shown in fig. 1b.

The short, wider and conical posterior ends of each strand are separated from the rest of the muscle by a visible gap which is the intramuscular slit (SL, fig. 1a). These posterior ends form a semi-circle which encloses the sense organ and the sensory ganglion (fig. 3b, c) and are attached directly to the shell valves.

The cruciform muscle fibres are 8-9 μm in diameter in stretched and 12-16 μm in contracted condition and myofibrils run parallel in stretched and spiral in contracted fibres. Each muscle fibre extends from its anterior attachment to the intramuscular slit. It terminates on collagen fibres on the basement membrane of the squamous epithelium of the slit. The muscle fibres which make up the posterior part of the cruciform muscle similarly originate from collagen fibres attached to the opposite basement membrane.

The sense organ (figs. 2 & 3) consists of a wide, thin-walled and blind-ending ventral chamber or sac (VS) which narrows in diameter as it leads dorsally to a ciliated groove or pit (GV) and a semi-circular intramuscular slit. The sac is almost perpendicular to the slit. The epithelium of the sac and slit is squamous, about 5 μm tall, and the slit has a continuous and thick basement membrane for the attachment of muscle fibres. The groove or pit is lined by cubical epithelium, 10 μm tall, and is penetrated by long dendritic processes or sensory nerve terminals (DP, fig. 2b; fig. 3e) emerging from the overlying ganglion cells (GC, SOG). These processes project 30-40 μm into the cavity or groove. Ganglion cells form a semi-circle around the groove and have characteristic large nuclei with numerous nucleoli. They are bipolar neurones with their axons (AX) forming the short nerve which is a branch of the posterior pallial nerve and their dendrons penetrating the epithelium of the groove. Tabel 1 shows the relative dimensions of various parts of the sense organ.

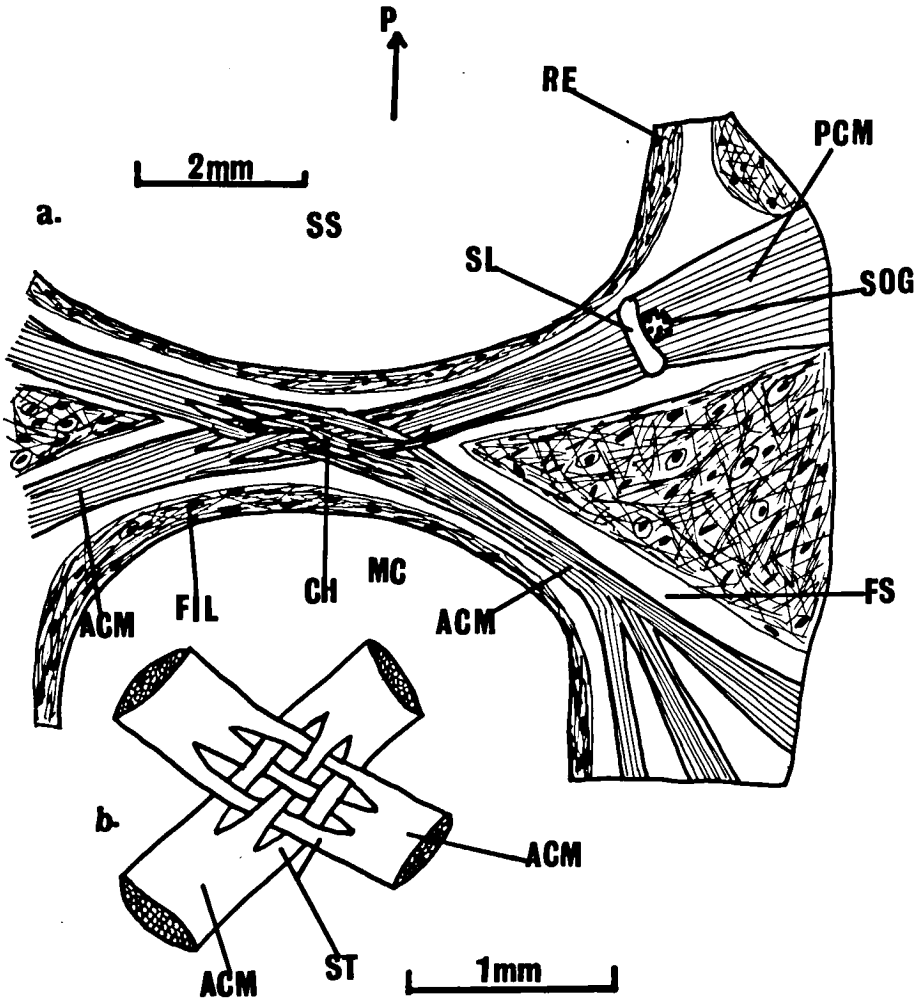

Fig. 1. a, Semi-diagrammatic ventral view of the posterior end of the fused mantle edge in *Egeria radiata* showing the cruciform muscle; b, the crossing or chiasma, magnified. ACM, anterior part of cruciform muscle; CH, crossing of strands; FIL, fused inner mantle lobes; FS, fluid-filled space surrounding cruciform muscle; MC, mantle cavity; P, posterior end of animal; PCM, posterior part of cruciform muscle; RE, right mantle edge; SL, intramuscular slit; SOG, sense organ ganglion; SS, siphonal space; ST, flat strips of muscle.

