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BIOLOGY AND EVOLUTION OF TOXOGLOSSAN GASTROPODS

John D. Taylor
Organizer

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John D. Taylor

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INTRODUCTION

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The families of the Conoidea (= Toxoglossa), namely the Turridae, Conidae, Terebridae and Pervicaciidae, are probably a monophyletic group, which share the autapomorphy of possessing a venom gland and muscular bulb (presumed lost in some taxa). As is well known, many taxa also have highly modified, radular teeth which may be used singly at the proboscis tip for the hypodermic injection of venom. The relationships of the Conoidea to other prosobranch gastropods are uncertain, with some characters suggesting a relationship with the Neogastropoda, whilst others indicate a separate derivation from the mesogastropods.

The four families differ greatly in the state of current knowledge. Much attention has been given to the species-level taxonomy of the Conidae, but the description of putative new species continues unabated. Far more is known about the biology and ecology of *Conus* than any other toxoglossan group, including details of their feeding, habitats and reproduction. However, apart from the radula and the venom apparatus, there have been few anatomical studies, and there is no understanding of relationships amongst the species groups or clades of *Conus*.

For the Terebridae, there has been a recent taxonomic monograph, but little is known of the anatomy and biology of the family. Relationships both within the family and with the other conoideans are uncertain. The anatomical data available suggest a lack of congruence between shell and anatomical characters. Controversy surrounds the status of the Pervicaciidae, first proposed by Rudman for terebrid-like gastropods with solid radular teeth and no venom apparatus.

The Turridae are an immensely diverse family with daunting taxonomic problems at all levels, with at least fifteen subfamilies in current use. The biology of only a few species is known in any detail, and the limited amount of anatomical work suggests an amazing diversity of foregut structures within the family. These anatomical characters have yet to be incorporated into any phylogenetic analysis or classification. Further understanding of the origin and evolution of the toxoglossan feeding mechanism clearly depends upon further anatomical studies of more turrid species.

It is clear from this brief summary that further progress in understanding the evolution of the Conoidea depends upon a much more detailed knowledge of relationships, both within and between the conoidean families. Shell characters have proved to be generally unsatisfactory in determining relationships and much more attention needs to be given to the analysis of anatomical characters. In both the Turridae and Terebridae there are many examples of gastropods with similar shells having quite different internal anatomies. Concurrent studies on biology and feeding behaviour are essential to any understanding of the functional significance of both anatomical and shell characters. Additionally, studies of larval development, particularly in the Turridae and Conidae, are contributing data of both systematic and biogeographical importance.

There has recently been an upsurge of interest in the systematics and evolution of toxoglossan gastropods, and the objectives of the Tübingen Symposium were to bring together workers specializing in different groups and aspects of the Conoidea, to review present research, and to highlight areas of importance and interest for the future. Six of the nine papers presented at the Symposium are published here.

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ANATOMICAL BASIS FOR THE ORIGIN AND EVOLUTION OF THE TOXOGLOSSAN MODE OF FEEDING

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ABSTRACT

Five types of feeding mechanism can be recognized in the Toxoglossa. The mechanism by which separate marginal teeth are used at the proboscis tip for stabbing and poisoning the prey with secretions from the venom gland originated in "lower" turrids possessing a radular membrane, solid marginal teeth, a central tooth and sometimes lateral teeth. The morphological prerequisite of the appearance of toxoglossan mode of feeding was firstly the appearance of the venom gland, which initiated the formation of the specialized intraembolic type of proboscis with the buccal mass situated at its base. Hollow marginal teeth originated repeatedly and independently in different phylogenetic lineages of Toxoglossa. It is supposed that the ancestors of Toxoglossa were primitive mesogastropods with a short acrembolic proboscis and taenioglossan radula. The separation of Toxoglossa from the Rachiglossa occurred at an early evolutionary stage, when the common ancestor had seven radular teeth in each transverse row.

Key words: Toxoglossa, evolution, feeding, radula.

INTRODUCTION

The order Toxoglossa is large, diverse, and well differentiated from the other prosobranch gastropods. It includes four Recent families: Turridae, Conidae, Pervicaciidae, and Terebridae. One of the most outstanding and well-known features of the order is the specialized feeding mechanism of its higher representatives. That is the use of separate hollow marginal teeth at the proboscis tip for stabbing and subsequent poisoning the prey, with the venom produced by a usually well-developed, tubular venom gland. Most representatives of the order (the "higher" Turridae, Conidae and part of the Terebridae) lack the radula membrane, and the radula itself consists of only hollow marginal teeth. The teeth being formed in the radula sheath are finally stored in the short arm of the radula sac, which is probably a homologue of the sublingual pouch.

At the same time, many toxoglossans (mainly "lower" turrids) have a normally developed radular membrane with two to five radular teeth per transverse row. Information on feeding mechanisms and the morphology of these "lower" toxoglossans is very limited, although the functional analysis of their digestive system and feeding mechanism may elucidate the pathways of origin and evolution of "toxoglossan" mode of feeding.

One of the most interesting problems is the origin of "toxoglossan" feeding mechanism. Does it have a single or repeated origin in evolution, and what are the morphological prerequisites for its appearance? The main aim of this study was to clarify these problems.

MATERIALS AND METHODS

Materials for the study were obtained mainly from the collections of the Zoological Museum of Moscow State University and Institute of Oceanology of the USSR Academy of Sciences (Moscow). Other material was kindly provided by Dr. James H. McLean (Los Angeles County Museum of Natural History, USA); the late Dr. Virginia O. Maes (Academy of Natural Sciences, Philadelphia, USA); Dr. Anders Warén (Naturhistoriska Riksmuseet, Sweden); and Dr. R. N. Kilburn (Natal Museum, South Africa).

The morphology of the digestive tract was studied using sections 8–10 μm thick, which were cut after dehydration and embedding in paraffin wax. The sections were usually stained with Masson's triple stain. Its second solution, which contains orange-G and aniline blue, was used for staining the radula. Large specimens were also dissected under the stereomicroscope. In total, the morphology of 18 species of Turridae belonging to six subfamilies was studied.

RESULTS AND DISCUSSION

Within the Toxoglossa there is significant variability both in the morphology of the radular teeth and their number in a transverse row (the radular formulae: 1-1-1-1-1, 1-0-1-0-1, 1-1-0-1-1, 1-0-0-0-1). The morphological changes in the radular apparatus and associated structures of the anterior digestive system form the main evolutionary trends of the order. Several authors have tried to classify the radular types of Toxoglossa according to both the morphology and probable mechanism of function (Thiele, 1929; Powell, 1966; Morrison, 1966; McLean, 1971). The most complex classification was proposed by Shimek & Kohn (1981), who isolated six functional types of toxoglossan radula, four of which are found in lower "non-toxoglossate" turrids (those with solid marginal teeth). However, one can say that only two general feeding mechanisms include all the isolated types: "toxoglossate" for those gastropods which have only hollow marginal teeth and lack a radular membrane, and "non-toxoglossate" for lower turrids. In the first feeding type, separate, hollow marginal teeth are used at the proboscis tip for stabbing and poisoning the prey; in the second type, the radula is used as a whole organ only within the buccal cavity. In their analysis, Shimek & Kohn (1981) used mainly isolated radulae, without taking into account the morphology of the digestive tract, and this led to some misinterpretation (Sysoev & Kantor, 1987).

A functional morphological analysis of the digestive system of the species studied suggests that there are at least four different types of feeding mechanism for toxoglossans possessing a radula and one type for radula-less species.

General Anatomy of Toxoglossa

Before a more detailed analysis of the feeding mechanism, a brief description of the anterior part of the digestive system of the Toxoglossa is necessary. One of the outstanding features of the order is the specialized intraembolic type of proboscis (Smith, 1967), which is characterized by the position of the buccal mass at the base of the proboscis or even behind it. This precludes the use of the radula as a whole organ for rasping and grazing, as in other gastropods. The second feature is the presence of the well-developed tubular venom gland entering the anterior oesophagus behind the buccal cavity. It has been shown that the venom gland produces a venom that immobilizes or kills prey animals (Kline, 1956; Pearce, 1966; Miller, 1980; Shimek & Kohn, 1981; Kohn, 1956, 1959, 1968, many others). The buccal tube leads from the buccal cavity to the mouth, which opens at the proboscis tip. The buccal tube has thick muscular walls in "lower" toxoglossans, but is thin-walled and practically lacking muscular fibres in higher representatives.

It should be noted that the functional analysis was carried out mainly using the anatomical evidence, because data on feeding behaviour and diet are scarce and chiefly concern species of Conidae, Terebridae and some higher Turridae. As our knowledge of the morphology of turrids becomes more precise, the proposed classification may change.

Feeding Mechanism Type 1

The first functional type of digestive system and feeding mechanism, that in which the radula is used as a whole organ only within the buccal cavity, was found among species of Pseudomelatominae (Turridae). This is an endemic subfamily from central west America, which includes three genera and several species (McLean, in Keen, 1971). The anatomy of two species—*Pseudomelatoma penicillata* (Carpenter, 1864) and *Hormospira maculosa* (Sowerby, 1834)—indicates the isolated position of the group among the Toxoglossa (Kantor, 1988). This is obvious, in particular, from the presence of long curve of the anterior part of the digestive tract, a rarely found and undoubtedly secondary feature in turrids. The curve is formed either by elongation of the part of the oesophagus between the nerve ring and the buccal mass (in *Pseudomelatoma penicillata* (Fig. 1), the buccal mass is situated at the proboscis base and far ahead of the nerve ring) or by the elongation of the posterior part of the buccal tube (in *Hormospira maculosa,* the buccal mass is situated in front of the nerve ring, distant from the proboscis base).

Both species have a well-developed venom gland, longer in *H. maculosa* (its length comprises 0.5 of the shell height). Although the diet of Pseudomelatominae is unknown, the presence of the large venom gland testifies to predatory mode of feeding. The gastropods have a muscular proboscis with a wide oral opening in the form of triangular or transverse slit and lack an oral sphincter. The radula of

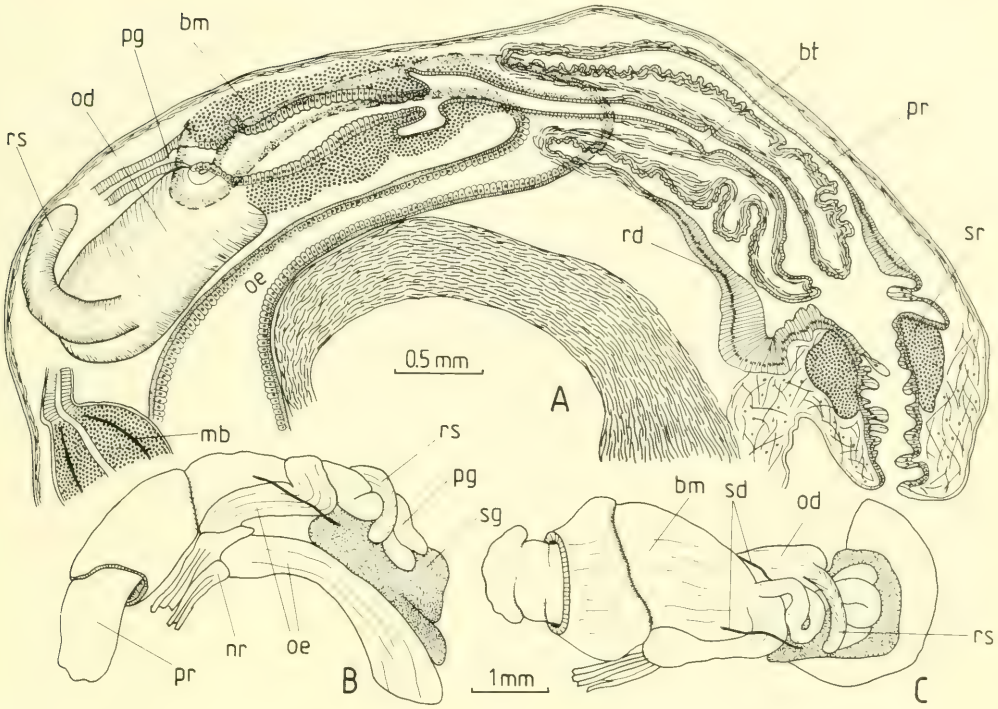

FIG. 1. Anatomy of *Pseudomelatoma penicillata* (Carpenter). A—semidiagrammatic longitudinal section of the anterior part of the molluscan body. Salivary glands with the duct and convolutions of the venom gland together with the nerve ring are not shown. B, C—organs of the body haemocoel (B: from the left, C: from above).

Pseudomelatominae consists of a large and well-developed central tooth, flanked by large, sharply pointed, scythe-like marginal teeth. Thus, although the morphology of the marginal teeth is primitive, the absence of lateral teeth indicates that the group has deviated greatly from the toxoglossan ancestor.

From the morphology of the digestive tract, one can suggest that prey capture probably occurs with the aid of the proboscis tip and is facilitated by the presence of a wide and highly extensible oral opening. The envenomation of the prey probably occurs in the anterior part of the proboscis, and this facilitates the transportation of the prey through the buccal tube into the buccal cavity by the peristaltic movements of well-developed circular muscles in walls of the buccal tube. The presence of a very large odontophore (the largest of all the turrids studied) suggests that the radula tears the prey in the buccal cavity. Thus, the radula of Pseudomelatominae is of the slicing-rasping type as determined by Shimek & Kohn (1981). The large inner volume of the buccal cavity and the curve of the anterior part of the digestive tract suggests that the prey is partially digested in the anterior part of the digestive tract.

In summary, the main features of this feeding mechanism are: prey capture with the aid of the proboscis tip, without using marginal teeth (since the oral opening lacks a sphincter and the shape of the marginal teeth prevents their being held at the proboscis tip); use of the large and powerful radula for slicing and rasping the prey; and, what is probably a secondary feature, at least partial digestion of the prey in the anterior part of the digestive tract. This feeding mechanism is the true "non-toxoglossate" and was probably characteristic of ancestors of the Toxoglossa. In my opinion, it is widespread among turrids, and occurs probably in the Clavinae and other taxa lacking an oral sphincter (for example, *Clavatula diadema*), although digestion of the prey in the anterior part of the digestive system is uncertain.

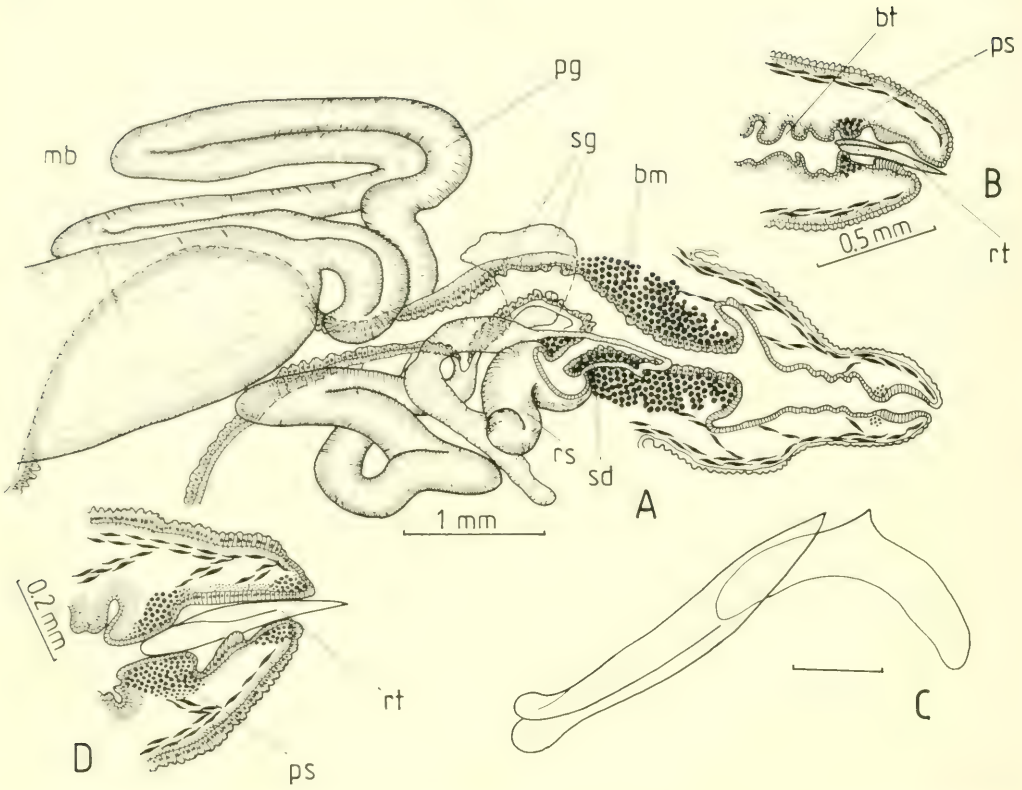

FIG. 2. Morphology of the digestive system of *Aforia* spp. A—C: *Aforia abyssalis* Sysoev et Kantor (A—semidiagrammatic section of the anterior part of the digestive system; B—magnified tip of the proboscis; C—radula); D—magnified tip of the proboscis of *Aforia kupriyanovi* Sysoev et Kantor.

Feeding Mechanism Type 2

The second functional type of digestive system is found in some turrids with a well-developed radular membrane (subfamilies Turriculinae, Clavinae) (Sysoev & Kantor, 1987, 1989). Its typical feature is the use of marginal teeth, which become detached from the radular membrane during its degeneration (in the sublingual pouch), at the proboscis tip for stabbing the prey. Meanwhile, the radula as a whole organ has a different function in the buccal cavity. This type of feeding mechanism can be probably found amongst species of almost all subfamilies of Turridae, except the Pseudomelatominae, Zonulispirinae and probably the Clavatulinae.

Since turrids belonging to this type have varied anatomies, it is difficult to distinguish morphological features common to all representatives of the group. For the species studied (*Aforia* spp., *Antiplanes* spp., *Splendrillia chathamensis* Sysoev & Kantor, 1989) the following features can be noted: a large or medium-sized odontophore, with well-developed radular muscles; a sac-like enlargement of the anterior part of the buccal tube; and a well-developed oral sphincter.

Individual solid marginal teeth were found at the proboscis tip, either held by the oral sphincter as in *Aforia* (Fig. 2 B,D), or attached by their bases to the "mat" of epithelial cells in the enlargement of the buccal tube as in *Splendrillia chathamensis* (Fig. 3B). It should be noted that separate teeth were not found in the sublingual pouch. This seems to indicate that the marginal teeth are not used at the proboscis tip of *Aforia* in every feeding act. On the contrary, the mechanism of tooth fixation in *Splendrillia* testifies to the long-term occurrence of the tooth at the proboscis tip, i.e. the enlargement of the anterior part of the buccal tube may be considered as a functional analogue of the short arm of the radular sac.

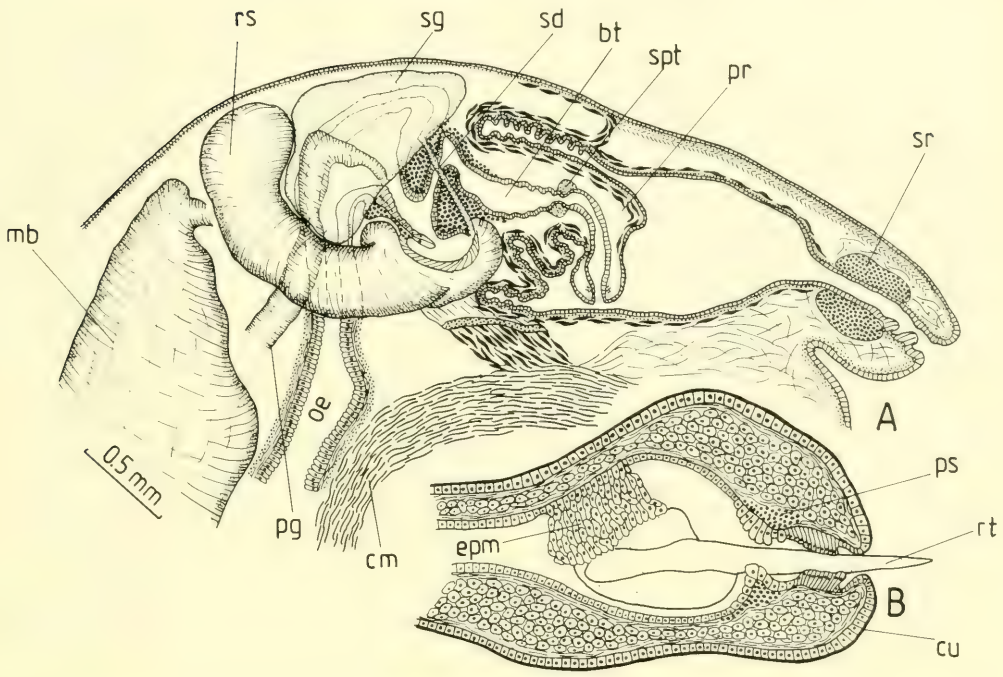

FIG. 3. Anatomy of *Splendrillia chatamensis* Sysoev & Kantor. A—semidiagrammatic longitudinal section of the anterior part of molluscan body; B—magnified tip of the proboscis.

Transportation of teeth to the proboscis tip in *Aforia* may occur with the flow of venom during contraction of the muscular bulb or also by peristaltic movements of circular muscle fibres of the buccal tube. *Splendrillia chathamensis* has an additional, well-developed sphincter in the middle part of the buccal tube (Fig. 3A, spt), which probably takes part in the transportation of the tooth. The marginal tooth is detached from the membrane and is pushed into the buccal cavity by the contracting walls of the buccal sac. The tooth length is about 1/3–1/4 of the contracted proboscis length. During the contraction of the proximal part of the proboscis, the tooth becomes held by the additional sphincter. When the distal part of the proboscis contracts, the tooth is passed into the oral sphincter.

The function of the radula as a whole organ within the buccal cavity is most probably for the transport of food from the cavity to the oesophagus. This may be confirmed, in particular, by the observations of Maes (1981), who noted the presence of intact sipunculans in the posterior part of the oesophagus of *Drillia cydia* (Bartsch, 1943) (Clavinae), although the large, pectinate lateral teeth might at first sight be thought to serve for tearing or rasping the prey.

The use of marginal teeth at the proboscis tip in turrids with a well-developed radular membrane is probably a widespread phenomenon amongst the Turridae. This may explain the origin of hollow marginal teeth in different groups possessing the radular membrane and odontophore. For example, *Imaclava* (Clavinae), most probably also uses the teeth at the proboscis tip for stabbing the prey in a way similar to higher toxoglossans.

In summary, the main features of this feeding mechanism are: the detachment of marginal teeth from the radular membrane during its degeneration; transportation of the teeth to the proboscis tip; and their use for damaging and poisoning the prey with the venom. A feature of the proboscis is the sac-like enlargement of the anterior part of the buccal tube, with the sphincter holding the base or the middle part of the tooth. The function of the radula as a whole organ is mainly for the transport of the food from the buccal cavity to the oesophagus, although in some turrids it may be used also for tearing and rasping. This could be confirmed by the investigation of the prey ob-

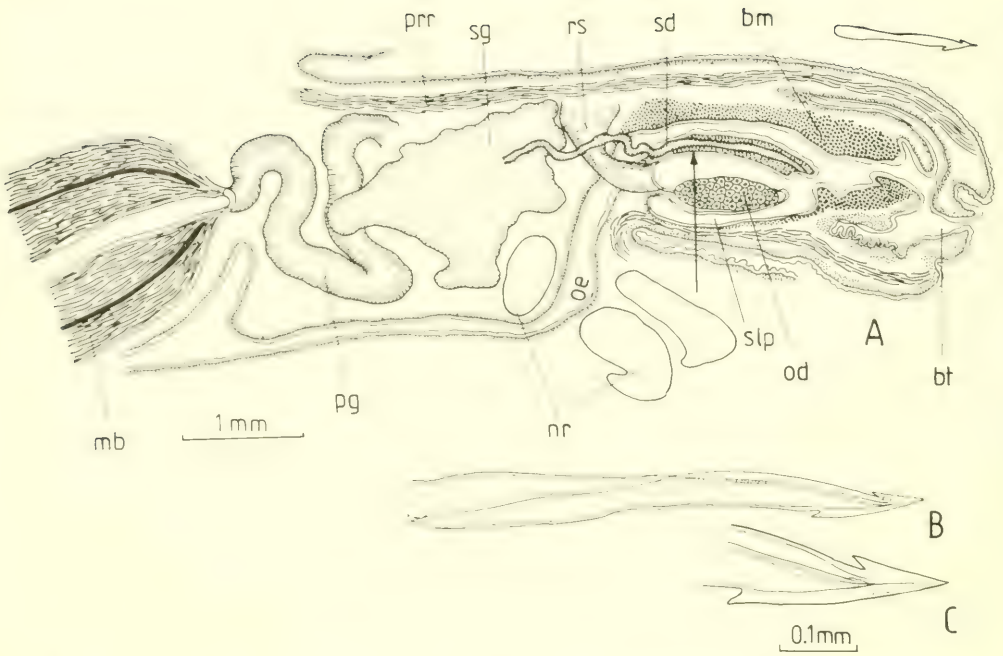

FIG. 4. Morphology of the digestive system of *Toxiclionella tumida* (Sowerby). A—semidiagrammatic longitudinal section of the anterior part of the digestive system. The convolution of the venom gland and posterior part of the radular sac are not shown. the arrow indicates the entrance of the venom gland in the oesophagus; B—marginal tooth; C—the tip of the tooth, enlarged.

tained from the buccal cavity and anterior oesophagus. Thus, the slicing, slicing-rasping, and slicing-stabbing types of radula described by Shimek & Kohn (1981) belong principally to the same functional type, which may be named "stabbing–transporting" type.

Feeding Mechanism Type 3

The third feeding mechanism has been found so far only in a single species of Turridae, *Toxiclionella tumida* (Sowerby, 1870) (Clavatulinae), although it probably exists in other species of this endemic south African genus. A feature of the morphology of the digestive system is the position of the buccal mass, with the odontophore near the proboscis tip (Fig. 4A). The oral sphincter is absent. The gastropod has a well-developed, long venom gland and an unpaired salivary gland with paired ducts, which is situated in the posterior part of the proboscis. The radula consists only of hollow, marginal teeth which are morphologically similar to the teeth of higher turrids (Fig. 4B,C); a radular membrane is present. The teeth are sufficiently long (the tooth, at the same scale, is figured above the proboscis on Fig. 4) that during protraction of the odontophore the tips would protrude through the oral opening. This leads to the conclusion that the mollusc uses the radula as a whole organ for stabbing the prey.

The main difference of this mechanism from all others in which a marginal tooth is used for stabbing and poisoning the prey, is that the radula is used as a whole organ, not as separate teeth. It is possible that a similar mechanism occurs in *Turricula nelliae spurius* (Hedley, 1922) (Taylor, 1985), which has a similar proboscis morphology.

Feeding Mechanism Type 4

The fourth feeding mechanism was found in higher toxoglossans that lack a radular membrane, i.e. higher Turridae, Conidae and some Terebridae. The main feature of the mechanism is the use of individual, hollow marginal teeth at the proboscis tip for stabbing the prey, and the completely reduced function of the radula as a whole organ within the buccal cavity. The feeding and the diet of

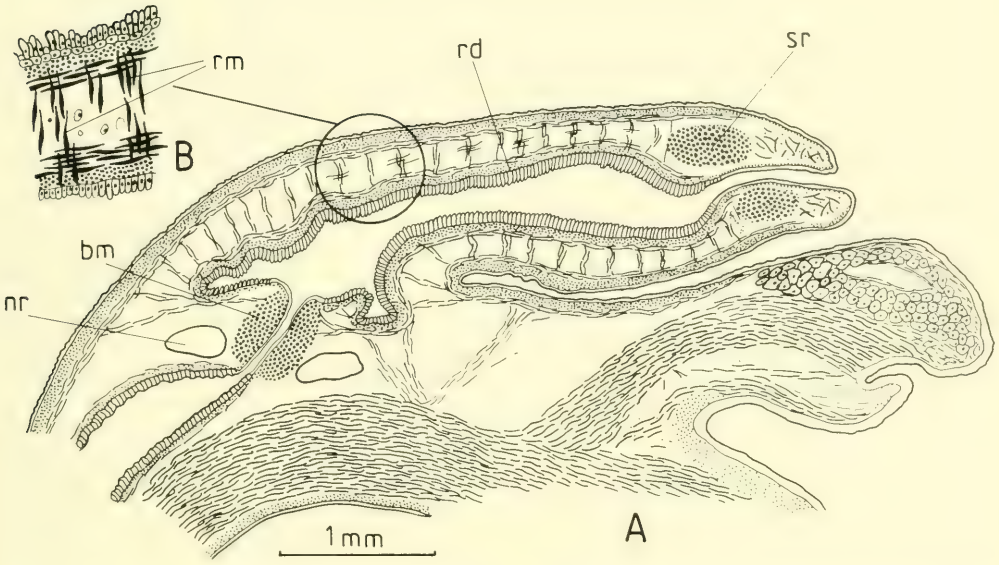

FIG. 5. Anatomy of *Teretiopsis abyssalis* Kantor & Sysoev. A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—enlarged part of the section through the body wall and rhynchodaeum.

species with this functional type is well known, and it is unnecessary to describe it in detail. Only the most important morphological features should be noted. These are the vestigial, or completely reduced, radular membrane; the absence of an odontophore; the presence of the short arm of the radular sac, where the fully formed marginal teeth are stored; and a well-developed, oral sphincter for tooth fixation. The radula is represented only by hollow marginal teeth, with the most specialized and complex morphology found within the prosobranchs. The tooth ligament (long flexible stalk attached to the tooth base) is probably the rudiment of the radular membrane. Amongst molluscs of this functional group, the enlarged rhynchostomal lips appeared. In some species, the lips are able to invert (i.e. to form a pseudoproboscis) and this is used in prey capture. It should be noted that in some representatives of the group—some vermivorous species of *Conus* (Marsh, 1970) and *C. geographus* L., 1758 (Johnson & Stablum, 1971)—stabbing is not a necessary part of each feeding act.

Judging from the morphology of the digestive system, Zonulispirinae occupy an intermediate position between the gastropods of the second and the fourth functional groups. They have hollow marginal teeth, attached to a rather strong radular membrane. This may indicate that separate teeth are used at the proboscis tip. Moreover, the gastropods have very small odontophore (Maes, 1983); this indicates that the function of the radula as a whole organ within the buccal cavity is probably rudimentary.

Feeding Mechanism Type 5

The fifth and last functional type is found among those Toxoglossa lacking a radula. Gastropods of this group belong to higher Turridae (according to the shell morphology) and some Terebridae. The most important features are: a reduced or completely absent proboscis; and absence of a radular sac, and venom and salivary glands. Most representatives of this group have either well-developed rhynchostomal lips or a large pseudoproboscis (Terebridae—Miller, 1975; *Philbertia linearis* (Montagu), Turridae—Sheridan et al., 1973). Some turrids (*Cenodagreutes* spp.—Smith, 1967; *Abyssobella atoxica* Kantor & Sysoev—Kantor & Sysoev, 1986; *Teretiopsis* spp.—Kantor & Sysoev, 1989), lacking a pseudoproboscis, have a vast rhynchocoel and have developed a cavity between the rhynchodaeum and body walls, which are connected by numerous muscles in the cavity

(Fig. 5). Species of the genus *Taranis* lack both a pseudoproboscis and a cavity.

The feeding mechanism is known for terebrids (Miller, 1970, 1975). Thus, species with a relatively short pseudoproboscis feed on the enteropneust *Ptychodera flava,* and species with a long pseudoproboscis feed on polychaetes. The capture and engulfment of the prey occurs with the aid of the pseudoproboscis. Turrids lacking a pseudoproboscis, but with a cavity between the rhynchodaeum and the body walls, probably engulf the prey with the aid of negative pressure, which arises in the rhynchocoel during contraction of the radial muscle fibres (at that moment the inner volume of the rhynchocoel increases). It is difficult at present to say anything certain about the feeding mechanism of *Taranis.*

The feeding of such aberrant groups as Strictispirinae (Turridae) is unclear. These gastropods lack a venom gland and have a very large odontophore. According to the figure of Maes (1983), *Strictispira paxillus* (Reeve, 1845) has a short buccal tube. Thus, there is a possibility that it can protrude the radula through the mouth opening and use it pincer-like, tearing off small pieces of food.

Origin of the Toxoglossan Mode of Feeding

In my opinion, the development of the unique "toxoglossan" mode of feeding is connected with certain morphological prerequisites. These were the appearance of the venom gland and the intraembolic type of the proboscis.

The mobile proboscis, which in the contracted state is situated in the special cavity of the body haemocoel, or proboscis-like structures (for example, the extrovert formed by the walls of the buccal cavity in Janthinidae—Graham, 1965) appeared independently in different groups of marine predatory gastropods. The presence of the proboscis allows an increase in the mobility of the buccal mass, and this is achieved by its shift from the ventral side of the head (as in herbivorous gastropods) in the terminal (axial) position. This also allows "distant" feeding, i.e. to feed on prey hidden in burrows, crevices, etc., and also on animals with external skeletons, for example on bivalves (inserting the proboscis between the open valves or through a drilled hole).

Usually three types of proboscis are defined: acrembolic, pleurembolic, and intraembolic, these are differentiated by the position of the buccal mass and the mode of eversion. Only the latter two types are found among Neogastropoda. In gastropods with the pleurembolic proboscis, the buccal mass with radular sac is situated near the proboscis tip, and proboscis eversion occurs with the aid of the posterior invaginable part of the rhynchodaeum (wall of the proboscis sheath or rhynchocoel). In many neogastropods with this proboscis type, the entire or nearly entire rhynchodaeum takes part in proboscis eversion. On the contrary, in gastropods with the intraembolic proboscis, the buccal mass is situated at the proboscis base or even behind it (*Pseudomelatoma penicillata,* Turridae—Fig. 1), the invaginable part of the rhynchodaeum is absent, and the proboscis eversion results only from its stretching. Recently, a proboscis somewhat intermediate between the typical pleurembolic and intraembolic types was described in *Turricula nelliae spurius* (Taylor, 1985) and *Toxiclionella tumida* (herein). In these gastropods, the buccal mass is situated near the proboscis tip, and the rhynchodaeum is capable of partial eversion.

Usually, the Neogastropoda are considered as a monophyletic group (Ponder, 1973; Taylor & Morris, 1988). On the other hand, doubts on the monophyletic origin of neogastropods were expressed by Golikov & Starobogatov (1975), with moreover the Toxoglossa (*sensu* Golikov & Starobogatov who included Mitroidea along with Conoidea and Terebroidea in the order) were separated from the rest. The problem of the ancestral group is also essential to the argument. Ponder (1973) considered that the Neogastropoda originated from archaeogastropods or primitive mesogastropods. Thus, the proboscis of neogastropods in general and of Toxoglossa in particular should be considered as *de novo* structure. Taylor & Morris (1988), on the contrary, suggested the possibility of the origin of Neogastropoda from higher, advanced Mesogastropoda and their proboscides thus should be homologous with the pleurembolic proboscis of predatory Mesogastropoda. Finally, Sheridan et al. (1973) stated that the intraembolic type of the proboscis originated from the acrembolic type.

For more careful consideration of the question some comments on the morphology of the buccal muscles are necessary.

In archaeogastropods and primitive mesogastropods lacking a proboscis, there are numerous buccal muscles that are connected to the columellar and pedal muscles. On the

contrary, in Mesogastropoda and Neogastropoda with a developed pleurembolic proboscis, the buccal muscles have lost such a connection and are attached to the proboscis walls (Graham, 1973; herein). In a species of Clavinae, which are considered to be the least-derived Toxoglossans, there is such a connection of supramedian, radular tensor and columellar muscles (Fig. 3A). In my opinion, this undoubtedly confirms the original basal position of the buccal mass in Clavinae. In the opposite case, the connection of the buccal and columellar muscles would be lost. Thus, one can state that the intraembolic proboscis has evolved independently from the pleurembolic type and not from the latter (by the shift of the buccal mass to the proboscis base) and that the origin of Toxoglossa and all Neogastropoda in general (if they are considered as a monophyletic group) from higher probosciferous mesogastropods is improbable. Proboscides of different groups of Neogastropoda probably appeared independently, and the detailed morphological studies of some poorly known groups would corroborate this supposition.

The appearance of the intraembolic proboscis in Toxoglossa may be connected with appearance and development of the venom gland. It is very likely that toxoglossan ancestors were carnivorous gastropods with a short acrembolic proboscis. The acrembolic proboscis is found among various primitive gastropods (for example, Naticidae, Triphoridae, Cerithiopsidae) and principally may be considered as an elongated buccal tube that has an ability to evert through the mouth opening as a glove finger. In the inverted position, the buccal mass is situated at the base of the proboscis, while in an everted position it is located at the proboscis tip (Fig. 6 A). During proboscis eversion the oesophagus is pulled through the nerve ring.

The elongation of the acrembolic proboscis allows gastropods to feed on animals hidden in deep burrows, crevices or tubes, for example on polychaetes. At the same time, the elongation of the proboscis limits the size of the oesophageal glands, which have to be pulled through the nerve ring during eversion.

It could be suggested that at early evolutionary stages, these gastropods started to use the secretion produced by the dorsal glandular folds of the oesophagus and squirted through the mouth for immobilization of the prey. This simplified the capture and swallowing of actively moving prey. After the appearance of such feeding mechanism, the proboscis may have elongated by the development of a tube in front of the mouth opening, which was situated in the sheath formed by the walls of introvert of the acrembolic proboscis (Fig. 7B). The main function of the proboscis was not to move the buccal mass forward, but to form the tube through which the venom reaches the prey.

Such elongation of the proboscis appears closely related to the enlargement of the dorsal oesophageal folds; as the inner volume of the proboscis grew, more venom was necessary to fill it. Gradually the glandular folds stripped off from the oesophagus and formed a tube, i.e. the venom gland. In the initial stages of the formation of the new proboscis type, the introvert was probably able to evert, but the enlarged size of the venom gland prevented its being pulled through the nerve ring. Finally, this caused fixation of the buccal mass in front of the nerve ring at the proboscis base, and the introvert ceased to evert. At that moment, the newly formed proboscis possessed all features of the intraembolic type (Fig. 6C). The functions of the radula were the same as in other gastropods (tearing and rasping the prey and its transportation to the oesophagus), but it acted only within the buccal cavity.

If this proposed scheme of origin of the intraembolic proboscis is accepted, then one can suppose that the rhynchodaeum is a homologue of the introvert wall of the acrembolic proboscis and the proboscis itself is *de novo* structure that is not homologous with the pleurembolic proboscis of other neogastropods.

The discovery of a mechanism by which individual solid marginal teeth are used at the proboscis tip in turrids with a well-developed radular membrane, allows us to reconstruct the development of the typical "toxoglossan" mode of feeding. In the process of radula growth, anterior (the oldest) rows of teeth are detached from the radular membrane, which in turn degenerates in the sublingual pouch. It is reasonable to suppose that some detached teeth are not removed through the digestive tract (as usually occurs in gastropods) but are somehow transported to the proboscis tip where they are used for damaging the prey integument. This intensifies the efficiency of venom action. Fixation of such a mechanism in evolution created the prerequisites and necessity of the appearance of hollow marginal teeth. This was an important stage in toxo-

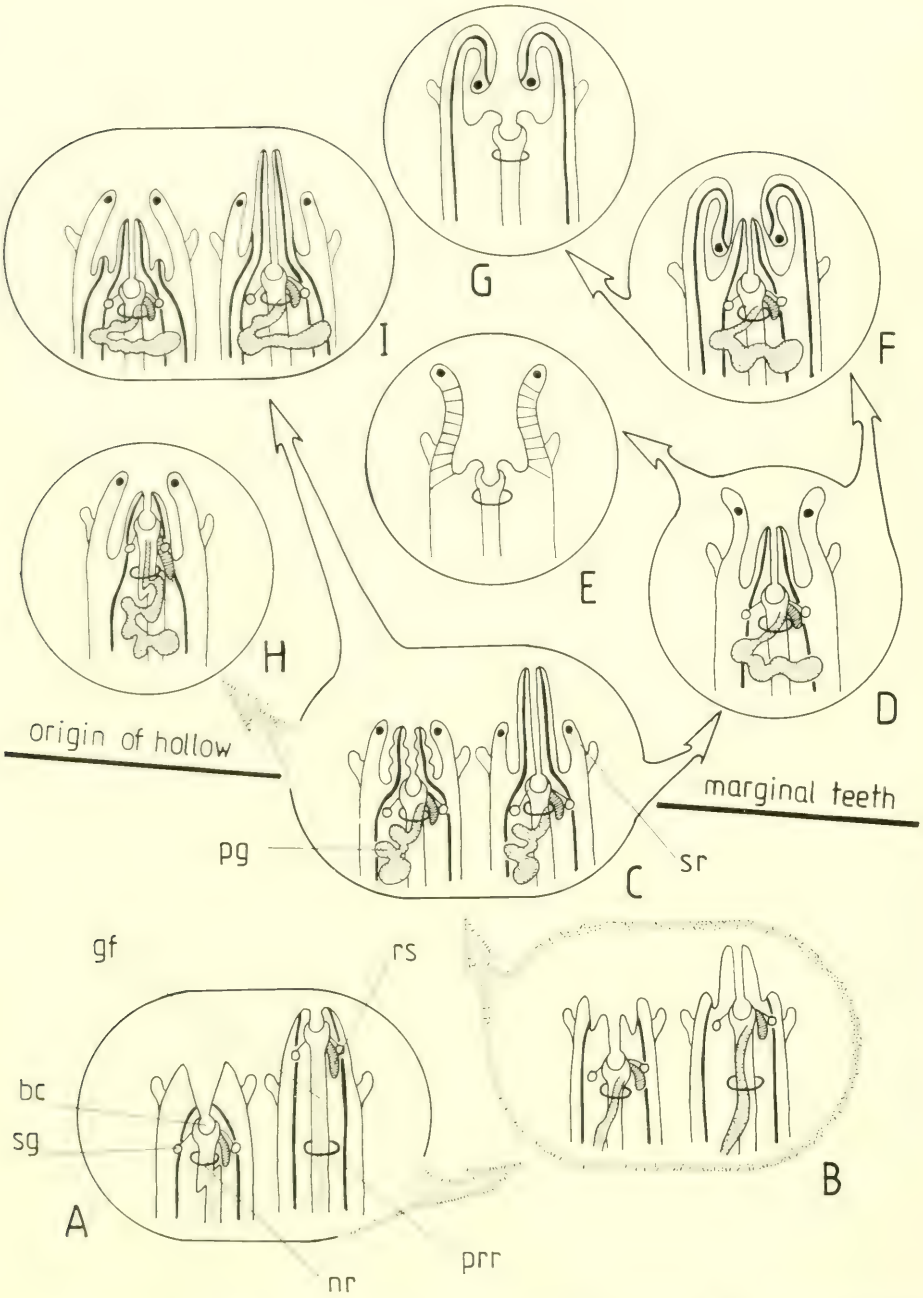

FIG. 6. A scheme for the origin and evolution of the proboscis of Toxoglossa. The dotted arrows indicate hypothetical connections. The hypothetical morphological stage is given on the dotted background. A—acrembolic proboscis of the ancestral group; B—intermediate morphological stage between the acrembolic and intraembolic proboscis types; C—the basal type of the intraembolic proboscis; D—origin of rhynchostomal lips; E—reduction of the proboscis, radula and venom and salivary glands; F—origin of pseudoproboscis; G—reduction of the proboscis, radula and venom and salivary glands; H—displacement of the buccal mass toward the proboscis tip and formation of the curve of the digestive tract; I—formation of the radial folds at the proboscis base.

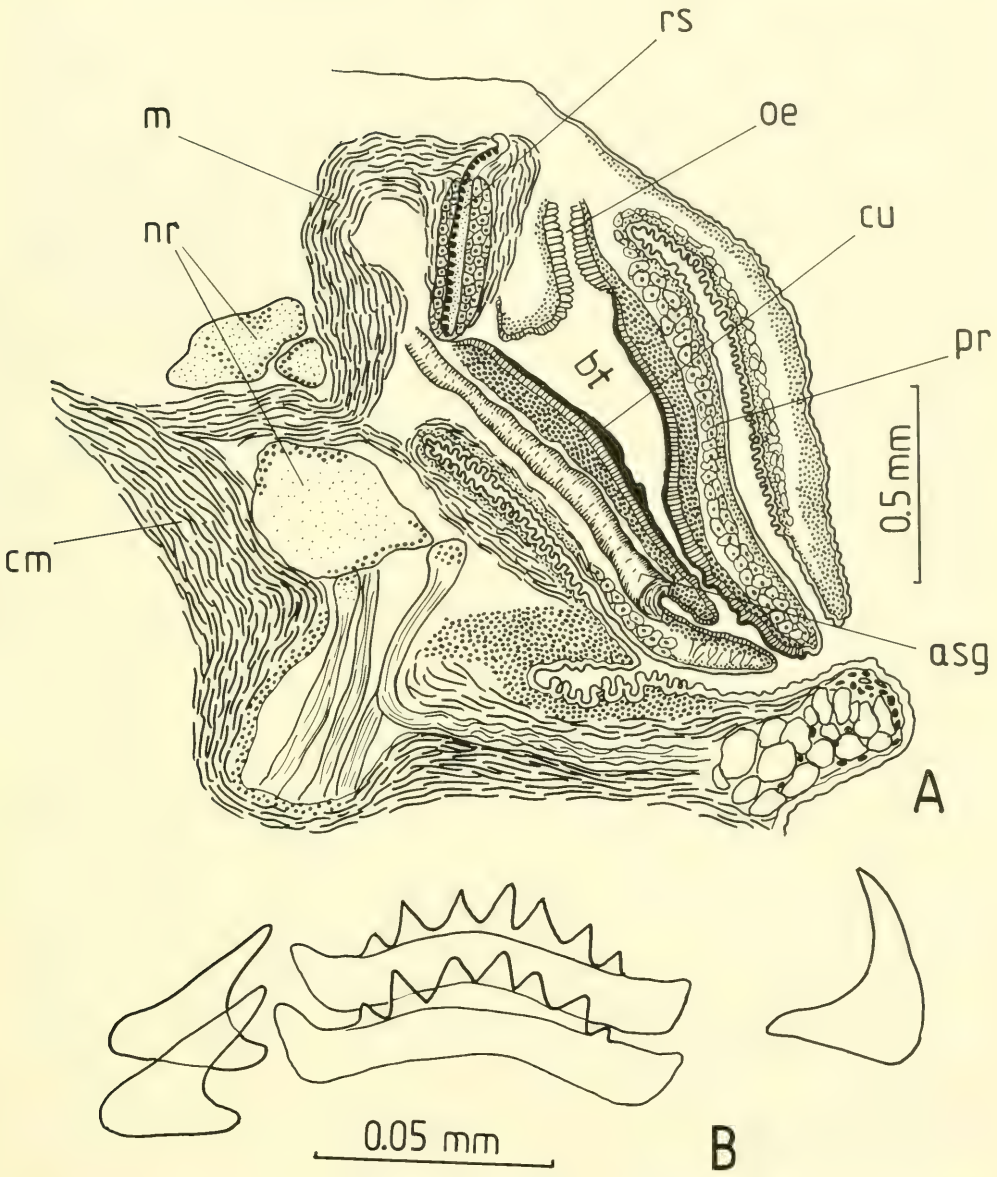

FIG. 7. The anatomy of *Benthobia* n.sp. A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—radula.

glossan evolution. As the mechanism of prey stabbing and poisoning by the teeth at the proboscis tip improved, the functions of the radula as a whole organ within the buccal cavity became less and less important. This finally led to reduction of the odontophore, central and lateral teeth, and as a final stage, the radular membrane.

Up until now the intraembolic proboscis has been found only amongst Toxoglossa. However, a similar proboscis type was found by the author in a species of the family Pseudolividae (Fig. 7), *Benthobia* n.sp. The buccal mass in this species is situated at the proboscis base; moreover, there is a connection of the buccal muscles with the columellar mus-

cle (this confirms the primary position of the buccal mass, see above). This gastropod also has a very large gland of Leiblein. According to Ponder (1973), the venom gland of the Toxoglossa and the gland of Leiblein were formed independently, but in similar way, by the stripping off of the glandular folds from the oesophagus. Thus, one can state that Pseudolividae and Toxoglossa are not related groups, and the similar proboscis type appeared independently. The radular morphology of *Benthobia* (Fig. 7B) (very similar to Olividae), as well as details of the morphology of the anterior part of the digestive tract, indicates that the marginal teeth are not used at the proboscis tip by *Benthobia.* Thus, the development of the venom gland rather than the position of the buccal mass at the proboscis base, was the main factor conditioning the appearance of "toxoglossan" mode of feeding in evolution.

The origin of hollow marginal teeth took place repeatedly and independently in different phylogenetic lineages of Toxoglossa. Hollow marginal teeth appeared at least twice among turrids, simultaneously with the retention of the radular membrane and the central and sometimes lateral teeth. Radulae of this type are found among *Imaclava unimaculata* (Sowerby, 1843) (Clavinae) (Shimek & Kohn, 1981) and *Toxiclionella elstoni* (Barnard, 1962) (Clavatulinae) (Kilburn, 1985).

The main trends of subsequent evolution of the Toxoglossa are variable and characterized by morphological changes in the anterior part of the digestive system. Thus, three main pathways of the morphological evolution of the proboscis may be defined. Some Toxoglossa have circular folds formed by the proboscis in the contracted state (Fig. 6I). This reduces the length of the contracted proboscis, and probably simplifies the transportation of the individual marginal teeth from the radular sac to the proboscis tip.

The second lineage is connected with origin and development of the mobile rhynchostomal lips, which take part in the prey capture (Fig. 6D). The progressive development of lips into an introvert results in the pseudoproboscis (Fig. 6F) of some turrids and most Terebridae. The action of prey capture gradually transferred from the proboscis to the rhynchostomal lips or pseudoproboscis, and this finally led to the complete reduction of the true proboscis (Fig. 6E, G). The process is evolutionarily connected with the complete reduction of the radula, venom and salivary glands, a process that occurred independently in different phylogenetic lineages.

Finally, the third, less studied trend is connected with the shift of the buccal mass toward the proboscis tip. Also the rhynchodaeum secondarily evolved the capability of partial eversion (this was made possible by the elongation of the oesophagus between the buccal mass and the nerve ring and formation of the curve of the oesophagus, as it takes place in Rachiglossa). The tendency is best seen in *Turricula nelliae spurius* (Turriculinae) and *Toxiclionella tumida* (Clavatulinae). An intermediate morphological stage is found in *Clavatula diadema* (Kiener, 1840) (Fig. 8), in which the buccal mass is situated inside the proboscis nearer to its base, and the rhynchodaeum is capable of partial eversion. The presence of two consecutive morphological stages in the same subfamily confirms the secondary character of this evolutionary lineage.

In conclusion, one more question should be discussed, the resolution of which may shed light on the ancestral group of Neogastropoda and Toxoglossa. Usually, the radula of Clavinae (Turridae), with a central tooth, flanked by pairs of lateral and marginal teeth, is considered as a plesiomorphic condition in neogastropods (Taylor & Morris, 1988). In pectinibranchiate gastropods, the radula is folded lengthways in the radular sac. The folds in the gastropods with differentiated groups of teeth are situated between the marginal and lateral teeth and between the lateral and central teeth. Thus, in gastropods with marginal and lateral teeth, there are two pairs of folds. A similar condition is observed in *Olivella,* except for the Clavinae, the only genus of neogastropods which has five teeth in a transverse row (Fig. 9A). Nevertheless, the clavine radula has only one pair of folds, which are situated between the central and lateral teeth (Fig. 9B). Species of the genus *Antiplanes* have the central formations which were considered as a reduced central tooth. Investigations of the radula indicate that it has only one fold (Fig. 9C). This may indicate that traditional interpretation of the radular teeth of Clavinae is wrong and their radula is formed by central and two pairs of marginal teeth, which have become greatly differentiated in evolution. In *Antiplanes,* the central tooth is possibly completely reduced, and the central formations are the rudiments of the inner pair of the marginal teeth.

Thus, one can suppose that the toxoglossan

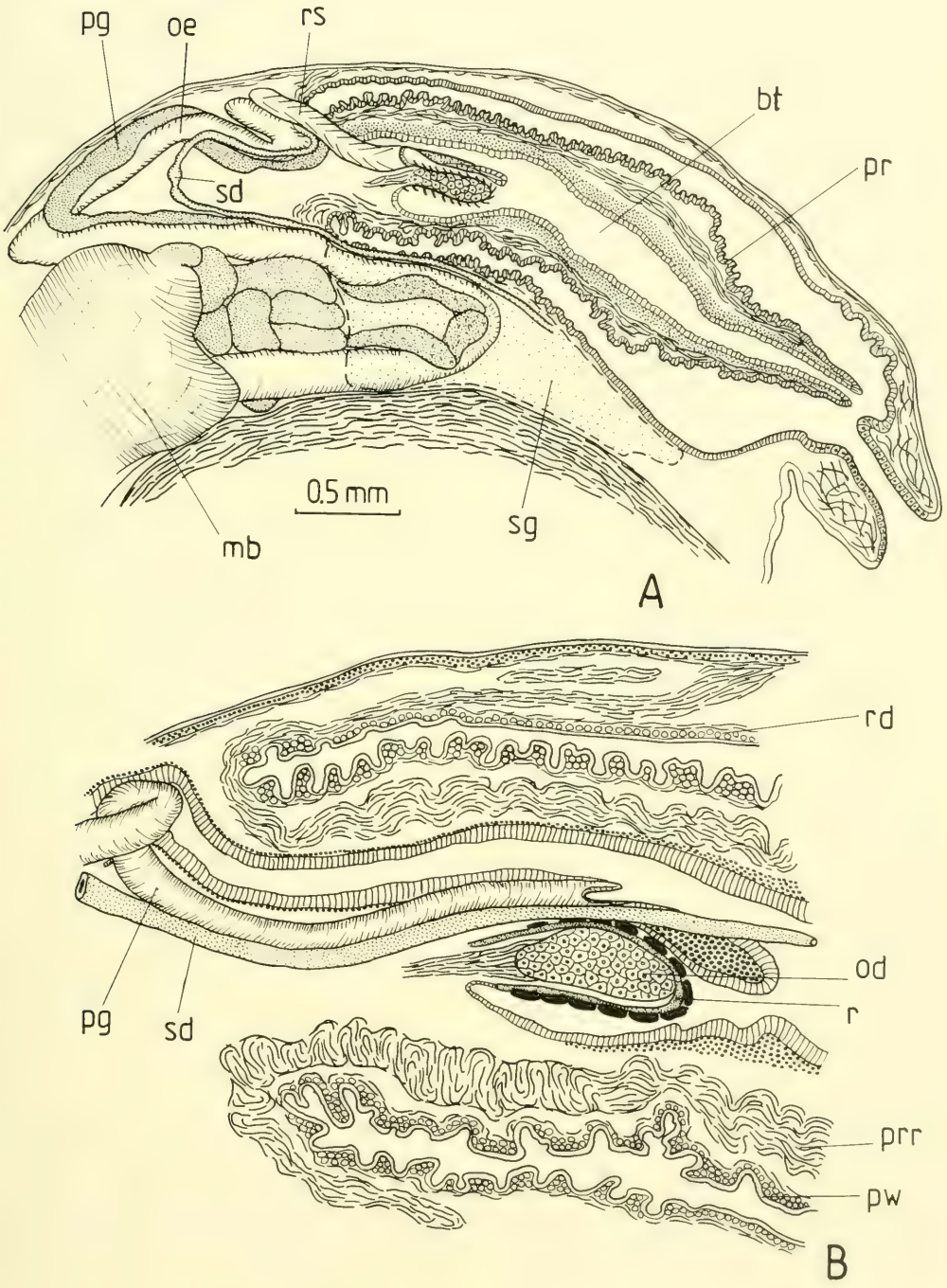

FIG. 8. The anatomy of *Clavatula diadema* (Kiener). A—semidiagrammatic longitudinal section of the anterior part of the molluscan body; B—magnified base part of the proboscis.

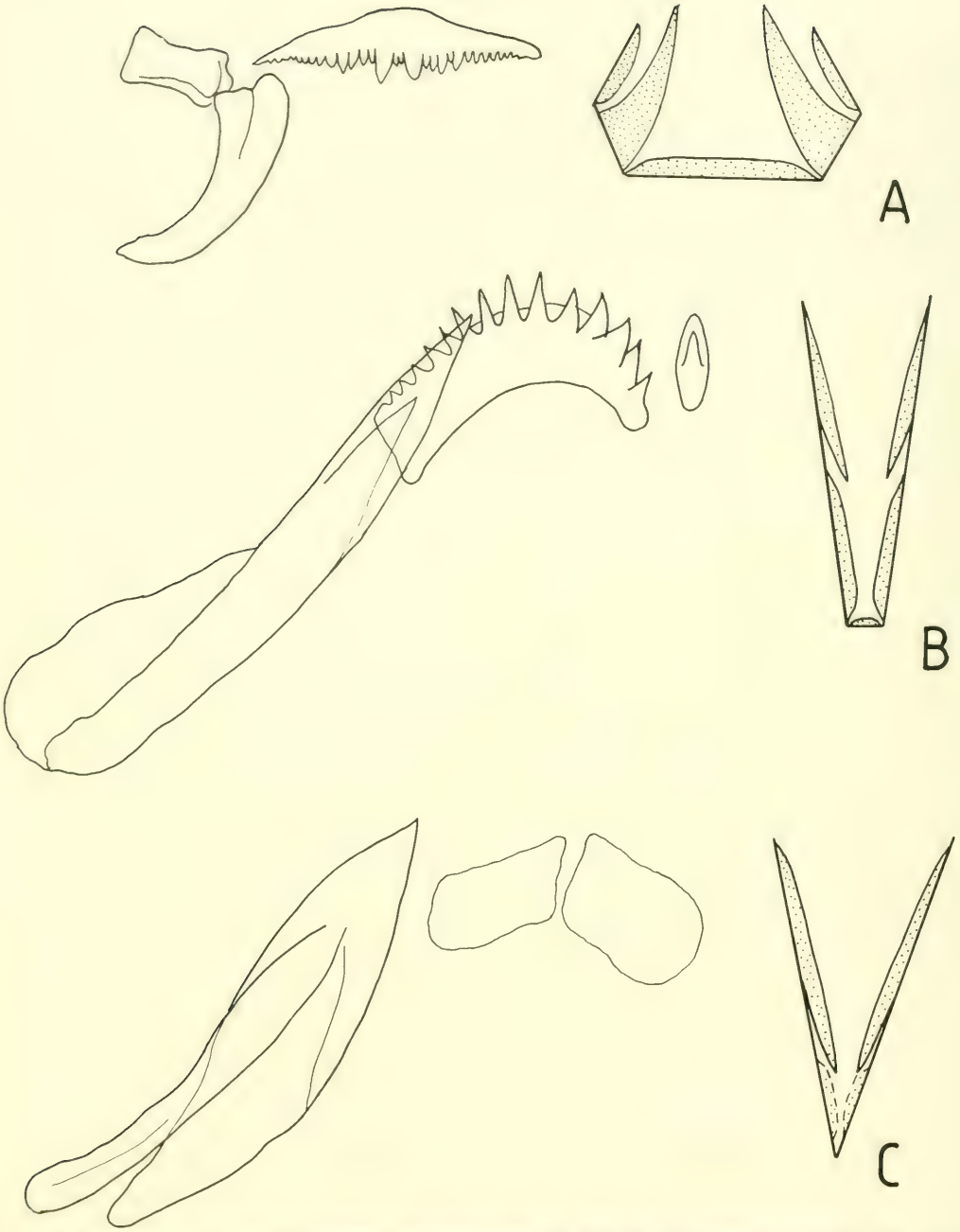

FIG. 9. The radular folding in different Neogastropoda. At the left—the shape of radular teeth, at the right—diagrammatic transverse section of the radula sheath. A—*Olivella*; B—*Splendrillia* (Clavinae); C—*Antiplanes* (Turriculinae).

radula originated from the taenioglossan (2-1-1-1-2) by the reduction of true lateral teeth and differentiation of the marginals. (The radular formula of Clavinae should be 2-0-1-0-2, of *Antiplanes*, 2-0-0-0-2.) On the contrary, in *Olivella* the radula is formed by the rudiments

of the marginal teeth, by a pair of laterals and a central, i.e. it originated from the taenioglossan by a reduction of the pair of marginal teeth (formula: 1-1-1-1-1). The present hypothesis supposes that if the Neogastropoda is a monophyletic group, their ancestor had the taenioglossan radula, and the derivation of Rachiglossa and Toxoglossa occurred at an early stage, when the ancestor had seven teeth per transverse row.

CONCLUSIONS

(1) The evolution of Toxoglossa as a separate taxon was connected with the origin and development of the venom gland. The development of the venom gland determined the appearance of the specialized intraembolic type of proboscis and the specific "toxoglossan" mode of feeding.

(2) The ancestors of Toxoglossa were probably lower mesogastropods with a short acrembolic proboscis and taenioglossan radula.

(3) In higher Toxoglossa, the specific "toxoglossan" mode of feeding, using separate, hollow marginal teeth at the proboscis tip, has originated repeatedly and independently in the Turridae. A similar feeding mechanism with the use of solid marginal teeth at the proboscis tip in some lower turrids with a well-developed radular membrane and odontophore may be considered as the intermediate evolutionary stage.

(4) In "higher" Toxoglossa with well-developed rhynchostomal lips or with a pseudoproboscis, a decrease of the proboscis size usually occurs and this leads finally to the complete reduction of the radula, venom and salivary glands.

ABBREVIATIONS

asg—accessory salivary gland; bc—buccal cavity; bm—buccal mass; bt—buccal tube; cm—columellar muscle; cu—cuticle; epm—"mat" of epithelial cells; gf—glandular folds of the oesophagus; m—buccal muscle, connected to the columellar muscle; mb—muscular bulb of the venom gland; nr—nerve ring; od—odontophore; oe—oesophagus; pg—venom gland; pr—proboscis; prr—proboscis retractor muscles; ps—proboscis sphincter; pw—proboscis wall; r—radula; rd—rhynchodaeum; rm—radial muscles, connecting the rhynchodaeum and the body wall; rs—radular sac; rt—marginal tooth, held at the proboscis tip; sd—salivary duct; sg—salivary gland; slp—sublingual pouch; spt—intermediate sphincter of the buccal tube; sr—rhynchostomal sphincter.

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THE ANATOMY OF THE FOREGUT AND RELATIONSHIPS IN THE TEREBRIDAE

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ABSTRACT

A study of foregut anatomy in the gastropod family Terebridae shows that two major groups of species are represented. Members of one group have hypodermic radular teeth, venom apparatus and an extensible buccal tube. Terebrids of the second group have a very short buccal tube, a radula consisting of two rows of solid, curved teeth and no venom apparatus. Furthermore, there are many terebrid species lacking a radula, venom apparatus and buccal tube and these could be derived from either group.

It is suggested that the two groups of Terebridae were derived independently from the Turridae, and each group should be given family status. This study confirms Rudmans's (1969) proposal of the family Pervicaciidae for *Terebra tristis,* and the family should now be extended to include perhaps all species of *Duplicaria* and a number of species currently referred to *Terebra.*

Key words: Terebridae, anatomy, feeding, functional morphology, radula.

INTRODUCTION

The Terebridae is a family of conoidean gastropods characterised by high-spired, multiwhorled shells with relatively small apertures. There are about 300 living species which inhabit soft-substrate habitats at tropical and sub-tropical latitudes (Bratcher & Cernohorsky, 1987). The family is particularly diverse and abundant in shallow-water sandy habitats of Indo-Pacific coral reefs (Miller, 1970; Taylor, 1986). The biology of Terebridae has been little studied and not only is little known about relationships within the family, but the relationship of terebrids with other conoideans is also obscure.

Anatomical work on the Terebridae has been very limited. Details of individual species have been described by Risbec (1953), Marcus & Marcus (1960), Rudman (1969), Auffenberg & Lee (1988), and Taylor & Miller (1990). By far the most significant studies were by Miller (1970, 1971, 1975, 1979). As a result of these studies, Miller (1970, 1971) proposed a classification of proboscis types within the family Terebridae which he thought represented natural groupings, although he made no attempt to examine relationships within the family.

Miller (1970, 1971) recognised three main proboscis types amongst the species he studied. They are briefly defined as follows:

Type Ia species have a long, extensible labial tube or introvert, a short buccal tube, no radula, a pair of salivary glands, and no venom gland or muscular bulb.

Type Ib species are simliar to type Ia in foregut anatomy, but have a very long labial tube, which is folded upon itself when retracted into the rhynchodeal cavity.

Type IIa species have a medium length labial tube, a long proboscis and buccal tube, a pair of fused salivary glands, a radula sac and caecum, with hollow hypodermic radular teeth, a large venom gland and muscular bulb.

Type IIb species are similar, but the buccal tube is shorter and the rhynchodeum may be partitioned by a septum.

Type III species have a labial tube of medium length, a very short or no buccal tube, salivary glands are vestigial or absent, and there is no radular or venom apparatus. A feature of this group of species is the presence of a club-shaped accessory feeding organ attached to the left wall of the rhynchodeal cavity.

Since Miller's scheme was published, the anatomy of a number of terebrid species has been described that do not fit into the classification, and it is clear that some reappraisal is necessary. Furthermore, the recent monograph by Bratcher & Cernohorsky (1987) has highlighted the inconsistencies and problems in the classification of the family, with apparent

incongruence between the anatomy and the shell characters used in the generic divisions.

Apart from a phenetic study of Miocene species (Davoli, 1977), there have been no previous attempts to establish phylogenetic relationships within the Terebridae, and only very generalised comments on the relationship of the terebrids with other toxoglossans. Because a number of terebrid species possess the toxoglossan feeding apparatus of hypodermic radular teeth, venom gland, and muscular bulb, the relationship with the families Turridae and Conidae has long been established. However, many terebrid species lack a radular and venom apparatus, and the structures are presumed to have been evolutionarily lost. The Terebridae are usually assumed to have been derived from the Turridae, although details of this relationship are obscure. Powell (1966, fig. 1) suggested, presumably following Cossmann, 1896), a derivation from the turrid subfamily Clavatulinae, probably based upon the superficial similarities of the smooth, rather elongated shells of *Pusionella* with some terebrids.

Because of the general uniformity of shell morphology, the Terebridae have been assumed to be monophyletic. The only serious dissenter from this view is Rudman (1969), who described the anatomy of the New Zealand and southern Australian species *Pervicacia tristis* (Deshayes, 1859) (*Terebra tristis* in Bratcher & Cernohorsky, 1987). This species has a radula consisting of two rows of short, solid and slightly curved marginal teeth and an odontophore, but lacks a venom apparatus. Rudman considered the species sufficiently distinct from other terebrids to justify the erection of a new family, the Pervicaciidae, which he thought was derived from the Turridae independently from the rest of the terebrids. The latter together with the Conidae were derived from the Turridae after the evolution of the hypodermic type of radular teeth. Subsequently, other authors (Ponder, 1973; Bratcher & Cernohorsky, 1987) have considered that the characters of *T. tristis* fall within the range of other Terebridae and that the separation as a separate family was not justified.

The objectives of this paper are to review what is known of foregut anatomy in the Terebridae, and to examine the use of these anatomical characters in determining relationships both within the family and with other conoideans.

MATERIALS AND METHODS

The basic data for this study were obtained from dissections and serial sections of the foregut made from 18 species of Terebridae. These are listed below, nomenclature following Bratcher & Cernohorsky, 1987, which for convenience is also followed throughout the paper: *Hastula aciculina* (Lamarck, 1822); *H. albula* Menke, 1843; *H. bacillus* (Deshayes, 1859); *H. hectica* (Linnaeus, 1758); *H. salleana* (Deshayes, 1859); *H. solida* (Deshayes, 1857); *Terebra affinis* Gray, 1834; *T. babylonia* Lamarck, 1822; *T. capensis* Smith, 1873; *T. cerithina* Lamarck, 1822; *T. dimidiata* (Linnaeus, 1758), *T. funiculata* Hinds, 1844; *T. maculata* Linnaeus, 1758; *T. nassoides* Hinds, 1844; *T. subulata* (Linnaeus, 1758); *T. tristis* Deshayes, 1844; *Duplicaria duplicata* (Linnaeus, 1758); *D. spectabilis* (Hinds, 1844).

REVIEW OF FOREGUT ANATOMY

This section consists of brief descriptions of the major features of the foregut anatomy of a number of terebrid species chosen to represent the variety of form so far known in the family. Further details of some of the species can be found in the publications cited.

Hastula cinerea (Born, 1778), *H. galleana,* and *H. inconstans* (Hinds, 1844) (see Marcus & Marcus, 1960; Miller, 1979; Taylor, unpub.)

These three species have a similar anatomy and are characteristic of Miller's type IIa foregut and of most other *Hastula* species. All three species have a short- to medium-length labial tube, a long buccal tube which can extend outside the rhynchodeum, a radular sac and caecum with hollow, hypodermic radular teeth, a pair of salivary glands, and a well-developed venom gland and muscular bulb.

Hastula hectica has a basically similar anatomy, but the labial tube is longer. The most interesting feature of this species is in the structure of the radular teeth. The large barbed and hollow radular teeth have an apparently unique feature. The mid-section of the tooth is formed of a network structure rather like chicken-wire (Figs. 1c, 2). The tooth is hollow but has a well-developed orifice near the tip which in other toxoglossans is where the venom emerges on penetration of the prey. The function of the perforated mid-section of the tooth is not known but may al-

FIG. 1. Single radular teeth of a. *Hastula bacillus* x95; b. *Terebra babylonia* x217; c. *Hastula hectica* x718.

low the delivery of venom along the full length of the tooth rather than just at the tip.

Terebra imitatrix Auffenberg & Lee, 1988

This recently described species has a shell morphology very similar to species of the *Hastula cinerea* group but differs in anatomy. *T. imitatrix* has a large, spoon-shaped labial tube; a large, club-shaped accessory proboscis structure with two rows of papillae on the ventral side; a very short buccal tube which probably cannot be extended out of the mouth of the rhynchodeum; a relatively short venom gland and a small muscular bulb. There is a radular sac and a caecum with rather elongate, slightly curved, barbless teeth. No salivary glands were located by the authors.

Auffenberg & Lee (1988) were puzzled by the combination of characters in this species and for this reason hesitated to include it in the genus *Hastula*. The shell and much of the anatomy resembles that of other *Hastula* species, but the presence of the large accessory proboscis structure they thought to be a feature usually restricted to terebrids with Miller's Type III proboscis. However, species in this latter group lack a buccal tube, radular apparatus, salivary glands, venom gland, and muscular bulb.

FIG. 2. Detail of mid-section of the middle shaft of the radular tooth of *Hastula hectica*. Scale bar 10 μm.

Hastula bacillus (see Taylor & Miller, 1990)

This small species was found abundantly on the surf beaches of the western side of Phuket Island, Thailand. There is a short, extensible labial tube, a long extensible buccal tube, and a large, muscular, branched accessory proboscis structure (**aps**), which is anchored to the left wall of the rhynchodeum (Fig. 3). The **aps** can be extended some distance out of the rhynchodeum, but when retracted is bent into an "s" shape within the cavity. Entering the buccal cavity is a radular sac, without a caecum. A small odontophore is present, and the radula consists of teeth that are scroll-like at the base but taper into a pointed barb-less, knife-like, blade at the tip (Fig. 1a). There is a pair of salivary glands and a single (right) accessory salivary gland. The venom gland is large, with a well-developed muscular bulb.

S.E.M. studies of the accessory proboscis structure show that regularly spaced tufts of short, stiff cilia are distributed over the suface. Associated with each tuft are pairs or triplets

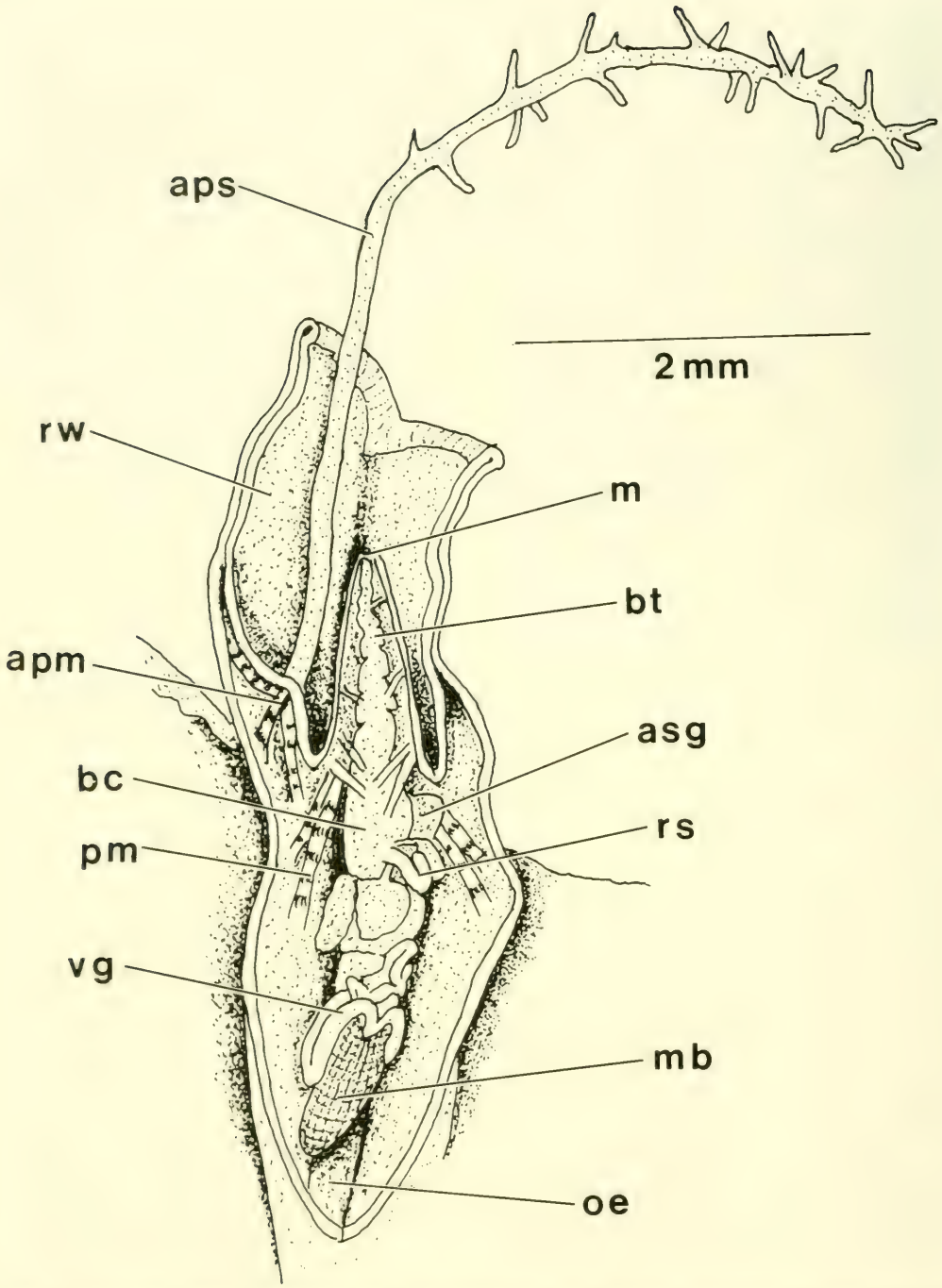


FIG. 3. Dissection of the head of *Hastula bacillus* showing the extended accessory proboscis structure and extended labial tube. The buccal tube is retracted into the rhynchodeal cavity but can be extended beyond the mouth of the cavity. apm, accessory proboscis retractor muscles; aps, accessory proboscis structure; asg, accessory salivary gland; bc, buccal cavity; bt, buccal tube; m, mouth; mb, muscular bulb; oe, oesophagus; pm, proboscis retractor muscles; rs, radular sac; rw, rhynchodeal wall; vg, venom gland.

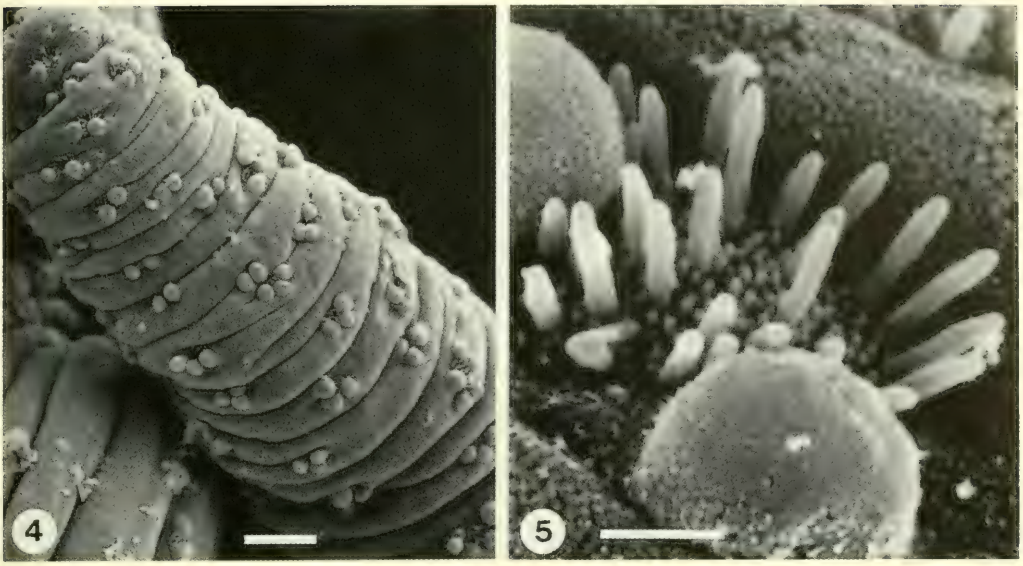


FIG. 4. Branch of the accessory proboscis structure of *Hastula bacillus* showing the ciliary tufts with pairs and triplets of domes. SEM of critical point dried material. Scale bar 10 μm.
FIG. 5. Detail of a ciliary tuft, showing short stiff cilia and the accompanying microvilli-covered domes. Scale bar 1 μm.

of microvilli-covered domes (Figs. 4, 5). The ciliary tufts are similar to those seen on the pallial or cephalic tentacles of other molluscs and which are thought to be either chemo- or mechanosensory in function. Because *Hastula bacillus* lives in a wave-disturbed habitat, Taylor & Miller (1990) suggested that the accessory proboscis structure was more likely to be chemosensory in function and used in finding the preferred prey of *Scolepis,* a spionid polycheate.

Although similar in basic anatomy to *Hastula cinerea, H. bacillus* shows a number of important differences. The presence of the odontophore and accessory salivary glands are plesiomorphic characters. The radular teeth are much simpler than the hollow, barbed, hypodermic teeth of *H. cinerea.* Additionally, the branched accessory proboscis structure is a unique feature, but almost certainly homologous with the club-shaped structure in *Terebra imitatrix* and *T. affinis.* Prior to its discovery in *H. bacillus* and *T. imitatrix,* the accessory proboscis structure was considered an advanced character, found only in species with Miller's type III proboscis.

Terebra subulata

Along with *T. babylonia* and *T. guttata,* this species has a long multiwhorled shell of more than 18 whorls. These species have an anatomy typical of Miller's type IIb. *Terebra subulata* has a labial tube introvert; a long buccal tube; a septum dividing the rhynchodeal cavity (Fig. 13); a short radular sac; a radular caecum; long, thin, hypodermic radular teeth, with small barbs and a constricted neck near the base of the tooth (Fig. 12f); a pair of salivary glands; a pair of accessory salivary glands (Fig. 6); and a large venom gland and muscular bulb.

Terebra maculata (see Miller, 1970)

This species possesses Miller's type Ib foregut. It has a very long labial tube introvert which is coiled within the rhynchodeal cavity (Fig. 13); a short buccal tube; a pair of salivary glands; no radula and no venom apparatus.

Terebra gouldi Deshayes, 1857 (see Miller, 1975)

This species which represents Miller's type Ia foregut has a medium length labial tube introvert; a very short buccal tube; a pair of salivary glands, with no radula or venom apparatus.

