

Ultrastructure of Euspermatozoa of Cerithiacean Gastropods (Prosobranchia: Mesogastropoda)

JOHN M. HEALY

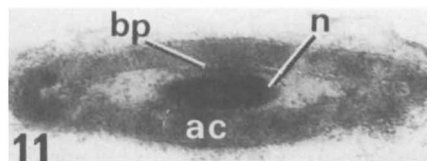
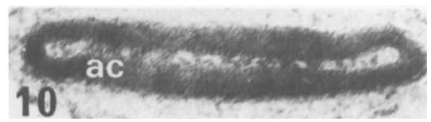
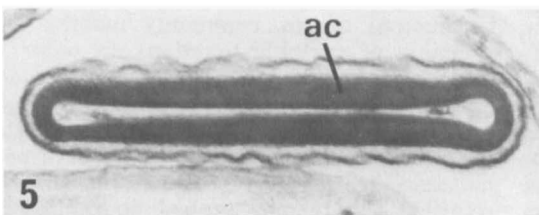
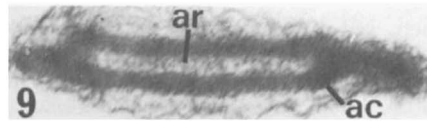
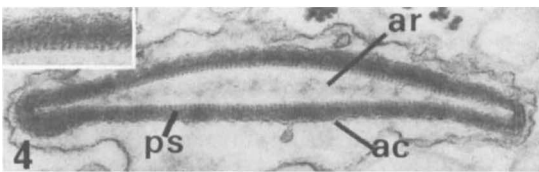
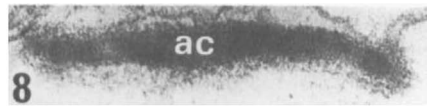
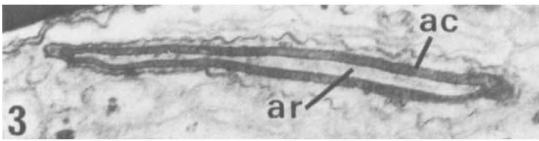
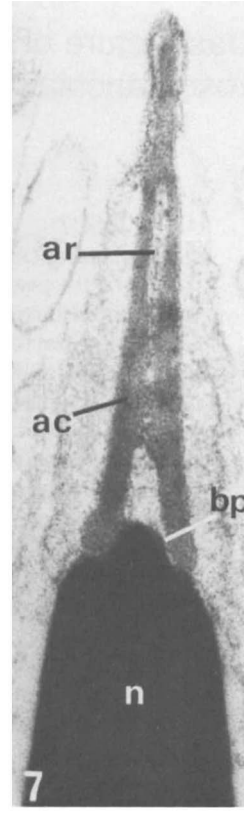
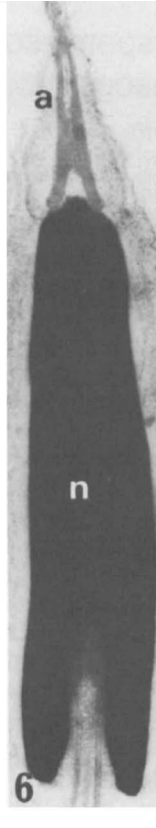
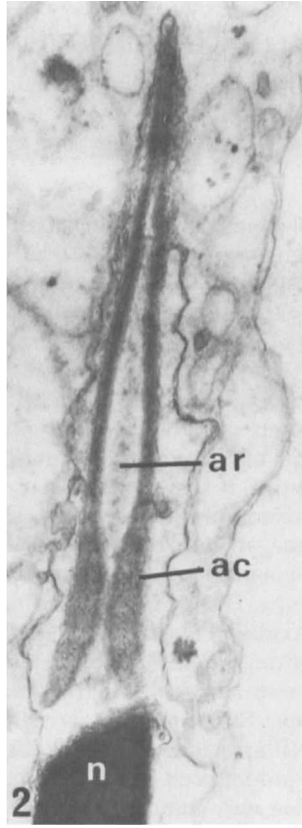
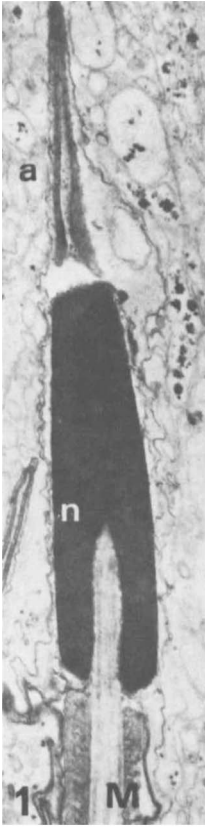
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ABSTRACT Euspermatozoa of selected cerithiacean gastropods have been studied using transmission electron microscopy and the results compared (primarily) with previous studies of mesogastropod and neogastropod euspermatozoa. Cerithiacean euspermatozoa each possess a well-defined acrosome (extremely varied in shape), a short (2.25–3 μm), very electron-dense nucleus, an elongate midpiece, and an elongate glycogen piece. A dense ring structure associated with the plasma membrane occurs at the junction of the midpiece and glycogen piece. While features such as the dense ring structure and the systematic periaxonemal arrangement of "glycogen" granules can be understood from a purely functional standpoint, it is suggested that euspermatozoon features also provide information of taxonomic and phylogenetic relevance. On the basis of euspermatozoon midpiece structure, true cerithiaceans can be easily distinguished from other mesogastropods and from neogastropods and are divided tentatively into two groups: Group 1 (Turritellidae, Cerithiidae, *Australaba* (family uncertain), Planaxidae, Potamididae (subfamily Batillariinae)), and Group 2 (Potamididae (subfamily Potamidinae), Modulidae, *Obtortio* (family uncertain)). Using midpiece and acrosomal features, group 1 can be further subdivided into two subgroups: Subgroup 1(i) (Turritellidae, Cerithiidae, *Australaba*) and Subgroup 1(ii) (Planaxidae, Potamididae (subfamily Batillariinae)). It is suggested that the pronounced differences existing between the two subfamilies of the Potamididae may indicate the necessity for a separate family for the Batillariinae.

Franzén ('56) recognized two basic types of sperm common within the Invertebrata: "primitive sperm" (occurring in species which exhibit external fertilization) and "modified sperm" (occurring in species with internal fertilization). Modified sperm are usually recognized by the presence of an elongate, postnuclear midpiece and rod-shaped (often elongate) nucleus. Within the Mollusca, primitive sperm occur in the Bivalvia (see Popham, '79 for references), Polyplacophora (Retzius, '04; Franzén, '55a, Pearce and Woollacott, '79) and Scaphopoda (Retzius '05; Franzén, '55a), while both primitive and modified sperm occur in the Aplousobranchia (Franzén, '55b) and Gastropoda (Retzius, '06; Franzén, '55a; see Healy, 82a,b for electron microscopic references). Spermatozoa of all cephalopods could be described as modified, although the morphological differences between spermatozoa of the major

groups (decapods, octopods, *Nautilus*) are very pronounced (Franzén, '67, '70; Longo and Anderson, '70; Maxwell, 1974; Fields and Thompson, '76; Arnold and Williams-Arnold, '78).

In many mesogastropod and neogastropod species, two distinct types of sperm are produced simultaneously within the gonad. These two types are commonly referred to as "typical spermatozoa" (sperm of the modified shape, presumably the true genetic sperm) and "atypical spermatozoa" (usually multi-axonemal sperm, commonly mobile, and probably of variable function). In order to remove any suggestion of aberrancy, Healy and Jamieson ('81) replaced the terms "typical spermatozoa" and "atypical spermatozoa" with "euspermatozoa" and "paraspermatozoa" (respectively). Melone et al. ('80) retained the terms "typical spermatozoa" and "atypical spermatozoa" but used the lat-



ter in connection with cells "which in their organization and morphological characters are close to typical spermatozoa" (p. 199). Melone et al. ('80) introduced the term "paraspermatic cell" to describe "cells that manifest very different morphology but derive from the same germinal line as typical spermatozoa" (p. 199)—essentially the "atypical spermatozoa" of mesogastropods and neogastropods. Healy and Jamieson ('81) suggested that the term "paraspermatic cell" could be used in a wider sense to include both paraspermatozoa and nurse cells (for example the nurse cells of *Littorina*—see Reinke, '12; Buckland-Nicks and Chia, '77). Buckland-Nicks et al. ('82) recognized the unsuitability of the terms "atypical spermatozoa" and "typical spermatozoa," but rejected the "euspermatozoa/paraspermatozoa/paraspermatic cell" system in favour of Meves' ('03) sperm classification based on the occurrence and relative size of the nucleus (that is: eupyrene oligopyrene and apyrene spermatozoa). It would, however, be equally valid to establish a morphological classification on the basis of other important spermatozoal features such as the occurrence and number of axonemes present (uniaxonemal, multiaxonemal, an-axonemal), the presence or absence of the acrosome, or the overall spermatozoal shape. The euspermatozoon/paraspermatozoon/paraspermatic cell system: (1) does not, as assumed by Buckland-Nicks et al. ('82), conflict with the continued usage of Meves' terminology in an accessory, descriptive capacity (as already practiced by some authors who additionally use the term "atypical spermatozoa"—including Zylberberg, '63; Fain-Maurel, '66; Friedlander and Miesel, '77; Giusti and Selmi, '82); (2) avoids the impli-

cation of aberrancy inherent in the "typical/atypical spermatozoa" system; and (3) is defined on lineal, functional, and morphological bases (see Healy and Jamieson, '81).