Table 1. The relative dimensions (in μm) of various parts of the sense organ in *Egeria radiata*

Part of sense organ	Width	Length	Height
Ventral chamber	192	200	461
Intramuscular slit (across ends)	51	700	-
Sensory groove	120	100	-

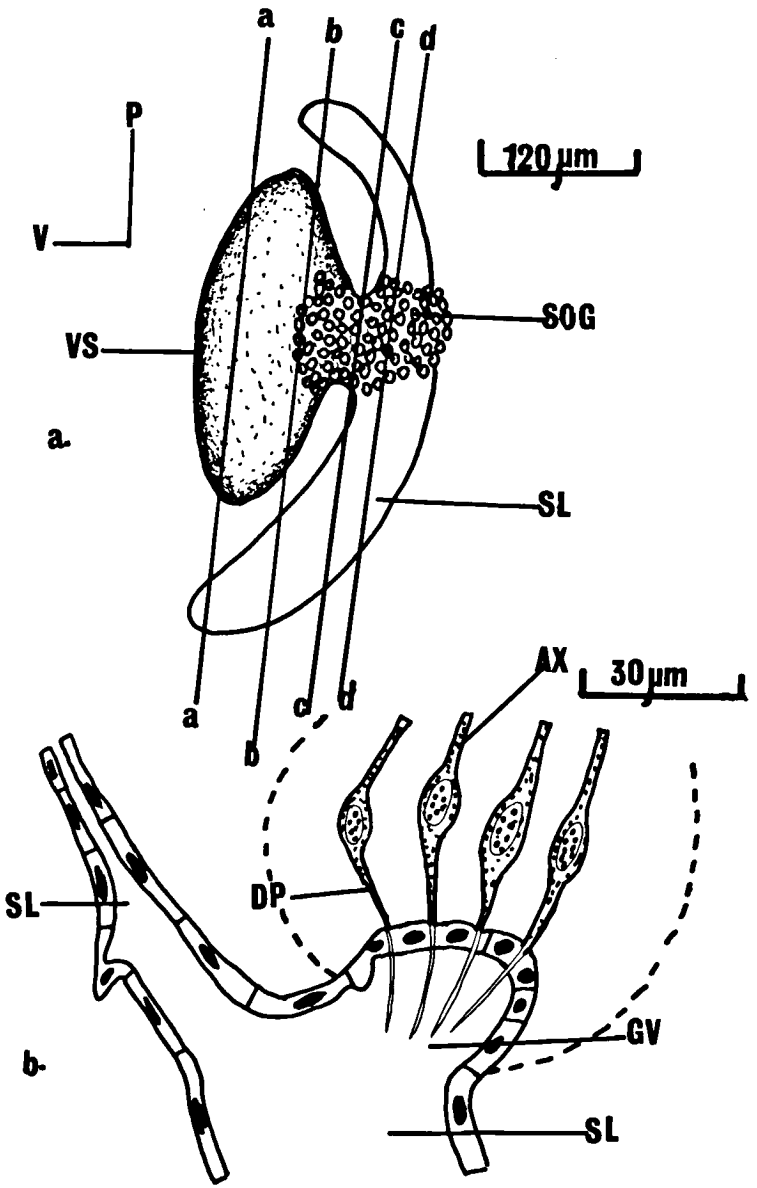

Fig. 2. a, Lateral view of sense organ (ganglion cells surround sensory groove or pit); b, details of ganglion cells and sensory pit epithelium. AX, axon; DP, sensory nerve terminal; GV, sensory groove or pit; P, posterior; SOG, sense organ ganglion; SL, intramuscular slit; V, ventral; VS, ventral sac or chamber; a-a, b-b, c-c, & d-d, plane of sections (horizontal) which give photomicrographs in fig. 3 a to d, respectively. Fig. 2a is a freehand drawing reconstructed from serial sections.