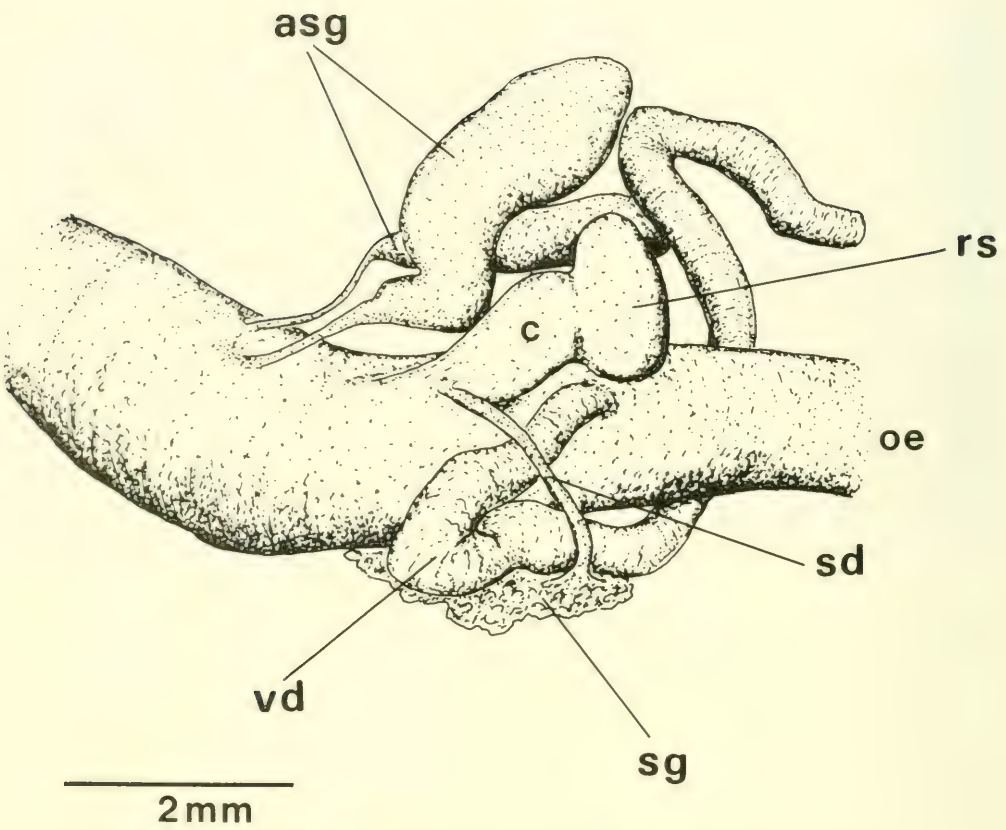


FIG. 6. Main organs of the buccal mass of *Terebra subulata*. asg, accessory salivary glands; c, radular caecum; oe, oesophagus; rs, radular sac; sd, salivary duct; sg, salivary gland; vd, venom duct.

Terebra affinis (see Miller, 1970)

This species represents Miller's Type III foregut. It possesses a long labial tube introvert; no buccal tube; no salivary glands; no radula or venom apparatus. Arising from the left wall of the rhynchodeum is the accessory proboscis structure (Fig. 13), an extensible muscular stalk, with a mace-like, papillate head.

Duplicaria spectabilis and *D. duplicaria*

Both of these species lack eyes and cephalic tentacles. They possess a long labial tube introvert, but the buccal tube is extremely short (Figs. 7, 8). The buccal cavity is large, and opening into it is a small radular sac, with an odontophore with a radular ribbon consisting of two rows of solid, sickle-shaped radular teeth (Fig. 9). Salivary ducts from a pair of salivary glands open either side of where the radular sac joins the buccal cavity. There is no venom gland or muscular bulb.

Terebra nassoides

This is a small species collected from intertidal sand patches in Oman. The anatomy is basically similar to that of the above *Duplicaria* species. It has no eyes or cephalic tentacles. The labial tube is hood-shaped, the dorsal part being much larger than the ventral. The buccal tube is very short, and there is a small odontophore (Fig. 11) and short radular ribbon with two rows of curved, solid teeth (Fig. 10). There are no salivary glands and no venom apparatus.

Terebra tristis

The anatomy of this New Zealand-southern Australian species was described by Rudman (1969) as *Pervicacia tristis*. There are no eyes

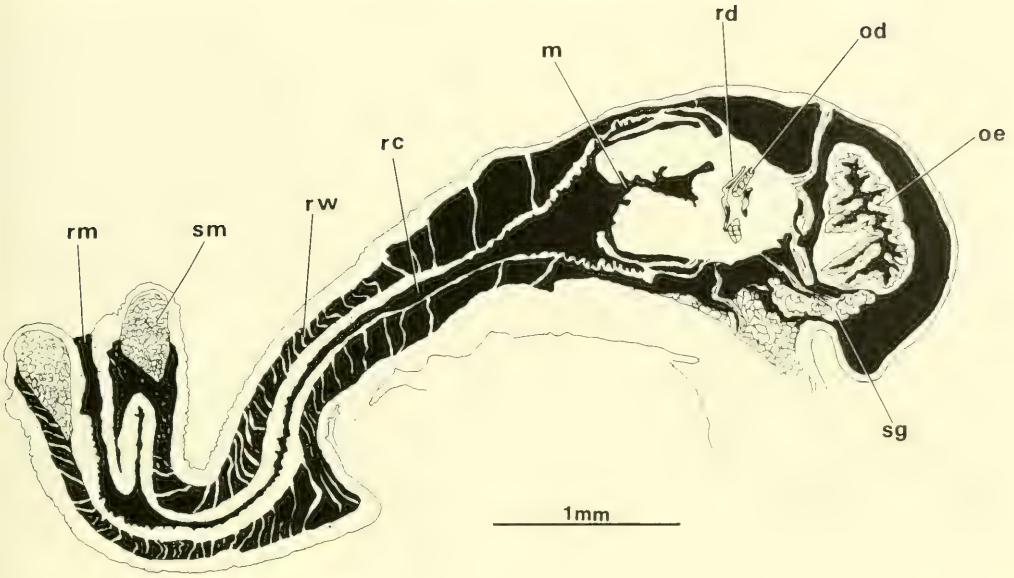


FIG. 7. Longitudinal section through the extended labial tube and buccal mass of *Duplicaria spectabilis*. m, mouth; od, odontophore; oe, oesophagus; rc, rhynchodeal cavity; rd, radula; rm, mouth of rhynchodeum; rw, rhynchodeal wall; sm, sphincter muscle; sg, salivary gland.

or tentacles. The dorsal part of the labial tube extends anteriorly over the ventral surface, forming a hood. Rudman stated that the labial tube appeared incapable of withdrawal, but sections of preserved specimens I have studied show that both dorsal and ventral parts of the labial tube can be folded back into the rhynchodeum. The buccal tube is very short. There is a radula ribbon and odontophore with two rows of solid, slightly curved radular teeth. There is a pair of fused salivary glands, and two salivary ducts enter the buccal cavity. There is no venom apparatus.

REVIEW OF FOREGUT CHARACTERS

In this section I review the distribution and variation in the main organs of the foregut amongst the terebrid species for which the anatomy is known.

Labial tube

The possession of an extensible labial tube (introvert formed by the extension of the walls of the rhynchodeum) is perhaps characteristic of all species of the Terebridae. This character is not confined to the terebrids, but is found in some turrids (subfamily Daphnellinae) which have a polyembolic proboscis, such as *Philbertia linearis* (Sheridan et al., 1973) and *Cenodagruetes* (Smith, 1967).

There are some differences in the form of the labial tube which may be important. In *Terebra tristis* and *T. nassoides,* the dorsal part of the tube is much larger than the ventral and when extended appears hood-like (Rudman 1967, Taylor, unpub. observ.). The ventral part of the tube in *T. nassoides* probably does not retract.

Other variation mainly concerns the length of the tube. In those species having a long buccal tube and hypodermic radula, the labial tube is relatively short. However, in those forms with a short buccal tube and also lacking a radula, the labial tube is much longer, and in *Terebra maculata* and similar species the labial tube, when withdrawn, is folded on itself several times within the rhynchodeal cavity (Miller, 1970).

In his account of feeding in *Terebra gouldi,* Miller (1975) has shown how this species, which lacks a radula and venom apparatus, and has only a very short buccal tube, uses the extensible labial tube to capture the enteropneust *Ptychodera* and transfer the prey to the short buccal tube. Similarly, the long labial tube of *T. maculata* probes in the sand for the capitellid polychaete *Dasybranchus*.

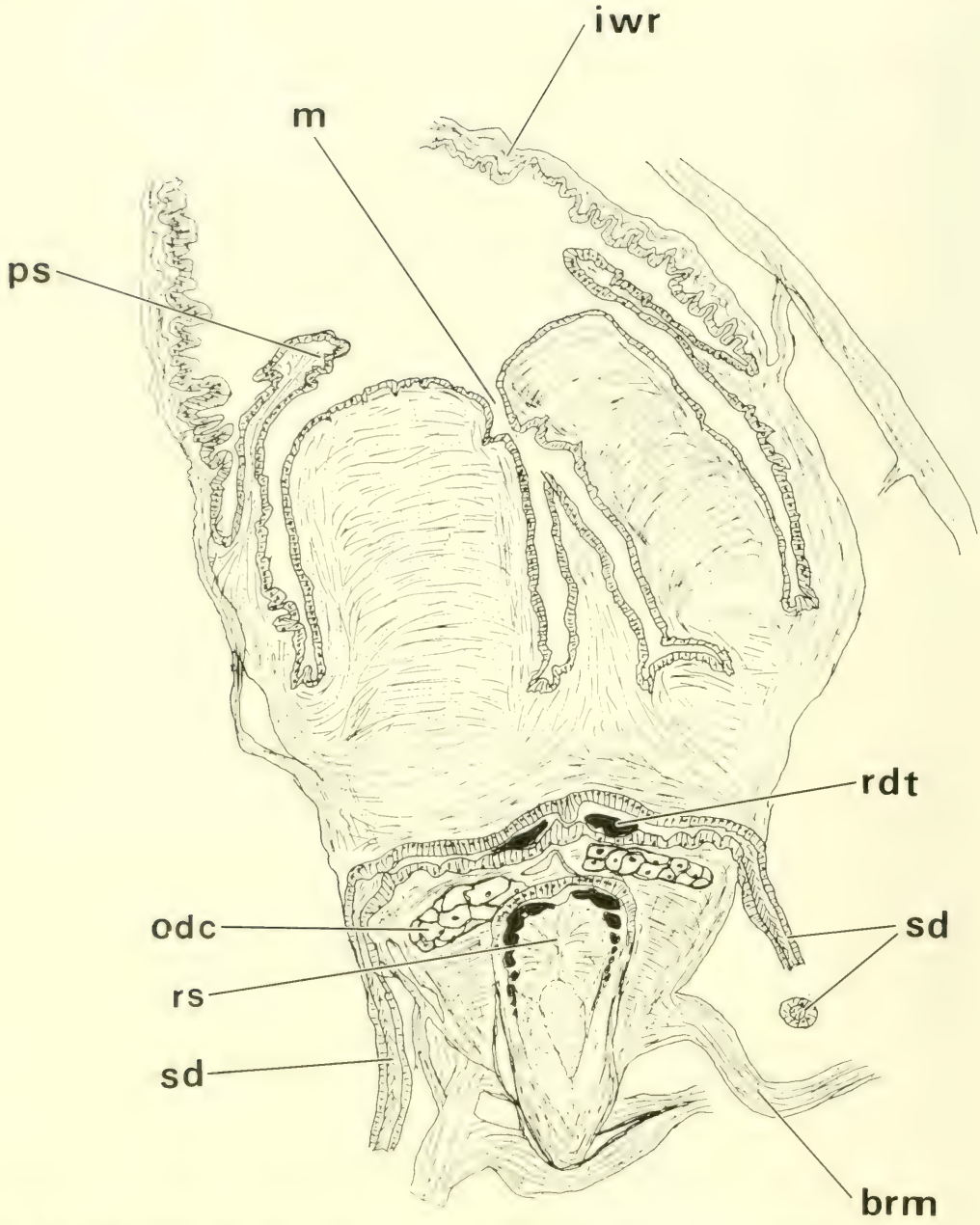
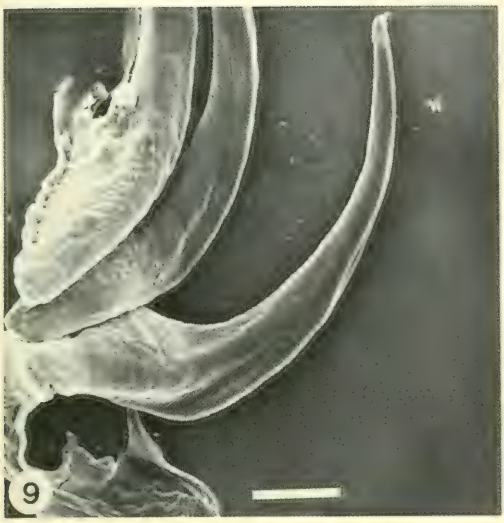


FIG. 8. Section through the buccal mass of *Duplicaria spectabilis* showing the short, muscular, buccal tube, the odontophore and radular sac. brm, buccal retractor muscle; bt, buccal tube; iwr, inner wall of rhynchodeum; m, mouth; od odontophore; odc odontophoral cartilage; ps, proboscis sheath; rdt, radular tooth; rs, radular sac; sd, salivary duct.

Buccal Tube

The buccal tube or true proboscis is long only in those species with hollow, hypodermic radula teeth. During the feeding process single teeth are transferred from the radular caecum to the tip of the buccal tube, where they are gripped by the sphincter muscle (e.g. *Has-*



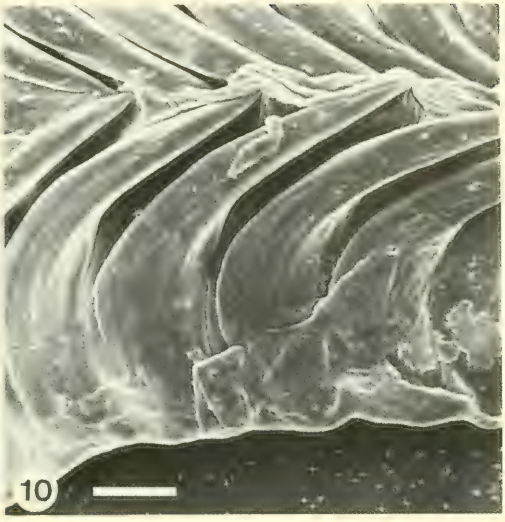


FIG. 9. Disaggregated radular teeth of *Duplicaria spectabilis*. Scale bar 20 μm.
FIG. 10. Side view of part of row of radular teeth of *Terebra nassoides*. Scale bar 20 μm.

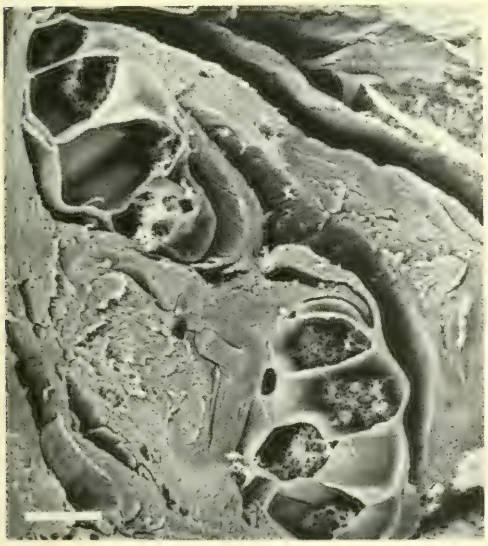


FIG. 11. Section through the odontophore of *Terebra nassoides* showing the pair of odontophoral cartilages. SEM of critical point dried material. Scale bar 30 μm.

tula inconstans; Miller, 1979). In these species, the proboscis wall is muscular and is capable of being extended well beyond the rhynchodeal cavity. Although they did not observe any living animals, Auffenberg & Lee (1988) thought that the short, but muscular, buccal tube of *Terebra imitatrix* could not be extended out of the rhynchodeal cavity.

Those terebrid species with solid radula teeth fixed on a ribbon have only a very short buccal tube (Fig. 13). This also applies to those species that have completely lost the radular apparatus.

Accessory Proboscis Structure

Miller (1970) described in *Terebra affinis* a retractile, club-shaped structure, which he called the accessory feeding organ. (Taylor & Miller [1990] prefer the functionally neutral term of accessory proboscis structure.) This consists of a muscular stalk with a distal papillate head that is attached at the base to the posterior left side of the wall of the rhynchodeal cavity. This structure occurs in species otherwise lacking a buccal tube, radula, salivary glands and venom apparatus. Miller thought, but without direct observations, that the organ was involved in prey capture.

The possession of the accessory proboscis structure is a major character defining Miller's Type III foregut. Miller (1970) mentioned, but did not illustrate, a number of other terebrids as having an **aps**.

Recently, an accessory proboscis structure was described from two other terebrid species, *Hastula bacillus* (by Taylor & Miller,

1990) and *Terebra imitatrix* (by Auffenberg & Lee, 1988). These species otherwise possess an extensible buccal tube, hypodermic radular teeth, salivary glands and venom apparatus. The anatomy is similar to other *Hastula* species and the Type IIa foregut of Miller (1970, 1971). *Hastula bacillus* has a long, branching **aps**, but in *T. imitatrix* it is club shaped. Both muscular structures are attached to the left side of the rhynchodeal cavity and are probably homologous with the structure in *Terebra affinis*.

As shown in Figures 4 and 5, the **aps** in *Hastula bacillus* possesses numerous ciliary tufts which T.E.M. analysis suggests are sensory, probably chemosensory, structures. Because *H. bacillus* and *T. imitatrix* both have a long functional buccal tube (true proboscis) it seems more likely that the **aps** is a sensory device, rather than part of the food-gathering apparatus. However, the fine structure of the **aps** in *T. affinis* and *T. imitatrix* has not been investigated. Nevertheless, it is now clear that the possession of an **aps** is not an autapomorphy of terebrids having the Type III foregut, but it can occur in terebrids, which compared with the outgroups in the Turrridae (Miller, 1989), are the least derived for the family.

Radula

There are basically two main types of radula found in the Terebridae: (1) radulas of solid, sickle or dagger-shaped teeth; (2) radulas of hollow, harpoon-like hypodermic teeth. Additionally, there are many terebrid species that have no radular apparatus at all.

Relatively few radulae of the solid-toothed variety have been described. Figures 9 and 10 illustrate the radula in two species, which are basically similar in morphology. The radula consists of two rows of marginal teeth attached to the short radular ribbon. In all species there is an odontophore with two odontophoral cartilages (Fig. 11). In *Terebra nassoides* and *T. tristis* the teeth are solid, broader at the base and curved; in *Duplicaria spectabilis* and *D. duplicaria* they are sickle shaped. Additionally, teeth like those in *T. tristis* are found in *Duplicaria kieneri* and *D. fictilis* from South Australia (radula mounts in BM(NH)). Troschel (1866) illustrates an unusual radula for *Myurella lamarckii* Kiener (= *Duplicaria lamarckii,* considered by Bratcher & Cernohorsky, 1987, as a form of *D. duplicata*). This has long sickle-shaped teeth as in *D. duplicata,* but with spur-like projections near the distal end of each tooth. I examined the radula of *D. lamarcki* from Kenya but found the teeth to be simple, with no sign of the spur-like cusps.

The solid, sickle-shaped marginal teeth of these terebrids resemble those found in some turrids, particularly from the subfamily Pseudomelatominae (e.g. *Tiariturris libya* (Dall, 1919), Shimek & Kohn, 1981, fig. 2; *Pseudomelatoma penicillata* (Carpenter, 1864), Kantor, 1988, fig. 1D-F). However, these turrids also have a large, unicuspid central tooth. The marginal teeth are erected into a basket structure as the radular passes over the bending plane. Shimek & Kohn (1981) thought that the central tooth functions as a slicing tooth and that the marginal teeth lacerate the prey, tearing off fragments and conveying them to the oesophagus.

Amongst those species having the hollow hypodermic teeth, there is some variety of form (Figs. 1, 12). Both the simplest and most complex forms are those of some *Hastula* species. In *Hastula bacillus* the teeth are rolled and hollow, but the anterior half consists of a knife-like blade. In *Hastula cinerea, H. penicillata* and *H. salleana* the teeth are robust with a harpoon-like, barbed tip, a large aperture near the tip and a broad base with a flared rim (Marcus & Marcus, 1960; Bandel, 1984). An additional feature of the teeth in these three species is the presence of "screw-thread"-like flanges separating the rolls of the tooth (Fig. 12). Bandel (1984) suggested that these flanges gave rigidity to the tooth by separating the rolls. Essentially similar teeth are seen in *T. taurinus* and *T. protexta* (Bandel, 1984, figs. 313, 314). The teeth of *Hastula hectica* with the perforated midsection are apparently unique. In *Terebra subulata, T. guttata, T. succinea,* and *T. anilis,* the radula teeth are long and thin, with pointed tips and small barbs (Mills, 1977a; Bandel, 1984; personal observations). Those of *Terebra babylonia* are similar but lack the barbed tips (Fig. 1). Additionally, all these latter species have a marked concavity near the base of the tooth produced by twisting of the tooth (Fig. 1b). Of the species with the hypodermic teeth, *Hastula bacillus* and *H. aciculina* are the only species so far found with an albeit small odontophore and odontophoral cartilages.

In *Hastula bacillus* and *H. aciculina,* the radular sac is relatively long and there is no radular caecum for the storage of detached

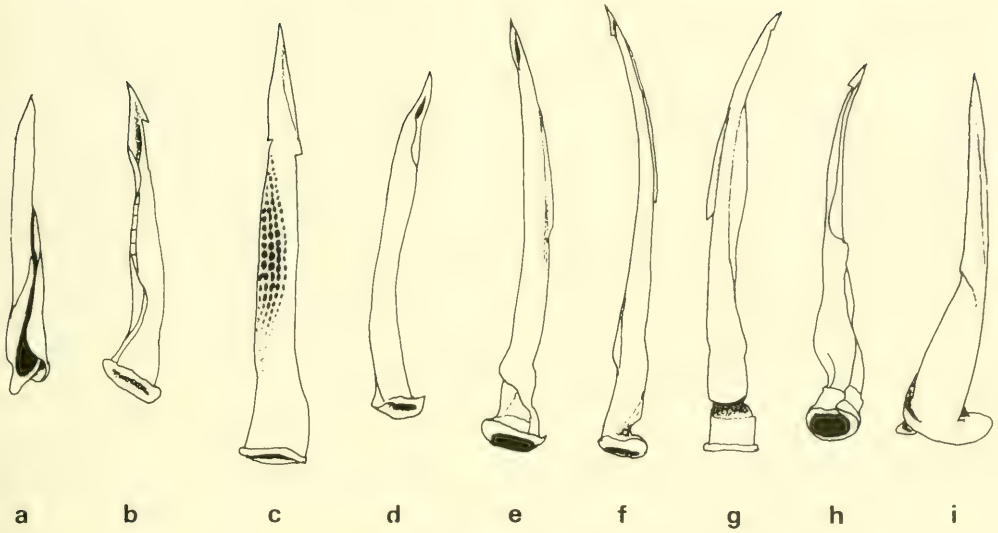


FIG. 12. Range of form found in the hypodermic-type radula teeth of Terebridae. Traced from original scanning electron micrographs or from references cited. a. *Hastula bacillus*, Thailand; b. *H. cinerea* Colombia (Bandel, 1984); c. *H. hectica* Kenya; d. *Terebra protexta* Colombia (Bandel, 1984); e. *T. babylonia* Guam; f. *T. subulata* Maldives; g. *T. guttata* Queensland (Mills, 1977a); h. *T. taurinus* Colombia (Bandel, 1984); i. *T. succinea* Queensland (Mills, 1977a). Not to scale.

radular teeth. In other species (e.g. *Hastula cinerea* and *H. inconstans*), the radular sac is shorter and there is a well-developed caecum. In *Terebra subulata* and *T. babylonia* the radular sac is very short, with a large caecum.

The hollow barbed radular teeth found in some terebrids are similar in form to those found in the Conidae and some turrids (subfamily Borsoninae) and which are considered to be the most derived type of radula to be found in the Conoidea. A great diversity of radular types is found in the Turridae, and Shimek & Kohn (1981) have developed an adaptive scenario to explain the evolution of the radula, from the primitive condition of five teeth in a row found in some Clavinae, to the advanced hypodermic marginal teeth of the Borsoninae. The main evolutionary elaborations concern the marginal teeth and include increasing size and complexity, with concomitant loss of the central and lateral teeth.

Although considerable variation is seen in the radula amongst the various subfamilies of Turridae (Powell, 1966; McLean, 1971; Shimek & Kohn, 1981), variation in both the Conidae and Terebridae is relatively small and concerns details of the form of the hypodermic teeth. Indeed, variation in the hypodermic teeth in the Terebridae is probably no greater than found in one subfamily of Turridae, the Oenopotinae (Bogdanov, 1989). No convincing intermediate condition between the solid teeth and the hypodermic teeth of terebrids has been seen. The teeth in *Hastula bacillus,* with the hollow, rolled proximal end and the solid, blade-like distal end, might be an intermediate condition or a variant of the hypodermic tooth.

Accessory salivary glands

Accessory salivary glands are an apomorphic character of the Neogastropoda and are known in some turrids and some *Conus* species (Ponder, 1973; Marsh, 1971; Schultz, 1983). Recently, a single accessory gland was found in *Hastula bacillus* (Taylor & Miller, 1990), but not in several other *Hastula* species examined. Furthermore, dissection and thin sections have also revealed a pair of accessory glands in *Terebra subulata* (Fig. 6), but only single glands in *Terebra babylonia* and *T. funiculata.*

Salivary glands

A pair of salivary glands is present in most terebrids. The glands are usually partially

fused together and appear as two distinct lobes of one mass. Separate salivary ducts enter the buccal cavity at the base of the radula sac, where this is present. Rudman (1969) described an apparently unusual feature of *Pervicacia tristis* where the salivary ducts fuse, entering the buccal cavity as a single duct. But my observations of serial sections of this species show two ducts entering the buccal cavity.

Salivary glands and ducts are present in many terebrids where the radula, buccal tube and venom apparatus has been lost. They are however, absent in some of Miller's Type III species, such as *Terebra affinis*.

Venom apparatus

The venom apparatus of venom gland and muscular bulb is an autapomorphic character of the Conoidea (Taylor & Morris, 1988). In the Terebridae it is present only in those species with hollow, hypodermic radular teeth and a long buccal tube. There is some variation in the length of the venom gland and the size of the muscular bulb. For instance, the venom apparatus is particularly large in *Terebra subulata* (Mills, 1977b). By contrast, Auffenberg & Lee (1988 p. 155) consider that the muscular bulb in *Terebra imitatrix* ". . . is weak, seemingly vestigial. . . .". Mills (1977b) reported differences in the secretory epithelia of the venom gland between *Terebra* and *Conus*, but these need further investigation.

Rhynchodeal septum

Miller (1970, 1971) briefly mentioned a septum across the rhynchodeal cavity in some terebrids with his Type IIb proboscis. In *Terebra subulata*, this structure divides the rhynchodeal cavity into two compartments. It consists of an invagination of the inner wall of the rhynchodeum with a central aperture. When withdrawn, the buccal tube lies to the posterior and the labial tube to the anterior of the septum. When extended, the buccal tube passes through the central aperture of the septum. The function of the septum is unknown, but may be concerned with retaining prey that has been pulled into the rhynchodeum by the buccal tube.

GEOLOGICAL HISTORY

No adequate analysis has been made of the geological history of the Terebridae. Various authors (Cossmann, 1896, Wenz, 1938; Taylor et al., 1980) have considered, with varying degrees of confidence, the Cretaceous (Santonian) species *"Fusus" cingulatus* Sowerby, from Gosau, Austria, to be an early terebrid (as *Strioterebrum*). However, the species appears to have an elongate siphonal canal and is more likely to be a member of the Turridae. Otherwise, the earliest terebrids appear to be *Hastula* species from the Eocene of France and England (Cossmann, 1896). The Terebridae diversified extensively in the Miocene, with the appearance of many of the shell forms seen amongst Recent species (Davoli, 1977).

DIET OF TEREBRIDAE

Most available dietary information for the Terebridae is from the genus *Hastula*, and nearly all the species investigated seem to feed upon spionid polychaetes. Miller (1979) gives a detailed account of the Hawaiian species *Hastula inconstans*, which feeds exclusively upon *Dispio magna*. Also in Hawaii, *H. hectica* and *H. strigillata* feed upon *Nerinides* sp. and *H. penicillata* upon an unidentified spionid. Marcus & Marcus (1960) report *H. cinerea* as feeding upon *Nerinides agilis*, as does *H. salleana* (Stewart, in Miller, 1979)

In Thailand, *Hastula bacillus* feeds upon *Scolepis* sp. (Taylor & Miller, 1990). The only exception to the spionid diet of *Hastula* is *H. solida* from Guam, which feeds upon a cirratulid polychaete, probably *Cirratula* sp. (Taylor, unpub.).

Species with Miller's foregut type IIb also eat spionids. Miller (1970) reports *Terebra textilis* from Hawaii as eating *Prionospio malmgreni*, and from Guam Taylor (1987) reports *T. cingulifera* and *T. subulata* feeding upon *Laonice cirrata*.

There is little dietary data available for terebrids with solid radular teeth. Dissection of many *Duplicaria spectabilis* from Hong Kong revealed no recognisable food remains. The only information available is for *Terebra nassoides* from Salalah, Oman, where three individuals contained setae of a capitellid polychaete (Taylor, unpub.).

Of the terebrids with no radula and venom apparatus, Miller (1975) has described feeding in *Terebra gouldi*, which eats the enteropneust *Ptychodera flava*. This diet is shared by *Terebra dimidiata*, *T. crenulata*, and *T. areolata*.

Amongst those species with a very long labial tube and no radula or venom apparatus, *Terebra felina, T. maculata* and *T. chlorata* all eat the capitellid polychaete *Dasybranchus caducus* (Miller, 1970, 1975).

Finally, the diet of the species with an accessory proboscis structure but no radula and venom apparatus is unknown. The digestive tract of *T. affinis* frequently contains amorphous red-brown material, which Miller (1970) and Taylor (1986) thought might be the branchial tentacles of cirratulid polychaetes.

DISCUSSION & CONCLUSIONS

From the foregoing descriptions it is clear that a wide range of foregut anatomies are present in the Terebridae (summarized in Fig. 13). There is clearly more complexity to be accounted for than in Miller's (1970, 1971) classification. Furthermore, only a small proportion of the nearly 300 living species have been examined anatomically, and the discovery of further foregut types is to be expected.

In considering the evolutionary relationships of the Terebridae, the first question to be asked is whether the family comprises a monophyletic group. Evidence from foregut anatomy suggests that there are two major divisions within the family. Firstly, there is the group of species with solid radular teeth, and a well-developed radular ribbon. These species have a short buccal tube, lack a venom apparatus and have no cephalic tentacles or eyes. Secondly, there is the group comprising the species possessing radular teeth of the hypodermic type. These species also possess a venom apparatus and elongate buccal tube. Additionally, there are terebrids which lack a radula and venom apparatus and have a very short buccal tube. These species could be derived from one or other of the radulate groups.

It is suggested that the two groups of terebrids represent separate derivations from the Turridae. The group with solid teeth comprise some species classified in the genus *Duplicaria* by Bratcher & Cernohorsky (1987), as well as *Terebra nassoides, T. capensis* and *T. tristis,* and probably many others.

In their analysis of the toxoglossan radula, Shimek & Kohn (1981) considered that the most derived condition was the hypodermic type consisting of long, hollow, barbed marginal teeth with only a vestigial radular membrane. The hypodermic radulae of such terebrids as *Hastula cinerea, H. salleana* and *Terebra subulata* are similar to those found in the Conidae and Borsoniinae. However, *Hastula bacillus* and *H. aciculina* have a less derived condition, with simpler radular teeth with no barbs, a small odontophore and odontophoral cartilages and a more substantial radular membrane. In *H. bacillus* there is no caecum to the radular sac in which teeth can be stored. However, thin sections showed a radular tooth held at the proboscis tip. This is similar to the situation in some turrids, where detached, non-hypodermic, solid marginal teeth are held at the proboscis tip (Sysoev & Kantor, 1987). The knife-like distal portion of the tooth is more likely a stabbing structure, rather than a true hypodermic tooth. The presence of this less-derived radular apparatus in *H. bacillus* suggests that the hypodermic radulae of the Terebridae and Conidae are parallel but independent developments.

Compared to outgroups in the Turridae and Conidae (Miller, 1989), species of the genus *Hastula* are the least derived for the family. They all possess the basic intraembolic proboscis condition, with a long buccal tube, venom apparatus, with in many species a true hypodermic radula. A major variant is seen in *Hastula bacillus,* which possesses an elongate, branching accessory proboscis structure. This may be homologous with the club-shaped structure seen in *Terebra imitatrix,* which has a reduced buccal tube and a small venom apparatus.

Terebra subulata and similar species (*T. guttata, T. babylonia, T. funiculata*) have long, thin radular teeth, and shells with many (18+) whorls. This group of species can be simply derived from the *Hastula* condition.

Many terebrids, however, lack a radula, venom apparatus and buccal tube, and the foregut provides less useful evidence of relationships. The trend in terebrids for the loss of most of the foregut structures except for the labial tube introvert, results in the condition known as the polyembolic proboscis (Smith, 1967). The whole foregut is essentially simplified into a muscular tube that ingests prey. The extensible labial tube becomes the main organ of prey capture and ingestion, the true proboscis having disappeared. This trend is paralleled in the Turridae, where the polyembolic proboscis occurs in some species of the subfamily Daphnellinae (Smith, 1967; Kantor & Sysoev, 1989). The simplified foregut of the terebrids could have been derived via a number of evolutionary routes. Corrob-

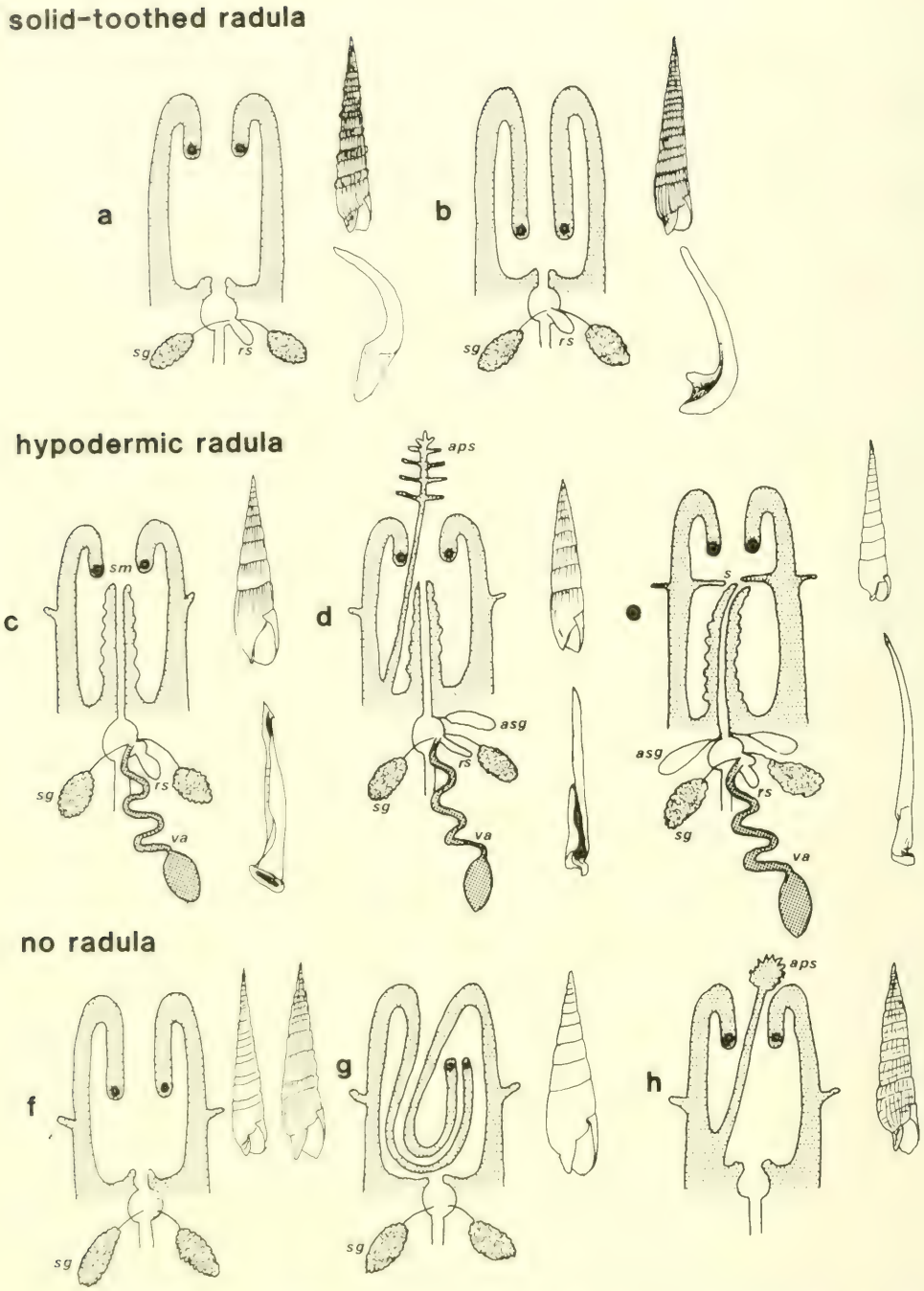


FIG. 13. Diagrammatic representation of the main types of foregut found in the Terebridae, with radular teeth. Key to abbreviations: aps, accessory proboscis structure; asg, accessory salivary gland; rs, radular sac; s, rhynchodeal septum; sg, salivary glands; sm, sphincter muscle at mouth of labial tube; va, venom apparatus. Key to species: a. *Duplicaria spectabilis*, b. *Duplicaria duplicata*, c. *Hastula cinerea*, d. *Hastula bacillus*, e. *Terebra subulata*, f. *Terebra gouldi* and *Terebra dimidiata*, g. *Terebra maculata*, h. *Terebra affinis*.

orative evidence from other anatomical characters is needed to establish the relationships of these terebrids. For example, *Terebra gouldi* has the simplified foregut structure, but it has the shell characters of the genus *Duplicaria* (placed there by Bratcher & Cernohorsky, 1988) and may conceivably have been derived from the solid-toothed group of terebrids. By contrast, *T. dimidiata* and *T. crenulata* similarly have the simple foregut, but shell characters more like (perhaps superficially) those in the *Terebra subulata* group of species.

The mace-like accessory proboscis structure described from *Terebra affinis* (Miller, 1970, 1971) occurs in a species that otherwise lacks a buccal tube, radula, venom apparatus or salivary glands. It was thought to be an autapomorphic character of Miller's type III proboscis. However, the discovery of probably homologous structures in the otherwise less-derived *Hastula bacillus* (Taylor & Miller, 1990) and *Terebra imitatrix* (Auffenberg & Lee, 1988), suggests that this structure could be more widespread amongst the Terebridae.

More species of Terebridae need to be examined using more characters before an adequate phylogenetic analysis can be made. However, the main conclusion of this paper is that Rudman (1969) was essentially correct in separating the Pervicaciidae as a separate family. What is now clear is that the family should accommodate many more "terebrids," perhaps all of the *Duplicaria* species and probably many others, such as *Terebra nassoides, T. capensis, T. kieneri,* and *T. fictilis.* The family Terebridae should accomodate all the species with hypodermic radular teeth and venom apparatus and derivatives from these. The great range of morphology found in the terebrid foregut coupled with the apparent incongruence between shell characters and anatomy will make detailed classification of the families difficult. It is clear that shell characters are a poor guide to relationships in the Terebridae.

A pressing problem concerns the anatomy, as yet unknown, of the south Australian species, *T. albida* Gray, 1834. This is the type species of the genus *Acus* Gray, 1847, on which the family Acusidae Gray, 1853, is based. If this species turns out to have solid radular teeth and no venom apparatus, then the name Acusidae will have priority over Pervicaciidae. Additionally, anatomical material is needed of *Pervicacia ustulata,* the type species of the genus *Pervicacia.*

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ONTOGENETIC CHANGE IN THE *CONUS* RADULA, ITS FORM, DISTRIBUTION AMONG THE RADULA TYPES, AND SIGNIFICANCE IN SYSTEMATICS AND ECOLOGY

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ABSTRACT

The radula teeth of some species of the carnivorous genus *Conus* undergo a morphological change during their ontogeny. This change is documented for four species in two feeding categories. The form of change differs in the different feeding types, but the initial juvenile tooth appears similar in all. The change from juvenile to adult tooth appears to occur quickly and presumably results from the initiation of the activity of the superior epithelial tissue. Not all species of *Conus* show an ontogenetic change in the radula tooth. For those species showing a change, however, there is a correlation of tooth morphology and diet that suggests a close coupling of the two. It is suggested that ontogenetic change in morphology will occur in those species in which there is a marked change in the diet between juveniles and the adult, but not in those in which the prey does not change.

Key words: *Conus,* radula, ontogeny, diet, evolution.

INTRODUCTION

The radula morphology of prosobranch gastropods is known to show a certain amount of morphological variability within a species (Bandel, 1974; Borkowski, 1975; Carriker, 1943; Cernohorsky, 1970; Houbrick, 1978; Howe, 1930; Merriman, 1967; Rosewater, 1970). Such variability has been most often reported for adult animals and has been occasionally correlated with sex (Arakawa, 1958, 1959; Maes, 1966; Robertson, 1971). Reports of the occurrence of morphological change in gastropod radular teeth during ontogeny have been less frequent. Reported ontogenetic changes in prosobranch and opisthobranch gastropods have included increases in number of teeth per row (Bertsch, 1976; Robertson, 1985) and alterations in the morphology of single teeth in a given row (Carriker, 1943; Fujioka, 1985; Hickman, 1980; Hollister, 1954; Page & Willan, 1988; Thompson & Brown, 1984). Despite these studies, until recently there do not appear to have been any studies that follow ontogenetic changes within a species from post-metamorphic juveniles to adults to ascertain when and how rapidly the changes occur, and to try to ascertain the reason for the changes.

Ontogenetic change in the radula of *Conus magus* was reported by Nybakken & Perron (1988), and a second suspected case in *Conus patricius* was reported by Nybakken (1988). Rolan (1986) has also reported a difference in radula tooth structure between juvenile and adults of *C. ermineus.*

Two of the three species for which ontogenetic change has been demonstrated in *Conus, C. magus,* and *C. ermineus,* are piscivores in which the juvenile is too small to consume fish. Hence it is probably not unexpected that the radula tooth morphology should change with change in diet as Nybakken & Perron (1988) have demonstrated for *C. magus.* However, the finding of a change in tooth morphology in a vermivore, *C. patricius,* suggests that ontogenetic change might be more widespread within the genus. This, coupled with the knowledge that the different radula types in *Conus* can be associated with certain diets (Lim, 1969; Nybakken, 1970), led me to embark on a study of the radula tooth morphology within a broad size range of *Conus* species representing as many of the different tooth types and feeding types as were available. The objects of this study were to see if I could uncover further instances of ontogenetic change, if these changes were correlated with a particular tooth type and diet or whether such changes were universal

throughout the genus, if the juvenile tooth was similar in all instances or different, and finally, to suggest or speculate as to the reasons for the observed changes.

In order to accomplish the above tasks, it was necessary to establish a somewhat more elaborate scheme of classification of tooth types than that originally established by Lim (1969) in order to accommodate all the morphological types of teeth known to occur in *Conus*.

METHODS AND MATERIALS

The *Conus* specimens used in this study came from a number of sources; *Conus magus* were furnished by Frank Perron and either collected by SCUBA in the field in Palau or raised in the laboratory from egg capsules; *C. pennaceus* were collected in Hawaii by Frank Perron. *C. patricius* specimens were obtained from the 1967 Pillsbury Expedition to the Gulf of Panama (Nybakken, 1971), and Los Angeles County Museum, the Academy of Natural Sciences of Philadelphia, and Alex Kerstitch; *Conus fergusoni* were obtained from the Los Angeles County Museum and Alex Kerstitch. Juvenile specimens of *C. ebraeus, C. miliaris,* and *C. coronatus* were furnished by Alan Kohn. Juvenile *C. pulcher* were furnished by Constance Boone. All other adult and juvenile specimens from the eastern Pacific were from the Pillsbury Expedition to the Gulf of Panama (Nybakken, 1971), or from the author's collection from the Gulf of California (Nybakken, 1979) and the Galapagos (Nybakken, 1978). Indo-Pacific and West African specimens were either in the author's collection or from Alan Kohn.

Each specimen was measured for total shell length with a vernier calipers. The shell was broken, the animal extracted, and the sex recorded. The radula sac was dissected out, transferred to a depression slide, and the radula teeth freed by treatment with a solution of bleach. Freed teeth were washed in two rinses of water and mounted directly from water into a polyvinyl-alcohol lactophenol medium on standard glass slides. Radulae were examined under a compound microscope equipped either with a differential interference contrast system after Normarski or Hoffman Modulation Contrast optics. Drawings of individual teeth were made using a drawing tube.

For specimens smaller than 2 mm in shell length, a different technique was employed. They were first measured using an eyepiece micrometer in a dissecting microscope. The shell was then broken away using a fine pair of forceps and the animal extracted entire. The whole animal was then transferred to the first depression on a spot plate and rinsed with water; then transferred to the next depression with acid fuchsin and left for 10–15 minutes to stain the radula. Next the animal was moved through four successive rinses of water, which removed much of the stain except from the radula. The animal was then soaked in tissue solubilizer (Beckman BTS-450 0.5N Quaternary Ammonium Hydroxide in Toluene) and heated on a slide warming tray at 40–65°C for 2–4 hours. The animal was then transferred through Toluene into 70% ethanol where the radula was usually visible as a series of red dots. The radula sac was excised and mounted in PVA-K on a slide for observation.

Radula teeth used for scanning electron microscopy were removed from water, air dried, and placed on double stick tape on standard stubs. They were coated with gold in a Polaron sputter-coater unit and examined with an ISI SX30 SEM. The SEM mounts were used primarily to verify the three-dimensional structure of the *Conus* radula.

A total of 89 species of *Conus* were examined for the establishment of radula types in the genus. They represented species from all oceans. (A complete list of species and their radula type is found in Appendix 1.)

In order to examine the ontogeny of the radula, I was more limited, both by time and by the availability of specimens. I used only specimens that I was able to identify or that were verified for me. Small specimens of any *Conus* species are not easy to come by; hence, this study is not as complete as I would have liked it to be. I was able to investigate a complete size series of specimens from post-metamorphic juveniles to adult only for *C. magus.* The only other species for which post-metamorphic juveniles and adults were available was *C. pennaceus,* but here the series was not as complete. Other species for which size series were available were: *C. arcuatus* (16.3–41.9 mm), *C. chaldeus* (7.4–25.1 mm), *C. coronatus* (8.2–20.1 mm), *C. ebraeus* (7.5–32.5 mm), *C. fergusoni* (26.1–51.9 mm), *C. lucidus* (14.4–38.5 mm), *C. patricius* (27.1–83.5 mm), *C. pulcher* (11.6–80.7 mm), *C. tornatus* (8.2–20.1 mm), and *C. virgatus* (14.9–56.5 mm). Fortunately, these species encompass all of the common

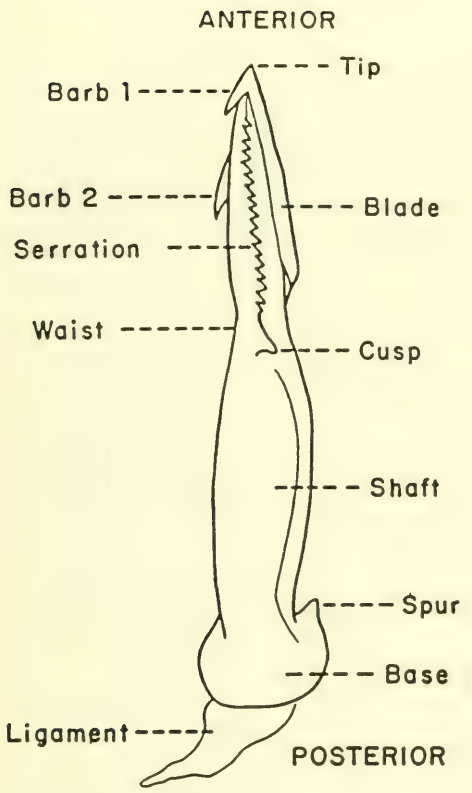

FIG. 1: A diagrammatic *Conus* radula tooth illustrating the various terms used in describing the morphology.

radula types except Type 3, so it was possible to obtain a good overview of the potential changes in the different radula types.

RESULTS

Morphological Classification of the *Conus* Radula

The individual *Conus* radula tooth is asymmetrical, three dimensional, and may be morphologically complex (Nybakken, 1970b). A system of terminology for the various parts of the tooth was provided by Nybakken (1970b) and Kohn et al. (1972) and is the one followed here. These terms are illustrated in Figure 1.

Lim (1967) first recognized that there were three morphologically different groups of radulae in *Conus.* These three groups were correlated with the three different feeding types within the genus, piscivores, molluscivores, and vermivores. Of these three, the vermivores are the most numerous and also the most diverse in terms of tooth morphology. Whereas the structure of the teeth of both the molluscivores and piscivores is unique and consistent, that of the vermivores is not. Vermivores include a number of different morphological types, only one of which, that possessed by those species which prey on amphinomid worms, has been directly correlated with a specific diet (Nybakken, 1970a).

In order to undertake this study, it was necessary to attempt to group the various different radula morphologies into a few more manageable groups. Because this had already been done for the molluscivores and piscivores by Lim (1969), that left only the vermivores. Personal observation of the radulas of 89 species of *Conus* from all feeding types and oceans, coupled with the analysis of another 21 species that have been illustrated in the literature (Bergh, 1895; Piele, 1939; Warmke, 1960), plus an unpublished analysis of 179 species by Tucker (personal communication), of which 113 were different from those I studied, suggested that the vermivores could be grouped into a relatively few morphological types, leaving only a few that did not fit and that I have chosen to call "unique" types. Those with which I am familiar are illustrated in Figure 2 and described here.

Group 1 radulae are the most common among all *Conus* species and were found in 34 of the 89 species examined (Fig. 2a). The individual tooth has the anterior and posterior parts (demarcation by the waist) approximately equal. The anterior half is terminated by a single barb and has opposite the barb, a blade that extends posteriorly more than halfway to the waist. It may or may not be terminated by a barb. A serration is present that extends posteriorly to the level of the end of the blade, or to the level of the waist. The serration usually terminates in a prominent cusp. Scanning electron microscopy shows that the serration and terminal cusp are in fact internal (Fig. 3). The posterior half of the tooth is usually slightly greater in diameter than the anterior and has a slightly enlarged, usually rounded base bearing a prominent but small spur. For the 17 species for which the food is known, all are vermivores (Table 1).

Two additional tooth types are similar to those of Group 1. In fact, Tucker groups them together with Group 1. However, they are both morphologically distinct and readily dis-

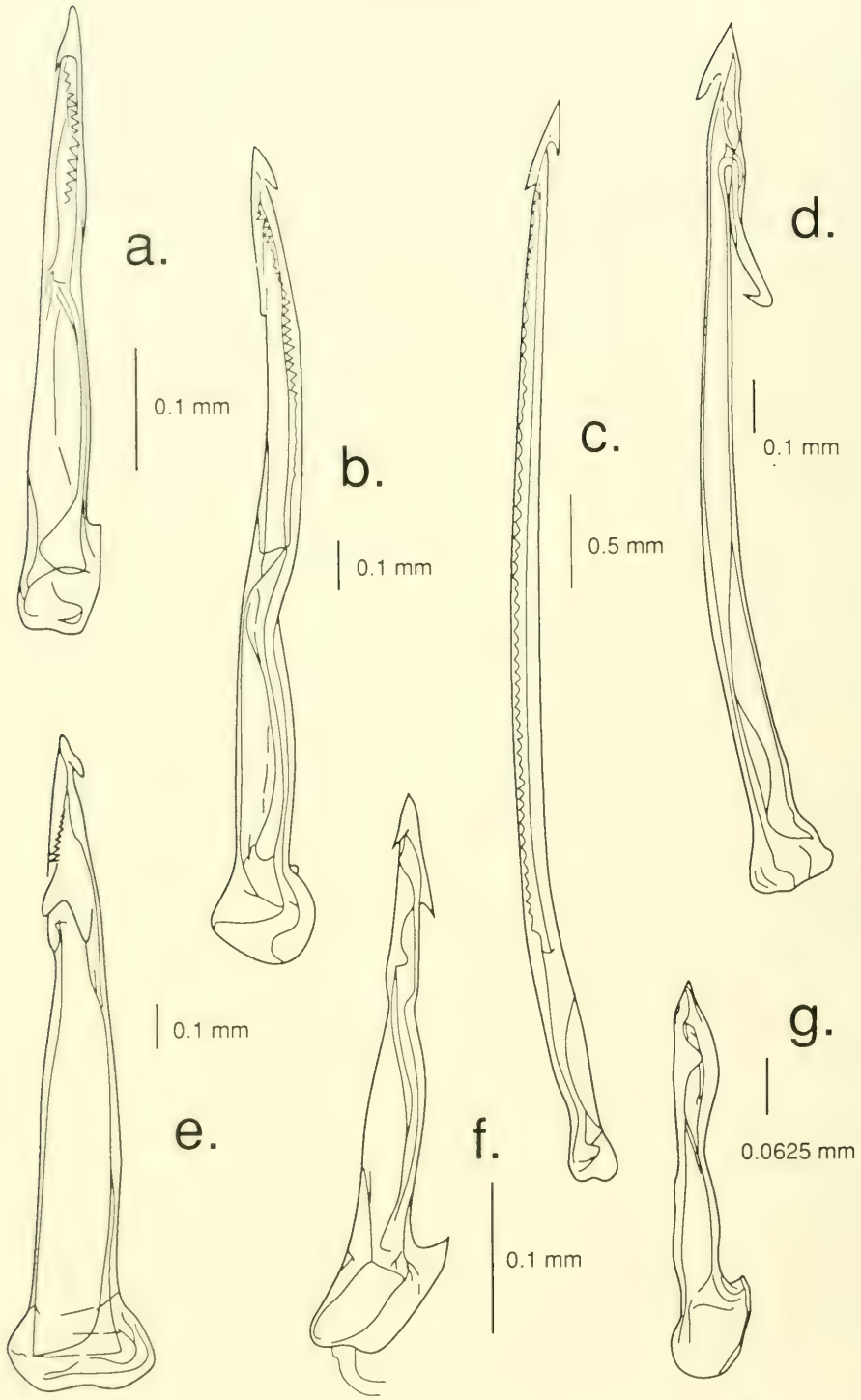

FIG. 2: The major morphological groups of *Conus* radulae. a. Type 1. b. Type 1a. c. Type 1b. d. Type 2. e. Type 3. f. Type 4. g. Radula of *C. ebraeus*.

FIG. 3. a. Scanning electron micrograph of the tooth of *C. virgatus* showing the internal position of the serration. b. Scanning electron micrograph of the waist of a tooth of *C. princeps* showing the internal position of the cusp.

TABLE 1. *Conus* Radula Types and Reported Food

Conus Species	Food	Reference
Radula Type 1		
C. chaldeus	*Platynereis dumerelii*	Kohn, 1959
	Palola siciliensis	
C. miles	*Palola siciliensis*	Kohn, 1959; Kohn & Nybakken, 1975
	Lysidice collaris	
	Eunice antennata	
C. abbreviatus	*Perinereis helleri*	Kohn, 1959
	Platynereis dumereli	
	Lysidice collaris	
	Eunice antennata	
	Eunice cariboea	
	Eunice filamentosa	
	Marphysa sanguinea	
	Lumbrinereis sarsi	
	Arabella iricolor	
C. sponsalis	*Nereis jacksoni*	Kohn, 1959
	Perenereis helleri	
	Platynereis dumereli	
	Lysidice collaris	
	Eunice cariboea	
	Lumbrinereis sarsi	
C. rattus	*Perenereis helleri*	Kohn, 1959
	Eunice antennata	
	Eunice afra	
C. tiaratus	*Nereis jacksoni*	Nybakken, 1978
	Neanthes spp.	
	Eunice afra	
	Eunice biannulata	
	Lumbrinereis sp.	
C. litteratus	*Dasybranchus caducus*	Kohn, 1980
C. leopardus	*Ptychodera flava*	Kohn, 1980
C. taeniatus	*Ceratonereis*	Taylor & Reid, 1984
	Platynereis	
	Eunicidae	
C. arenatus	*Perinereis*	Kohn & Nybakken, 1975
	Ceratonereis	
	Palola	
C. ceylanensis	*Perenereis*	Kohn & Nybakken, 1975
	Nereis	
	Ceratonereis	
	Lysidice	
C. scabriusculus	*Palola siciliensis*	Kohn & Nybakken, 1975
C. capitaneus	*Nereis*	Kohn & Nybakken, 1975
	Eunice afra	
C. vexillum	*Eunice australis*	Kohn & Nybakken, 1975
C. balteatus	*Eunice afra*	Kohn & Nybakken, 1975
C. miliaris	*Onuphis* sp.	Kohn, 1968a
	Perinereis spp.	
	Lysidice collaris	
	Eunice afra	
	Eunice rubra	
	Palola siciliensis	
	Eunice cariboea	
C. coronatus	*Palola siciliensis*	Marsh, 1971
	Lysidice collaris	
	Arabella iricolor	
	Glycera tessellata	Kohn & Nybakken, 1975
C. nux	Nereidae	Nybakken, 1979
	Eunicidae	Nybakken, 1971
	Syllidae	

TABLE 1. (*Continued*)

Conus Species	Food	Reference
	Polynoidae	
C. gladiator	*Eunice afra*	Nybakken, 1979
	Eunice filamentosa	
	Platynereis polyscalma	
C. regularis	*Nothria elegans*	Nybakken, 1979
C. pulicarius	*Dasybranchus caducus*	Kohn, 1959
	Nematonereis unicornis	Taylor, 1986
C. vexillum	*Eunice antennata*	Kohn, 1959
	Marphysa sanguinea	
Radula Type 1a		
C. princeps	*Eunice afra*	Nybakken, 1979
	Eunice filamentosa	
	Palola siciliensis	
C. flavidus	*Dasybranchus caducus*	Marsh, 1971
	Ampharetidae	Kohn, 1959
	Capitellidae	
	Maldanidae	
	Terebellidae	
	Eunicidae	
C. frigidus	*Dasybranchus caducus*	Kohn, 1968b
	Terebellidae	
C. virgo	*Loimia medusa*	Kohn & Nybakken, 1975
C. patricius	Aphroditidae	Nybakken, 1988
	Spionidae	
C. ventricosus	*Perinereis*	Taylor, 1987
	Palola	
	Capitella	
Radula Type 1b		
C. dalli	gastropods	Nybakken, 1968
C. pennaceus	*Cypraea, Dolabrifera*	Kohn & Nybakken, 1975
C. marmoreus	molluscs	Kohn, 1980
C. textile	*Conus*	Kohn, 1968
C. episcopus	gastropods	Kohn & Nybakken, 1975
Radula Type 2		
C. catus	fish	Kohn & Nybakken, 1975
C. striatus	fish	Kohn & Nybakken, 1975
C. purpurascens	fish	Nybakken, 1967
C. magus	fish	Nybakken & Perron, 1988
Radula Type 3		
C. brunneus	amphinomid worms	Nybakken, 1970; Nybakken, 1979
C. zonatus	*Eurythoe*	Kohn & Nybakken, 1975
C. imperialis	*Eurythoe*	Kohn, 1959
Radula Type 4		
C. lucidus	*Ampharete*	Nybakken, 1978
	Lygadamis	
	Sabellariidae	
	Sabellinae	
	Capitellidae	
	Nereidae	Nybakken, 1979
C. arcuatus	Onuphidae	
Radula Type—Unique		
C. ebraeus	Nereidae	Kohn & Nybakken, 1975
C. lividus	Terebellidae	Kohn, 1959
	Nereidae	Nybakken, 1979
	Cirratulidae	
	Ptychodera	
	Platynereis	
	Phyllodocidae	
	Maldanidae	

(*continued*)

TABLE 1. (*Continued*)

Conus Species	Food	Reference
C. diadema	Eunicidae *Eurythoe* Terebellidae gastropods	Nybakken, 1979
C. californicus	gastropods bivalves cephalopods polychaetes amphipods fish	Kohn, 1966
C. tornatus	Nephtyidae	Nybakken, 1979

cernable from Type 1; hence, I choose to give them separate status. The tooth type I have designated as Type 1a differs from Type 1 in that the anterior part of the tooth is elongated, the serration is proportionately longer, and the blade shorter than Type 1 (Fig. 2b). Usually the cusp is more prominent also. As with Type 1, the serration is internal for most of its length. For the five species for which food is known, all are vermivores, usually taking tube-dwelling polychaetes. I found this type in 14 species investigated.

The second related type, which I have designated Type 1b, is more different from Type 1 than is Type 1a (Fig. 2c). In this radula type, the anterior portion is extremely elongated, usually several times the length of the posterior region, and the serration runs the entire length of the anterior part. The serration may be external, as in *C. pennaceus* (Fig. 4a), or completely internal, as in *C. dalli* (Fig. 4b). There is no waist. In addition, the anterior tip has two unequal-sized barbs, the smaller of which is inflated laterally so as to appear as a spear blade (Fig. 4c). There is no blade and no spur. This tooth type is characteristic molluscivores (Table 1). I found this radula in 14 species studied.

The radula tooth type I have designated as Type 2 is unique to piscivorous *Conus* (Fig. 2d, Table 1). Each tooth is very large, consisting of a very elongated shaft with no evidence of a waist or a serration. The anterior tip of the tooth has an armature of two opposing barbs followed posteriorly by a very large third barb that protrudes outward. There is no spur. There appears to be a slight difference in the teeth of Indo-Pacific piscivores and those of the eastern Pacific and Atlantic. Those from the former have the tip of the large third barb recurved at the end, whereas those from the latter do not. I have found this tooth type in eight species.

Another highly distinctive tooth type is that designated as Type 3 (Fig. 2e). Teeth of this morphological construction are characteristic of cones feeding on amphinomid worms (Nybakken, 1970a; Table 1). Diagnostic of these teeth is the presence of four barbs near the shortened anterior end. One of these barbs juts out from the tooth to form a prominent angle with the shaft. This barb also bears a short serration. The most prominent barb is the one with the greatest length and terminates a large blade. All barbs are pointed and none are recurved or hooked. Posterior to the barbs is a slight waist. Posterior to the waist the shaft expands to its maximum diameter and ends in a massive base that bears a large spur. There is no cusp. Tucker includes this tooth with Type 1. I have found this tooth type in eight species.

The tooth type designated as Type 4 is characterized by a shortened anterior section that bears two or three barbs but no serration and no blade (Fig. 2f). The barb nearest the anterior tip is always pointed, but the remaining one or two may be pointed or blunt. In addition, these teeth usually show evidence of a peculiar anterior fold. The waist is usually prominent, and the posterior part of the shaft is usually longer and broader than the anterior half. The base is very large and bears a very large spur. There is no cusp. Tucker has divided this group into two different groups based upon barb number. *Conus* species

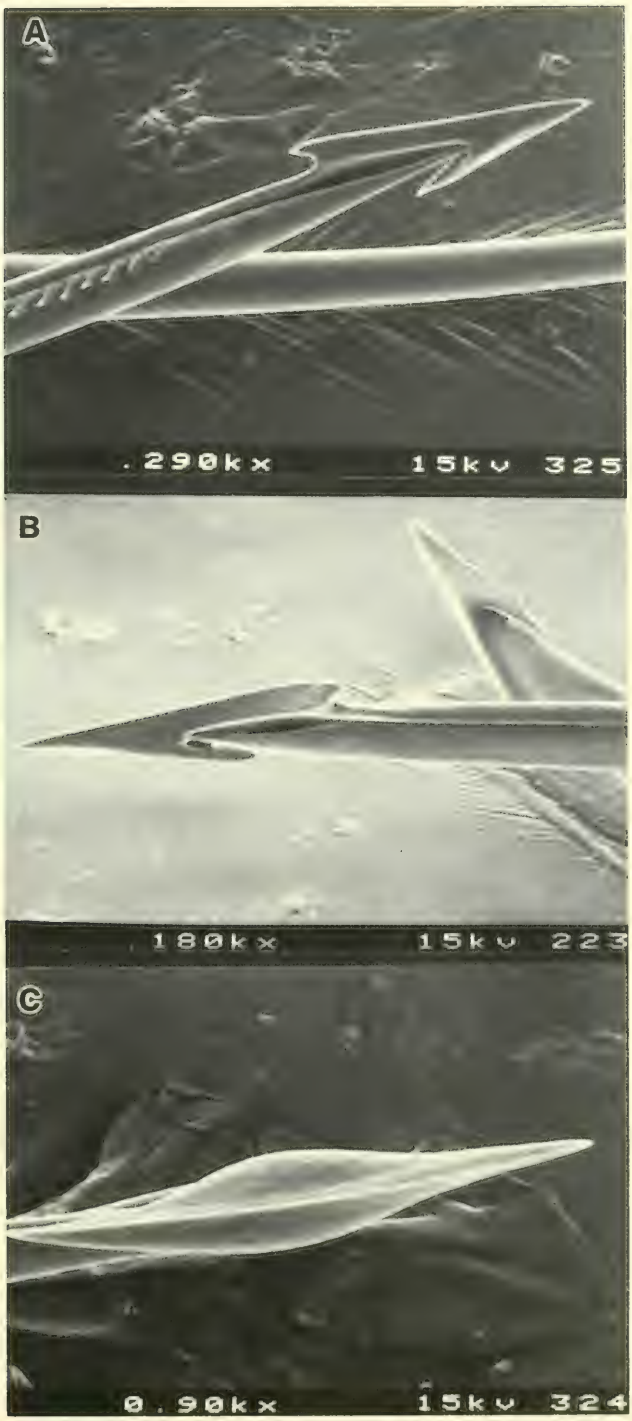

FIG. 4. a. Scanning electron micrograph of the anterior tip of the tooth of a *C. pennaceus* showing the external position of the serration. b. Scanning electron micrograph of the anterior tip of the tooth of a *C. dalli* showing the internal position of the serration. c. Scanning electron micrograph of the anterior tip of the tooth of a *C. pennaceus,* showing the inflated barb.

showing this radula type appear to be mainly deeper water dwellers on soft substrates. Food data for this tooth type are quite sparse, but they appear to feed on worms. I found this type in only five species, but this may be due to the lack of deeper water cones available for study.

There are also some teeth that I would designate as unique, apparently confined to one or two species. Those of which I am aware are shown in Figures 2g and 5. Of these, *C. californicus* has the most catholic diet, feeding upon molluscs, polychaetes, Crustacea and fish; *C. ebraeus* feeds on nereid polychaetes; *C. tornatus* on nephtyid polychaetes; and *C. lividus* and *C. diadema* both feed primarily on polychaetes (Table 1).

It is by no means certain that the above designations represent all the tooth types present in the living Conidae. However, given the probable number of species (350–380) and the total number of species examined here (110), it does not seem likely that any large radula group remains unrepresented.

Radula Classification and Correlation with Food in the Vermivorous *Conus*

Whereas the molluscivores and piscivores seem to each possess a single characteristic radula morphology, the same does not appear to be true for vermivores. Types 1, 1a, 3, 4, and at least two of the unique types (*C. lividus* and *C. ebraeus*) are all tooth types associated with vermivory (Table 1). With the exception of radula Type 3, which seems to be specific for polychaetes of the family Amphinomidae, the other vermivores cannot be correlated with a single worm family. The radula tooth type represented by *C. tornatus* may yet prove to be associated with a single polychaete family, because the only food remains found have been of the family Nephtyidae, a family otherwise not present in any other *Conus* for which food data are available (Nybakken, 1979).

Analysis of Table 1 suggests that most of *Conus* species with Type 1 radulae feed on errant polychaetes primarily of the families Nereidae and Eunicidae. Those with Type 1a radulas feed more often on polychaetes of the families Terebellidae and Capitellidae. However, because one species with this radula morphology, *C. princeps,* feeds on eunicids and nereids, this evidence is hardly conclusive.

Food data are very scarce for *Conus* species with radula Type 4. The data for *C. lucidus* indicated that cones with this tooth type are vermivores feeding on several families of sedentary polychaetes (Table 1).

Conus lividus and *C. diadema* share a radula tooth morphology that so far has not been found in any other *Conus* species. It is most like Type 1b but lacks a serration. For vermivores, these two species consume the widest variety of food taxa, six families of polychaetes, both errant and sedentary, as well as enteropneusts and other gastropods.

The most catholic diet of any *Conus* is that of *C. californicus,* which is known to consume other gastropods, bivalves, fish, worms, and Crustacea. This species also has a unique radula tooth.

Ontogenetic Change

In order to attempt to document whether or not an ontogenetic change occurred within each of the major radula types, it was necessary to dissect as broad a size range of individuals in each category as possible. Unfortunately, very small cones are not abundant in collections and immediate post-metamorphic specimens are even more rare. As a result of these difficulties, I was able to obtain post-metamorphic individuals of only radula Types 1b and 2. Good size ranges were available for some species of radula Types 1 and 1a, and that of *C. ebraeus,* but there were no small specimens of Type 3.

The most conclusive data documenting a profound ontogenetic change in the radula are found in those *Conus* species that consume fish (Type 2 tooth). This change was documented by Nybakken & Peron (1988) for *Conus magus* and Rolan (1986) for *C. ermineus.* Both showed that the juvenile radula differed from that of the adult in lacking all three barbs, in size, and in presence of a spur.

Since that time, a set of post-metamorphic specimens of *C. magus* has become available, and dissection of these animals, all below 2.0 mm in shell length, has revealed the presence of even more changes. The immediate post-metamorphic radula tooth is less than 0.08 mm in length (in an animal of 1.7 mm shell length), has no barbs or blades, and is only slightly folded such that the central lumen appears to be at least partially open for the entire length. The base is large but lacks the spur found in the later juvenile tooth (Fig. 6).

Analysis of a size series of *Conus penna-*

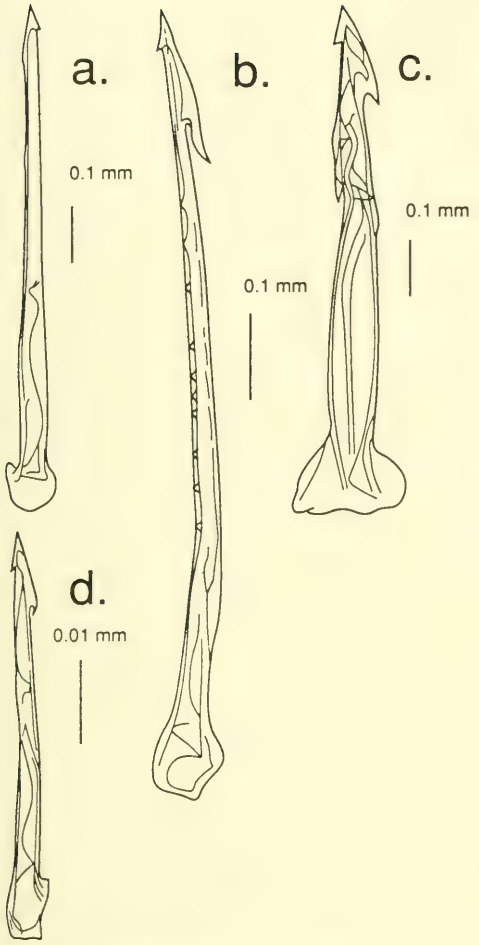

FIG. 5. Unique radula types. a. Radula of *C. lividus* and *C. diadema*. b. Radula of *C. ximenes* and *C. mahogani*. c. Radula of *C. californicus*. d. Radula of *C. tornatus*.

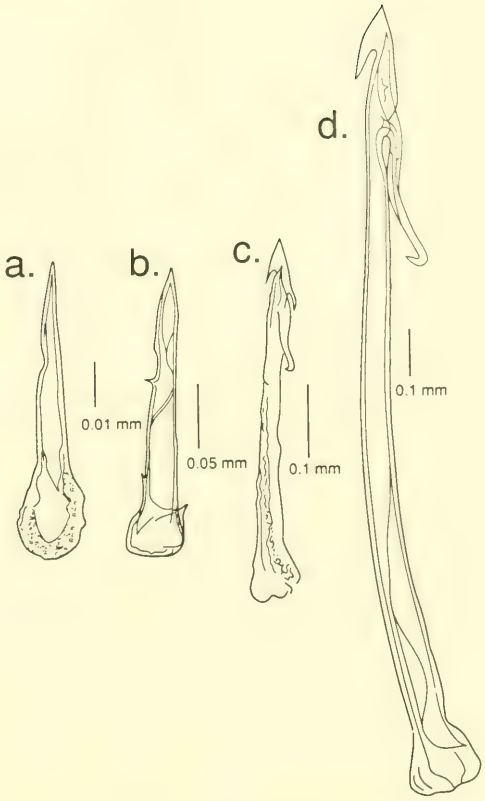

FIG. 6. Ontogeny of the radula tooth in *C. magus*. a. Radula tooth of a post-metamorphic juvenile. b. Radula tooth of a juvenile. c. Transitional radula tooth. d. Radula tooth of an adult.

ceus, a molluscivore, from 9.6 mm to 33.4 mm revealed no change in the radula morphology (Fig. 7a,b). However, a series of post-metamorphic *Conus omaria* was available from Perron. These animals had shell lengths of about 1.4 mm. Dissection of these animals revealed a radula tooth almost identical to that found in the post-metamorphic *C. magus* (Fig. 7c). This tooth was less than 0.06 mm in length, had no barbs, blades, or serrations, and the central lumen was open throughout its length.

Although radula Type 1 is by far the most common, very small specimens of species exhibiting this type were difficult to come by. I examined a series of teeth from *C. virgatus* ranging in size from 56.5 mm to 14.9 mm but found no change. I examined a series of *C. chaldeus* ranging in size from 25.1 mm down to 7.4 mm. In this series, the smallest individual had a tooth that differed from the adult in lacking a serration and a blade (Fig. 8b). The tooth was folded but did have a very large anterior lumen.

A series of specimens of *C. ebraeus* from 33.2 mm down to 7.5 mm in shell length was dissected. In this case, the smallest individual possessed a radula clearly of the juvenile type without serration, barb, or blade (Fig. 8c, d) and resembling the juvenile tooth of Types 1 and 1a.

For radula tooth Type 1a, the presence of a juvenile tooth differing from the adult has been described for *C. patricius* by Nybakken (1988) (Fig. 9a, b). In this study two additional

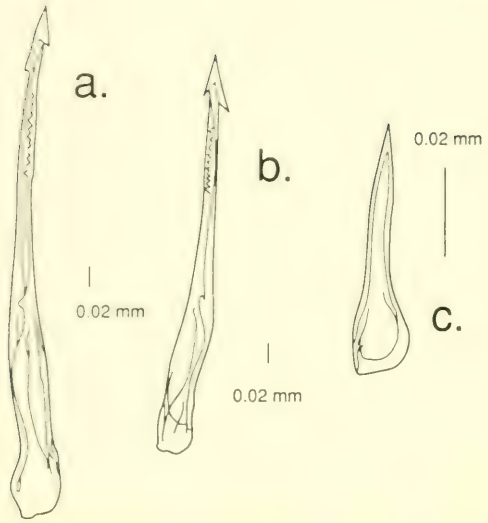

FIG. 7. Ontogeny of the radula tooth in *C. pennaceus*. a. Radula tooth of an adult (shell length 33.4 mm). b. Radula tooth of an animal of shell length 9.6 mm. c. Radula tooth of a post-metamorphic *C. omaria* of shell length 1.4 mm.

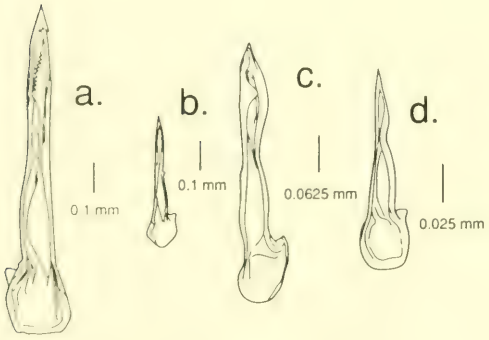

FIG. 8. a. Adult tooth of *C. chaldeus*. b. Juvenile tooth of *C. chaldeus*. c. Adult tooth of *C. ebraeus*. d. Juvenile tooth of *C. ebraeus*.

species, *C. pulcher* and *C. fergusoni,* have also been discovered to have different juvenile teeth (Figs. 10 and 11). In *C. fergusoni,* the smallest individual dissected was only 26.1 mm and the tooth was similar to tooth Type 1 (Fig. 10a). In *C. pulcher* the smallest specimen dissected was 11.6 mm. Each tooth in this specimen was more similar to that of the juvenile *C. patricius* and lacked a serration, cusp, and blade and had a single barb (Fig. 11c).

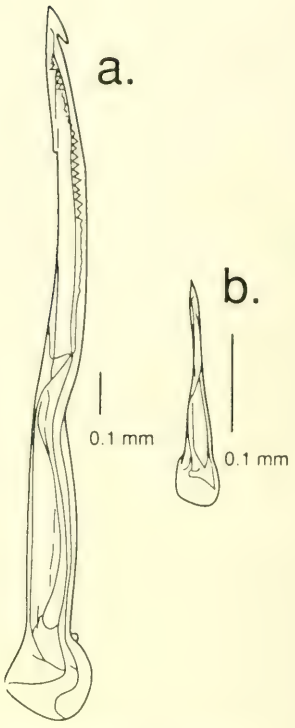

FIG. 9. a. Tooth of an adult *C. patricius*. b. Tooth of a juvenile *C. patricius*.

No very small *Conus* bearing Type 4 teeth were available for dissection. A size series of *C. arcuatus* from 41.9 mm down to 21.0 mm failed to reveal any radula change. Similarly, a size series from *C. lucidus* of 38.5 mm down to 14.4 mm also failed to reveal any radula change. Since no animals of 10 mm or less in shell length were available, we cannot at present assess if there is an ontogenetic change in this radula type.

DISCUSSION

These studies have established that there is an ontogenetic change in the radula of *Conus* species of a number of different tooth types that include all three main feeding types. These changes are documented for the greatest range of shell size for Type 1b (molluscivores) and Type 2 (piscivores) where immediate post-metamorphic juveniles were available for study. The striking similarity between the tooth types of the post-metamorphic juveniles in these two otherwise very

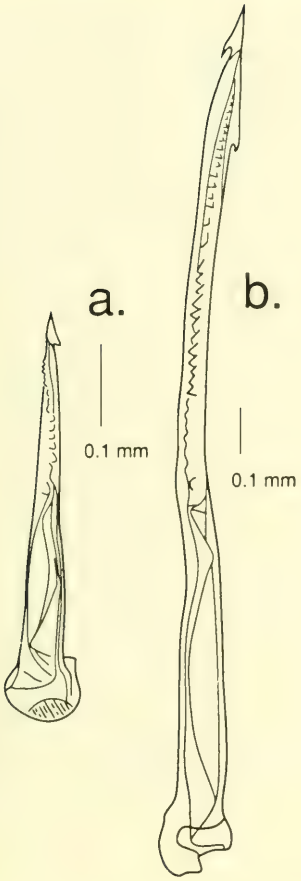

FIG. 10. a. Tooth of a juvenile *C. fergusoni.* b. Tooth of an adult *C. fergusoni.*

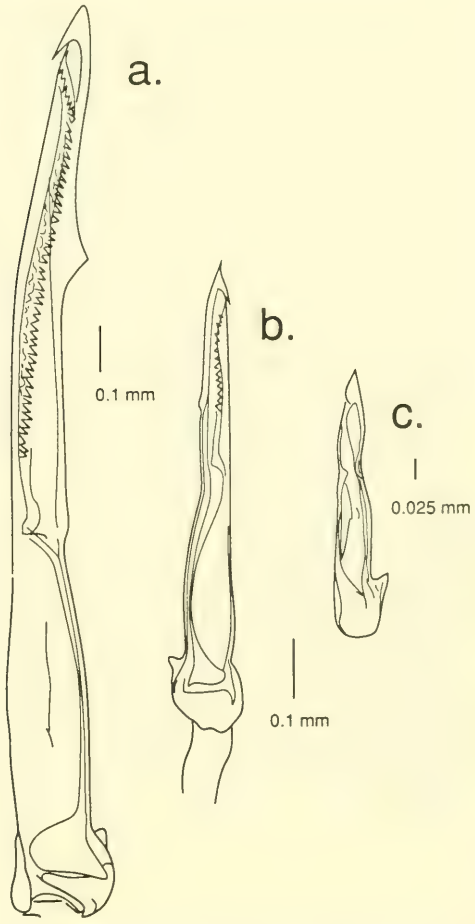

FIG. 11. a. Radula tooth of an adult *C. pulcher* of shell length 79.2 mm. b. Radula tooth of an animal of shell length 27.8 mm. c. Radula tooth of a juvenile of shell length 11.6 mm.

different feeding groups, as opposed to the differences in the adult teeth, strongly suggests that perhaps all immediate post-metamorphic juvenile *Conus* have similar teeth. It also suggests that the food may well be similar, because Nybakken & Perron (1988) have demonstrated that the food of juvenile *C. magus* is worms, not fish.