Many studies now exist dealing with the ultrastructure of mesogastropod and neogastropod euspermatozoa (including Kaye, '58; Yasuzumi, '62; Walker and MacGregor, '68; Giusti, '69, '71; Anderson and Personne, '70; Hachiri and Higashi, '71; Buckland-Nicks, '73; Giusti and Mazzini, '73; West, '78; Grifond, '80; Kohnert, '80; Healy, '82a) or euspermatozoa and paraspermatozoa (Ishizaki and Kato, '58; Tanaka, '58; Yasuzumi and Tanaka, '58; Gall, '61; Bulnheim, '62; Hachiri and Higashi, '72, '74; Koike and Nishiwaki, '80; Selmi and Giusti, '80; Healy and Jamieson, '81; Buckland-Nicks et al., '82; Healy, '82c). No study has, however, dealt with more than two or three species in any one superfamily and consequently little is known concerning the morphological diversity of euspermatozoa within genera, families, and superfamilies. The present study examines such diversity in structure of euspermatozoa within genera of three cerithiacean families—Potamididae (*Telescopium*, *Terebralia*, *Cerithidea*, *Pyrazus*, *Velacumantus*), Cerithiidae (*Rhinoclavis*, *Clypeomorus*), Planaxidae (*Planaxis*), and one species of *Australaba* (the relationship of this genus to other cerithiaceans being uncertain). Recent (unpublished) work by the author on some features of euspermatozoa of *Modulus tectum* (Modulidae: Cerithiacea) is also referred to. Both euspermatozoa and paraspermatozoa were examined in all species but only euspermatozoa are described in the present paper. A comparative account of cerithiacean paraspermatozoa is currently in preparation.

MATERIALS AND METHODS

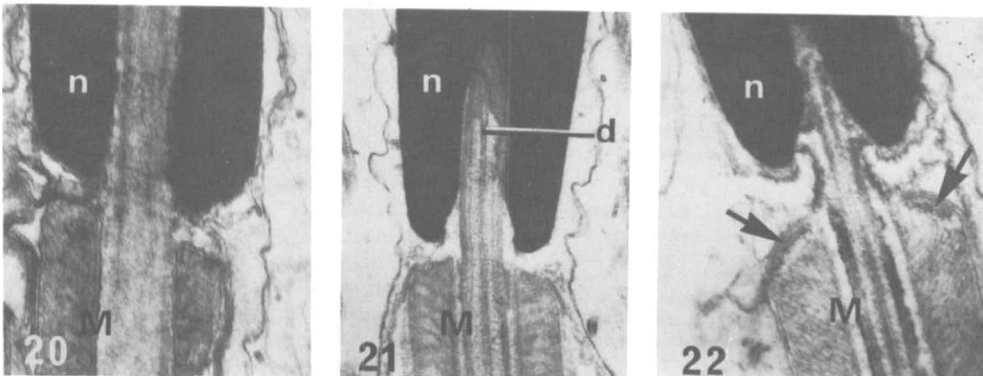
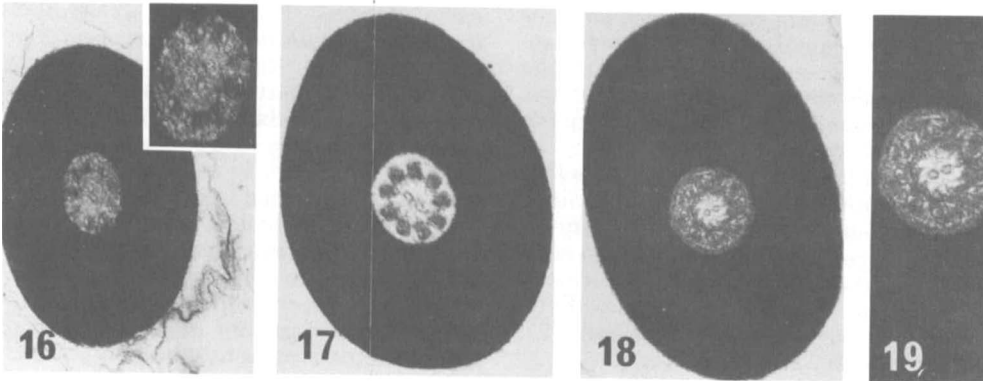
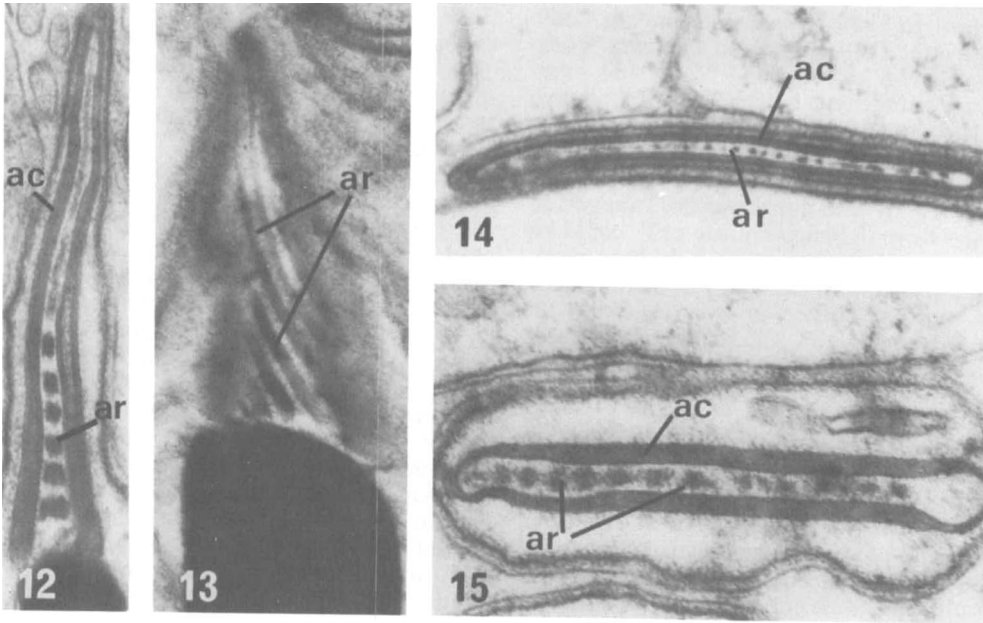
Live, reproductively mature specimens of each species were collected (and processed) between 1979 and 1981 from the following localities: Lota, Moreton Bay, southern Queensland (*Cerithidea largillierti* Philippi, *Cerithidea obtusa* (Lamarck), *Australaba* sp.¹); Sandgate, Moreton Bay, southern Queensland (*Clypeomorus moniliferus* (Kiener), *Velacumantus australis* (Quoy and Gaimard); Low Isles, northern Queensland (*Rhinoclavis vertagus* (Linnaeus)); Cairns, northern Queensland (*Telescopium telescopium* (Linnaeus)); Yule Point, northern

Figs. 1-5. *Clypeomorus moniliferus*. 1) Longitudinal section of euspermatozoon head ($\times 20,000$). 2) Acrosome ($\times 42,000$). 3) Transverse section of anterior region of acrosome ($\times 40,000$). 4) Middle region of acrosome ($\times 50,000$). Inset: Detail of plate substructure in wall of acrosomal cone ($\times 100,000$). 5) Posterior region of acrosome ($\times 50,000$).

Figs. 6-11. *Rhinoclavis vertagus*. 6) Euspermatozoon head ($\times 30,000$). 7) Longitudinal section of acrosome ($\times 60,000$). 8) Transverse section of acrosome above level of basal invagination ($\times 80,000$). 9) Transverse section of acrosome at upper level of basal invagination ($\times 80,000$). 10) Middle region of basal invagination of acrosomal cone ($\times 80,000$). 11) Basal region of acrosomal cone invagination ($\times 80,000$).

Abbreviations: a, acrosome; ac, acrosomal cone; ar, axial rod material; bp, basal plate; M, midpiece; n, nucleus; ps, plate substructure within wall of acrosomal cone.

¹Species name not determined.



Queensland (*Terebralia palustris* (Linnaeus), *Cerithidea cingulata* (Gmelin), *Planaxis sulcatus* (Born)); Pebbly Beach, northern Queensland (*Clypeomorus breviculus* (Sowerby)). Sperm ducts and gonad tissue from *Terebralia palustris*, *Clypeomorus moniliferus*, *Clypeomorus breviculus*, *Cerithidea largillierti*, *Cerithidea obtusa*, *Velacumantus australis*, and *Planaxis sulcatus* were fixed in 2.5% 0.1 M phosphate-buffered glutaraldehyde for two hours, rinsed in phosphate buffer, post-fixed in 1% phosphate-buffered osmium tetroxide for 80 minutes, again rinsed in buffer, dehydrated in a graded ethanol series (20, 40, 60, 70, 90, 100%), and infiltrated and embedded in Spurr's medium. Sperm ducts and gonadal tissues of *Telescopium telescopium*, *Rhinoelavis vertagus*, and *Australaba* sp. were processed in the same manner but with sucrose added to fixatives and buffer to give a 5% solution in each case. All stages up to and including 70% ethanol were maintained at approximately 0–4°C. Ultrathin sections were cut using either an LKB 3 or LKB 4 Ultratome, collected on coated or uncoated 200 mesh copper grids, stained with uranyl acetate and lead citrate, and examined with both Siemens Elmiskop I and AEI 500 Corinth transmission electron microscopes.