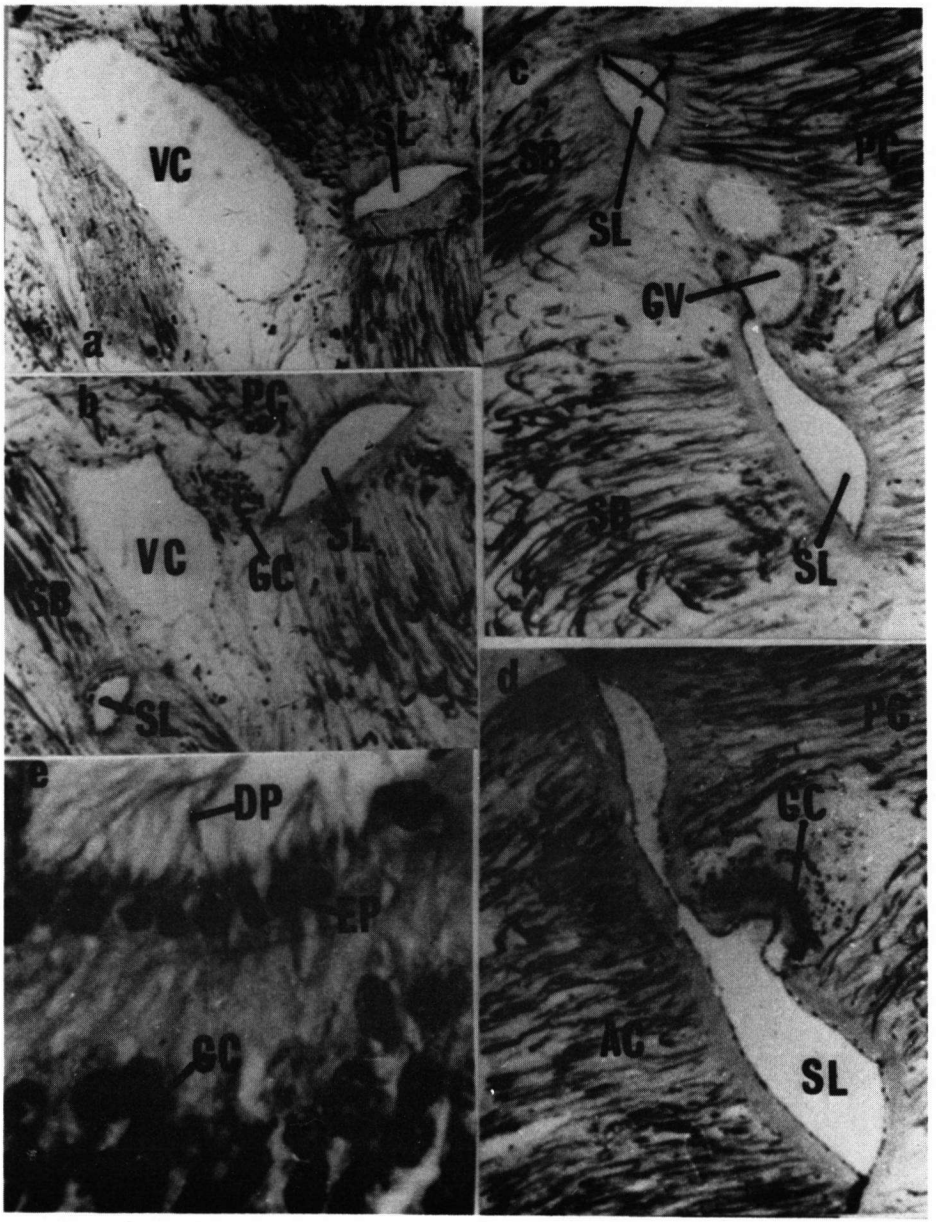

Fig. 3. Horizontal sections through sense organ and cruciform muscle of *Egeria radiata* corresponding to plane of section as shown in fig. 2a. a & b, x 240; c & d, x 480; e, x 1920. Lettering as in fig. 2. AC, anterior part of cruciform muscle before slit; EP, sensory pit epithelium; GC, ganglion cells; PC, posterior part of cruciform muscle; SB, bundles of cruciform muscle, on both sides of slit, forming a semi-circle.

DISCUSSION

In bivalve molluscs possessing the cruciform muscle, the sense organ consists of an intramuscular slit opening into a ciliated pit. In *Gari tellinula* (Lam.) and *Tellina crassa* Penn. (Graham, 1934) the pit opens directly to the exterior at the siphonal space. In *Scrobicularia plana* (Da C.) (Odiete, 1978), *Macoma balthica* (L.) and *Solecurtus scopula* (Turton) (Graham, 1934) a relatively long outer chamber connects the pit to the exterior. All these species have open sense organs. In *Donax vittatus* (Da C.) (Graham, 1934), *D. trunculus* L., *D. semistriatus* Poli (Moueza & Frenkiel, 1974), *Tagelus dombeii* (Lam.) (Hoffmann, 1914), *T. californianus* (Conr.), *T. divisus* and *Sanguinolaria nuttalli* (Conr.) (Frenkiel, 1979) the ciliated pit leads to a blind-ending outer chamber and the sense organ is, thus, of the closed type. Being closed, the sense organ in *Egeria radiata* resembles this last type.