The post-metamorphic tooth does not appear to be strongly chitinized, as it only weakly takes up dyes specific for chitin (acid fuchsin). Furthermore, it is only slightly rolled, such that the lumen is open for the entire length. Whether or not the tooth is functional is not known, but Shimek (personal communication) has observed in certain turrids a similar type of tooth in which the tooth is rolled to form a tube by the proboscis before use.

If the teeth of immediate post-metamorphic specimens eventually prove to have the same structure in all *Conus* species, then the difference in morphology observed among adult teeth would seem to be initiated in the juvenile teeth as this study suggests. Although teeth different in morphology from the adult were found in juveniles in all three major feeding types, the morphology of tooth was not the same in each juvenile. The most prevalent juvenile tooth type, and very similar in adult Types 1, 1a, 2, 4, is a tooth with a single fold closing the lumen but leaving a very large anterior opening; having no, or at most one, barb; no blade; no serration, and a large base. In *C. magus,* Nybakken & Perron

FIG. 12. Scanning electron micrograph of a juvenile *C. magus* showing the development of the bulge that will become the large, recurved barb of the adult.

(1988) have demonstrated that this tooth is correlated with feeding on syllid polychaetes. In the molluscivores (Type 1b tooth), dissection of a series of specimens of *C. pennaceus* from 33.4 down to 9.6 mm failed to reveal any change from the adult radula. Yet, as noted above, the immediate post-metamorphic animals of a closely related species, *C. omaria,* have a very similar tooth to post-metamorphic *C. magus* of the same shell length. Perron (personal communication) has noted that juveniles of *C. pennaceus* feed on small gastropods, so the food type is similar to the adult. It is not in *C. magus.* Therefore, it may be suggested that the reason a different juvenile tooth is not seen in *C. pennaceus* is that there is not significant change in diet such as seen in *C. magus.* However, until we can examine radulae from specimens of *C. pennaceus* between 9.0 mm and 2.0 mm, this must remain only a suggestion.

In these juvenile teeth, although similar, there are indications of the morphological changes that will shape the adult teeth. Thus, in *C. magus* there is at this stage the development of a prominent bulge on the tooth at the level where the adult will have the characteristic recurved barb (Fig. 12). *Conus patricius* has an elongated anterior portion of the tooth corresponding to the elongated anterior portion in the adult (Fig. 13). In *C. fergusoni,* although we lack small specimens, those with shell lengths of 26 mm show an advanced juvenile tooth indistinguishable from a Type 1 tooth (Fig. 10). In this case, the adult tooth would seem to be derived from the juvenile by simple differential growth of the anterior region.

A significant gap in the current analysis is the unavailability of very small specimens of cones with radula Types 3 and 4. It is especially unfortunate for radula Type 3 because of our knowledge that the adults consume only one family of polychaetes, Amphinomi-

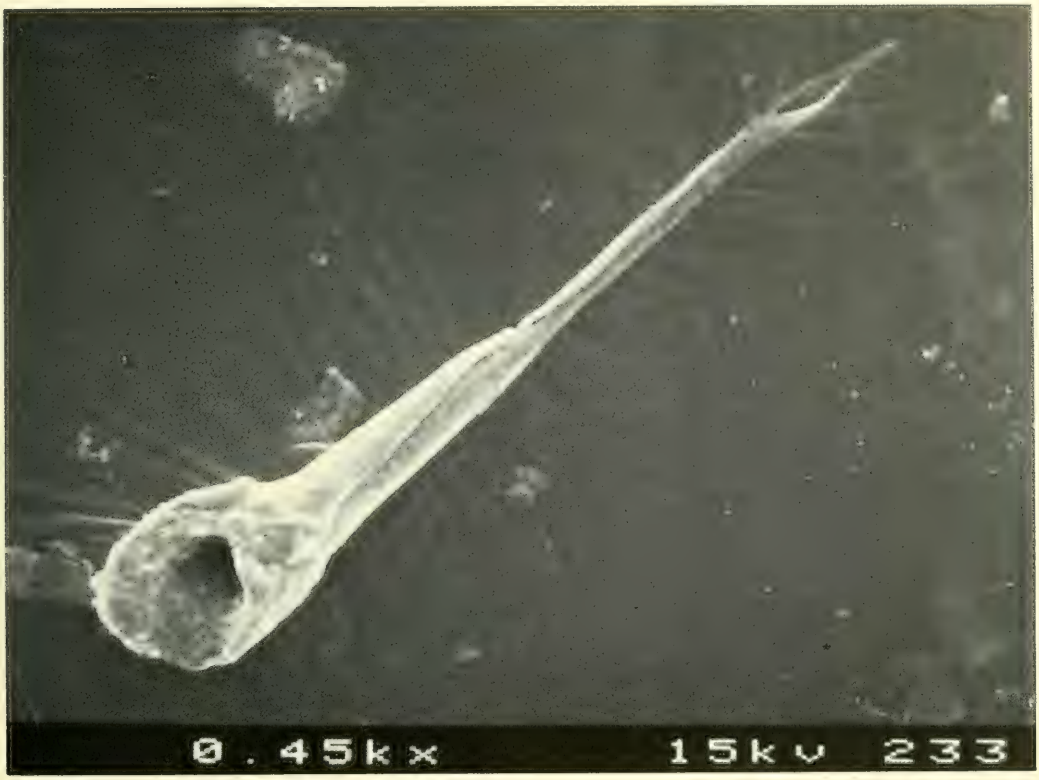

FIG. 13. Scanning electron micrograph of the juvenile tooth of *C. patricius* showing the slender, elongated anterior end.

dae. Although a fairly good size series of species with Type 4 radula was available in *C. arcuatus* and *C. lucidus,* no change in tooth morphology was discernable; the need for smaller sizes and post-metamorphic specimens is apparent.

Observation of all of the above radula types and comparison of the adult and juvenile suggests that the location of the greatest change from juvenile to adult is in the distal half of the tooth. The basal portion seems to change little from juvenile to adult (Figs 8–11), whereas the distal half undergoes significant changes.

It is also significant to note that it appears that the serration, where it is present, may be external or internal. If internal, it is of little or no use in any cutting or penetrating action. Where it is exposed, such as in *C. pennaceus,* it lies very close to the overlapping fold, suggesting that only a little change in growth or folding could make it internal. However, relatively few molluscivores were available for SEM work, so the extent of either internal or external serrations in this group is not known. It is also not known if this internal or external position of the serration correlates with any particular molluscan prey item.

What initiates the radula change? This is unknown at present, but Marsh (1977) has shown that the *Conus* tooth is actually the product of two tissues, the odontoblasts, which make the initial tooth, and the superior epithelium which finishes the tooth. It is possible that the form of the juvenile tooth is the product of the odontoblasts and that the adult tooth represents the finishing work of the superior epithelium.

The establishment of the existence of a change in radula morphology within a single species with ontogeny and the finding that this change is widespread in the genus among all food types has implications for systematics and ecology in *Conus.*

In the first place, Nybakken & Perron (1987) and Nybakken (1988) have demonstrated that the change in radula morphology

can occur rapidly and within a narrow range of shell lengths. This means that specimens of different shell lengths that have different radulas may not necessarily be different species. Now that we have established the likely morphology of the juvenile tooth in this study and that morphology seems to have certain recognizable characteristics, it would seem that this should facilitate juvenile recognition and reduce errors with respect to use of the radula in taxonomy. It is also of importance, therefore, to note the shell length of any specimens used in radula studies and when comparing specimens to compare only specimens of the same shell size. Given the fact that in *C. patricius* the juvenile radula may persist into animals with shells and shell lengths of the adult aspect and morphology, this means there may be no *a priori* way to predict whether in some species a specimen of a given size will have the adult radula. However, this may be a feature restricted to only a few feeding types, because there is no evidence for it over a rather large size range in molluscivores (*C. pennaceus*) and some vermivores (*C. lucidus, C. virgatus, C. arcuatus*).

The fact that Nybakken & Perron (1988) conclusively demonstrated that the juvenile radula in piscivores is correlated with a different diet than the adults suggests that many of the other species in which the juvenile radula is different from the adult may also prey upon different food items when small. However, at this time no data exist to prove or disprove this contention.

The results from Nybakken & Perron (1988) and Nybakken (1988) with *C. magus* and *C. patricius,* respectively, have also demonstrated that the observed radula change is not due to sexual dimorphism. Juvenile radulae were found in both sexes.

Given the various radula types and their distribution among the species, which is likely the most primitive type and which are the derived? There are several ways of looking at this problem. The simplest is to employ the commonality principle, otherwise stated as "common equals primitive" (Wiley, 1981). This principle simply states that if a character is widely distributed within a taxon, then the character is likely primitive. Employing this principle and considering that Type 1 is by far the most common type suggests it is also the most primitive.

Another criterion for determining primitive or derived is that of ontogenetic precedence (Hennig, 1966). This criterion assumes that the ontogenetic transformation toward a particular character reflects the phylogenetic development of that ontogeny. Employing this criterion and observing all the juveniles in this study suggests that the development of at least one anterior barb is a primitive feature and that it comes before the development of a serration.

My tentative conclusion, therefore, is that a modified Type 1 tooth would seem to be the most primitive, perhaps without a serration, and that the others are derived. The likelihood that the primitive tooth is without a serration is also given support by the fact that the toxoglossan teeth in the more primitive family Turridae also lack a serration (Shimek & Kohn, 1981).

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APPENDIX 1
Alphabetical List of *Conus* Species Examined for Radula Tooth Structure

C. abbreviatus	Type 1
C. aemulus	?
C. amadis	Type 1b
C. ambiguus	Type 1
C. araneosus	Type 1b
C. archon	Type 3
C. arcuatus	Type 4
C. arenatus	Type 1
C. aurora	Type 1
C. balteatus	Type 1
C. bartschi	Type 3
C. brunneus	Type 3
C. bulbus	?
C. californicus	Unique
C. capitaneus	Type 1
C. catus	Type 2
C. centurio	Type 4
C. ceylanensis	Type 1
C. chaldeus	Type 1
C. coronatus	Type 1
C. dalli	Type 1b
C. diadema	Unique
C. dispar	Type 1
C. distans	Modified Type 3
C. dorriensis	Type 1
C. ebraeus	Type 5
C. elongatus	Type 1
C. emaciatus	Type 1a
C. episcopus	Type 1b
C. ermineus	Type 2
C. fergusoni	Type 1a
C. frigidus	Type 1a
C. furvus	Type 1b
C. genuanus	Type 3
C. geographus	Type 1b
C. gladiator	Type 1
C. gloriamaris	Type 1b
C. gubernator	Type 2
C. imperialis	Type 3
C. litteratus	Type 1
C. lividus	Unique
C. loroisi	Type 1
C. lucidus	Type 4
C. magus	Type 2
C. mahogoni	Unique
C. marmoreus	Type 1b
C. mercator	?
C. miles	Type 1
C. miliaris	Type 1
C. monile	Type 1a
C. natalensis	Type 1b
C. nicobaricus	Type 1a
C. nigropunctatus	Type 2
C. nux	Type 1
C. omaria	Type 1b
C. orion	Type 1
C. paniculus	Type 1b
C. patricius	Type 1a
C. pennaceus	Type 1b
C. perplexus	Type 4
C. piperatus	Type 1
C. poormani	Type 1
C. princeps	Type 1a
C. pulcher	Type 1a
C. purpurasceus	Type 2
C. rattus	Type 1a
C. recurvus	Type 4
C. regularis	Type 1
C. scabriusculus	Type 1
C. scalaris	Type 1
C. scitulus	Type 1
C. simplex	Type 1
C. stercomuscarum	Type 2
C. striatellus	Type 1
C. textile	Type 1b
C. tiaratus	Type 1
C. tornatus	Unique
C. tulipa	Type 1b
C. varius	Type 1
C. ventricosus	Type 1a
C. venulatus	Type 1
C. vexillum	Type 1
C. victor	Type 1
C. victoriae	Type 1b
C. vidua	Type 1a
C. virgatus	Type 1
C. vittatus	Type 1
C. ximenes	Unique
C. zonatus	Type 3

Total Examined = 89

By Type:
- Type 1 = 34
- Type 1a = 11
- Type 1b = 15
- Type 2 = 7
- Type 3 = 7
- Type 4 = 5
- Type 5 = 1

? or unique = 9

APPENDIX 2
Conus Radulae Studied from Drawings and Photos in the Literature

C. acuminatus	Type 1b	(Piele, 1939)
C. anemone	Type 1a	(Bergh, 1895, as *C. maculosus*)
C. betulinus	Type 1	(Piele, 1939)
C. daucus	Type 1	(Warmke, 1960)
C. ermineus	Type 2	(Warmke, 1960, as *C. ranunculus*)
C. generalis	Type 1a	(Piele, 1939, as *C. maldivus*)
C. inscriptus	Type 4	(Piele, 1939)
C. jaspideus	Type 4	(Warmke, 1960)
C. juliae	Type 1	(Warmke, 1960)
C. leopardus	Type 1	(Bergh, 1895, as *C. millipunctatus*)
C. mercator	Type 1	(Bergh, 1895)
C. mindanus	Type 4	(Piele, 1939, as *C. agassizii*)
C. monachus	Type 2	(Piele, 1939)
C. mucronatus	Type 2	(Bergh, 1895)
C. nussatella	Type 1	(Piele, 1939)
C. pulicarius	Type 1	(Bergh, 1895)
C. regius	Type 3	(Warmke, 1960)
C. spurius	Type 1a	(Warmke, 1960)
C. striatus	Type 2	(Bergh, 1895)
C. taeniatus	Type 1	(Bergh, 1895)
C. tessulatus	Type 1	(Piele, 1939)

Total = 21

By Type
- 1 = 9
- 1a = 3
- 1b = 1
- 2 = 4
- 3 = 1
- 4 = 3
- 5 = 0

Total *Conus* spp. examined = 110

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TEMPO AND MODE OF EVOLUTION IN CONIDAE

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ABSTRACT

I examined the paleontological literature of the Conidae, here limited to the genus *Conus,* in order to detect temporal patterns in its evolutionary history. All 20 Mesozoic species originally described as *Conus* are likely opisthobranchs, or if *Conus* they are from strata now known to be of Eocene age. The few reports of Paleocene species are probably also incorrect. The earliest *bona fide* fossils of *Conus* appear to be from the Lower Eocene (50–55 mybp) of England and France, where the contemporaneous land flora indicates tropical climatic conditions. Collation of the paleontological literature places the first radiation of *Conus* in the Middle and Upper Eocene. Diversity decreased in the Oligocene, one or more major radiations occurred in the Miocene, and diversity decreased again in the Pliocene, followed by very rapid increase to the present approximately 500 species. The observed pattern is compared with four alternative models of taxonomic diversification: exponential, logistic, and exponential interrupted by periods of stasis or by periods of reduced diversity. The data fit the last model most closely, as do gastropods and other fossilizable marine invertebrates in general from the same era. Important evolutionary trends in *Conus* include (1) increasing shell size, thickness, and ratio of diameter to length, and decreasing spire height, and (2) inhabiting shallower, higher-energy marine environments. Shell form may have been the most important innovation leading to the major radiations.

Key words: fossil history, evolutionary origins, adaptive radiation, Conidae.

> "One finds very few papers that give us an objective account of the evolution and adaptive radiation of any group of Mollusca."
>
> G. M. Davis (1981)

INTRODUCTION

During the past 35 years, comparative biological studies of the Conidae have elucidated many aspects of the habitats and habits, feeding and reproductive biology, and diversity and community ecology of assemblages of co-occurring species (Table 1). This geologically youthful yet unusually species-rich family of gastropods is now probably as well known biologically as any tropical marine invertebrate taxon. Yet despite this wealth of neontological information, and the existence of a quite respectable fossil record, the origin and evolutionary history of the family, and the historical and ecological factors that have been important in its remarkable evolutionary radiation, remain virtually unknown.

CLASSIFICATION OF THE FAMILY CONIDAE

Conidae as a family-level taxon was first validly proposed by John Fleming (1822), and has been generally accepted since about 1850, but its scope has been variably perceived. Twentieth-century workers generally consider the neogastropod Superfamily Conoidea (or Conacea or Toxoglossa) to comprise two families, Conidae and Terebridae, (Thiele, 1931; Seed, 1983), or three, with separation of Turridae from Conidae (Wenz, 1942; Powell, 1966; Ponder & Warén, 1988). As this paper focuses on the evolution of Conidae in the narrower sense, I employ the latter classification here.

Characterizing the distinction between Turridae and Conidae is not straightforward. Several genera intermediate in shell form, most with extant representatives, appear to link the two families, and different authors have drawn different lines between them. Cossmann (1896) and Powell (1966) described each of these genera and noted their similarities and distinguishing features. Most 20th century authors include in the Conidae only *Conus,* and *Hemiconus* if they consider this extinct genus or subgenus (Table 2).

TABLE 1. Summary of comparative biology of Indo-Pacific *Conus*

Aspect	Patterns
Geographic distribution	Species ranges: narrowly endemic to entire Indo-Pacific region. Range extent: correlated with dispersal ability of planktonic larvae.
Species diversity	Lowest (1 species) in geographically peripheral regions. Low (5–9 species) in topographically simple, intertidal habitats. Highest (12–27 species) in complex subtidal coral reefs.
Habitat occupation*	Fine to coarse soft sediments; algal turfs; rubble to reef limestone. Some differential specialization by co-occurring species.
Habits and activity	Infaunal to epifaunal. Nocturnally active; diurnally sheltered.
Feeding biology*	Predators on worms (mainly polychaetes), gastropods, or fishes. Markedly differential specialization by co-occurring species.
Reproductive biology*	Embryonic period 7–24 days. Precompetent planktonic veliger larval period 0–30 days. Strong gradients in developmental patterns related to egg size.

*Species of *Conus* vary widely from specialists to generalists in these aspects.

Cossmann's (1896) criteria that distinguish Coninae and Cryptoconinae are clear and applicable to both fossil and Recent forms. Partial resorption of inner walls, a hallmark of *Conus* (Kohn et al., 1979), also occurs in *Conorbis* and *Hemiconus* (Coninae) but not in *Cryptoconus* (Cryptoconinae). The spire and aperture in *Cryptoconus* each comprise about half the total shell length, whereas the spire of *Conorbis* is always shorter than the aperture length. In Coninae, shell form is generally conic or biconic with the sides of the aperture parallel. *Hemiconus* and *Conorbis* thus share important shell features with *Conus*. Members of the Cryptoconinae do not resorb inner shell walls and have fusiform shells with ovate apertures. Here I follow Cossmann's (1896) distinction between Cryptoconinae and Coninae, but in agreement with other 20th century workers I assign the Cryptoconinae to Turridae. I restrict the Conidae to the genera comprising the subfamily Coninae.

Conorbis (Eocene-Miocene and the Recent *C. coromandelicus* Smith) and *Hemiconus* (Middle Eocene-Lower Miocene) each include about 20 species (Glibert, 1960; Powell, 1966). Thus neither of these genera has undergone a striking radiation. Traditionally, they are considered the most closely related to *Conus* (e.g. Thiele, 1931; Powell, 1966), but we remain ignorant of the evolutionary history and phylogenetic relationships of these groups. I consider only *Conus* in the rest of this discussion.

ORIGIN OF *CONUS*

The oldest fossils described as *Conus* are from the Lias of Normandy near Caen; they are of Pliensbachian age (188–196 mybp; absolute dates in this paper are taken from Harland et al., 1982, and Haq & Van Eysinga, 1987). Charles Lyell read an informal account of the discovery of these specimens in a publication of the Linnaean Society of Normandy ([Eudes-Deslongchamps], 1837). He collected at the site in 1840, and later that year (Lyell, 1840), in collaboration with G. B. Sowerby, he described *Conus cadonensis* and *C. concavus*. Deshayes & Milne Edwards (1845:7) questioned the assignment of these species to *Conus,* and soon d'Orbigny (1850, 1852) confirmed their suspicion by demonstrating in sectioned specimens that the last whorls are thin and that internal shell walls are not resorbed. In *Conus,* the last whorl is thick and inner walls are often reduced to 50 μm (Kohn et al., 1979), in Eocene as well as modern species (Kohn, 1982). *Conus abbreviatus* Eudes-Deslongchamps, 1849, and *C. caumontii* Eudes-Deslongchamps, 1849, were described later from the same formation. *Conus minimus* D'Archiac, 1843, was described from the Middle Jurassic (Bajocian, 172–177 mybp) of Aisne, but it was assigned questionably to *Conus.* It is clearly an opistobranch, on the same grounds. D'Orbigny (1850, 1852) assigned all of these taxa to the opisthobranch genus *Actaeonina,* and they have generally been considered members of the family Actaeonidae

TABLE 2. Boundaries between Turridae and Conidae of selected authors.

Genera:	*Genota*	*Cryptoconus*	*Conorbis*	*Hemiconus*	Conus	
Geologic Range:	Eocene-Recent	Eocene-Miocene	Eocene-Recent	Eocene-Pliocene	Eocene-Recent	
	[CONIDAE: CRYPTOCONINAE]		[CONIDAE: CONINAE]			Cossman (1896)
...	CONIDAE: CYTHARINAE]		[CONIDAE CONINAE]			Thiele (1931)
...	TURRIDAE: CRYPTOCONINAE]		[CONIDAE]			Wenz (1942), Glibert (1960)
[	TURRIDAE: CONORBIINAE]					Powell (1966)
[	TURRIDAE: CONORBIINAE .....]			[CONIDAE]		Ponder & Warén (1988)

ever since (Meek, 1863; Cossmann, 1895; Zilch, 1959) (Table 3).

The remaining Mesozoic fossils originally described as *Conus* are all reported as Cretaceous. The next oldest is *C. verneuilli* Vilanova, from the Neocomian of Spain (123–140 mybp). This also appears to be an opisthobranch (Tomlin, 1937). One species, *C. primitivus* Collignon, was described from the Albian (98–109 mybp) of Madagascar. Definitely Albian (N. Sohl, *in litt.*), the single specimen is a partial internal mold lacking any shell material. It is too fragmentary to assign to any genus with confidence, but it is possibly an opisthobranch. The one Cretaceous species described from Italy, C. schiosensis Böhm, 1895 (Cenomanian-Turonian; 89–98 mybp), is also an opisthobranch (Sohl & Kollmann, 1985).

Three species of *Conus* were described from the Cretaceous of France, one Turonian (88–91 mybp) and two Santonian (83–86 mybp). *Conus marticensis* Matheron, 1843, was described from the Turonian at Martigues. The original description and figures in Matheron (1843) do not permit its rejection from *Conus,* and its source formation, "Craie ligno-marneuse," is definitely Cretaceous. One of the Santonian species, *C. tuberculatus* Dujardin, 1837, from the Touraine, was the first Cretaceous *Conus* to be described. The great French protozoologist Dujardin described the species mainly from molds, but in the original figured specimen a partial cast replaced some of the original shell. This specimen is now assigned to the genus *Gosavia,* family Volutidae (Cossmann, 1896; Wenz, 1943). The second Santonian species, *C. senessei* Delpey, 1938, from Corbières, is probably neither a conid nor a turrid.

Three additional species described from the Upper Cretaceous, *Conus cylindraceus* Geinitz, 1850, from Silesia, *C. semicostatus* Goldfuss, 1843, from Westphalia, and *C. latus* Eichwald, 1869, from the Crimea, are also opisthobranchs. Geinitz (1850) stated that his generic assignment of his 4 mm-long fossil was doubtful.

Of the six remaining species originally described as Cretaceous *Conus, C. canalis* Conrad, 1858, from Mississippi is now placed in the Volutidae, and the remaining five (three from California and two from Brazil) are now known to be from Eocene and Miocene strata (Table 3).

Finally, one Cretaceous species was originally assigned to *Conorbis.* Powell (1966) retained this species, *C. mcnairyensis* Wade, 1917, in *Conorbis* and thus extended the range of that genus from Cretaceous to Recent. However, the shell aperture of *C. mcnairyensis* is not straight and its sides are not parallel, and there is no evidence either of the exhalent sinus or the arcuate outer lip characteristic of the Turridae, including Conorbinae. Sohl (1964) retained *C. mcnairyensis* in the Turridae, questionably assigning it to *Cryptoconus* (Table 3).

Thus all 20 species of *Conus* and the one of *Conorbis* originally described from Mesozoic

TABLE 3. Present disposition of species described originally as Mesozoic *Conus* (and *Conorbis*)

Original Designations						Current Dispositions				
Species	Author, Date	Locality	Period	Epoch	Stage	Genus	Period	Epoch	Stage	Reference
cadonensis	Lyell & G. Sowerby, 1840	near Caen, France	Jurassic	Lias	Pliensbachian	*Conactaeon* (OPISTHOBRANCHIA)	Jurassic	Lias	Pliensbachian	d'Orbigny (1850), Zilch (1955)
concavus	Lyell & G. Sowerby, 1840	near Caen, France	Jurassic	Lias	Pliensbachian	*Conactaeon* (OPISTHOBRANCHIA)	Jurassic	Lias	Pliensbachian	d'Orbigny (1850), Zilch (1955)
abbreviatus	Eudes-Deslongchamps, 1849	near Caen, France	Jurassic	Lias	Pliensbachian	*Actaeonina* (OPISTHOBRANCHIA)	Jurassic	Lias	Pliensbachian	d'Orbigny (1850)
caumontii	Eudes-Deslongchamps, 1849	near Caen, France	Jurassic	Lias	Pliensbachian	*Actaeonina* (OPISTHOBRANCHIA)	Jurassic	Lias	Pliensbachian	d'Orbigny (1850)
minimus	D'Archiac, 1843	Aisne, France	Jurassic	Dogger	Bajocian	*Actaeonina* (OPISTHOBRANCHIA)	Jurassic	Lias		d'Orbigny (1852)
verneuilli	Vilanova, 1859	Castellon?, Spain	Cretaceous	Neocomian		*Acteon* (OPISTHOBRANCHIA)	Cretaceous?	Neocomian?		Tomlin (1937)
primitivus	Collignon, 1949	W. Analavory, Madagascar	Cretaceous		Albian	indeterminate	Cretaceous	K_1	Albian	Sohl (*in litt.*)
schiosensis	Böhm, 1895	Venetian Alps, Italy	Cretaceous		Cenomanian-Turonian	*Trochactaeon*? (OPISTHOBRANCHIA)	Cretaceous	K_2	Cenomanian-Turonian	Sohl & Kollmann (1985)
marticensis	Matheron, 1843	Martigues, France	Cretaceous		Turonian	*Conus*?	Cretaceous	K_1		Sohl (*in litt.*)
tuberculatus	Dujardin, 1837	Tours, France	Cretaceous		Turonian	*Gosavia* (Volutidae)	Cretaceous	Senonian	Santonian	Cossmann (1896), Wenz (1943)
senessei	Delpey, 1938	Corbières, France	Cretaceous			not *Conus*; probably not a turrid	Cretaceous	Senonian	Santonian	

mcnairyensis	Wade, 1917 (*Conorbis*)	McNairy Co., Tennessee	Cretaceous			*Cryptoconus*?	Cretaceous	Senonian	Maastrichtian	
cylindraceus	Geinitz, 1850	Kieslingswalda, Czechoslovakia	Cretaceous	Senonian	Coniacian	*Cylichna* (OPISTHOBRANCHIA)	Cretaceous	Senonian	Coniacian	Tomlin (1937)
semicostatus	Goldfuss, 1843	Westphalia, Germany	Cretaceous			(OPISTHOBRANCHIA)	Cretaceous	K_2		
latus	Eichwald, 1869	Crimea, USSR	Cretaceous			(OPISTHOBRANCHIA)	Cretaceous			
canalis	Conrad, 1858	Tippah Co., Mississippi	Cretaceous			*Liopeplum* (Volutidae)	Cretaceous	Senonian	Maastrichtian	Sohl (1964)
hornii	Gabb, 1864	near Fort Tejon, Kern Co., Calif.	Cretaceous			*Conus*	Tertiary	Eocene-Miocene		Stewart (1927), Keen & Benson (1944)
remondii	Gabb, 1864	near Fort Tejon, Kern Co., Calif.	Cretaceous			*Conus*	Tertiary	Eocene		Waring (1917), Stewart (1927)
sinuatus	Gabb, 1864	near Fort Tejon, Kern Co., Calif.	Cretaceous			*Surculites**	Tertiary	Eocene		Stewart (1927)
conditorius	White, 1875	Rio Piabas, Para, Brazil	Cretaceous			*Conus*	Tertiary	Miocene		Sohl (*in litt.*)
restitutus	White, 1875	Rio Piabas, Para, Brazil	Cretaceous			*Conus*	Tertiary	Miocene		Sohl (*in litt.*)

*Family uncertain (Powell, 1966).

strata are probably either not Mesozoic or not Conidae or both. I conclude that the family Conidae originated after the Cretaceous-Tertiary boundary.

The few reports of Paleocene *Conus* are equally suspect. Only *C. rouaulti* D'Archiac, 1850, from the "Groupe Nummulitique" of southern France, occurs in beds that are mainly Eocene but may possibly include Thanetian material (Danizot, 1957). *Conus rouaulti* and the quite similar *C. concinnus* J. deC. Sowerby, 1821, from the Lower Eocene (Ypresian) of France and England respectively, seem to represent the earliest *bona fide* records of *Conus, s.s.* In addition, Lower Eocene fossils of two other species have been reported from Sind, Pakistan (Cossmann & Pissarro, 1909).

SMALL BEGINNINGS?

New groups of animals tend to originate from small ancestors, and a common trend in the evolutionary history of a supra-specific taxon is increase in body size. This is Cope's well known "law," proposed for vertebrates but shown to hold quite generally as well for invertebrates with fossilizable hard structures (Newell, 1949). Does a pattern of increasing shell size characterize the evolutionary radiations within *Conus*? If so, does the overall distribution of shell size in the genus shift upward, or, as Gould (1988) proposed as more likely, is apparent size increase due mainly to increasing variance in shell size? If *C. concinnus* and *C. rouaulti* are accepted as early, if not the earliest, members of the genus, their size can be compared with later species, particularly those at and just before the initiation of major radiations. Detailed analyses remain to be carried out, but preliminary data suggest trends. The type specimen of *C. rouaulti* is 11 mm, and that of *C. concinnus* is 14 mm, in shell length. The largest specimen of the latter species in The Natural History Museum, London, is 32 mm, and the mean length of the largest specimen in five Lower Eocene (London Clay) lots is 26 mm.

Although many *Conus* species of about the same size occur in Middle Eocene deposits, much larger species are also prominent then, the time of the first known radiation of the genus. For example, a syntype and several other specimens of *C. edwardsi* Cossmann in The Natural History Museum, London, from the Middle Eocene Bracklesham Beds in southern England are about 70 mm long. This species also has a relatively shorter spire than *C. concinnus,* averaging about 16% of total shell length vs. 30% in the latter species.

While further analyses of the size frequency distributions of Paleogene and Neogene *Conus* remain to be carried out, the sizes of extant species, representing the most diverse radiation in the group's history, are reasonably well known. The size of modern *Conus* species varies markedly in different habitat types. In the Indo-Pacific region where most species occur, median shell lengths are 23 mm on intertidal benches, 35 mm on subtidal coral reefs, and 80 mm in subtidal sandy bays (Kohn, 1980, 1981). Species similar in size to the hypothesized ancestral species thus persist commonly today. Coral reef platforms support the highest modern diversity; these species are of somewhat larger body size. Shallow reef-associated lagoons rank next in *Conus* diversity; they support assemblages mainly of even larger species (Kohn, 1981), including the largest extant species, with shell length of more than 200 mm. A few Indo-Pacific *Conus* species with maximum shell size less than the Lower Eocene species also occur today, and more exist in other parts of the geographic range of the genus.

Thus size increase has characterized the evolution of *Conus,* in the sense of increasing upper size limits and increasing size variance. As in other groups of organisms to which Cope's law applies (Bonner, 1988), small species not only persist but may be quite diverse.

PATTERNS OF EVOLUTION IN TIME AND SPACE

Alternative Hypotheses of Diversity Patterns

As a simplified model of diversification rates, Stanley (1979) plotted the logarithm of the number of extant species in a taxon against the time since its origin. The slope of a line drawn between this point and the origin (assuming a single species initiated each taxon) can be interpreted as the exponential rate of species proliferation. This method underestimates, as Stanley (1979) noted, because it omits extinct species. Moreover, diversification rates are unlikely to remain constant over long periods, for reasons involving earth history, ecological factors, and the inherent attributes of evolutionary lin-

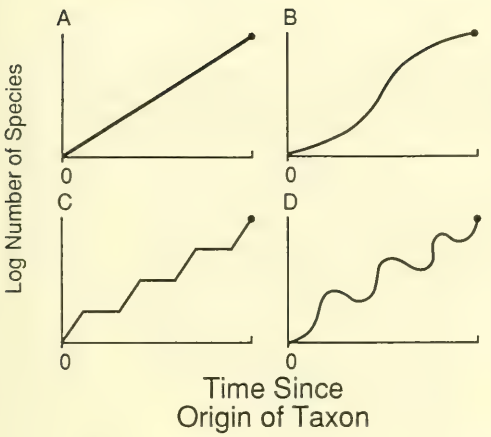

FIG. 1. Alternative patterns of species proliferation of a diversifying taxon in time; semilogarithmic plots. A, Exponential. $dD/dt = r_dD_o$. Speciation rate per species (r_s) and species extinction rate (r_e) are constant; $r_d = r_s - r_e$. B, Logistic. $dD/dt = r_oD(1-D/\hat{D})$. r_o = initial diversification rate. $\hat{D}$ = equilibrium value. C, Periods of exponential diversification alternate with periods of stasis. r_d varies, as $r_s \geq r_e$. D, Periods of diversification ($r_s > r_e$) alternate with periods of net extinction ($r_s < r_e$).

eages. Figure 1 shows several possible alternative patterns. The simplest case is the exponential or log-linear model (Stanley, 1975, 1979) (Fig. 1A), for speciation by each daughter species at a constant rate and a constant species survival rate. A constant exponential rate of increase damped by the imposition of a saturation value results in a logistic curve (Sepkoski, 1978; Walker, 1985) (Fig. 1B). The remaining models in Figure 1 incorporate factors that cause periods of diversification to alternate with periods of stasis or slow net change (Fig. 1C), or with periods of reduced diversity due to extinction rate exceeding speciation rate (Fig. 1D).

Temporal Characteristics of the *Conus* Fossil Record

In order to determine the history of taxonomic diversification in *Conus,* I developed a database of all records I could locate in the paleontological literature (2,500 from 1792 to the present) that indicated stratigraphic age and geographic location of fossil *Conus* species. For Middle Eocene-Pleistocene records, I generally accepted at face value the species identification and stratigraphy of original authors; no effort has yet been made toward critical evaluation of the data, and all of the biases that characterize paleontological data in general apply (see e.g. Raup, 1976a). Figure 2 shows the result in the form of a spindle diagram of the number of *Conus* species through the Cenozoic, including Lyellian percentages for each epoch. At times when the number of species is increasing from stage to stage, turnover becomes an important aspect of diversification. Is increasing richness due to a modest number of originations combined with persistence of most species from the previous stage, or to modest persistence and the origination of many new species?

Figure 3 presents patterns of *Conus* species turnover during the Cenozoic; these data are also accepted uncritically from the paleontological literature. First and last appearances are expressed in absolute numbers (plotted on a logarithmic scale; Fig. 3A), relative to the total number of species present during the interval (Fig. 3B), and as apparent rates of speciation and extinction (Fig. 3C). Figure 3D shows turnover calculated as the number of originations plus extinctions per species present and the rate of diversification per species per million years, because the intervals used vary considerably in absolute time. The notations used (after Sepkoski, 1978) are:

S = number of first appearances in interval (apparent speciations);
E = number of last appearances in interval (apparent extinctions);
D = number of species present in interval (apparent diversity);
$\triangle t$ = duration of interval in millions of years;
Turnover = $(S+E)/D$;
Diversification rate = $r_d = r_s - r_e$,
where
Rate of speciation $r_s = S/(D\triangle t)$, and
Rate of extinction $r_e = E/(D\triangle t)$.

The main aspects of the patterns that emerge from analyses of the data as originally reported are:

(1) The genus *Conus* originated during Lower Eocene time. Mesozoic and Paleocene records are rejected or dubious.

(2) The first real radiation of the genus occurred in the Middle Eocene (Fig. 2). Many species persisted into the Upper Eocene, but 75% of all Upper Eocene species are first reported then (Fig. 3B). In all, about 100 species are recorded from this epoch. Species turnover was maximal in Middle Eocene because of the large numbers of both origina-

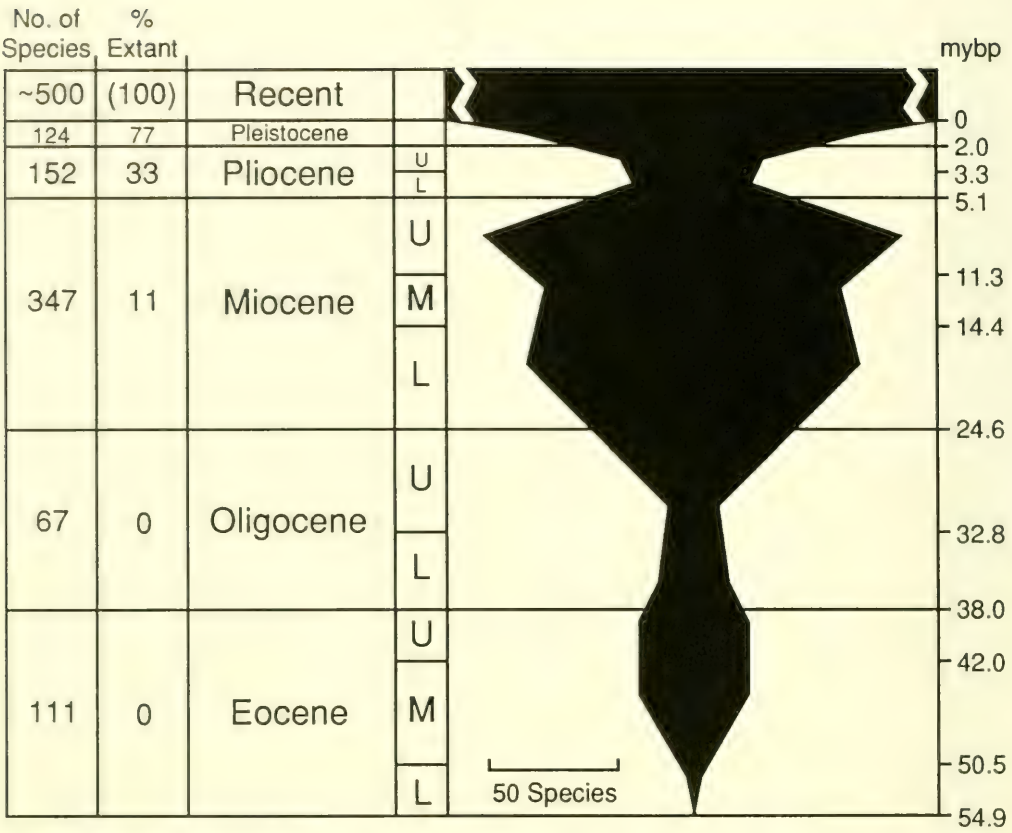

FIG. 2. Kite diagram showing the number of species of *Conus* throughout Tertiary and Quaternary time, based on an uncritical analysis of the paleontological literature. Ages of epochs and subdivisions from Harland et al. (1982); the two columns at left give the total number of species reported from each epoch and the fraction extant. Numbers of species are: Lower Eocene: 5; Middle Eocene: 42; Upper Eocene: 42; Lower Oligocene: 28; Upper Oligocene: 19; Lower Miocene: 127; Middle Miocene: 111; Upper Miocene: 158; Lower Pliocene: 43; Upper Pliocene: 53; Pleistocene: 124.

tions and disappearances (Fig. 3A), but because the interval was long, the rate of diversification was low (Fig. 3D). "Per species" rates of origination and extinction were higher in the Upper Eocene (Fig. 3C).

(3) Species diversity decreased in the Oligocene, a pattern common to the Gastropoda and marine invertebrates in general (Raup, 1976b). Numbers and rates of originations and extinctions declined (Figs. 3A,C), as did species turnover (Fig. 3D); about 70% of species present originated in the Lower and Upper Oligocene while extinction rates were 52% and 32%, respectively (Fig. 3B).

(4) One or more major radiations occurred in the Miocene. Nearly 300 species are recorded from this epoch. Originations of new species increased to 82% of all species present in the Lower Miocene, when turnover was second only to the Middle Eocene (Figs. 3B,D). As in that radiation, the Lower Miocene diversification rate was low because the interval was long (Figs. 3C,D). The rates were higher although absolute and relative numbers of originations and extinctions declined in the shorter Middle Miocene (Figs. 3A,B,C). Originations then declined to about 50% of species present by Upper Miocene, extinctions increased, but rates of both declined (Figs. 3A,B,C).

(5) Species diversity again declined in the Pliocene (152 species recorded). Generally reduced diversity of gastropods and other invertebrates is characteristic of this epoch (Raup, 1976b). Both the numbers (Fig. 3A) and proportions (Fig. 3B) of originations and

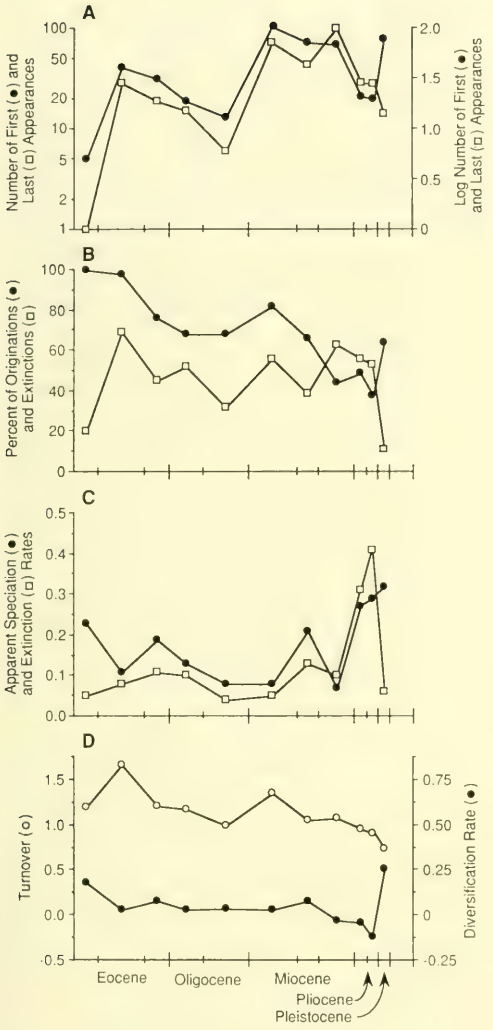

FIG. 3. A. The numbers of originations (•) and extinctions (□) of *Conus* species, determined from reports of first and last appearances in the fossil record, throughout the Cenozoic. B. Species turnover, calculated as the sum of the numbers of originations (S) and extinctions (E) (from Fig. 3A) divided by the number of species reported during each interval (D) (see text). C. The apparent rates of speciation (origination) (r_s = S/Dt; •) and extinction (r_e = E/Dt;□) during each interval. D. Species turnover ([S + E]/D; ○) and species diversification rate ($r_d = r_s - r_e$;•).

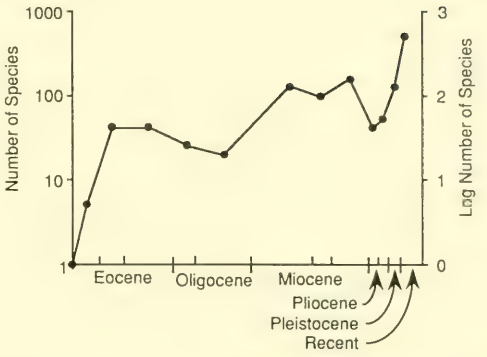

FIG. 4. The numbers of species of *Conus* reported from Tertiary and Quaternary epochs and stages. Data from Fig. 2, plotted to conform with the models in Fig. 1.

extinctions of *Conus* species declined, but their rates increased (Fig. 3C) in this temporally brief epoch.

(6) Very rapid speciation (Figs. 3A,B) and a large disparity between origination and extinction rates (Fig. 3C) occurred during the even briefer Pleistocene, leading to modern high diversity. Nearly 65% of Pleistocene species are not known from earlier in the fossil record.

(7) Only 11% and 33% respectively of Miocene and Pliocene species survive, but 77% of Pleistocene species are extant.

In his graph of nine extant radiating marine prosobranch clades according to model A (Fig. 1), Stanley (1979) gave a mean net exponential rate r = 0.067 my^{-1}. At this rate, the number of species in a clade doubles in 10.3 my. For Conidae, he indicated 500 extant species and an age of 70 my, or r = 0.103 my^{-1}, equivalent to a doubling time of 6.7 my. Taking the age of Conidae as 55 my based on the evidence presented here increases r to 0.113 my^{-1} and decreases the doubling time to 6.1 my. As noted above, this model inevitably underestimates the rate of diversification.

If the data in Figure 2 are replotted according to Figure 1, the resulting pattern approaches model D most closely (Fig. 4); the fossil record of *Conus* indicates alternating periods of rapid radiation and of reduced diversity. As this closely parallels the temporal diversity patterns of other marine invertebrate groups during Cenozoic time (Raup, 1976b), extrinsic environmental factors were likely important causes.

Geographic Features of the *Conus* Fossil Record

Preliminary paleobiogeographic analysis of the *Conus* fossil record suggests that:

(1) The Lower Eocene origin of the genus is coastal European; the earliest verified records are from England and France.

(2) The first real radiation, in the Middle Eocene, likely occurred in the same geographic region; about 3/4 of Middle Eocene species are from Britain and Europe, but the genus also expanded its range broadly. Middle Eocene species are also recorded from Egypt, Nigeria, Pakistan, California, and the U.S. Gulf Coast.

(3) After the Middle Eocene, extinctions of *Conus* species outpaced originations in the European seas, but modest, localized diversity increases occurred on the Indo-Australian plate (Upper Eocene), and in the Asian region of the Eurasian plate (Upper Oligocene). Whether or not different *Conus* species assemblages occurred in each geographic region remains to be addressed. Piccoli (1984) concluded that Paleogene molluscan assemblages of the Mediterranean region were generally Indo-Pacific in composition; Rosen (1988) emphasized regional differences in contemporaneous corals and echinoids.

(4) Europe and the Indo-Australian regions were the sites of major Miocene radiations, the latter predominantly early in the epoch and the former continuing throughout Miocene time.

(5) Throughout its history, the genus *Conus* appears to have been confined to warm seas, with all of the major radiations occurring in tropical conditions. In Britain, "in Eocene times the climate, as reflected in the land flora, was that of tropical lowlands such as those of south-east Asia today" (Melville & Freshney, 1982). The same likely applies to the Miocene seas occupied by the genus, and its modern geographic distribution remains predominantly tropical.

(6) The data fail to reveal the geographic sources of the group's most important radiation, resulting in several hundred extant species. Most species known as Pleistocene fossils are distributed similarly to their modern counterparts, with the majority in the Indo-Australian plate and western Pacific regions, and fewer but substantial numbers in the Americas. This remains a critical area for future investigation.

NEW ADAPTIVE ZONES? KEY INNOVATIONS?

Of necessity I address these topics with a high degree of speculation, and I urge others to gather relevant data to test the hypotheses advanced.

New Adaptive Zones?

An adaptive zone, as the concept was introduced by Simpson (1953) and clarified by Van Valen (1971), is the "niche" of a taxon above the species level. Its two basic, more or less independent components comprise the resources used by the members of the focal taxon, and their resistance to predation and parasitism. Did the evolutionary radiations of *Conus* depend on successful invasion of a different adaptive zone and different ways of acquiring resources and defending against enemies, from those of the ancestral and sister taxa?

The answer is by no means clear. During the early evolutionary history of *Conus,* the fossils are typically associated with fine sediments characteristic of continental shelf and greater depths, similar in general to the habitats of many species in the hypothetically ancestral family Turridae. (Such habitats are also particularly favorable sites for fossilization.) Successful invasions of shallower bay and lagoon environments probably began in Middle Eocene time. The conical shape of the last whorl with the apex of the cone anterior would certainly facilitate locomotion by the gastropod through soft substrata. Evolutionary trends toward (1) increased shell size, thickness and ratio of diameter to length, and decreased spire height, and (2) occupation of ever shallower and high energy marine environments probably occurred during all Middle Eocene and Miocene radiations of *Conus* but at present remain largely undocumented. These changes in shell form could well have expanded the taxonomic and size ranges of suitable prey organisms without sacrificing defensive shell strength. Simultaneously, the habitat shifts likely involved use of hard as well as soft but coarser substrata associated with coral reefs, a biogenic environment increasing in complexity and geographic extent contemporaneously with the radiations of *Conus* (Rosen, 1988).

Key Innovations?

The rapid evolutionary radiation of a taxon is often assumed and sometimes documented (e.g. Liem, 1973) to be associated with the origin of key evolutionary novelties, i.e. the development of new, usually morpho-

logical, attributes that satisfy several criteria (as modified from Herrera, 1989):

(1) The novel feature is significant to the taxon and absent from its sister or ancestral groups;

(2) Taxa with the feature diversify early in their evolutionary history;

(3) Taxa with the feature become structurally and taxonomically more diverse than sister taxa lacking it.

Coddington (1988) uses a cladistic framework to test whether innovations are adaptations in the strict sense (of Gould & Vrba, 1982) of selection on a specific function promoting the origin, spread and maintenance of the innovative attribute, and driving taxonomic diversification. Lauder & Liem (1989) provide additional criteria and an explicit procedure for testing the key innovation hypothesis. It involves mapping the hypothesized key innovation onto a phylogeny of the taxon and comparing morphometric analyses of this taxon and of outgroups.

What innovative features of *Conus* might qualify? Hallmarks of the genus include:

(1) the detachable, hollow, barbed, harpoon-like radular tooth individually injected via an extensile intraembolic proboscis during prey capture (Kohn et al., 1972);

(2) the peptide venoms injected through the tooth that rapidly immobilize the prey (Olivera et al., 1985);

(3) the characteristically broadly conical or biconical shell with parallel-sided aperture, typically with the last whorl covering most of the prior whorl so that the spire is quite low; and

(4) the thick, heavy and strong crossed-lamellar last whorl of the shell, with the protected inner walls later mainly dissolved away during extensive interior renovation (Kohn et al., 1979).

At present, data are lacking in *Conus* to test these features against even those predictions of the key innovation hypothesis that do not require phylogenetic evidence. Moreover, the present lack of detailed comparative anatomical information on *Conus* means that other important innovative characters may remain to be discovered. At best we can indicate the present status of knowledge:

(1) The general features of the *Conus* radular tooth mentioned above are shared by numerous turrids, especially the subfamily Borsoniinae; whether this is a sister taxon of *Conus,* its ancestral taxon, or neither is unknown. The functional morphology of the proboscis of *Conus* and turrids is also very similar (Greene & Kohn, 1989; Kantor, 1990).

(2) A venom apparatus morphologically similar to that of *Conus* also occurs in many taxa of Turridae, but nothing is known of the chemical nature of the venom in the latter family.

(3) Shell size, shape and thickness may meet all of the criteria.

(4) Internal wall resorption occurs, but to a lesser extent than in *Conus,* in some Olividae as well as in *Hemiconus* and *Conorbis.*

Key innovations may be quite subtle. As Mayr (1960) said, "Most evolutionary changes take place without the origin of new structures. . . . Most differences are merely shifts in proportions, fusions, losses, secondary duplications, and similar changes," that nevertheless can lead to "evolutionary avalanches." In addition, the causal relationship of key innovations with subsequent taxonomic diversification may be quite indirect. Anatomical changes that provide selective advantages early in the evolution of a taxon may fortuitously support organisms of larger size at a later time in the evolution of a clade, as Bonner (1988) points out, as well as promoting speciation and the clade's radiation in a new adaptive zone.

Shell form is the most likely candidate for the critical key evolutionary innovation of *Conus.* The depressed spire and broadly conical form permits the aperture to expand, particularly anteriorly and posteriorly. This in turn may have permitted thickening of the last whorl without reducing aperture size, and internal wall thinning to retain a large living space within the shell, thus accommodating large prey organisms. The latter is likely especially important in a predator that must engulf and swallow whole prey. A thick, resistant shell is an important defense against both crushing predators and physical factors in shallow, high-energy Cenozoic marine environments. The development of a shell form with these features, involving no anatomically new structures but mainly changes in proportions, and in combination with prior possession of a well-developed harpoon-like radular tooth and venom apparatus, may have been the key innovation leading to the major radiations of *Conus.* At present this hypothesis is speculative, and tests, such as those proposed by Coddington (1988) and Lauder & Liem (1989), must await improved knowledge in an area presently completely unknown but certainly amenable to study, the phylogeny of

the Conidae. However, available evidence from the Paleogene and especially Neogene radiations suggest that strongly but stylishly shelled, *Conus* is a young, upwardly mobile, progressional genus, albeit at a snail's pace.

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TURRID GENERA AND MODE OF DEVELOPMENT: THE USE AND ABUSE OF PROTOCONCH MORPHOLOGY

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ABSTRACT

Two contrasted protoconch morphologies (multispiral vs. paucispiral) are correlated in Turridae, as in other Caenogastropoda, with modes of larval development (respectively planktotrophic vs. non-planktotrophic). The multispiral vs. paucispiral dichotomy has been used extensively to denote phylogeny and recognize genera, a practice unique to Turridae that resulted in Powell's "phenomenon" of "turrid pairs." Because planktotrophy can be lost repeatedly and independently from a given ancestor, Powell's system fails to provide a phylogenetic classification: it leads to artificial polyphyletic genera, each characterized by a single protoconch type, but not necessarily deriving from a common ancestor. A group of turrid species possessing multispiral and paucispiral protoconchs should not be split into different (sub)genera when their teleoconch, radula and anatomical characters otherwise indicate that a single clade is involved. However, sculptural types among planktotrophic type protoconchs are considered to have taxonomic utility at supraspecific levels.

Key words: Turridae, protoconch, larval development, taxonomy, phylogeny.

INTRODUCTION

With 679 genus-group taxa and probably as many as 10,000 Recent and fossil nominal species, the family Turridae ranks as the most speciose of all marine gastropods. Tryon (1884) was the last author to try to monograph the Recent species of the family worldwide. This task has probably been considered unrealistic by later authors, who have mostly been working on a regional and/or stratigraphic basis. Species-level taxonomy in the Turridae offers no more problem than in other marine gastropod families, except perhaps that large series of specimens are only rarely available for an appraisal of variation. By contrast, considerable difficulty in recognizing good classificatory characters at supraspecific levels has been frequently expressed in the literature, emphasis being variously laid by different authors on conchological, radular or anatomical characters.

Controversy as to the value of the protoconch as a guide to phylogeny has continued unabated over the years (Kilburn, 1983). In the present paper, I review how the protoconch has been used by paleontologists and zoologists in supraspecific turrid taxonomy. I demonstrate that mode of larval development alone cannot be used to recognize genera or subgenera. I conclude that the so-called "turrid pairs" of genera are most likely to be polyphyletic and should be abandoned in taxonomic practice in the family. Finally, I discuss the taxonomic utility of styles of ornamentation and conclude that such morphological details are useful in planktotrophic protoconchs.

REVIEW

The "Phenomenon" of "Turrid-pairs"

As other marine prosobranchs, Turridae exhibit two major types of protoconchs: (a) a multispiral—Powell (1942) also used the term "polygyrate"—protoconch, with a small protoconch I, and a protoconch II consisting of 2-5 whorls, often with an elaborate sculpture of ribs and cords; and (b) a paucispiral protoconch, with no distinction between protoconchs I and II, consisting of 1-2 whorls with a large nucleus, and a simpler, stouter sculpture, or no sculpture at all.

Although protoconchs had been previously used by malacologists before in gastropod taxonomy, it was certainly Powell who first formalized a system using protoconchs in routine supraspecific taxonomy in the Turridae. Through his monumental work on New Zealand and worldwide turrids (Powell, 1942, 1966), Powell has profoundly influenced modern taxonomic practice, and these two papers are cited in almost every paper on tur-

rid supraspecific taxonomy published in the last few decades.

Powell's (1942) opinion is worth citing in full here: "A certain number of genera appear to occur in parallel series, being alike in adult shell features and evidently of common origin, but by their respective protoconchs they are separable into polygyrate and paucispiral series. In all these instances I have treated these parallel developments as distinct genera, for differences in the embryo are surely of basic biological importance." And further: "Much criticism has been levelled at the employers of protoconch criteria in the family, but in all these objections the fault seems to lie in the failure of rigid application of these criteria. If we refuse to admit more than one style of protoconch in a genus these anomalies disappear."

On Powell's authority, this opinion later became an established, almost unchallenged dogma entrenched in turrid taxonomic practice, and genera have been and are being recognized based on this single character (e.g. Powell, 1942, 1964; van Aartsen & Fehrde Wal, 1978; Gougerot & Le Renard, 1981; van Aartsen et al., 1984; Bernasconi & Robba, 1984; van Aartsen, 1988). Examples of such "turrid pairs" include:

Mangelia Risso, 1826 (multispiral) / *Mangiliella* Bucquoy, Dautzenberg & Dollfus, 1883 (paucispiral) (Fig. 1).
Raphitoma Bellardi, 1847 (multispiral) *Philbertia* Monterosato, 1884 (paucispiral).
Bela Gray, 1847 (multispiral) / *Fehria* van Aartsen, 1988 (paucispiral).
Lophiotoma Casey, 1904 (multispiral) / *Lophioturris* Powell, 1964 (paucispiral).
Parasyrinx Finlay, 1924 (multispiral) / *Lirasyrinx* Powell, 1942 (paucispiral).

Protoconch Morphology and Turrid Larval Development

A general correlation between protoconch morphology and mode of larval development has been demonstrated (Thorson, 1946; Shuto, 1974; Robertson, 1976; Jablonski & Lutz, 1980, 1983) and may be examined here with reference to what is known of turrid larval biology.

Most described turrid egg-capsules are ovoid and lenticular, with a central dorsal plug, and attached by the ventral side to the substrate (Lebour, 1934; Thorson, 1946; Knudsen, 1950; Bandel, 1976; Bouchet & Warén, 1980). A notable exception is the egg-capsules of the subfamily Clavatulinae, which are stalked and purse-shaped (Kilburn, 1985). A capsule contains several dozens to a few hundred eggs. Nurse eggs have not been reported.

As is frequent with species with planktotrophic larval development, the complete development, from oviposition to metamorphosis, has not been followed for any single specimen, but evidence can be derived from numerous scattered and fragmentary data. Turrid veligers, although never abundant, are frequently recorded in meroplankton samples (Franc, 1950; Richter & Thorson, 1975; Lebour, 1934; Thiriot-Quiévreux, 1969, 1972) and exhibit a broad range of morphological/sculptural types (Kay, 1979, and personal observations). From published observations, the behaviour of such veligers is similar to that in other gastropod planktotrophic veligers, i.e. the larvae actively swim in the epipelagic layers of the water column while feeding on phytoplankton. These veligers have protoconchs of the multispiral type (Fig. 1a); the larvae of the many deep-sea turrids that undertake ontogenetic vertical migrations (Bouchet & Fontes, 1981; Killingley & Rex, 1985) enter into this category. The planktonic phase is a period of active feeding and very active growth, and the whole protoconch II is secreted during this planktonic planktotrophic phase. The total length of the planktonic phase is not known with precision and certainly varies between species, but by comparison with other prosobranch families a range from three to eight weeks is a likely estimate.

The complete larval development of *Oenopota levidensis* (Carpenter, 1864), a species with paucispiral larval shell, has been described with considerable detail based on laboratory observations (Shimek, 1986). Development to a veliger occurs within the egg-capsule in about 50 days. After hatching, the larvae swim actively for a period of a few days, and then live a demersal life on the bottom of the culture vessel. The larvae were experimentally fed with algal suspensions; shell and velar dimensions increase during the swimming phase, after which the veliger does not get appreciably larger, and by the 15th posthatching day, the protoconchs are fully formed. Demersal development then continues without shell growth and the veligers metamorphose after 25 days.

Based on these observations, Shimek (1986) concludes that paucispiral proto-

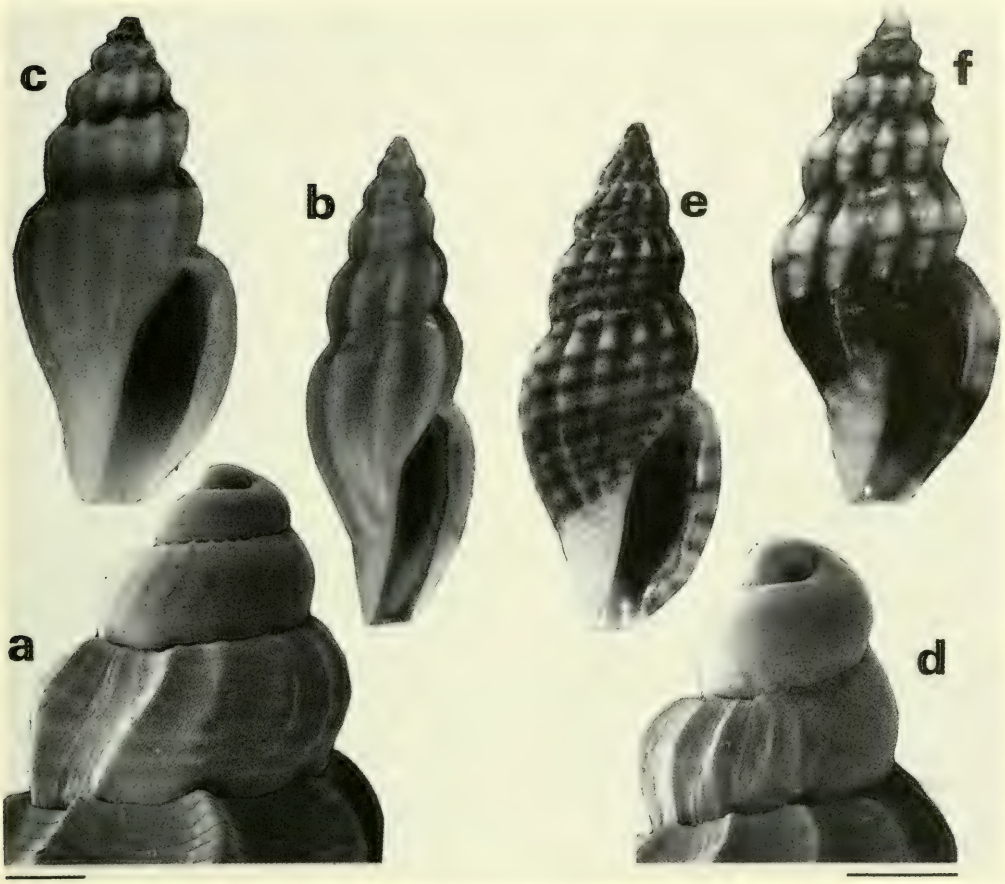


FIG. 1. The multispiral (1a) and paucispiral protoconch (1d) define respectively the genera *Mangelia* and *Mangiliella*. There is no evidence that *Mangelia striolata* Risso, 1826, (1b) and *M. vauquelini* (Payraudeau, 1826) (1c) are more closely related to each other than they are to *Mangiliella multilineolata* (Deshayes, 1833) (1e) or *M. taeniata* (Deshayes, 1833) (1f). *Mangiliella* should be synonymized with *Mangelia*. 1b = 7.8 mm; 1c = 9.0 mm; 1e = 5.7 mm; 1f = 5.5 mm. Scale lines 200 μm.
All specimens from Calvi, Corsica.

conchs in turrids cannot be interpreted as evidence for lack of a planktonic stage, as claimed by Thorson (1935, 1946). A development with intracapsular metamorphosis had been inferred in Atlantic Arctic *Oenopota* by Thorson from the contents of egg capsules, because there is no appreciable size difference between the shells of intracapsular embryos ready to hatch and the smallest benthic juveniles. Shimek's observations certainly demonstrate that a long demersal phase may occur in species with paucispiral larval shells. However they do not, in my opinion, weaken the distinction between planktotrophic and non-planktotrophic larval development. I fully admit that the duration of the post-hatching phase in *O. levidensis* may probably equal the duration of some of the shorter-lived planktonic planktotrophic veligers. The short initial free-swimming planktonic phase aside (though this is admittedly important in terms of dispersal), the biology of the veliger of *O. levidensis* is markedly different from that of planktotrophic veligers: it does not swim, except for brief moments following artifical stimulation, and it does not grow or secrete pro-

toconch shell material. By contrast with species with multispiral protoconchs, the isotopic composition of the shells of deep-water turrids with paucispiral protoconchs indicates that a vertical ontogenetic migration does not occur (Killingley & Rex, 1985).

Just as the duration of the planktonic phase varies among species with planktotrophic development, the duration of the swimming and demersal phases may be expected to vary considerably between species with non-planktotrophic development. Whether the case of *Oenopota levidensis* represents an average duration or an extreme is not known. Kilburn's (1985) observation that in the paucispiral protoconch of *Clavatula tripartita* (Weinkauff, 1876) "the defining varix precedes the veliconch lip by about one-sixth of a whorl" may be an indication that a swimming phase is also present. Clearly, more data are needed on the the larval biology of additional species. In particular, it would be of great interest to know if the larval biology of warm-water turrids with paucispiral larval shells conforms to the pattern described for the cold-water *Oenopota levidensis*. Knudsen (1950) described the egg-capsules and contained embryos of several West African continental shelf turrids, and inferred lecithotrophic or "direct" development. Non-planktotrophic larval development has been inferred from protoconch morphology in numerous temperate, tropical and deep-water turrids.

Available evidence in the family Turridae therefore confirms the general correlation between protoconch morphology and mode of development. This correlation, which had been assumed by Powell (1942 and later papers) based on the data then available in other prosobranch families, is applicable to Recent as well as fossil turrids.

Polarity of Changes in Protoconch Morphology

Although the mode of development, and hence protoconch morphology, is a species-specific character throughout the range of a species (Hoagland & Robertson, 1988; Bouchet, 1989), it is known to change through time in monophyletic lineages (see references below).

Powell (1942), certainly influenced by Finlay (1931), believed the paucispiral protoconch / "sedentary larva" type to represent the ancestral condition, and the multispiral protoconch / "free swimming larva" type to represent the derived condition. He moreover believed this change ot be irreversible: "When once the radical embryonic change from a sedentary to a free swimming larva takes place, both types appear to develop independently, for there is no evidence suggesting indiscriminate change and rechange between these two types of embryos. It would seem rather that the 'Sinusigera' apex is an evolutionary culmination from the less efficient paucispiral type." This is, I think, a good example of circular reasoning. How can changes in protoconch morphology be recognized if, by definition, they are used to distinguish genera?

Contrary to Powell's assumption, the evidence throughout marine invertebrates is that planktotrophic larval development represents the ancestral (plesiomorphic) condition and the loss of planktotrophy is a derived (apomorphic) condition (Strathmann, 1978, 1985). Strathmann (1978), however, argues that the loss of planktotrophy is in theory reversible as long as the larval ciliary opposed band system of feeding is not lost during intracapsular development. Such is the case in *Oenopota levidensis* (Shimek, 1986), so that reacquisition of planktotrophy is in theory possible in a descendant of that species.

The final answer to this question can only be found in the study of modes of development in fossil and Recent species, because biological time is too short for an approach other than theoretical. However, in the Turridae, there are presently no available data that combine (a) description of a small lineage through time, and (b) description of protoconch types without a preconceived idea on their significance in classification.

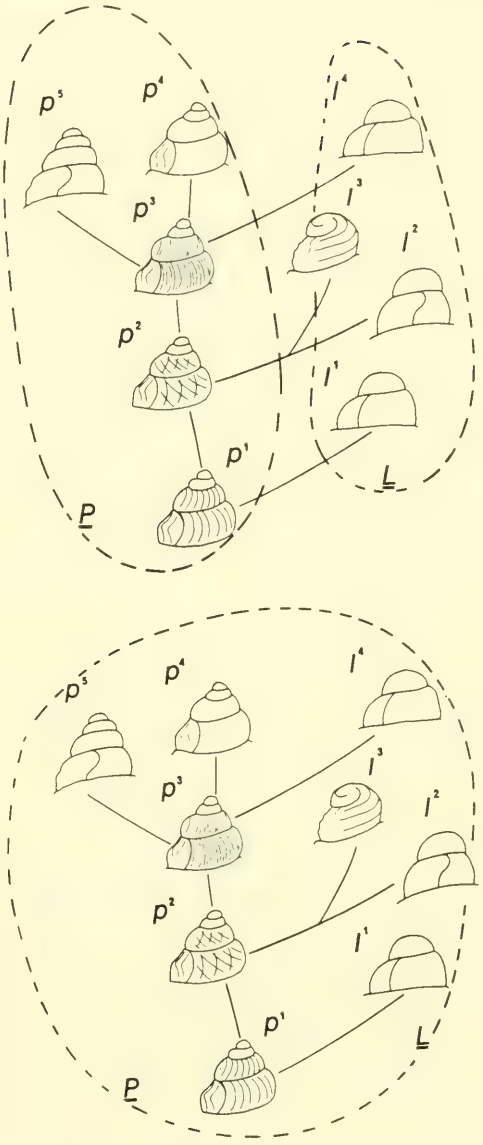
Fragmentary data are scattered throughout the taxonomic literature on Caenogastropoda: in Neogene to Recent eastern Atlantic Terebridae (Bouchet, 1981); in Paris Basin Eocene *Triforis* (Gougerot & Le Renard, 1980); in Pliocene to Recent Mediterranean nassariids (Martinell & Cuadras, 1977) and *Trophon* (Bouchet & Warén, 1985); in Neogene to Recent eastern American *Ficus* (Smith, 1945); in North American Paleogene Volutidae (Hansen, 1983). All these papers point out many examples of changes from multispiral to paucispiral protoconchs (loss of planktotrophy), but not a single case of change from paucispiral to multispiral protoconchs (reacquisition of planktotrophy) is recorded. Therefore, although reacquisition of planktotrophy is theoretically embryologically

feasable, evidence is still wanting, and in this paper my working hypothesis is that the loss of planktotrophy in Turridae is, as a rule, not a reversible phenomenon.

Refutation of Mode of Development as a Generic Character

If Powell's system of genera was applicable to Turridae, it should equally be applicable, on the same basis, to other families of marine gastropods. As reviewed above, protoconch morphology correlates with mode of development. If the planktotrophic / non-planktotrophic dichotomy is to be given generic value in the Turridae, then logically it should also be given the same value in other Caenogastropoda. However, there are many examples of genera (e.g. *Nassarius, Chicoreus, Alvania, Littorina*) that are believed to be monophyletic and that contain both species with planktotrophic and non-planktotrophic larval development. As a matter of fact, there are sibling species in many genera that are distinguished only on the basis of their mode of development (Hoagland & Robertson, 1988; Bouchet, 1989). Recognition of genera based only on the paucispiral vs. multispiral dichotomy has been explicitly rejected by Robertson (1976) in general and by Marshall (1978, 1983) in the families Cerithiopsidae and Triphoridae. The practice is indeed quite restricted to Turridae (but has already been challenged by Kilburn, 1983), but it is not justified by any larval biology feature that would be unique to turrids.

Genera that are established on the paucispiral vs. multispiral dichotomy are prone to be artificial and polyphyletic. I have in Figures 2 and 3 presented a hypothetical evolutionary tree starting from an ancestor with multispiral larval shell. Through speciation and anagenetic evolution, this ancestral species (P 1) gives rise to local shorter-lived species that have lost planktotrophy (L 1 to L 4), and longer-lived species that retain planktotrophy (P 2 to P 5). That species with non-planktotrophic development are more local and outlived by species with planktotrophic development has been both predicted (Scheltema, 1977), and noticed (Powell, 1942; Hansen, 1978, 1980, 1983; Jablonski, 1982, 1986) in the fossil record. Loss of planktotrophy can occur independently several times through various evolutionary scenarios, such as insular endemism or relict distribution resulting from changes in the climatic and/or geo-



FIGS. 2–3. Hypothetical evolutionary tree of a turrid lineage. In Powell's system of genera (Fig. 2, above), the species with paucispiral protoconchs are grouped in one genus, although they do not share a common ancestor, and the species with multispiral protoconchs in another genus. Such genera are respectively polyphyletic and paraphyletic. In the absence of detailed knowledge on the tree (and this is by far the most frequent situation in Turridae), the most parsimonious solution is a single genus comprising species both with multispiral and paucispiral protoconchs (Fig. 3, below).

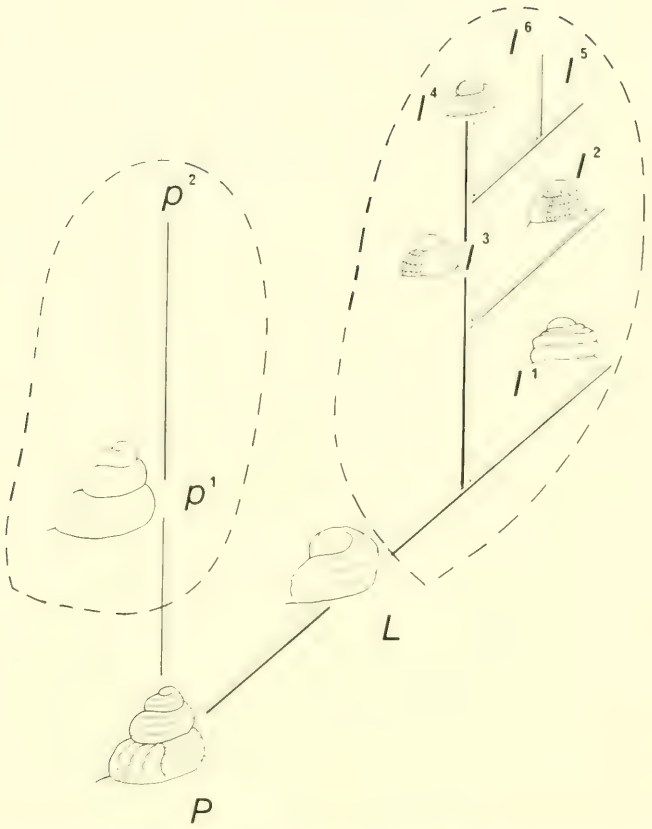


FIG. 4. Loss of planktotrophy may permit an adaptive radiation. This character may then be expressed in classification. A genus defined by a paucispiral protoconch is monophyletic and perfectly acceptable. All species with paucispiral protoconch are derived from a common ancestor.

graphic environments. According to Powell's system, all species with paucispiral larval shells (L 1 to L 4) are classified into one genus, and species with multispiral larval shells (P 1 to P 5) in another. It is obvious that any one of species L 1, L 2, or L 4 is more closely related to its immediate ancestor with multispiral larval shell than it is to other species with the same protoconch morphology. The genus *L* is not based on parental affinities and should therefore be rejected. I would therefore regard as valid a single genus encompassing all the species descended from P 1, whatever their mode of larval development.

In other words, when teleoconch, radula and anatomical characters indicate that a single evolutionary clade is involved, protoconch morphology should not be used to split it into different genera based on the mode of development. Subgenera based on the same concept are no more acceptable, since their polyphyletism would not be more justifiable. This view is not revolutionary in turrid taxonomy, and a number of authors have already allowed differing modes of development to coexist within a single turrid genus (e.g. Bouchet & Warén, 1980; Kilburn, 1983; Maes, 1983).

It may be worth noting, at this point, that even if the loss of planktotrophy was, contrary to my assumption, reversible, then the above conclusion remains valid.

This does not of course necessarily mean that all turrid genera have or should have both species with paucispiral and species with multispiral protoconchs. Loss of planktotrophy may represent the onset of an adaptive radiation, such as in an insular or polar environment (Fig. 4). All known Recent *Oenopota* have paucispiral protoconchs (Bogdanov, 1989), and all Pliocene *Oenopota* apparently already had the same mode of development (Harmer, 1914-19; Beets, 1946). Although I

fully expect that somewhere in the ancestry of *Oenopota* there is a species with multispiral larval shell, it is obvious that the loss of planktotrophy has permitted an adaptive radiation in the arctic/subarctic environment where planktotrophy is selected against, and a paucispiral protoconch is now certainly a hallmark of *Oenopota*.

Admittedly, each of the successive speciation events by loss of planktotrophy in Figure 2 represents a discrete radiation event, and one could imagine a nomenclature with L 1, L 2 + L 3, and L 4 each in a different genus. In my view, this should not be recommended in the present state of our knowlege: much of our genus-level and species-level taxonomy is based on shell characters only, and this is all we will ever have in the many fossil taxa. The state of the art in turrid taxonomy is such that these discrete monophyletic genera cannot be easily recognized. Splitting and recognition of many monotypic genera with paucispiral larval shell will not help our understanding of turrid evolution and, considering the sheer size of the family, is most likely to result in absolute chaos.

What Future for the Turrid Protoconch as a Supraspecific Character?

After all that has been said above, is there a future left for the use of protoconch in turrid taxonomy? That the paucispiral vs. multispiral dichotomy has no supraspecific taxonomical significance does not imply that just any kind of protoconch is to be expected in a turrid genus.

The consequence of the genus concept advocated here is that paucispiral protoconchs should only be compared with paucispiral protoconchs, and multispiral protoconchs with multispiral protoconchs.

Accompanying the loss of planktotrophy, paucispiral protoconchs have few distinctive characters (see however Bodganov, 1989), and extensive parallelism and convergence between distant, unrelated taxa is the rule. It is very unlikely that these protoconchs have a promising future in turrid classification. By contrast, as has been noted above, the morphology and sculpture of planktotrophic turrid veligers is remarkably diverse and present a vast array of characters that have not yet been fully appreciated. I believe that different sculptural types within the multispiral protoconch have a profound taxonomic meaning, just as teleoconch characters happen not to be random within a genus. *Neopleurotomoides* was segregated from *Pleurotomella* despite extremely similar teleoconchs, because the sculpture of their multispiral protoconchs differ fundamentally (Shuto, 1971): respectively two spiral keels with axial pillars, and diagonal cancellation extending over most of the whorl. (It is worth noting here that, at this stage of our knowledge, a species with paucispiral larval shell cannot be attributed to *Pleurotomella* or *Neopleurotomoides,* an obvious difficulty with the genus concept advocated in the present paper.)

What remains for the future is to identify what are the basic sculptural types, evaluate the degree of convergence (for instance, has the diagonally cancellated sculpture appeared only once?), and understand how secondary sculptural types can be derived from more fundamental ones. There is certainly a rich and rewarding future use of turrid protoconchs in taxonomy.

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TURRID FAUNAS OF PACIFIC ISLANDS

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ABSTRACT

Of the more than 300 species in 45 genera and seven subfamilies of Turridae described or recorded from the shallow waters (<100 m) of the tropical Pacific, 160 species are recognized as occurring on the islands of the central Pacific. Compared with the turrids of continental shorelines (tropical west America and New Zealand), the Daphnellinae are better represented and the Clavinae less well represented on central Pacific islands. The turrids in general comprise a lesser proportion of the gastropod fauna, and shells in all turrid subfamilies are smaller on average. Species distribution is patchy and endemism is high in the Hawaiian Islands (47%) and at Easter Island (80%). Less than 30% of the central Pacific turrids are widespread in the Indo-Pacific, nearly 40% also occur in the western Pacific, and about 30% are known only from the Pacific Plate. Nearly 50% of the genera represented on the Pacific Plate apparently lack a fossil record.