Figs. 12–15. *Australaba* sp. 12) Longitudinal section of acrosome ($\times 48,000$). 13) Oblique longitudinal section of acrosome through wide axis ($\times 37,000$). 14) Transverse section (slightly oblique) through anterior region of acrosome ($\times 50,000$). 15) Transverse section near basal region of acrosome ($\times 70,000$).

Fig. 16. *Clypeomorus moniliferus*. Transverse section through nuclear invagination ($\times 40,000$). Inset: Detail of axoneme embedded in attachment material ($\times 70,000$).

Fig. 17. *Rhinoelavis vertagus*. Transverse section through nuclear invagination ($\times 60,000$).

Fig. 18. *Australaba* sp. Nuclear invagination ($\times 50,000$).

Fig. 19. *Australaba* sp. Detail of Fig. 18 showing embedded axoneme ($\times 76,000$).

Fig. 20. *Clypeomorus moniliferus*. Nucleus–midpiece junction ($\times 35,000$).

Fig. 21. *Rhinoelavis vertagus*. Nucleus–midpiece junction. Note persistence of central microtubules of axoneme into attachment material. ($\times 35,000$).

Fig. 22. *Australaba* sp. Nucleus–midpiece junction. Note dense bodies at initial portion of midpiece (arrows) ($\times 35,000$).

Abbreviations: ac, acrosomal cone; ar, axial rod material; d, central microtubules of axoneme; M, midpiece; n, nucleus.

Some confusion exists regarding the use of the name *Cerithidea obtusa* (Lamarck) for the species used in this study. Bishop ('79) concludes that *Cerithidea kieneri*, Hombron and Jaquinot, is the correct name for this species and that true *C. obtusa* is distinguishable from *C. kieneri* on radular and shell characters. However, Bishop also states that *C. obtusa* and *C. kieneri* are sometimes difficult to separate on shell characters. Hinton ('77) figures the shell and operculum of a specimen similar to those used in this study and refers to this specimen as *Cerithidea anticipata*, Iredale. Cernohorsky ('72) lists both *C. anticipata* and *C. kieneri* as synonyms of *C. obtusa* and figures the shell of a Moreton Bay specimen. Voucher specimens of all species used in this study have been lodged with the Australian Museum (*Terebralia palustris*, C. 138053; *Planaxis sulcatus*, C. 138054; *Rhinoelavis vertagus*, C. 138055; *Clypeomorus moniliferus*, C. 138057; *Velacumantus australis*, C. 138058; *Clypeomorus breviculus*, C. 138060; *Telescopium telescopium*, C. 138061; *Cerithidea cingulata*, C. 138062; *Australaba* sp., C. 138063, C. 138064; *Cerithidea largillierti*, C. 138066, C. 138067; *Cerithidea obtusa*, C. 138068, C. 138069).

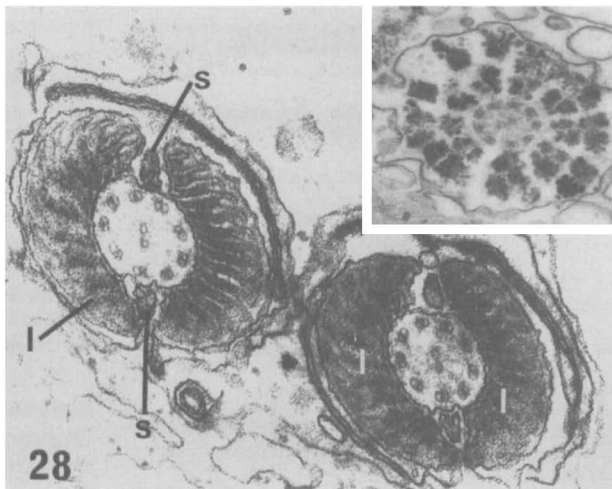
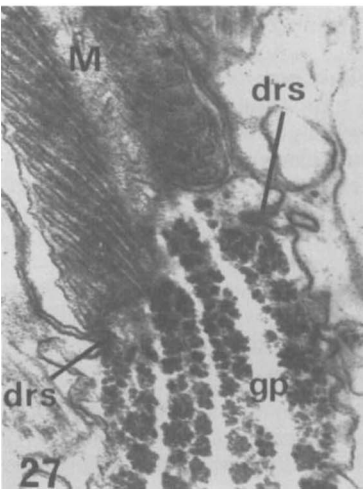
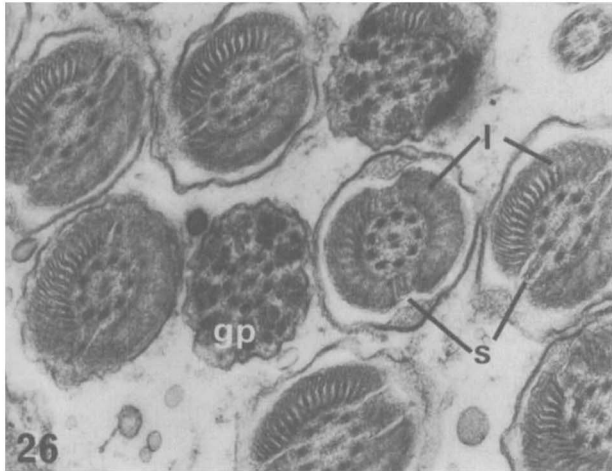
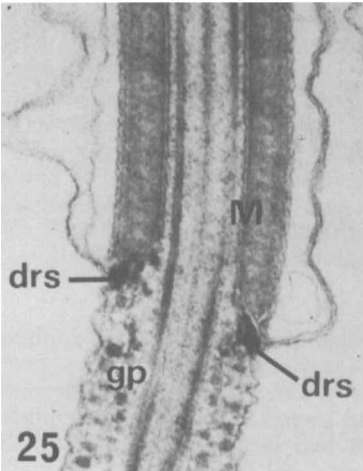
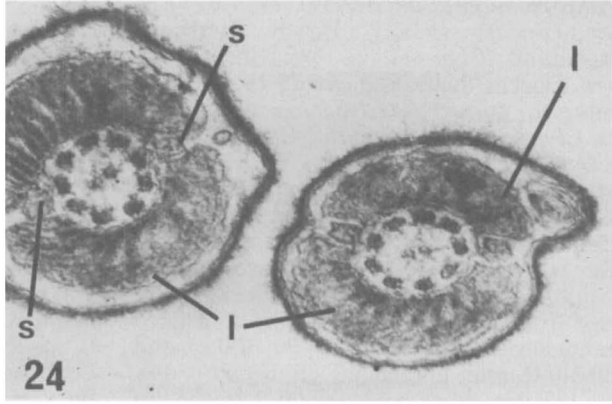
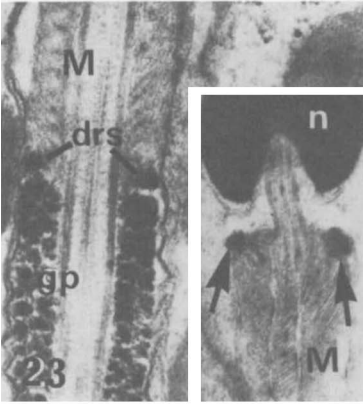
RESULTS

On the basis of euspermatozoon midpiece structure, it is possible to divide the species studied into two major groups. Euspermatozoa of Group 1 species all possess a midpiece composed of two large and two small midpiece elements—all four elements arranged nonhelically around the axoneme. Euspermatozoa of Group 2 species are characterized by a midpiece composed of four equal-sized midpiece elements, (nonhelically arranged around the axoneme) and prominent flange structures which occur at the initial (and apparently the terminal) portions of the midpiece. The structure of the paraspermatozoa lends support to this two group scheme (Healy and Jamieson, '81; Healy, '82c; personal observations). Group 1 has been divided into two subgroups using midpiece and acrosome features, which will be referred to as Subgroup 1(i) and Subgroup 1(ii).

Group 1

Subgroup 1(i): *Clypeomorus moniliferus*, *Clypeomorus breviculus*, *Rhinoelavis vertagus* (all Cerithiidae); *Australaba* sp. (family uncertain)

(a) *Acrosome*. All species of Subgroup 1(i) possess euspermatozoa with acrosomes com-



posed of a flat acrosomal cone and (sometimes diffuse) axial rod material within the cone invagination. In *Clypeomorus moniliferus* (Figs. 1–5; see also Figs. 85–88) and *Clypeomorus breviculus* (unfigured), the acrosomal cone is 1.8 μm in length and almost totally invaginated. The invagination is constricted basally by bulges in the cone wall (Figs. 2, 5, 85, 88). The axial rod material is most apparent in the central region of the cone invagination and in transverse sections taken at this level (Figs. 4, 87) fine parallel plate-like substructure is visible within the acrosomal cone wall. In *Rhinoclavis vertagus*, the cone invagination only penetrates three quarters of the 1.1 μm long acrosomal cone and the cone base is seated on a thin basal plate covering a wedge-like protuberance of the nuclear apex (Figs. 7, 11; see also Figs. 78–81). Transverse sections sometimes show evidence of plate substructure within the acrosomal cone wall but these are not clearly apparent in the material studied (Figs. 6–11). Although both *Australaba* and *Clypeomorus* possess deeply invaginated acrosomal cones, the longitudinal profiles differ markedly. The axial rod material of *Australaba* is organized into a series of inclined rods within the cone invagination (Figs. 12–15; see also Figs. 82–84).

(b) *Nucleus*. Euspermatozoan nuclei of all species of this subgroup are similar in shape to all species of Subgroup 1(ii) and Group 2—

being laterally compressed, 2.5–3 μm in length and posteriorly invaginated (Figs. 1, 6, 16–22). Inside the nuclear invagination, the proximal portion of the axoneme is embedded in dense granular material which probably attaches the axoneme to the nucleus. The central pair of axonemal microtubules persists into the attachment material (Figs. 16–19, 21).