Sensory nerve endings penetrate the epithelium of the pit in *Egeria* as in *Donax*, where electronmicroscopic studies of the sense organ by Moueza & Frenkiel (1976) have confirmed this penetration.

The ventral outer sac or chamber of the sense organ in *Egeria* is extremely thin-walled and is separated from the blood spaces in the mantle edge. Therefore, it should not contain any haemolymph.

The cruciform muscle complex in *Egeria* differs from those of other species in some respects. In *Egeria* each cruciform muscle strand is subdivided into three or more long and flat strips at the chiasma. These loosely interlock with the strips of the other strand. This condition is obviously necessitated by the fact that the adductor muscles in *Egeria* are far dorsally placed (see also Purchon, 1963). The mussel thus gapes very widely when the adductor muscles are fully relaxed and, as there is no ventral mantle fusion except at the cruciform muscle, the strands could break during extensive gaping. It has been demonstrated in *Scrobicularia* that the cruciform muscle strands are stretched during gaping and contracted during adduction (Odiete, 1978). The long interlocking muscle strips will allow the shell valves to gape without much strain on or injury to the cruciform muscle which would have been the case were the muscle fibres to interdigitate at the chiasma as in other species.

Another point of difference with other species is, that in *Egeria* the posterior ends of the cruciform muscle and hence the intramuscular slit, form a semi-circle and enclose part of the outer chamber, the ciliated pit and sensory ganglion. Furthermore, the ventral outer chamber is much more enlarged compared with species with a closed sense organ such as in *Donax*.

The results of a study on *Iphigenia*, the other freshwater genus of the Tellinacea, could not be included in this presentation because of doubtful identification. Yoloye (1977) described the biology of *Iphigenia truncata* (Von Martens) which is abundant in the Lagos lagoon. Specimens have separate siphons, very extensive ventral mantle fusion and no evidence of a cruciform muscle. A report of the condition in this genus will be made after proper identification.

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SUMMARY

The cruciform muscle complex in the freshwater bivalve *Egeria radiata* L. is highly developed and probably more complicated than in any previously described species. The muscle strands divide at the chiasma into long flat strips which are loosely interlocking. The sense organ consists of a blind-ending, thin-walled and wide ventral sac, becoming progressively narrower dorsally as it leads to a ciliated pit or groove and a semi-circular intramuscular slit. The posterior ends of the cruciform muscle consist of muscle bundles similarly arranged in a semi-circular manner so that the large sac, ciliated pit and sensory ganglion are enclosed between the muscle bundles. Dendritic or sensory nerve endings from the ganglion cells penetrate the epithelium of the pit as in *Donax*. The sense organ is of the closed type as in *Donax*, *Tagelus* and *Sanguinolaria*.

REFERENCES

FRENKIEL, L., 1979. L'organe sensoriel du muscle cruciforme des Tellinacea: importance systématique chez les Psammobiidae. - J. molluscan Stud. 45: 231-237.

GHOSH, E., 1920. Taxonomic studies on the soft parts of the Solenidae. - Rec. Indian Mus. 19: 47-78.

GRAHAM, A., 1934. The cruciform muscle of lamellibranchs. - Proc. R. Soc. Edinb. 54: 17-30.

HOFFMANN, F., 1914. Beiträge zur Anatomie und Histologie von Tagelus dombeyi (Lamarck). - Jena. Z. Naturw. 52: 521-566.

IHERING, H. VON, 1900. The musculus cruciformis of the order Tellinacea. - Proc. Acad. nat. Sci. Philad.: 480-481.

MOUEZA, M. & L. FRENKIEL, 1974. Contribution à l'étude des structures palléales des Tellinacea. Morphologie et structure du manteau de Donax trunculus L. - Proc. malac. Soc. Lond. 41: 1-19.

————, 1976. Premières données sur l'ultrastructure de l'organe sensoriel du muscle cruciforme de Donax trunculus L. (Mollusque, Lamellibranche, Tellinaces). - Archs Zool. exp. gén. 117: 485-492.

ODIETE, W.O., 1978. The cruciform muscle and its associated sense organ in Scrobicularia plana (Da Costa). - J. molluscan Stud. 44: 180-189.

PURCHON, R.D., 1963. A note on the biology of Egeria radiata L. (Bivalvia, Donacidae). - Proc. malac. Soc. Lond. 35: 251-271.

THIELE, J., 1934. Handbuch der systematischen Weichtierkunde. 2(3): 779-1022. Jena.

YOLOYE, V., 1977. The biology of Iphigenia truncata (Monterosato) (Bivalvia, Tellinacea). - Malacologia 16: 295-301.

YONGE, C.M., 1949. The structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. - Phil. Trans. R. Soc. Lond. B 234: 29-76.