Key words: Turridae, biogeography, Indo-Pacific, distribution, island faunas.

INTRODUCTION

Members of the neogastropod family Turridae are among the most numerous of marine gastropods. The family may include as many as 2,000 Recent species (Kilburn, 1983), 550 (Powell, 1966; McLean, 1971) to 679 (Bouchet, 1990) generic and subgeneric units, and from 9 to 15 subfamilies (Powell, 1966; McLean, 1971). Turrids are found throughout the world from the poles to the tropics, and from intertidal coral reefs to depths of more than 5,000 m in the abyssal regions of the sea. They can be both abundant and speciose. In the deepwaters of the Atlantic, they are the most abundant mollusc group in terms of both number of specimens and number of species (Bouchet & Warén, 1980), and more than 30% of the described Alaskan, Arctic, and North Pacific boreal shallow-water gastropods are turrids (Shimek, 1986). Turrids of the tropical Pacific Ocean are not so easily quantifiable, despite the fact that more than 900 species names have been proposed or recorded for turrids in that area.

This study represents an initial analysis of turrid species composition and distribution in three major island groups in the central Pacific, the Marshall Islands (Enewetak), the Hawaiian Islands, Tahiti and the Tuamotus (French Polynesia). The turrids from these islands are also examined in terms of several of the generalizations now recognized as pertaining to the distribution of marine organisms in the Pacific (cf. Kay, 1980; Kay, 1984). Is there an attenuation of species and higher taxonomic groups from west to east across the Pacific? Are the relationships of Pacific island turrids to the west rather than the east? Is there a distinctive Pacific Plate element in the fauna?

MATERIALS AND METHODS

Collections

A long-term study of the turrids of Pacific islands, particularly those of the Hawaiian Islands; Enewetak, Marshall Islands; Fanning Island, Line Islands; and Guam, Mariana Islands, has permitted collection in the field and comparison of field-collected material with type and reference collections in the Academy of Natural Sciences Philadelphia (Pease and Garrett types); Australian Museum, Sydney (Hedley and Laseron collections); B. P. Bishop Museum, Honolulu, Hawaii (Thaanum collection of Okinawan turrids and material identified by Dall); The Natural History Museum, London (Cuming collection, Reeve types, Melvill and Standen material); the Musée d'Histoire Naturelle, Paris (Hervier, Crosse and Souverbie types); the Museum of Comparative Zoology, Harvard University (Pease collection); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Dall, Pease and Garrett

TABLE 1. Numbers of turrid species described from the Pacific 1800–present. Western Pacific includes the Philippines, Queensland, Malayan archipelago, Lifu, Fiji. Fossil species included.

YEAR	WESTERN PACIFIC	PRINCIPAL AUTHORS	CENTRAL PACIFIC	PRINCIPAL AUTHORS
1800–1825	3	Lamarck		
1826–1850	138	Reeve, Hinds	14	Reeve
1851–1875	48	Garrett, Gould, Souverbie	61	Garrett, Pease, Dunker
1876–1900	203	Hervier, Melvill and Standen	8	Dall, Smith
1901–1925	241	Hedley, Schepmann	4	Dall
1926–Present	74	Ladd, McNeil, Shuto, Noda	26	Kay, Powell

material: Ladd Enewetak and Bikini fossil types); and the National Museum of Wales, Cardiff (Tomlin collection). I rely also on the published work of Dautzenberg & Bouge (1933), Hedley (1922), Hervier (1896–1898), Melvill & Standen (1895–1897), and Richard (1982) to augment species lists compiled from museum and field collections.

Turrid Taxonomy

Turrid taxonomy remains a major problem in the understanding of turrid systematics and distribution. The importance of radular studies in the Turridae has been discussed by McLean (1971) and Kilburn (1983, 1985, 1988). The nature of the material that serves as the bases for this study for the most part precluded study of radulae, and placement of turrids in subfamilies herein is largely based on conchological features recognized by Powell (1942, 1966), that is, position of the sutural gap and protoconch type. Although it is widely recognized that shell type can no longer be considered a valid generic or subgeneric criterion, I nevertheless find that protoconch form does seem to provide insight into subfamilial placement of many turrid species.

Seven subfamilies are recognized here as occurring in the island Pacific, the Turrinae of Powell (1966, 1967, but excluding *Turridrupa*); Crassipirinae (of Kilburn, 1983, including *Turridrupa*); the Drilliinae *sensu* McLean (1971) and Kilburn (1988); the Mangeliinae and Daphnellinae *sensu* Powell (1966); the Borsoniinae, as recognized by Kilburn (1986); and the Cochlespirinae (of Powell, 1966).

To arrive at an estimate of the numbers of turrid species associated with the tropical Pacific *sensu lato* and specifically with the islands of the central Pacific, the number of turrid species described from the western Pacific (Philippines, Queensland, Lifu, New Caledonia, Fiji) and the central Pacific (Hawaii, French Polynesia, Samoa, etc.) was counted, and other species referred to the Pacific included in the list. More than 850 turrid species have been described from the Pacific (*sensu lato*) since 1800, of which less than 15% were described from islands in the central Pacific (Table 1). An additional 75-100 species have been recorded from the tropical Indo-Pacific, for example species described from Réunion by Deshayes and the northern Indian Ocean by Nevill. The total list was then culled for synonyms and other errors and is here reduced to about 160 species referable to the central Pacific islands.

Pacific Island Biogeography

Definitions utilized to delimit the islands of the central Pacific and their associated biogeographic regions, the Indo-Pacific and the western Pacific (Fig. 1) are as follows. By Indo-Pacific is meant "the Indian Ocean including contiguous seas, and the Pacific Ocean as far east as Easter Island but excluding the area occupied by the coast and offshore islands . . . of the Western Hemisphere" (Springer, 1982). The western Pacific is distinguished as the Pacific Ocean west of the western margin of the Pacific lithospheric plate which includes such inland seas as the South China Sea, Arafura Sea, and Coral Sea (Springer, 1982), and the islands of Lifu (Loyalty Islands), Fiji, Okinawa (Ryukyu Islands) and Guam (Mariana Islands). The "Pacific islands" of this study (Enewetak, Marshall Islands; Hawaii; and Tahiti and Tuamotus, French Polynesia) are primarily on non-marginal portions of the Pacific Plate.

THE TURRIDS OF PACIFIC ISLANDS

The distribution of the currently recognized 160 species in six subfamilies is shown in Fig-

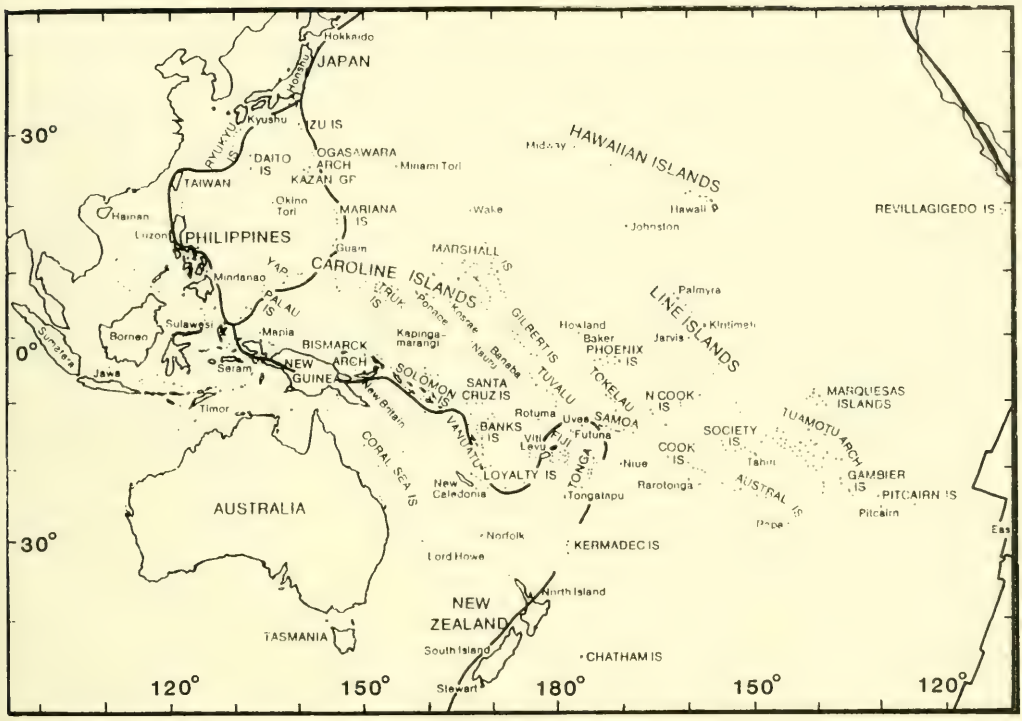

FIG. 1. The Pacific Ocean showing the margins of the Pacific Plate and major island groups.

ure 2. About 90% of the Pacific island turrids represent four subfamilies: the Mangeliinae (43%), the Daphnellinae (29%), the Drilliinae (9%), and Turrinae (7%). The remaining turrids include the Crassispirinae (7%), Borsoniinae (4%), and Cochlespirinae (1%). Subfamily representation confirms Powell's (1966) summary of turrid distribution in the Pacific: "In the atolls, reefs and small isolated island groups of the Indo-Pacific, large turrids are either absent or poorly represented: *Lophiotoma acuta* is almost the only exception, the faunules being composed mainly of small mangelinids and daphnellids. The most characteristic mangelinid genera of the islands of the Indo-west Pacific are *Eucithara, Lienardia, Etrema, Macteola,* . . .".

More than 80% of the turrid species associated with central Pacific islands are small (<5 mm in length), and the shells are sturdy and colorful. Except in the turrines and the deep-water daphnellines, shell form is marked by a short siphonal canal and usually reinforced labial extremity. Most of the shells also represent subfamilies that are characterized by elaborate protoconchs (i.e. Daphnellinae and Mangeliinae). Veligers of daphnellines and mangelines in Hawaii have been raised for periods of several weeks (J. B. Taylor, 1975). *Iredalea exilis* (Pease, 1868) (Drilliinae) among the shallow water turrids is the only species with the protoconch of the type associated with direct or lecithotrophic development.

Most of the central Pacific island turrids are known from depths of less than 30 m, and are commonly found at depths of 10–20 m on the fore-reef in rubble and sand. Only one species, *Iredalea exilis,* is frequently found in the intertidal on reef flats. Eleven species are recorded from depths of more than 300 m, nine species dredged in the Hawaiian Islands and two-*Pleurotomella dubia* Schepmann, 1913, and *P. allisoni* Rehder & Ladd, 1973-dredged from depths of more than 1,000 m on guyots in the mid-Pacific mountains (Rehder & Ladd, 1973).

The shallow water turrids of central Pacific islands are neither numerous nor abundant. Turrids feed mainly on polychaetes (J. D. Taylor, 1977; Maes, 1983), and they comprise about 15% of the predatory gastropod spe-

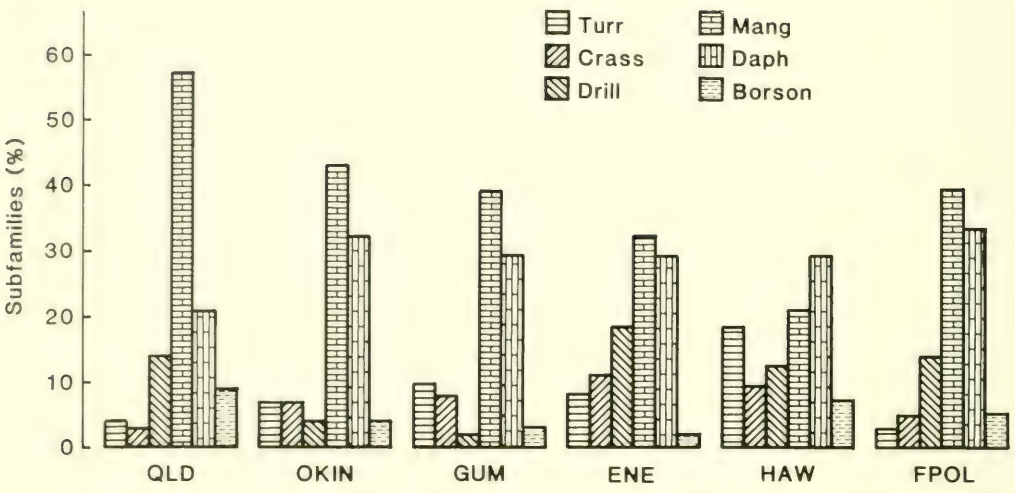

FIG. 2. Subfamily composition in Pacific Turridae. QLD, Queensland; OKIN, Okinawa; GUM, Guam; ENE, Enewetak, HAW, Hawaii; FPOL, French Polynesia. Turr, Turrinae; Crass, Crassispirinae; Drill, Drilliinae; Mang, Mangeliinae; Daph, Daphnellinae; Borson, Borsoniinae.

cies, in contrast to 27% and 25% respectively in New South Wales and New Zealand (Iredale & McMichael, 1962; Powell, 1979); 31% on the tropical west American coast (Keen, 1971); and an average of 7% on islands in the Indian Ocean (J. D. Taylor, 1977). Little is known of turrid biology in the Pacific, although J. D. Taylor (1984, 1986) notes the polychaete diet of four species on Guam, and refers (J. D. Taylor, 1984) three species to the polychaete feeding guild in a partial food web on a fringing reef on Guam.

The distribution of species among the islands is patchy (Table 2). Only 10 species (6%) are recorded from all three island groups. Enewetak and Hawaii share 19% of the 114 species occurring in both island groups, and French Polynesia and Hawaii share 15% of 123 species.

From west to east across the Pacific, the numbers of turrid species decrease from 180 species recorded along the Queensland coast of Australia (Hedley, 1922) to 76 species in French Polynesia, and from 100 species in the Philippines and Okinawa (Kuroda, 1960) to about 70 species respectively at Enewetak (Kay & Johnson, 1987) and in the Hawaiian Islands (Kay, 1979) (Figure 3). The decrease in number of turrid species is not the same in all subfamilies. The Turrinae gradually increase in percentage composition across the Pacific from 5% on the Queensland coast to 18% in Hawaii, but are apparently reduced in importance in French Polynesia, where only two species are recorded (Richard, 1982; Salvat & Rives, 1979). The Mangeliinae, representing 57% of the Queensland turrid list decrease to 21% of the Hawaiian list and increase to 39% of the list in French Polynesia (Fig. 2).

Biogeographic Components

Three biogeographical components are identified: 39% of the Pacific island turrids also occur in the western Pacific but are not reported further west in either the Indo-Malayan archipelago or the Indian Ocean; 31% are recorded only from the Pacific Plate; and 29% are widespread within the Indo-Pacific, many of them found as far west as the coast of Natal. Two species, *Microdaphne trichodes* Dall, 1910 (McLean, 1971), and *Kermia maculosa* (Pease, 1860) (Shasky, 1983), also occur on the west coast of the Americas; both appear to be Indo-Pacific species that have crossed the East Pacific Barrier.

The relative importance of the subfamilies differ among the three regional components of the fauna: in the Indo-Pacific faunal component, 47% of the turrids are daphnellines; and in the western Pacific and Pacific Plate components, 45% and 35% of the turrids respectively are mangelines (Fig. 4). There is a conspicuous component of Pacific Plate endemism in all the subfamilies, but it is especially noticeable in the Turrinae (56%), all of which are endemic to the Hawaiian Islands.

TABLE 2. Distribution records for 25 turrid species recorded from central Pacific Islands. Single island occurrences are not included. Xs represent occurrence.

SPECIES	ENEWETAK, MARSHALL IS.	HAWAIIAN ISLANDS	FRENCH POLYNESIA
Mitromorpha metula (Hinds, 1843)	xxxxxxxxx	xxxxxxxxx	xxxxxxxxx
Carinapex minutissima (Garrett, 1873)	xxxxxxxxx	xxxxxxxxx	xxxxxxxxx
Iredalea exilis (Pease, 1868)	xxxxxxxxx	xxxxxxxxx	xxxxxxxxx
Daphnella ornata (Hinds, 1844)	xxxxxxxxx	xxxxxxxxx	xxxxxxxxx
Lienardia crassicostata (Pease, 1860)	xxxxxxxxx	xxxxxxxxx	xxxxxxxxx
Daphnella flammea (Hinds, 1843)	xxxxxxxxx		xxxxxxxxx
Kermia clandestina (Deshayes, 1863)	xxxxxxxxx		xxxxxxxxx
Psudodaphnella tincta (Reeve, 1846)	xxxxxxxxx		xxxxxxxxx
Clavus pica (Reeve, 1843)	xxxxxxxxx		xxxxxxxxx
Xenuroturris cingulifera (Lamarck, 1822)	xxxxxxxxx		xxxxxxxxx
Lophiotoma acuta (Perry, 1811)	xxxxxxxxx	xxxxxxxxx	
Xenuroturris kingae (Powell, 1964)	xxxxxxxxx	xxxxxxxxx	
Turridrupa albofasciata (Smith, 1877)	xxxxxxxxx	xxxxxxxxx	
Tritonoturris amabilis (Hinds, 1843)	xxxxxxxxx	xxxxxxxxx	
Daphnella olyra (Reeve, 1845)	xxxxxxxxx	xxxxxxxxx	
Mitromorpha alphonisana (Hervier, 1899)		xxxxxxxxx	xxxxxxxxx
Kermia pumila (Mighels, 1845)		xxxxxxxxx	xxxxxxxxx
Clavus exilis (Pease, 1868)		xxxxxxxxx	xxxxxxxxx
Lienardia lutea (Pease, 1860)		xxxxxxxxx	xxxxxxxxx
Lienardia mighelsi (Iredale, 1917)		xxxxxxxxx	xxxxxxxxx

Guam, in the southern Marianas Islands, and Okinawa, both of which are on the Philippine Plate, have turrid faunas that are similar in species composition and habit to those of the central Pacific islands (Fig. 2). As with the central Pacific island turrids, there is a strong Daphnellinae and Mangeliinae component in these faunas.

Fossil Record

There is no clear direction to the fossil record of Pacific island turrids, unless it is that about 50% of the genera represented in the islands of the central Pacific apparently lack a fossil record. There are Miocene and Pliocene records for *Mitromorpha* (Borsoniinae) and *Daphnella* and *Philbertia* (Daphnellinae) in Okinawa and Europe respectively, for *Inquisitor* and *Clavus* (Drilliinae) in the Pliocene of Java and Miocene of Borneo respectively, for *Anacithara, Etrema, Eucithara,* and *Lienardia* (Mangeliinae), and Miocene and Pliocene records for *Gemmula, Lophiotoma, Turris* (Turrinae) and *Turridrupa* (Claviinae) (Powell, 1966; Robba, 1987; Shuto, 1984). Among the genera and subgenera for which a fossil record is apparently lacking are: *Eucy-*

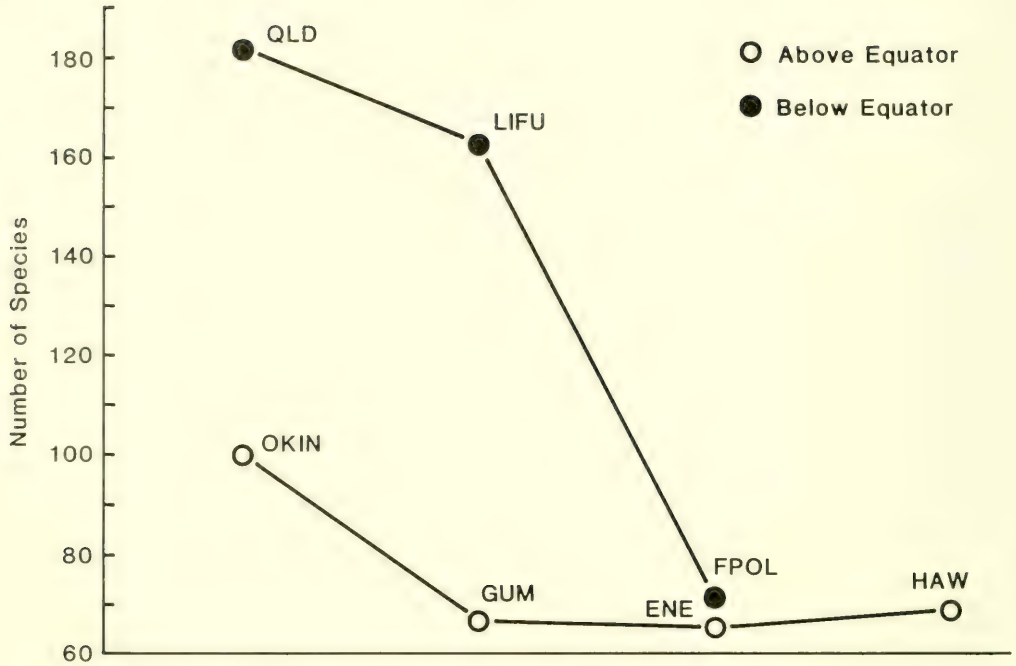

FIG. 3. Numbers of turrid species from west to east across the Pacific. Locality abbreviations as in Figure 2.

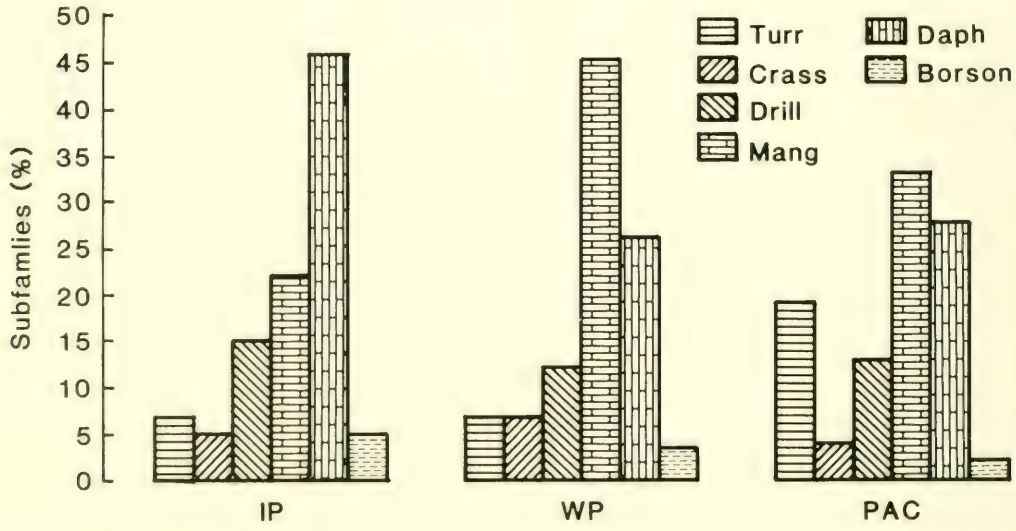

FIG. 4. Subfamily composition of Indo-Pacific species, Western Pacific species, and Pacific Plate species. IP, Indo-Pacific, WP, Western Pacific, PAC, Pacific Plate. Subfamily abbreviations as in Figure 2.

clotoma, *Kermia*, *Microdaphne*, *Pseudodaphnella*, *Tritonoturris*, *Iredalea*, *Macteola*, and *Paramontana*.

The evolution of the Indo-Pacific molluscan fauna can be traced to the ancient Tethys seaway which, from Triassic to Miocene time,

connected the Mediterranean and Indo-Pacific across what is now the Middle East and Pakistan (Kay, in press). The seaway was closed in Early Miocene (Adams, 1981), and the faunas of the Mediterranean and the Indo-Pacific evolved separately. Among the earliest turrids of Pakistan-India are Drilliinae in the Palaeocene *Cardita beaumonti* beds of the Upper Ranikot of Pakistan. In Indonesia, the earliest recognizable molluscan faunas are middle Miocene (Shuto, 1976), and there are representatives of the Drilliinae, Turrinae, Borsoniinae in that area. In the Pacific, several Miocene turrids (*Daphnella, Clavus, Inquisitor, Etrema, Anacithara, Eucithara, Lienardia, Gemmula, Lophiotoma,* and *Turris*) are recorded from Fiji and Okinawa. *Euclathurella, Gemmula,* and *Lophiotoma* are all recorded from the Pliocene of Fiji. The furthest east that fossil turrids are known is in the Marshall Islands, where Ladd (1982) described *Eucithara marshellensis* from the Miocene of Bikini and Enewetak.

DISCUSSION

Pacific island turrid faunas are characterized by a suite of characters consonant with insular coral reef habitats separated one from another by great distances. The relatively high proportions of mangelines and daphnellines result in faunas with small, sturdy shells and with protoconchs indicative of long larval life. Indeed, Kilburn (1988) has suggested that the shell form of short, sturdy shells with reinforced labial lips may have evolved as an adaptation to a reef or under-rock existence, as opposed to shells with a produced siphonal canal and non-reinforced labial extremity (the 'turrid facies') of the predominantly sand-dwelling Turrinae and Cochlespirinae. The Pacific island turrid assemblages, with their prominent daphnelline and mangeline components, with colorful shells and long larval lives, and comprising less than 15% of the predatory gastropods, contrast with a Caribbean island assemblage described by Maes (1983), which is rich in drillines with dark shells, most of which apparently have direct development.

The pattern of turrid distribution among Pacific islands follows a generally recognized pattern of a marine fauna of the Indo-Pacific (Kay, 1980): decreasing diversity west to east in the Pacific Ocean (Kay, 1980; Springer, 1982); patchy distribution (Kay, 1980; 1984); disproportionate representation in certain groups; and a recognizable component of species that are endemic to the Pacific Plate (Kay, 1980; Springer, 1982). On the Pacific Plate, the pattern of endemism follows that of other mollusks, with a group of species that is widespread, and with others of the turrids endemic to two foci, the Hawaiian Islands where 60% of the turrids are reported as endemic, and French Polynesia with 9%. No single island endemics as distinguished by Springer (1972) have been identified.

Although in broad outline the Pacific island turrid faunas fit the pattern of history and distribution of other marine mollusks, three aspects of the current review of Pacific island turrid faunas are vulnerable to the criticism of insufficient and biased collection: (1) the apparent concentration of species in the western Pacific; (2) the records of patchy distribution; and (3) the apparent lack of fossil record.

The prominent western Pacific element in the distributional pattern may be an artifact of collecting simply because of the enormous numbers of species described from the Philippines, Loyalty Islands, New Caledonia, and Queensland by Reeve, Hervier, Melvill and Standen, Hedley, and others. As the taxonomy of the several hundred species is worked out, many of the species may be shown to be invalid, and new collecting records will possibly extend the presently known ranges. The apparent patchy distribution of turrid species among the islands may also be misleading and with further collection such anomalies as the virtual absence of Turrinae in Tahiti may be rectified. The fossil history of Pacific island turrids is similarly subject to criticism in that so few fossil are actually known from Pacific islands.

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ULTRASTRUCTURAL CHANGES IN THE DIGESTIVE SYSTEM OF *DEROCERAS RETICULATUM* (MOLLUSCA; GASTROPODA) INDUCED BY LETHAL AND SUBLETHAL CONCENTRATIONS OF THE CARBAMATE MOLLUSCICIDE CLOETHOCARB

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ABSTRACT

Specimens of the grey garden slug, *Deroceras reticulatum,* were fed lethal (2%, 1%, 0.5%, 0.1%) or sublethal concentrations (0.01%, 0.001%) of the carbamate molluscicide Cloethocarb (BASF) as either pellets or wheat-germ agar. To investigate the influence of the chemical on the ultrastructure of the cells in the digestive tract, samples of oesophagus, crop, stomach, intestine and hepatopancreas were taken at six time intervals. Reactions of lethal intoxication (e.g. elongation of cells, damage to nuclei and mitochondria, destruction of membranes) were distinguished from those appearing most intensely after sublethal intoxication (e.g. reactions of the endoplasmic reticulum, Golgi apparatus, mucous cells) and finally from features that appear after both lethal and sublethal poisoning (e.g. reduction of storage products).

It could be shown that higher concentrations of the pesticide do not necessarily produce stronger effects at the ultrastructural level. Because it is effective in elucidating cellular injury following lethal and sublethal intoxication, electron microscopy is a sensitive method for diagnosing the animals' response to stress.

Key words: molluscicide, carbamate, ultrastructure, digestive tract, Gastropoda, *Deroceras reticulatum.*

INTRODUCTION

The increasing importance of slugs as field and garden pests (Martin & Kelly, 1986), demands continued efforts to identify and produce more effective and selective molluscicides. For commercial reasons, however, most molluscicides have been detected only incidental to screening programmes for the development of insecticides (Henderson & Parker, 1986). It is highly probable, therefore, that most potential molluscicides will also be insecticides having considerable side-effects on useful animals, as soil arthropods and annelids.

Little is known about the mollusc-specific effects of even the most widely used commercial molluscicides, metaldehyde and methiocarb, owing to the fact that most pesticide research is restricted to LD_{50} tests, which provide information about lethal or non-lethal effects of the substances tested. Such acute toxicity tests have demonstrated the advantages of carbamate or metaldehyde application under specific conditions (Kemp & Newell, 1985; Glen & Orsman, 1986; Prystupa et al., 1987), and have also revealed optimal molluscicidal concentrations for different active substances (Wright & Williams, 1980). Such tests, however, do not yield any further information about either the targets for the molluscicides or the mollusc-specific mechanisms induced in the slugs' bodies. Because this knowledge is essential for the development of new, more selective substances, much basic research is required.

Basic biochemical and physiological studies, for instance, have shown the inhibitory effect of methiocarb on cholinesterases (Pessah & Sokolove, 1983; Young & Wilkins, 1989) and the influence of metaldehyde on feeding motoneurons in the buccal ganglia (Mills et al., 1989).

In the present study, the influence of lethal ($\geq$0.1%) and sublethal ($\leq$0.01%) oral doses (OD) of the carbamate Cloethocarb on the cells of the digestive system of *Deroceras reticulatum* was investigated by electron microscopy. Sublethal concentrations are defined as those not leading to any mortality during the test (up to 30 h).

Diagnosis at the cellular level was chosen for its high sensitivity (Braunbeck, 1989), and for its providing information about reactions to

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TABLE 1. Amount of ingested food containing various concentrations of Cloethocarb and calculated values for absolute quantity of active substance ingested / g wet weight.

active substance	Food ingested (mg/g wet weight)	Active substance ingested (μg/g wet weight)
2% Cloethocarb (pellet)	70.0±50.5	1400
2% Cloethocarb (agar)	69.0±25.2	1380
0.1% Cloethocarb	83.9±44.0	83.9
0.01% Cloethocarb	105.2±47.5	10.5
0.001% Cloethocarb	105.3±29.9	1.05
Control	102.8±38.3	—

both lethal and sublethal intoxication. Thus, it should be possible to distinguish primary carbamate-specific cell reactions from symptoms resulting from cell death, and to differentiate irreversible damage from such cellular injury that might be compensated by the animal's detoxification mechanisms.

MATERIALS AND METHODS

The carbamate molluscicide Cloethocarb (BASF) was given to laboratory-reared *Deroceras reticulatum* by a single feeding of either pellets produced by BASF containing 2% of the active substance, phenol-2-(2-chloro-1-methoxyethoxy)-methylcarbamate, or wheatgerm agar containing 2%, 1%, 0.5%, 0.1%, 0.01%, or 0.001% of this toxin. The amount of food ingested was determined by weighing the treated food, which was dried before and after feeding. Finally, the quantity of active substance taken up with the food was calculated (Table 1). Doses in the 0.02% and 0.001% formulation proved to be sublethal.

Behavioral and macroscopic changes of the animals were recorded during the first hour after the beginning of feeding. For determination of cellular reactions, three animals feeding at each of the molluscicide concentrations were dissected after 30 min, 1 h, 3 h, 5 h, 24 h and 30 h. For primary fixation of excised tissue, a 2% glutaraldehyde solution in cacodylate buffer (0.01 M, pH 7.4) was injected into the body cavity. The oesophagus, crop, stomach, intestine and hepatopancreas were isolated under fixative and fixed for 2 h at 4°C. The tissues were then rinsed in cacodylate buffer and postfixed in 1% osmium ferrocyanide (Karnovsky, 1971) for 2 h at 4°C. After rinsing in cacodylate and maleate buffer (0.05 M, pH 5.2), the specimens were stained *en bloc* overnight in 1% uranyl acetate dissolved in maleate buffer (0.05 M, pH 5.2) at 4°C. The samples were rinsed in maleate buffer, dehydrated and embedded in Spurr's medium (Spurr, 1969). Semithin and ultrathin sections were cut on a Reichert ultramicrotome. Semithin sections were stained with methylene blue-azur (Richardson et al., 1960) and used for light microscope overviews. Ultrathin sections were counterstained with lead citrate for 30 sec. The tissues were examined in a Zeiss EM 9. The following cell types of the digestive system were investigated:

Oesophagus: storage cells, secretory cells of an eccrine type, secretory cells of a holocrine type (mucous cells);

Crop: storage cells;

Stomach: storage cells, secretory cells of a holocrine type (mucous cells);

Intestine: storage cells, secretory cells of an eccrine type, secretory cells of a holocrine type (mucous cells);

Hepatopancreas: digestive cells, crypt cells, excretory cells. The muscle and nerve layers underlying the epithelia were also studied.

RESULTS

Macroscopic Observations

Table 2 shows the mortality after Cloethocarb application. More animals were killed after the application of low lethal concentrations (0.1–1%) than after that of 2%. After ingestion of the 2% agar, however, animals died sooner than after that of all other concentrations. Furthermore, the mortality after 2% agar was higher than that after 2% pellets.

The macroscopically visible reactions of animals to intoxication with Cloethocarb cor-

TABLE 2. Mortality (absolute number of dead animals) after application of Cloethocarb. For each concentration, 20 animals were tested.

Concentration Cloethocarb	Time							
	0.5 h	1 h	3 h	5 h	10 h	16 h	24 h	30 h
Control	0	0	0	0	0	0	0	0
0.001%	0	0	0	0	0	0	0	0
0.01%	0	0	0	0	0	0	0	0
0.1%	0	0	0	0	0	0	3	10
0.5%	0	0	0	0	0	2	4	14
1%	0	0	0	0	0	0	3	16
2% agar	0	0	0	1	2	2	2	8
2% pellet	0	0	0	0	0	0	1	4

respond to typical symptoms of carbamate intoxication (Godan, 1979): ten minutes after taking up pellets or wheat-germ agar containing 2%, 1%, 0.5% or 0.1% of the poison, the animals show muscle convulsions that become more intense in the following 30 minutes. During this period, they lose large amounts of a lucent mucus. Whereas during the first 30 minutes after intoxication, the animals still move actively, after 1 h, the animals are alternately active and immobile. The anterior part of the body begins to swell while the posterior part flattens. After a period longer than 16 h, most of the animals lie motionless on their sides and only occasionally move. Reactions to 0.1%, 0.5% and 1% OD are as intense as those to 2%, whereas behavioral reactions to both sublethal concentrations are absent.

Electron Microscope Investigations

Table 3 summarizes the most important reactions of investigated components in cells of the digestive system of *Deroceras reticulatum* after intoxication with different concentrations of Cloethocarb.

Thirty minutes after the onset of poisoning, reactions were confined to single cells and especially to the anterior part of the digestive tract (oesophagus and crop). During the following hours, reactions spread over the epithelia, then appeared in the cells of the posterior part of the digestive system (stomach, intestine and hepatopancreas), with lapse of time corresponding to the rate of transport of toxic feedstuff by the alimentary canal or by the hemolymph (Triebskorn et al., 1990).

In general, cells of the hepatopancreas are more strongly damaged than are those of the digestive tract. In the cells of the crop, the reactions are less severe than those in epithelia characterized by high percentages of mucous cells.

In most cases, there are no differences in the cellular responses to 2%, 1%, 0.5% or 0.1% OD. Such differences as exist appear less intense after 2% than after 0.1% (Table 3: indented arrows). Cellular reactions of slugs exposed to pellets containing 2% of the carbamate substance are similar to those of animals fed the 2% treated agar.

Cellular Outline

In control animals, most of the epithelial cells of the digestive tract are columnar (Figs. 1, 2). Their apical surfaces are characterized by microvilli (storage and secretory cells of oesophagus and crop, digestive cells of the midgut gland; Figs. 6, 8) or by cilia and microvilli (storage and secretory cells of oesophagus, stomach and intestine; Fig. 9). Infoldings of the basal surfaces of these cells are small or absent, and the basal membrane is very thin (Fig. 12).

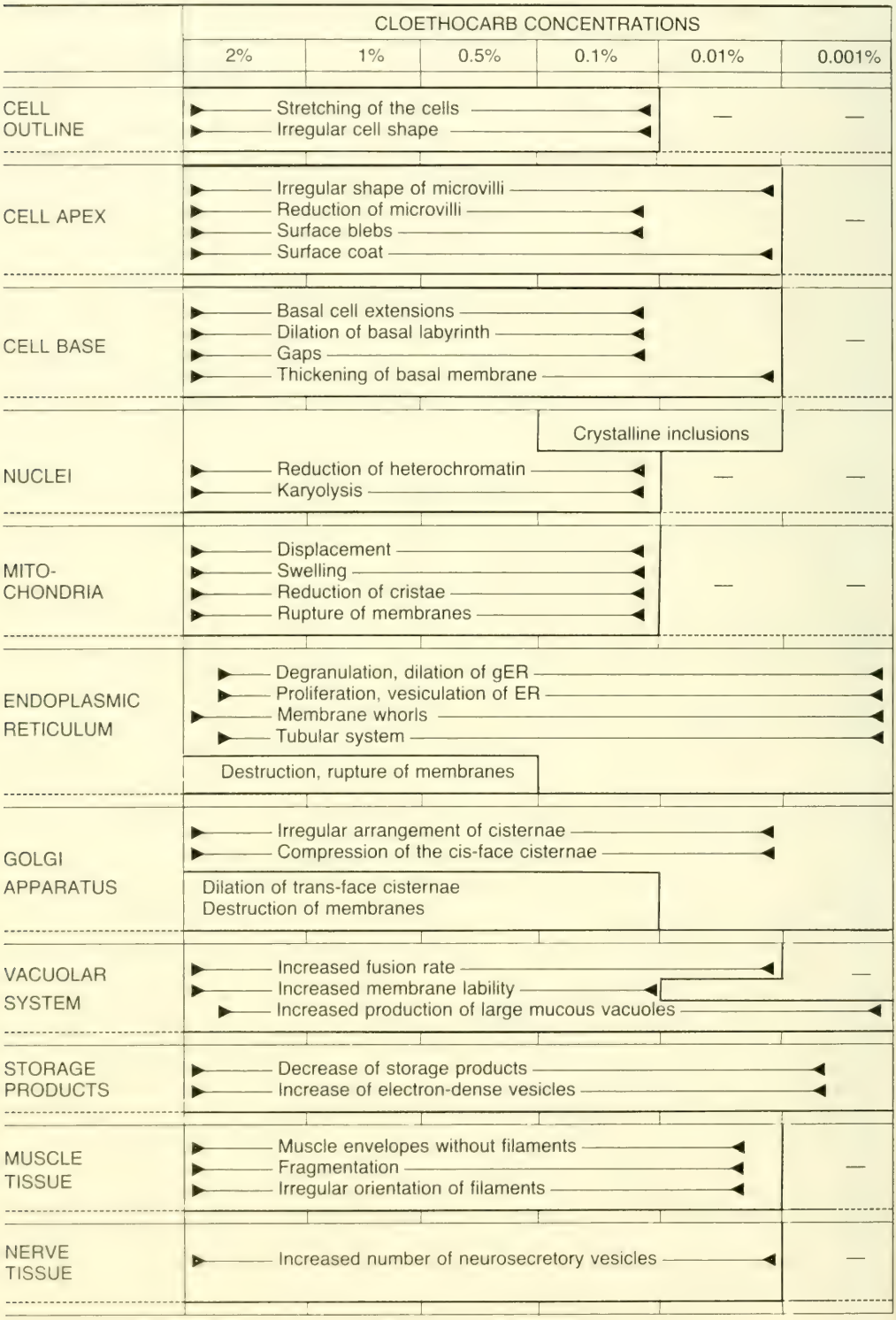
The mucus-producing cells of oesophagus, stomach and intestine are pyriform (Fig. 2). They bear small microvilli. Immature mucous cells do not reach the lumen.

In the hepatopancreas, two other cell types can be distinguished in addition to the digestive cells: conical crypt cells (Fig. 3), with a microvillous border and a prominent basal labyrinth, and the bellied excretory cells, characterized by large excretory vacuoles and long microvilli.

The molluscicide produces cytopathological changes in the general outline of cells and in their apical and basal surfaces.

Most of the cells in the digestive system change their typical cellular outline after 5 h, and more intensely 24 h and 30 h after the application of food containing between 0.1% and 2% poison. The columnar cells of the di-

TABLE 3. The most striking reactions of cellular components after lethal and sublethal intoxication with Cloethocarb.



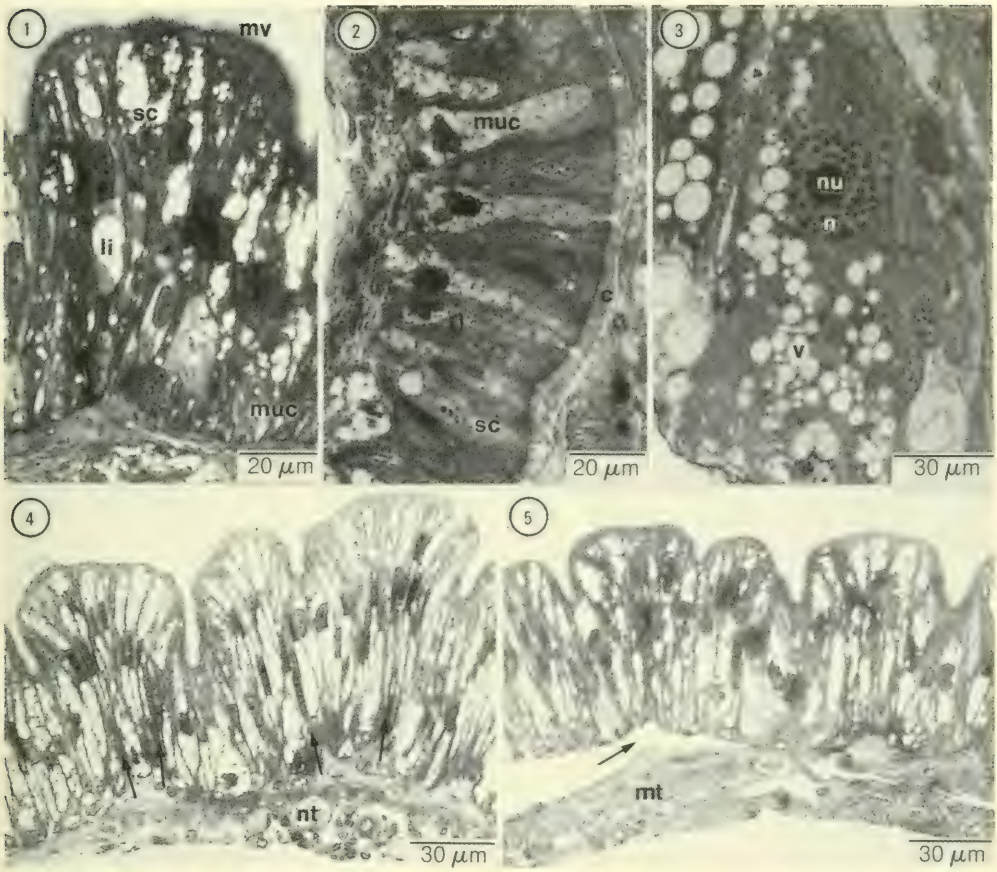
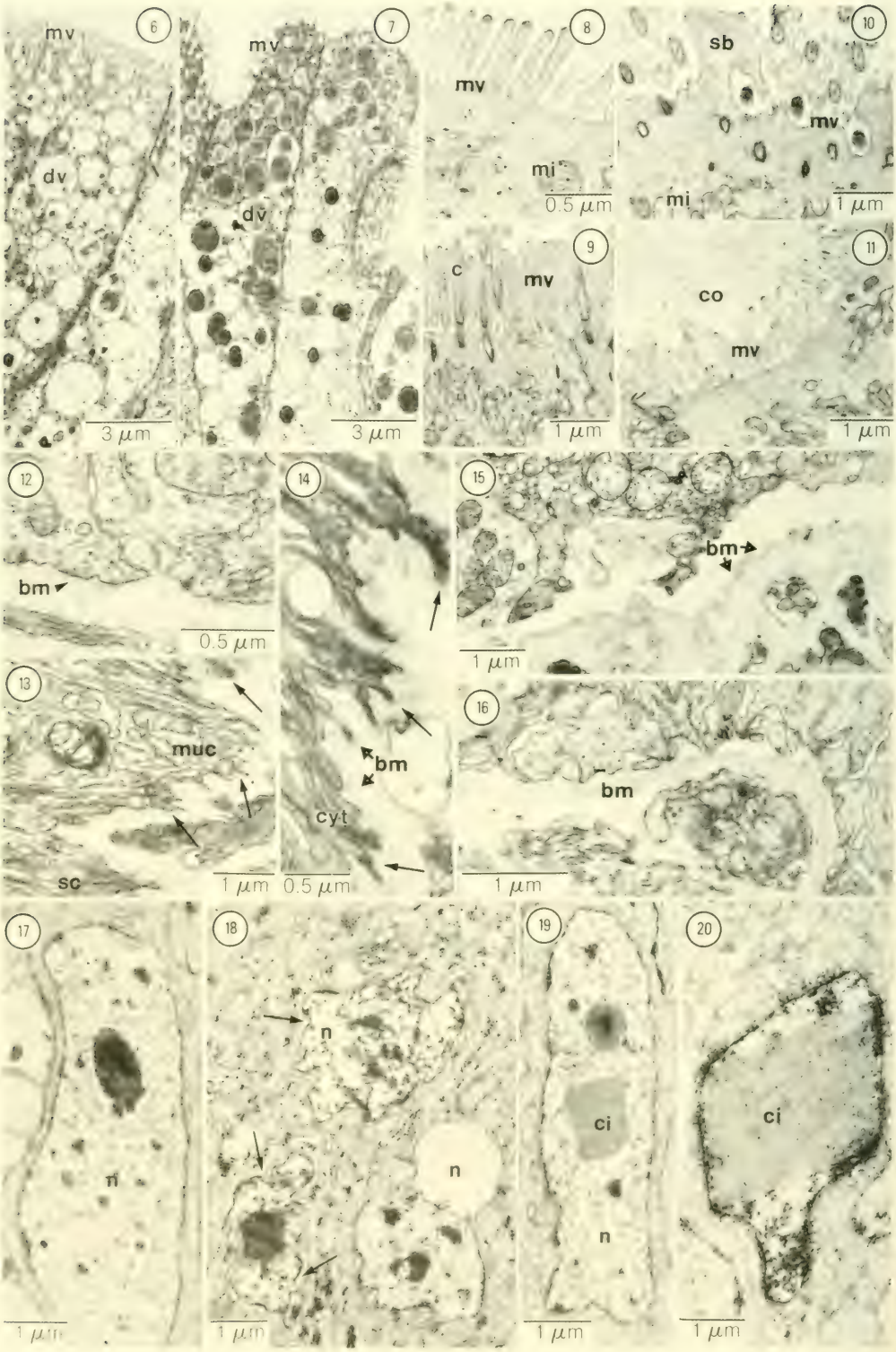


FIG. 1. Crop (control). Storage (sc) and mucous cells (muc) in epithelium of crop. Storage cells contain large amounts of lipid (li) and bear microvilli (mv). LM.
FIG. 2. Stomach (control). Storage (sc) and mucous cells (muc) in epithelium of stomach. c: cilia. LM.
FIG. 3. Hepatopancreas (control). Light-microscopial overview of crypt cell characterized by round nucleus (n) with prominent nucleolus (nu) and numerous vesicles (v).
FIG. 4. Crop (2% Cloethocarb, 5h). Epithelial cells elongated (arrows), nuclei condensed. nt = nerve tissue.
FIG. 5. Stomach (2% Cloethocarb, 5h). Gap (arrow) between muscle tissue (mt) and epithelial cells.

gestive tract become greatly elongated, especially after 0.1% OD, and often gaps open between the epithelial cells and the underlying muscle and nerve tissue (Figs. 4, 5). The cells of the hepatopancreas are already irregularly shaped after 1 h (Fig. 7). Sublethal concentrations (0.01%, 0.001%) do not affect cell shape.

The most striking reactions of the cell apices are reduction of microvilli, formation of surface blebs and production of a hyaline surface coat. Thirty minutes after the application of a lethal concentration, reduced microvilli and apical cytoplasmic protrusions (blebs) already can be observed in the columnar cells of the oesophagus and crop. Both reactions occur in all epithelia of the digestive system after 5, 24 and 30 h (Fig. 10), most severely in the cells of the intestine 24 h after ingestion of 0.1% toxin and in the hepatopancreas as soon as 1 h after ingestion of any lethal concentration. Food containing 0.01% poison leads to formation of small blebs and irregularly shaped microvilli in isolated cells. Ingestion of food containing 0.001% poison produced no evident reaction.

A further phenomenon appearing after both sublethal and lethal intoxication is a surface coat consisting of a hyaline material overlying the microvilli or the cilia, or both (Fig. 11). This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surface coat is less electron-dense in the digestive tract than in the hepatopancreas. It is already present in the anterior parts of the tract 1 h after administration of the poison and is very prominent in all regions of the digestive system after 5 h.

Application of 0.001% of the molluscicidal agent does not produce a detectable surface coat.

The most striking changes in the basal surface of the cell are development of basal cell extensions, thickening of the basement membrane, and development of gaps between the epithelium and the basement membrane.

After 30 minutes, small basal infoldings already have formed in the oesophagus, particularly after 0.1% OD. After 5 and 24 h, however, bases of the cells of the digestive tract, but not of the hepatopancreas, show considerable extensions (Figs. 13, 14). These extensions are most prominent in the region of the stomach and intestine.

In the hepatopancreas, the basal labyrinth of the crypt cells is extended. Thirty hours after the application of 0.01% OD the basal infoldings are comparable to those in the oesophagus 30 minutes after lethal intoxication.

From 24 h to 30 h after ingestion of lethal concentrations, gaps form between the basal parts of the epithelial cells and the underlying connective, muscle and nerve tissues (Fig. 15).

A further reaction detectable after the ingestion of sublethal concentrations is the thickening and increased electron-density of the basement membrane (Figs. 14, 16), which appears as early as 1 h after the ingestion of food containing $\geq$0.01% Cloethocarb.

Nuclei

In the storage and secretory cells of the digestive tract and in the digestive cells of the hepatopancreas, the nuclei are ovoid (Fig. 17). In the crypt cells of the hepatopancreas and in the mucuous cells, however, they are roundish (Figs. 2, 3). The nuclei of the crypt cells are rich in heterochromatin and have a prominent, round nucleolus (Fig. 3).

The most typical cytopathological changes in the nuclei are lightening of the karyoplasm, reduction of the heterochromatin, dilation of the nuclear envelope and formation of crystalline inclusions.

Thirty minutes after the onset of intoxication, the nuclear envelope is locally dilated and the karyoplasm becomes more electronlucent in individual cells. After 5 h these phenomena occur in many cells (Fig. 18). The nuclei show the effects of lytic processes. In the crypt cells the nucleoli assume irregular shapes.

The most severe nuclear damage occurs in the posterior part of the digestive tract and in the cells of the hepatopancreas. Twenty-four hours after ingestion of food containing 0.1% or 0.01% of the molluscicide, large crystalline inclusions form in the nuclei, especially in the region of the stomach and the intestine (Fig.

FIG. 6. Hepatopancreas (control). Digestive cells, characterized by microvillous border (mv) and system of digestive vacuoles (dv).
FIG. 7. Hepatopancreas (0.1% Cloethocarb, 1h). Irregularly shaped digestive cells. Digestive vacuoles (dv) contain electron-dense material. mv: microvilli.
FIG. 8. Crop (control). Apex of a storage cell bearing microvilli (mv). Beneath microvillous border mitochondria (mi) visible.
FIG. 9. Stomach (control). Apices of two storage cells bearing microvilli (mv) and cilia (c).
FIG. 10. Oesophagus (2% Cloethocarb, 5h). Apex of storage cell with reduced microvilli (mv) and surface blebs (sb). Mitochondria (mi) severely damaged.
FIG. 11. Oesophagus (2% Cloethocarb, 1h). Storage cells with coat (co) overlying microvilli (mv).
FIG. 12. Crop (control). Basal part of storage cell with thin basal membrane (bm).
FIG. 13. Stomach (2% Cloethocarb, 5h). Basal parts of mucous (muc) and storage cells (sc) with basal cell extensions (arrows).
FIG. 14. Crop (2% Cloethocarb, 24h). Storage cell with basal cell extensions (long arrows), electron-dense cytoplasm (cyt) and thickened basal membrane (bm, short arrows).
FIG. 15. Crop (2% Cloethocarb, 30h). Gap between epithelium and basal membrane (bm, short arrows).
FIG. 16. Intestine (0.1% Cloethocarb, 5h). Thickening of basal membrane (bm).
FIG. 17. Oesophagus (control). Nucleus (n) of storage cell.
FIG. 18. Stomach (2% Cloethocarb, 5h). Nuclei (n) with envelope dilated (arrows), karyoplasm lightened and heterochromatin reduced.
FIG. 19. Stomach (0.1% Cloethocarb, 5h). Nucleus (n) with crystalline inclusion (ci).
FIG. 20. Stomach (0.1% Cloethocarb, 5h). Crystalline inclusion (ci) filling greater part of karyoplasm.

19). In some cases, these crystals occupy an appreciable part of the nucleus (Fig. 20).

A molluscicide concentration of 0.001% failed to induce any reaction in the nuclei.

Mitochondria

The storage cells have a layer of mitochondria beneath the microvillous border (Figs. 8, 9), whereas in the other cells, these organelles are irregularly dispersed throughout the cytoplasm.

Reduction of cristae and swelling are the most important reactions of mitochondria to Cloethocarb intoxication. One hour after lethal intoxication, the regular arrangement of mitochondria beneath the microvillous border begins to be disturbed. The organelles swell, the cristae become reduced (Figs. 21, 22), and after 5 h, the outer membranes rupture (Fig. 23). Damage to mitochondria is most severe in the stomach and intestine.

After sublethal intoxication, changes in the mitochondria could not be observed.

Endomembrane System

Large amounts of granular endoplasmic reticulum (ER) occur in the secretory cells of the oesophagus and intestine, in the mucous cells of oesophagus, crop, stomach and intestine (Fig. 24), and in the crypt cells of the hepatopancreas (Fig. 25). The cisternae are almost parallel, mostly within the basal or medio-basal parts of the cells.

The granular endoplasmic reticulum of the mucous cell is of the wide-luminar type, the width of the cisternae ranging from 120 to 280 nm. In the lumen of the cisternae, there are typical tubular structures with an average diameter of 30 nm (Fig. 24). In the other cell types, only small amounts of granular endoplasmic reticulum are present. Additionally, there are some cisternae of smooth endoplasmic reticulum in the storage cells and excretory cells.

The most prominent cytopathological changes in the endoplasmic reticulum after Cloethocarb intoxication are dilations of the cisternae, degranulation of the granular ER, proliferation and vesiculation of ribosome-free ER, and formation of membrane whorls and tubular structures.

Within 30 minutes after ingestion of lethal and sublethal concentrations, degranulation of the granular endoplasmic reticulum and dilation of the cisternae occur (Fig. 26). After 1 h, the cisternae of both granular and degranulated/smooth endoplasmic reticulum are greatly dilated (Fig. 27). Furthermore, the amounts of degranulated/smooth endoplasmic reticulum in the storage, secretory, crypt and excretory cells have increased. In the storage cells, the cisternae often touch (Fig. 28) or surround lipid droplets (Figs. 29, 30). After 5 h, vesicles of endoplasmic reticulum occur throughout the cytoplasm of storage, secretory and crypt cells. This reaction is also evident after 0.01% OD (Fig. 31), but is most intense after intoxication with the sublethal concentration of 0.001%. The proliferation becomes stronger with time. In addition to the dilation of the cisternae, characteristic concentric whorls of the endoplasmic reticulum and other membrane whorls form 5, 24 and 30 h after all lethal and both sublethal concentrations (Figs. 29, 30). After ingestion of lethal concentrations, the membranes of the endoplasmic reticulum often rupture (Fig. 32).

Another phenomenon appearing 5 h after both lethal and sublethal intoxication is a system of tubules arising from and connected with the degranulated/smooth endoplasmic reticulum (Figs. 33, 34). It occurs especially in the storage and excretory cells. After 0.001% OD, there are fewer tubules than after 0.01%, whereas their number after 0.01% is similar to that after lethal intoxication.

Large Golgi fields characterize the mucous and crypt cells (Figs. 35, 36). In both kinds of cells, small vesicles originating from the granular endoplasmic reticulum fuse with the cis-face cisternae. Most trans-face cisternae also fuse with small vesicles of unknown origin, become spherical, and finally as large vacuoles become free from the Golgi fields.

In the other cell types, the Golgi complex is less prominent.

Disorganisation of the cisternae, compression of the cis-face and dilation of the trans-face cisternae and destruction of membranes are the most common cytopathological responses of the Golgi apparatus to Cloethocarb.

One hour after both lethal and sublethal concentrations of the toxin are ingested, the normally regular arrangement of the cisternae in large and small Golgi apparatus is disrupted. The cis-face cisternae become tightly stacked (Figs. 37, 40). In the mucous cells, very many mucous vacuoles originate from the trans-face cisternae, and vesicles arising from the endoplasmic reticulum become more numerous (Fig. 38). With sublethal intoxication these reactions occur after 30 h.

Five hours after lethal intoxication, how-

ever, damage to large and small Golgi complexes becomes greater. The trans-face cisternae, especially those of the small Golgi apparatus in the storage and secretory cells, are grossly swollen (Fig. 39) and the membranes often rupture (Figs. 37, 41).

Within the digestive cells of the hepatopancreas are typical vacuolar and lysosomal systems, the vacuoles of which fuse with each other and with lysosomes, vary in size, and are generally largest towards the basal regions of the cells (Fig. 42). The small endocytotic vesicles, located in the most apical parts of the cells and the lysosomes, are more electron-dense than the large vacuoles (Fig. 43).

A second type of cell that is dominated by vacuoles is the mucous cell (Fig. 2). Its vacuoles fuse on their way from the base to the apex and are thus largest towards the apical part of the cell.

In immature mucous cells, only a few mucous vacuoles occur and seem not to fuse with one another.

The most striking cytopathological reactions of the vacuolar system are the intensified fusion of vacuoles and the increased lability of membranes.

Within one hour after lethal intoxication, reaction of the digestive vacuoles and the lysosomes is already evident. Endocytotic vesicles in the apical part of the cell are fewer, and the large vacuoles contain material of appreciable electron-density (Fig. 7). From 3 to 5 h, wide cisternae appear as a result of the intensified fusion of small vesicles and of small and large vacuoles (Figs. 44, 45). Whereas the membranes of the resulting large cisternae often rupture, those of the remaining small vesicles remain intact. After 16 h, most of the vacuolar membranes are heavily damaged (Fig. 46) and the vacuolar system thus is disrupted.

The molluscicide acts on the mucous cells to produce a greater number of cells entirely filled with mucous vacuoles. Furthermore, even in immature mucous cells, many large vacuoles fuse. This intensified production of mucous occurs after lethal oral dosage but is more intense after sublethal intoxication (Fig. 47).

Storage Products

In control animals, there are large deposits of lipid and glycogen in storage and crypt cells (Fig. 48), but few storage products occur in the secretory, digestive and excretory cells. In the storage cells, most lipid droplets are slightly electron-dense and only a few lipid-containing vesicles are totally electron-dense.

Cloethocarb intoxication results in a reduction of storage products and a concomitant increase in electron-dense vesicles. As soon as 1 h after ingestion of all lethal concentrations and of 0.01% Cloethocarb (Fig. 49), the glycogen content is slightly reduced in the storage cells of the oesophagus and crop, and lipid droplets fuse and appear less electron-dense.

After 3 h, lipid droplets have become fewer while electron-dense vesicles have become more numerous (Fig. 50). Peroxisomes are frequently associated with lipid droplets and ER cisternae surround them (Figs. 28–30).

After 5, 16 and 24 h, the amount of storage products is obviously diminished. There is still some lipid present, but very little glycogen remains in the storage cells.

The reduction of storage products is less intense after application of sublethal concentrations than after that of any of the lethal concentrations. Both the decrease in lipid and glycogen content and the increase in the number of electron-dense vesicles can be related to the concentration of molluscicide in the food ingested.

Muscle and Nerve Tissue

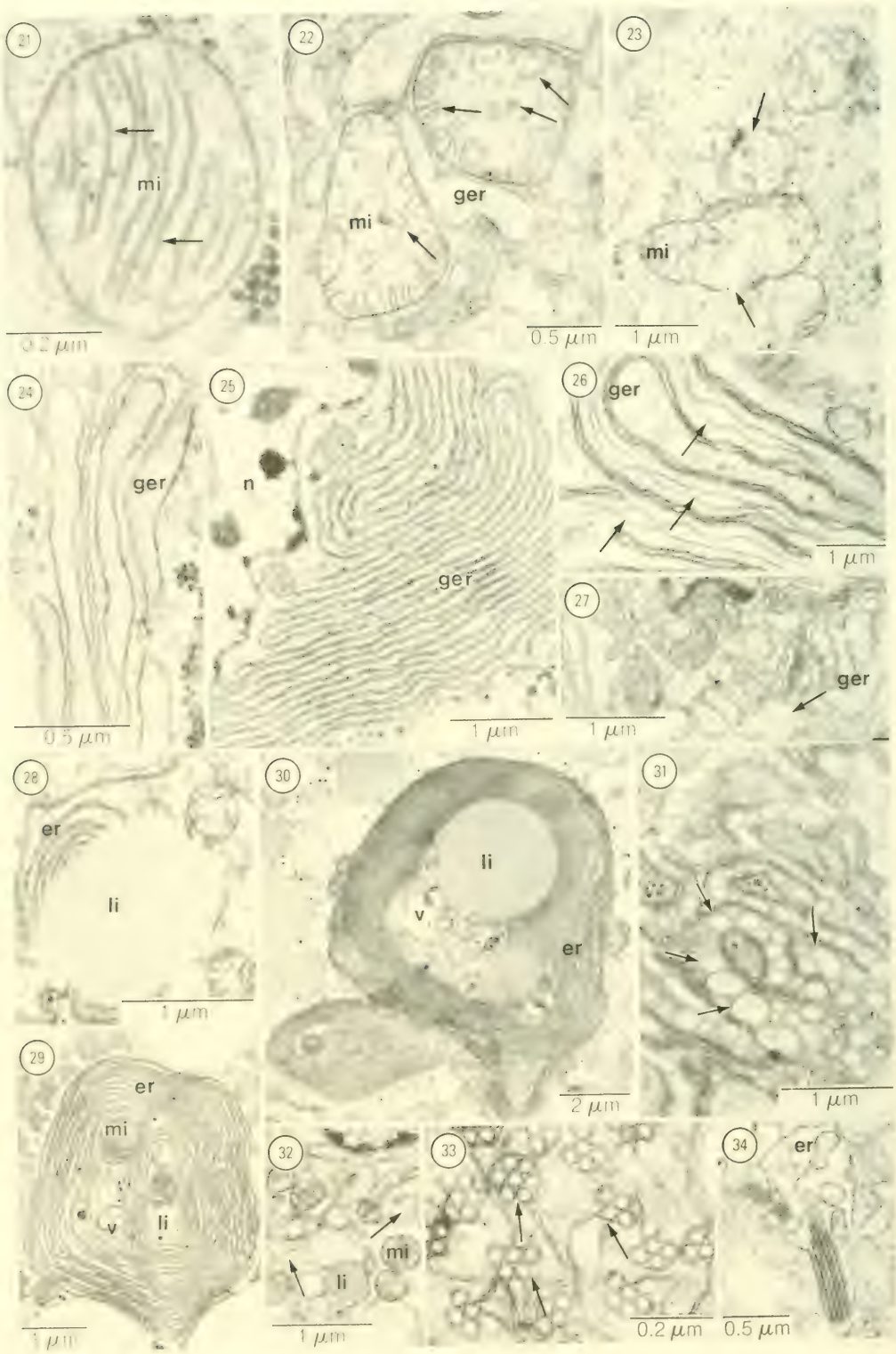
In control animals, a conspicuous layer of muscle tissue, the filaments of which are longitudinal and transverse, underlie the epithelia of the oesophagus, stomach and intestine (Fig. 51). The filamentous portions are surrounded by a plasma membrane and an envelope of connective tissue. Underlying the epithelia of the crop and hepatopancreas is a very thin layer of muscle.

Nerves, characterized by various neurosecretory vesicles, lie close to the muscle tissue. The neurosecretory vesicles vary from electron-dense to electron-lucent and are surrounded by an electron-lucent halo.

Connective tissue occurs between nerves, muscles and the epithelia of the digestive system.

The most prominent cytopathological responses of muscles and nerve tissues to the molluscicide are disorientation of muscle filaments, appearance of muscle envelopes devoid of muscle filaments and augmentation of neurosecretory vesicles.

At 1, 3 and 5 h after lethal intoxication, the muscle filaments are irregularly oriented in the oesophagus, stomach and intestine (Fig. 52). After 24 h, the muscle tissue is frag-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mented and plasma membranes surround cytoplasm lacking muscle filaments (Fig. 53). The most severe damage observed is in the stomach and the intestine.

Furthermore, neurosecretory vesicles become more numerous (Figs. 54–56), and dense connections form between muscle and nerve tissue (Fig. 56).

Intoxication with 0.01% molluscicide also disarrays the muscle fibers. In some cases, muscle envelopes without muscle fibres underlie the epithelium of the intestine after 24 h and 30 h. The number of neurosecretory vesicles also increase. After 0.001% OD, there is no apparent reaction of either muscle or nerve tissue.

DISCUSSION

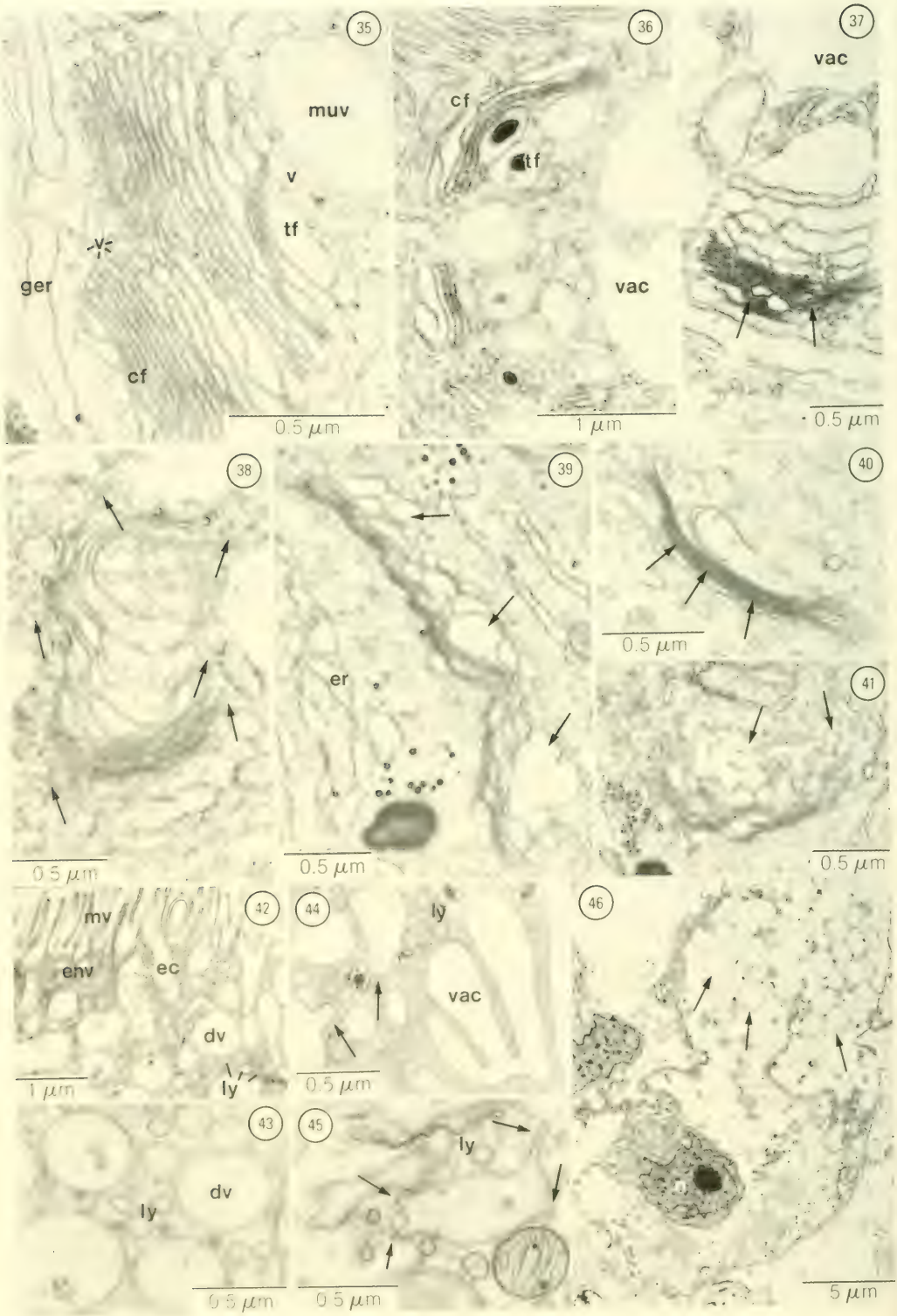
The present paper was designed as a baseline study of cellular reactions in the slugs' bodies to carbamate intoxication. Because the molluscicide was orally applied, the cells of the digestive system were investigated as targets for effects of poisoning. In a prior investigation, the passage of ^{14}C-labeled Cloethocarb through the digestive system could be traced and labeled material could be shown to penetrate the cells (Triebskorn et al., 1990), thus indicating that all cells of the digestive tract are in direct contact with the poison.

Whereas earlier workers report the influence of carbamates on the nervous system alone (Pessah & Sokolove, 1983; Young & Wilkins, 1989), we showed that carbamate intoxication produces conspicuous cellular reactions in the digestive system as well, even though sublethal poisoning did not induce overt reactions at the macroscopic, organismic, level. The results of the study support the statement of Armstrong & Millemann (1974) that "damage to the nervous system through cholinesterase inhibition may not be the only or even the primary cause of death of exposed clams."

In the present study, three types of cellular reaction in the digestive system of *Deroceras reticulatum* can be distinguished: those that are detectable only after lethal intoxication, those that occur with the same intensity after lethal and sublethal poisoning, and reactions that are most intense after the application of sublethal concentrations.

Reactions typical of lethal intoxication are damage to nuclei and mitochondria; alterations to the general cell outline, to the basal cell surfaces and to muscle and nerve tissue; and formation of clefts between the epithelia and the underlying connective, muscle and nerve tissues. Most of these reactions are absent after 0.001% OD, but they appear at 0.1% OD in a few cells and with less intensity after 30 h. The fact that these reactions become visible only after lethal intoxication might indicate either that these cellular structures have a lower sensitivity to the poison, or that those reactions are secondary responses of the cells. In the first case, only high concentrations of the toxin would lead to unspecific stress reactions that finally induce cell

FIG. 21. Oesophagus (control). Mitochondrion (mi) in storage cell (arrows: cristae).
FIG. 22. Intestine (2% Cloethocarb, 1h). Mitochondria (mi) swollen, cristae (arrows) partly reduced. ger: granular endoplasmic reticulum.
FIG. 23. Stomach (2% Cloethocarb, 5h). Mitochondria (mi) with ruptured membranes (arrows).
FIG. 24. Intestine (control). Wide-luminar granular ER (ger) of mucous cell.
FIG. 25. Hepatopancreas (control). Granular ER (ger) of crypt cell. n: nucleus.
FIG. 26. Hepatopancreas (0.01% Cloethocarb, 1h). Degranulation of granular ER (ger) in crypt cell (arrows).
FIG. 27. Oesophagus (2% Cloethocarb, 1h). Cisternae of granular ER (ger) in mucous cell grossly dilated.
FIG. 28. Crop (2% Cloethocarb, 5h). Cisternae of ER (er) touching lipid droplet (li).
FIG. 29. Hepatopancreas (2% Cloethocarb, 1h). Cisternae of ER (er) surrounding lipid droplet (li), mitochondria (mi) and vesicles (v) in crypt cell.
FIG. 30. Hepatopancreas (2% Cloethocarb, 16h). Membrane whorls of ER (er) surrounding lipid droplet (li) and vesicles (v).
FIG. 31. Hepatopancreas (0.01% Cloethocarb, 5h). Vesicles of ER (arrows) in basal part of crypt cell.
FIG. 32. Hepatopancreas (0.1% Cloethocarb, 30 min). Ruptured membranes (arrows) of ER. li: lipid; mi: mitochondrion.
FIG. 33. Intestine (0.1% Cloethocarb, 5h). Transverse and longitudinal section of tubular system arising from ER. Arrows: lumen of cisternae.
FIG. 34. Intestine (0.1% Cloethocarb, 5h). Transverse and longitudinal section of tubular system arising from ER. Tubules open into wide-luminar ER cisterna (er).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death. In the second case, interaction of the toxin with other targets in the slug's body might cause the reactions and these would follow other symptoms of cell death.

Carbamates, as nerve toxins, induce uncontrolled muscle contractions that do not appear after sublethal concentrations. As a consequence of these muscle convulsions, the epithelial cells might be stretched, leading to basal cell extension, such as to induce detachment of the cells from the basal membrane. This phenomenon has also been described by Vogt (1986) for the hepatopancreas of *Penaeus monodon* after exposure to dimethoate, which is also an inhibitor of cholinesterases. It might be that the toxin distorts the cytoskeleton, thereby changing the shape of the cell and displacing the mitochondria.

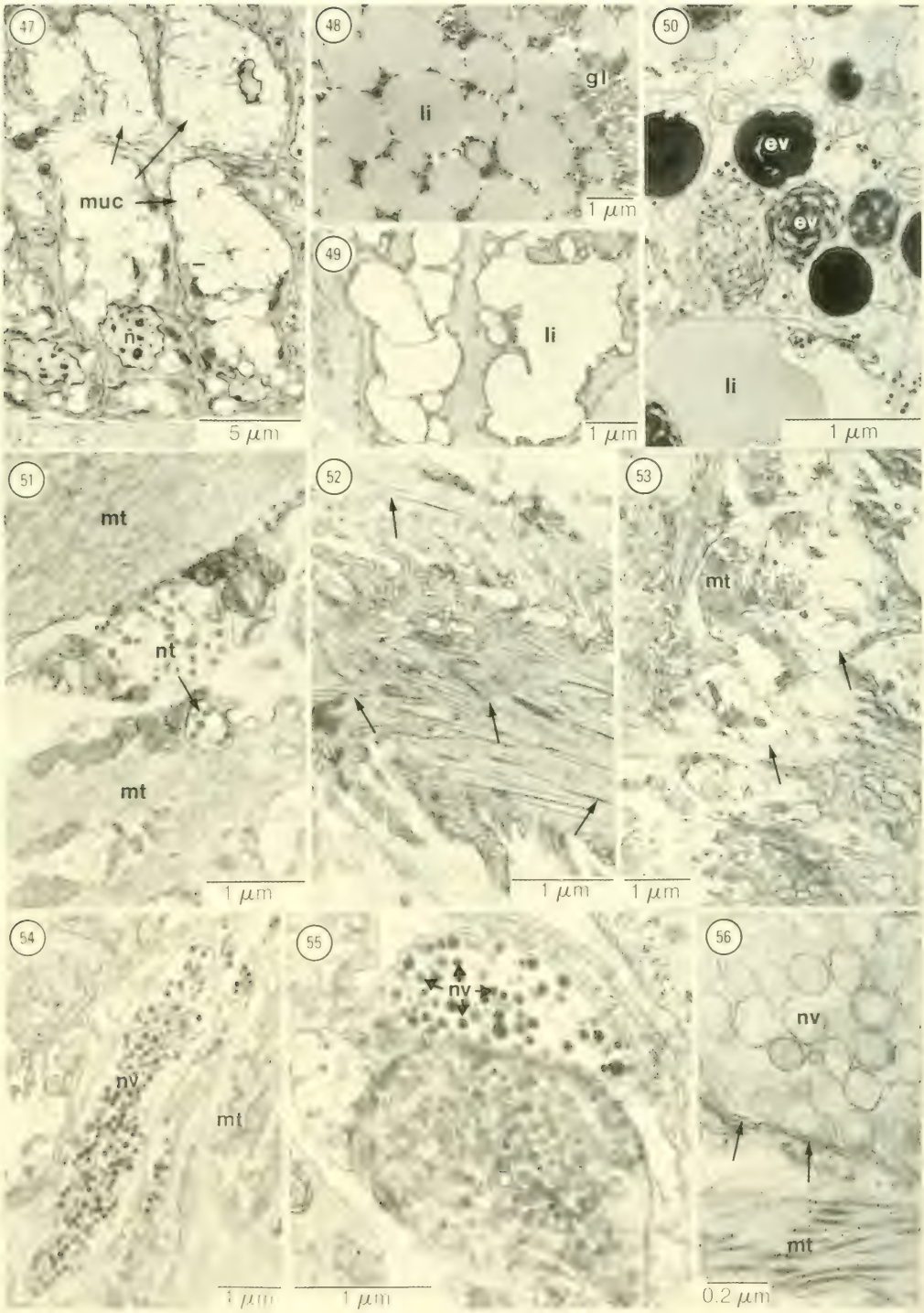
Besides damaged nuclei, fully intact nuculei and others with conspicuous crystalline inclusions in the karyoplasm occur. This observation accentuates the importance of the heterogeneity of the cellular reaction.

The crystalline inclusions in the karyoplasm might result from either intensified productivity or serious injury to metabolic or regulatory processes.

The reactions of the mitochondria, swelling and reduction of the cristae, are often considered unspecific stress symptoms (Rez, 1986). We have demonstrated in earlier studies (Triebskorn, 1988; 1989a), however, that there are several other modes of mitochondrial response to different molluscicides. Swelling of the organelles and reduction of cristae can ensue immediately upon intoxication, but can also result from other reactions such as an increase in number or size of intramitochondrial granules or the appearance of glycogen-like particles in the matrix. Furthermore, swelling of the mitochondria could also be induced in other cellular systems, such as the fish liver, by poisoning or by certain diets (Braunbeck et al., 1989; Segner et al., 1987). We assume, therefore, that swelling of the organelles and reduction of the cristae can be induced in various ways by exogenous or endogenous stresses. Even if the symptoms are similar, the causes of the response might be totally different. One attempt to explain the reaction is that of Goyer & Rhyne (1975), who propose that the swelling of the organelles results from inhibition of ion transport and protein synthesis. It also seems possible that the toxin interacts with the mitochondrial membrane so as to change its permeability to ions.