(c) *Midpiece*. The euspermatozoan midpieces of all Subgroup 1(i) species are long (45–60 μm —phase-contrast observations) and in transverse section (Figs. 24, 26, 28; see also Fig. 71) are each constituted of two large elements (showing multiple cristal plates) and two very small elements (showing at most one cristal invagination). These small elements are consistently aligned with the central pair of axonemal microtubules. In *Australaba*, electron-dense bodies (possibly a continuous collar) are incorporated into the initial portion of the midpiece (Figs. 22, 23 inset; see also Fig. 75) and are not observed in *Clypeomorus* (Fig. 20) or *Rhinoclavis* (Fig. 21; see also Fig. 74).

(d) *Dense ring structure, glycogen piece*. Posterior to the midpiece the axoneme becomes ensheathed by electron-dense granules which have been shown in other mesogastropod euspermatozoa to be glycogen (Anderson and Personne, '70, '76; Hachiri and Higashi, '72; Giusti and Mazzini, '73). A dense ring structure applied to the inside surface of the plasma membrane occurs at the junction of midpiece and glycogen piece in all Subgroup 1(i) species (Figs. 23, 25, 27), Subgroup 1(ii) species and Group 2 species.

Subgroup 1(ii): *Planaxis sulcatus* (Planaxidae); *Velacumantus australis* (Potamididae)

(a) *Acrosome*. The acrosomes of *Planaxis* and *Velacumantus* are very similar to that demonstrated by Healy and Jamieson ('81) and Healy ('82a) for *Pyrazus ebeninus* (Potamididae) and consist of a conical acrosomal cone invaginated in the basal half (Figs. 29–31, 35–37; see also Figs. 89–91). Axial rod material is found within the cone invagination and a thin basal plate caps the apex of the nucleus and probably aids in connecting the acrosomal cone and axial rod material to the nucleus.

(b) *Nucleus*. As described for Subgroup 1(i) species (*Velacumantus*, Fig. 29; *Planaxis*, Figs. 35, 38; see also Fig. 76).

(c) *Midpiece*. The midpieces of Subgroup 1(ii) species are considerably shorter (12–18

Fig. 23. *Australaba* sp. Junction of midpiece and glycogen piece showing dense ring structure ($\times 43,000$). Inset: Dense structures at initial region of midpiece ($\times 27,000$).

Fig. 24. *Australaba* sp. Transverse section through midpieces showing cristal plate structure and large and small midpiece elements ($\times 50,000$).

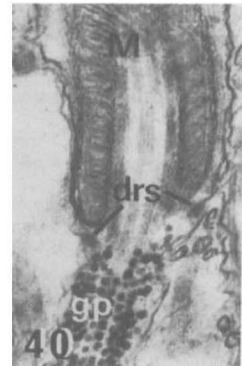
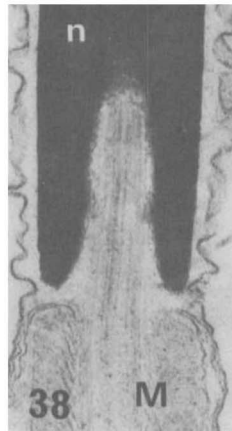
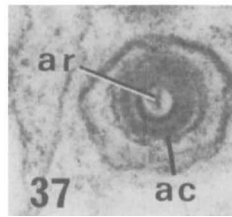
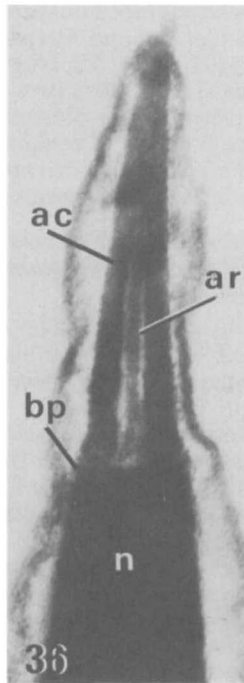
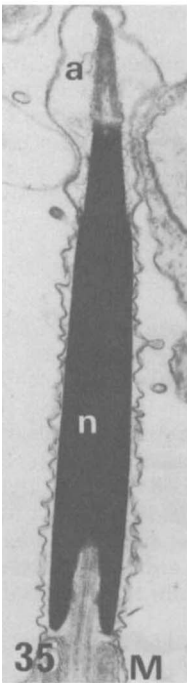
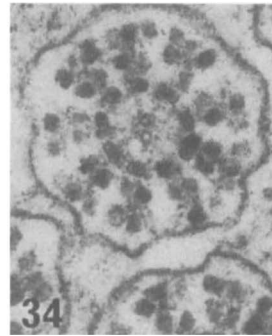
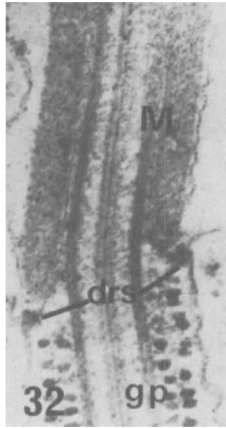
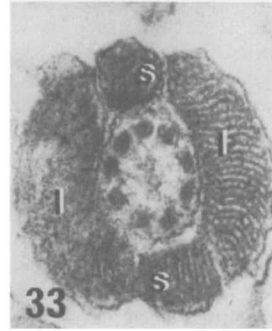
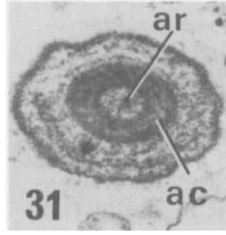
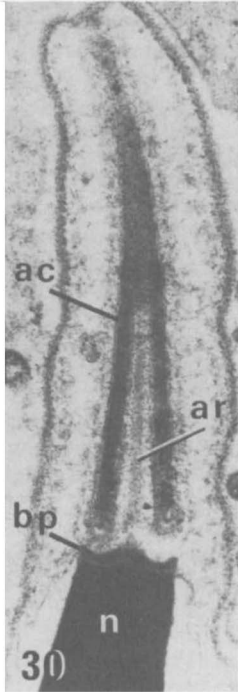
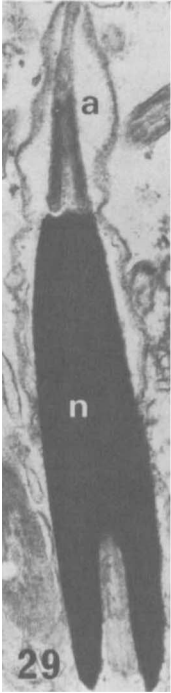
Fig. 25. *Rhinoclavis vertagus*. Midpiece–glycogen piece junction and dense ring structure ($\times 45,000$).

Fig. 26. *Rhinoclavis vertagus*. Transverse sections through glycogen pieces and midpieces ($\times 25,000$).

Fig. 27. *Clypeomorus moniliferus*. Oblique longitudinal section through midpiece–glycogen piece junction. Note cristal plates and longitudinal tracts of glycogen granules ($\times 50,000$).

Fig. 28. *Clypeomorus moniliferus*. Transverse sections through midpieces ($\times 50,000$). Inset: Transverse section of glycogen piece ($\times 34,000$).

Abbreviations: drs, dense ring structure; gp, glycogen piece; l, large midpiece element; M, midpiece; n, nucleus; s, small midpiece element.



μm) than midpieces of Subgroup 1(i) species. In *Velacumantus*, the midpiece is composed of two large and two small elements (Fig. 33; see also Fig. 72). The small elements are larger than those of Subgroup 1(i) species and usually exhibit four or five cristal plates. In *Planaxis*, the size difference between large and small midpiece elements is less pronounced (Fig. 39) than *Velacumantus* (or *Pyrazus*) and in this respect to some extent approaches the condition seen in Group 2 euspermatozoa. However, the structure of *Planaxis* paraspermatozoa is as observed in *Pyrazus* (see Healy and Jamieson, '81), *Velacumantus*, and other Group 1 species (i.e. Subgroup 1(i)), and *Planaxis* euspermatozoa do not possess the midpiece flanges of Group 2 species euspermatozoa.

(d) *Dense ring structure, glycogen piece.* As observed in Subgroup 1(i) species, the glycogen pieces of *Velacumantus* (Figs. 32, 34) and *Planaxis* (Fig. 40) consist of the axoneme surrounded by nine tracts of glycogen granules (one tract associated with each of the axonemal doublets). The dense ring structure is as observed in Subgroup 1(i) and Group 2 species.

Group 2

Cerithidea cingulata, *Cerithidea largillierti*,
Cerithidea obtusa, *Terebralia palustris*,
Telescopium telescopium (all Potamididae)

(a) *Acrosome.* The acrosomal cones of Group 2 species are all elongate (as observed in Group 1 species) and varied in shape (Figs. 41–54; see also Figs. 92–103). In *Cerithidea cingulata* and *Terebralia palustris*, the acrosomal cones are invaginated basally. In

transverse section the acrosomal cones of both species are oval in the basal region and become flattened further anteriorly (*C. cingulata*, Figs. 41–45; *Terebralia palustris*, Figs. 46–49; see also Figs. 99–103). A very diffuse deposit of axial rod material is usually present inside the cone invagination, whereas the cone is composed of a dense outer region and less dense inner region (*C. cingulata*, Figs. 41, 43; *Terebralia*, Figs. 46, 48; see also Figs. 99–103). The acrosomal cones of *Cerithidea largillierti* (Figs. 50–53; see also Figs. 95–98), and *Cerithidea obtusa* (not figured) differ from the acrosomal cones of *Cerithidea cingulata* and *Terebralia* in being distinctly less flattened anteriorly and relatively more deeply invaginated. Figure 52 suggests that plate-like substructure may exist within the wall of the acrosomal cone of *Cerithidea largillierti* (see also Fig. 49 *Terebralia*). The acrosomal cone of *Telescopium telescopium* differs from all other Group 2 species in being conical throughout its entire length. Axial rod material is possibly present but was not detected in the material studied (Figs. 54, 92–94).