Reactions that are discernible after the sublethal molluscicide concentration of 0.01% and are intense after lethal intoxication are: reduction of microvilli, often associated with formation of apical protrusions of the cytoplasm (surface blebs); presence of a coating upon the apical surfaces of the cells; thickening of the basal membrane; intensification of fusion between small vesicles and vacuoles

FIG. 35. Stomach (control). Golgi apparatus of mucous cell. Small vesicles (v) arising from granular ER (ger) fuse with cis-face cisternae. On trans-face (tf), small vesicles (v) and mucous vacuole (muv) are visible.
FIG. 36. Hepatopancreas (control). Golgi apparatus producing large vacuoles (vac). cf: cis-face; tf: trans-face.
FIG. 37. Crop (0.1% Cloethocarb, 5h). Golgi apparatus in mucous cell with cis-face cisternae (arrows) closely stacked. vac: vacuole.
FIG. 38. Intestine (2% Cloethocarb, 5h). Increased number of small vesicles (arrows) surrounding Golgi apparatus in mucous cell.
FIG. 39. Oesophagus (2% Cloethocarb, 5h). Storage cell. Trans-face cisternae of small Golgi apparatus greatly inflated (arrows). er: granular ER.
FIG. 40. Oesophagus (2% Cloethocarb, 5h). Storage cell. Small Golgi apparatus with cis-face cisternae tightly stacked (arrows).
FIG. 41. Oesophagus (2% Cloethocarb, 30h). Storage cell. Small Golgi apparatus with disorganized cisternae; membranes irregularly arranged and sometimes ruptured (arrows).
FIG. 42. Hepatopancreas (control). Apex of digestive cell with microvilli (mv), endocytotic channels (ec), endocytotic vesicles (env), lysosomes (ly) and digestive vacuoles (dv).
FIG. 43. Hepatopancreas (control). Digestive vacuoles (dv) and lysosomes (ly) in digestive cell.
FIG. 44. Hepatopancreas (0.1% Cloethocarb, 5h). Lysosomes (ly) fusing with vacuolar system (vac; arrows) in digestive cell.
FIG. 45. Hepatopancreas (0.1% Cloethocarb, 5h). Fusion of lysosomes (ly) with vacuoles (arrows) in digestive cell.
FIG. 46. Hepatopancreas (2% Cloethocarb, 16h). Autolytic digestive cell with severely damaged vacuolar system. (arrows: intact vacuoles; n: nucleus).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in the digestive cells of the hepatopancreas; reduction of storage products; condensation of the cis-face stacks of the Golgi apparatus and formation of membrane whorls by ER cisternae.

The first four reactions described are regarded as effects induced by the direct contact of toxin and cell surfaces. The thickening of the basement membrane and the formation of an apical coat protect the apical and basal surfaces of the cell, preventing further penetration of the toxin from either the lumen of the digestive tract or from the hemolymph space. The origin of the coat is not known. Perhaps the cells themselves produce it but maybe the mucous cells of the stomach and the intestine form it, inasmuch as exudation of mucus intensifies after intoxication (Triebskorn & Ebert, 1989).

The reduction of microvilli, the formation of blebs and the increased fusion of vesicles and vacuoles in the digestive cells of the hepatopancreas might result from the interaction of the lipophilic molluscicide with membranes. This interaction might induce changes in composition, fluidity and finally stability of the membranes (Axiak et al., 1988; Moore, 1982, 1985; Moore et al., 1982).

Although the reactions mentioned above have often been described as unspecific cell responses to any stress (Rez, 1986), e.g. starvation (Segner et al., 1987), we assume that the plasma and the lysosomal membranes are very unstable and sensitive systems that react quickly to any alteration of cellular homeostasis. Lysosomal instability in mussels has been used as a measure of environmental pollution (Moore, 1982, 1985; Moore et al., 1982; Lowe et al., 1981).

In such studies, the reduction of membrane stability has been investigated with light microscopy and enzyme-histochemistry but not with the electron microscope. In the present study, we could show that the membranes of the small vesicles in the digestive cells of the hepatopancreas were not affected. As a consequence of the intensified fusion between small and large vacuoles, the number of large vacuoles increases after intoxication. Moore et al. (1982) assumed that changes in membrane fluidity induce this altered rate of vesicle fusion. The membranes of the resulting large autolysosomes are less stable and often rupture. Bayne et al. (1985) distinguish between these autolysosomes, a typical response to stress, and the heterophagosomes, large vacuoles involved in pinocytosis and intracellular digestion in untreated animals.

The decrease in stability of the ER and Golgi membranes, especially after ingestion of lethal concentrations, might also result from the capacity of the carbamate to interact with membranes. The more important reactions of the ER, however, are those to sublethal concentrations; these will be discussed later.

An increased call upon energy resources to initiate protective or detoxification processes might lead to a quick reduction of lipid and glycogen in the storage cells. Recio et al. (1988) also describe a reduction of storage products in *Arion ater* induced by zinc. They characterize the reaction to intoxication as similar to the effects of starvation. Because in our recent study peroxisomes and ER cisternae were often observed in close contact with lipid droplets, and because our histochemical enzyme tests revealed that catalase was induced by Cloethocarb (Triebskorn, 1989b), it seems possible that β-oxidation, or peroxida-

FIG. 47. Oesophagus (0.001% Cloethocarb, 30 min). Increased number of mature mucous cells (muc). n: nucleus.
FIG. 48. Crop (control). Lipid (li) and glycogen storage (gl) in storage cell.
FIG. 49. Crop (2% Cloethocarb pellet, 1h). Reduction of glycogen, fusion of lipid droplets (li).
FIG. 50. Oesophagus (2% Cloethocarb, 3h). Decrease of lipid storage (li) and increased numbers of electron-dense vesicles (ev).
FIG. 51. Oesophagus (control). Muscle (mt) and nerve tissues (nt) underlying epithelium.
FIG. 52. Oesophagus (2% Cloethocarb, 5h). Irregularly oriented muscle filaments (arrows).
FIG. 53. Crop (2% Cloethocarb, 24h). Fragmentation of muscle tissue (mt) and muscle envelope lacking muscle filaments (arrows).
FIG. 54. Oesophagus (2% Cloethocarb, 30 min). Nerve with increased numbers of neurosecretory vesicles (nv). mt: muscle tissue.
FIG. 55. Stomach (0.5% Cloethocarb, 5h). Nerve with increased number of neurosecretory vesicles (nv).
FIG. 56. Oesophagus (2% Cloethocarb, 30 min). Dense connection between muscle (mt) and nerve tissues (nt; arrow).

tive processes, or both, are involved in the reduction of lipid stores. Furthermore, there is perhaps a relation between peroxidation and membrane destruction, as has often been described for vertebrates (Tappel, 1975; Recknagel, 1967).

The intensity of the alterations and damage after lethal intoxication are shown to be more severe than after sublethal intoxication. Although, in this case, a dose-response relationship is obvious, no positive correlation could be found between dose and effect, if the reactions after low and high lethal concentrations were observed. That 0.1% OD frequently causes more severe damage than 2% could be explained by the fact that high concentrations induce protective mechanisms or potential defense reactions, such as exudation of mucus, more quickly than low concentrations. Given the capacity of the mucus to dilute the toxin with the passage of time, the relative amount of the chemical in the lumen of the digestive tract might therefore be lower after 2% than after 0.1%, even if a higher concentration were ingested. Furthermore, Bowen & Jones (1985) assume that high concentrations of molluscicides prevent the animal from taking up lethal doses of the pesticide owing to quickly induced paralysis of the crop. A higher concentration of the pesticide thus might not be related necessarily to a higher efficiency as postulated by Fries & Tripp (1976).

In the third category are responses to lethal oral doses that are more intense after sublethal intoxication. Such is the case of degranulation and dilation of the granular endoplasmic reticulum (ER), the proliferation and vesiculation of the ER, the formation of a tubular system and of membrane whorls by the ER and the production of large mucous vacuoles.

Reactions of the ER to intoxification similar to those described in this study have often been seen in both vertebrates (Sivarajah et al., 1978; Klaunig et al., 1979) and mussels (Nott & Moore, 1987). Because transitions between smooth and granular ER were visible, especially in the crypt cells of the hepatopancreas, and because Klaunig et al. (1979) describe a continuity between two forms of ER, we hesitate to refer to degranulated ER as smooth ER. It is unclear, moreover, whether ribosome-free ER necessarily functions as smooth ER. Klaunig et al. (1979) interpret the circular arrays of ER as a response to substances that induce enzymes of the mixed function oxygenases system. A similar conclusion can be drawn from our enzyme-histochemical tests, which showed an increase of NADPH-neotetrazolium reductase in cell areas in which ER-proliferation and whorls of ER cisternae occurred (Triebskorn, 1989a, b).

Reactions of the endoplasmic reticulum are stronger after sublethal intoxication than after a lethal dose, most probably because destructive effects are less important than induced reactions of a potentially protective nature. Any new molluscicide developed should not induce such defence mechanisms.

A second mechanism that intensifies after sublethal intoxication is the production of large mucous vacuoles owing to an increased activity of the secretory system (ER, Golgi apparatus). Such large mucous vacuoles occurred even in cells having the shape typical of immature mucous cells, which generally have prominent Golgi complexes, large amounts of granular ER and only few mucous vacuoles. Large amounts of mucus are exuded as an immediate response to the ingestion of lethal doses of the molluscicide. As already mentioned above, the mucus might serve the animal to dilute the toxin. Moreover, as shown in an earlier study, the animals are capable both of increasing the quantity, and of varying the quality, i.e. the chemical composition, of the mucus (Triebskorn & Ebert, 1989). In the case of Cloethocarb, the exudation of acidic mucus can be regarded as a kind of incidental detoxification, because the toxin is less stable under acidic conditions (Künast, pers. comm.). Nevertheless, the reason for the alteration in the chemical composition of the mucus is not known. Because we could demonstrate activity of γ-glutamyltransferase and an increase in amount of SH-groups in the mucous cells of the digestive system (Triebskorn, 1988), we assume that conjugation processes (glutathione conjugation) might be related to secretion of mucus. An increase in the number of mucous cells, such as described by Neff et al. (1987) as a response of Arctic marine bivalves to experimentally spilled oil, could not be detected.

Although it might serve slugs as a defense mechanism, intensified exudation of mucus can also kill them; specific molluscicides can not only enhance secretion of mucus but also damage the ultrastructure of cells, especially immature ones. That is the reason that induction of mucus secretion would finally lead to a desiccation of the animal and loss of mucous

cells would prevent production of the very mucus that protects the surface of the animal from desiccation and that is necessary for digestion in the intestinal lumen. We therefore agree with the conclusions of Airey et al. (1989), who regard the mucous cells as one of the targets for specific molluscicial interference.

Bowen & Jones (1985) also advocate pursuing baseline studies in the development of new substances and suggest that molluscicides should be "packaged so as to effect a slow release and combined with a phagostimulant and pinocytosis inducer."

We think that such basic studies revealing specific sites with which molluscicides could interfere are a necessary adjunct to screening programs in industrial research, of which the objectives are the discovery of new, more specific and less hazardous molluscicides.

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THE PELAGIC FAMILY ATLANTIDAE (GASTROPODA: HETEROPODA) FROM HAWAIIAN WATERS: A FAUNISTIC SURVEY

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ABSTRACT

The atlantid heteropod fauna of Hawaiian waters is composed of 13 species, including *Oxygyrus keraudreni, Protatlanta souleyeti* and 11 species of *Atlanta*. Species characterizations are accompanied by scanning electron micrographs of the shells for all species, color photographs of six live species and a key to the Hawaiian atlantids.

Key words: Atlantidae, Heteropoda, Hawaii, taxonomy, shell morphology, operculum morphology, eye morphology.

INTRODUCTION

Among the several groups of pelagic gastropods, the family Atlantidae (Heteropoda: Mesogastropoda) is perhaps the most poorly understood taxonomically by most zooplankton biologists. This is undoubtedly due to their highly similar shell morphologies and the fact that species identifications have been based almost entirely on shell structure. In addition, the atlantids are difficult to work with because of their microscopic size; shell diameters of most individuals from Hawaiian waters range from about 0.6-0.7 mm in recently metamorphosed individuals to about 2 mm in adults, although two species are as much as 4 mm and one species is nearly 9 mm in diameter. Identifications are usually made under a dissection microscope. The important taxonomic features of the shell spire (the number, shape and sculpture of the whorls) are often difficult to see, however, even at higher magnifications. In this and other recent studies, discussed below, the scanning electron microscope (SEM) has proven to be essential in resolving fine details of spire structure.

The first comprehensive review of the taxonomy of the atlantids was that of Tesch (1949). He reduced the number of recognized species from about 30 to ten based on the voluminous collections made during the Dana Expedition to the Atlantic, Pacific and Indian Oceans. Two of the genera, *Oxygyrus* and *Protatlanta*, in the family Atlantidae were monotypic and remained unchanged, although Tesch reduced the number of species in the third genus, *Atlanta*, to eight. Since the monograph by Tesch, only one major faunistic study (Richter, 1974) and one taxonomic review (van der Spoel, 1976) have been completed. In addition to the eight species recognized by Tesch, Richter (1974) included six others. Of these six, *A. oligogyra* Tesch, 1906, *A. gibbosa* Souleyet, 1852, and *A. affinis* Tesch, 1906, had been described prior to Tesch's revision. The remaining three, *A. echinogyra* Richter, 1972, *A. plana* Richter, 1972, and *A. meteori* Richter, 1972, were subsequently described. In his review of the atlantids in 1976, van der Spoel also added six species, *A. pacifica* Tokioka, 1955, *A. peresi* Frontier, 1966, *A. gibbosa, A. tokiokai* van der Spoel & Troost, 1972, *A. echinogyra* and *A. plana*, to the eight recognized by Tesch in 1949. Among these six, however, only three, *A. gibbosa, A. echinogyra* and *A. plana*, overlapped with those identified by Richter (1974) from the Indian Ocean.

Identification of the various species of *Atlanta* has been based almost exclusively on shell morphology, although eye, opercular and radular morphology can be very important characteristics for the recognition of certain species. Tokioka (1961) described the opercula of a number of atlantids. He found that the opercula of most species were similar and differed only in overall shape and location of the gyre (or spiral portion). In two species, however, the opercular gyres were uniquely ornamented. Tokioka characterized the operculum of *A. inflata* Souleyet, 1852, as having a spiral row of claw-like structures around the central portion of the gyre and that of *A. turriculata* d'Orbigny, 1836, as having two rows of short spines that spiral outward from the

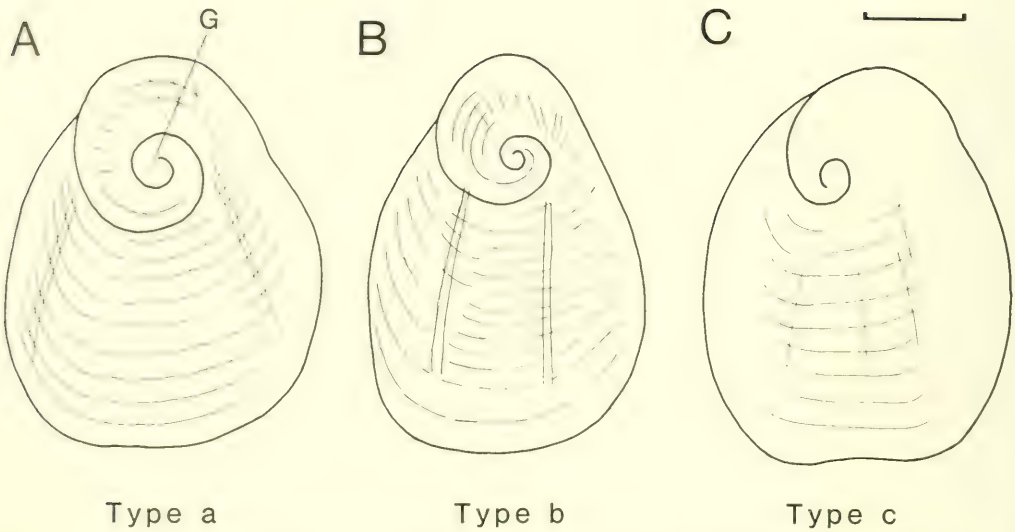

FIG. 1. The three morphological types of opercula found in the Atlantidae (after Richter, 1974). The opercula were drawn from specimens collected during this study. A. Type a (macro-oligogyre) operculum is from a 1.6 mm *Protatlanta souleyeti*. B. Type b (micro-oligogyre) operculum is from a 2.2 mm *Atlanta meteori*. C. Type c (monogyre) operculum is from a 1.4 mm *Atlanta helicinoides*. G: opercular gyre. Scale bar is 0.2 mm.

center of the gyre. Richter (1972) subsequently showed that the operculum of *A. inflata* lacked spiral sculpture on the gyre, however, and that Tokioka had actually figured the opercula of two undescribed species, which Richter had collected from the Indian Ocean and had named *A. echinogyra* and *A. plana*. Three basic types of opercula, termed macro-oligogyre, micro-oligogyre and monogyre, were recognized by Richter (1961). In his 1974 paper Richter termed these Types a, b and c. They differ in overall shape and in the position and number of turns of the gyre (Fig. 1). Among the Indian Ocean species, seven had Type b opercula, while five had Type c and three had Type a opercula (Table 1).

Eye morphology has been little used in distinguishing the species of atlantids. This may be due to difficulties encountered in seeing details of eye structure through the shell of preserved animals, inasmuch as the shell can become very opaque following preservation. Van der Spoel (1972) described a procedure for clearing such specimens without destroying the shell so that the soft parts can be seen. In this same paper van der Spoel illustrated the eyes of nine species of *Atlanta*, among which only one (*A. helicinoides* Souleyet, 1852) possessed a distinctive morphology. This eye type was characterized by a very broad pigmented base into which the spherical lens was recessed. Richter (1974) concluded that three basic eye types (termed Types a, b and c) could be distinguished among the species of atlantids (Fig. 2). The broad-based eye of *A. helicinoides* (termed Type c) is markedly different from the more cuboidal shape of the other two eye types. In all three eye types the lens rests in a cup of pigmented tissue. This pigmented tissue is continuous (Type c) or is interrupted by an approximately triangular, unpigmented window (Types a and b). The latter two eye types are easily distinguished by the presence (Type b) or absence (Type a) of a narrow, transverse slit in the distal portion of the pigmented tissue (Fig. 2). Among those species identified by Richter (1974) from the Indian Ocean, Type c eyes occurred in only *A. helicinoides* and *O. keraudreni*, while Type a and b eyes were equally distributed among the remaining species (Table 1).

Radular morphology has been largely disregarded as a taxonomic character in the Atlantidae (Tesch, 1949; van der Spoel, 1976), although Richter (1986, 1987, 1990) has used radular differences to separate species having very similar shell morphologies. Earlier, Richter (1961) characterized the radulae of nine species of *Atlanta* and concluded that two types (I and II) could be distinguished

TABLE 1. Species in the family Atlantidae recognized by Richter (1974, 1986, 1987, 1990). Whorl number refers to shell whorl in which whorl width increases rapidly (see text). Eye types (a, b and c) and opercular types (a, b and c) are those characterized by Richter (1974). Radular types (I and II) are those described for nine species by Richter (1961).

Species	Whorl number	Eye type	Opercular type	Radular type
**Oxygyrus keraudreni* (Lesueur, 1817)	**	c	***	I
**Protatlanta souleyeti* (Smith, 1888)	3	a	a	I
**Atlanta lesueuri* Souleyet, 1852	3	b	b	II
**Atlanta oligogyra* Tesch, 1906	3	a	b	—
**Atlanta peroni* Lesueur, 1817	4	b	b	II
Atlanta gaudichaudi Souleyet, 1852	4	b	b	II
**Atlanta plana* Richter, 1972	4	a	b	—
**Atlanta echinogyra* Richter, 1972	4	a	c	—
**Atlanta fusca* Souleyet, 1852	5	a	a	I
**Atlanta turriculata* d'Orbigny, 1836	5	a	a	—
**Atlanta inflata* Souleyet, 1852	5	a	c	I
**Atlanta helicinoides* Souleyet, 1852	5	c	c	I
Atlanta inclinata Souleyet, 1852	5	b	c	—
**Atlanta tokiokai* van der Spoel & Troost, 1972	6	b	c	II
Atlanta gibbosa Souleyet, 1852	6	b	b	—
**Atlanta meteori* Richter, 1972	6	b	b	—

*Denotes species identified from Hawaiian waters
**Whorl counts not made because this species has involute spire
***Operculum broadly triangular to trapezoidal; not comparable with the opercula of *Protatlanta* and *Atlanta*

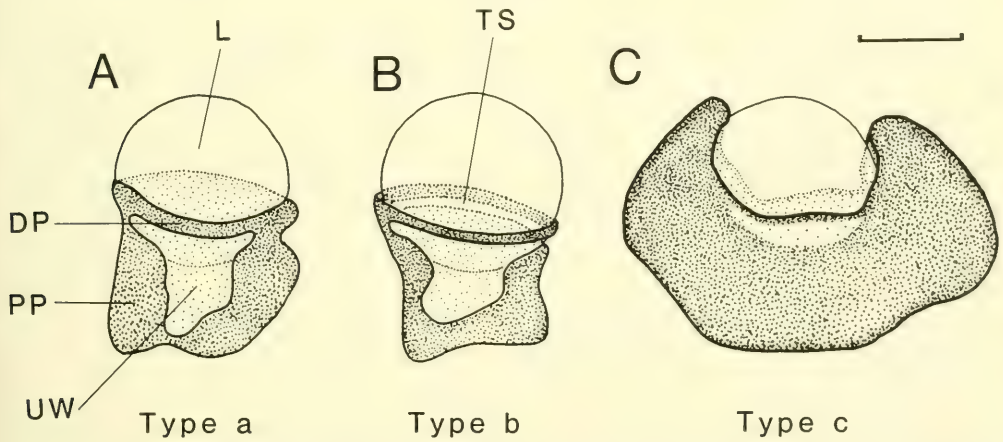

FIG. 2. The three morphological types of eyes found in the Atlantidae (after Richter, 1974). Illustrations of Type a and b eyes modified from drawings in Richter (1974, Fig. 3). Type c eye is from a specimen of *Atlanta helicinoides* (shell length = 1.6 mm) from Hawaiian waters. DP: distal portion of pigmented tissue; L: lens; PP: proximal portion of pigmented tissue; TS: transverse slit in distal pigment; UW: unpigmented window. Scale bar (0.2 mm) applies only to Type c eye. Sizes of Type a and b eyes not given by Richter (1974).

(Table 1). These two species groups were also distinguished on the basis of eye and opercular morphology (Richter, 1974); those species with Type I radulae had Type a or c eyes and Type a or c opercula, while species with Type II radulae had Type b eyes and Type b opercula, except for *A. tokiokai,* which had a Type c operculum.

The present paper characterizes *Oxygyrus keraudreni* (Lesueur, 1817), *Protatlanta souleyeti* (Smith, 1888), and 11 species of *Atlanta* based on material from plankton net samples collected off the island of Oahu between 1984 and 1986. Species descriptions are accompanied by scanning electron micrographs of all species and color photographs of live an-

TABLE 2. Numbers of specimens per sample examined from plankton net tows taken during cruises off western coast of Oahu in April 1984, March 1986, August 1986, and November 1986, and off northern coast of island of Hawaii in August 1986. See text for types of nets used, depths and volumes of water filtered during tows.

Species	Apr 1984	Mar 1986	Aug 1986*	Aug 1986**	Nov 1986	Total
Atlanta lesueuri	1,060	75	202	181	513	2,031
Atlanta turriculata	171	115	555	58	186	1,085
Atlanta plana	299	388	144	198	30	1,059
Atlanta inflata	352	274	209	104	113	1,052
Atlanta peroni	332	437	44	43	7	863
Protatlanta souleyeti	306	191	9	19	64	589
Atlanta meteori	120	75	51	90	2	338
Atlanta oligogyra	21	9	52	18	94	194
Atlanta helicinoides	58	35	42	8	30	173
Atlanta fusca	34	18	2	3	0	57
Atlanta echinogyra	0	0	27	1	19	47
Atlanta tokiokai	2	15	5	3	0	25
Oxygyrus keraudreni	11	3	0	0	0	14

*Oahu
**Hawaii

imals for six species. A key to the Hawaiian atlantids is included at the end of the paper.

MATERIALS AND METHODS

A total of 7,527 specimens of atlantids were examined (Table 2). The animals were removed from plankton samples collected during cruises of research vessels from the University of Hawaii in waters off the western coast of Oahu (21°15′N, 158°20′W) and off the northwestern shore of Hawaii (19°43′N, 156°06′W). During a 10-14 April 1984 cruise off Oahu, 40 tows were taken with paired, opening-closing Bongo nets (70 cm mouth diameter), constructed of 0.5 mm mesh Nytex gauze. Oblique tows of 30 min duration were taken within 50 m depth intervals between the surface and 200 m and from 200 to 300 m. An average of 2,600 m^3 of water was filtered during each tow. During a 22-29 March 1986 cruise off Oahu, 15 oblique tows between the surface and about 300 m were taken with an open ring net (226 cm mouth diameter), constructed of 0.5 mm mesh Nytex gauze. The tows averaged 35 min in duration, and an average of 7,300 m^3 of water was filtered during each tow. Oblique tows to 300 m were taken using the 226 cm ring net during a 6–9 August 1986 cruise off Oahu (three tows) and off Hawaii (three tows). Average tow duration was 35 min, and the average volume of water filtered was 7,600 m^3. During daytime hours on 23 November 1986 off Oahu, oblique tows to a target depth of 50 m were taken with the 226 cm ring net (three tows; average of 5,100 m^3 filtered) and open 70 cm Bongo nets (three tows; average of 1,800 m^3 filtered). Unless used to obtain specimens for observation or photography, plankton samples were preserved aboard ship in 4% formalin solution in buffered sea water immediately after collection and were transferred to 40% isopropanol within 14 days. All shell measurements were made to the nearest 0.1 mm with an ocular micrometer in a Wild M5 dissection microscope. Because the keel of the shell was frequently damaged, all shell diameters were measured exclusive of the keel.

During the March and August 1986 cruises, specimens were sorted from the fresh plankton samples for live photography using a Zeiss dissection microscope with Kodachrome 64 color slide film and Kodak VRG 100 color negative film. Specimens were placed in filtered sea water in clear glass petri dishes. Vivitar 285 strobes were positioned on either side of the microscope stage and were angled obliquely to produce a dark background.

A minimum of four specimens of each species were examined under a JEOL JSM-35CF scanning electron microscope (SEM). The shells were mounted on aluminum stubs to which double-sided tape had been attached, and were then cold sputter-coated with gold-palladium (60:40), 21 nm thickness, in a

Pelco Model 3 sputter coater. Photographs were taken on Kodak T-MAX 120 black-and-white negative film. During preparation of specimens of *Atlanta*, drying did not produce any changes in the shape of the calcareous shell (composed of aragonite; Batten & Dumont, 1976). However, because the adult shell and keel of *Oxygyrus keraudreni* and the keel of *Protatlanta souleyeti* are made of conchiolin (Richter, 1974; Batten & Dumont, 1976), drying resulted in shriveling and collapse of these organic shell components. To retain their original shape, a critical point drying procedure was used prior to sputter-coating. Briefly, individual specimens were held between filter paper hats in specimen holders. They were transferred from ethanol solutions of 30% to 50% to 90% and to 100% (three times at each concentration), then placed in Freon 113 (transferred three times) and then critical point dried in carbon dioxide.

Complete synonymies of the species characterized in this paper were given by van der Spoel (1976) and are not repeated here. Voucher specimens of each species were deposited with the Bishop Museum, Honolulu, Hawaii, and the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

RESULTS AND DISCUSSION

A total of 13 species of atlantids were recorded from Hawaiian waters (Table 1). Two of the genera (*Oxygyrus* and *Protatlanta)* are monospecific, while the third (*Atlanta*) includes the remaining eleven species. Descriptions of these species are presented below.

Because the shell morphologies of the larvae and adults of a species are quite different, and because the larvae and adults commonly occur together in plankton samples, shell differences are described here before proceeding to the species characterizations. The most conspicuous difference is that the keel of the adults is lacking in the larvae (Fig. 3A–D). In addition, the shell terminates in an apertural lip that is quite different in the adults and larvae. In adults the aperture is approximately triangular to oval in cross-sectional outline and is formed by the two halves of the outermost (final) shell whorl and the base of the preceding shell whorl. In the larval shell the aperture is formed by two large lobes that are separated from the preceding shell whorl by broad lateral notches (Fig. 3A-D). The surface sculpture of the larval and adult shells of each species can be quite different. The larval shells of eight of the Hawaiian species possess raised sculpture, which ranges in the extent of development from simple (e.g. *A. plana* [Fig. 3A], with a small number of weakly-elevated spiral ridges) to complex (e.g. *A. echinogyra* [Fig. 3C], with prominent spiral ridges, angled cross-ridges and punctae). The postlarval whorls of the adult shell generally lack elevated ridges, although punctae are present in some species. Thus, the transition from the larval to the adult shell is often very distinct (e.g. *A. echinogyra*; Fig. 8E,F).

Oxygyrus Benson, 1835

Oxygyrus keraudreni (Lesueur, 1817)
(Fig. 3E-H)

Material: A total of 14 specimens was examined (Table 2), which ranged from larvae (less than 1.1 mm) to a 3.4 mm adult. Four individuals, ranging from 1.4 to 2.7 mm, were examined under the SEM.

Species characterization: The adult shell and keel are of conchiolin, although the larval shell is calcareous and has prominent, zigzag spiral sculpture (Fig. 3E,G). The shell spire is involute (Fig. 3G). With age, the calcareous larval shell is overgrown by the conchiolin adult whorls. The conchiolin keel is tall and terminates abruptly at the shell aperture (Fig. 3E). Also, the keel is truncate along its anterior margin. The color of the adult shell and keel is a translucent, light bluish-purple. The eyes are large and Type c (Fig. 2C). The operculum (Richter, 1961: Fig. 18; van der Spoel, 1976: Fig. 133C) is very different from those of other atlantids. It is broadly triangular (nearly trapezoidal) and lacks the spiral portion (or gyre).

Discussion: This species is collected infrequently and in low numbers in Hawaiian waters (Table 2). A maximal shell diameter of 10 mm was reported by Tesch (1949) and van der Spoel (1976). Richter (1982) recorded animals between 3 and 8 mm from the guts of immature dolphin fish. The largest specimen captured in the present study was only 3.4 mm.

The shell of *O. keraudreni* is unique among the atlantids because it has an involute spire, rather than the outwardly-produced spire on the right side of the shell of the other two gen-

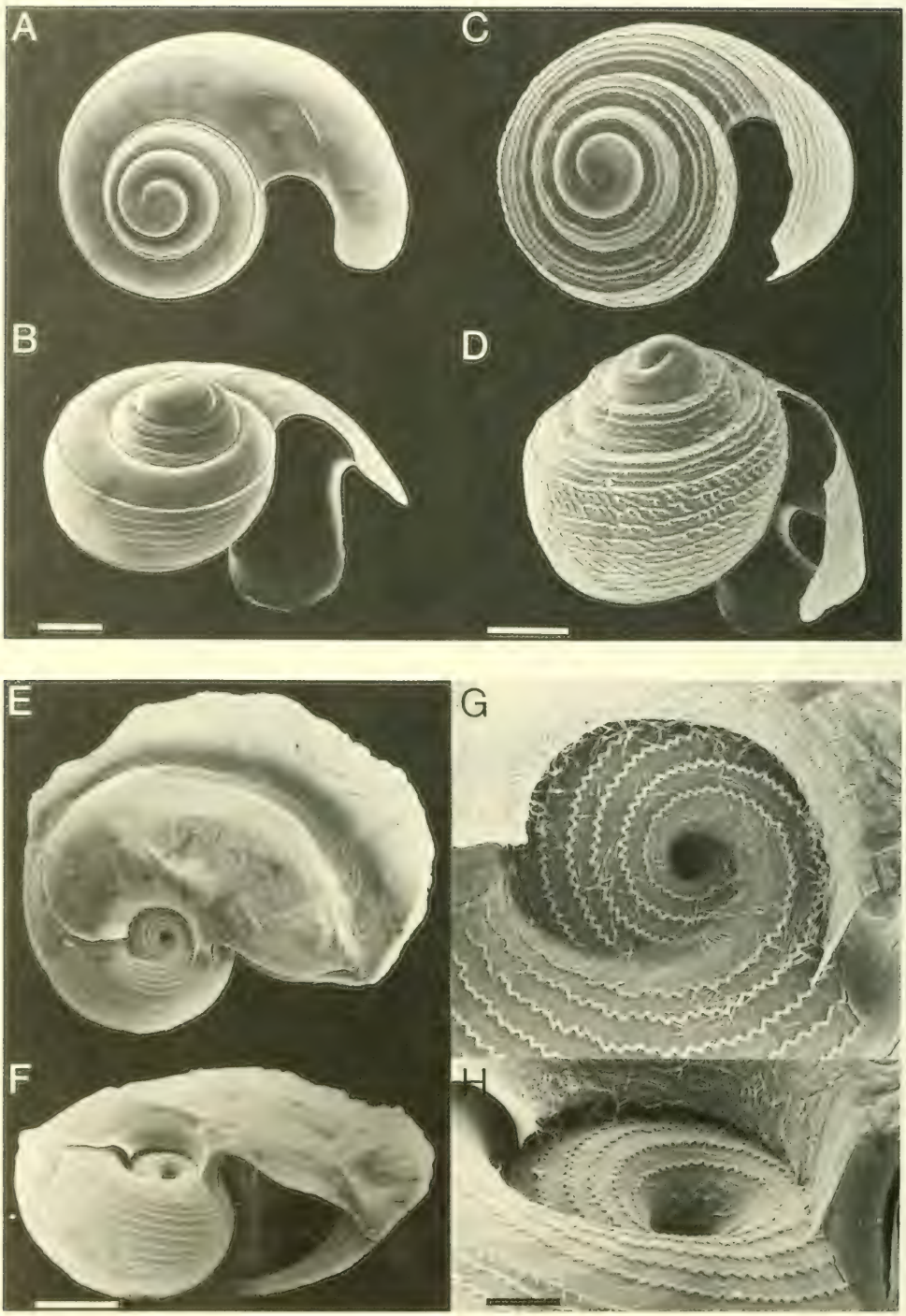

FIG. 3. Scanning electron micrographs of larval shells of *Atlanta plana* (A,B) and *A. echinogyra* (C,D), and of adult shell of *Oxygyrus keraudreni* (E-H). All photographs are of right side of the shell taken either perpendicular to the shell plane or at a 60 tilt. Scale bars are 0.1 mm for larval shells; 0.5 mm for *O. keraudreni* at low magnification (E,F), and 0.1 mm for *O. keraudreni* at high magnification (G,H).

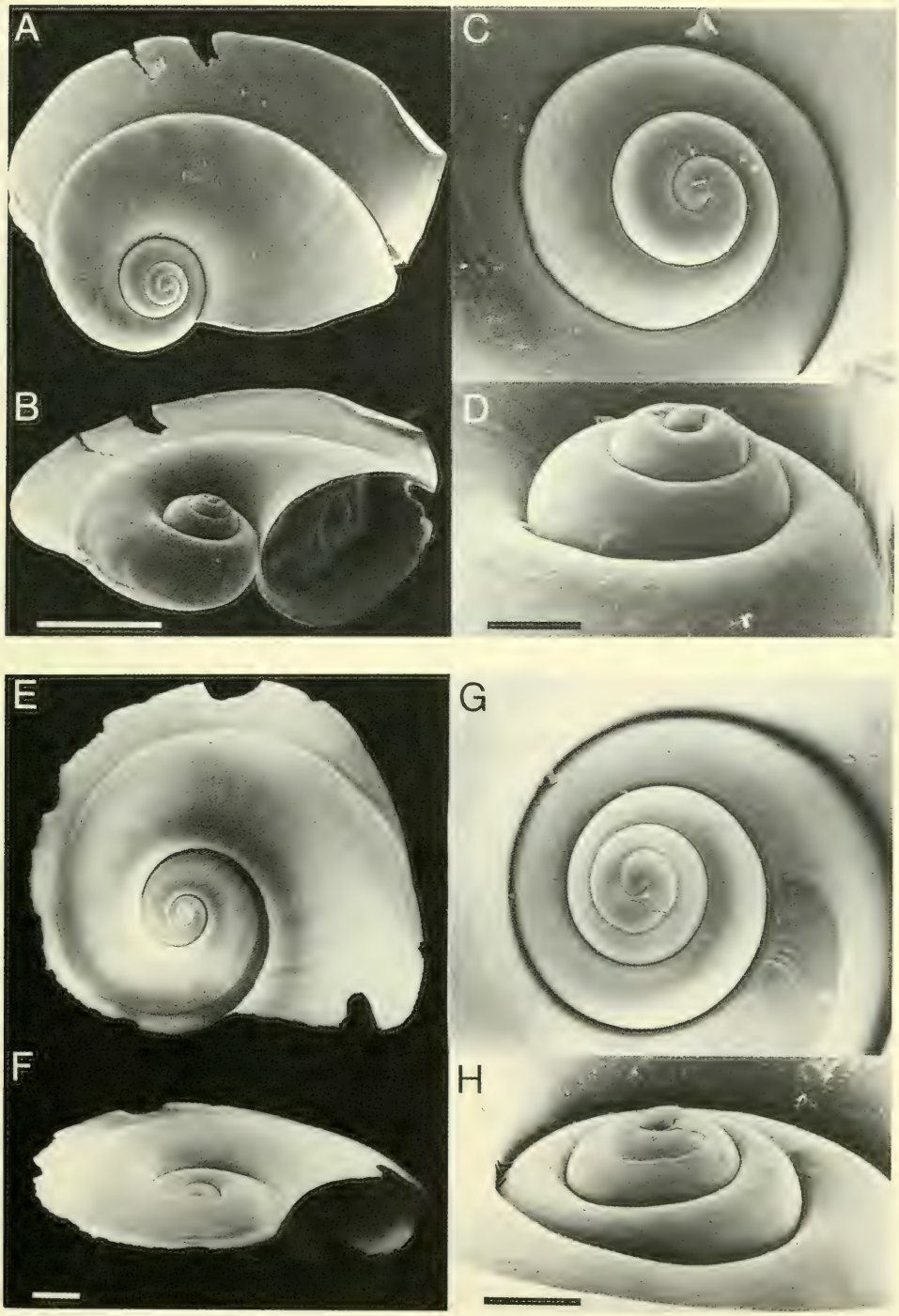

FIG. 4. Scanning electron micrographs of *Protatlanta souleyeti* (A-D) and *Atlanta peroni* (E-H). For each species four views are included; low magnification of right side of shell (upper left) and at 60° tilt (lower left); high magnification of spire (upper right) and at 60° tilt (lower right). Scale bars are 0.5 mm for low magnification, 0.1 mm for high magnification.

era. Further, the adult shell is composed entirely of conchiolin (Richter, 1974; Batten & Dumont, 1976), the sclerotized protein that forms the outer periostracum layer of the gastropod shell (Hyman, 1967). In young individuals, such as the 1.9 mm shell illustrated by Tesch (1949: Fig. 1C) and in the 2.2 mm specimen shown here in Fig. 3E-H, the junction between the larval and adult shell is clearly marked. During the critical point drying procedure used in this study, this junction was exaggerated by the partial elevation of the adult shell from the underlying larval shell.

Protatlanta Tesch, 1908

Protatlanta souleyeti (Smith, 1888)
(Figs. 1A, 4A-D, 5A)

Material: A total of 589 specimens was examined (Table 2), which ranged from larvae (less than 0.7 mm) to a 1.9 mm adult. Eight individuals, ranging from 0.9 to 1.7 mm were examined under the SEM.

Species characterization: The shell is calcareous and the keel is of conchiolin. The shell spire is smooth, lacking sculpture, and is slightly elevated (Fig. 4B,D). The keel has a glass-like transparency (Fig. 5A) and a curved, rectangular shape (Fig. 4A), extending from the shell aperture to about one-half the circumference of the shell. The anterior margin of the keel is sharply truncate. The digestive gland is contained within the shell spire and is usually a light brownish-orange to reddish-brown (Fig. 5A). The eyes are Type a, and the operculum is Type a.

Discussion: The maximal size of *P. souleyeti* in this study was only 1.9 mm, although this is greater than the adult size range of 1.0 to 1.5 mm cited by Tesch (1949) and van der Spoel (1976).

The transparency and shape of the keel immediately distinguishes this species from all other atlantids. *Protatlanta souleyeti* is most similar in appearance to *Atlanta lesueuri* Souleyet, 1852, and *A. oligogyra*, for all three species have a compact spire comprised of a low number of smooth whorls. When the keel has broken off, as sometimes happened in the Hawaiian material, *P. souleyeti* can be somewhat difficult to separate from these two species of *Atlanta*. In such instances the color of the shell spire can be used to separate *P. souleyeti* (brownish-orange to reddish-brown) from *A. lesueuri* (clear to light pink) and *A. oligogyra* (light violet).

Atlanta Lesueur, 1817

The genus *Atlanta* differs from *Oxygyrus* and *Protatlanta* in having a shell and keel that are both calcareous. Separation of the species of *Atlanta* has been based largely on shell characteristics, as discussed above. One of the features of the shell that is easy to determine and has been used commonly in the past is the total number of whorls comprising the adult shell. This number is not constant, however, but increases with shell growth. Alternatively, the number of whorls comprising the inner portion of the shell is a feature that is not affected by the size of the adult animal at the time of capture. In her review of the heteropods, Thiriot-Quiévreux (1973) referred to the number of whorls comprising the spire for each of the atlantid species. In the present paper, a similar approach is used.

Under the dissection microscope, the whorl in which the shell morphology of atlantids changes from that of the larva to that of the adult is often clearly demarcated. Even if this point of change cannot readily be detected, the dramatic increase in overall whorl size, indicated by a rapid increase in whorl width, that begins in the last larval whorl and continues following metamorphosis is very distinctive. The shell whorl in which this region of rapid increase in whorl width occurs is used here as a taxonomic character. To make whorl counts, the shell must be oriented in a consistent manner. The specimen must be rotated until the protoconch is directed away from the viewer (Fig. 6). In *A. lesueuri* (Fig. 6A), for example, the protoconch comprises most of the first whorl and is followed by a narrow second whorl and a rapidly expanding third whorl. In *A. peroni* Lesueur, 1817 (Fig. 6C), on the other hand, the second and third whorls are narrow and the fourth whorl expands rapidly. Among the 11 Hawaiian species, the whorl that expands rapidly is the third shell whorl in *A. lesueuri* (Fig. 6A) and *A. oligogyra* (Fig. 6B); the fourth whorl in *A. peroni* (Fig. 6C), *A. plana* (Fig. 6E) and *A. echinogyra* (Fig. 6F); the fifth whorl in *A. fusca* Souleyet, 1852 (Fig. 6G), *A. turriculata* (Fig. 6H), *A. inflata* (Fig. 6I) and *A. helicinoides* (Fig. 6J); and the sixth whorl in *A. tokiokai* (Fig. 6K) and *A. meteori* (Fig. 6L). For purposes of comparison with *A. peroni* and *A. plana*, a sketch of *A. gaudichaudi* Souleyet, 1852 (Fig. 6D), from Australian waters is included, although this species was not collected from Hawaiian waters.

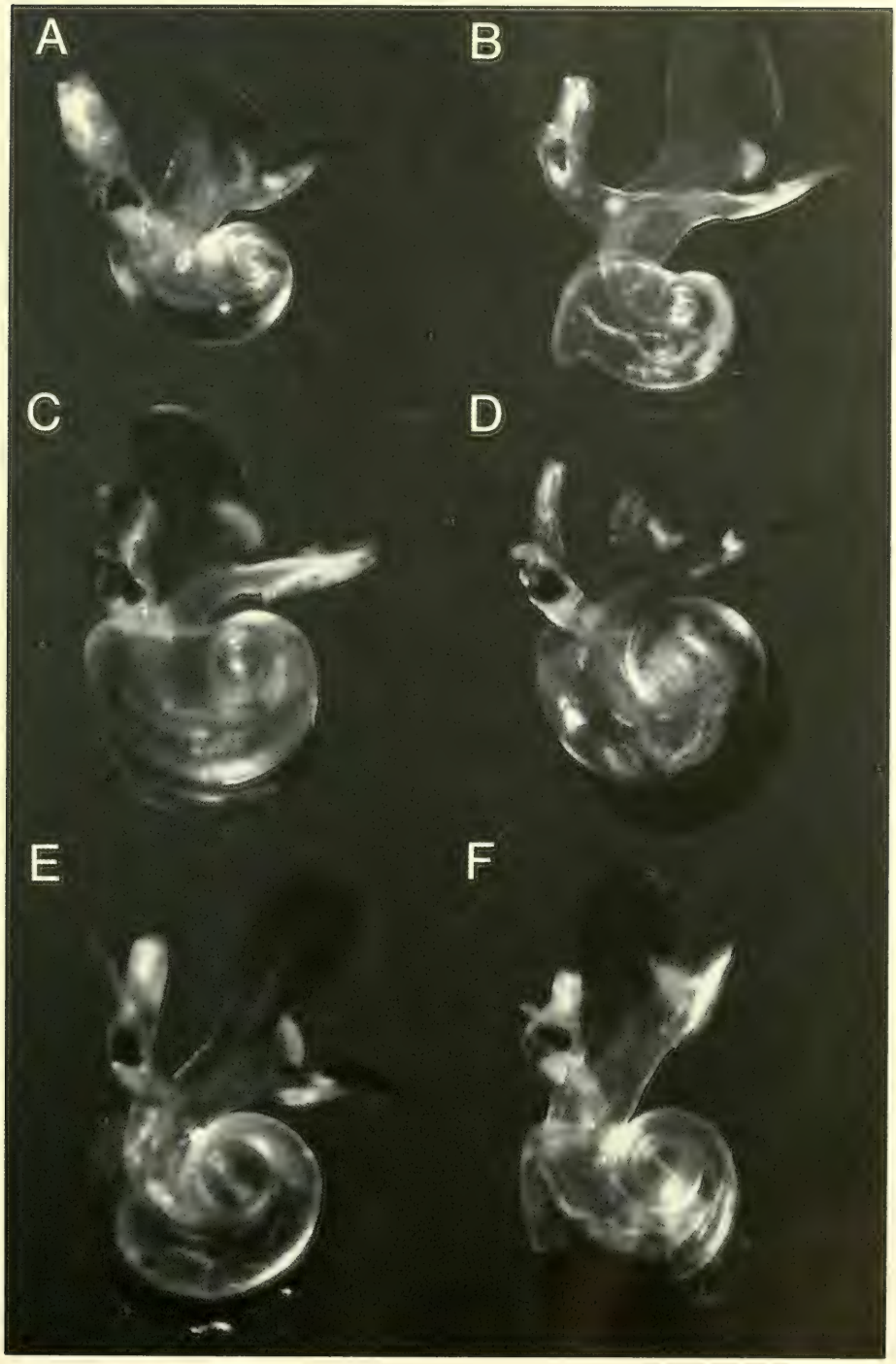

FIG. 5. Laboratory photographs of live atlantids collected from southwest side of Oahu May 1987. A. *Protatlanta souleyeti* (0.8 mm). B. *Atlanta lesueuri* (1.2 mm). C. *A. turriculata* (0.9 mm). D. *A. tokiokai* (1.5 mm). E. *A. echinogyra* (1.0 mm). F. *A. inflata* (0.9 mm).

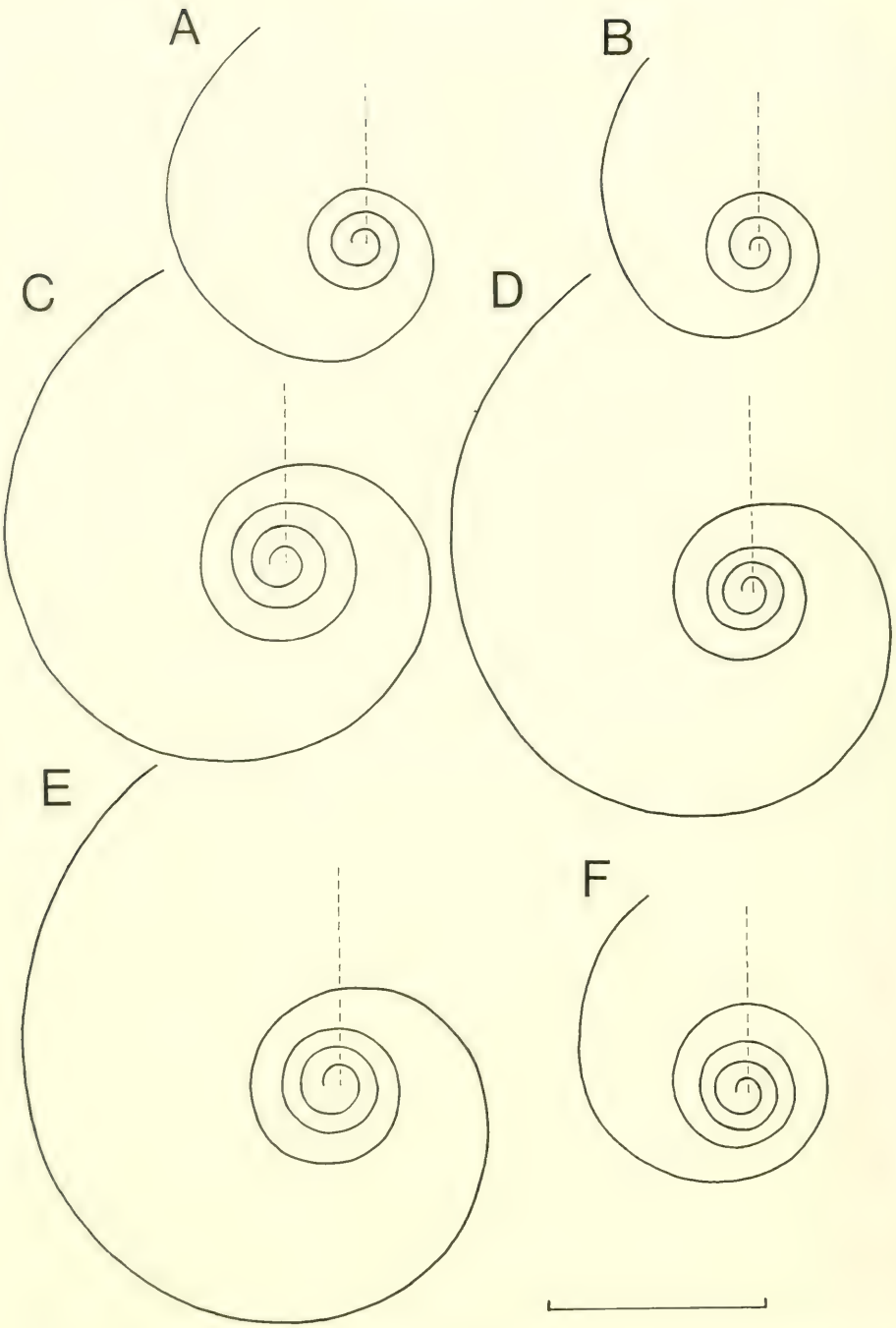

FIG. 6. Sketches of atlantid shell spires viewed at right angles to axis of spire and oriented with protoconch directed upwards. Dashed line in each sketch to aid in counting of shell whorls. A. *A. lesueuri*. B. *A. oligogyra*. C. *A. peroni*. D. *A. gaudichaudi*. E. *A. plana*. F. *A. echinogyra*. G. *A. fusca*. H. *A. turriculata*. I. *A. inflata*. J. *A. helicinoides*. K. *A. tokiokai*. L. *A. meteori*. Scale bars are 0.5 mm. All sketches from specimens of atlantids collected off Hawaii, except for that of *A. gaudichaudi*, which was based on animals from Australian waters.

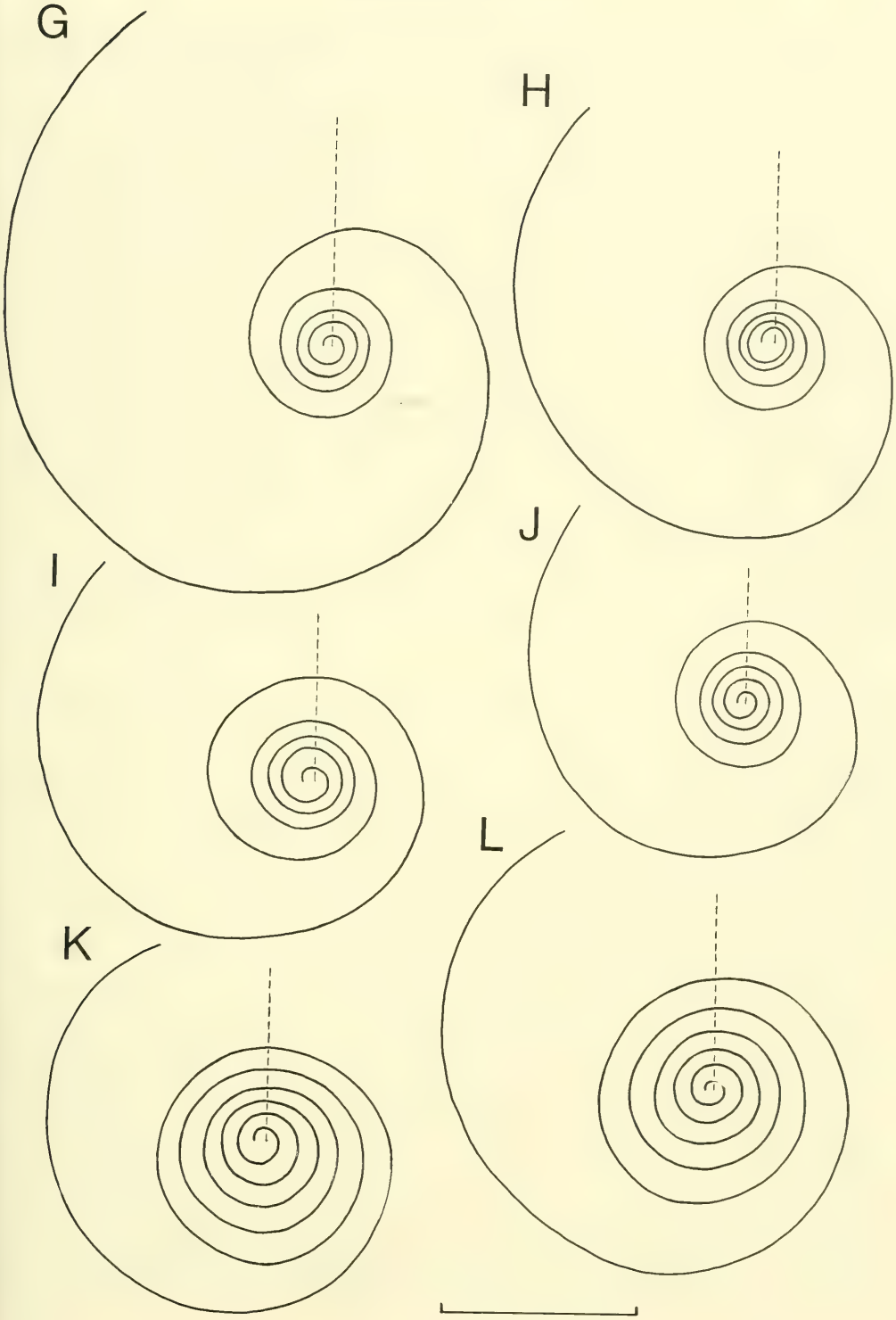

FIG. 6G-L.

Atlanta lesueuri Souleyet, 1852
(Figs. 5B, 6A, 7A-D)

Material: A total of 2,031 specimens was examined (Table 2), which ranged from larvae (less than about 0.6 mm) to 1.9 mm adults. Seven specimens, ranging from 1.0 to 1.7 mm, were examined under the SEM.

Species characterization: The shell spire is compact and low (Fig. 7B). The spire whorls are smooth, lacking any sculpture (Fig. 7C). The sutures between the whorls are incised (Fig. 7D). Rapid increase in whorl width occurs in the third shell whorl (Fig. 6A). The keel is high with a truncated anterior edge (Fig. 7A). Because it is quite fragile, however, the keel is commonly damaged and the truncated anterior margin might not be evident. The shell of the animal is clear (Fig. 5B), although the inner whorls can take on a light pink color (darkest in the sutures) in older specimens. The body is also clear (Fig. 5B), except for purple-red pigmentation at the end of the proboscis and at middle and distal locations on the opercular lobe. This pigmentation becomes darker and more prominent in older individuals. The eyes are Type b, the operculum is Type b.

Discussion: *Atlanta lesueuri* is among the most abundant species of atlantids in Hawaiian waters (Table 2). It resembles only one other species, *A. oligogyra*. Features that distinguish the two species are discussed below under *A. oligogyra*.

Atlanta oligogyra Tesch, 1906
(Fig. 7E-H)

Material: A total of 194 specimens was examined (Table 2), which ranged from larvae (less than 0.6 mm) to a 1.9 mm adult. Four specimens, ranging from 0.9 to 1.9 mm, were examined under the SEM.

Species characterization: The shell spire is compact and low (Fig. 7F). The spire whorls are smooth, lacking any sculpture (Fig. 7G). The sutures between the first and second whorls are shallow, while those between the second and subsequent whorls are incised (Fig. 7G,H). The sutures have a very light violet color. The keel is moderately tall and rounded in lateral profile (Fig. 7E). The eyes are Type a and the operculum is Type b.

Discussion: The shell of *A. oligogyra* can be difficult to distinguish from that of the preceding species, *A. lesueuri*. Features used by Richter (1974) to characterize the shell of *A. oligogyra* and to separate it from that of *A. lesueuri* included a lower keel, a brown keel base and light violet inner surface of the aperture (in adults). The eyes of the two species, however, are distinctly different: Type a and small in *A. oligogyra*, and Type b and large in *A. lesueuri*. Despite these differences, van der Spoel (1976) treated *A. oligogyra* as a synonym of *A. lesueuri*. In defense of his separation of the two species in his 1974 paper, Richter (1986) expanded on the species characterizations and included differences in the radulae.

In the Hawaiian material, *A. oligogyra* could be distinguished from *A. lesueuri* on the basis of the Type a eyes (Type b in *A. lesueuri*), the relatively lower and more rounded keel (tall and truncated at the anterior edge in *A. lesueuri*), and the light violet color of the spire sutures (clear in *A. lesueuri*). The keel base of Hawaiian *A. oligogyra* is clear, not brown as reported by Richter for Indian Ocean specimens.

Atlanta peroni Lesueur, 1817
(Figs. 4E-H, 6C)

Material: A total of 863 specimens was examined (Table 2), which ranged from larvae (less than about 0.7 mm) to an 8.4 mm adult. Six specimens, ranging from 1.6 to 3.8 mm, were examined under the SEM.

Species characterization: The shell spire is low (Fig. 4H). The whorls comprising the spire are smooth, lacking any sculpture (Fig. 4G). The sutures between the first and second whorls are shallow, while those between subsequent whorls are deeply incised (Fig. 4H). Rapid increase in whorl width occurs in the fourth shell whorl (Fig. 6C). The moderately tall keel is rounded in profile (Fig. 4E). The keel base is clear in young individuals (i.e. less than about 2 mm), but changes from a light to a dark golden-brown in progressively older animals. The keel inserts between the fifth and sixth whorls in individuals greater than about 2 to 3 mm. The eyes are Type b, the operculum is Type b.

Discussion: This species achieves the largest size (up to a diameter of 10 mm) in the genus *Atlanta* (Richter, 1974; van der Spoel, 1976). The largest specimen that I collected in Hawaiian waters was 8.4 mm, which approaches a total diameter of 10 mm when the keel is included.

Except for the golden-brown pigmentation that develops at the base of the keel with in-

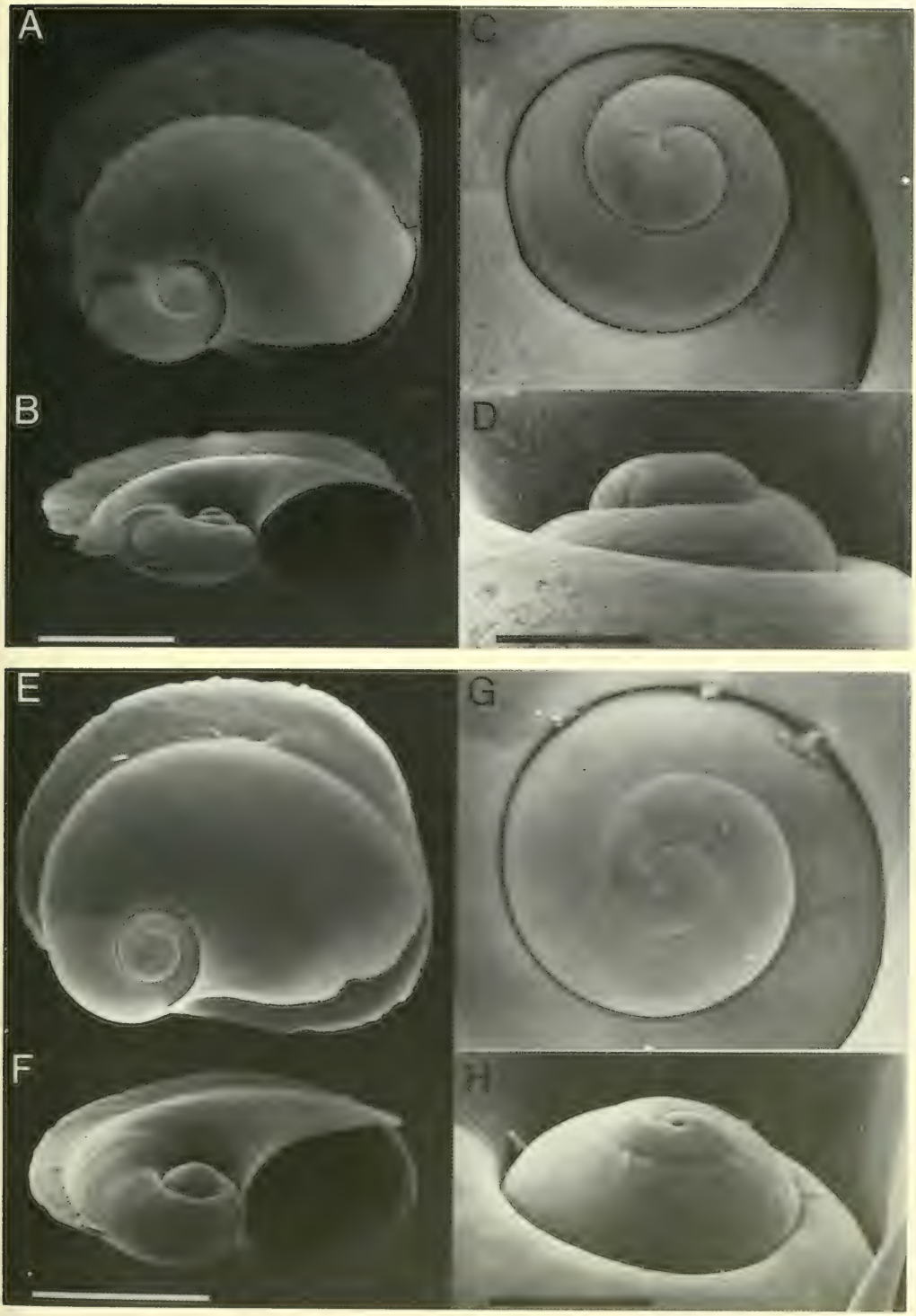

FIG. 7. Scanning electron micrographs of *Atlanta lesueuri* (A-D) and *A. oligogyra* (E-H). Views and scale bars as in Fig. 4.

creased age, most of the shells examined were clear. In some instances, however, the shell in juveniles was found to be light pink, which presumably persists and would account for the light pink color seen in some adults (also reported by Thiriot-Quiévreux, 1973).

The present characterization of the shell spire for Hawaiian *A. peroni* agrees with the descriptions of Tesch (1949) and van der Spoel (1976). In the *A. peroni* from the Indian Ocean examined by Richter (1974: Fig. 7), however, the whorls comprising the shell spire had an elevated, thin spiral ridge along the outer margin of each whorl. This elevated ridge was also indicated in the drawing by Frontier (1966: Fig. 4) of *A. peroni* from the Indian ocean. Such a ridge would appear to be lacking in the *A. peroni* from the Pacific and Atlantic oceans. Van der Spoel's description of the species and illustrations of a specimen from the Atlantic Ocean (1976: Fig. 135A,B) do not include this ridge, nor does the scanning electron micrograph of a specimen in Thiriot-Quiévreux (1973: Fig. 1C). Presumably, the specimen used by Thiriot-Quiévreux came from the North Atlantic or the Mediterranean Sea. Tesch's (1949) description and drawing (1949; p. 16-17, Fig 9) of *A. peroni* also did not indicate such a ridge. The presence of an elevated spiral ridge on the shells of specimens collected from the Indian Ocean is problematical. The species identified by Frontier and Richter as *A. peroni* could represent a morphological variant of *A. peroni* that is unique to the Indian Ocean. However, Richter (pers. comm.) now thinks that it is either an undescribed species or is a species that was described previously and is not currently recognized.

The shell morphology of *A. peroni* is close to that of only one other species from Hawaiian waters, *A. plana*. Differences between these two species and *A. gaudichaudi* will be discussed below under *A. plana*.

Atlanta plana Richter, 1972
(Figs. 3A-B, 6E, 8A-D, 9A-B)

Material: A total of 1,059 specimens was examined (Table 2), which ranged from larvae (less than about 0.7 mm) to a 3.4 mm adult. Six specimens, ranging from 1.3 to 2.5 mm, were examined under the SEM.

Species characterization: The shell spire forms a low cone (Fig. 8D). Under the dissection microscope the spire can appear to lack spiral sculpture. Under the SEM, however, two weakly-developed spiral ridges are seen on the second and third whorls (Fig. 8C,D). In the last half of the third whorl, the spiral ridges break up and are replaced by spirally arranged rows of small punctae (Fig. 8C). The sutures of the spire are violet. The shell whorl in which a rapid increase in width occurs is the fourth (Fig. 6E). The keel is rounded and somewhat low (Fig. 8A). The keel base is a copper-brown to golden-brown color. The eyes are Type a. The operculum is Type b (Fig. 9A) and possesses a low gyre with about 20 flattened, outwardly directed spines (Fig. 9B).

Discussion: Like Richter (1974), I consider *A. plana* to be most similar in appearance to *A. gaudichaudi*. In turn, these two species are perhaps most similar to *A. peroni*. In all three species the shell whorl that expands rapidly in width is the fourth (Figs. 6C,D,E). All three species also have Type b opercula (Table 1). The operculum of *A. plana* is unique, however, in that it has a spinose gyre (Fig. 9B). Further, the Type a eyes distinguish *A. plana* from *A. gaudichaudi* and *A. peroni* (Type b eyes), and the whorl sculpture (two weakly developed spiral lines) in *A. plana* is lacking in the other two species. The violet suture pigmentation of the spire in *A. gaudichaudi* distinguishes this species from *A. peroni*, which has clear to light pink sutures.

Richter reported both *A. gaudichaudi* and *A. plana* from the Indian Ocean. Newman (pers. comm.) has recorded both species in waters off Heron and Lizard islands, Australia, and has indicated that *A. gaudichaudi* is the most common species of atlantid. It is therefore surprising that I have never identified *A. gaudichaudi* from Hawaiian waters, although I have routinely checked the eye type and, periodically, the operculum of specimens identified as *A. plana*.

Atlanta echinogyra Richter, 1972
(Figs. 3C-D, 5E, 6F, 8E-H, 9C,D)

Material: A total of 47 specimens was examined (Table 2), which ranged from larvae (less than 0.7 mm) to a 1.7 mm adult. Four specimens, ranging from 1.1 to 1.7 mm, were examined under the SEM.

Species characterization: The spire of this small species forms a low cone that can be slightly tilted relative to the shell plane (Fig. 8F,H). The shell whorl that expands rapidly is

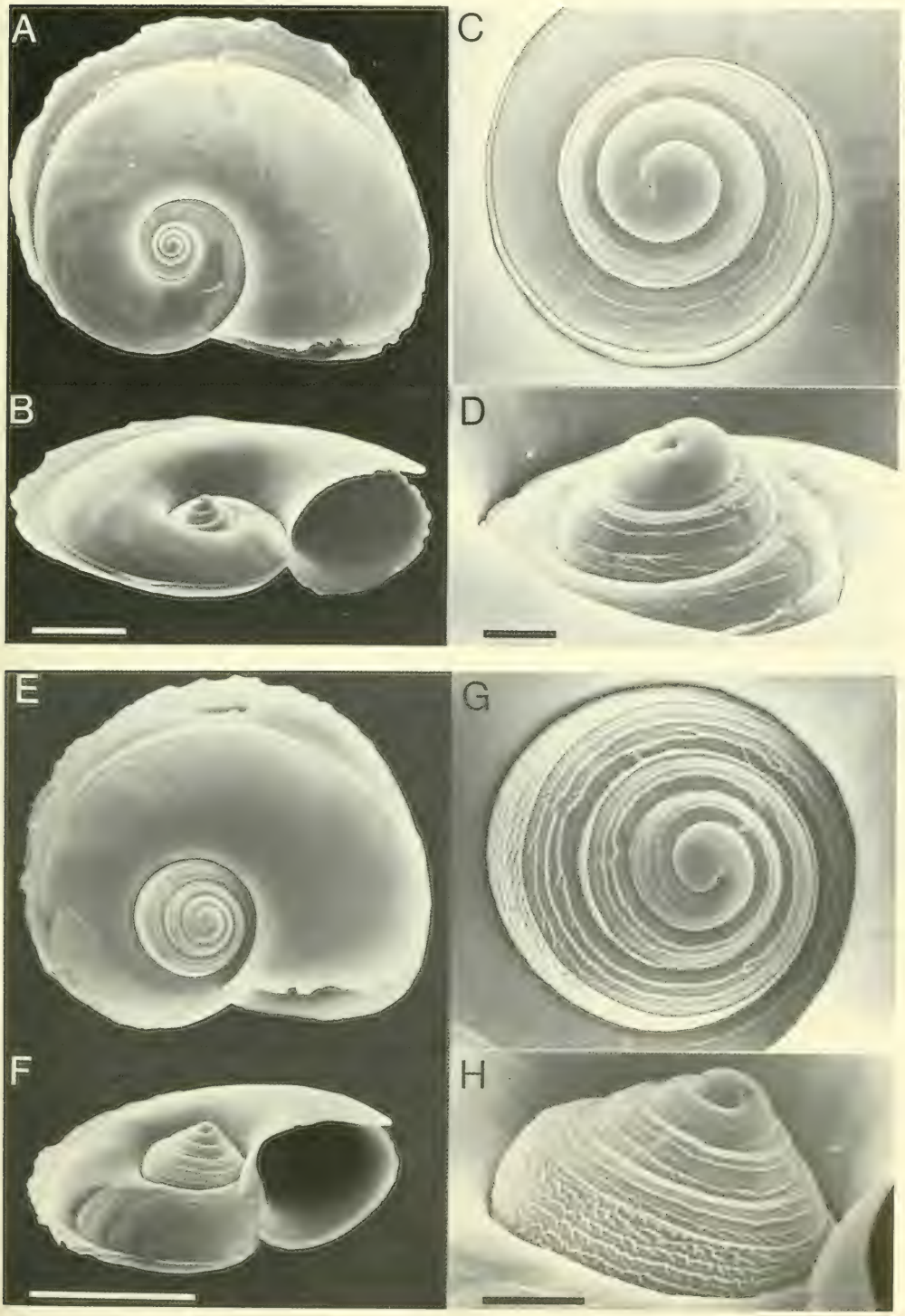

FIG. 8. Scanning electron micrographs of *Atlanta plana* (A-D) and *A. echinogyra* (E-H). Views and scale bars as in Fig. 4.

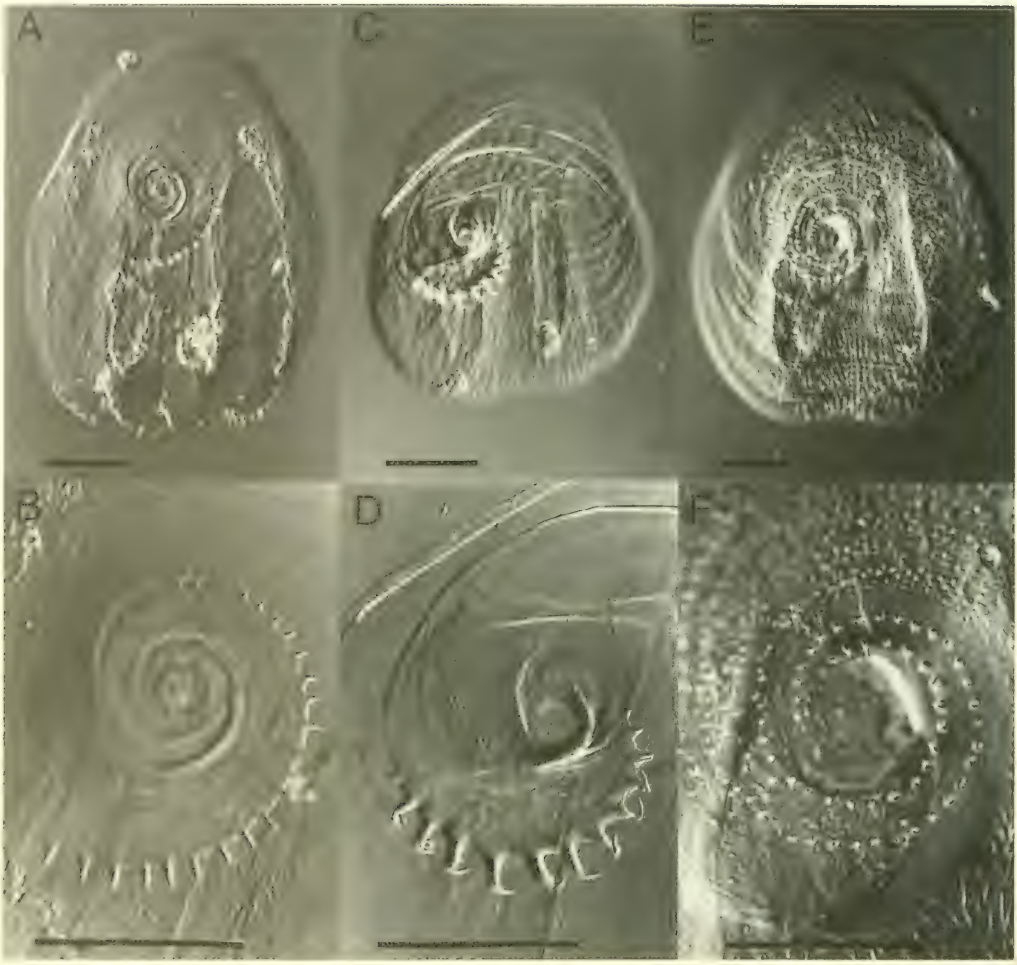

FIG. 9. Photographs of operculum and spiral portion (gyre) of operculum in *Atlanta plana* (A,B), *A. echinogyra* (C,D), *A. turriculata* (E,F). Scale bars are 0.1 mm.

the fourth (Fig. 6F). The second, third and about half of the fourth whorl bear prominent spiral ridges and secondary sculpture (Fig. 8G,H). The shell spire is a uniform reddish-brown, whereas the remaining whorls of the shell and keel are clear (Fig. 5E). The eyes are Type a, and the operculum is Type c. The opercular gyre is elevated and bears about 12 broad-based spines (Fig. 9C,D).

Discussion: This species is immediately recognized in fresh material by the moderately elevated, reddish-brown shell spire. The characteristic spire sculpture is also clear under the high magnification of a dissection microscope. The elevated opercular gyre with the broad-based spines is also unique to this species. When the operculum is mounted on a slide (for viewing beneath a compound microscope), the tips of the spines bend under the pressure of the cover slip, causing them to have the hook-like appearance seen in Figure 9C,D.

I have collected *A. echinogyra* infrequently and in comparatively low numbers from Hawaiian waters (Table 2). Richter (1974), however, reported this species to be abundant in the western Indian Ocean. Richter (1987) also recorded a larger maximum shell size

(2.5 mm) for *A. echinogyra* than I obtained from Hawaiian waters (1.7 mm).

Atlanta fusca Souleyet, 1852
(Figs. 6G, 10A-D)

Material: A total of 57 specimens was examined (Table 2), which ranged from larvae (less than 0.6 mm) to a 1.9 mm adult. Four specimens, ranging from 1.0 to 1.6 mm, were examined under the SEM.

Species characterization: The shell spire forms a strongly elevated cone (Fig. 10B,D) The spire whorls are sculptured by a complex pattern of ornamentation (Fig. 10C,D). A prominent spiral ridge is located along the outer margin of the spire whorls (Fig. 10C,D). This ridge is low on the second shell whorl and progressively increases in height to a maximum on the fourth and fifth whorls. The complex spire ornamentation ends on the larval shell and is replaced by rows of small punctae on the adult shell (Fig. 10A,C). The keel is tall and rounded (Fig. 10A). In animals larger than about 1.5 mm, such as the animal used in Fig. 10A-D, the keel inserts between the fifth and sixth shell whorls. The shell is yellowish-brown (amber) to brown. The eyes are Type a and the operculum is Type a.

Discussion: The largest specimen of *A. fusca* collected in the present study approaches the maximal size of 2 mm reported by Richter (1974) for this species from the Indian Ocean. Van der Spoel (1976) indicated an upper size limit of 4 mm, however.

This species is distinguished by its conspicuous brown to yellowish-brown color and by its tall, conical spire. The species that is most similar in appearance to *A. fusca* is *A. turriculata* (see below).

Atlanta turriculata d'Orbigny, 1836
(Figs. 5C, 9E-F, 10E-H)

Material: A total of 1,085 specimens was examined (Table 2), which ranged from larvae (less than 0.6 mm) to a 1.7 mm adult. Six specimens, ranging from 1.0 to 1.6 mm, were examined under the SEM.

Species characterization: The shell spire protrudes laterally from the right side of the shell as an elongate 'turret' (Fig 10F), formed by the strongly elevated second and third whorls capped by the protoconch (Fig. 10H). When the shell is viewed at right angles to the shell plane (Fig. 10G), a prominent spiral ridge is evident along the periphery of the spire whorls. When oriented in the plane of the shell (Fig. 10H), however, this spiral ridge is seen to be situated in the middle of the second and third whorls. The spiral ridge also increases in height to a maximum on the fourth and fifth whorls (Fig. 10H). The light reddish-brown color of the shell spire grades into a clear outer shell whorl and keel (Fig. 5C). The keel is well developed and rounded in lateral profile (Fig. 10E). The eyes are Type a, the operculum is Type a. The operculum is unique in having two parallel rows of numerous short spines that spiral outward from the gyre center (Fig. 9E,F).

Discussion: The strongly turreted, light reddish-brown shell spire and the spinose operculum immediately distinguish *A. turriculata* from the other species of atlantids. The species of atlantid that is most similar to *A. turriculata* in appearance is *A. fusca*. Both species are small (maximal size of 2.0 mm or less in Hawaiian waters), have pigmented spires, have an elevated ridge in the same position on the spire whorls and have Type a eyes and Type a opercula.

Atlanta inflata Souleyet, 1852
(Figs. 5F, 6I, 11A-D)

Material: A total of 1,052 specimens was examined (Table 2), which ranged from larvae (less than 0.6 mm) to 1.5 mm adults. Twenty-eight specimens, ranging from 0.9 to 1.4 mm, were examined under the SEM.

Species characterization: The shell of this small species is laterally inflated (shell width is about 40% of shell diameter). The spire is relatively flat (Fig. 11B,D). The shell whorl that increases rapidly in width is the fifth (Fig. 6I). The spire whorls and sutures are weakly defined owing to the presence of thick, evenly spaced spiral ridges (Fig. 11A,C). The keel is tall (Fig. 11A) and its anterior margin is truncate in undamaged specimens (not shown by the specimen used in Figure 11A-D, but illustrated clearly in Figure 4 of Richter, 1974). The digestive gland, contained within the shell spire, is mottled reddish-brown to yellowish-brown (Fig. 5F). The eyes are Type a, the operculum is Type c.

Discussion: A second color morph of *A. inflata* was common in the Hawaiian fauna. It was immediately distinguished in fresh and recently preserved specimens by a uniform violet to light purple color of the spire. This appears only to be a color variant, however,

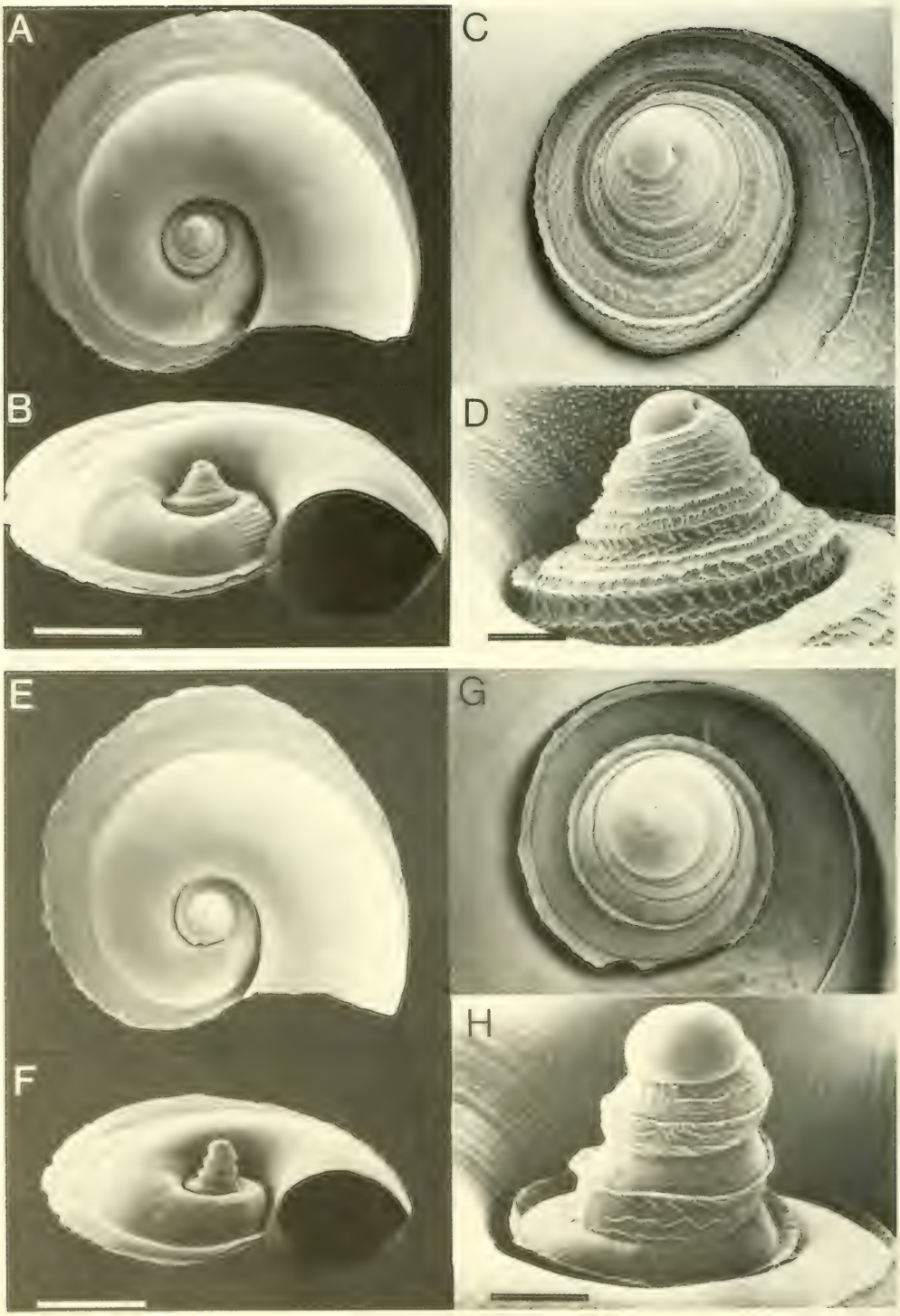

FIG. 10. Scanning electron micrographs of *Atlanta fusca* (A-D) and *A. turriculata* (E-H). Views and scale bars as in Fig. 4.

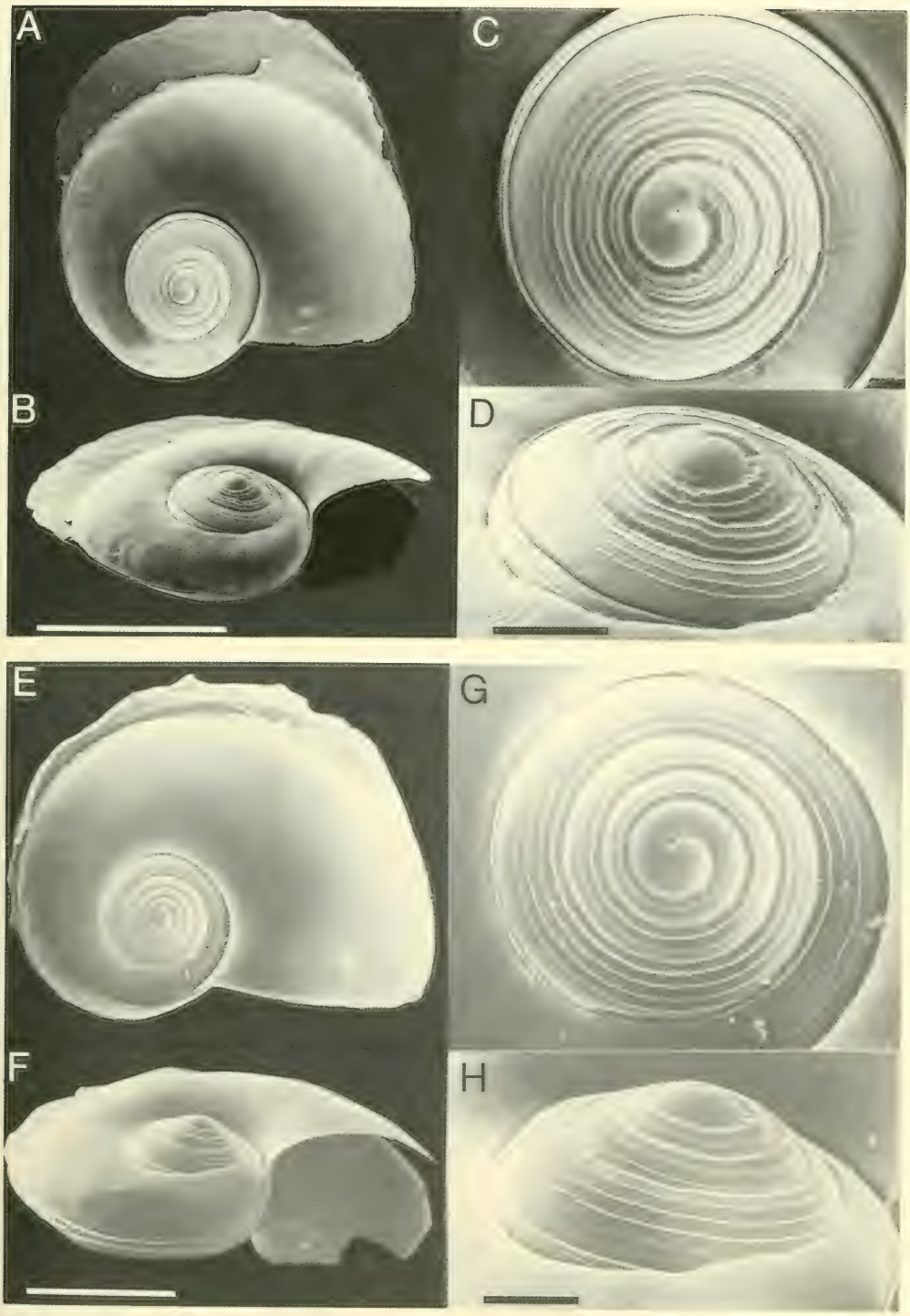

FIG. 11. Scanning electron micrographs of *Atlanta inflata* (A-D) and *A. helicinoides* (E-H). Views and scale bars as in Fig. 4.

because eye and opercular morphologies were indistinguishable from those of typical *A. inflata*, as were the shells when viewed under the SEM.

Like Richter (1987), I have observed considerable variability in the presence and degree of expression of the spiral ridges on the whorls of the shell spire. In the majority of the individuals that I examined under the SEM, however, the spiral ridges were well developed. The shell spire of *A. inflata* is very similar in appearance to that of *A. helicinoides*, and these two species can be easily confused unless other taxonomic characters are used (discussed below).

Atlanta helicinoides Souleyet, 1852
(Figs. 1C, 2C, 6J, 11E-H)

Material: A total of 173 specimens was examined (Table 2), which ranged from larvae (less than about 0.7 mm) to a 2.0 mm adult. Twelve specimens, ranging from 1.1 to 1.9 mm, were examined under the SEM.

Species characterization: The shell of this small species is laterally inflated (shell width is about 40% of the shell diameter). The spire is slightly elevated (Fig. 11H). The shell whorl that increases rapidly in width is the fifth (Fig. 6J). The second through fourth whorls have evenly spaced, thin spiral ridges (Fig. 11G). Because the spiral ridges are relatively narrow, the sutures can be clearly distinguished, particularly under a dissection microscope. On the fifth whorl the spiral ridges break down and are replaced by rows of low, small punctae (Fig. 11G). The keel is rounded and moderately tall in undamaged specimens. The eyes are Type c and the operculum is Type c.

Discussion: In the Hawaiian fauna two distinct color morphs of *A. helicinoides* were encountered in approximately equal proportions; a light yellow-tan form and a light purple-pink form. I could not see any structural differences in eye, opercular or shell morphologies that would justify their taxonomic separation, however.

Referring to *A. helicinoides*, Tesch (1949: 19) stated, "This species is at first sight so extremely like the preceding one (*A. inflata*) that it requires considerable attention to distinguish them." Richter (1987) also noted the strong similarities of the two species, particularly in the appearance of the shell spire. In SEM photographs (compare Figs. 11A, 11E), the gross morphologies of the shells can be seen to be nearly identical. The spires are relatively flat and about the same size, and the number and spacing of the spiral ridges on the spire whorls are the same (compare Figs. 11C, 11G). Further, both species are small and the shells are laterally inflated. The only obvious differences between the shells of the two species are, first, the spiral ridges on the spire whorls are thinner and less prominent in *A. helicinoides* than in *A. inflata*, with the result that the whorls comprising the spire are more clearly defined in *A. helicinoides*, and, second, the keel of *A. helicinoides* is somewhat low and rounded, whereas that of *A. inflata* is tall and truncate along the anterior edge. The two species can be immediately separated on the basis of their eyes, however, which are Type c in *A. helicinoides* and Type b in *A. inflata*.

Atlanta tokiokai van der Spoel & Troost, 1972 (Figs. 5D, 6K, 12A-D)

Material: A total of 25 specimens was examined (Table 2), which ranged from larvae (less than about 0.8 mm) to a 2.6 mm adult. Four specimens, ranging from 1.2 to 2.4 mm, were examined under the SEM.

Species characterization: The shell spire is tilted (or inclined) relative to the shell plane (Fig. 12A). The spire is globose in side view (Fig. 12B,D), forming an apical angle of about 80°. Spirally arranged rows of small, low punctae are present on the spire (Fig. 12D). The punctae become more prominent on the last whorls of the spire. The shell whorl that increases rapidly in width is the sixth (Fig. 6K). The shell is a light yellow-tan color (Fig. 5D). The keel is tall and rounded (Fig. 12A). The eyes are Type b, and the operculum is Type c.

Discussion: Specimens of *A. tokiokai* collected from Hawaiian waters were small; the largest individual measured only 2.6 mm. This maximal size is close to that (2.8 mm) reported by Richter (1990).

Prior to Richter's 1990 revision of the group of *Atlanta* species having tilted spires, he (1974) and, subsequently, I (1990a, 1990b) had identified this species as *A. inclinata* Souleyet, 1852. Among the atlantids from Hawaiian waters, this and the next species, *A. meteori*, are the only two species belonging to the group of four species having tilted spires. Features that distinguish *A. tokiokai* from A. meteori are given below under the latter species.

The species that is most similar to *Atlanta*

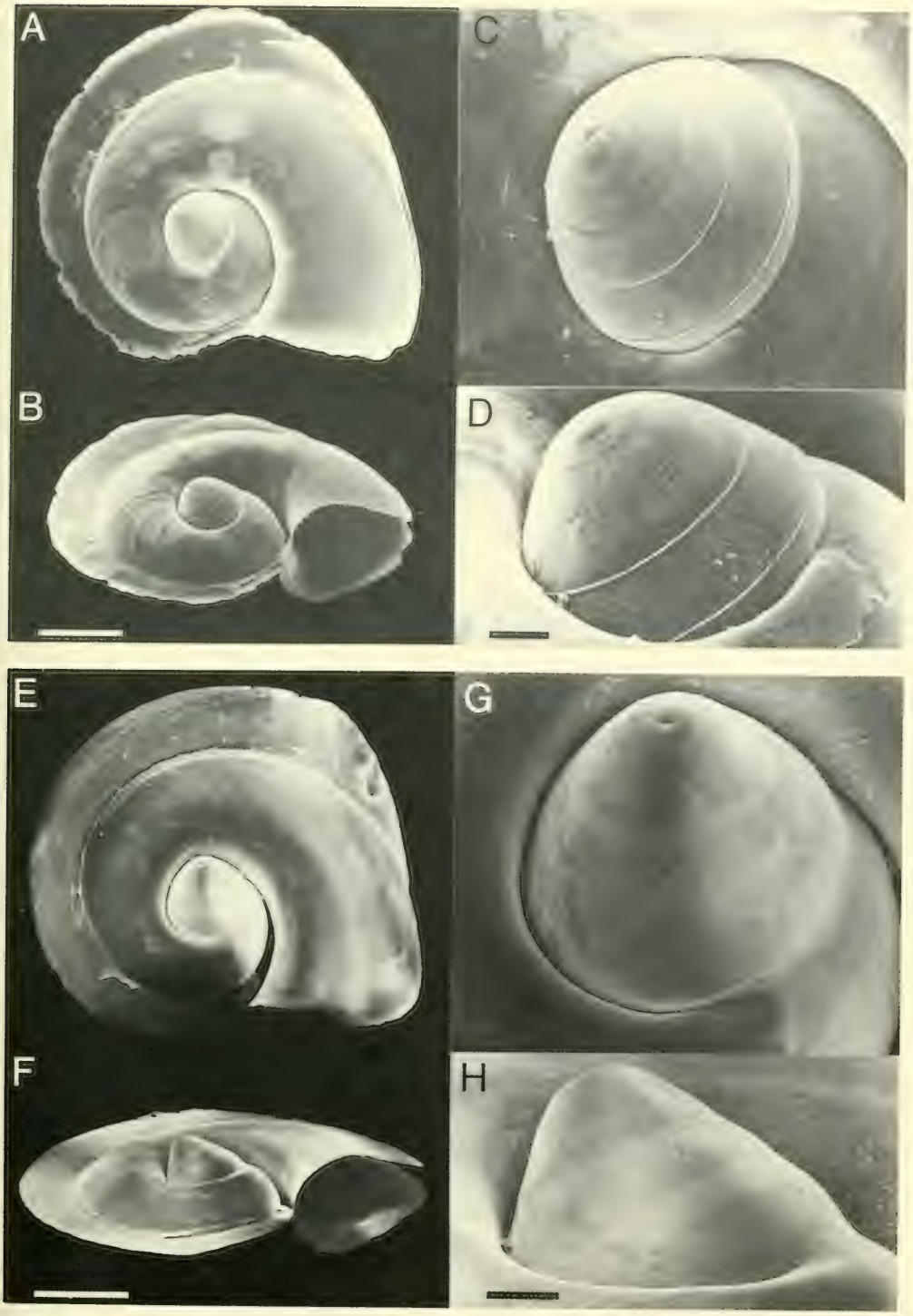

FIG. 12. Scanning electron micrographs of *Atlanta tokiokai* (A-D) and *A. meteori* (E-H). Views and scale bars as in Fig. 4.

tokiokai is *A. inclinata* (Richter, 1990). Both species have a globose spire, with an apical angle of about 80°. However, the spire of *A. inclinata* consists of four whorls, while that of *A. tokiokai* is comprised of five whorls. In *A. inclinata* the last shell whorl is colorless and the spire is a weak rose color, whereas the entire shell of *A. tokiokai* is a light yellow-tan. When viewed with the SEM, the prominent spiral rows of punctae on the spire whorls of *A. tokiokai* are greatly reduced or lacking on *A. inclinata*, with the result that the shell surface is essentially smooth. However, when viewed with the light microscope, the spire whorls of *A. inclinata* show fine radial markings, which are due to the internal shell structure. Lastly, *A. inclinata* attains a larger size (to 6 mm) than *A. tokiokai* (2.8 mm).

Atlanta meteori Richter, 1972
(Figs. 1B, 6L, 12E-H)

Material: A total of 338 specimens was examined (Table 2), which ranged from larvae (less than about 0.7 mm) to a 3.7 mm adult. Nine specimens, ranging from 1.2 to 2.8 mm, were examined under the SEM.

Species characterization: The shell spire is tall and strongly tilted (Fig. 12E). Viewed in the plane of the shell (Fig. 12F), the spire is conical and steep sided, with an apical angle of about 70°. The spire whorls are smooth and relatively flat, and are separated by very shallow sutures that are difficult to resolve under the SEM (Fig. 12G,H). The shell whorl that increases rapidly in width is the sixth (Fig. 6L). The prominent keel is rounded in lateral profile, except at the anterior edge, where it is truncate (Fig. 12E). The eyes are Type b, the operculum is Type b.

Discussion: In live material *A. meteori* is the clearest and most glass-like of the Hawaiian atlantids. Richter (1972, 1974) also commented upon this feature in *A. meteori* from the Indian Ocean. *Atlanta meteori* is most similar to *A. gibbosa* (Richter, 1990). Both species are clear and glass-like, but the spire of *A. gibbosa* forms a pointed cone (apical angle of about 85°), and the spire whorls are rounded with incised and distinct sutures. The umbilicus is conspicuously wider in *A. gibbosa* than in *A. meteori*.

As indicated above, the only two species in the Hawaiian fauna with distinctly tilted spires are *A. meteori* and *A. tokiokai*. In the former species the shell is clear, whereas in the latter species it is light yellowish-tan. Further, the spire of the former species forms a tall cone (about a 70° apical angle) and has smooth whorls, whereas that of the latter species is lower, globose (about an 80° apical angle) and is ornamented by spiral rows of numerous, small punctae. The opercula are also different; Type b in *A. meteori* and Type c in *A. tokiokai*.

CONCLUSIONS

The atlantid fauna of Hawaiian waters is highly diverse, and includes 13 of the 16 species reported by Richter (1974) from the extensive plankton sampling program of the Meteor Expedition to the Indian Ocean. The number of worldwide species in the genus *Atlanta* is at least twice as many as the eight species recognized by Tesch in 1949. The total of 16 species does not include two species described since 1949 (*A. peresi* and *A. pacifica*), which were characterized in the taxonomic review of van der Spoel (1976). Neither species was reported from the Indian Ocean by Richter (1974) or from the central Pacific Ocean in the present study. In his study on atlantid opercula, Tokioka (1961) concluded that *A. pacifica* was not a valid species. The validity of these two species remains uncertain and confirming studies are needed.

KEY TO HAWAIIAN ATLANTIDAE

1. a. Spire whorls involute, projecting spire lacking from right side of shell; adult shell and keel of conchiolin . . . *Oxygyrus keraudreni* (Fig. 3E-H)
   b. Spire projects laterally, to varying degrees, from the right side of the shell; adult shell calcareous; keel calcareous or of conchiolin 2
2. a. Keel of conchiolin and transparent . . . *Protatlanta souleyeti* (Fig. 4A-D)
   b. Keel calcareous and translucent . . . . . (genus *Atlanta*) 3
3. a. Shell whorl that increases rapidly in width is the third 4
   b. Shell whorl that increases rapidly in width is the fourth, fifth or sixth . . 5
4. a. Eyes Type b; shell and keel base unpigmented, although inner whorls can become light pink in older specimens; keel tall with anterior edge truncated . . . . *A. lesueuri* (Fig. 8A-D)

b. Eyes Type a; shell unpigmented except spire whorls (faint violet) and sutures (light violet); keel moderately elevated and rounded . . *A. oligogyra* (Fig. 8E-H)

5. a. Shell whorl that rapidly increases in width is the fourth or fifth; axis of spire not inclined relative to the shell plane 6
   b. Shell whorl that rapidly increases in width is the sixth; axis of spire inclined relative to the shell plane 12
6. a. Shell whorl that rapidly increases in width is the fourth 7
   b. Shell whorl that rapidly increases in width is the fifth 9
7. a. Spire whorls smooth, lacking spiral sculpture; spire slightly rounded; sutures of spire whorls unpigmented or light pink; eyes Type b . . . . . *A. peroni* (Fig. 4E-H)
   b. Spire whorls with weak to well-developed spiral ridges; spire forms a low cone; spire whorls clear with violet sutures or reddish-brown; eyes Type a 8
8. a. Spire weakly conical; second and third spire whorls with two weakly expressed spiral ridges and violet sutures; gyre of Type b operculum with about 20 narrow, projecting spines (Fig. 11B) . . . . *A. plana* (Fig. 10A-D)
   b. Spire forms a low cone; spire reddish-brown, with well-developed spiral ridges and secondary sculpture on the second through fourth whorls; gyre of Type c operculum elevated, with about 12 broad-based, thick projecting spines (Fig. 11D) . . . *A. echinogyra* (Fig. 10E-H)
9. a. Spire projects conspicuously as a high cone or a turret 10
   b. Spire flattened, not conical or turreted 11
10. a. Spire forms a high cone (spire angle about 65-75°); shell distinctive yellowish-brown (or amber) color; gyre of operculum lacking ornamentation . . . . . *A. fusca* (Fig. 13A-D)
    b. Spire turreted and steep-sided (spire angle about 35-45°); shell (especially the spire) light reddish-brown; gyre of operculum with double row of short, projecting spines (Fig. 11F) . . . . . *A. turriculata* (Fig. 13E-H)
11. a. Eyes Type a; spire with prominent spiral ridges on whorls; sutures separating second from third whorls and third from fourth whorls difficult to distinguish; keel tall, with anterior edge truncated . . . . . *A. inflata* (Fig. 12A-D)
    b. Eyes Type c; spire with weakly developed spiral ridges on whorls; sutures separating second from third whorls and third from fourth whorls distinct; keel moderately low and rounded in profile . . . *A. helicinoides* (Fig. 12E-H)
12. a. Shell light yellow-tan color; spire globular and moderately inclined relative to the shell plane; surface of spire whorls with numerous, small and regularly spaced spiral rows of punctae that are most strongly developed on the fourth and fifth whorls; operculum Type c. . . . . *A. tokiokai* (Fig. 9A-D)
    b. Shell clear and glass-like; spire tall, conical and steeply inclined relative to the shell plane; surface of whorls smooth, lacking punctate sculpture; operculum Type b . . . . . *A. meteori* (Fig. 9E-H)

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ON THE VARIOUS EDITIONS OF TETSUAKI KIRA'S "COLOURED ILLUSTRATIONS OF THE SHELLS OF JAPAN" AND "SHELLS OF THE WESTERN PACIFIC IN COLOR VOL. I," WITH AN ANNOTATED LIST OF NEW NAMES INTRODUCED

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ABSTRACT

At least 37 printings of Tetsuaki Kira's "Coloured Illustrations of the Shells of Japan" (CISJ) and nine of its English-language version, "Shells of the Western Pacific in Color Vol. I" (SWPC), published between 1954 and 1989, are in existence. Some of the editions, often incorrectly dated on the title page, differ greatly in text and illustrations. They are of taxonomic importance as they contain descriptions of new taxa and so-called "manuscript names," spanning 30 molluscan families. Of the 54 species-group and one genus-group names in question, five had been introduced before Kira's work, two are not available for taxonomic purposes, and eight were subsequently introduced by other authors after Kira had listed them as nude names only. The remaining 40 species-group names, only five of which were designated as new taxa, were made available with this work. The majority, 34 names, date from Kira (1959, CISJ), two from Kira (September 1954, CISJ), two from Kira (1960, CISJ), one from Kira (1962, SWPC), and one from Kira & Habe in Kira (1962, SWPC). New taxa and "manuscript names" are traced through the various editions, and annotated lists of the printings and of the nominal taxa are supplied.

INTRODUCTION

Tetsuaki Kira's "Coloured Illustrations of the Shells of Japan," first published in 1954, in Japanese, has become one of the standard reference works on Indo-Pacific mollusks. A revised edition in English, first published in 1962, is known as "Shells of the Western Pacific in Color <Vol. I>." For convenience, they will hereafter be referred to as CISJ and SWPC, respectively. The work is of taxonomic interest as it contains the descriptions of at least 40 new species-group names. One new genus-group name appears, but is not validly introduced. However, the frequent use of manuscript names, the lack of dates given with the taxa, rampant misspellings, and the erratic use of parentheses around authors' names, make use of the book extremely difficult and have resulted in many erroneous citations by subsequent authors. While working on such problems, we discovered that there are at least 37 Japanese and nine English-language printings of this work, published between 1954 and 1989. Of the Japanese version, two editions are generally recognized, the original and the "enlarged & revised" edition, which was first published in 1959. We found, however, many of the so-called new printings to be revised editions. They were often newly typeset, and contained not only technical corrections and additions (such as indexes) but had major taxonomic changes in the figure captions, and figures were replaced or renumbered on some of the plates. Only five new species are clearly designated as such, but about 50 manuscript names, inconsistently assigned to various authors, appear in the different editions (there may be additional nude names or available descriptions of taxa wrongly assigned to other authors in this work that have escaped us). A further complicating fact is that the date on the English-language title page of the Japanese editions is often incorrect, as can be shown by the Japanese date (day, month and year of emperor Hirohito's reign) in the colophon (inscription at the end) of each copy. Some English-language title pages were apparently used for a number of subsequent printings ("1955," for instance, still appears on the 1958 printing). Issues of CISJ and SWPC of the same year do not necessarily agree in taxonomic treatment, as the two were apparently independently revised and edited (Kira mentions in the SWPC preface that "Dr. Habe took the trouble of revising the Latin names into the latest and authorized way of use").

The taxonomic mess created by author and publisher of this work proves the inappropriateness (1) of introducing manuscript names

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into the literature, and (2) of describing new taxa in commercial book publications.

LISTING OF NEW AND "MANUSCRIPT" NAMES

(1) *"Cantharidus kanekonis* Oyama"
(2) *Gaza sericata* Kira, 1959
(3) *Pseudastralium henicus gloriosum* Kira, 1959
(4) *Galeoastraea millegranosa* Kuroda & Habe in Habe, 1958
(5) *Papyriscala bifasciata* Kira & Habe in Kira, 1962
(6) *Cirsotrema (Elegantiscala) kurodai* Kira, 1960
(7) *Canarium microurceum* Kira, 1959
(8) *Neverita (Glossaulax) hosoyai* Kira, 1959
(9) *Simnia xanthochila* Kuroda, 1928
(10) *Pustularia margarita tetsuakii* Kira, 1959
(11) *Erosaria tomlini maturata* Kira, 1959
(12) *Semicassis persimilis* Kira, 1959
(13) *Bursa dunkeri* Kira, 1959
(14) *Eudolium inflatum* Kuroda & Habe, 1952
(15) *Murex kiiensis* Kira, 1959
(16) *Ceratostoma (Pteropurpura) vespertilio* Kira, 1959
(17) *Coralliobia akibumii* Kira, 1960
(18) *Coralliophila pyriformis* Kira, 1959
(19) *Latiaxis kawamurai* Kira, 1959
(20) *Babylonia pallida* Kira, 1959
(21) *Neptunea fukueae* Kira, 1959
(22) *Buccinum isaotakii* Kira, 1959
(23) *Nassarius (Zeuxis) kiiensis* Kira, 1959
(24) *Granulifusus kiranus* Shuto, 1958
(25) *Fusinus gemmuliferus* Kira, 1959
(26) *Fusinus crassiplicatus* Kira, 1959
(27) *Turrancilla apicalis* Kira, 1959
(28) *Baryspira urasima* Kira, 1959
(29) *Oliva hirasei* Kuroda & Habe, 1952
(30) *Mitropifex hirasei* Kira, 1962
(31) *Mitra (Cancilla) yagurai* Kira, 1959
(32) *Ancistrosyrinx pulcherrissima* Kira, 1959
(33) *Daphnella nobilis* Kira, 1959
(34) *Chelyconus kinoshitai* Kuroda, 1956
(35) *Asprella (Conasprella ?) ichinoseana* Kuroda, 1956
(36) *Euhadra roseoapicalis* Kira, 1959
(37) *Euhadra grata gratoides* Kira, 1959
(38) *Cadulus (Platyschides) novilunatus* Kira, 1959
(39) *Entalina majestica* Kira, 1959
(40) *Dentalium (Episiphon) candelatum* Kira, 1959
(41) *Dentalium (Pictodentalium) formosum hirasei* Kira, 1959
(42) Genus-group name *Pictodentalium*
(43) *Acila schencki* Habe, 1958
(44) *Nuculana (Thestyleda) acinacea* Habe, 1958
(45) *Limopsis tajimae emphaticus* Kira, 1959
(46) *Fragum loochooanum* Kira, 1959
(47) *Clinocardium uchidai* Habe, 1955
(48) *Vasticardium compunctum* Kira, 1959
(49) *"Vasticardium serricostatum"*
(50) *Leukoma japonica* Kira, 1954
(51) *Irus ishibashianus* Kuroda & Habe, 1952
(52) *Solecurtus dunkeri* Kira, 1959
(53) *Nuttallia solida* Kira, 1953
(54) *Heteromacoma oyamai* Kira, 1954
(55) *Lanceolaria oxyrhyncha cuspidata* Kira, 1959

LISTING OF PRINTINGS AND REVISED EDITIONS

Table 1 lists the various printings and editions encountered by us. We were unable to examine in detail all of the printings for which we established printing dates. To properly date a copy, locate the *bottom line* of the date information in the colophon (e.g. "..35..6..5.."), and add 1925 to the first number which is the Year of the Showa Era; the second number is the month, and the third number is the day. This example translates to June 5th, 1960, which is the second printing of the second edition (the number of printing appears in kanji to the right of the last Arabic numeral; beginning with the tenth printing, the number of printing is shown in Arabic numerals).

Table 1. List of printings and revised editions of Kira's "Coloured Illustrations of the Shells of Japan" (CISJ) and "Shells of the Western Pacific" (SWPC). Asterisks (*) mark those in which taxonomic names were first made available.

(a) Coloured Illustrations of the Shells of Japan

All Japanese editions are cloth-bound octavo volumes, with gold lettering in Japanese and a muricid-icon imprinted on the spine. The First Edition (before 1959) has a greenish cloth binding with photographs of three ranellid specimens on the front cover; the Second Edition has a blue binding featuring a *Latiaxis* photograph on the front cover. The dust cover has a small buccinid (*Pusiostoma*) photo-

graph on the spine and a *Spondylus* photograph in front; the cardboard slip case of the First Edition features photographs of *Chlamys* and *Pleurotomaria* shells, and in the Second Edition photographs of an *Architectonica* and two *Strombus* shells.

Printing	Publication date	Notes
First Edition		
* 1	1954a (September 5)	[1]
2	1954b (November 1)	[2]
3	1955 (August 15)	[3]
4	1956 (June 1)	
5	1957 (June 15)	[4]
6	1958 (May 1)	[5]
Second Edition		
* 1	1959 (March 10)	[6]
* 2	1960 (June 5)	[7]
3	?	[not seen]
4	1961 (October 1)	
5	?	[not seen]
6	1963 (February 5)	
7–9	?	[not seen]
10	1965 (August 1)	[8]
11	1966 (August 1)	
12	?	[not seen]
13	1968 (May 1)	
14–15	?	[not seen]
16	1971 (March 1)	[9]
17	?	[not seen]
18	1972 (October 1)	
19	?	[not seen]
20	1974 (July 1)	[not seen]
21–24	?	[not seen]
25	1979 (July 1)	
26	?	[not seen]
27	1981 (April 1)	
28–30	?	[not seen]
31	1989 (February 1)	

Notes:

[1]Contents (1954a): Japanese title page; [8 pp.] preface and introduction, dated August 1954; [1 p.] schematic drawings; pp. 1–135 figure captions [p. 1 = series title page], including 67 pls.; [p. 136 blank]; pp. 137–172 discussion of plates in Japanese, with black-and-white drawings (incl. description of two new taxa); pp. 1–4 index of family names in Latin and Japanese; pp. 5–24 index of figured taxa in Japanese. Apparently due to misnumbering, neither this nor any other printing of the first edition contains pages 41, 42, or 105, 106.

[2]1954b. Changes from preceding (1954a): Correction of many printer's errors, correction of gender in Latin species names, re-identifications, change of genus-group names as well as authorships (affecting most plates); renumbering of figures (pls. 9, 29, 55, 65, 66); correction of transposed figure legends (pls. 27, 37); change of family names (pls. 23, 39); replacement of two figures by photographs of different specimens (*Oliva emicator, Oliva erythrostoma*; pl. 31 figs. 10, 14); change and introduction of manuscript names; slight changes in text and indexes reflecting changes in plates.

[3]Title page design changed and title given in English for the first time. The Japanese title did not change, but the translation of the title of the first two printings was sometimes rendered as "Illustrations of Japanese Shells in Natural Colour" when cited by Japanese authors. Other changes from preceding printings: consecutive page numbering (pp. [8], 1–204), new index of generic names in Latin (pp. 177–184); very few corrections/changes in figure captions, most differences due to printer's error.

[4]Changes from 1955 (1956 not examined): minor correction in text (p. 36, *Sulcerato*); background color of plates changed from light-blue to gray or black (pl. 40).

[5]Changes from preceding (1957): Minor technical adjustments (such as color of pl. 64).

[6]Japanese/English title page now stating "Enlarged & Revised Edition." Contents: [4 pp.] + [1 p. new foreword in Japanese]; i–vii introduction in Japanese and index of family names in Japanese and Latin; [2 pp.] schematic drawings; pp. 1–195 figure captions, descriptions in Japanese (including black-and-white photographs and line drawings) **plus** 1 unnumbered (rare cowries) and 71 numbered pls.; pp. 196–210, introduction to shell collecting (including line drawings and

black-and-white photographs); pp. 211–218 index of generic names in Latin; pp. 219–239 index of figured taxa in Japanese + [241] colophon.

Major changes from preceding (1958): Figure captions now containing descriptions; 5 additional color plates (1 unnumbered, pls. 68–71), black-and-white photographs and line drawings in text; many re-identifications and new printer's errors; use of additional family names (e.g. Stomatiidae, p. 16, pl. 8); plates renumbered (pls. 16, 50); and many replacements of photographs in plates (pl. 4: *Tugali gigas*; pl. 7: *Monodonta perplexa, M. neritoides*; pl. 11: *Clython sowerbyanus*; pl. 12: *S. quaria cumingi, Serpulorbis imbricatus*, pl. 14 *Xenophora corrugata*; pl. 15: *Tibia fusus*; pl. 20: *Erronea hiraseı* replaced by *E. caurica*; pl. 21: *Cassis cornuta*; pl. 30: *Baryspira urasima, Oliva emicator, O. erythrostoma*; pl. 50: *Spondylus cruentus*, addition of *Spondylus sanguineus*; pl. 55: *Tridacna squamosa*; pl. 57: *Sunetta concinna*).

[7]Changes from preceding (1959): re-identifications, frequently on the generic level, and corrections of typographic errors for most plates.

[8]Figures 5–16 on plate 8 have been renumbered to accommodate *Stomatia rubra* in the Stomatiidae.

[9]This is the first printing that we have seen which gives dates (years only) of previous printings on the verso of the title page. It is also the first printing seen which has "<<Vol. I>>" added to the title.

(b) Shells of the Western Pacific in Color

All English-language editions are larger (quarto) cloth-bound volumes, with gold lettering in English and a *Latiaxis*-icon imprinted on the front cover. The dust cover features color photographs of various gastropod and scaphopod shells. An odd feature of <<Vol. I>>, in contrast to the later <<Vol. II>> by Habe not covered here, is that the odd-numbered pages are on the left instead of the right.

In contrast to the many different Japanese versions of this work, the English-language "editions" do not differ from each other, with the exception of minor technical details (such as the loss of figure-number 16 on plate 12 after 1962, probably due to printer's error).

Printing	Publication date	Notes
First Edition		
* 1	1962 (September)	
2	1965 (November 1)	[1]
Second (or "Revised") Edition		
—	1965 (October)	[not seen][2]
—	1966	[not seen][3]
—	1967	[4]
—	1968	[5]
—	1970	
Third (or "Second") Edition		
—	1972 (May)	[6]
—	1975	[7]

Notes:

[1]Inscribed "2nd printing, 1965" with copyright date of 1962.

[2]The Revised Edition copyright date is October 1965.

[3]From dates of printing listed in 1968 printing.

[4]Stated to be "Third Edition January 1967," but it bears only the 1962 copyright date and not the copyright date of the Second Edition. As the copyright date for a "Third Edition" is later given as "May 1972," this is believed to be an error for "Third Printing," but we have no explanation for the 1962 copyright date.

[5]This is the first printing seen which has "<<Vol. I>>" appended to the title.

[6]The 1972 printing is referred to as the "Third Edition" on the verso of the title page, whereas the 1970 and earlier printings show "Revised Edition."

[7]The 1975 printing is again referred to as the "Second Edition" on the verso of the title page.

Neither the new copyright date (1965), nor the term "Revised Edition" are understood by us, as the 1962 and 1968 printings we have examined differ only in the 1968 (and later) being styled "<<Vol. I>>," but the 1967 printing still omits this addition to the title.

ANNOTATED LISTING OF NEW TAXA AND "MANUSCRIPT NAMES"

List of names that were recognized as either of Kira's or as "manuscript names" in Kira's work, following Kira's arrangement of molluscan families.[3]

Such names were traced through the printings and editions available to us. If published elsewhere, the proper citation of the original description is given in brackets. Printings in which the new names were first made available are indicated by asterisks (*). It should be noted that the listing is **not** a synonymy but reflects a chronological order of figure captions. In cases where the first two printings of CISJ differ, they are marked as "1954a" or "1954b."

GASTROPODA

Trochidae

(1) "*Cantharidus kanekonis* Oyama" [*nomen nudum*]

1954–1958 (CISJ): *Cantharidus kanekonis* Oyama, MS.; p. 15, pl. 7, fig. 5 [*nom. nud.*].
1959 (CISJ): *Cantharidus yokohamensis* (Bock); p. 13, pl. 7, fig. 5.
1960–1989 (CISJ): *Cantharidus (Kanekotrochus) infuscatus* (Gould); p. 13, pl. 7, fig. 5.
1962–1968 (SWPC): *Cantharidus (Kanekotrochus) infuscatus* (Gould); p. 10, pl. 8, fig. 5.

Taxonomic note: Apparently the name was never made available.

(2) *Gaza sericata* Kira, 1959

1954–1958 (CISJ): *Gaza sericata* Kuroda, MS.; p. 16, pl. 8, fig. 13 [*nom. nud.*].
*1959 (CISJ): *Gaza sericata* Kuroda, MS.; p. 17, pl. 8, fig. 13 [with short description in Japanese].
1960–1963 (CISJ): *Gaza sericata* Kira; p. 17, pl. 8, fig. 13.
1962–1968 (SWPC): *Gaza sericata* Kira; p. 14, pl. 9, fig. 12.
1965–1989 (CISJ): *Gaza sericata* Kira; p. 17, pl. 8, fig. 12.

Turbinidae

(3) *Pseudastralium henicus gloriosum* Kira, 1959

1954a (CISJ): *Pseudastralium henicus gloriosa* Kuroda et Habe, MS.; p. 20, pl. 10, fig. 2 [*nom. nud.*].
1954b–1958 (CISJ): *Pseudastralium henicus gloriosum* Kuroda et Habe, MS.; p. 20, pl. 10, fig. 2 [*nom. nud.*].
*1959 (CISJ): *Pseudastralium henicus gloriosum* Kuroda et Habe, MS.; p. 19, pl. 10, fig. 2 [with short description in Japanese].
1960–1961 (CISJ): *Guildfor or dia* [*sic*] *(Pseudastralium) gloriosa* Kira; p. 19, pl. 10, fig. 2.
1963 (CISJ): *Guildforordia* [*sic*] *henicus gloriosum* Kira; p. 19, pl. 10, fig. 2.
1962–1968 (SWPC): *Pseudastralium henicus gloriosum* (Kira); p. 18, pl. 11, fig. 2.
1965–1989 (CISJ): *Pseudastralium henicus gloriosum* (Kira); p. 19, pl. 10, fig. 2.

(4) *Galeoastraea millegranosa* Kuroda & Habe in Habe, 1958 [1958a, Venus, 20(1): 45, pl. 3, fig. 1]

1954–1958 (CISJ): *Bolma ? millegranosa* Kuroda et Habe, MS.; p. 20, pl. 10, fig. 3 [*nom. nud.*].
1959 (CISJ): *Bolma ? millegranosa* Kuroda & Habe, MS. [*sic*]; p. 20, pl. 10, fig. 3.
1960–1963 (CISJ): *Galeoastraea (Harisazaea) millegranosa* Habe [*sic*]; p. 20, pl. 10, fig. 3.
1962–1968 (SWPC): *Galeostraea* [*sic*] *millegranosa* Habe [*sic*]; p. 18, pl. 11, fig. 3.
1965–1989 (CISJ): *Galeoastraea millegranosa* Habe [*sic*]; p. 20, pl. 10, fig. 3.

Epitoniidae

(5) *Papyriscala bifasciata* Kira & Habe in Kira, 1962

1954a (CISJ): *Epitonium (Papyriscala) halimense* Makiyama; p. 27, pl. 13, fig. 16.
1954b–1958 (CISJ): *Epitonium (Papyriscala)* sp.; p. 27, pl. 13, fig. 16.
1959–1963 (CISJ): *Epitonium (Papyriscala)* sp.; p. 31, pl. 13, fig. 16.
*1962 (SWPC): *Papyriscala bifasciata* Kira et Habe (n. sp.); p. 30, pl. 14, fig. 16.
1965–1968 (SWPC): *Papyriscala bifasciata* Kira et Habe (n. sp.) [*sic*]; p. 30, pl. 14, fig. 16.
1965–1989 (CISJ): *Papyriscala bifasciata* Kira et Habe; p. 31, pl. 13, fig. 16.

Taxonomic note: Listed in synonymy of "*Papyriscala yokoyamai* (Suzuki & Ichikawa, 1936)" by Kuroda et al. (1971: 257). Also listed this way by Inaba & Oyama (1977: 27), but authorship of *P. yokoyamai* is correctly given as "Suzuki & Ichimura, 1936."

[3]Kira's collection is now located in the Osaka City Museum, Japan (Inaba & Oyama, 1977: 36).

(6) *Cirsotrema (Elegantiscala) kurodai* Kira, 1960

1954–1958 (CISJ): *Cirsotrema (Elegantiscala)* sp.; p. 27, pl. 13, fig. 17.
1959 (CISJ): *Cirsotrema (Elegantiscala)* sp.; p. 32, pl. 13, fig. 17.
*1960 (CISJ): *Cirsotrema (Elegantiscala) kurodai* Kira; p. 32, pl. 13, fig. 17.
1961–1963 (CISJ): *Cirsotrema (Elegantiscala) kurodai* Kira; p. 32, pl. 13, fig. 17.
1962–1968 (SWPC): *Cirsotrema (Elegantiscala) varicosum* Kuroda; p. 30, pl. 14, fig. 17.
1965–1989 (CISJ): *Cirsotrema (Elegantiscala) rugosum* Kuroda et Ito; p. 32, pl. 13, fig. 17.

Taxonomic note: In the original description of *Cirsotrema (Elegantiscala) rugosum* Kuroda & Ito, 1961, the authors list *Cirsotrema (Elegantiscala)* sp. of Kira in the synonymy. Hanshin Shell Club (1986: 100–101) does not mention Kira as one of those "persons who dedicated taxonomic names to Dr. T. Kuroda."

Strombidae

(7) *Canarium microurceum* Kira, 1959

1954–1958 (CISJ): *Canarium microurceum* Kuroda, MS.; p. 31, pl. 15, fig. 5 [*nom. nud.*].
*1959 (CISJ): *Canarium microurceum* Kuroda, MS.; p. 35, pl. 15, fig. 5 [with short description in Japanese].
1960–1989 (CISJ): *Canarium microurceum* Kira; p. 35, pl. 15, fig. 5.
1962–1968 (SWPC): *Canarium microurceum* Kira; p. 34, pl. 16, fig. 5.

Taxonomic note: Cited by Habe & Kosuge (1964a: 4) as of Kira (1958).

Naticidae

(8) *Neverita (Glossaulax) hosoyai* Kira, 1959

*1959 (CISJ): *Neverita (Glossaulax) hosoyai* Kuroda & Kira, MS.; p. 42 [with short description in Japanese].
1960–1989 (CISJ): *Neverita (Glossaulax) hosoyai* Kira; p. 42.
1962–1968b (SWPC): *Neverita (Glossaulax) hosoyai* Kira; p. 43.

Taxonomic note: Listed as synonym of *Glossaulax didyma* (Röding, 1798) by Majima (1987: 62).

Amphiperatidae / Ovulidae [depending on printing]

(9) *Simnia xanthochila* Kuroda, 1928 [Venus, 1(1): pl. 1, fig. 5; Venus, 1(3): 78 (1929)]

1954a (CISJ): *Pellasimnia xanthochila* Kuroda, MS. [*sic*]; p. 36, pl. 18, fig. 13.
1954b–1958 (CISJ): *Pellasimnia hirasei xanthochila* (Kuroda); p. 36, pl. 18, fig. 13.
1959–1989 (CISJ): *Pellasimnia hirasei xanthochila* (Kuroda); p. 44, pl. 18, fig. 13.
1962–1968 (SWPC): *Pellasimnia hirasei xanthochila* (Kuroda); p. 45, pl. 19, fig. 13.

Taxonomic note: Placed in genus *Xandarovula* Cate, 1973, by Cate (1973: 35) and Azuma (1976: 115).

Cypraeidae

(10) *Pustularia margarita tetsuakii* Kira, 1959

1954–1958 (CISJ): *Pustularia margarita tetuakii* [*sic*] Kuroda, MS.; p. 36, pl. 18, fig. 17 [*nom. nud.*].
*1959 (CISJ): *Pustularia margarita tetsuakii* Kuroda, MS.; p. 45, pl. 18, fig. 17 [with short description in Japanese].
1960–1989 (CISJ): *Pustularia margarita tetsuakii* Kuroda [*sic*]; p. 45, pl. 18, fig. 17.
1962–1968 (SWPC): *Pustularia margarita tetsuakii* Kuroda [*sic*]; p. 46, pl. 19, fig. 17.

Taxonomic note: Considered "Japanese-Hawaiian race" of *Pustularia cicercula* (Linné, 1758) by Cernohorsky (1967: 72). Listed as subspecies of *Pustularia (Pustularia) globulus* (Linné, 1758) by M. Schilder & F. A. Schilder (1971: 57).

(11) *Erosaria tomlini maturata* Kira, 1959

1954–1958 (CISJ): *Erosaria tomlini maturata* Kuroda, MS.; p. 39, pl. 19, fig. 11 [*nom. nud.*].
*1959 (CISJ): *Erosaria tomlini maturata* Kuroda, MS.; p. 47, pl. 19, fig. 11 [with short description in Japanese].
1960–1963 (CISJ): *Erosaria tomlini maturata* Kira; p. 47, pl. 19, fig. 11.
1962–1968 (SWPC): *Erosaria tomlini ogasawarensis* Schilder; p. 48, pl. 20, fig. 11.
1965–1989 (CISJ): Erosaria tomlini ogasawarensis Schilder; p. 47, pl. 19, fig. 11.

Taxonomic note: Listed in synonymy of *Erosaria tomlini ogasawarensis* Schilder, 1944, by Kuroda et al. (1971: 105).

Cassididae [Cassidae]

(12) *Semicassis persimilis* Kira, 1959

1954a (CISJ): *Semicassis persimile* [*sic*] Kuroda, MS.; p. 43, pl. 21, fig. 3 [*nom. nud.*].
1954b–1958 (CISJ): *Semicassis persimilis* Kuroda, MS.; p. 43, pl. 21, fig. 3 [*nom. nud.*].
*1959 (CISJ): *Semicassis persimilis* Kuroda,

MS.; p. 52, pl. 21, fig. 3 [with short description in Japanese].
1960–1963 (CISJ): *Semicassis persimilis* Kira; p. 52, pl. 21, fig. 3.
1962–1968 (SWPC): *Semicassis persimilis* Kuroda [*sic*]; p. 54, pl. 22, fig. 3.
1965–1989 (CISJ): *Semicassis persimilis* Kuroda [*sic*]; p. 52, pl. 21, fig. 3.

Taxonomic note: Abbott (1968: 129) lists this as synonym of *Phalium bisulcatum* (Schubert & Wagner, 1829) and states "Kira's type of *persimilis* may be lost."

Bursidae

(13) *Bursa dunkeri* Kira, 1959

1954–1958 (CISJ): *Bursa dunkeri* Kuroda, MS.; p. 43, pl. 21, fig. 18 [*nom. nud.*].
*1959 (CISJ): *Bursa dunkeri* Kuroda, MS.; p. 54, pl. 21, fig. 18 [with short description in Japanese].
1960–1989 (CISJ): *Bursa dunkeri* Kira; p. 54, pl. 21, fig. 18.
1962–1968 (SWPC): *Bursa dunkeri* Kira; p. 57, pl. 22, fig. 18.

Taxonomic note: Listed as of Kira (1962) by Kuroda et al. (1971: 133).

Tonnidae

(14) *Eudolium inflatum* Kuroda & Habe, 1952 [Check List, p. 56]

1954a (CISJ): *Eudolium lineatum inflatum* Kuroda et Habe; p. 44, pl. 22, fig. 4.
1954b–1958 (CISJ): *Eudolium lineatum inflatum* Kuroda et Habe, MS. [*sic*]; p. 44, pl. 22, fig. 4.
1959–1960 (CISJ): *Eudolium lineatum inflatum* Kuroda et Habe, MS. [*sic*]; p. 55, pl. 22, fig. 4.
1963 (CISJ): *Eudolium lineatum inflatum* Kuroda et Habe; p. 55, pl. 22, fig. 4.
1962–1968 (SWPC): *Eudolium inflatum* Kuroda et Habe; p. 59, pl. 23, fig. 4.
1965–1989 (CISJ): *Eudolium inflatum* Kuroda et Habe; p. 55, pl. 22, fig. 4.

Taxonomic note: Introduced by Kuroda & Habe (1952: 56) as a new name for *Eudolium lineatum* Schepman as figured by Osima (1943, Conch. Asiat. 1, pl. 5, fig. 1). As Osima's figure is accompanied by a description, Kuroda & Habe's (1952) name can be accepted.

Muricidae

(15) *Murex kiiensis* Kira, 1959

1954–1958 (CISJ): *Murex kiiensis* Kuroda, MS.; p. 47, pl. 23, fig. 10 [*nom. nud.*].
*1959 (CISJ): *Murex Kiiensis* [*sic*] Kuroda, MS.; p. 58, pl. 23, fig. 10 [with short description in Japanese].
1960–1989 (CISJ): *Murex kiiensis* Kira; p. 58, pl. 23, fig. 10.
1962–1968 (SWPC): *Murex kiiensis* Kira; p. 63, pl. 24, fig. 10.

Taxonomic note: Listed as of Kira (1962) by E. H. Vokes (1971: 62).

(16) *Ceratostoma (Pteropurpura) vespertilio* Kira, 1959.

1954a (CISJ): *Ceratostoma (Pteropurpura) vespertilis* [*sic*] Kuroda, MS.; p. 48, pl. 24, fig. 10 [*nom. nud.*].
1954b–1958 (CISJ): *Ceratostoma (Pteropurpura) vespertilio* Kuroda, MS.; p. 48, pl. 24, fig. 10 [*nom. nud.*].
*1959 (CISJ): *Ceratostoma (Pteropurpura) vespertilio* Kuroda, MS.; p. 61, pl. 24, fig. 10 [with short description in Japanese].
1960–1963 (CISJ): *Ceratostoma (Pteropurpura) vespertilio* Kira; p. 61, pl. 24, fig. 10.
1962–1968 (SWPC): *Pteropurpura vespertilio* Kira; p. 66, pl. 25, fig. 10.
1965–1989 (CISJ): *Pteropurpura vespertilio* (Kira); p. 61, pl. 24, fig. 10.

Taxonomic note: Listed as of Kuroda in Kira (1955) by E. H. Vokes (1971: 115).

Rapidae [Coralliophilidae]

(17) *Coralliobia akibumii* Kira, 1960

1954a (CISJ): *Coralliobia inflata* (Dunker); p. 51, pl. 25, fig. 3.
1954b–1958 (CISJ): *Coralliobia* sp.; p. 51, pl. 25, fig. 3.
1959 (CISJ): *Coralliobia* sp.; p. 63, pl. 25, fig. 3.
*1960 (CISJ): *Coralliobia akibumii* Kira; p. 63, pl. 25, fig. 3 [with short description in Japanese].
1961–1989 (CISJ): *Coralliobia akibumii* Kira; p. 63, pl. 25, fig. 3.
1962–1968 (SWPC): *Coralliobia akibumii* Kira (n. sp.) [*sic*]; p. 68, pl. 26, fig. 3.

Taxonomic note: Listed as of Kira (1959) in synonymy of *Coralliophila inflata* (Dunker, 1847) by Kosuge & Suzuki (1985: 34).

(18) *Coralliophila pyriformis* Kira, 1959

1954–1958 (CISJ): *Coralliophila pyriformis* Kuroda, MS.; p. 51, pl. 25, fig. 12 [*nom. nud.*].
*1959 (CISJ): *Coralliophila pyriformis* Kuroda, MS.; p. 64, pl. 25, fig. 12 [with short description in Japanese].
1960–1989 (CISJ): *Coralliophila pyriformis* Kira; p. 64, pl. 25, fig. 12.
1965–1968 (SWPC): *Coralliophila pyriformis* Kira; p. 69, pl. 26, fig. 12.

Taxonomic note: Listed in synonymy of *Coralliophila radula* (A. Adams, 1855) by Kosuge & Suzuki (1985: 39).

(19) *Latiaxis kawamurai* Kira, 1959

1954–1958 (CISJ): *Latiaxis kawamurai* Kuroda, MS.; p. 51, pl. 25, fig. 20 [*nom. nud.*].
*1959 (CISJ): *Latiaxis kawamurai* Kuroda, MS.; p. 65, pl. 25, fig. 20 [with short description in Japanese].
1960 (CISJ): *Latiaxis kawamurai* Kira; p. 65, pl. 25, fig. 20.
1961–1989 (CISJ): *Laticxis* [*sic*] *kawamurai* Kira; p. 65, pl. 25, fig. 20.
1962–1968 (SWPC): *Latiaxis kawamurai* Kira; p. 70, pl. 26, fig. 20.

Taxonomic note: Kuroda, in October 1958 [Venus, 20(2)], published an illustration and figure caption of what he intended to describe as "*Latiaxis kawamurai* Kuroda, n.sp." The text describing the new species appeared only in November 1959 [Venus, 20(4)], eight months after Kira had given a description in CISJ. Kuroda (1959), recognizing Kira's priority, correctly cited "*Latiaxis kawamurai* Kira, 1959" in the text (1959: 319). Placed in genus *Babelomurex* by Kosuge & Suzuki (1985: 14).

Buccinidae

(20) *Babylonia pallida* Kira, 1959 [preoccupied, replaced by *B. kirana* Habe, 1965]

1954–1958 (CISJ): *Babylonia pallida* Kuroda, MS.; p. 52, pl. 26, fig. 28 [*nom. nud.*].
*1959 (CISJ): *Babylonia pallida* Kuroda, MS.; p. 69, pl. 26, fig. 28 [with short description in Japanese].
1960–1963 (CISJ): *Babylonia pallida* Kira; p. 69, pl. 26, fig. 28.
1962–1968 (SWPC): *Babylonia pallida* Kira; p. 75, pl. 27, fig. 28.
1965–1989 (CISJ): *Babylonia pallida* Kuroda [*sic*]; p. 69, pl. 26, fig. 28.

Taxonomic note: Placed in synonymy of *Babylonia kirana* n.sp. by Habe (1965: 119), who found Kira's name preoccupied by *Ancilla pallida* Perry, 1811 (secondary homonymy). Altena & Gittenberger (1981: 28–29) considered *B. kirana* as a *nomen novum* for *B. pallida* Kira, *non* Perry, and selected the shell figured by Kira (1959: pl. 26, fig. 28) as the lectotype of *B. pallida* Kira, and, consequently, of *B. kirana* Habe. However, ICZN Article 72(e) [a replacement name for a prior species-group name has the same name-bearing type] demands that "an author proposes a new species group-name expressly as a replacement name for a prior one." It can be argued that *B. kirana* Habe was not indicated "expressly as a replacement name," as it is only after Habe (1965: 119) has illustrated and described the species and named a type specimen, that he mentions that the species had previously been named. Altena & Gittenberger (1981: 29) also state that "*B. pallida* Hirase, 1934, and *B. pallida* Kira, 1959, have been introduced independently for the same species and, therefore, are primary homonyms and synonyms," and they select the specimen figured by Hirase (1934: pl. 104, fig. 9) as the lectotype of *B. pallida* Hirase. The listing and illustration of *B. pallida* Hirase, 1934, however does not fulfill the requirements of ICZN Article 13(a) [criteria of availability to be satisfied by new names published after 1930] and has to be regarded as a *nomen nudum*. The nude name "*Babylonia pallida* Hirase" may have been what Kira meant when he first listed "*Babylonia pallida* Kuroda, MS."

(21) *Neptunea fukueae* Kira, 1959

1954–1958 (CISJ): *Neptunea fukueae* Kuroda, MS.; p. 55, pl. 27, fig. 4 [*nom. nud.*].
*1959 (CISJ): *Neptunea fukueae* Kuroda, MS.; p. 69, pl. 27, fig. 4 [with short description in Japanese].
1960–1963 (CISJ): *Neptunea fukueae* Kira; p. 69, pl. 27, fig. 4.
1962–1968 (SWPC): *Neptunea fukueae* Kira; p. 76, pl. 28, fig. 4.
1965–1989 (CISJ): *Neptunea fukueae* Kuroda [*sic*]; p. 69, pl. 27, fig. 4.

Taxonomic note: Listed as of Kira (without date) by Habe & Sato (1973: 2) when they made it type species of the new genus *Golikovia*.

(22) *Buccinum isaotakii* Kira, 1959

1954–1958 (CISJ): *Buccinum leucostoma* (Lischke); p. 55, pl. 27, fig. 8.
*1959 (CISJ): *Buccinum isao-takii* Oyama, MS.; p. 70, pl. 27, fig. 8 [with short description in Japanese].
1960–1989 (CISJ): *Buccinum isao-takii* Kira; p. 70, pl. 27, fig. 8.
1962–1968 (SWPC): *Buccinum isaotakii* Kira; p. 76, pl. 28, fig. 8.

Nassariidae

(23) *Nassarius (Zeuxis) kiiensis* Kira, 1959

1954a (CISJ): *Nassarius (Alectrion) kiiensis* Kuroda, MS.; p. 56, pl. 28, fig. 21 [*nom. nud.*].
1954b–1958 (CISJ): *Nassarius (Zeuxis) kiiensis* Kuroda, MS.; p. 56, pl. 28, fig. 21 [*nom. nud.*].
*1959 (CISJ): *Nassarius (Zeuxis) kiiensis* Kuroda, MS.; p. 73, pl. 28, fig. 21 [with short description in Japanese].
1960–1963 (CISJ): *Nassarius (Zeuxis) kiiensis* Kira; p. 73, pl. 28, fig. 21.
1962–1968 (SWPC): *Zeuxis kiiensis* Kira; p. 81, pl. 29, fig. 21.
1965–1989 (CISJ): *Zeuxis kiiensis* (Kira); p. 73, pl. 28, fig. 21.

Taxonomic note: Listed in synonymy of *Nassarius castus* (Gould, 1850) by Cernohorsky (1984: 131).

Fasciolariidae

(24) *Granulifusus kiranus* Shuto, 1958 [Trans. Proc. Paleont. Soc. Japan, 31: 258, pl. 38, fig. 1]

1954a (CISJ): *Fusinus kirana* [*sic*] Kuroda, MS.; p. 60, pl. 30, fig. 3 [*nom. nud.*].
1954b–1958 (CISJ): *Granulifusus kiranus* Kuroda, MS.; p. 60, pl. 30, fig. 3 [*nom. nud.*].
1959 (CISJ): *Granulifusus kiranus* Kuroda, MS. [*sic*]; p. 77, pl. 30, fig. 3.
1960–1989 (CISJ): *Granulifusus kiranus* Shuto; p. 77, pl. 30, fig. 3.
1962–1968 (SWPC): *Granulifusus kiranus* Shuto; p. 85, pl. 31, fig. 3.

(25) *Fusinus gemmuliferus* Kira, 1959

1954–1958 (CISJ): *Fusinus gemmuliferus* Kuroda, MS.; p. 60, pl. 30, fig. 5 [*nom. nud.*].
*1959 (CISJ): *Fusinus gemmuliferus* Kuroda, MS.; p. 77, pl. 30, fig. 5 [with short description in Japanese].
1960–1989 (CISJ): *Fusinus gemmuliferus* Kira; p. 77, pl. 30, fig. 5.
1962–1968 (SWPC): *Fusinus gemmuliferus* Kira; p. 85, pl. 31, fig. 5.

(26) *Fusinus crassiplicatus* Kira, 1959

1954–1958 (CISJ): *Fusinus crassiplicatus* Kuroda, MS.; p. 60, pl. 30, fig. 6 [*nom. nud.*].
*1959 (CISJ): *Fusinus crassiplicatus* Kuroda, MS.; p. 78, pl. 30, fig. 6 [with short description in Japanese].
1960–1989 (CISJ): *Fusinus crassiplicatus* Kira; p. 78, pl. 30, fig. 6.
1962–1968 (SWPC): *Fusinus crassiplicatus* Kira; p. 85, pl. 31, fig. 6.

Olividae

(27) *Turrancilla apicalis* Kira, 1959

1954–1958 (CISJ): *Turrancilla apicalis* Is. Taki, MS.; p. 63, pl. 31, fig. 2 [*nom. nud.*].
*1959 (CISJ): *Turrancilla apicalis* Is. Taki, MS.; p. 79, pl. 31, fig. 2 [with short description in Japanese].
1960–1989 (CISJ): *Turrancilla suavis* (Yokoyama); p. 79, pl. 31, fig. 2.
1962–1968 (SWPC): *Turrancilla suavis* (Yokoyama); p. 88, pl. 32, fig. 2.

(28) *Baryspira urasima* Kira, 1959

1954a (CISJ): *Baryspira hinomotoensis* (Yokoyama); p. 63, pl. 31, fig. 3.
1954b–1958 (CISJ): *Baryspira urasima* Is. Taki, MS.; p. 63, pl. 31, fig. 3 [*nom. nud.*].
*1959 (CISJ): *Baryspira urasima* Is. Taki, MS.; p. 80, pl. 31, fig. 3. [From here on different shell figured! With short description in Japanese].
1960–1989 (CISJ): *Baryspira urasima* Kira; p. 80, pl. 31, fig. 3.
1962–1968 (SWPC): *Baryspira hinomotoensis* (Yokoyama); p. 88, pl. 32, fig. 3.

Taxonomic note: Listed as synonym of *Baryspira hinomotoensis* (Yokoyama, 1922) by Kuroda et al. (1971: 195).

(29) *Oliva hirasei* Kuroda & Habe, 1952 [Check List, p. 74]

1954–1958 (CISJ): *Oliva hirasei* Kuroda, MS. [*sic*]; p. 63, pl. 31, fig. 8.
1959 (CISJ): *Oliva hirasei* Kuroda, MS. [*sic*]; p. 80, pl. 31, fig. 8.
1960–1989 (CISJ): *Oliva hirasei* Kira [*sic*]; p. 80, pl. 31, fig. 8.
1962–1968 (SWPC): *Oliva hirasei* Kira [*sic*]; p. 89, pl. 32, fig. 8.

Taxonomic note: Kuroda & Habe (1952: 74) give this name for a figure in Hirase (1909: pl. 4, fig. 26). As Hirase's work (1909: 45, 46) contains a description of the cited figure, "*Oliva irisans* Lam. Var. ?," the name can be accepted as of Kuroda & Habe (1952) [ICZN Art. 13(a)(ii)]. Petuch & Sargent (1986) list this name in their index as of Kuroda & Habe (1952), but in their text as of Kira (1959).

Mitridae

(30) *Mitropifex hirasei* Kira, 1962

1954a (CISJ): *Mitra (Scabricola) japonica* A. Adams; p. 68, pl. 34, fig. 2.
1954b–1958 (CISJ): *Vexillum (Uromitra)* sp.; p. 68, pl. 34, fig. 2.

1959–1963 (CISJ): *Vexillum (Uromitra)* sp.; p. 88, pl. 34, fig. 2.
*1962 (SWPC): *Mitropifex hirasei* Kira (n.sp.); p. 98, pl. 35, fig. 2.
1965–1968 (SWPC): *Mitropifex hirasei* Kira (n.sp.) [*sic*]; p. 98, pl. 35, fig. 2.
1965–1989 (CISJ): *Mitropifex hirasei* Kira; p. 88, pl. 34, fig. 2.

(31) *Mitra (Cancilla) yagurai* Kira, 1959

1954a (CISJ): *Mitra (Cancilla) yagurai* Kuroda, MS.; p. 68, pl. 34, fig. 3 [*nom. nud.*].
1954b–1958 (CISJ): *Mitr* [*sic*] *(Cancilla) yagurai* Kuroda, MS.; p. 68, pl. 34, fig. 3 [*nom. nud.*].
*1959 (CISJ): *Mitra (Cancilla) yagurai* Kuroda, MS.; p. 88, pl. 34, fig. 3 [with short description in Japanese].
1960–1963 (CISJ): *Mitra (Tiara) yagurai* Kira; p. 88, pl. 34, fig. 3.
1962–1968 (SWPC): *Tiara yagurai* (Kira); p. 98, pl. 35, fig. 3.
1965–1989 (CISJ): *Tiara yagurai* (Kira); p. 88, pl. 34, fig. 3.

Taxonomic note: Listed as synonym of *Mitra interlirata* Reeve, 1844, by Cernohorsky (1970: 46).

Turridae

(32) *Ancistrosyrinx pulcherrissima* Kira, 1959

1954a (CISJ): *Ancistrosyrinx pulcherissima* [*sic*] Kuroda, MS.; p. 71, pl. 35, fig. 1 [*nom. nud.*].
1954b–1958 (CISJ): *Ancistrosyrinx pulcherrissima* Kuroda, MS.; p. 71, pl. 35, fig. 1 [*nom. nud.*].
*1959 (CISJ): *Ancistrosyrinx pulcherrissima* Kuroda; p. 90, pl. 35, fig. 1 [with short description in Japanese].
1960–1963 (CISJ): *Ancistrosyrinx pulcherrissima* Kira; p. 90, pl. 35, fig. 1.
1962–1968 (SWPC): *Ancistrosyrinx pulcherrissimus* Kira; p. 100, pl. 36, fig. 1.
1965–1989 (CISJ): *Ancistrosyrinx pulcherrissimus* Kira; p. 90, pl. 35, fig. 1.

Taxonomic note: Listed as of Kuroda, 1958, by Powell (1966: 42).

(33) *Daphnella nobilis* Kira, 1959

1954a (CISJ): *Daphnella nofilis* [*sic*] Kuroda, MS.; p. 71, pl. 35, fig. 4 [*nom. nud.*].
1954b–1958 (CISJ): *Daphnella nobilis* Kuroda, MS.; p. 71, pl. 35, fig. 4 [*nom. nud.*].
*1959 (CISJ): *Daphnella nobilis* Kuroda, MS.; p. 90, pl. 35, fig. 4 [with short description in Japanese].
1960–1989 (CISJ): *Daphnella nobilis* Kira; p. 90, pl. 35, fig. 4.
1962–1968 (SWPC): *Daphnella nobilis* Kira; p. 100, pl. 36, fig. 4.

Conidae

(34) *Chelyconus kinoshitai* Kuroda, 1956 [Venus, 19(1): 6, text-fig. 7]

1954–1955 (CISJ): *Floraconus ? kinoshitai* Kuroda, MS.; p. 75, pl. 37, fig. 18 [*nom. nud.*].
1957–1958 (CISJ): *Floraconus ? kinoshitai* Kuroda, MS. [*sic*]; p. 75, pl. 37, fig. 18.
1959–1989 (CISJ): *Chelyconus kinoshitai* Kuroda; p. 97, pl. 37, fig. 18.
1962–1968 (SWPC): *Chelyconus kinoshitai* (Kuroda); p. 108, pl. 38, fig. 18.

(35) *Asprella (Conasprella ?) ichinoseana* Kuroda, 1956 [Venus, 19(1): 10, pl. 1, fig. 5]

1954a (CISJ): *Asprella (Conasprella) ichinoseana* Kuroda [*sic*]; p. 76, pl. 38, fig. 3 [*nom. nud.*].
1954b–1955 (CISJ): *Asprella ichinoseana* Kuroda, MS.; p. 76, pl. 38, fig. 3 [*nom. nud.*].
1957–1958 (CISJ): *Asprella ichinoseana* Kuroda, MS. [*sic*]; p. 76, pl. 38, fig. 3.
1959–1989 (CISJ): *Asprella (Conasprella) ichinoseana* Kuroda; p. 98, pl. 38, fig. 3.
1962–1968 (SWPC): *Asprella (Conasprella) ichinoseana* Kuroda; p. 109, pl. 39, fig. 3.

Bradybaenidae

(36) *Euhadra roseoapicalis* Kira, 1959

1954a (CISJ): *Euhadra brandtii* (Kobelt); p. 132, pl. 66, fig. 16.
1954b–1958 (CISJ): *Euhadra brandtii* (Kobelt); p. 132, pl. 66, fig. 15 [renumbered].
*1959 (CISJ): *Euhadra roseoapicalis* Kuroda, MS.; p. 182, p. 66, fig. 15 [with short description in Japanese].
1960–1963 (CISJ): *Euhadra brandti* [*sic*] (Kobelt); p. 182, pl. 66, fig. 15.
1962–1968 (SWPC): *Euhadra brandti roseoapicalis* Kira; p. 197, pl. 67, fig. 15.
1965–1989 (CISJ): *Euhadra brandti roseoapicalis* Kira; p. 182, pl. 66, fig. 15.

(37) *Euhadra grata gratoides* Kira, 1959

1954a (CISJ): *Euhadra grata gratoides* Kira, MS.; p. 132, pl. 66, fig. 19 [*nom. nud.*].
1954b–1958 (CISJ): *Euhadra grata gratoides* Kira, MS.; p. 132, pl. 66, fig. 17 [renumbered] [*nom. nud.*].
*1959 (CISJ): *Euhadra grata gratoides* Kira; p. 182, pl. 66, fig. 17 [with short description in Japanese].
1960–1989 (CISJ): *Euhadra grata gratoides* Kira; p. 182, pl. 66, fig. 17.
1962–1968 (SWPC): *Euhadra grata gratoides* Kira; p. 197, pl. 67, fig. 17.

SCAPHOPODA

Siphonodentaliidae

(38) *Cadulus (Platyschides) novilunatus* Kira, 1959

1954a (CISJ): *Gadila novilunata* Kuroda, MS.; p. 80, pl. 40, fig. 2 [*nom. nud.*].
1954b–1958 (CISJ): *Cadulus (Platyschides) novilunatus* Kuroda, MS.; p. 80, pl. 40, fig. 2 [*nom. nud.*].
*1959 (CISJ): *Cadulus (Platyschides) novilunatus* Kuroda, MS.; p. 104, pl. 40, fig. 2 [with short description in Japanese].
1960–1963 (CISJ): *Cadulus (Platyschides) novilunatus* Kira; p. 104, pl. 40, fig. 2.
1962–1968 (SWPC): *Gadila (Platyschides) novilunata* (Kira); p. 116, pl. 41, fig. 2.
1965–1989 (CISJ): *Pulsellum virginalis* (Boissevain); p. 104, pl. 40, fig. 2.

Taxonomic note: Listed as "*Gadila novilunata* Kira, 1959," in synonymy of *Platyschides virginalis* (Boissevain, 1906) by Habe (1964: 49), and in synonymy of "*Cadulus (Polyschides) virginalis* Biossevain [*sic*]" by Habe & Kosuge (1964b: 12); listed as "*Gadila (Platyschides) noviluna* [*sic*] Kira, 1959," under *Polyschides (Platyschides) virginalis* by Habe (1977: 342).

(39) *Entalina majestica* Kira, 1959

1954–1958 (CISJ): *Entalina majestica* Kuroda, MS.; p. 80, pl. 40, fig. 3 [*nom. nud.*].
*1959 (CISJ): *Entalina majestica* Kuroda, MS.; p. 105, pl. 40, fig. 3 [with short description in Japanese].
1960–1963 (CISJ): *Entalina majestica* Kira; p. 105, pl. 40, fig. 3.
1962–1968 (SWPC): *Entalina majestica* Kira; p. 116, pl. 41, fig. 3.
1965–1989 (CISJ): *Entalina quadriangularis* [*sic*] (Boissevain); p. 105, pl. 40, fig. 3.

Taxonomic note: Listed as synonym of *Entalina quadriangularis* [error for *quadrangularis*] Boissevain, 1906, by Habe (1964: 39; 1977: 339), and of *E. quadrangularis* by Habe & Kosuge (1964b: 8).

Dentaliidae

(40) *Dentalium (Episiphon) candelatum* Kira, 1959

1954–1958 (CISJ): *Dentalium (Episiphon) candelatum* Kuroda, MS.; p. 80, pl. 40, fig. 5 [*nom. nud.*].
*1959 (CISJ): *Dentalium (Episiphon) candelatum* Kuroda, MS.; p. 105, pl. 40, fig. 5 [with short description in Japanese].
1960–1963 (CISJ): *Dentalium (Episiphon) candelatum* Kira; p. 105, pl. 40, fig. 5.
1962–1968 (SWPC): *Episiphon candelatum* (Kira); p. 116, pl. 41, fig. 5.
1965–1989 (CISJ): *Episiphon candelatum* (Kira); p. 105, pl. 40, fig. 5.

(41) *Dentalium (Pictodentalium) formosum hirasei* Kira, 1959

1954–1958 (CISJ): *Dentalium formosum* Adams et Reeve; p. 80, pl. 40, fig. 11.
*1959 (CISJ): *Dentalium (Pictodentalium) formosum hirasei* Kuroda, MS.; p. 105, pl. 40, fig. 11 [with short description in Japanese].
1960–1963 (CISJ): *Dentalium (Pictodentalium) formosum hirasei* Kira; p. 105, pl. 40, fig. 11.
1962–1968 (SWPC): *Pictodentalium formosum hirasei* (Kira); p. 117, pl. 41, fig. 11.
1965–1989 (CISJ): *Dentalium (Pictodentalium) formosum hirasei* (Kira); p. 105, pl. 40, fig. 11.

Taxonomic note: Placed in synonymy of *Dentalium formosum* Adams & Reeve, 1850, by Habe (1964: 15; 1977: 332) and Habe & Kosuge (1964b: 4).

(42) Genus-group name *Pictodentalium*

Taxonomic note: With his introduction of *Dentalium formosum hirasei,* Kira (1959 and following years, see above) used the genus-group name *"Pictodentalium,"* without description or indication that it was new. Authorship for this name was credited to Kira (1959) by Habe & Kosuge (1964b: 4) and Palmer (1974: 118); the latter lists *D. formosum hirasei* as type species. However, Kira's use of the name does not fulfill the ICZN requirements [Articles 13(a),(e), criteria of availability to be satisfied by new names published after 1930], and *Pictodentalium* Kira has to be considered a *nomen nudum.* As ICZN Article 13(a)(i) does not apply any degree to differentiation, the name might date from Palmer (1974: 118) who lists the name for a group comprising "the multicoloured dentaliids."

BIVALVIA

Nuculidae

(43) *Acila schencki* Habe, 1958 [1958b, Publ. Seto Mar. Biol. Lab., 6(3): 243]

1954–1958 (CISJ): *Acila schencki* Kuroda, MS.; p. 83, pl. 41, fig. 6 [*nom. nud.*].

1959 (CISJ): *Acila schencki* Kuroda, MS. [*sic*]; p. 107, pl. 41, fig. 6.
1960–1963 (CISJ): *Acila schencki* Kira [*sic*]; p. 107, pl. 41, fig. 6.
1962–1968 (SWPC): *Acila schencki* Kira [*sic*]; p. 119, pl. 42, fig. 6.
1965–1989 (CISJ): *Acila schencki* Kuroda [*sic*]; p. 107, pl. 41, fig. 6.

Taxonomic note: Habe (1958b: 243) lists this as "*Acila schencki* Kuroda (MS)," and in synonymy shows that it is "*Acila divaricata submirabilis* Makiyama" Schenck, 1936, *non* Makiyama, 1926 (p. 151, pl. 12, fig. 9). As there is a description of *submirabilis* in Schenck (1936: 88–90), the name *A. schencki* is here considered valid as of Habe (1958) [ICZN Art. 13(a)(ii)]. Habe (1977: 15) lists it as "*Acila (Acila) divaricata schencki* Kira, 1959."

Nuculanidae

(44) *Nuculana (Thestyleda) acinacea* Habe, 1958 [1958b, Publ. Seto Mar. Biol. Lab., 6(3): 247]

1954–1958 (CISJ): *Nuculana (Thestyleda?) acinacea* Habe, MS.; p. 83, pl. 41, fig. 9 [*nom. nud.*].
1959 (CISJ): *Nuculana (Thestyleda?) acinacea* Habe, MS. [*sic*]; p. 107, pl. 41, fig. 9.
1960–1963 (CISJ): *Nuculana (Thestyleda?) acinacea* Habe; p. 107, pl. 41, fig. 9.
1965–1989 (CISJ): *Nuculana (Thestyleda) acinacea* Habe; p. 107, pl. 41, fig. 9.
1962–1968 (SWPC): *Nuculana (Thestyleda) acinacea* Habe; p. 119, pl. 42, fig. 9.

Limopsidae

(45) *Limopsis tajimae emphaticus* Kira, 1959

1954a (CISJ): *Limopsis tajimae emphaticus* Kuroda, MS.; p. 88, pl. 44, fig. 4 [*nom. nud.*].
1954b–1958 (CISJ): *Limopsis tajimae emphaticus* Kira [*sic*], MS.; p. 88, pl. 44, fig. 4 [*nom. nud.*].
*1959 (CISJ): *Limopsis tajimae emphaticus* Kira; p. 112, pl. 44, fig. 4 [with short description in Japanese].
1960–1989 (CISJ): *Limopsis tajimae emphaticus* Kira; p. 112, pl. 44, fig. 4.
1962–1968 (SWPC): *Limopsis tajimae emphaticus* Kira; p. 125, pl. 45, fig. 4.

Taxonomic note: Listed in synonymy of *Limopsis tajimae* Sowerby, 1914, by Kuroda et al. (1971: 338) and Habe (1977: 48).

Cardiidae

(46) *Fragum loochooanum* Kira, 1959

1954a (CISJ): *Fragum loochooanus* Kuroda, MS.; p. 108, pl. 54, fig. 13 [*nom. nud.*].
1954b–1958 (CISJ): *Fragum loochooanum* Kuroda, MS.; p. 108, pl. 54, fig. 13 [*nom. nud.*].
*1959 (CISJ): *Fragum loochooanum* Kuroda, MS.; p. 137, pl. 54, fig. 13 [with short description in Japanese].
1960–1989 (CISJ): *Fragun* [*sic*] *loochooanum* Kira; p. 137, pl. 54, fig. 13.
1962–1968 (SWPC): *Fragum loochooanum* Kira; p. 154, pl. 55, fig. 13.

(47) *Clinocardium uchidai* Habe, 1955 [Publ. Akkeshi Mar. Biol. Stat., 4: 11, pl. 2, figs. 5, 6]

1954–1955 (CISJ): *Clinocardium uchidai* Habe, MS.; p. 111, pl. 55, fig. 1 [*nom. nud.*].
1957–1958 (CISJ): *Clinocardium uchidai* Habe, MS. [*sic*]; p. 111, pl. 55, fig. 1.
1959 (CISJ): *Clinocardium uchidai* Habe, MS. [*sic*]; p. 138, pl. 55, fig. 1.
1960–1989 (CISJ): *Clinocardium uchidai* Habe; p. 138, pl. 55, fig. 1.
1965–1968b (SWPC): *Clinocardium uchidai* Habe; p. 156, pl. 56, fig. 1.

Taxonomic note: Placed in synonymy of *Clinocardium californiense* (Deshayes, 1839) by Habe (1977: 172).