(b) *Nucleus.* Although nuclear length is similar in most species of this group (2.5–3 μm), the nuclei of *Terebralia* are relatively shorter (2.25 μm) (Figs. 55–57). As observed in Group 1 species, the axonemal microtubules become obscured within the basal invagination of the nucleus (Figs. 60, 61).

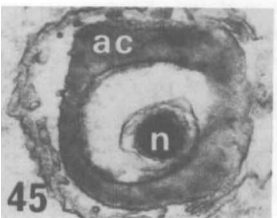
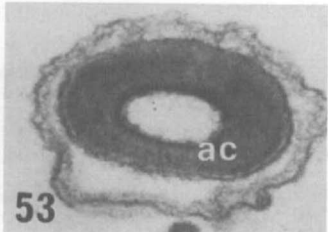
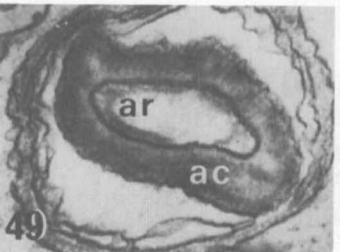
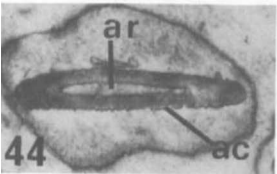
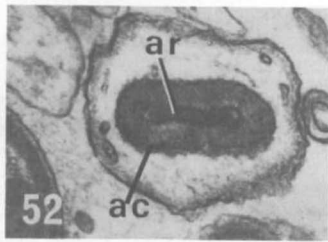
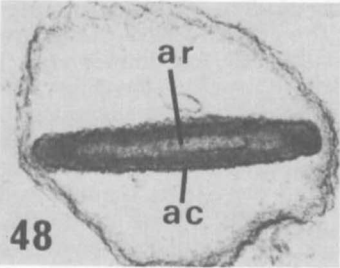
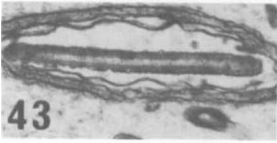
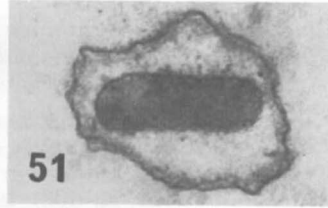
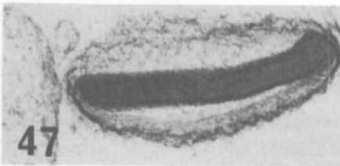
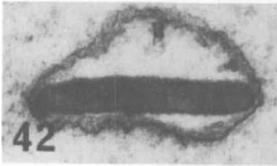
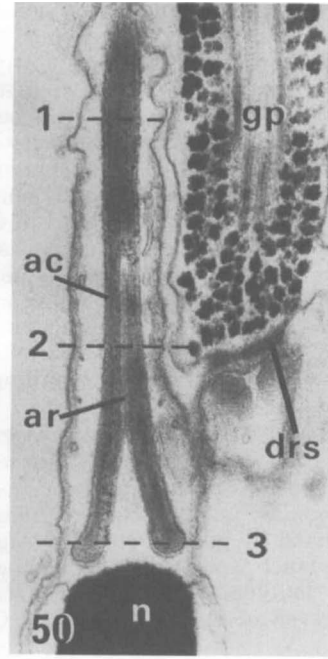
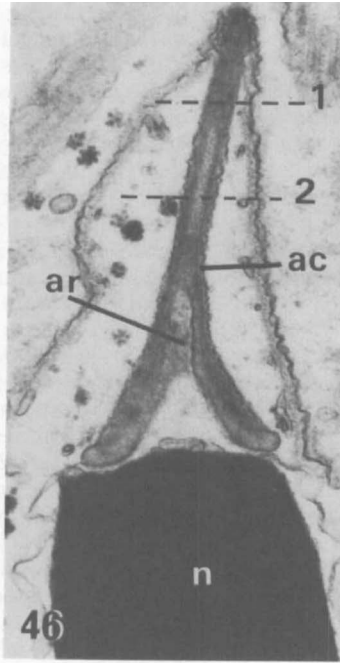
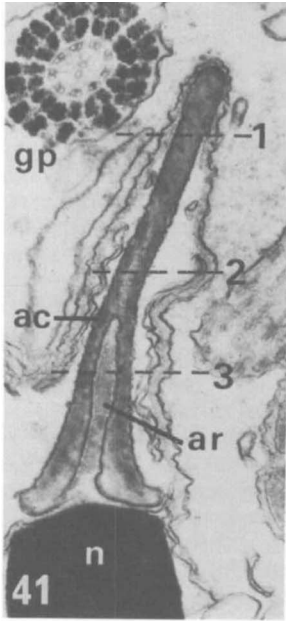
(c) *Midpiece.* The initial region of the midpiece of all Group 2 euspermatozoa exhibit flange structures (Figs. 55–58, 62, 68, 77). No cristal plates are visible in these structures (or immediately below them) in longitudinal section (Figs. 58, 59). Oblique transverse sections taken through this region indicate that probably four flanges (one per midpiece element) are present (Fig. 68). In transverse section, the four midpiece elements are of equal size (Figs. 63–65, 73) with each midpiece element showing seven to eight cristal plates (probably owing to the inclined orientation of these plates (see Fig. 62), they are often obscured in transverse section). Flange structures similar to those observed at the initial region of the midpiece also occur at the terminal region of the midpiece in *Telescopium* (Fig. 66) but are relatively small. Presumably these additional flanges are present in euspermatozoa of all Group 2 species.

(d) *Dense ring structure, glycogen piece.* As observed for Group 1 species (Figs. 65–67, 69). Figure 70 shows the transition between the glycogen piece and end piece of a *Tere-*

Figs. 29–34. *Velacumantus australis*. 29) Euspermatozoon head ($\times 30,000$). 30) Longitudinal section of acrosome ($\times 70,000$). 31) Transverse section of acrosome ($\times 70,000$). 32) Midpiece–glycogen piece junction and dense ring structure ($\times 50,000$). 33) Transverse section of midpiece. Note cristal plates of large and small midpiece elements ($\times 70,000$). 34) Transverse section of glycogen piece ($\times 70,000$).

Figs. 35–40. *Planaxis sulcatus*. 35) Euspermatozoon head ($\times 20,000$). 36) Longitudinal section of acrosome ($\times 70,000$). 37) Transverse section of acrosome ($\times 70,000$). 38) Nucleus–midpiece junction ($\times 55,000$). 39) Transverse section of midpiece ($\times 70,000$). 40) Midpiece–glycogen piece junction and dense ring structure ($\times 36,500$).

Abbreviations: a, acrosome; ac, acrosomal cone; ar, axial rod material; bp, basal plate (of acrosome); drs, dense ring structure; gp, glycogen piece; l, large midpiece element; M, midpiece; n, nucleus; s, small midpiece element.



bralia euspermatozoon. It is likely that this junction is similar in all Group 1 and Group 2 species.

DISCUSSION

Nucleus and acrosome

Euspermatozoa of cerithiacean species (Healy, '82a,c; this study) and many other mesogastropods that have been studied ultrastructurally (including Bulnheim, '62; Giusti, '69, '71; Giusti and Mazzini, '73; Grifond, '80; Kohnert, '80; Koike and Nishiwaki, '80) have nuclei which are shallowly invaginated in the basal region. Euspermatozoan nuclei of all neogastropods that have to date been studied (Walker and MacGregor, '68; Feral, '77; West, '78; personal observations) and at least some mesogastropods (Buckland-Nicks, '73; Buckland-Nicks et al., '82; personal observations) are almost completely invaginated (the axoneme commencing immediately below the nuclear apex). It appears likely that the extent of the nuclear invagination is the product of both environmental and phylogenetic influences.

The extreme structural diversity of the acrosomal cone and axial rod material of cerithiacean euspermatozoa is remarkable—the acrosomal cone varying from truly conical to flat while the axial rod material may be represented by a single rod, multiple rods or diffuse deposits (Hachiri and Higashi, '71; Healy and Jamieson, '81; Healy, '82a,c; this

study). Although flat acrosomes have been observed in euspermatozoa of some rissacean mesogastropods (Giusti, '71; Kohnert, '80; personal observations) most mesogastropod and neogastropod euspermatozoa have acrosomes which consist of a single axial rod and truly conical acrosomal cone (see Bulnheim, '62; Walker and MacGregor, '68; Buckland-Nicks, '73; Giusti and Mazzini, '73; Feral, '77; Koike and Nishiwaki, '80). In opisthobranch and pulmonate gastropods (Euthyneura), the acrosome consists of an apical vesicle (usually rounded) resting on a (usually columnar) acrosomal pedestal attached to the nuclear apex (Takaichi and Sawada, '73; Takaichi, '75; Atkinson, '82; Healy '82b, '83). Nothing is as yet known concerning the ultrastructure of the acrosome reaction or events of fertilization in mesogastropod or neogastropod prosobranchs or euthyneuran gastropods. Lewis et al. ('80) presented details of the acrosome reaction in the archaeogastropod prosobranch *Haliotis rufescens* (a primitive sperm producer) and observed elongation of the actin-cored acrosome process (= axial rod material) and the dissolution of the acrosome granule (= acrosomal cone). An examination of the acrosome reaction within mesogastropods, neogastropods, and euthyneuran gastropods would be of great value in establishing both the function and homology of acrosome components within the Gastropoda.

Midpiece

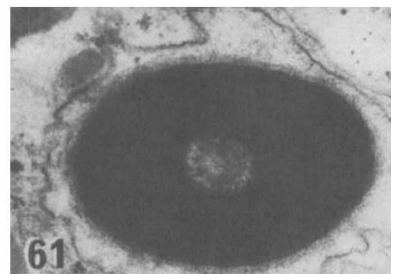
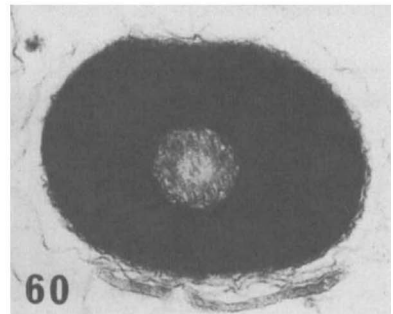
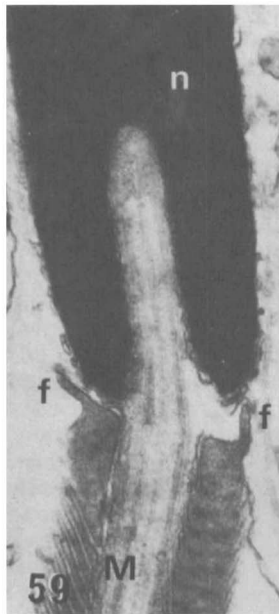
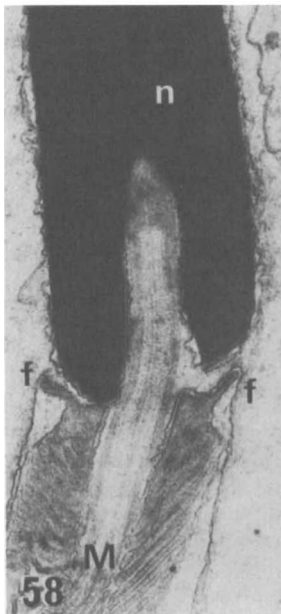
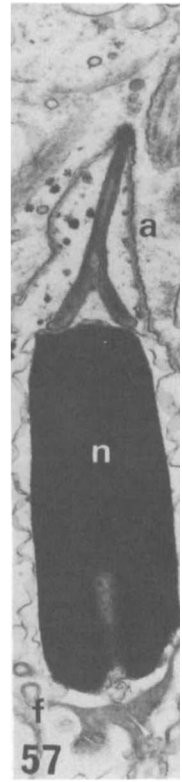
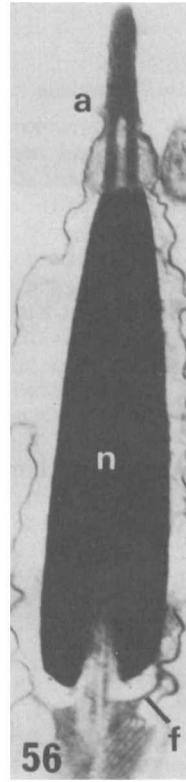
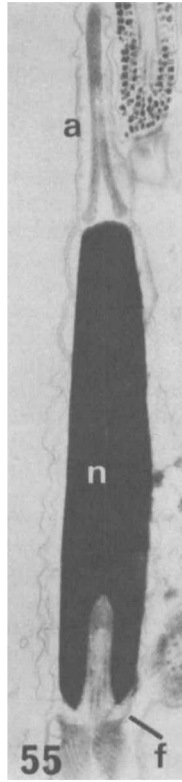
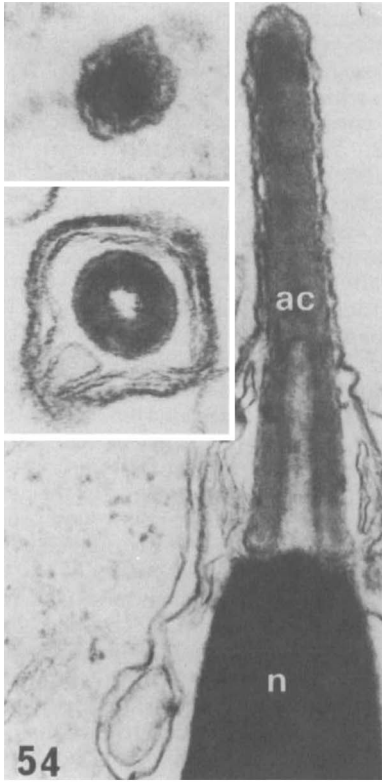
Midpieces of cerithiacean euspermatozoa are each composed of four distinct elements (exhibiting parallel cristal plate structure) arranged nonhelically around the axoneme (Healy, '82a,c; this study). In most other mesogastropod euspermatozoa and in neogastropod euspermatozoa, the midpiece elements (usually seven to nine) are helically arranged around the axoneme and do not exhibit parallel cristal plates (see Bulnheim, '62; Giusti, '69, '71; Giusti and Mazzini, '73; West, '78; Kohnert, '80). Koike and Nishiwaki ('80) have reported parallel cristae in the midpieces of strombid euspermatozoa, but this configuration does not appear to be similar to that occurring in cerithiaceans. However, in euspermatozoa of viviparaceans, the midpiece elements (although helically arranged around the axoneme) exhibit cristal plate fine structure very similar to that observed in cerithiaceans (see Kaye, '58; Yasuzumi and Tanaka, '58; Anderson, '70; Personne and Anderson, '70; Hachiri and Higashi, '74).

Figs. 41–45. *Cerithidea cingulata*. 41) Longitudinal section of acrosome and transverse section of glycogen piece ($\times 40,000$). 42) Transverse section through acrosome at level 1 of Fig. 41 ($\times 40,000$). 43) Transverse section of acrosome at level 2 of Fig. 41 ($\times 40,000$). 44) Transverse section of acrosome at level 3 of Fig. 41 ($\times 40,000$). 45) Transverse section through base of acrosomal cone ($\times 40,000$).

Figs. 46–49. *Terebralia palustris*. 46) Longitudinal section of acrosome ($\times 40,000$). 47) Transverse section of acrosome at level 1 of Fig. 46 ($\times 50,000$). 48) Transverse section of acrosome at level 2 of Fig. 46 ($\times 50,000$). 49) Transverse section of acrosome near base of acrosomal cone ($\times 50,000$).

Figs. 50–53. *Cerithidea largillierti*. 50) Longitudinal section of acrosome and oblique section of midpiece-glycogen piece junction ($\times 45,000$). 51) Transverse section of acrosome at level 1 of Fig. 50 ($\times 50,000$). 52) Transverse section of acrosome at level 2 of Fig. 50 ($\times 50,000$). 53) Transverse section of acrosome at level 3 of Fig. 50 ($\times 50,000$).

Abbreviations: ac, acrosomal cone; ar, axial rod material; drs, dense ring structure; gp, glycogen piece; n, nucleus.



Studies conducted by some workers (Ishizaki and Kato, '58; Gall, '61; Griffond, '80) indicate that four midpiece elements are present in euspermatozoa of viviparaceans (as occurs in cerithiaceans). These results, together with the general similarity of viviparacean and cerithiacean paraspermatozoa (Ishizaki and Kato, '58; Yasuzumi and Tanaka, '58; Gall, '61; Griffond, '80; Healy and Jamieson, '81) would suggest that a close relationship may exist between these two mesogastropod superfamilies. It should be pointed out that the work of Kaye ('58) suggests that four or five midpiece elements may be present in euspermatozoa of viviparaceans while other workers (Tanaka, '58; Yasuzumi and Tanaka, '58; Yasuzumi, '62) conclude that as few as two midpiece elements are present. Recently, Selmi and Giusti ('80) have demonstrated cristal plate organization in midpieces of the mesogastropod *Cochlostoma montanum* (Cyclophoracea). In this species crystalline deposits were shown to be associated with the cristal plates.

Glycogen piece

The periaxonemal arrangement of (presumed) glycogen granules of the glycogen piece in cerithiacean euspermatozoa (Giusti,

'71; Hachiri and Higashi, '71; Healy, '82a,c; this study) is common in euspermatozoa of other mesogastropods and of neogastropods that have been studied (Giusti, '71; Kohnert, '80; Koike and Nishiwaki, '80; Selmi and Giusti, '80; Buckland-Nicks et al., '82; personal observations). The same arrangement has also been observed in sperm of cephalopods (Anderson and Personne, '70; Longo and Anderson, '70; Baccetti et al., '76) where nine tracts of granules are associated with the periaxonemal coarse fibres. Sperm of oligochaetes also show an ordered arrangement of glycogen granules around the axonemal doublets (Henley, '73a; Jamieson, '78). Buckland-Nicks et al. ('82) recently have shown that nine radial links connect the axonemal doublets to the plasma membrane in immature "eupyrene" sperm (immature euspermatozoa) and that at maturity, these radial links become obscured by the nine tracts of glycogen granules. It therefore seems most likely that the ordered arrangement of glycogen granules is linked with motility in those species in which it occurs. It is interesting to observe that in opisthobranch and pulmonate sperm which possess a glycogen piece, glycogen granules are randomly packed around the axoneme and (presumably) such sperm lack radial links (Ohsako, '71; Anderson and Personne, '70, '76; Thompson, '73; Kitajima and Paraense, '76; Maxwell, '80; Healy, '82b, '83).