(48) *Vasticardium compunctum* Kira, 1959

1954–1958 (CISJ): *Vasticardium compunctum* Kuroda, MS.; p. 111, pl. 55, fig. 9 [*nom. nud.*].
*1959 (CISJ): *Vasticardium compunctum* Kuroda, MS.; p. 139, pl. 50, fig. 9 [with short description in Japanese].
1960–1989 (CISJ): *Vasticardium compunctum* Kira; p. 139, pl. 55, fig. 9.
1962–1968 (SWPC): *Vasticardium compunctum* Kira; p. 156, pl. 56, fig. 9.

(49) "*Vasticardium serricostatum*"

1954–1958 (CISJ): *Vasticardium serricostatum* Kuroda, MS.; p. 111, pl. 55, fig. 11 [*nom. nud.*].
1959 (CISJ): *Vasticardium serricostatum* Kuroda, MS.; p. 139, pl. 55, fig. 11 [with short description in Japanese].
1960–1963 (CISJ): *Vasticardium serricostatum* Melvill et Standen [*sic*], var.; p. 139, pl. 55, fig. 11.
1962–1968 (SWPC): *Vasticardium okinawaense* Kuroda; p. 157, pl. 56, fig. 11.
1965–1989 (CISJ): *Vasticardium okinawaense* Kuroda; p. 139, pl. 55, fig. 11.

Taxonomic note: The name "*serricostatum* Kuroda" is an error for what was meant to be described as a variety of *Cardium (Trachycar-*

dium) serricostatum Melvill & Standen, 1899 (p. 191, pl. 11, fig. 20). It was subsequently named by Kuroda (1960: 82) as "*Trachycardium (Acrosterigma)* {*serricostatum* Melvill & Standen var?} *okinawaense* Kuroda (nov.)," referring to Kira's illustration (1959: pl. 55, fig. 11). Peculiarly, Fischer-Piette (1977) lists "*Vasticardium serricostatum* Kuroda" as illustrated by Kira (1955) in the synonymy of *Laevicardium (Vasticardium) flavum* (Linné, 1758), but has "*Vasticardium okinawaense* Kuroda" as illustrated by Kira (1962), using the same figure, in synonymy with *Cardium enode* Sowerby, 1834.

Veneridae

(50) *Leukoma japonica* Kira, 1954

1954a (CISJ): *Leucoma* [*sic*] *japonica* Kira, MS.; p. 115, pl. 57, fig. 17 [*nom. nud.*].
*1954a (CISJ): *Leukoma japoniac* [*sic*] sp. nov.; p. 163.
1954b–1958 (CISJ): *Leukoma japonica* Kira, MS. [*sic*]; p. 115, pl. 57, fig. 17.
1954b–1958 (CISJ): *Leukoma japonica* Kira sp. nov. [*sic*]; p. 163.
1959–1963 (CISJ): *Leukoma japonica* Kira; p. 147, pl. 57, fig. 17.
1962–1968 (SWPC): *Glycydonta marica japonica* (Kira); p. 164, pl. 58, fig. 17.
1965–1989 (CISJ): *Glycydonta marica japonica* (Kira); p. 147, pl. 57, fig. 17.

Taxonomic note: As "*Leuboma* [*sic*] *marica japonica* Kira, 1954," placed in synonymy of *Glycodonta marica* (Linné, 1758) by Habe (1977: 250).

(51) *Irus ishibashianus* Kuroda & Habe, 1952 [Check List: 21]

1954–1958 (CISJ): *Irus ishibashianus* Kuroda et Habe; p. 115, pl. 57, fig. 25.
1959 (CISJ): *Irus ishibashianus* Kuroda, MS. [*sic*]; p. 148, pl. 57, fig. 25.
1960–1963 (CISJ): *Irus ishibashianus* Kuroda et Habe; p. 148, pl. 57, fig. 25.
1962–1968 (SWPC): *Notirus ishibashianus* (Kuroda et Habe); p. 165, pl. 58, fig. 25.
1965–1989 (CISJ): *Notirus ishibashianus* Kuroda et Habe; p. 148, pl. 57, fig. 25.

Taxonomic note: Kuroda & Habe (1952: 21) introduced this as a new name for "*Venerupis irus* (Linné)," Yokoyama, 1924 (1924: 44, pl. 2, fig. 23), *non Donax irus* Linné, 1758. Kuroda et al. (1971: 427), Hanshin Shell Club (1986: 45), Inaba & Oyama (1977: 52), and Habe (1977: 268) list it as of Kuroda & Habe, 1952. Habe (1981: 166) lists it as of Kira (1959).

Asaphidae/Psammobiidae [depending on printing]

(52) *Solecurtus dunkeri* Kira, 1959

1954–1958 (CISJ): *Solecurtus dunkeri* Kuroda, MS.; p. 116, pl. 58, fig. 22 [*nom. nud.*].
*1959 (CISJ): *Solecurtus dunkeri* Kuroda, MS.; p. 152, pl. 58, fig. 22 [with short description in Japanese].
1960–1963 (CISJ): *Solecurtus dunkeri* Kira; p. 152, pl. 58, fig. 22.
1962–1968 (SWPC): *Solecurtus dunkeri* Kira; p. 169, pl. 59, fig. 22.
1965–1989 (CISJ): *Solecurtus dunkeri* Kuroda, MS. [*sic*]; p. 152, pl. 58, fig. 22.

Taxonomic note: Listed in synonymy of *Solecurtus divaricatus* (Lischke, 1869) by Habe (1977: 224).

(53) *Nuttallia solida* Kira, 1953 [Venus, 17(3): 149, figs. 1c, 1d, 2c]

1954–1958 (CISJ): *Nuttallia solida* Kira; p. 119, pl. 59, fig. 10.
1959–1989 (CISJ): *Nuttallia solida* Kira; p. 154, pl. 59, fig. 10.
1962–1968 (SWPC): *Nuttallia solida* Kira; p. 171, pl. 60, fig. 10.

Taxonomic note: Listed in synonymy of *Nuttallia japonica* (Reeve, 1857) by Habe (1977: 224).

Tellinidae

(54) *Heteromacoma oyamai* Kira, 1954

1954a (CISJ): *Heteromacoma oyamai* Kira, MS.; p. 119, pl. 59, fig. 21 [*nom. nud.*].
*1954a (CISJ): *Heteromacoma oyamai* sp. nov.; p. 164.
1954b–1958 (CISJ): *Heteromacoma oyamai* Kira, MS. [*sic*]; p. 119, pl. 59, fig. 21.
1954b–1958 (CISJ): *Heteromacoma oyamai* Kira sp. nov. [*sic*]; p. 164.
1959 (CISJ): *Heteromacoma oyamai* Kira; p. 155, pl. 59, fig. 21.
1960–1963 (CISJ): *Macoma oyamai* (Kira); p. 155, pl. 59, fig. 21.
1962–1968 (SWPC): *Heteromacoma oyamai* Kira; p. 172, pl. 60, fig. 21.
1965–1989 (CISJ): *Heteromacoma oyamai* (Kira); p. 155, pl. 59, fig. 21.

Taxonomic note: Listed as *Heteromacoma irus oyamai* Kira, 1959, by Habe (1977: 210).

Unionidae

(55) *Lanceolaria oxyrhyncha cuspidata* Kira, 1959

1954–1958 (CISJ): *Lanceolaria oxyrhyncha cuspidata* Kuroda, MS.; 127, pl. 63, fig. 18 [*nom. nud.*].
*1959 (CISJ): *Lanceolaria oxyrhyncha cuspidata* Kuroda, MS.; p. 172, pl. 63, fig. 18 [with short description in Japanese].
1960–1989 (CISJ): *Lanceolaria oxyrhyncha cuspidata* Kira; p. 172, pl. 63, fig. 18.
1962–1968 (SWPC): *Lanceolaria oxyrhyncha cuspidata* Kira; p. 187, pl. 64, fig. 18.

Taxonomic note: Listed in synonymy of *Lanceolaria grayana* (Lea, 1834) by Habe (1977: 115).

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SPERM STORAGE MECHANISMS AND FERTILIZATION IN FEMALES OF TWO SOUTH AMERICAN ELEDONIDS (CEPHALOPODA:OCTOPODA).

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ABSTRACT

Octopod species of the genus *Eledone* do not have spermathecae in the oviducal glands. Sperm masses are found within the ovary, where fertilization takes place. In two South American species, *Eledone massyae* and *Eledone gaucha,* unusual filamentous structures were observed in the animal pole of the oocyte and were entangled greatly with the sperm masses. These structures are extensions of the surrounding layers of the oocytes. The sperm penetrate the filaments forming agglomerates surrounded by a layer of follicular cells. The filaments shorten as the oocyte grows, drawing the enclosed spermatozoa to the ooplasm, in which fertilization occurs. These filaments allow sperm to be stored for long periods and might be analogous to spermathecae in the oviducal gland of Octopodinae.

Key words: Cephalopoda, *Eledone,* fertilization, sperm storage, Octopodidae, Brazil.

INTRODUCTION

Female incirrate octopods can store sperm for a long time after mating. In two of the four Octopodidae subfamilies, the Octopodinae and Bathypolypodinae, internal sperm storage mechanisms and fertilization have been described (Petersen, 1959; Froesch & Marthy, 1975; Wells & Wells, 1977, O'Dor & Malacaster, 1983). Less is known about the Eledoninae and Graneledoninae. In *Eledone cirrhosa,* a time lag between copulation and spawning has been established in aquaria experiments (Mangold et al., 1971) but mechanisms of sperm storage are uncertain (Boyle,1983).

Eledone massyae Voss, 1964, and *Eledone gaucha* Haimovici,1988, were described recently and are little known. Haimovici & Andriguetto (1986) and Haimovici (1988) described morphological differences between these species and commented on their apparent geographical coexistence on the southern Brazilian shelf. Some unusual oocyte structures were observed in the ovaries of both species. In this paper these structures are described and evidence is given for their involvement in sperm storage and fertilization.

MATERIAL AND METHODS

Reproductive organs of nine females of *Eledone massyae* and four females of *E. gaucha* were examined (Table 1). Octopuses were collected with a bottom trawl and fixed in 10% formalin or seawater Bouin solution. Oocytes and oviducal glands were dissected and embedded in paraffin (58°C) according to standard histological techniques (Gabe, 1968). Longitudinal and transverse sections (5 to 7 μm) were stained with Harry's hematoxilin-eosin.

Terms applied to cephalopods and used in this paper:

Spermatangia: Also called sperm sac. Evaginated spermatophores; bladders enclosing the sperm mass.

Spermatophore: Complex sperm package used for transfer of sperm from male to female.

Spermatheca: Seminal receptacle. Pouch in females in which male gametes are stored at mating.

RESULTS

Oocytes

Maturing oocytes remain attached by stalks to the inner epithelium of the ovary (Fig. 1A). Each oocyte is enveloped by three layers: externally, a stratified epithelium of squamous cells; internally, a layer of follicular cells; and between these, a layer of connective tissue

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TABLE I. Females of *Eledone massyae* Voss, 1964, and *Eledone gaucha* Haimovici, 1988, used for histological analyses.

Species	Number	Locality	Date	DML range (mm)	Oocyte length range (mm)	Fixative
E. massyae	5	off Rio Grande do Sul state	Oct. 1988	25.0–65.0	0.7–10.0	Formalin 10%
E. massyae	4	off Rio de Janeiro state	Nov. 1988	64.0–73.3	3.8–6.6	Seawater Bouin
E. gaucha	4	off Rio Grande do Sul state	April 1983	25.0–39.0	0.5–5.4	Formalin 10%
E. gaucha	1	*	Nov. 1983	36.0	5.8	Formalin 10%

with cells of different sizes and shapes, fibroblasts and blood vessels. The follicular cells proliferate and penetrate the ooplasm, forming longitudinal folds that give the oocyte a striped appearance. At final stages of oogenesis these cells secret the chorion. At the stalked end of the oocyte the chorion becomes drawn out into a stalk (Fig. 2d).

At the animal pole, opposite the stalked end, there is a conical filamentous projection (Fig. 1B). Filament sizes range from twice the length of a 3 mm long oocyte to one-fourth that of the 11 mm long oocytes. Microscopically, the oocyte-surrounding layers are drawn out from the oocyte to form these extensions (Fig. 3D). The external epithelium and the intermediate connective tissue line the filament throughout its length. The follicular cells of the inner layer differentiate and penetrate the filament, filling it as a compact tissue. In the initial stages of maturation (Fig. 3A), follicular cells are dispersed irregularly and are fusiform with elongated nuclei. As maturation advances, these cells become regularly dispersed and cuboidal with large oval nuclei (Fig. 3B). Finally, in advanced stages of maturity, they have smaller nuclei with dense chromatin, which suggests a degeneration of the tissue (Fig. 3C).

Oviducal glands

In the mid-portion of each oviduct is an oviducal gland structurally divided into two concentric glands around the oviduct and separated by a thin sheet of connective tissue (Fig. 3E). Spermatheca are absent (Fig. 4), as in *E. cirrhosa* and *E. moschata* (Froesch & Marthy, 1975). The peripheral gland is formed by groups of concentric cells with basal nuclei and a central lumen; in females close to maturity their cytoplasm is densely packed with reddish grains. The central gland is composed of 22-23 ducts around the oviduct, each lined by an epithelium with ciliated cells having superficial nuclei and glandular cells having basal nuclei. Spermatozoa were not seen to be associated with the oviducts.

Sperm storage and fertilization

In females that had mated, spermatangia and free sperm were seen within the ovaries. As many as seven spermatangia were inside an ovary, often attached to the head of the spermatophoric tunic (Fig. 1D). Free sperm masses occurred around the oocytes and were much entangled with the oocyte apical filaments (Fig. 1 C, 1D). Sperm were attached to the filament tips, and apparently penetrated them. Longitudinal sections of apical filaments of the oocyte showed hair-like masses of spermatozoa, regularly dispersed and surrounded by flattened differentiated follicular cells forming dark purple agglomerates along the filament (Fig. 3 G, H; Fig. 5). During development, the evolving layers degenerate, thus shortening the filament. The filament-enclosed spermatozoa are thus drawn to the ooplasm, in which fertilization occurs, probably very shortly before spawning (Fig. 2).

Oocytes in females of *Eledone massyae* bearing spermatangia, free sperm and traces of fertilization ranged from 3.0 to 9.0 mm. In *E. gaucha* they ranged from 0.8 to 5.0 mm. In the former, the largest oocyte, although striped, was 12.0 mm; in the latter, it was 7.5 mm (Perez & Haimovici, MS).

DISCUSSION

The potential for storage of sperm is known for octopods of the subfamilies Octopodinae and Bathypolypodinae. The sperm released into the oviducts after the "spermatophoric re-

FIG. 1. Photomicrographs of ovary and maturing oocytes of Brazilian *Eledone* species. A. Cluster of maturing oocytes. B. General view of ovary. C. Detail of apical filament attachment to free sperm mass. D. Ovary of mated female. Spermatangia, spermatophore tunics and free sperm mass present. Arrow indicates apical filament attached to sperm mass. Scale bar — 1 mm. af, apical filament; s, stalk; sf, spermatophore tunic; sg, spermatangium; sm, sperm mass.

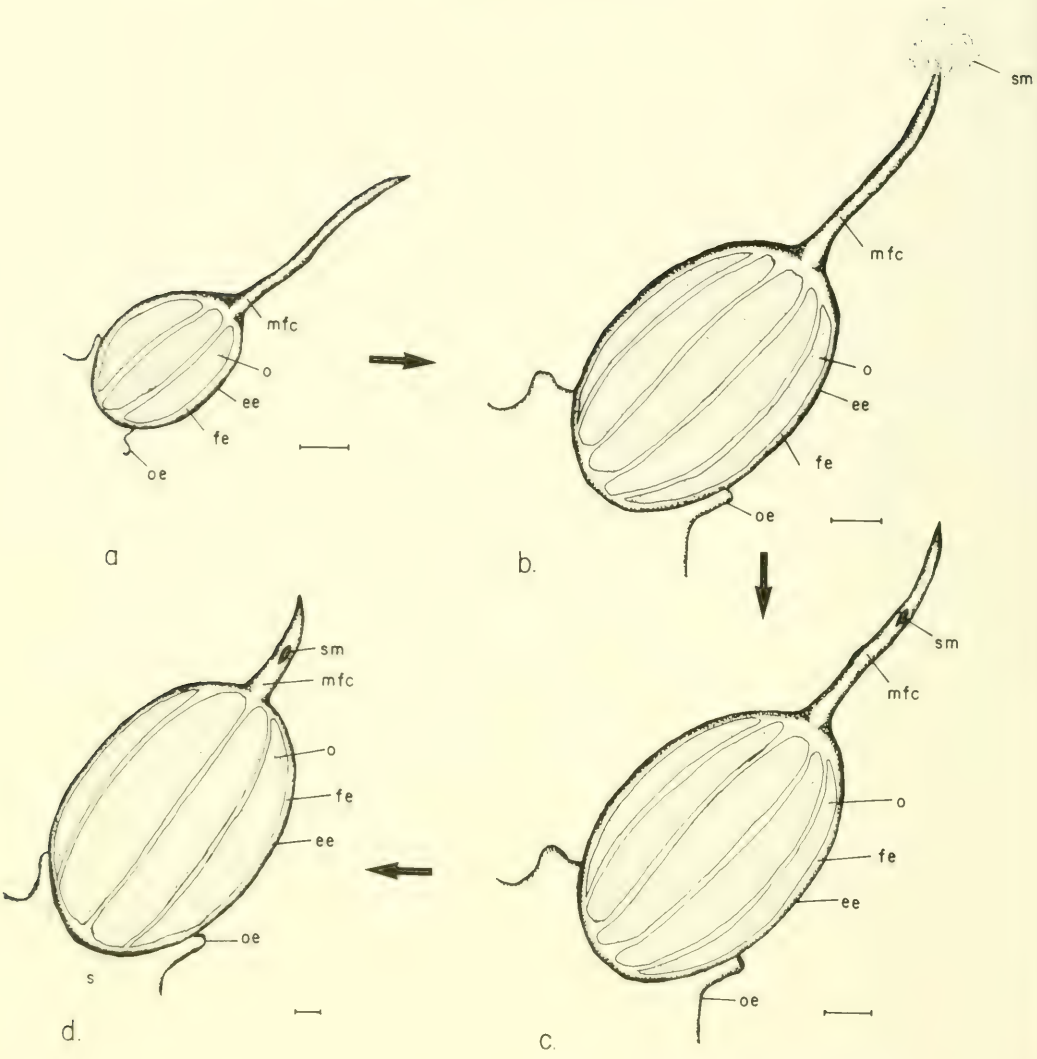

FIG. 2. Schematic diagram of fertilization in *Eledone massyae* and *Eledone gaucha*. a. Oocyte in early stage of maturation. Apical filament is almost twice oocyte length. b. Maturing oocyte. Apical filament as long as oocyte and attached to free sperm mass. c. Maturing oocyte. Sperm mass penetrates filament and is surrounded by modified follicular cells. d. Oocyte in advanced stage of maturation. At this stage, apical filament is very short and sperm mass close to ooplasm. Note position at which it will form chorionic stalk. ee, external epithelium; fe, follicular epithelium; mfc, modified folicular cells; o, ooplasm; oe, ovarian epithelium; sm, sperm mass.

action" (Mann et al., 1970) enter the oviducal glands, where they remain attached to the epithelium of the spermatheca (Froesch & Marthy, 1975). Spermatozoa can be maintained as long as ten months, as observed in *Bathypolypus arcticus* (O'Dor & Malacaster, 1983); thus, mating can occur long before maturation. Mature eggs are fertilized in the lumina of the oviducal glands just before spawning.

There is evidence of sperm storage in both European and South American species of *Eledone*. Aquaria observations of Mediterranean E. cirrosa suggested that sperm might be stored for at least six weeks (Mangold et

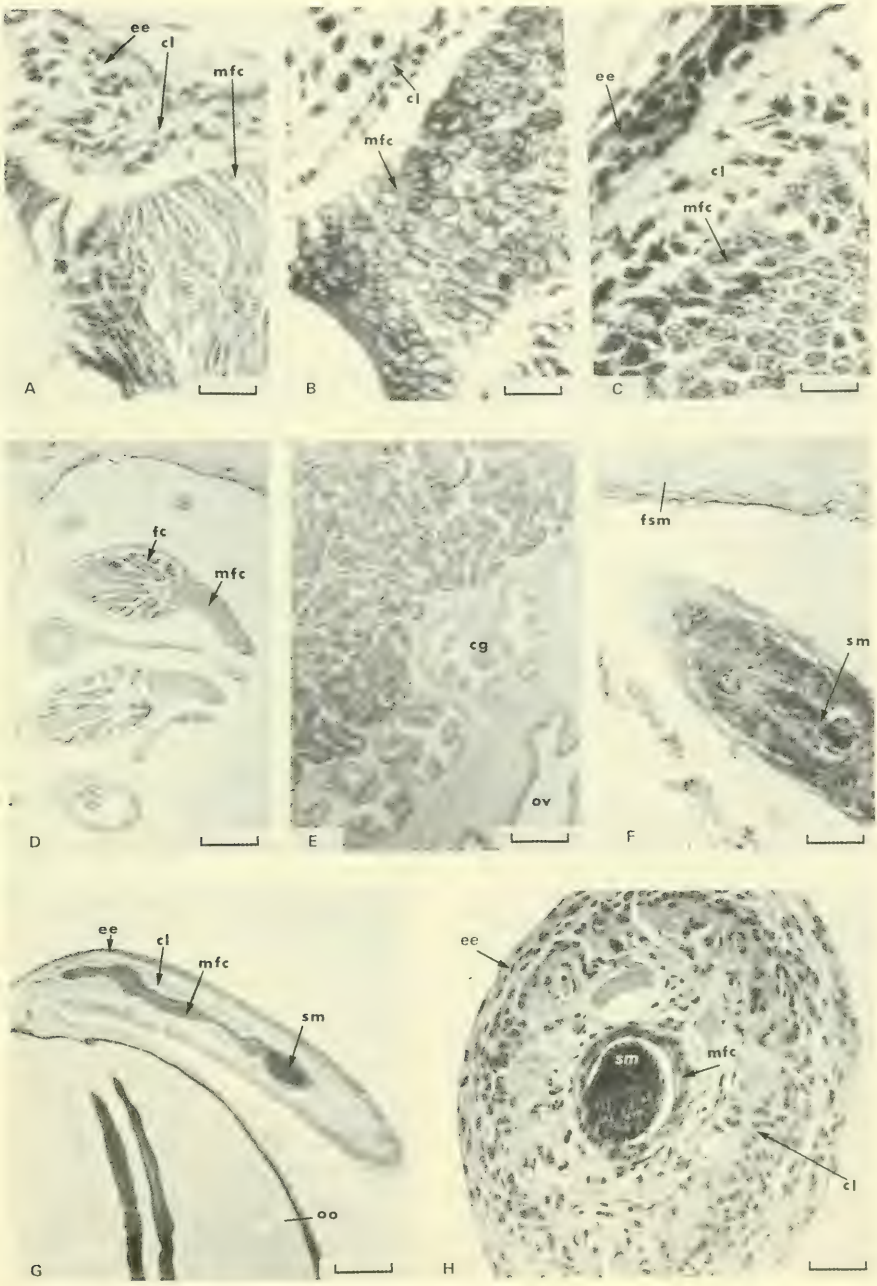

FIG. 3. Photomicrographs of cross-sections of apical filaments, oviducal glands and oocytes of Brazilian *Eledone* species. A–C. Differentiation of follicular cells at base of apical filament, at successive stages of maturation. A,B, scale bar = 20μm; C, scale bar = 100μm. D. Oocytes in initial maturation stages showing oocyte surrounding layers forming apical filaments. Scale bar = 300μm. E. Transverse section of oviducal glands. Scale bar = 300μm. F. Apical filament tip in contact with free sperm mass. Scale bar = 140μm. G. Longitudinal sections of apical filament showing surrounding layers and enclosed sperm mass. Scale bar 300μm. H. Transverse section of apical filament showing three surrounding layers and central spermatozoa. Scale bar = 70μm. cg, central gland; cl, connective layer; ee, external epithelium, fc, follicular cells; fsm, free sperm mass; mfc, modified follicular cells; oo, oocyte; ov, oviduct; pg, peripheral gland; sm, sperm mass.

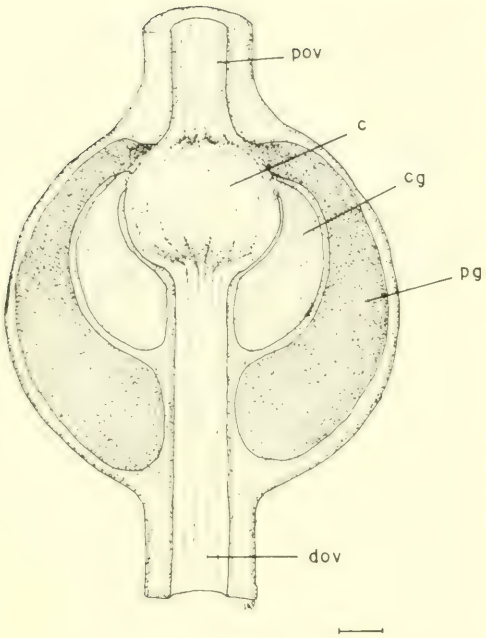

FIG. 4. Schematic diagram of longitudinal cut of oviducal gland of South American *Eledone*. c, central cavity of oviducal gland; cg, central gland; dov, distal oviduct; pg, peripheral gland; pov, proximal oviduct.

al., 1971). A maximal lapse of three months between copulation and spawning was estimated for *E. massyae* (Perez & Haimovici, MS). Maturing females bearing spermatangia within their ovaries were observed in South American species of *Eledone* and Mediterranean *E. cirrosa* (Mangold-Wirz, 1963). In populations of *E. cirrosa* in the North Sea (Boyle & Knobloch, 1983) and *E. moschata* in the Mediterranean (Mangold, 1983) mating was assumed to occur just before spawning because females bearing spermatangia within their ovaries were scarce and nearly mature.

The absence of spermathecae in the oviducal glands seems to be a consistent characteristic of the genus *Eledone* since it was observed in four species. Spermatophores penetrate the oviducts and oviducal glands reaching the ovarian cavity, in which the spermatophoric reaction takes place. Sperm masses occur either freely around the oocytes or enclosed in bladders known as spermatangia (Fort, 1937; Mangold-Wirz, 1963) or sperm sacs (Boyle, 1983; Mangold, 1986). In *Eledone massyae* and *Eledone gaucha*, the apical filaments provide a site for sperm storage and a fertilization mechanism. Modified follicular cells surrounding the sperm mass inside the filament are supposed to keep spermatozoa viable until oocytes are ripe. Whether the apical-filament mechanism is an adaptation of the entire genus is still unclear. In *E. cirrhosa* and *E. moschata*, sites and timing of fertilization, as well as the means to keep sperm viable, are not known. Early descriptions of the reproductive system of *E. cirrhosa* (Insgrove, 1909; Morales, 1958) do not mention structures similar to the apical filaments. Photographs of ovarian eggs of the same species in Mangold-Wirz (1963: plate II, d, e, f) show delicate expansions at the animal pole of the eggs, although they are quite different from those of the South American species (Fig. 1B). Boyle (pers. comm.) observed white masses of sperm attached to the apical end of each egg. Whether these structures indeed form part of the egg-surrounding layers is not known. Comparisons could not be made with the three remaining but poorly-known described species of the genus, *E. caparti* Adam, 1950, *E. thysanophora* Voss, 1962, and *E. nigra* (Hoyle, 1910) from the West African coast.

In species of *Eledone* that have been studied, as well as in most Octopodinae and Bathypolypodinae, males mature earlier and remain sexually active for a greater part of life than do females. The ability of females to store sperm means that mating can occur long before spawning. Histological study of *E. massyae* and *E. gaucha* shows that at least in the South American eledonids, females can copulate a considerable time before maturation and store sperm until fertilization shortly before spawning. The apical filament and the oviducal glands' spermatheca both allow storage of sperm and are important facets of the reproductive strategy of these octopods.

There are some slight differences between these adaptations, however. In the Octopodinae and Bathypolypodinae, each mature oocyte is fertilized as it descends through the lumen of the oviducal gland (Froesch & Marthy, 1975). Spermatozoa stored in the outer parts of the spermathecae will compete to fertilize the eggs; the last male to copulate with the female will be most likely to sire the offspring. In the South American eledonids the sperm of the first male to copulate are likely to fertilize most of the eggs. This fact could explain the difference in body sizes of the sexes of *E. massyae* at maturity (Perez & Haimovici, MS). If they can mate successfully, young

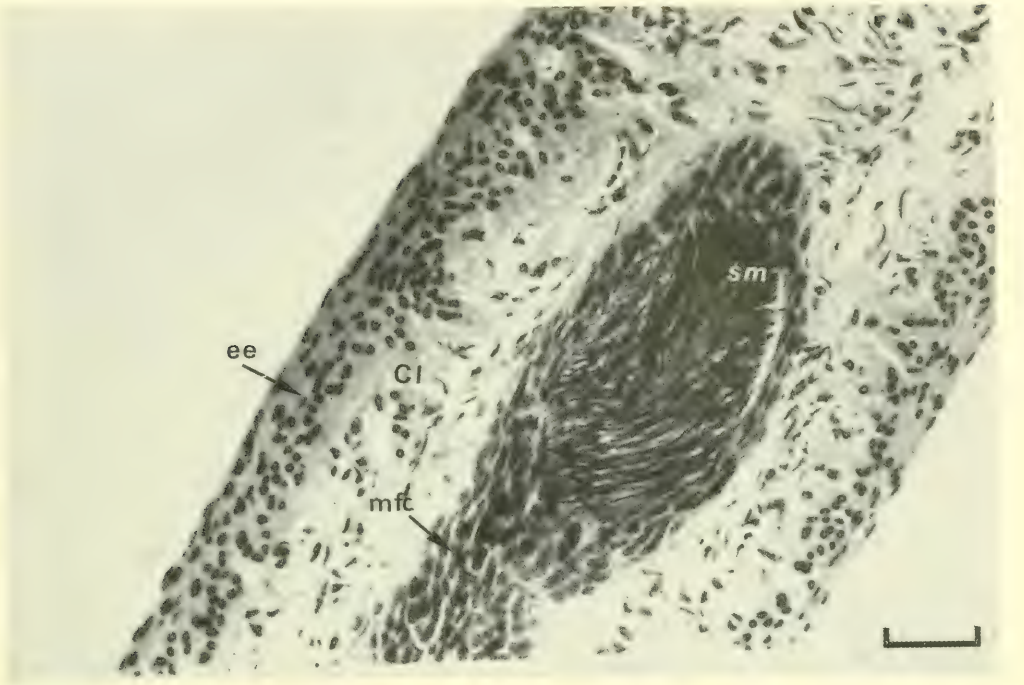

FIG. 5. Longitudinal sections of oocyte apical filament of *Eledone massyae* showing surrounding layers and enclosed sperm mass. cl, connective layer; ee, external epithelium; mfc, modified follicular cells; sm, sperm mass. Scale bar = 40 μm.

males need not grow so large or live so long as females. Indirectly this difference in size could be particularly advantageous during the spawning and brooding seasons because males would not be in the same areas at the same time with mature females; this separation would not only reduce intraspecific competition for food but also avoid cannibalism on the hatchlings.

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PREDATORY ECOLOGY OF NATICID GASTROPODS WITH A REVIEW OF SHELL BORING PREDATION

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ABSTRACT

This review provides a critical synthesis and analysis of the extensive body of knowledge of predation by the Naticidae, a cosmopolitan family of burrowing marine gastropods. First, the diversity of shell boring predation is reviewed and documented for ten taxa (nine marine, one terrestrial), in order to facilitate comparative analyses. These predators are: Naticidae, Muricidae, Cassidae and Capulidae (Gastropoda, Prosobranchia); *Okadaia* (Gastropoda, Opisthobranchia); *Aegopinella* (Gastropoda, Pulmonata); *Octopus* (Cephalopoda); *Pseudostylochus* (Turbellaria); Nematoda; and *Asemichthys* (Pisces). Second, the proximate mechanisms of naticid predation are explicated. Third, the known prey of naticids are tabulated; over 80 families of gastropods and bivalves are subject to naticid predation which is essentially restricted to soft-substrate prey taxa. Fourth, the fossil record of naticid predation is summarized; this predation dates from the Cretaceous, with a possible boring "experiment" in the early Triassic. The diagnostic countersunk naticid boreholes are recognizable in fossil and Recent faunas; naticid predation is a readily documented aspect of the otherwise elusive soft-bottom food web. Fifth, the studies on physiology and ecology of naticid predation are integrated into a conceptual framework. These aspects of naticid predation (energy budgets, prey size and species choice, unsuccessful predation) indicate a successful albeit rather stereotyped mode of predation. The macroevolutionary implications (escalation, or "arms races") suggest generalized predator-prey coevolution.

Key words: Naticidae, predation, boring.

DIVERSITY OF BORING PREDATION

In the Mollusca, many of the post-Paleozoic Gastropoda are predators, and an extensive body of research has developed around various aspects of predation by mollusks (Kohn, 1983). Most of these studies treat Recent mollusks, including the community ecology, behavior and physiology of predation. Other, more restricted, studies on fossils analyzed those elements of predation revealed by fossil shells (boreholes and other signs of shell damage and repair) (Kohn, 1985). Among the predatory gastropods, several families include shell borers which excavate a hole in the prey shell to provide access to the prey flesh. Earlier overviews of boring by gastropods by Fischer (1922, 1966), Carriker (1961), Fatton & Roger (1968), Sohl (1969), Bishop (1975), Boucot (1981: 200 ff.), Bromley (1981), Benton (1986) and Vermeij (1987) have summarized some of this research. More general reviews of gastropod feeding biology were provided by Ankel (1938), Fretter & Graham (1962: 240–262), Taylor et al. (1980), Kohn (1983) and Tsikhon-Lukanina (1987). Inevitably, numerous previous studies have been overlooked by subsequent researchers; this paper seeks to provide some unity and a coherent framework to the body of knowledge of shell boring predation by gastropods of the family Naticidae.

The objectives of this paper are: (1) to document the diversity of shell boring predation and related phenomena; (2) to summarize the mechanical or proximate aspects of naticid prey capture and boring; (3) to tabulate the known naticid prey taxa in order to indicate the prey diversity in relation to the overall diversity of marine mollusks; (4) to review the fossil record of naticid predation in the Mesozoic and Cenozoic; and (5) to integrate and synthesize the ecological and evolutionary aspects of naticid predation into a broader conceptual framework.

The diversity of molluscan shell boring predators is briefly reviewed, in order to be able to distinguish amongst the traces of predation left by the various taxonomic groups of predators. Based on this review, it is obvious that predation by boring in taxa other than the Naticidae and Muricidae is seldom studied.

Shell breaking predators, particularly crustaceans and fish, represent an entire field of study in themselves; valuable reviews are provided by Vermeij (1978, 1983c). Not mentioned herein are the diverse groups of symbiotic (non-predatory) epibionts and endolithic shell burrowers, such as certain cyanobacteria, fungi, algae, sponges, polychaetes, sipunculans, barnacles, lithophagid and pholadid bivalves, brachiopods and bryozoans (reviewed by Boekschoten, 1966, and the 1969 *American Zoologist* [vol. 9, #3] symposium on calcibiocavitology). Generally speaking, the latter "bore holes" can be recognized by their large number on a single shell, the lack of complete penetration, and their obvious burrowing aspect. An exception is the pedicle attachment scar of brachiopods, which may show complete penetration in the host shell (often another brachiopod); these scars or holes (common in the Paleozoic) could be confused with those of other, unknown, Paleozoic borers.

Within the Prosobranchia, there are two major groups of shell boring (or drilling) predators, the Naticidae (Mesogastropoda) and the Muricidae (Neogastropoda). I have summarized only a small part of the extensive research on muricid predation, and have limited it to the principal means of distinguishing their predation from naticid predation. A comprehensive review of muricid predation will be most useful but remains to be written.

An heuristic definition of gastropod boreholes was provided by Carriker & Yochelson (1968: 2) as "an excavation of characteristic size and form drilled by a predatory snail in the calcareous exoskeleton of a prey organism by means of chemical weakening and radular abrasion of the prey shell for the purposes of obtaining food." Refinements of this definition were provided by Chatterton & Whitehead (1987: 68). Specifically, naticid boreholes are parabolic holes (straight or oblique), formally referred to as a "truncated spherical paraboloid"; the borehole is countersunk (i.e., the enlarged outer margin is beveled or tapered, forming a chamfer) (Fig. 1), and incomplete naticid boreholes are characterized by a prominent central boss (rounded elevation) on the bottom surface (Fig. 2).

The Muricoidea (Neogastropoda) is a diverse group containing a variety of eclectic predators, including shell borers, carrion feeders, and other specialized predators, as well as several herbivores. The majority of muricids are shell borers and are distinguished by the presence of the accessory boring organ (ABO) in the sole of the foot. The muricid borehole is cylindrical, with nearly straight edges (Fig. 3); the naticid borehole, in contrast, has a more parabolic form and beveled edges. Much of the research carried out on the oyster drill, *Urosalpinx cinerea,* and other shellish pests by Carriker, along with research on other muricoideans by Taylor, has greatly added to our knowledge of the feeding biology of this superfamily (Carriker, 1981; Taylor et al., 1980).

The Nassariidae, or mudsnails, are carnivorous or scavenging members of the Neogastropoda. Fischer (1962a: 75) and Reyment (1966: 34) stated in passing that nassariids are shell borers. Subsequently, Ilina (1987: 23) also mentioned that they probably are shell borers. This appears to be mistaken, as no documentation has ever been provided for boring by mudsnails. Similarly, Stevanovic (1950) thought that the boreholes in mollusks from the Serbian Upper Miocene were caused by the hydrobiid gastropod *Sandria* [= *Pseudamnicola*] *atava;* Ilina (1987: 25) rejected this conclusion and attributed the boreholes to the naticid *Euspira helicina.*

The Cassidae (Tonnoidea, Mesogastropoda) are important predators of tropical echinoids, using sulfuric acid from their proboscis gland along with the radula to penetrate the echinoid test (by cutting out a disc, rather than drilling a hole) (Fig. 4). Hughes & Hughes (1981) provided a comprehensive review of the biology and ecology of cassid predation, and pointed out that other tonnoideans which feed on mollusks do so without boring (i.e., by penetrating between the gastropod operculum and shell, or between the valves of a clam). The numerous unique aspects of cassid predation clearly suggest an independent origin from that of naticids or muricids. Tertiary echinoids with cassid holes were documented by Sohl (1969: figs. 7–8) and Beu et al. (1972).

The Capulidae (Mesogastropoda) are specialized ectoparasitic symbionts of mollusks and echinoderms. They are known to drill holes into the shell of their mollusk host for the purpose of obtaining small amounts of fluids from the host's feeding current for nutrition. Matsukuma (1978) reviewed shell boring by capulids and recorded several fossil records of capulid boreholes: these are sharp-sided cylindrical holes, similar to those produced by muricids. However, capulid

boreholes can be recognized by the surrounding attachment scar on the host shell, where the edge of the capulid shell had slightly worn away the host shell (Figs. 5, 6).

In the Opisthobranchia, the nudibranch *Okadaia elegans* (Vayssiereidae) is known to drill holes into the calcareous tubes of serpulid and spirorbid polychaete annelids (Young, 1969). These minute bore holes (Figs. 7, 8) are similar in shape to those of muricids; however, muricids are not known to prey on these polychaetes, whereas *Okadaia* does not feed on mollusks.

In the Pulmonata, the terrestrial *Aegopinella* (Zonitidae) are known as shell-boring predators of other gastropods. Mordan (1977: 65) described predation by *A. nitidula,* in which prey snails (typically other zonitids) are first attacked through the aperture (followed by consumption of the head-foot); subsequently, a quite irregular hole on the umbilical surface of the last whorl is bored (Fig. 11), allowing the predator access to the rest of the prey flesh. Pulmonate shell boring may have evolved from simple shell "radulation," or the scraping of the outer surface of prey shells (Mordan, 1977: 70–1).

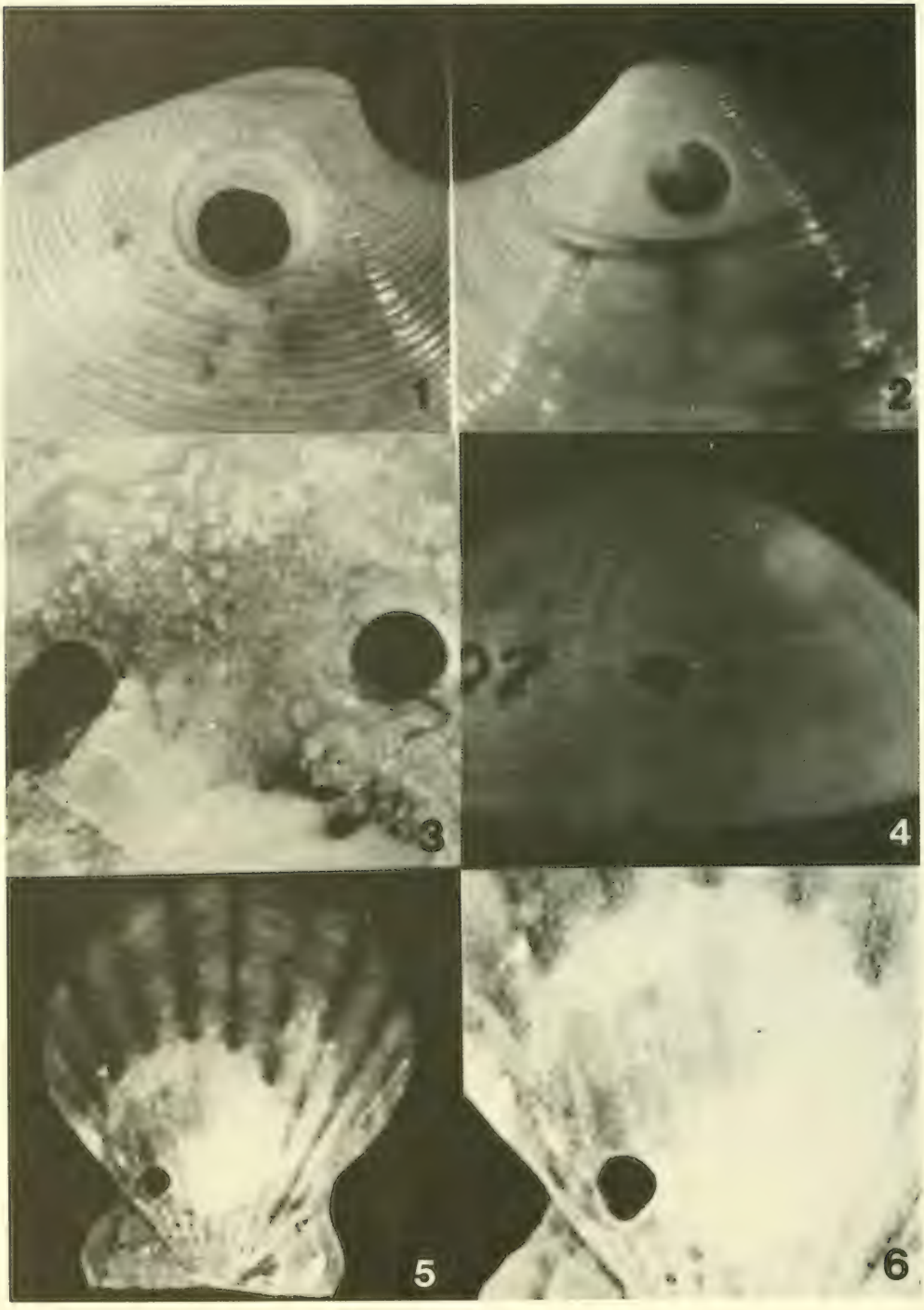
In the Cephalopoda, the octopuses are shell boring predators of a variety of marine shelled mollusks (Ambrose, 1986; Nixon & Maconnachie, 1988). Octopus boreholes can be recognized by their distinctly irregular or oval (but not circular) outline and their extremely small inner borehole diameter, in contrast to the large outer borehole diameter (Ambrose et al., 1988) (Fig. 9). Furthermore, the purpose of the hole is solely for the injection of venom to relax or kill the prey, which is then extracted through the aperture or valve opening. One problem with the analysis of octopus predation is that octopuses frequently break open the shell or otherwise capture the prey without drilling the shell (Ambrose, 1986: table 1). Hence, octopus boreholes represent only part of their trophic activities. Probable octopus boreholes from the Pliocene were reported by Robba & Ostinelli (1975: 338–344).

An unusual polyclad turbellarian flatworm, *Pseudstylochus ostreophagus,* is known to bore a hole in the shell of juvenile oysters (spat), effecting separation (or relaxation) of the prey adductor muscle, which causes the shell valves to gape, facilitating entry of the predator between the valves leading to prey consumption. The irregular oval holes are quite small (typically 150 × 190 μm); further details are provided by Woelke (1957). Many polyclads are known predators of mollusks, but shell boring has not been shown for other species (Galleni et al., 1980: table 1).

Nematode worms are known to prey upon the microscopic Foraminifera (Granuloreticulosa), boring one or more holes in the test, entering the chamber, and slowly consuming the prey. In the past, such holes were thought to be produced by juvenile gastropods (Livan, 1937: 149; Saïdova & Beklemishev, 1953; but see Fischer, 1962a: 70–1); however, their size (less than 60 μm in diameter) is smaller than those produced by newly hatched predatory gastropods (boreholes 100–160 μm in diameter). Sliter (1971) found that nematodes were responsible for this predation, and illustrated the various borehole morphologies (irregular oval to bevelled round). Subsequently, Arnold et al. (1985) described even larger boreholes (10–125 μm in diameter) in Foraminifera from the Galápagos hydrothermal vent mounds, and concluded that naticid gastropods were probably responsible (despite the fact that naticids are not known from such habitats). These are also likely to be the product of nematodes.

Decapod crustacean predation on mollusks is well known, and typically takes the form of shell breaking or cracking followed by extraction of the prey. Occasionally, the prey is able to escape and repair the broken shell, leaving diagnostic shell repair scars (Fig. 10) as a sign of unsuccessful predation (Schäfer, 1972: 408–411; Vale & Rex, 1988). Usually, the shell is fragmented; in a few cases, the predator may only effect a smaller, very irregular hole in the otherwise intact prey shell. Papp et al. (1947), provided an extensive discussion of crab predation; subsequent authors have documented the presence of shell fragments or subsequent shell repair attributable to predation attempts (successful and unsuccessful, respectively) by crabs and other decapods. However, because of fragmentation, one cannot account for all the remains of such predation. Shell fragmentation may also occur because of wave action; Cadée (1968: 87–88) noted that this is usually accompanied by signs of abrasion and fragmentation in subtidal shells is probably restricted to predation.

A most novel recent discovery is that of Norton (1988) who documented holes made in gastropod shells by a marine cottid fish, *Asemichthys taylori.* This species has a special set of vomeral teeth that are used to punch a hole or series of holes in the prey



FIGS. 1–6.

shell (Fig. 12). The holes (which are not truly "bored") allow the entry of digestive enzymes while the shell is in the digestive tract of the fish. Shells which are unpunched generally pass through undigested and emerge alive (except, of course, for limpets which have an exposed ventral aspect). Similar rows of punctures in Paleozoic brachiopods, conulariids and nautiloids were attributed to shark predation (Mapes et al., 1989, and references therein).

Shell boring or burrowing is little known in the freshwater environment, with a few exceptions, such as the endolithic burrowing polychaete *Caobangia* (Jones, 1969). Recently, the Soviet paleontologist Ilina (1987) found shells of *Unio* and *Viviparus* (freshwater mollusks) with regular, round boreholes, one to four per shell, with an outer diameter up to 2 mm and an inner diameter from 1.0 to 1.5 mm. Ilina (1987: 29) suggested that these holes were made by ". . . ants that for reasons not yet known use their formic acid to etch perforations in the shells of molluscs . . ."; E. O. Wilson (*in litt.*) stated that "I don't know of any documented cases of ants boring mollusk shells, and I doubt very much if they do . . . it's hard to imagine their cutting through a clam shell even with the aid of formic acid." In any case, since ants are terrestrial, it seems unlikely that these freshwater mollusks were drilled and consumed *in situ;* it is more likely that empty shells were washed ashore and (post-mortem) excavated by some other organism, perhaps for a refuge. Further study is clearly indicated.

Finally, there is an extensive and scattered literature on shell borings in Paleozoic fossils. While providing lengthy descriptions of the bore holes and of the prey organisms, these studies generally have not elucidated the nature of the predator (known predatory gastropods did not evolve until the Mesozoic). Carriker & Yochelson (1968) suggested that these holes were made by soft-bodied, sessile, non-predatory organisms of unknown taxonomic affinity (this hypothesis is essentially non-testable!); Sohl (1969: 728–9) further discussed this problem. More recently, Smith et al. (1985) and Chatterton & Whitehead (1987) reviewed the Paleozoic boreholes and suggested that they were, indeed, predatory in origin although the identity of the predator remains unknown. Vermeij (1987: 176–7) hypothesized that ectoparasitic platyceratid gastropods (ecologically analogous to capulids) were the Paleozoic borers.

The remainder of this paper is restricted to analysis of predation by naticids. The preceding review of the diversity of shell borers indicates that predation by boring has evolved independently in a number of taxa; any similarities are undoubtedly cases of convergent evolution. The following section, on the proximate mechanisms, demonstrates the numerous unique (derived) aspects of naticid predation, and should be compared with what is known for other shell-boring taxa.

MECHANISMS OF NATICID PREDATION

For a detailed review and critique of the previous morphological studies on naticid feeding mechanisms, see Carriker (1981). Essentially, early controversies concerning naticid boring involved the means of boring: i.e., was it solely by mechanical means (radular rasping of the prey shell) or did it also involve chemical action (acid secretion). It was the careful work of Carriker and colleagues (Carriker, 1981) which demonstrated that the latter hypothesis is the case for naticids and muricids.

FIG. 1. Naticid bore hole (complete) in valve of *Dosinia discus* (Reeve, 1850) [Cocoa Beach, Florida; MCZ 145801]. Shell dimensions 52.7 mm × 48.8 mm; outer bore hole diameter 5.2 mm; inner borehole diameter 2.8 mm.

FIG. 2. Naticid bore hole (incomplete) in valve of *Dosinia concentrica* (Born, 1778) [Punta Guanajibo, Puerto Rico; MCZ 212607]. Shell dimensions 55.7 mm × 52.3 mm; outer bore hole diameter 2.7 mm.

FIG. 3. Muricid bore holes [presumably by *Urosalpinx* or *Eupleura*] in adjacent valves of *Crassostrea virginica* (Gmelin, 1791) [Stono River, South Carolina; MCZ 226338]. Shell lengths 86 mm and 65 mm; outer bore hole diameter 2.5 mm; inner bore hole diameter 2.3 mm.

FIG. 4. Cassid bore hole in *Cassidulus pacificus* (A. Agassiz, 1863) [Punta Pescadero, Baja California Sur, Mexico; USNM 32907]. Test dimensions 34.9 mm × 28.9 mm, height 16.1 mm; bore hole diameter 2.1 mm.

FIG. 5, 6. *Capulus danieli* (Crosse, 1858) bore hole in valve of *Comptopallium vexillum* (Reeve, 1853) [Noumea, New Caledonia; ANSP 272383]. Scallop shell dimensions 32.5 mm × 29.5 mm; outer bore hole diameter 1.75 mm; capulid shell dimensions 4.9 mm × 15.0 mm.

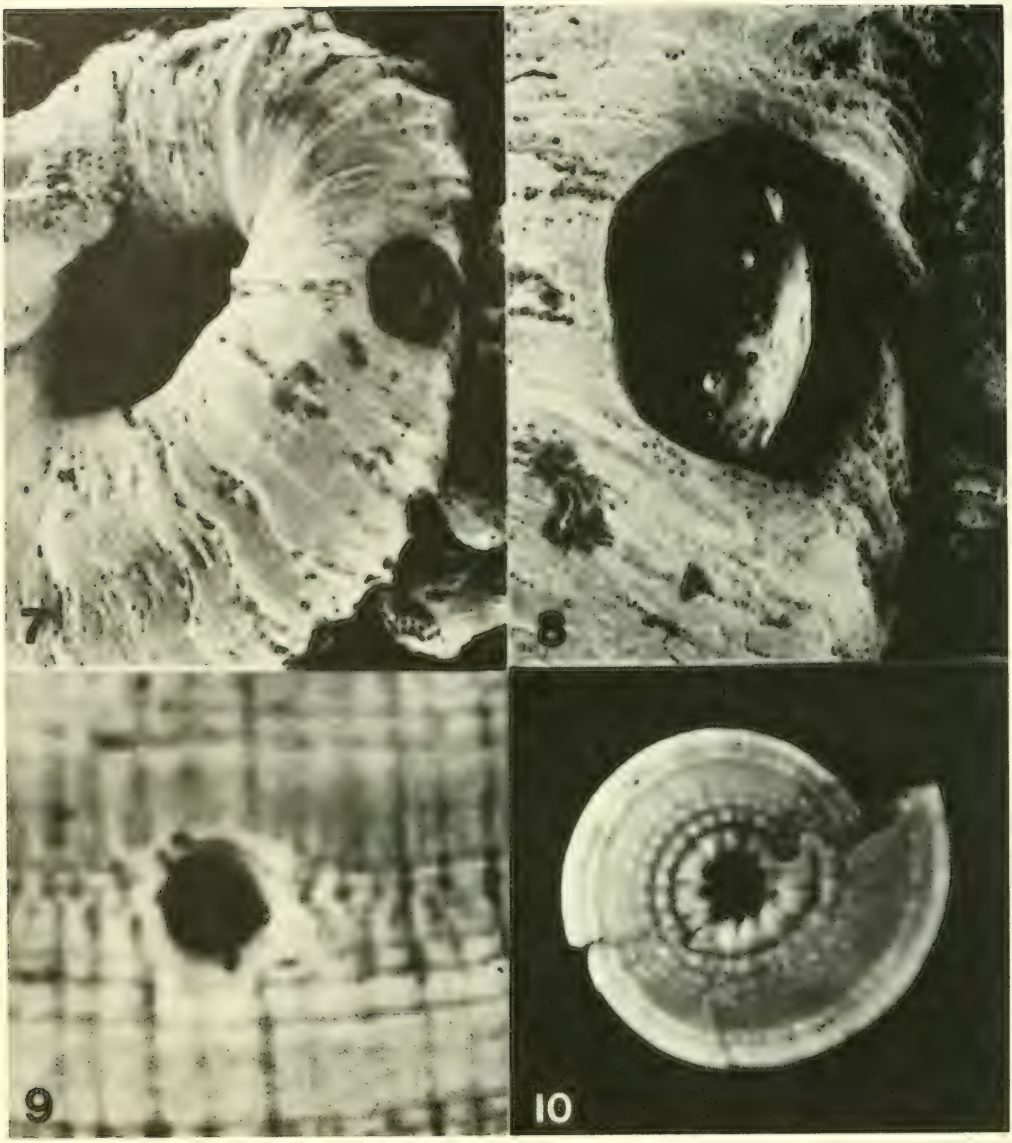


FIG. 7, 8. *Okadaia elegans* Baba, 1930 [Nudibranchia] bore hole in tube of spirorbid polychaete [Oahu, Hawaii]. Bore hole diameter ca. 115 μm; worm tube diameter at bore hole ca. 300 μm. SEM photographs courtesy J. D. Taylor. [Magnifications; Figure 7 at 110×; Figure 8 at 350×].
FIG. 9. *Octopus bimaculatus* Verrill, 1883 bore hole in *Ventricolaria fordi* (Yates, 1890) [Anacapa Island, off Ventura, California; MCZ 298337]. Shell dimensions 33.7 mm × 31.2 mm; outer bore hole diameter 2.2 mm, inner bore hole diameter 0.6 mm. Specimen courtesy R. F. Ambrose.
FIG. 10. Unsuccessful crustacean predation: shell repair scars in *Architectonica nobilis* Röding, 1798 [Puerto Plata, Dominican Republic; MCZ 106825]. Shell dimensions 8.8 mm × 17.5 mm.

A fundamental and little studied problem concerns the methods by which naticids detect their prey. For many predatory gastropods, chemoreception (detection of prey "chemical odors" by the osphradium) is typically the initial mechanism for determining the presence and direction of potential prey (Kohn, 1961; Croll, 1983). With infaunal nati-

cids, the sediment habitat not only decreases the diffusion rate of chemical substances, but also may perturb its directionality; hence naticids may forage with the siphon extending to the surface where diffusion is more direct and rapid. Kitching & Pearson (1981) found that the Australian "*Polinices*" [= *Conuber*] *incei* responded to artificial sound waves directed through the substrate, which presumably mimicked the vibration of burrowing prey. Mechanoreception may well serve as an additional prey detection mechanism for the naticids.

Regardless of how the prey are initially detected, one can analyze the behavioral perspective: namely, recognition of suitable prey serves as a releasing mechanism which elicits a stereotyped sequence of behaviors [= fixed action patterns] (Ansell, 1960). Naticids have been little studied with respect to classical ethological principles, probably because most activity occurs while they are buried.

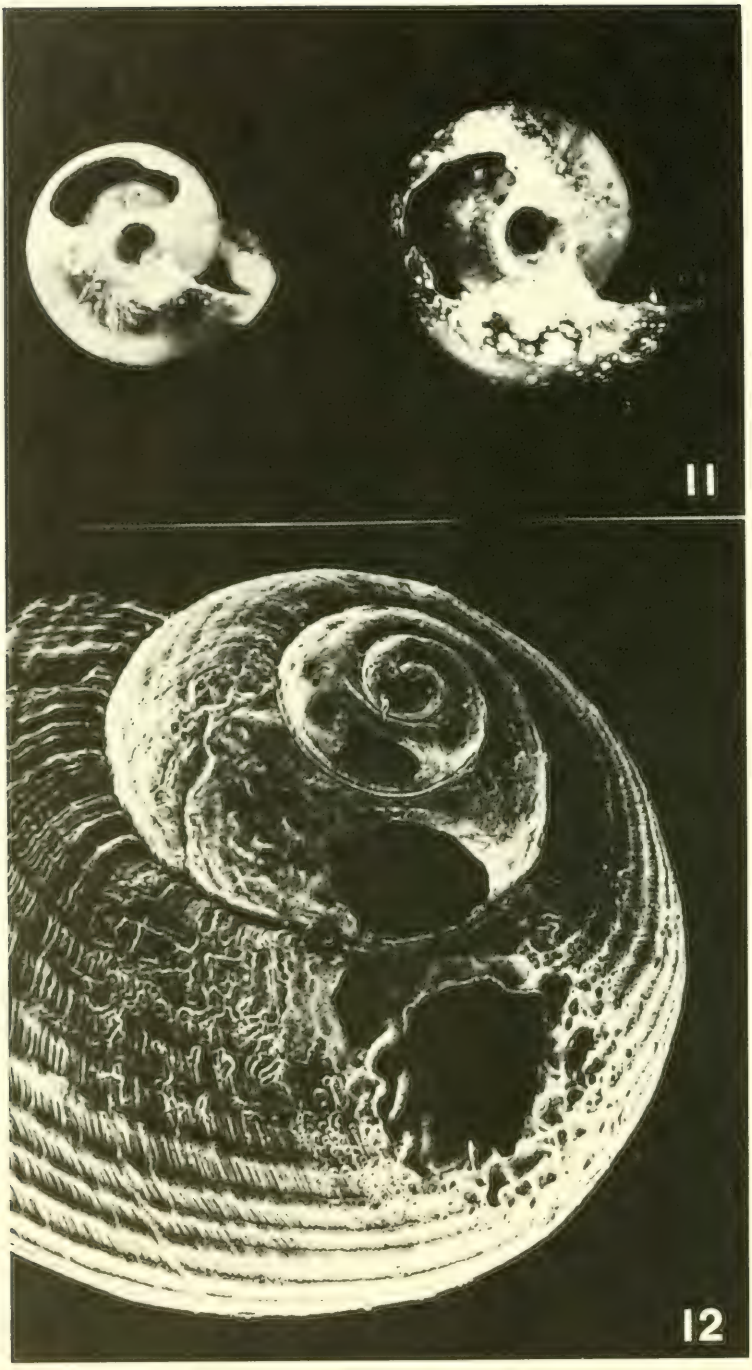
Edwards (1969), Schäfer (1972: 242–3), Stenzler & Atema (1977) and Hughes (1985) discussed the sequence of prey capture events: the prey is detected, evaluated, seized, covered and immobilized with copious pedal mucus, wrapped in the dilated foot of the naticid, dragged for some distance, and finally carried deep into the sand for commencement of boring.

The mechanism of naticid boring involves a complex sequence of events. There is alternate application of the predator's radula and accessory boring organ (ABO) to the bore hole site on the prey shell. The ABO is found on the ventral surface of the proboscis in naticids (but in the sole of the muricid foot); the two ABO types represent a case of convergent evolution and no homologues in other taxa are known. The ABO histology was described by Bernard & Bagshaw (1969), who characterized it as a "fungiform papilla" containing numerous epithelial secretory cells. The biochemistry of ABO secretions was discussed by Carriker & Williams (1978). The ABO secretes a complex mixture of presumed enzymes, chelators, and inorganic acid (HCl) in a saline, hypertonic solution which effects dissolution of the prey shell layers (both calcareous and organic matrix). During boring, the proboscis becomes engorged, everting both the radula and the ABO. The radula is protracted and scrapes at the surface of the bore hole. The proboscis is rotated in 90° sectors and the scraping is from the outer edge to the center, resulting in the diagnostic boss in the center of incomplete bore holes (Ziegelmeier, 1954: fig. 7; Carriker, 1981: 410). The prey shell fragments are ingested but subsequently excreted without digestion (Carriker, 1981: 411). The prey tissue is ingested by the proboscis through the borehole; Reid & Gustafson (1989) determined that external digestion does not occur.

Most studies have documented that naticids capture and consume their prey entirely within the sediment. Previous reports of naticid predation on the sediment surface were usually a result of aquaria studies wherein the sediment depth was too shallow and consequently abnormal behavior patterns were manifested. Recently, field observations of *Natica gualteriana* from the Philippines (Savazzi & Reyment, 1989) have documented that this species was capable of searching for and capturing its prey on sand bars at low tide (i.e., while exposed to the air). Further study is needed to ascertain whether other naticid species can also feed on the sediment surface (exposed or subtidally). As such, this would result in greater competitive interactions between those naticids and the epifaunal muricids.

For temperate and boreal naticids, the water temperature can determine the active periods of feeding. Hanks (1953) showed that the northwest Atlantic *Neverita duplicata* and *Euspira heros* had a marked temperature-dependence, with no feeding at temperatures below 5°C and 2°C, respectively. Similarly, salinity (brackish or estuarine waters) also affects feeding rates; these two naticid species did not feed at artificial salinities below 10‰ (normal seawater about 35‰).

For the calculation of energy budgets, the rates of shell boring and of prey tissue ingestion must be determined. Determining the time for infaunal prey capture and subjugation would be extremely difficult and yields variable results (here, especially, aquaria studies would be of little value). In general, the relative sizes of predator and prey (both dimensional and shell thickness) must be taken into account; there will undoubtedly be great interspecific variation in these rates. Ziegelmeier (1954) found a boring rate of 0.6 mm/day, or 0.025 mm/hour by *Euspira nitida.* Similarly, Kitchell et al. (1981: fig. 2) observed that in *Neverita duplicata* preying on various bivalves, the boring rate was a nearly constant 0.0223 mm/hour, regardless of prey species, predator size, or elapsed time. Bayliss (1986) noted that for *Mya* and *Spisula* prey, *Euspira*



FIGS. 11, 12.

alderi bored at an average rate of 0.0097 mm per hour; the prey tissue was consumed in 19.5 hours (*M. arenaria*), 21.5 hours (*S. subtruncata*), or 60 hours (*S. elliptica*).

For the analysis of naticid boring predation, especially in fossils, the primary source of data for the predator is the size of the borehole. Kitchell et al. (1981: 539, fig. 4) proved that the borehole diameter is constant for a given predator size, regardless of the prey size. Most studies have used the inner borehole diameter as the basis for analysis, as this represents the size of the predator's proboscis. Wiltse (1980a: 189, fig. 1) used the diameter ". . . at the junction of the prismatic and nacreous shell layers"; this does not facilitate comparisons with other prey taxa (given that the depth of this junction is not constant for all taxa). Usually, the outer borehole diameter is also directly proportional to the predator size; but due to the chamfered borehole edge, it is more difficult to measure. However, for corbulid bivalve prey, there is an exception in that the outer borehole is disproportionately much larger than the inner borehole; this reflects the conchiolin layer in the prey shell (De Cauwer, 1985). Arua & Hoque (1989b), based solely on analysis of outer borehole sizes, concluded that the opening was more oval than circular; regrettably, their data on inner borehole sizes was not presented.

It is unfortunate that a recent paleoecological study (Arua & Hoque, 1989a, 1989c) seems to have confused several muricid boreholes with those of naticids, and *vice versa.* Their "hole types" A, B and D were claimed to be muricid; C, E and F as naticid. The authors had stated that naticid boreholes are countersunk, with tapering sides, and incomplete ones have a central boss; yet, they claimed that their "hole type E," which lacks a boss and has vertical sides, was naticid! My re-analysis of their descriptions leads to the conclusion that their "hole types" E and (maybe) A are muricid; whereas B, C, D, and F are naticid. This confusion undoubtedly has arisen in other studies, and should be considered when interpreting community-level analyses (because the variety of observed boreholes are rarely illustrated therein).

A more general aspect of naticid predation is the suitability of the substrate for naticid locomotion. It is well known that naticids are restricted to infaunal sedimentary habitats; it is less appreciated that extremely fine or smooth grained substrates (silt-mud-clay) are precluded because they are too tightly packed to burrow through readily, in contrast to coarser sand substrates (Yochelson et al., 1983: 12; Maxwell, 1988: 31).

Vermeij (1980) and Ansell & Morton (1987) discovered that the tropical *Polinices "tumidus" [= mammilla],* after wrapping its prey in a mucus coat within the foot, retained the prey until suffocation and gaping occurred. Subsequently, the prey was consumed without boring. Ansell & Morton (1987: 117) suggested that a "narcotizing toxin" may play a role in causing prey gaping, such as by thaidine gastropods preying on barnacles. This was questioned by Reid & Gustafson (1989), who determined that prey suffocation alone caused shell gaping. The ecological and evolutionary implications of this non-boring predation will be discussed below.

A preposterous view of the evolution of naticid feeding mechanisms was advanced by Stafford (1988), who claimed that naticids originated at Ediacaran-Cambrian times (570 million years ago), as swimming filter feeders, and gradually shifted to benthic feeding entailing eversion of the stomach (as in asteroids) to effect external digestion of the prey.

To summarize the proximate mechanisms of naticid shell boring: (a) Prey are detected by chemoreception using the osphradium, though mechanoreception may also play a role. (b) Suitable prey are seized, covered with pedal mucus and wrapped in the foot. (c) The proboscoideal acid-enzyme secretory accessory boring organ (ABO) together with the radula is used to excavate a countersunk (bevelled) hole in the prey shell, and the prey tissues are extracted through this borehole. The size of the borehole (inner diameter) is

FIG. 11. *Aegopinella nitidula* (Draparnaud, 1805) [Zonitidae] bore holes in (left) *A. pura* (Alder, 1830) [bore hole 1.5 mm × 0.7 mm] and (right) *A. nitidula* [bore hole 1.6 mm × 1.0 mm] [Monks Wood, England]. Photographic negative courtesy P. B. Mordan; original in the *Biological Journal of the Linnean Society* (1977), 9: 65, plate 1A. [Copyright 1977 by The Linnean Society of London].

FIG. 12. *Asemichthys taylori* Gilbert, 1912 [Pisces], punched holes in *Margarita* sp. [San Juan Island, Washington]. Shell width ca. 2 mm. Maximum hole diameters: 165 μm; 350 μm; 380 μm. SEM negative courtesy S. F. Norton; original in *Science* (1988), 241(1): cover. [Copyright 1988 by the AAAS].

positively correlated with predator size. (d) Some tropical Indo-Pacific naticids are able to immobilize their bivalve prey until shell gaping occurs, allowing direct access to the prey tissues; thus, no borehole need be made.

THE PREY OF NATICIDS

The Appendix tabulates the known prey of naticid gastropods (fossil and Recent). The genera are arranged alphabetically by family; the reference is given in brackets following the species name [*n.b.* this is not the author of the taxon!]; some species were reported in several studies but only one such is indicated herein. This compilation includes an unpublished data set on Fijian Pleistocene mollusks collected by A. J. Kohn. I have corrected for obvious changes in generic nomenclature; species names were not given for several reports, as indicated by an asterisk. Many records of naticid predation are purely incidental or even parenthetical (e.g., "by the way, some of the shells of X were bored . . ."), which does not facilitate critical comparative analyses.

Generally, the records herein are limited to ecological or paleoecological studies emphasizing predation; it is too time-consuming to search through the general systematic and faunistic literature for scattered records of naticid predation (which are usually not thoroughly documented in such papers). Needless to say, aquarium studies of naticid feeding should be based on prey found in the same habitat as naticids. Unfortunately, some papers (Hayasaka, 1933; Fischer, 1966; Sander & Lalli, 1982; and De Cauwer, 1985) provided lists of taxa with gastropod boreholes, but without specifying naticid or muricid boreholes. Nonetheless, based on the available data, it appears that naticids prey on the majority of benthic, infaunal shelled mollusks.

A. Class Gastropoda

Since most archaeogastropods (e.g. Pleurotomaroidea, Fissurelloidea and Patelloidea) are rocky-habitat dwellers, they are not subject to naticid predation. Beebe (1932: 212, fig.) made the unusual statement that, in Bermuda, *Natica canrena* preyed upon the rocky intertidal limpet *Fissurella barbadensis,* leaving a diagnostic borehole in the limpet shell. My subsequent re-analysis of this situation reveals that Beebe had confounded the excurrent slit or foramen ("keyhole") of these limpets with naticid boreholes and erroneously assumed that naticid predation was responsible for the limpet keyholes!

Many of the soft-substrate taxa in the Mesogastropoda are subject to naticid predation. Not included herein are the extensive reports of confamilial predation on naticids themselves (sometimes referred to as "cannibalism") (Kabat & Kohn, 1986). Reports of naticid boreholes in *Xenophora* [Xenophoridae] and *Lamellaria* [Lamellariidae] by Adegoke & Tevesz (1974) are questionable, given the epifaunal habitat of these taxa. While it may appear that neogastropod genera are more frequent in the list, this could be a taxonomic artifact of generic lumping *vs.* splitting.

Most of the neogastropods are active predators themselves; the epifaunal and rocky-habitat species generally escape naticid predation. It is entirely possible that some of these records, especially of Muricidae, are of misidentified muricid boreholes.

B. Class Bivalvia

Most infaunal bivalves are subject to naticid predation. In particular, the venerids, tellinids, and lucinids (the last two often with relatively thin or little-sculptured shells) are frequent victims. The infaunal Solemyidae live in reducing sediments where naticids are not found. Bivalve taxa that are in rocky habitats, epifaunal byssate or cemented (Dimyoidea, Plicatuloidea, Anomioidea, Chamoidea, Leptonoidea and Cyamioidea) effectively escape naticid predation; the few cases of naticid boreholes in the Pterioidea, Limoidea, Ostreoidea and Pectinoidea are unusual exceptions. Those that are rock or wood burrowers (Lithophagidae, Gastrochaenoidea and Pholadoidea) are also inaccessible to naticids. The Pinnoidea and Tridacnoidea have encrusted and sculptured shells; the Glossoidea, Clavagelloidea and Pholadomyoidea are too rare to have been reported in this context.

C. Class Scaphopoda

A thorough review of naticid predation on scaphopods by Yochelson et al. (1983) found that scaphopods were the occasional prey of naticids from the Late Cretaceous to the Recent. Usually, there is moderate stereotypy of borehole siting, with most being laterodorsal

and about midway along the shell axis. It was found that coarse-ribbed scaphopods (which live in coarse sediments) were much more likely to be bored; those with smooth (or no) ribs, living in fine sediments, escaped naticid predation by virtue of their habitat which is inimical to active naticid burrowing (Yochelson et al., 1983).

D. Other Mollusk classes

Naticid predation has not been recorded on the Aplacophora, Monoplacophora, Polyplacophora, or the Cephalopoda. The shell-less Aplacophora would not leave traces of naticid predation. The Monoplacophora (clay-mud habitats) and the Polyplacophora (rocky habitats) are usually not encountered by naticids. The epifaunal and pelagic cephalopods, predators themselves, are unlikely to be captured by the slower naticids.

E. Polychaetes

Paine (1963: 69) found one specimen of *Neverita duplicata* from Florida that fed on the polychaete *Owenia fusiformis;* this is the only known record of naticids preying on annelids. It is not clear whether this represents normal behavior or a single, aberrant event.

F. Crustaceans

Significantly, Gonor (1965: 229) found that naticids would not feed on hermit crab occupied shells. This is of importance as it indicates that not only can naticids recognize such "prey" (of course, the active epibenthal hermit crabs may be beyond the range of naticids), but also that boreholes found in shells with recognizable signs of hermit crab occupancy (worn lips, unrepaired damage, epibionts) were the cause of the gastropod mortality, freeing the shell for hermit crab use.

Ostracods represent a potentially important prey source for juvenile naticids. Livan (1937) and Reyment (1966, 1967) attributed numerous boreholes in ostracods to predatory gastropods. Maddocks (1988) reviewed the various types of boreholes in ostracods (Cretaceous to Holocene of Texas) and concluded that juvenile naticids were responsible for most. However, because of the thin ostracod test, there is a wide variety of "holes" and it is difficult to attribute them to known causes (Reyment et al., 1987).

G. Brachiopods

Most articulate brachiopods live in rocky habitats (rock walls or boulder grounds), thereby escaping naticid predation because of habitat incompatibility. However, Witman & Cooper (1983: 71, figs. 8c–d) reported "naticid" boreholes in values of *Terebratulina septentrionalis* from the Gulf of Maine, which they attributed to either *Natica clausa* or *N. pusilla.* The illustrated boreholes resemble those of muricids (albeit with slightly sloping sides); further study is recommended.

H. Pisces

Perry (1940: 116) reported that the tropical western Atlantic *Naticarius canrena* "preys on bivalves and has been seen to devour dead fish." This remarkable observation, if true, represents the only known record of piscivory in the Naticidae. However, if it is based on aquarium observations, then it may simply reflect aberrant behavior by starved individuals (see the next paragraph).

I. Scavenging

Most studies have shown that naticids will only feed on fresh prey; carrion-feeding (as in the neogastropod Buccinidae and Nassariidae) is not manifested. A few studies (typically in aquaria) have shown that gaping (dying) bivalve prey may be consumed directly without boring (Ansell & Morton, 1985). It is not clear if this laboratory behavior is also shown in the field.

J. Egg Capsules

Several authors have reported "naticid" boreholes in the egg capsules of various deep-sea organisms. These observations include Thorson (1935: 12–13, figs. 4a–c) in egg capsules of the neogastropod buccinid *Sipho* [= *Colus*] *curtus* from East Greenland; Jensen (1951, fig. 1) in egg capsules of the ray (*Raia*) from Davis Strait (the boreholes ranged from 0.75 to 2.5 mm in diameter; a few capsules had multiple boreholes); and Ansell (1961) in egg capsules of the dogfish (*Scyliorhinus canicula*) with countersunk boreholes. It must be emphasized that naticids were not observed boring these holes; these authors had merely conjectured that naticids were the most likely causative agents. These boreholes were clearly effected from the out-

side (i.e., they are not the hatching-out holes of the juveniles within). First, for the buccinid egg capsules, it is probable that a muricid bored the holes, as is known for some other muricids (Abe, 1985). Second, for the elasmobranch egg cases, a more likely predator is the unusual deep-sea archaeogastropod family Choristellidae, which are typically associated with skate egg capsules upon which they feed (Hickman, 1983: 86).

The primary prey sources for naticids are infaunal gastropods and bivalves. The data [Appendix] document that 47 gastropod families (out of 129 shelled marine gastropod families) and 35 bivalve families (out of 109 marine bivalve families) are known to be subject to naticid predation. The major gastropod prey sources are the Turritellidae and Naticidae (Mesogastropoda) and the Turridae (Neogastropoda). The major bivalve prey sources are the Lucinidae, Tellinidae and Veneridae (Heterodonta).

FOSSIL RECORD OF NATICID PREDATION

This section tabulates the reports of fossil naticid predation and is arranged by geological time period. In general, only brief summaries are provided; discussion of any broader ecological aspects is deferred to the following section in combination with related conclusions from Recent studies. It must be emphasized that it is difficult to track down all the paleoecological studies, especially those that are "buried" within lengthy systematic monographs (no attempt has been made to search through the latter). Indeed, it seems better that extensive paleoecological researches should be published separately from narrower taxonomic studies, in order to bring them to wider notice.

A. Triassic

Fürsich & Wendt (1977: 299) mentioned "naticid" boreholes from the Cassian Formation of northern Italy (Tirol). Subsequently, Fürsich & Jablonski (1984) illustrated the boreholes, showing the diagnostic countersunk appearance of incomplete boreholes, and discussed the implications thereof. The bivalve prey were *Cassianella* and *Palaeonucula;* the gastropod predators were referred to several species of the naticid genus "*Ampullina.*" Newton (1983; Newton et al., 1987: fig. 25.2) independently documented "naticid" boreholes in the epibyssate limid *Mysidioptera* from the Wallowa Terrane of the Hells Canyon (Oregon-Idaho); this suggests that the Triassic borers were somewhat widespread, before becoming extinct. However, the taxonomy of Triassic "naticids" remains a morass, and their familial assignment is still uncertain. Further discussion of the evolutionary consequences of Triassic boring predation is deferred to the next section. Indeed, if these countersunk Triassic boreholes are **not** those of naticids, then it remains uncertain whether all the younger occurrences of countersunk boreholes are correctly attributed to naticid predation.

Sohl (1969: 726) expressed some doubt as to whether the Triassic forms were true naticids; in any event, his spindle diagram of naticid clade diversity (his fig. 1) clearly shows that from the Triassic to the mid-Cretaceous, there are never more than five genera in any epoch; naticid diversification did not commence until the Upper Cretaceous, with the evolution of the boring habit. Bandel (1988: 270) claimed that "Thus Triassic 'naticids,' to a large extent, are neritoideans, some belong to other groups, but none appear to be naticids"; this needs further documentation.

B. Jurassic

Sohl (1969: 729) searched through various paleontological monographs and collections of Jurassic mollusks and found no signs of molluscan boreholes. Fürsich & Jablonski (1984) also concluded that there were no gastropod borers in the Jurassic.

C. Cretaceous

Fischer (1962a) reviewed some reports of Cretaceous boreholes and attributed most to naticids, as there were relatively few muricids at that time. Subsequently, Sohl (1969: 731) more carefully analyzed Cretaceous boreholes and found a few from the Cenomanian (100 myr) and a much greater abundance from the Campanian (75 myr). The Ripley Formation (Campanian) was studied in greater detail by Vermeij & Dudley (1982) who also found extensive shell repair and a size refuge from boring predation. The oldest Cretaceous records were shifted further back by Taylor et al. (1983) who documented naticid predation from the Blackdown Greensand of

England (Albian, 105 myr). They found that the vast majority (92%) of boreholes were naticid, with a nearly equal ratio of gastropod to bivalve prey (in contrast to the few muricid boreholes, found primarily on bivalve prey). The diversification of naticids (and other modern marine families) at this time represents the "Mesozoic marine revolution" of Vermeij (1977), and is discussed in the next section.

Vermeij & Dudley (1982) reported no predation on naticids in the Ripley Formation (Tennessee); subsequently, Kitchell et al. (1986: 293, fig. 1h) found a multiple-bored specimen of *Euspira rectilabrum,* from the same outcrops. This is the earliest record of confamilial naticid predation in the fossil record.

D. Paleocene

I have not found any paleoecological studies from the Paleocene reporting on naticid boreholes. Naticids were present then; future studies of these faunas would be most worthwhile.