Dense ring structure

A dense ring structure or "annulus" such as that demonstrated in cerithiaceans (Healy, '82a,c; this study) is also found in other mesogastropods (Buckland-Nicks, '73; Kohnert, '80; Koike and Nishiwaki, '80; personal observations), neogastropods (Buckland-Nicks et al., '82; personal observations), the architectonic gastropod *Philippia* (Healy, '82d), and some opisthobranchs and pulmonates (Ohsako, '71; Thompson, '73; Ackerson and Koehler, '77; Healy '82b, '83). A similar structure occurs posterior to the midpiece in sperm of certain polychaete species (see Franzén, '82). The annulus of vertebrate sperm (occurring at the junction of the midpiece and fibrous principal piece) is well documented (see Fawcett, '70). The annulus of certain cephalopod spermatozoa (junction of midpiece and glycogen piece) resembles more closely that occurring in vertebrate spermatozoa and not the dense ring structures of mesogastropod or neogastropod euspermatozoa (see Longo and Anderson, '70). Functions

Fig. 54. *Telescopium telescopium*. Longitudinal section of acrosome ($\times 70,000$). Inset: Transverse sections of upper and lower regions of acrosome ($\times 76,000$).

Fig. 55. *Cerithidea largillierti*. Euspermatozoon head and proximal portion of midpiece. Note flange structures ($\times 20,000$).

Fig. 56. *Telescopium telescopium*. Euspermatozoon head and proximal portion of midpiece showing flange structures ($\times 20,000$).

Fig. 57. *Terebralia palustris*. Euspermatozoon head and proximal portion of midpiece showing flange structures ($\times 20,000$).

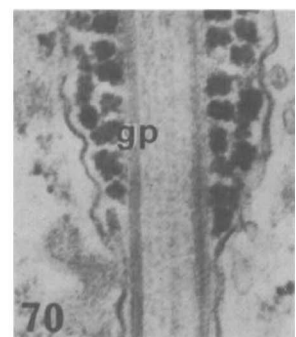
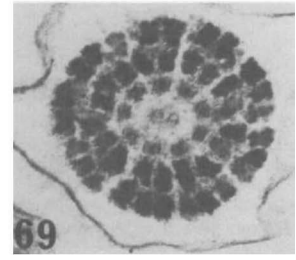
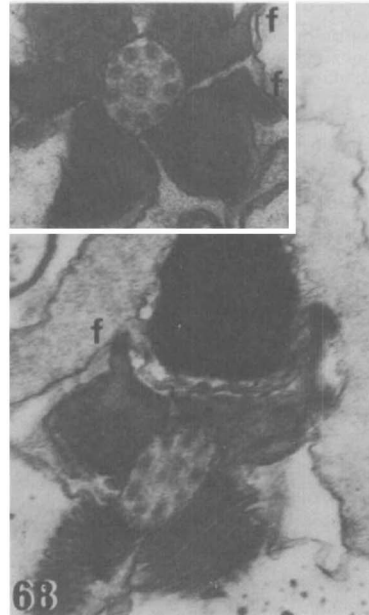
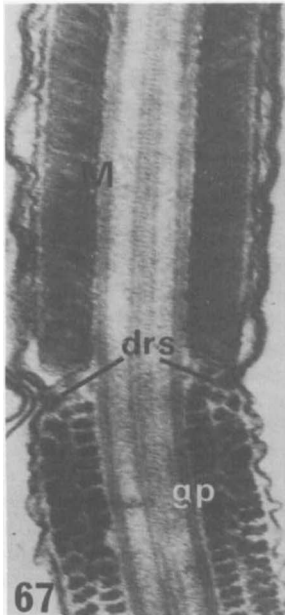
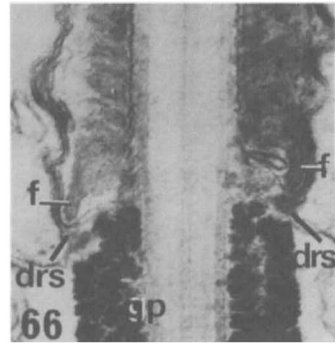
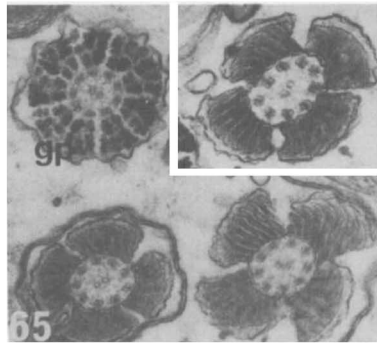
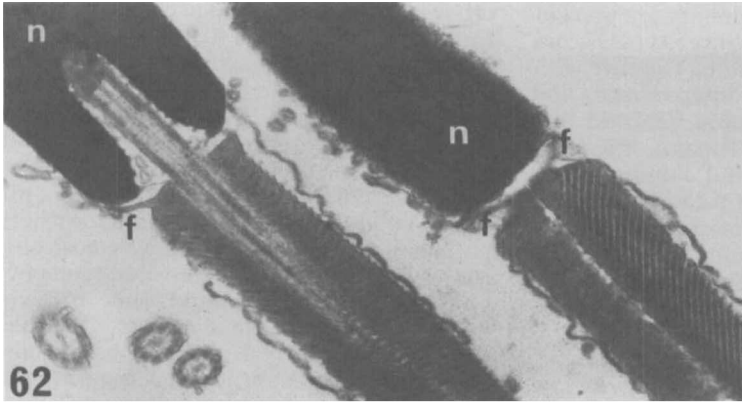
Fig. 58. *Terebralia palustris*: Nucleus-midpiece junction showing flanges ($\times 43,000$).

Fig. 59. *Telescopium telescopium*. Nucleus-midpiece junction showing flanges ($\times 43,000$).

Fig. 60. *Terebralia palustris*. Transverse section of nuclear invagination with axoneme embedded in attachment material ($\times 50,000$).

Fig. 61. *Telescopium telescopium*. Transverse section of nuclear invagination with embedded axoneme ($\times 35,000$).

Abbreviations: a, acrosome; ac, acrosomal cone; f, flange structures of midpiece; M, midpiece; n, nucleus.



that have been suggested for the dense ring structure (or annulus) include: (1) the prevention of axonemal constriction during movement (Buckland-Nicks, '73); (2) the prevention of "caudal displacement of the mitochondria during tail movements" (Fawcett, '70 p. 112); (3) as an additional kinetic centre (Buckland-Nicks and Chia, '81). Possibly the dense ring structure/annulus performs all three suggested functions.

Taxonomic implications of euspermatozoon structure

Using results presented in this study in addition to previous ultrastructural work (Giusti, '71; Melone et al., '80; Healy and Jamieson, '81; Healy, '82a,c) it is possible to establish two major groups of cerithiaceans using euspermatozoon structure. Figures 71 to 103 summarize the characteristic features of euspermatozoa of Group 1 and Group 2 species. It has been demonstrated that euspermatozoa of Group 1 species have midpieces composed of the axoneme surrounded by two large and two small midpiece elements (Figs. 71, 72) and that euspermatozoa of Group 2 species possess four equal-sized midpiece elements and midpiece flange structures (Figs. 73, 77). Group 1 is subdivided on the shape of the small midpiece elements (in transverse section) and the shape of the acrosome. From the midpieces shown in the micrograph of Giusti ('71), *Cerithium vulgatum*, like other cerithiids, can be placed within Subgroup 1(i). The acrosomal cone of *Cerithium vulgatum* (see plate LXXV, Fig. 1 of Giusti, '71), although long

and deeply invaginated as in *Clypeomorus*, differs markedly in longitudinal profile from all Subgroup 1(i) species. It is significant that the two species of *Clypeomorus* investigated in this study possess very similar acrosome structure and that the acrosomes of *Rhino-clavis*, *Australaba*, and *Cerithium* (of the species that have been studied) are recognizably different from each other. Further investigations of acrosome structure in other species of these (and other) genera will, however, be necessary in order to ascertain whether the features of the acrosome provide useful taxonomic data—at least within the Cerithiacea.

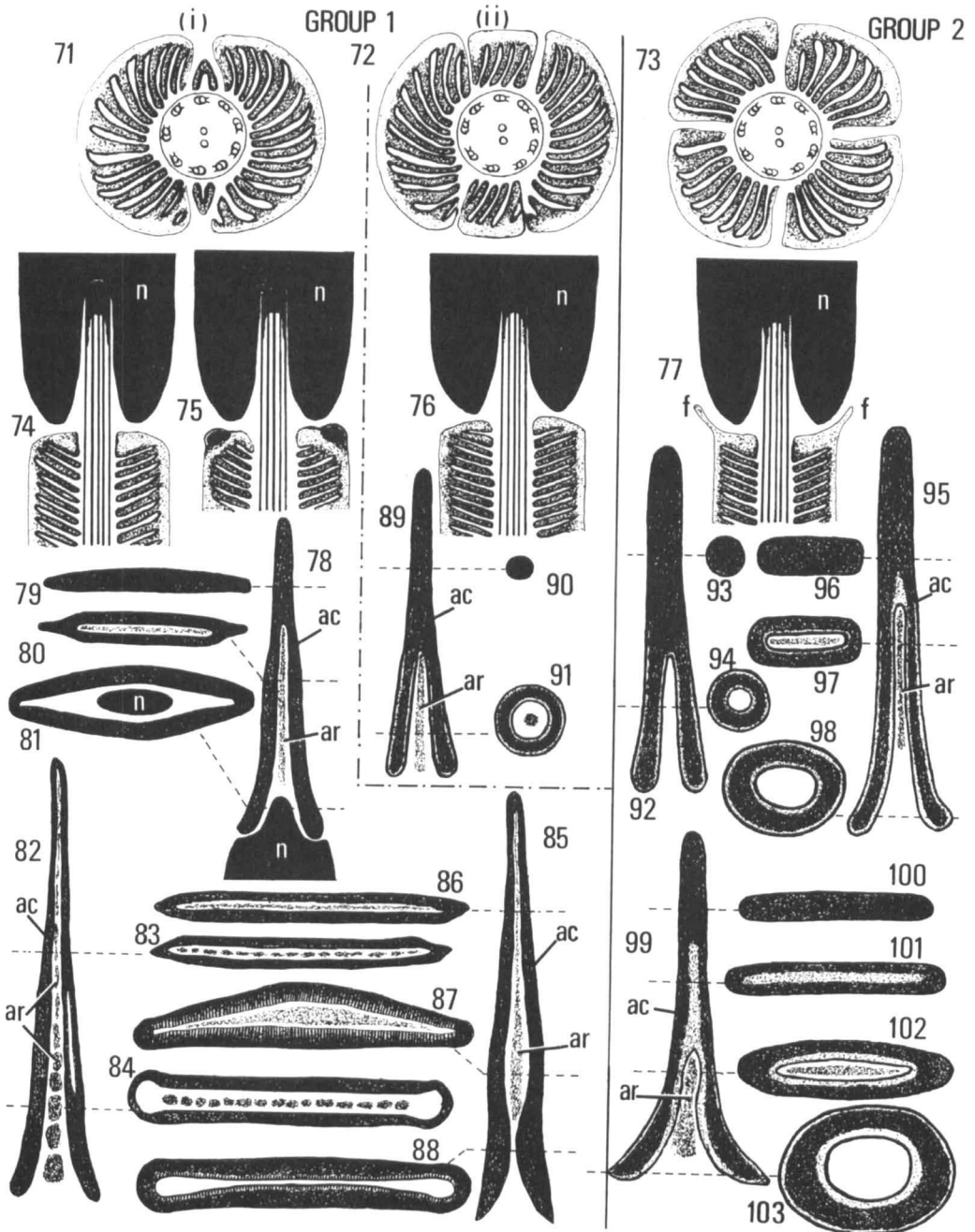
Melone et al. ('80) demonstrated some features of the paraspermatozoa of *Turritella communis* which also occur in paraspermatozoa of *Pyrazus ebeninus* (Healy and Jamieson, '81) and it is probable that all Group 1 species (both Subgroups 1(i) and 1(ii)) possess similar paraspermatozoa, distinct from those of Group 2 species (personal observations). The midpiece structure of *Turritella communis* euspermatozoa (see Fig. 2 of Melone et al. ('80)) places this species within Subgroup 1(i). Although the acrosome has not been figured for any turritellid, it seems likely that like the Cerithiidae, the entire Turritellidae have midpiece organization characteristic of Subgroup 1(i) species.

The euspermatozoon midpiece of *Australaba* sp. is, in transverse section, as observed in other Subgroup 1(i) species. However, the dense bodies (possibly a continuous collar?) associated with the midpiece immediately posterior to the nucleus are similar to dense bodies observed in the same region of *Viviparus* euspermatozoa (Griffond, '80) and are slightly reminiscent of the midpiece flange structures of Group 2 euspermatozoa. In the absence of information on euspermatozoa of other species of *Australaba* (and, more generally, the many cerithiacean genera that have not been investigated), it is impossible to assess the taxonomic significance of the dense bodies in the species considered here. It is anticipated that further studies of euspermatozoa (and paraspermatozoa) will prove extremely useful in determining the taxonomic relationships between many other small-shelled cerithiaceans.

Subgroup 1(ii) contains species assigned to the Potamididae (*Pyrazus ebeninus*—Healy, '82a; *Velacumantus australis*—this study) and Planaxidae (*Planaxis sulcatus*—this study). The euspermatozoon midpiece structure (and paraspermatozoon structure—Healy and Ja-

Figs. 62-70. 62) *Cerithidea obtusa*. Nucleus-midpiece junction showing flange structures and cristal plates of midpiece elements ($\times 30,000$). 63) *Cerithidea largillierti*. Transverse section through midpiece ($\times 60,000$). 64) *Telescopium telescopium*. Transverse section of midpiece ($\times 60,000$). 65) *Terebralia palustris*. Transverse sections of midpiece and glycogen piece ($\times 30,000$). Inset: Transverse section of midpiece of *Cerithidea cingulata* ($\times 40,000$). 66) *Telescopium telescopium*. Midpiece-glycogen piece junction showing flange structures and dense ring structure ($\times 60,000$). 67) *Terebralia palustris*. Midpiece-glycogen piece junction ($\times 60,000$). 68) *Terebralia palustris*. Oblique transverse section of nucleus-midpiece junction showing one flange structure ($\times 60,000$). Inset: Transverse section of midpiece showing position of flange structures in two adjacent midpiece elements ($\times 50,000$). 69) *Cerithidea largillierti*. Transverse section of glycogen piece ($\times 60,000$). 70) *Terebralia palustris*. Glycogen piece-end piece junction ($\times 60,000$).

Abbreviations: drs, dense ring structure; f, flange structures of midpiece; gp, glycogen piece; M, midpiece; n, nucleus.



mieson, '81; personal observations) clearly linking the species of this subgroup with Subgroup 1(i) (that is, Cerithiidae, Turritellidae and *Australaba*). According to the classification scheme of Thiele ('31), the Potamididae can be divided into two subfamilies: Potamidinae (including, among other genera, *Cerithidea*, *Terebralia*, *Telescopium*, *Pyrazus*) and Batillariinae (including, among other genera, *Batillaria*, *Zeacumantus*). Primarily on the basis of radular features, Bishop ('79) maintains this two subfamily system but transfers *Pyrazus* from the Potamidinae to the Batillariinae. The two subfamilies (as modified by Bishop) correspond to Group 2 (Potamidinae) and Group 1 (Subgroup 1(ii)) (Batillariinae) of the present study.

Although some differences in acrosome shape and nuclear length exist between Group 2 genera, the distinctive midpiece structure clearly separates these genera from the Batillariinae (Subgroup 1(ii)). Recent work by the author has revealed that the euspermatozoa of *Obtortio* (family uncertain, see Healy, '82c) and *Modulus* (Modulidae, unfigured) also have Group 2 midpiece structure. This may also be true for the Pleuroceridae since Henley ('73b) describes four "paracrystalline" mitochondrial derivatives without any mention of size disparity. Given that the same midpiece element arrangement exists in different cerithiacean families (for example Turritellidae and Cerithiidae share Subgroup 1(i) pattern; Potamididae (subfamily Potamidinae), Modulidae,

and *Obtortio* share Group 2 pattern, it would seem that the pronounced differences in euspermatozoon midpiece structure between the potamidid subfamilies Potamidinae and Batillariinae may indicate the necessity to separate the latter subfamily as a distinct family (tentatively the Batillariidae). On the basis of euspermatozoon (and paraspermatozoon) features the "Batillariidae" would be most closely allied to the Planaxidae and (to a lesser degree) the Turritellidae and Cerithiidae.

It is of interest that the acrosome of *Cerithidea cingulata* resembles that of *Terebralia palustris* and not other species of *Cerithidea* studied (*C. obtusa*, *C. largillierti*). These results could be interpreted equally well as support for the inclusion of "*Cerithidea cingulata*" in a separate genus *Cerithideopsilla* (Allan, '59; Bishop, '79) or as support for Thiele's ('31) subgeneric division of *Cerithidea*.

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LITERATURE CITED

- Figs. 71-103. Diagrammatic summary of cerithiacean euspermatozoa in species studied. Figs. 71, 72, 73 simultaneously show the cristal plates of all four midpiece elements and are not intended to represent actual transverse sections through midpieces. 71) Subgroup 1(i); 72) Subgroup 1(ii); 73) Group 2 (all $\times 50,000$). 74) Subgroup 1(i) Nucleus-midpiece junction of *Clypeomorus* and *Rhinoclavis* ($\times 35,000$). 75) Subgroup 1(i) Nucleus-midpiece junction of *Australaba* ($\times 35,000$). 76) Subgroup 1(ii) Nucleus-midpiece junction ($\times 35,000$). 77) Group 2 Nucleus-midpiece junction. ($\times 35,000$).
- Figs. 78-88. Acrosome structure of Subgroup 1(i) species. 78-81) *Rhinoclavis* (all $\times 45,000$). 82-84) *Australaba* (all $\times 45,000$). 85-88) *Clypeomorus* (all $\times 35,000$).
- Figs. 89-91. Acrosome structure of Subgroup 1(ii) species (all $\times 45,000$).
- Figs. 92-103. Acrosome structure of Group 2 species. 92-94) *Telescopium* (all $\times 50,000$). 95-98) *Cerithidea largillierti*, *Cerithidea obtusa* (all $\times 35,000$). 99-103) *Cerithidea cingulata*, *Terebralia* (all $\times 35,000$).
- Abbreviations: ac, acrosomal cone; ar, axial rod; f, flange structures of midpiece; n, nucleus.

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