E. Eocene

Fischer (1960, 1962a, 1963) reported on naticid predation in the Lutétien Stage of France and found that for the bivalve *Petunculus* [= *Glycymeris*], 4.6% of the specimens were bored, primarily the smaller ones. For the gastropod *Mesalia,* 70.9% were bored by naticids (of which only 7.7% were incomplete holes), and some had multiple complete or incomplete boreholes. For *Corbula* spp., there was a rather high rate of boring failure (to 26% of the specimens). This fauna was also analysed by Taylor (1970) who found numerous naticid and muricid boreholes and an overall confamilial naticid predation rate of 11.3%.

Siler (1965) briefly reported on the Gosport Formation of Texas and found both naticid and muricid boreholes on the bivalve *Lirodiscus tellinoides.* A more comprehensive study on the Stone City Formation of Texas (Stanton & Nelson, 1980; Stanton et al., 1981) recorded a naticid mortality rate of 15% and a crustacean mortality rate of 20% for molluscan prey. The latter studies entailed considerable efforts to reconstruct the food web and paleocommunity structure.

Several studies were carried out on the Ameki Formation of Nigeria by Adegoke & Tevesz (1974), Arua (1989) and Arua & Hoque (1987, 1989a, 1989c). They found that turrids and terebrids were the preferred gastropod prey; the latter authors also found extensive predation on bivalves. However, as discussed earlier, some of the boreholes seem to have been misidentified (vis á vis naticid *vs.* muricid) by Arua & Hoque. An analysis of bivalve prey (*Arcopsis* and *Limopsis*) from the Pallinup Siltstone in Western Australia found that 9.2% of the bivalves had gastropod boreholes, one fifth naticid and four fifths muricid (Darragh & Kendrick, 1980).

F. Oligocene

Klähn (1932) analyzed naticid predation on other naticids from the Sternberg Formation of Germany and found high predation rates from 53.3% (the second smallest prey size class) to 15%–26% (the other classes); the documentation provided does not facilitate further analysis.

G. Miocene

Hoffman et al. (1974) conducted an extensive study on the Korytnica clays of Poland and found a confamilial naticid predation rate of about 10%; unfortunately, their data (table 1) do not fully partition the boreholes by naticid or muricid sources. Subsequently, Hoffman (1976a) attributed most of the bivalve mortality to sedimentation, rather than predation; similarly, abiotic factors accounted for much of the gastropod mortality (Hoffman, 1976b). Other Miocene outcrops from Poland were studied by Hoffman & Szubzda (1976), primarily with respect to food webs and community structure. Kojumdjieva (1974) studied the Tortonian and Sarmatian outcrops of Bulgaria and found a variety of naticid and muricid prey taxa; very few unsuccessful or multiple boreholes were observed.

Thomas (1976) analyzed naticid predation on glycymerid bivalves from various Neogene (Miocene-Pliocene) outcrops in the eastern United States and concluded that predation rates in the Miocene were comparable to those on Recent glycymerids; however, the size-selectivity data seemed questionable. This research was reanalyzed by Kitchell et al. (1981: 545–548), who determined that the seemingly contradictory results of Thomas could be explained by the fact that there were actually two different naticid predators (of markedly different sizes) in the various fossil faunas; this meant that the observed "changes" in preda-

tion intensity or prey size were merely an artifact of which naticid predator was present.

A series of studies on the Chesapeake Group of Maryland was conducted by Kelley (1982a–1989b), with an emphasis on bivalve prey. Nearly three-fourths of the mortality could be attributed to naticid predation; for some prey there was an increase (over geological time) of prey size and shell thickness. This was hypothesized to be an evolutionary response to naticid predation. Dudley & Dudley (1980) made a briefer analysis of boring predation on three mollusk species from these outcrops, and observed a size refuge from predation for the two bivalves studied.

Colbath (1985) reported on the outcrops of the Astoria Formation of Oregon and noted extensive naticid predation, primarily of bivalves; other predation sources were not analyzed. The Wimer Formation of northern California was analyzed by Watkins (1974), who found low levels of naticid predation on several bivalves.

Maxwell provided a thorough systematic and paleoecological analysis of the Stillwater Mudstone of New Zealand and observed considerable naticid predation on various gastropods and bivalves. The data were used to reconstruct food webs (Maxwell, 1988: 34, fig. 3) as part of an overall trophic analysis which also considered non-fossilized aspects of the community. There was extensive confamilial naticid predation, especially of the smaller-sized species. This monograph is an excellent model of integrating systematics with paleocommunity reconstructions.

H. Pliocene

Boekschoten (1967) studied the fauna of the Tielrode Sands of Belgium and reported some confamilial naticid predation, although crustacean predation was a far more important source of mortality for the naticids. The Emporda of Spain was analyzed by Hoffman & Martinell (1984), who observed high selectivity in prey size and borehole site choices. Guerrero & Reyment (1988b) used multivariate analysis to differentiate between naticid and muricid boreholes in *Chlamys* from the Lower Pliocene near Malaga, Spain. Robba & Ostinelli (1975) analyzed gastropod, cephalopod and crustacean predation in the Albenga outcrops of Italy and noted that 13.9% of all specimens were bored, nearly all by naticids. Hingston (1985) reported on the Muddy Creek assemblage from Victoria, Australia, and determined that about 75% of the boreholes were naticid and the remainder muricid; edge drilling of bivalves was rare, and prey shell sculpture resulted in a greater frequency of unsuccessful boreholes.

I. Pleistocene

Kabat & Kohn (1986) analyzed predation on naticids from the Nakasi Beds of Fiji and observed rather high naticid predation rates on *Natica* spp., but considerably lower confamilal predation on species of *Polinices* and *Sinum*. Unsuccessful crustacean predation was quite common; successful crustacean predation probably accounted for a greater amount of mortality than did confamilial predation. Berg & Nishenko (1975) found that 26% of the shells of *Nassarius perpinguis* from the San Pedro deposits of California showed naticid boreholes; stereotypy of borehole siting was shown, although no data on predator or prey sizes were given. A much more detailed analysis of the nearly contemporaneous Puerto Libertad deposits of Sonora, Mexico, and a thorough trophic web reconstruction was conducted by Stump (1975: fig. 18).

J. Sub-Holocene

Yochelson et al. (1983) analyzed naticid predation on scaphopods from the elevated "mud lumps," or diapir structures from the Mississippi River delta (ca. 15,000 years old), and found (in two large samples) that almost 58% of *Dentalium laqueatum* had boreholes. They noted that other scaphopod assemblages (fossil and Recent) showed far fewer naticid boreholes (usually less than 10%); this assemblage undoubtedly reflected exceptional naticid feeding.

Since the end of the Early Cretaceous (Albian), naticid predation has been documented through Holocene faunas (except for the Paleocene), although probable naticids are known from the Jurassic. Potential "naticiform" boreholes from the Triassic are known; the evidence is not conclusive as to whether or not the Triassic predators actually were naticids. The available data do not show any clear trends in the rates of gastropod boring predation since the Cretaceous (Vermeij, 1987: fig. 7.6); however, comparisons between assemblages should be based on ecologically analogous taxa, and studies of a sin-

gle prey family need to consider possible changes in defense mechanisms (especially shell form) over time.

Another area of interest is the use of bore holes in the field of ichnology, or the study of trace fossils. Most paleontologists recognize animal locomotory tracks as trace fossils; however, this field includes any and all remains of the activities of living organisms. Thus, a borehole found in a fossil specimen is, per se, a trace fossil, and can be described and discussed in the absence of exact knowledge of the causative agent. Needless to say, there has been some controversy over the "nomenclature" of trace fossils; the International Code of Zoological Nomenclature (ICZN, 1985: Articles 1d, 10d, 42b) currently does recognize "ichnotaxon names," as a parallel nomenclatural system. Häntzschel (1975), Warme & McHuron (1978) and Ekdale et al. (1984) provided excellent reviews of trace fossils.

Predatory boreholes in fossil specimens can be referred to the ichnotaxon "*Praedichnia*" Ekdale, 1985; those produced specifically by mollusks to the ichnotaxon "*Oichnus*" Bromley, 1981; and those identical with naticid boreholes to the ichnotaxon "*Oichnus paraboloides*" Bromley, 1981. Maddocks (1988: 641–2) "arbitrarily defined" 20 "ichnophena" corresponding to different forms of boreholes in ostracod tests; this diversity is unrealistic and meaningless. These names have no heuristic value: if they can be attributed to a known predator, then they should be referred to as "borehole of _____", whereas those of unknown predators should not be given formal names.

ECOLOGICAL ASPECTS OF NATICID PREDATION

This section attempts to integrate and synthesize, from an ecological perspective, the varied aspects of naticid predation. It is hoped that this will not only indicate what has been well documented but also reveal promising (or neglected!) areas for future research. I have not attempted statistically to re-analyze previous studies or to provide detailed criticisms of previous methodologies, unless it seemed directly warranted. Subsequent researchers would be well advised to re-check the relevant previous studies. My section on "Mechanisms of naticid predation" above included the more proximate aspects of naticid prey detection, capture and boring; this section covers the broader, ultimate aspects of naticid predation, as well as several topics from the "prey's viewpoint."

A. Prey Size and Species Choice

The embryos of naticids feed on dissolved organic matter (DOM); some species have yolk reserves or infertile nurse eggs which serve as additional food resources, especially for those with direct development. Naticid species with planktotrophic larvae feed on the phytoplankton while in the swimming stage; those with lecithotrophic larvae undoubtedly rely on DOM in addition to their yolk reserves (Ansell, 1982c).

The feeding habits of juvenile naticids have been much less studied. For example, Ansell (1982c) reported that they ate various unspecified gastropods or bivalves of small size; Berg (1976) was able to feed them *Bittium* and *Rissoella,* although this was limited to aquarium studies. Wiltse (1980a) found that juvenile *Neverita duplicata* at Barnstable Harbor (Massachusetts) consumed the diminutive venerid *Gemma gemma;* because of the high density of the latter, naticid predation accounted for less than 15% of total prey mortality. Maddocks (1988) concluded that juvenile naticids represented significant predators of ostracods; with ontogeny, the naticids shift to larger-sized molluscan prey.

Adegoke & Tevesz (1974: 22) claimed that "no direct correlation was found between prey size and predator size"; but no statistical data were presented to support this statement. Other studies, however, have shown that there is usually a good correlation between predator size (as determined by the inner borehole diameter) and the prey size (e.g. Ansell 1960; Bayliss, 1986; Griffiths, 1981; Kabat & Kohn, 1986; Kitchell et al., 1981; Macé, 1978; Martinell & De Porta, 1982; Robba & Ostinelli, 1975; Selin et al., 1986; Wiltse, 1980a). Colbath (1985) reported little correlation between borehole diameter and prey size, except for *Katherinella* prey. However, these results are a consequence of Colbath's use of bivalve shell "width" rather than the more conventional length as the dimensional measure.

Also of importance is the relative size of the prey taxa and the naticid predators. Large prey species are often less susceptible to pre-

dation by naticids than are small prey species. Similarly, within a species, smaller individuals usually suffer greater naticid mortality (e.g. Franz, 1977; Jackson, 1972). Penney & Griffiths (1984) used three-dimensional predation contour diagrams to display the relationships between predator size, prey size, and quantity of prey consumed. Alternatively, Hoffman (1976b: 296) showed no size-selectivity for some (but not all) gastropod prey from the Poland Miocene. However, Green (1968) found that mortality from naticid boring of the bivalve *Notospisula parva* actually increased with prey shell size; similar results were shown by Mukai (1973) and Wilson (1988). As discussed below, increased prey size over geological time may represent an evolutionary response to naticid predation (or is of adaptive value to escape predation) (Kelley, 1984, 1989b).

Prey switching, or prey choice, has been a contentious point; the fundamental question of "why" a given naticid will pick a certain prey species given an equal choice of several species can lead to teleological explanations. Ansell (1983) found that dietary switching will not occur and suggested that "preconditioning" may play a rôle in species choice. Broom (1983) found that younger *Natica maculosa* fed on *Pelecyora trigona,* whereas older predators fed on *Anadara granosa;* ontogenetic dietary switching thus occurred.

Several studies, using a variety of prey items, have determined a hierarchy of preferred prey choices. For *Euspira alderi,* Bayliss (1986: 40) found that the preferred bivalve prey, in descending order, were: *Mya, Spisula, Cerastoderma* and *Parvicardium; Arctica* and *Corbula* were not preyed upon. Similarly, George (1965) found that mortality due to naticids was most prevalent in *Glycymeris glycymeris,* and less so in *Donax semistriatus* and *D. trunculus* (the latter the larger species). Kitchell et al. (1981) found that for *Neverita duplicata,* the preferred prey, in descending order, were: *Mya, Mercenaria, Mytilus* and *Neverita.* Although *Neverita* was actually the highest in energetic value, the handling costs were such that only much smaller conspecific prey could be captured by the naticid predator. Kelley (1989a) found that bivalve prey from the Maryland Miocene were preferentially bored, in descending order, as: *Eucrassatella, Anadara, Astarte* (the latter two roughly equivalent) and *Corbula,* with slight differences from one formation to another.

The same naticid species, in different localities, may have markedly different diets. Thus, *Natica maculosa* in Penang (Malaya) feeds wholly on gastropod prey, especially the trochid *Umbonium vestiarium,* whereas this species at Kuala Selangor (Sumatra) feeds on bivalve prey, particularly *Anadara granosa.* In this case, it is the relative availability of prey taxa which determines (in part) the diet of a given naticid species (Broom, 1982; Berry, 1982).

A recent series of studies by Kitchell and colleagues (Kitchell et al., 1981; DeAngelis et al., 1984, 1985, 1989) have attempted to model the energetic and coevolutionary aspects of naticid ecology. The first study was of value in providing a useful model for the testing of naticid predation; however, the subsequent papers incorporated multiple assumptions which decreased their representation of the real world into a series of parameters couched in advanced equations. This reductionist approach cannot account for complex, stochastic, and hierarchial ecological communities.

It is worthwhile to elaborate briefly the basic principles of the Kitchell models. Essentially, the cost:benefit ratio for various prey species is determined (costs being the time and energy to recognize, capture/subdue, bore, and digest the prey; benefits the energetic value or gain of prey tissues) and related to both prey size and predator size, given that the cost of a specific prey will vary according to the predator size. From this, one can graphically represent the cost-benefit functions with prey size as the dependent variable and cost: benefit ratios as the independent variable. The lowest curve represents the optimal prey choice. These curves show that optimum prey are of intermediate sizes; too-small prey are of low energy value and too-large prey can usually escape the predator. Kitchell (1987) found that these models lead to the prediction that "larger naticid predators should be more highly selective than smaller-sized naticids," all other factors being equal. Discussion of their later models, dealing primarily with predator-prey coevolution has been deferred to section F, under the evolutionary aspects.

Kelley (1982b, 1987, 1989a–b) used these methods to analyze naticid predation in the Maryland Miocene fauna, and confirmed that the models predict prey selection patterns, but with some exceptions. She found that over time, bivalve prey shell thickness (= cost) increased while there was no overall

trend in shell volume (= benefit). Commito (1987) questioned the validity of the Kitchell models and noted that their assumptions neglected several important factors with respect to prey defense strategies (or adaptations): ignored were the possibilities of depth refuges, shell ornamentation, chemical defenses, or behavioral responses, all of which could deter naticid predation. DeAngelis et al. (1987) acknowledged these criticisms and suggested that yet further modelling would be able to incorporate these aspects of prey biology. It is difficult to account fully for all the parameters or variables that determine or influence predation processes; any model that attempts to do so would likely be so unwieldy or incomprehensible as to be of little heuristic value.

Interestingly, Ansell (1982b) found that *Euspira alderi* would not feed on opened bivalves—only live, closed prey items were chosen. These same results were found by Kitchell et al. (1986: 297) for *Neverita duplicata.* This suggests that the stereotypy of prey choice restricts the naticids to fresh prey, and rules out scavenging or carrion-feeding.

Predation by naticids on other naticids can be quite widespread and represents a significant source of naticid mortality. Although occasionally referred to as "cannibalism," that term is inappropriate since this predation does not necessarily involve conspecifics. Studies from the Nigerian Eocene showed that about 15% of naticid shells had naticid boreholes (Adegoke & Tevesz, 1974); Colbath (1985) observed only 2.7% such in the Oregon Miocene; Hoffman et al. (1974) noted 10% such in the Poland Miocene. Boekschoten (1967) found that 7.8% of the naticids from the Belgian Pliocene had naticid boreholes. Kabat & Kohn (1986) determined that in the Fijian Pleistocene, naticid predation on *Natica* spp. accounted for 27% of mortality, whereas that on *Polinices* and *Sinum* spp., for only 3% of mortality. The latter genera have more globose shells and a larger foot which may provide faster locomotion and hence facilitate escape from confamilial predators. Maxwell (1988) concluded that smaller-sized naticids of the New Zealand Miocene had much higher naticid predation rates, confirming size-selectivity aspects of naticid predation. Several studies on Recent naticids have also shown extensive confamilial predation (Burch & Burch, 1986; Fretter & Manly, 1979). Obviously, there is considerable variation as to the extent of confamilial naticid predation; disease and predation by fish or crustaceans may represent more important naticid mortality pressures.

B. Stereotypy of Boring on Prey Shell

For gastropod prey, there has been some confusion among studies with respect to the siting of successful boreholes, with some "results" actually of no consequence. Thus, Arua & Hoque (1989a: 55) emphasized that the "preferred drilling site" on the apertural side was on the last whorl; however, because of whorl overlap, most of the exposed prey shell surface **is** the last whorl, and thus purely non-random borehole siting would lead to most boreholes located there (their other results combine 11 prey species into a single table which does not facilitate further analysis). Yet, for some gastropod prey, there is a predominance of predation on the dorsal (abapertural) side over the ventral (apertural) side; this reflects the increased ability of the prey to escape in the latter position (Adegoke & Tevesz, 1974). However, other studies suggested that predation on the ventral side is preferred since the predator's foot seals off the aperture, blocking escape (Berg, 1976: 3; Berry, 1982). Some studies have shown that certain gastropod prey are preferentially bored on the penultimate whorl (rather than the last whorl); this, too, reflects prey handling factors (Dudley & Dudley, 1980; Hoffman & Martinell, 1984). Boreholes that are at either extreme end (apical or abapical) may not allow the proboscis to penetrate the entire shell; more centrally located boreholes may facilitate complete consumption of the prey tissues.

For gastropod prey, it is convenient to analyze the stereotypy of borehole siting by the various geometrical subsets of the shell. Not only can one distinguish between the outer (body) whorl and the older, apical whorls [i.e. the horizontal dimension], but one can also partition the prey gastropod shell whorls into semicircular sectors, or longitudinal zones [i.e. the vertical, or axial dimension]. Thus, Berg (1976) and Berg & Nishenko (1975) developed two conflicting numbering schemes for the latter division. In the 1975 paper (their figure 1b), the sectors (numbered 1–8) started with the apertural plane and proceeded counterclockwise (when viewed from the apex); thus, their clockwise "pie chart" (their figure 1c) of the sectors is actually viewed abapically. But, in the 1976 paper (his

figure 2a) the sectors (also numbered 1–8) started with the apertural plane and proceeded clockwise (when viewed from the apex); their clockwise "pie chart" (his figure 2b) is, this time, viewed apically! It is not clear what has been done here; my recommendation is that future investigators explicitly specify which scheme they are using.

Kabat & Kohn (1986: fig. 4), using the first scheme, observed that for naticid prey, boreholes were found in four of the eight shell sectors, with nearly 90% occurring in two 90° sectors; however, there was little overall evidence for stereotypy of borehole siting. Robba & Ostinelli (1975: 327) independently depicted an angular measurement system which corresponds to the first scheme of Berg. Stump (1975: figs. 19–21) devised an elaborate "equal-area projections" system to show frequency-contours (in percentages) of borehole siting on the various prey shells. Regrettably, this method is difficult to visualize and does not lend itself to comparison with the other, more direct schemes; it does not seem to have been used by subsequent authors.

Some studies have shown that most boring occurs near the shell margin of bivalve prey, where the shell is thinner and there is no sculpture (e.g., Ansell, 1960; Ansell & Morton, 1985). Other studies, however, have shown a preference by other naticids for boring near the umbones (e.g. Ansell & Morton, 1985; Arua & Hoque, 1989; Bernard, 1967; Colbath, 1985; George, 1965; Jacobson, 1968; Kitchell et al., 1981; Leidy, 1878; Matsukuma, 1976; Negus, 1975; Piéron, 1933; Thomas, 1976; Vignali & Galleni, 1986); or in the mid-region (Bayliss, 1986; Griffiths, 1981; Vermeij et al., 1989). The strongly inequilateral *Periploma margaritaceum* was primarily bored on the anterior slope, due to its shell form (Rosewater, 1980). Some earlier studies had suggested that naticids preferentially bored near the prey gonads or digestive tissues (Pelseneer, 1924; Verlaine, 1936); however, borehole siting is primarily a function of the manipulation of the prey during boring and may depend on the prey shell morphology. In a few cases, little stereotypy is manifested. Berg & Porter (1974) found that, for the same bivalve prey, there were significant differences between naticid species as to the preferred borehole position; Berg (1975) suggested that behavioral differences in prey capture and handling influenced species-specific patterns.

Probably of greater importance are (1) the size of the prey relative to the predator; (2) the shell thickness and presence or absence of sculptural elements; (3) the relative convexity of the prey shell; (4) other factors relating to the predator's manipulation of the prey. Based on this review, no one element solely determines the locus of borehole siting among bivalve prey.

The majority of studies have shown little preference for right *vs.* left valves of bivalve prey, as would be expected given the equivalve nature of most infaunal bivalves. Some studies have shown 10–20% "differences" in the frequency of boreholes between valves, but no clear trends are apparent. Needless to say, for each valve with a borehole, there is a matching, unbored valve; hence the naticid mortality rate is twice the number of bored valves divided into the total number of valves. It is incomprehensible as to what Lever et al. (1961: 341) meant when they stated that "the percentual mortality may in some cases exceed 100 [%]."

Adegoke & Tevesz (1974) stated that *Varicorbula* from the Nigerian Eocene was pleurothetic and invariably bored on the right valve which is closer to the surface. However, as noted below, the left valve of corbulids has a thick periostracum which deters boring predation; the position of the corbulid shell in the substrate is of less import (De Cauwer, 1985). More generally, since naticids usually manipulate their prey prior to boring, the life position may be of little relevance. Newton (1983) found that the Triassic limid *Mysidioptera* was always bored through the left valve; this taxa is an epibyssate recliner and the left valve is adjacent to the substrate (Newton et al., 1987: fig. 27).

C. Incomplete and Multiple Boreholes; Non-boring Predation

Incomplete boreholes are usually interpreted to represent a sign of interruption of predation, whether by prey escape, arrival of another predator, or other disturbance. In some cases, the same naticid (or another) will recapture the prey and commence boring a new borehole, elsewhere on the prey shell. Sometimes the new hole will coincidentally overlap the older hole; but studies have shown that naticids cannot recognize their own previous borehole and resume drilling there (thereby saving considerable time) (Kitchell et al., 1981: 539). The related prob-

lem of multiple complete boreholes again suggests interruption of predation after the completion of a borehole. Obviously there is an evolutionary disadvantage in not recognizing previous boreholes (complete or incomplete); the stereotypy of naticid predatory patterns may not be sufficiently flexible (Vermeij, 1982: 707; Kitchell et al., 1986).

In an analysis of the Miocene *Strioterebrum monidum* from the Caribbean, Kitchell et al. (1986: 294–5) found extremely large numbers of shells with multiple boreholes; one such had 15, of which 12 were incomplete and three had penetrated the prey shell but were not sufficiently wide to allow passage of the proboscis. Further studies on living terebrids by these authors confirmed that some species of this prey family are highly agile and can repeatedly escape naticid predation during the boring actions. Earlier, Vermeij et al. (1980: table 2) showed rather high rates (to 40%) of incomplete boreholes in various Recent terebrids; G. J. Vermeij (*in litt.*) suggested that the pungent odor of terebrids and olivids may represent a chemical defense against predation.

Fischer (1962b: 97) found that in a large sample (n = 1,126) of the Eocene turritellid *Mesalia,* 70.9% had naticid boreholes. Of the bored specimens, 84.8% had a single complete borehole (of which a tenth also had one to several incomplete boreholes); 4.2% had multiple complete boreholes; 8.7% had a single incomplete borehole; and 2.3% had multiple incomplete boreholes. Kitchell et al. (1981: 542) observed that the lucinid *Pseudomiltha floridana* had a ratio of incomplete to complete boreholes of 0.54:1. This taxon was stated to be polymorphic for shell thickness; the thicker shells were more likely to have incomplete boreholes.

An important recent discovery was that some bivalve prey, primarily in the tropics, are preferentially bored through the edge of the valves (Taylor, 1980: 175; Vermeij, 1980: 330); not only is the shell thinner there, but also the prey shell is unsculptured and easier to bore (Ansell & Morton, 1985). The latter authors found that some species (i.e. of *Polinices*) regularly edge-bored *Bassina,* while *Glossaulax* did not; that genus may preferentially bore other prey taxa. Some elements of "learning" (conditioning) may be involved in these responses to shell sculpture.

The razor clams (*Ensis, Solen*) have been shown to be typically consumed by naticids without boring, because when the valves are contracted, there are still sizable pedal and siphonal gapes through which the naticid proboscis can be inserted (Turner, 1955; Edwards, 1975; Schneider, 1981; Frey et al., 1987); this was also shown for *Tresus* (Reid & Fiesen, 1980: 32). Edwards & Huebner (1977) noted that *Mya* was not consumed directly through its large siphonal gape; instead, naticids always bored through the valve; possibly the siphonal tissue deters feeding activities. Earlier, Agersborg (1920: 421) had claimed that *Mya* and various other clams could be suffocated and directly consumed by *Euspira lewisii;* this now seems doubtful. Vermeij & Veil (1978) found that the frequency of gaping bivalves in marine faunas decreased from the Arctic to the tropics and noted that this was correlated with the increase in shell boring and other predation sources in warmer habitats.

Some gastropod prey can be attacked through the aperture, as the corneous operculum is flexible enough for the proboscis to be inserted around the margins (Hughes, 1985). Edwards (1969: 327) found that some *Olivella* prey were consumed without boring, and suggested that either the naticid could force the operculum, or else the prey "suffocates while wrapped in the predator's foot and relaxes," allowing the predator direct access to prey tissues. Interestingly, Yochelson et al. (1983: 11) speculated that the stereotypy of naticid boring precluded their attacking scaphopods directly through the open apertural end; but they suggested that it was more likely that once the scaphopod had retracted posteriorly, the naticid proboscis would not be able to reach the prey tissues.

As mentioned earlier, the tropical Indo-Pacific *Polinices mammilla* is able to "suffocate" and consume bivalve prey without boring. Ansell & Morton (1987) documented that this non-boring predation, in aquarium experiments, accounted for 14% to 54% of the bivalve mortality (according to prey species). This example, and those in the preceding two paragraphs, would greatly complicate community analyses (especially of fossils!) since no "traces" of naticid predation would be left on the post-mortem prey shell.

It should be noted that the results of several studies of naticid predation were misinterpreted as concluding that a significant number of the prey were consumed without boring (Kitchell et al., 1986: 297). Thus, Edwards (1975: 17) found that about 75% of the prey were bored and the remainder died of other

causes; Taylor et al. (1980: 397) erroneously took this to mean that the latter 25% of the prey were consumed (by naticids) without being bored. Similarly, Medcof & Thurber (1958) misinterpreted their own data to assume that all the empty, non-bored bivalve prey shells were consumed by naticid predators without boring; this overlooked other mortality sources. Another study (Bernard, 1967) stated that "in limited aquarium observation, over 60% of *Saxidomus* consumed showed no drill marks" (p. 9); and, again, ". . . in aquaria tests 25% of clams [*Saxidomus giganteus*] consumed by *Polinices* [= *Euspira*] *lewisi* bore no marks at all" (p. 10); the discrepancy in numbers is irreconcilable and all bivalve mortality was erroneously attributed to naticid predation.

D. Prey Defense Mechanisms

Ansell (1969) and Carter (1968) provided a general overview of defense mechanisms in various marine mollusks. Many bivalves show leaping or rapid burrowing in response to contact by naticids. Laws & Laws (1972: fig. 1) described the escape response of the Australian *Donacilla angusta,* which leaps or pops out onto the surface, thereby evading the burrowing naticid predator; similar responses were shown for *Ensis directus* (Turner, 1955; Schneider, 1982) and *Ruditapes philippinarum* (Rodrigues, 1986). Either rapid or deep burrowing (or both), can serve as an escape mechanism (Vermeij, 1983a) for bivalve prey.

Ansell & Morton (1985: 656) found that the anomalodesmatan bivalves *Lyonsia* and *Pandora* seemed to escape naticid predation "by coating the posterior edge of the shell with mucus to which sand grains adhere"; presumably this somehow deterred naticid predation.

Corbulid bivalves have been the object of several paleoecological studies; corbulids are noteworthy for their well-developed conchiolin layer (within the valve) which serves as a fairly effective deterrent to gastropod predation (Lewy & Samtleben, 1979). Furthermore, most successful boreholes are in the right valve, since there is well-developed periostracum on the left valve of corbulids which also deters predators. Complete boreholes in corbulid valves have a special form, with a considerably narrowed inner margin below the conchiolin layer (De Cauwer, 1985: figs. 1d, 1e). Kelley (1989a: 446–7) also found considerably reduced successful predation on *Corbula* and suggested that the low level of selectivity of prey size and borehole siting may also account for the high rate of unsuccessful predation (60% of boreholes nonfunctional). Lewy & Samtleben (1979: 350) suggested that the conchiolin layer serves as a compensation for the slow mobility and shallow burrowing of corbulids.

Alternative "defense" strategies of two bivalves were discussed by Commito (1982); *Mya arenaria* grows rapidly to a large size (and deferring reproduction until then), thereby escaping naticid predation [= size refuge], whereas *Macoma balthica* instead grows slowly, reproduces early, and escapes most naticid predation by deep burrowing [= spatial refuge]. Of course, *Mya* is subject to naticid predation while it is still small. The former mechanism was used by Hutchings & Haedrich (1984) to explain the size structure of deep-water nuculanids subject to naticid and fish predation. Actually, these "alternative" life history patterns may represent phylogenetic constraints rather than direct adaptations to naticid predation, per se.

Ansell & Morton (1985) discovered that removal of the sculptural lamellae on the shells of the venerid *Bassina* led to increased boring predation through the shell sides. Otherwise the naticids bored through the valve edges which do not have sculpture. This experimental observation demonstrated the function of sculpture as a prey shell defense mechanism in addition to stabilizing the bivalve in soft sediments.

Bayliss (1986) found that among bivalve prey, the species with the thinnest shell was preferentially preyed upon by naticids. Hingston (1985: table 4) noted that increased prey shell sculpture led to increased frequency of unsuccessful (incomplete) boreholes. Dudley & Vermeij (1978: 439) concluded that strong spiral ribs usually deterred boring in turritellids. Kelley (1982a: 46) reported that uncrenulated (male) shells of *Astarte* were more likely to be bored than were crenulated (female) shells; however this genus is protandrous, and the resulting size differences (between sexes) may be sufficient to explain differences in predation rate (given that the smaller males are less likely to escape predation).

Boggs et al. (1984), using *Mercenaria mercenaria* prey, artificially ground-down the shell surface to half the normal thickness, and tested the effects on predation by *Neverita duplicata.* They found that naticids could not

learn to differentiate between normal and thin-shelled prey, although the latter took considerably less time to bore. The same results were found by Rodrigues et al. (1987) for *Neverita didyma* preying on *Ruditapes philippinarum*. In some respects, these studies are of questionable value since it has not been shown that gastropods have any sensory mechanism for "determining" shell thickness (or shell weight). It is true that preying on thinner prey freed up additional time for foraging; surely the snails are incapable of this realization because they have no method for recognizing the thinner prey. This is an interesting case of a hypothetical coevolutionary response that does not initiate an "arms race."

E. Food Webs, Energy Flow and Physiological Efficiencies

Food webs are attempts to diagram the overall trophic structure of an ecological community (predators, herbivores, primary producers, detritivores). Elucidation of the structure of a food web and the strength (or quantity of interactions) of each link (chain) facilitates analyses of community energy flow and population dynamics. As infaunal predators, naticids (with other infaunal polychaetes, crustaceans, and nemerteans) represent an often overlooked level of predation, in addition to the more conspicuous epibenthic predators (asteroids, fish and crabs) (Commito & Ambrose, 1985). An example of the complexity involved is that both asteroids and naticids prey on bivalves, whereas some asteroids also prey on naticids (Christenson, 1970: 67); the same multiple interactions also occur with respect to crabs and fishes. Relatively little research has been done on determining the complete food webs for soft-bottom communities, in contrast to better-known rocky intertidal communities; this reflects the ease of access and analysis of the latter fauna.

Several paleocological studies have attempted to elucidate community structure and food webs, based primarily on an analysis of shell boring and breaking predation (Hoffman & Szubzda, 1976; Stanton & Nelson, 1980; Stanton et al., 1981; Stump, 1975; Taylor et al., 1983). While of great heuristic value in facilitating comparisons between fossil communities (as well as with Recent communities), these studies are limited by the indeterminate nature of mortality that leaves no "traces," as well as shell-removing agents, the latter skewing the results towards the remaining predatory agents.

It is important to realize that naticid predation represents only a part of the sum of all predation in soft-bottom communities; several authors have carefully reviewed the diversity and importance of other predators in these habitats (Cadée, 1968; Carter, 1968; Vermeij, 1978). Thus, Green (1969) found that naticids accounted for 9% of the mortality of the tropical bivalve *Notospisula parva;* shell-crushing skates were responsible for over 60% of the mortality; the remainder was due to other factors (disease or abiotic agents). The latter, non-predatory sources of mortality are just as important but virtually impossible to determine precisely from fossil or beach assemblages (i.e., an empty, undamaged shell may be the outcome of parasitism, other disease, sedimentation, or other agents) (Hoffman, 1976a).

A series of excellent physiological studies was conducted by Ansell and Macé on the European *Euspira alderi*. Distinct periods of shell growth were followed by egg collar production; feeding was considerably greater during the latter stage, since over 90% of non-respired assimilated energy is used for reproduction (Ansell & Macé, 1978; Ansell, 1982a–b). Predation rates increased with temperature (Macé, 1981a); and oxygen consumption rates (= respiration) were affected by the prey type and quantity (Macé, 1981b; Macé & Ansell, 1982). Each week, an adult naticid consumed up to its own (dry) weight in prey tissue [*Tellina tenius*] (Ansell, 1982a); this is limited by the extensive time spent in obtaining suitable prey. Macé (1981c) found that energy assimilation efficiency is about 60% during reproductive periods, and only 40% at other times. About 50–60% of the consumed energy is, however, "lost": not accounted for by growth, respiration (maintenance) or reproduction. Ansell (1982b) suggested that some of this may be accounted for by the mucus that is essential for prey capture and predator avoidance; much of the remainder is represented by feces and unconsumed prey tissue, but Berry (1983) was unable to calculate the energetic costs or losses due to mucus or feces. Bayliss (1986), using the same naticid species, found that about 24% of the time was spent drilling, 11%–18% ingesting prey tissue, and the remaining time in other activities, typically quiescent.

Related physiological studies on the temperate *Neverita duplicata* (in Massachusetts)

showed that the feeding season was only about 35 weeks, during which approximately 1.85 prey (*Mya arenaria*) were consumed per week. The naticids consumed about 1% of their body weight in prey on a daily basis, and the overall growth efficiency rates (snail growth in kilojoules per clam tissue consumed in kilojoules) declined from almost 50% in young snails to 16% in older snails (Edwards & Huebner, 1977; Huebner & Edwards, 1981).

Another factor of importance in calculating energy budgets is whether or not all the prey tissue is consumed. Thus, for a high-spired gastropod prey, some of the apical tissues may not be reached by the proboscis. Edwards & Huebner (1977) found that when feeding on *Mya,* only about 80% of the prey tissues were consumed (i.e. the "energy rich, low-ash content tissues"); proboscoidal access is not at issue here and this may reflect the less-palatable nature of the mantle edge and siphonal tissues of *Mya.*

Broom (1982) determined the "consumption rate" equation of feeding efficiency: this represents the mg dry weight of prey consumed per day, as a function of predator body (wet) weight. Thus, for *Natica maculosa* feeding on *Anadara granosa,* the allometric equation was $CW = 9.13\ (W)^{1.0086}$, where W = predator wet weight (in grams). Similarly, Griffiths (1981) found that the consumption rates (of bivalve prey, *Choromytilus meriodionalis*) increased 4.5 fold over a 55% increase in predator (*Natica tecta*) size.

Many of these studies were based on laboratory (aquaria) observations. These, of course, are a simplification or modification of reality (field behavior). Bayliss (1986: 46) cogently noted that "the artificial and enclosed environment in an aquarium increases the predator's ability to detect and capture a prey item as well as reducing the prey's ability to avoid and escape from the predator." Also, intertidal naticids are usually quiescent during low tide; in aquaria where they are continually submerged, the duration of activity is more extensive. Many laboratory studies (e.g. Rodrigues, 1986) used an aquarium sand depth barely greater than the prey or predator size; this does not allow for normal burrowing patterns. Kitchell et al. (1986: 297) noted that in their aquaria, the prey frequently "die, gape and decompose without the predator taking any part in the process"; this suggests that their prey were usually moribund or otherwise unhealthy, and leads one to question the validity of predation studies on these weakened prey. These caveats should be considered when calculating feeding rates, energy budgets, and related trophic measurements based on laboratory studies.

A typical example of the effects of naticid predation on prey population dynamics is that of Ansell (1960) who found that of first-year *Venus* [= *Chamelea*] *striatula,* 40% of the total mortality [= 15% of all individuals] was due to naticids; for the second-year cohort, only 15% of all mortality [= 5% of the cohort] was naticid predation; and for the third-year cohort [the last], only about 1% of all mortality was due to naticids. Clearly, predation by *Euspira alderi* affects primarily the younger cohorts; disease or other predators affect the older cohorts.

Another interesting taphonomic-ecological phenomenon is that of "beach sorting" or the differential post-mortem "survival" of valves of different bivalves (interspecific and intraspecific analyses), comparing both right *vs.* left valves and bored *vs.* unbored valves (Lever et al., 1961; Lever & Thijssen, 1968; Martinell & De Porta, 1980). The critical question is whether or not bored valves are differentially susceptible to post-mortem damage which would affect their representation in the fossil (or "beach shell") assemblage (Dudley & Vermeij, 1978: 437). One must also determine the extent of other shell-breaking predation that wholly removes the shells from the assemblage.

The studies of Lever and colleagues found that valves with boreholes (natural or artificial) traveled shorter distances but were more likely to end up higher on the shore (than nonbored valves), because of the biomechanics of fluid flow through and around bored valves. Thus, the "hole effect" is the upward transport of bored valves. The differential transport of right and left valves may also occur, resulting in greatly distorted ratios thereof in a beach assemblage. Indeed, it is possible that some paleontological studies showing "differences" in boring rates between valves may actually be a consequence of this differential sorting. A problem with such studies is that the hydrodynamic properties of bivalve shells can vary between taxa, and the biomechanical effects of one shell morphology may well be the opposite of those of a different morphology.

F. Enemies and Control of Naticids

Asteroids (starfishes or seastars) are important predators of naticids (Agersborg,

1920; Christenson, 1970); some naticid prey will ward off the asteroid by extension of the foot over the shell followed by mucus secretion (Ansell, 1969; Margolin, 1975). The latter author documented that *Natica stercusmuscarum* could respond to *Astropecten* by rasping off the spines and consuming the tube feet, deterring the starfish. Clarke (1956) noted that *Nassarius trivittatus* feeds upon the egg collars of *Euspira heros,* serving as a means of control. Ironically, this nassariid is, in turn, preyed upon by adult naticids!

Frequently, naticids are "blamed" for observed declines in populations of commercial shellfish (soft shell clams, quahogs, etc.), and oyster beds may be disrupted as naticids burrow through them in search of other prey items (Agersborg, 1920: 420). Because oysters are now more commonly cultivated on stakes or lines off the substrate, this may now be less of a problem. Edwards & Huebner (1977: 1231) cogently noted that "bored shells . . . are thus an exaggerated indicator of [naticid] mortality . . ." because other predators (arthropods, fish, birds, humans) remove or otherwise destroy bivalve shells. These authors further stated that naticid predators are an easy scapegoat to take the blame for ". . . human exploitation patterns, a sensitive issue." The various mechanisms and their success (or lack thereof) for the control of "pests" of shellfish were reviewed by Korringa (1952: 347–351); hand collecting is particularly ineffective (Turner et al., 1948; Medcof & Thurber, 1958). Carriker (1981: 417) suggested that ecological control, involving species-specific pheromones or deterrents, might be successful. There remains the often unacknowledged dilemma that not only is it impractical (or even impossible) to eliminate these predators, but also the resulting impact on the overall community structure and food web may actually be more deleterious than the effects of the predators themselves on the shellfish.

G. Macroevolutionary Patterns and Evolutionary Escalation

If, as claimed by Fürsich & Jablonski (1984), the Triassic boreholes are attributable to naticids, then the parallel evolution of the naticid boring habit twice (Triassic and Cretaceous) undoubtedly reflected the canalization or phylogenetic constraints of shell-boring: there are only so many ways a shell can be bored, and the underlying mechanisms may have remained quiescent in the Naticidae during the Jurassic. However, it remains unclear whether the Triassic predators are indeed naticids, or how the Jurassic naticids may have fed (possibly as scavengers).

Taylor et al. (1980: fig. 16) presented a hypothetical scenario of the evolutionary radiation of gastropod predation. Generalized proboscis probing was subsequently supplemented by pedal manipulation, which led variously to shell boring, wedging, chipping, or pedal suffocation. It can be assumed that these initial stages represented preadaptations to shell boring; however, the specific origins of the complex accessory boring organ remain uncertain. The independent evolution of shell boring in a number of molluscan taxa represents convergent evolution; the structures and processes are not necessarily homologous. (See "Diversity of Boring Predation" above for further comparisons).

The Cretaceous radiation of naticids is part of the Mesozoic marine revolution, involving the increase in diversity of many modern marine predators as a consequence of the "increase in shelled food supply resulting from the occupation of new adaptive zones by infaunal bivalves and by shell-inhabiting hermit crabs" (Vermeij, 1977: 245). Specifically, the shift of bivalves from predominantely epifaunal and byssate forms to infaunal, siphonate forms served as an escape from the then-dominant epifaunal and pelagic predators [cephalopods, asteroids, sharks and marine reptiles] (see also Taylor, 1981: 236) and subsequently led to selection favoring infaunal predators. If the early Mesozoic naticids were not burrowers (as suggested by their shell morphology), then burrowing in combination with shell boring would have opened up a new adaptive zone for the Cretaceous naticids. At the same time, the diversification of other sandy-habitat gastropods (especially turritellids, turrids and terebrids) provided further infaunal prey for naticids (Taylor et al., 1980: 399).

An important biogeographical phenomenon is the pattern of latitudinal diversity (pole–equator) of predatory prosobranch gastropods. For most of these marine families, including the Naticidae, there is a strong increase in species diversity from the poles to the tropical regions (the two exceptions are the Buccinidae and Turridae) (Taylor & Taylor, 1977; Taylor et al., 1980: 381–3). Correlated with this gradient, Dudley & Vermeij (1978: 439) showed a marked equatorward

increase in boring predation in *Turritella.* Subsequently Vermeij et al. (1989), for bivalve prey, actually observed an equatorward decrease in the frequency of complete boreholes (and a correlated equatorward increase in the frequency of incomplete boreholes); they suggested that the turritellids were an unexplained exception to this more general pattern.

It appears that since the Cretaceous, the general mechanisms and consequences of naticid predation have not greatly changed. To be sure, the prey sources have changed, not only due to origination and extinction of prey taxa, but also because of changes in prey defense mechanisms. However, the overall "strategy" of naticid predation has persisted for the last 100 million years (Kitchell, 1987). It is possible that the naticids, following their late Cretaceous–early Tertiary adaptive radiation, have now reached their maximum taxonomic diversity (e.g. Sohl, 1969: fig. 1) and are at stasis which may lead to eventual decline in the absence of evolutionary innovations facilitating further expansion. The highly stereotyped nature of naticid predation suggests that their canalization may be so great as to preclude further breakthroughs (but consider the non-boring, suffocation predation of *Polinices mammilla*).

With the rise of muricids in the later Tertiary, the naticids may have shifted from gastropod to bivalve prey, as suggested by Adegoke & Tevesz (1974). Hoffman et al. (1974) noted that in a Miocene assemblage, naticid boreholes were found mostly in smooth prey whereas muricid boreholes were primarily in ribbed (sculptured) prey; however the former prey are more likely to be infaunal than the latter, which may affect these results. Within the Maryland Miocene, Kelley (1982a) found that naticid predation shifted from predominantly bivalve prey in the Calvert and Choptank formations to gastropod prey in the St. Marys Formation, correlated with the increase in diversity of prey gastropods in the latter formation. Kelley's results may be a preservational artifact, as the St. Mary's has a much better representation of gastropods than do the earlier formations (G. J. Vermeij, *in litt.*). Clearly, one also needs to account for changes in the relative abundances of infaunal prey sources; trends as suggested by Adegoke & Tevesz (1974) may not be applicable on a global scale. In addition, the study of naticids has been primarily in a few restricted habitats; more comprehensive analyses of tropical sub-littoral communities may show other naticid predation patterns.

Kelley (1982a) suggested that extensive naticid and other predation on bivalves increased prey species diversity, perhaps by reducing competitive interactions. Although ecologists recognize several factors that affect species diversity, predation is undoubtedly one of the more important, and one that can be easily recognized in the fossil record. Perturbation experiments involving predator-exclusion cages were used by Wiltse (1980b) to analyze the role of the western Atlantic *Neverita duplicata* in its community structure; she found that snail predation and disturbance (due to burrowing) actually decreased the community species diversity by eliminating the rare species and blocking strong competitive interactions.

Kitchell and colleagues (Kitchell et al., 1981; Kitchell, 1982, 1983, 1986; DeAngelis et al., 1984, 1985, 1989) expanded upon their model of the energetics of naticid predation to develop models of coevolution of naticids and their prey. Coevolution, or the reciprocal evolutionary interactions of two taxa, is an important, albeit difficult to quantify, aspect of evolutionary biology. There has been considerable disagreement as to how tightly or broadly coevolution should be defined or restricted. Indeed, almost any evolutionary trend can be "explained" as part of a coevolutionary process (Vermeij, 1982: 711–2). Instead of recognizing coevolution as "all evolution resulting from biological interactions," it is much more useful to restrict it to "reciprocal adaptation involving the heritable traits of two or more species" (Vermeij, 1983b: 311). These models of naticid-prey coevolution are subject to the same caveats mentioned earlier under the discussion of the previous models. Nevertheless, I shall attempt to summarize their scenarios.

First, one can hypothesize that some sorts of evolutionary "arms races" are involved, with the prey evolving various antipredatory adaptations, but with the predator also evolving new or changed features. One consequence is that "multiple adaptive tactics produce multiple directionality" (Kitchell et al., 1981: 550), meaning that diversity may result as different prey follow alternative strategies and the same is true for different predators. This may result in character displacement or other isolating mechanisms resulting in speciation (Kitchell, 1983).

A direct test of these coevolutionary pro-

cesses, at least for naticid predators, was conducted by Kitchell (1982) who analyzed Marincovich's stratigraphic data for the eastern Pacific Neogene naticid fauna and concluded that predator "efficiency" increased over geological time. Specifically, size, globosity and streamlining of the shell all increased, as did the proportion of apertural area to shell area and the general diversification of morphology (the latter not fully explained). In some respects these are all a consequence of general phyletic size increase, and may not be directly due to coevolution.

Further refinements of their coevolutionary models predicted that in the absence of predators, prey will reproduce early (i.e., at small sizes); whereas in the presence of predators, prey will show delayed reproduction at larger sizes (DeAngelis et al., 1984). More complex age-structured models tested the prey energy-allocation functions (growth vs. reproduction) as a consequence of predation levels, and resulted in three alternative ecological strategies for bivalve prey as coevolutionary responses: delayed reproduction to large size, early reproduction, or increased shell thickness. Needless to say, the numerous assumptions (DeAngelis et al., 1985: 836) severely constrain the value of their coevolutionary model. In particular, they assume that no other factors affect the population dynamics of the naticids or their prey; this overlooks other predators, disease and parasitism, and abiotic mortality sources, all of which (together and severally) are often of greater importance to the prey than are naticids, as has been documented in the other studies discussed herein. Of course, with respect to the evolution of shell morphology, the latter factors are not easily measured or of great significance. The results of their models largely corroborated the conclusions of previous ecological studies.

Edge-boring of bivalve prey represents an escalation in the evolutionary "arms race" as an adaptive response to the presence of prey sculptural elements and shell-thickening. Similarly, non-boring predation (suffocation) also represents an alternative strategy (Ansell & Morton, 1987: 117); the selective advantages presumably entail a reduction in the energetic costs of boring. Further study should reveal whether some prey taxa are resistant to these novel predation mechanisms. The phylogenetic correlations of these two traits remain uncertain; at the present time, they are only known for a few species from the tropical Indo-Pacific.

To briefly summarize these ecological studies: (a) There is a general positive correlation between predator and prey size; size selectivity is shown as larger prey often have a size refuge from predation. (b) Prey defense mechanisms not only help prevent prey capture, but also may lead to interruptions of predation as shown by incomplete boreholes in the prey shell. (c) The successful mode of naticid predation is limited by its seeming stereotypy (inflexibility). (d) The intriguing possibilities of predator-prey coevolution (arms races) remain unproven for specific cases.

FUTURE DIRECTIONS

This review has suggested several areas needing further research. They are tabulated below; readers will undoubtedly recognize yet other problems amenable to future studies.

The detection of prey by naticids remains a puzzle: elucidation of the potential interactions of chemosensory mechanisms (osphradium) vs. echolocation (Kitching & Pearson, 1981). A related mechanistic problem is to determine the precise biochemical constituents of the accessory boring organ secretion in naticids and the mode of function of shell dissolution.

More ecologically oriented approaches could include sophisticated field analyses of prey choice, entailing controlled manipulations and perturbation experiments (remove one species at a time). Further quantification of the various links of soft-bottom community food webs to determine more precisely the quantitative role of naticids in this habitat. Development of methods of ecological control of naticid predators of shellfish.

Paleontologists could analyze Paleocene faunas for gastropod boring predation; and conduct more detailed studies of Jurassic and Early Cretaceous faunas to supply information on changes in predation and shell form during that time (Vermeij, 1987: 238–9). Further study of the phylogenetic position of the Triassic shell borers and the early fossil record of naticids to unravel the complexities of the origin(s) of shell boring of the naticid type.

Study of boring predation from the cold temperature southern oceans and the sub-Antarctic would be most desirable. The presence of several phylogenetically primitive nat-

icid taxa in those faunas would provide further clues as to the relationships between naticid phylogeny and boring predation. It remains uncertain whether the most primitive subfamily, the Ampullospirinae [Triassic?—Recent] are shell borers.

Further research on the geographical and phylogenetic extent of epifaunal predation, non-boring suffocation, and edge-boring would also add to our knowledge of the phylogenetic correlations of predation mechanisms.

CONCLUSIONS

(A) Bored or punched holes in prey shells are made by nine taxa of marine predators: naticid, muricid & capulid snails, octopods, *Pseudostylochus* (Turbellaria) and *Asemichthys* (Pisces), all in mollusk shells; cassid snails in echinoids; *Okadaia* (Nudibranchia) in calcareous polychaete tubes; and nematodes in foraminiferal tests. Some terrestrial zonitid snails are also shell-borers. Shell-crushing predators (sharks, crustaceans) sometimes leave holes in otherwise intact prey shells.

(B) Following prey capture, naticid boring is accomplished by alternate application to the prey shell of the radula and the proboscoideal secretory accessory boring organ. The distinctive naticid borehole is countersunk, with beveled edges.

(C) The data on naticid prey show that many soft-bottom families of bivalves and gastropods are subject to naticid predation. Rocky-habitat taxa escape the infaunal naticids.

(D) Boring predation potentially attributable to naticids originated in the Triassic but shortly became extinct. The naticid boring habit definitively evolved in the Late Cretaceous and has been documented through Holocene faunas, with an unstudied gap in the Paleocene. No clear trends in rates of boring predation since the Cretaceous are obvious.

(E) Most studies have shown a positive correlation between predator size and prey size; also, smaller prey are usually subject to higher rates of naticid predation. Incomplete boreholes reflect interruptions of predation; multiple boreholes demonstrate inflexible stereotypy of naticid boring. Prey defense can take several forms: leaping or burrowing; thick or sculptured shells; chemical defenses; growth to large size; and the corbulid conchiolin layer. Non-boring predation, either through gaping shells or pedal suffocation, greatly confounds ecological studies since no signs of predation are left on the prey shell.

(F) Naticid predation is an important and easily documented link in the food web of marine soft-bottom communities; other predators often crush or remove their prey without leaving recognizable remains.

(G) The evolution of naticid boring predation is part of the Mesozoic marine revolution entailing the diversification of infaunal bivalves and other gastropods which greatly increased naticid prey sources. Evolutionary escalation (defenses) on the part of prey taxa may have occurred since the Cretaceous; attempts to prove specific coevolutionary trends have been unsuccessful.

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APPENDIX

An * indicates that no species was given; "spp." indicates that more than two species of that genus were reported on in one reference. I have not included the taxa reported on by Arua (1989) or Arua & Hoque (1989a–c) due to the questionable nature of their borehole determinations.

A. Class Gastropoda. Subclass Prosobranchia.
Order Archaeogastropoda. Trochoidea. Trochidae:
Calliostoma laugieiri [Vignali & Galleni, 1987]
Gibbula varia [Vignali & Galleni, 1987]
Helicocryptus radiatus [Taylor et al., 1983]
Jujubinus exasperatus [Vignali & Galleni, 1987]
Margarites monolifera [Taylor et al., 1983]
*Monilea** [Kohn, unpub.]
Umbonium vestiarium [Berry, 1982]
Cyclostrematidae:
*Pseudoliotina** [Taylor et al., 1983]
Turbinidae:
*Turbo** [Kohn, unpub.]

Neritoidea. Neritidae:
Nerita funiculata [Hughes, 1985]
N. scabricosta [Hughes, 1985]
Neritina virginea [Jackson, 1972]
Theodoxus luteofasciatus [Stump, 1975]

Order Mesogastropoda. Littorinoidea. Littorinidae:
Littorina littorea [Edwards, 1975]

Rissoidea. Hydrobiidae:
Hydrobia andrussowi [Kojumdjieva, 1974]
Rissoidae:
Alvania alexandrae [Hoffman et al., 1974]
Ihungia ponderi [Maxwell, 1988]
Mohrensternia angulata [Kojumdjieva, 1974]
M. inflata [Kojumdjieva, 1974]
Rissoa inconspicua [Fretter & Manly, 1979]
Rissoina podolica [Hoffman et al., 1974]

Caecidae:
Caecum glabrum [Hoffman et al., 1974]
Vitrinellidae:
*Circulus** [Hoffman et al., 1974]

Cerithioidea. Cerithiidae:
*Argyropeza** [Kohn, unpub.]
*Bittium** [Berg, 1976; Taylor, 1970]
B. reticulatum [Hoffman et al., 1974]
Cerithium europeum [Kojumdjieva, 1974]
C. variabile [Jackson, 1972]
C. vulgatum [Vignali & Galleni, 1987]
*Rhinoclavis** [Kohn, unpub.]
Procerithiidae:
Cirsocerithium gracile [Taylor et al., 1983]
Diastomatidae:
Sandbergeria perpusilla [Hoffman et al., 1974]
Fossariidae:
"Fossarus" granosus [Taylor et al., 1983]
Turritellidae:
Archimediella spirata [Robba & Ostinelli, 1975]
Mesalia spp. [Fischer, 1962]
M. amekiensis [Adegoke & Tevesz, 1974]
M. regularis [Taylor, 1970]
Turritella spp. [Dudley & Vermeij, 1978]
T. badensis [Kojumdjieva, 1974]
T. bieniaszi [Kojumdjieva, 1974]
T. granulata [Taylor et al., 1983]
T. subangulata [Kojumdjieva, 1974]
T. tricarinata [Hoffman & Martinell, 1984]

Stromboidea. Aporrhaidae:
Aporrhais pespelecani [Martinell & Marquina, 1980]
A. uttingerianus [Martinell & Marquina, 1980]
Drepanocheilus calcarata [Taylor et al., 1983]
D. neglecta [Taylor et al., 1983]
Strombidae:
Rimella fissurella [Taylor, 1970]
*Strombus** [Kohn, unpub.]
Tibia unidigitata [Adegoke & Tevesz, 1974]
Hipponicoidea. Hipponicidae:
*Hipponix** [Kohn, unpub.]
Vanikoriidae:
"Vanikoropsis" cf. *albus* [Taylor et al., 1983]

Tonnoidea. Cassidae:
Semicassis wannoensis [Hingston, 1985]
Cymatiidae:
*Cymatium** [Kohn, unpub.]

Suborder Heteroglossa. Cerithiopsioidea. Cerithiopsidae:
Cerithiopsis tubercularis [Hoffman et al., 1974]

Triphoroidea. Triphoridae:
Triphora perversa [Hoffman et al., 1974]

Epitonioidea. Epitoniidae:
Confusiscala fittoni [Taylor et al., 1983]
Epitonium spinosa [Hoffman et al., 1974]

Eulimoidea. Eulimidae:
Eulima subulata [Hoffman et al., 1974]
Strombiformis glaber [Vignali & Galleni, 1987]

Rissoelloidea. Rissoellidae:
*Rissoella** [Berg, 1976]

Order Neogastropoda. Muricoidea. Muricidae:
Blackdownea quadrata [Taylor et al., 1983]
Eupleura caudata [Flower, 1954]
Hadriania craticulata [Martinell & Marquina, 1980]
Hexaplex benedeica [Adegoke & Tevesz, 1974]
*Morula** [Kohn, unpub.]
Nassa restitutiana [Kojumdjieva, 1974]
N. dujardini [Hoffman et al., 1974]
Paramorea lineata [Taylor et al., 1983]
*Pterynotus** [Adegoke & Tevesz, 1974]
Terefundus lamelliferus [Maxwell, 1988]
Urosalpinx [Flower, 1954]
Buccinidae:
*Cantharus** [Kohn, unpub.]
*Phos** [Kohn, unpub.]
*Siphonalia** [Kohn, unpub.]
Columbellidae:
*Mitrella** [Adegoke & Tevesz, 1974]
M. minor [Hoffman & Martinell, 1984]
M. nassoides [Kojumdjieva, 1974]
Nassariidae:
Amyclina spp. [Robba & Ostinelli, 1975]
*Cyllene** [Adegoke & Tevesz, 1974]
Dorsanum duplicatum [Kojumdjieva, 1974]
Nassarius elatus [Hoffman & Martinell, 1984]
N. italicus [Martinell & Marquina, 1980]
N. obsoletus [Edwards, 1975]
N. perpinguis [Berg & Nishenko, 1975]
N. pygmaeus [Hoffman & Martinell, 1984]
N. semistriatus [Hoffman & Martinell, 1984]
N. tiarula [Stump, 1795]
N. trivittatus [Edwards, 1975]
Niotha crassigranosa [Hingston, 1985]
Plicarcularia leptospira [Broom, 1983]
Fasciolariidae:
*Colubraria** [Kohn, unpub.]
Falsicolus tangituensis [Maxwell, 1988]
*Fusinus** [Kohn, unpub.]
*Granulifusus** [Kohn, unpub.]
Iscafusus rigidus [Taylor et al., 1983]
Latirus moorei [Stanton et al., 1981]
*Peristernia** [Kohn, unpub.]
Turbinellidae [= Vasidae]:
Exilla wellmani [Maxwell, 1988]
Olividae:
Alocospira papillata [Hingston, 1985]
Ancilla buccinoides [Taylor, 1970]
Olivella biplicata [Edwards, 1969]
Marginellidae:
Marginella spp. [Taylor, 1970]
Protoginella bembix [Maxwell, 1988]
Mitridae:
*Cancilla** [Kohn, unpub.]
Mitra orientalis [Kojumdjieva, 1974]
*Scabricola** [Kohn, unpub.]
*Subcancilla** [Kohn, unpub.]
Volutomitridae:
Microvoluta nodulata [Maxwell, 1988]

Costellariidae [= Vexillidae]:
*Austromitra** [Hingston, 1985]
*Vexillium** [Kohn, unpub.]

Cancellarioidea. Cancellariidae:
Bonellitia amekiensis [Adegoke & Tevesz, 1974]
B. serrata [Martinell & Marquina, 1980]
Inglisella parva [Maxwell, 1988]
I. allophyla [Maxwell, 1988]
Sydaphera wannonensis [Hingston, 1985]

Conoidea. Conidae:
Conus dujardini [Kojumdjieva, 1974]
C. parisiensis [Taylor, 1970]
Turridae:
Bela brachystoma [Hoffman & Martinell, 1984]
B. vulpecula [Hoffman & Martinell, 1984]
Brachytoma obtusangula [Martinell & Marquina, 1980]
*Clavatula** [Adegoke & Tevesz, 1974]
Clavus spp. [Robba & Ostinelli, 1975]
Comitas nana [Maxwell, 1988]
*Crassispira** [Kohn, unpub.]
Cythara subcylindrata [Hoffman et al., 1974]
Eopleurotoma spp. [Adegoke & Tevesz, 1974]
*Gemmula** [Kohn, unpub.]
Genota ramosa [Kojumdjieva, 1974]
Hesperiturris nodocarinatus [Stanton et al., 1981]
Heterocithara marwicki [Maxwell, 1988]
*Lophitoma** [Kohn, unpub.]
Mauidrillia occidentalis [Maxwell, 1988]
Michela trabeatoides [Stanton et al., 1981]
Mioawateria personata [Maxwell, 1988]
Paracomitas beui [Maxwell, 1988]
*Pleurotoma** [Adegoke & Tevesz, 1974]
Raphitoma hispidula [Hoffman et al., 1974]
*Rugobela** [Maxwell, 1988]
Splendrillia vellai [Maxwell, 1988]
*Tomopleura** [Maxwell, 1988]
Turricula africana [Adegoke & Tevesz, 1974]
T. dimidiata [Martinell & Marquina, 1980]
Viridoturris powelli [Maxwell, 1988]
Terebridae:
Gemmaterebra catenifera [Hingston, 1985]
Strioterebrum monidum [Kitchell et al., 1986]
S. pliocenicum [Martinell & Marquina, 1980]
Terebra spp. [Vermeij et al., 1980]
T. dislocata [Kitchell et al., 1986]
Zeacuminia viapollentia [Maxwell, 1988]

Subclass Heterobranchia. Superorder Allogastropoda.
Architectonicoidea. Architectonicidae:
Architectonica bendeica [Adegoke & Tevesz, 1974]
A. olicatum [Taylor, 1970]
Philippia meditteranea [Vignali & Galleni, 1987]
Pyramidelloidea. Pyramidellidae:
Eulimella conulus [Hoffman et al., 1974]
Evelynella doliella [Maxwell, 1988]
*Odostomia** [Adegoke & Tevesz, 1974]
O. conoidea [Hoffman & Martinell, 1984]
Pyramidella digitalis [Hoffman et al., 1974]
P. plicosa [Hoffman & Martinell, 1984]
Pyrgulina interstincta [Hoffman et al., 1974]
Tubonilla rufa [Hoffman & Martinell, 1984]
T. zesulcata [Maxwell, 1988]
Waikura elevata [Maxwell, 1988]

Subclass Opisthobranchia. Order Cephalaspidea.
Philinoidea. Acteonidae:
Acteon reussi [Hoffman et al., 1974]
A. semistriatus [Hoffman & Martinell, 1984]
A. tornatilis [Vignali & Galleni, 1987]
Tornatellaea affinis [Taylor et al., 1983]
T. unisulcata [Taylor et al., 1983]
Ringiculidae:
Avellana incrassata [Taylor, et al., 1983]
Ringicula auriculata [Hoffman et al., 1974]
R. buccinea [Hoffman & Martinell, 1984]
Scaphandridae:
Acteocina lajonkaireana [Kojumdjieva, 1974]
Cylichna melitopolitana [Kojumdjieva, 1974]
C. rubignosum [Kojumdjieva, 1974]
*Scaphander** [Adegoke & Tevesz, 1974]
Tornatina heraclitica [Hoffman et al., 1974]
T. trunculata [Hoffman et al., 1974]
Hamineidae:
Atys miliaris [Hoffman et al., 1974]
Retusidae:
Retusa kelloggi [Stanton et al., 1981]
R. truncatula [Hoffman & Martinell, 1984].

B. Class Bivalvia. Subclass Protobranchia. Order Nuculoida.
Nuculoidea. Nuculidae:
Acila conradi [Colbath, 1985]
Ennucula kalimnae [Hingston, 1985]
Nucula antiquata [Taylor et al., 1983]
N. mixta [Taylor, 1970]
N. nucleus [Hoffman & Szubzda, 1976]
N. obtusa [Taylor et al., 1983]
N. turgida [Wilson, 1988]
Palaeonucula strigilata [Fürsich & Jablonski, 1984]

Nuculanoidea. Nuculanidae:
Mesosaccella angulata [Taylor et al., 1983]
M. lineata [Taylor et al., 1983]
*Nuculana** [Adegoke & Tevesz, 1974]
Nuculana spp. [Colbath, 1985]
N. fragilis [Kojumdjieva, 1974]
N. pella [Vignali & Galleni, 1987]
N. pernula [Hutchings & Haedrich, 1984]
Yoldiidae:
*Yoldia** [Colbath, 1985]
Y. thraciaeformis [Hutchings & Haedrich, 1984]
Malletiidae:
*Malletia** [Kohn, unpub.]

Subclass Pteriomorphia. Order Mytlioida.
Mytiloidea. Mytilidae:
Choromytilus meriodionalis [Griffiths, 1981]
Crenella orbicularis [Taylor et al., 1983]
Modiolus auriculatus [Vermeij, 1980]
M. reversa [Taylor et al., 1983]
Mytilus edulis [Edwards, 1975]

Order Arcoida. Arcoidea. Arcidae:
Anadara spp. [Kelley, 1989a]
A. elevata [Dudley & Dudley, 1980]
A. granosa [Broom, 1982]
A devincta [Colbath, 1985]
A. diluvii [Kojumdjieva, 1974]
A. thisphila [Dudley & Dudley, 1980]
Barbatia irregularis [Taylor, 1970]
*Bathyarca** [Maxwell, 1988]
Noetiidae:
Arcopsis dissimilis [Darragh & Kendrick, 1980]
Pachecoa declivis [Kitchell, 1982]
Cucullaeidae:
Idonearca glabra [Taylor et al., 1983]

Limopsoidea. Limopsidae:
Limopsis chapmani [Darragh & Kendrick, 1980]
L. beaumarisensis [Hingston, 1985]
L. minuta [Kojumdjieva, 1974].
Glycymeridae:
Glycymeris spp. [Thomas, 1976]
G. albolineata [Matsukuma, 1977]
G. halli [Hingston, 1985]
G. insubrica [Vignali & Galleni, 1987]
G. pulvinata [Taylor, 1970]
G. vestita [Matsukuma, 1977]
Glycymerita sublaevis [Taylor et al., 1983]
G. umbonata [Taylor et al., 1983]

Pterioida. Pterioidea. Cassianellidae:
Cassianella ampezzana [Fürsich & Jablonski, 1984]

Order Limoida. Limoidea. Limidae:
Mysidioptera williamsi [Newton, 1983]

Order Ostreoida. Ostreoidea. Gryphaeidae:
Amphidonte obliquata [Taylor et al., 1983].

Pectinoidea. Pectinidae:
Chlamys radians [Guerrero & Reyment, 1988]
Pectin opercularis [Boekschoten, 1967]
Pseudamussium similis [Smith, 1932].

Subclass Paleoheterodonta. Order Trigonioida.
Trigonioidea. Trigoniidae:
Rutitrigonia eccentrica [Taylor et al., 1983]

Subclass Heterodonta. Order Veneroida.
Lucinoidea. Lucinidae:
Codakia bella [Vermeij, 1980]
C. orbicularis [Jackson, 1972]
Ctena decussata [Vignali & Galleni, 1987]
C. orbiculata [Jackson, 1972]
Divaricella ornata [Kojumdjieva, 1974]
D. divaricata [Vignali & Galleni, 1987]
*Epicodakia** [Kohn, unpub.]
Loripes dentatus [Hoffman et al., 1974]
L. lacteus [Vignali & Galleni, 1987]
Lucina anodonta [Kelley, 1989a]
L. approximata [Stump, 1975]
L. spinifera [Kojumdjieva, 1974]
Lucinella divaricata [Hoffman & Martinell, 1984]
Myrtea papatikiensis [Maxwell, 1988]
Parvilucina costata [Jackson, 1972]
Pseudomiltha floridana [Kitchell et al., 1981]
*Wallucina** [Vermeij, 1980]
Fimbriidae:
Mutiella canaliculata [Taylor et al., 1983]
Ungulinidae:
Diplodonta subquadrata [Vermeij et al., 1989]

Carditoidea. Carditidae:
Beguina diversicosta [Kojumdjieva, 1974]
Cardita spp. [Adegoke & Tevesz, 1974]
C. chamaeformis [Boekschoeten, 1967]
Cyclocardia subtenta [Colbath, 1985]
Venericardia greggiana [Kitchell, 1982]
V. serrulata [Taylor, 1970]
*Vetericardiella** [Kitchell, 1986]

Crassatelloidea. Astartidae:
Astarte spp. [Boekschoten, 1967; Kelley, 1989a]
Astarte triangularis [Smith, 1932]
Eriphyla striata [Taylor et al., 1983]
Lirodiscus tellinoides [Siler, 1965]
Nicaniella formosa [Taylor et al., 1983]
Crassatellidae:
Crassatella spp. [Taylor, 1970]
C. vadosa [Sohl, 1969]
*Crassatellites** [Kohn, unpub.]
Eucrassatella spp. [Kelley, 1982a]

Cardioidea. Cardiidae:
Acanthocardia tuberculata [Vignali & Galleni, 1986]
Cardium spp. [Smith, 1932]
C. politionanei [Kojumdjieva, 1974]
Cerastoderma edule [Bayliss, 1986]
Clinocardium nuttallii [Bernard, 1967]
Dinocardium robustum [Kornicker et al., 1963]
Fragum fragum [Vermeij, 1980]
Laevicardium elenense [Vermeij et al., 1989]
Loxocardium bouei [Taylor, 1970]
Parvicardium scabrum [Bayliss, 1986]
Protocardia hillana [Taylor et al., 1983]
Thetis laevigata [Taylor et al., 1983]

Mactroidea. Mactridae:
Mactra angulata [Taylor et al., 1983]
M. australis [Laws & Laws, 1972]
M. chinensis [Vermeij et al., 1989]
M. fragilis [Paine, 1963]
M. stultorum [Vignali & Galleni, 1987]
Mactrellona exoleta [Vermeij et al., 1989]
Notospisula parva [Green, 1968]
Pseudocardium sachalinense [Vermeij et al., 1989]
Spisula elliptica [Bayliss, 1986]
S. solidissima [Franz, 1977]
S. subtruncata [Bayliss, 1986]
Tresus nuttallii [Reid & Friesen, 1980]
Mesodesmatidae:
Atactodea striata [Ansell & Morton, 1987]
Coecella chinensis [Ansell & Morton, 1987]
Donacilla angusta [Laws & Laws, 1972]
Ervilia ousilla [Hoffman & Szubzda, 1976]
E. dissita [Kojumdjieva, 1974]

Solenoidea. Solenidae:
Ensis directus [Schneider, 1982]
Solen conradi [Colbath, 1985]
S. strictus [Frey et al., 1987].

Tellinoidea. Donacidae:
Donax spp. [Vermeij et al., 1989]
D. faba [Ansell & Morton, 1987]
D. semistriata [Vignali & Galleni, 1987]
D. trunculus [Vignali & Galleni, 1987]
D. vittatus [Negus, 1975]
Plebidonax deltoides [Kitching & Pearson, 1981]
Psammobiidae:
Gari hamiltonensis [Hingston, 1985]
Tagelus peruvianus [Vermeij et al., 1989]
Scrobiculariidae:
Scrobicularia plana [Richter, 1962]
Solecurtidae:
Solecurtus antiquatus [Kojumdjieva, 1974]
Tellinidae:
Arcopagia robusta [Vermeij, 1980]
Macoma albaria [Colbath, 1985]
M. arctata [Colbath, 1985]
M. balthica [Commito, 1982]
M. calcarea [Aiken & Risk, 1988]
M. nasuta [Reid & Gustafson, 1989]
Palaeomoera inaequalis [Taylor et al., 1983]
Peronidia venulosa [Vermeij et al., 1989]
Quidnipagus palatam [Vermeij, 1980]
*Scissulina** [Vermeij, 1980]
Tellina spp. [Vermeij et al., 1989]
T. donacina [Vignali & Galleni, 1987]
T. emacerata [Colbath, 1985]
T. lux [Broom, 1983]
T. planata [Kojumdjieva, 1974]
T. pudica [Broom, 1983]
T. pulchella [Vignali & Galleni, 1987]
T. tenuis [Ansell, 1982a–c]
Tellinella virgata [Nakamine & Habe, 1983]
Temnoconcha cognata [Vermeij et al., 1989]

Arcticoidea. Arcticidae:
Arctica islandica [Christensen, 1970]
Epicyprina angulata [Taylor et al., 1983]
E. subtruncata [Taylor et al., 1983]
Venilicardia lineolata [Taylor, et al., 1983]

Veneroidea. Veneridae:
Anomalocardia squamosa [Ansell & Morton, 1987]
A. squamosa [Taylor, 1980]
Aphrodina nitidula [Taylor, 1970]
Bassina calophylla [Ansell & Morton, 1985]
Callistina plana [Taylor et al., 1983]
Calpitaria distincta [Taylor, 1970]
Calva subrotunda [Taylor et al., 1983]
Chamelea gallina [Guerrero & Reyment, 1988a]
Chimela caperata [Taylor et al., 1983]
Chione spp. [Smith, 1932]
C. basteroti [Kojumdjieva, 1974]
C. californensis [Stump, 1975]
C. cancellata [Paine, 1963]
C. subrugosa [Vermeij et al., 1989]
C. undatella [Peterson, 1982]
Circomphalus subplicatus [Hoffman & Szubzda, 1976]
Costacallista laevigata [Taylor, 1970]
Dosinia dunkeri [Vermeij et al., 1989]
D. lupinus [Vignali & Galleni, 1987]
Flaventia ovalis [Taylor et al., 1983]
Gafrarium minimum [Smith, 1932]
G. pectinatum [Vermeij, 1980]
Gemma gemma [Wiltse, 1980a]
Gouldia minima [Vignali & Galleni, 1987]
Katelysia scalarina [Laws & Laws, 1972]
Katherinella angustifrons [Colbath, 1985]
Macrocallista nimbosa [Paine, 1963]
Megapitaria squalida [Vermeij et al., 1989]
Mercenaria mercenaria [Berg & Porter, 1974]
M. campechiensis [Paine, 1963]
Meretrix lusoria [Vermeij et al., 1989]
Paraesa faba [Taylor et al., 1983]
Pelecyora trigona [Broom, 1983]
Periglypta reticulate [Vermeij, 1980]
Pitar spp. [Vermeij et al., 1989]
P. morrhuana [Jacobson, 1965]
Placamen subroboratum [Hingston, 1985]
Protothaca spp. [Vermeij et al., 1989]
P. staminea [Peterson, 1982]
Ruditapes philippinarum [Rodrigues, 1986]
Saxidomus giganteus [Bernard, 1967]
Sunetta gibberula [Hingston, 1985]
Tapes japonica [Hamada, 1961]
T. philippinarum [Ansell & Morton, 1987]
Timoclea marica [Vermeij, 1980]
Tivela spp. [Vermeij et al., 1989]
Venerupis aurea [Vignali & Galleni, 1987]
V. senegalensis [Vignali & Galleni, 1987]
Venus multilamella [Kojumdjieva, 1974]
V. striatula [Ansell, 1960]
V. verrucosa [Vignali & Galleni, 1987]
Veremolpa micra [Mukai, 1973]
Glauconomidae:
Glauconome chinensis [Ansell & Morton, 1987]

Order Myoida. Myoidea. Myidae:
Cryptomya californica [Watkins, 1974]
Mya arenaria [Edwards, 1975]
Corbulidae:
*Caestocorbula** [Kitchell, 1986]
Caryocorbula deusseni [Kitchell, 1982]
Corbula spp. [De Cauwer, 1985]
Corbula carinata [Kojumdjieva, 1974]
C. elegans [Taylor et al., 1983]
C. gibba [Vignali & Galleni, 1987]
C. idonea [Kelley, 1989a]
C. rugosa [Taylor, 1970]
C. truncata [Taylor et al., 1983]
Notocorbula ephamilla [Hingston, 1985]
N. innerans [Maxwell, 1988]
Varicorbula amekiensis [Adegoke & Tevesz, 1974]
Vokesula aldrichi [Kitchell, 1982]

Hiatelloidea. Hiatellidae:
Hiatella arctica [Aitken & Risk, 1988]
Panopea mandibula [Taylor et al., 1983]

Subclass Anomalodesmata. Pandoroidea. Periplomatidae:
Cochlodesma leanum [Rosewater, 1980]
Periploma spp. [Rosewater, 1980]

Poromyoidea. Cuspidariidae:
Cuspidaria cuspidata [Hoffman & Martinell, 1984]

C. Scaphopoda.

Dentaliidae:
Dentalium complexum [Fankboner, 1969]
D. bedensis [Kojumdjieva, 1974]
D. spp. [Yochelson et al., 1983]
Fustiaria miocaenica [Hoffman et al., 1974]
Entalinidae:
Entaliopis brevis [Yochelson et al., 1983]
Gadilidae:
*Cadulus** [Yochelson et al., 1983]

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LETTERS TO THE EDITOR

TOWARDS A PHYLOGENETIC SYSTEM OF GASTROPODA PART I: TRADITIONAL METHODOLOGY—A REPLY

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ABSTRACT

Bieler (1990) provides a critique of the methodology of a phylogenetic analysis of the Gastropoda by Haszprunar (1988). His criticism of an incomplete and inconsistent presentation of character-states and methodology is answered by explaining by examples the way in which the character analysis and the construction of the cladogram were done. I argue that any maximum parsimony analysis with equal weighting of characters will fail to produce the "true" phylogeny because of the high degree of parallelism and convergence within the group. The method presented applies *a priori* criteria for estimating the probabilities of homology and apomorphy (i.e. significance) of characters and constructs the cladogram according to that significance. In the proposed classification, higher taxa are thought to reflect stem-lines of high probability.

Key words: Gastropoda, systematics, classification, phylogeny, cladistics, critique.

INTRODUCTION

Bieler (1990) gives a critique of the methodology of the recently published phylogenetic analysis of streptoneuran Gastropoda by Haszprunar (1988) from a strictly cladistic point of view. Here I want, first, to correct certain points of the original paper (Haszprunar, 1988; cf. appendix); second, to explain briefly the reasons that the analysis was not done by application of accepted cladistic methodology; and third, to provide significant examples of the way in which I weighted the characters and did the analysis. Doing the latter, I accept the major points of Bieler's (1990) critique—no one is perfect.

Thus, I agree with Bieler (1990) that for any "scientific question, it is an integral part of any study to present the data unambiguously, to employ reproducible methods, and to offer testable hypotheses." Maybe I have underestimated the difficulty of following my arguments. I therefore wish at least to show the principles.

PRESENTATION OF DATA

Bieler (1990) is correct in assuming that my analysis was not done by computer, because during the original study adequate hardware to run phylogenetic software was unavailable. Since then, adequate hardware has become available, and I have become familiar with the advantages and disadvantages of programs like PHYLIP, PAUP and in particular HENNIG'86.

Admittedly there are some mistakes in the text, tables and figures, all of which are of minor importance, however. Nevertheless, I welcome this opportunity to correct those of which I am aware.

Bieler (1990) criticized the fact that I did not provide a comprehensive data-matrix. The way in which I did the analysis, however, does not require a data-matrix (see below), and the main results of the character-analysis have been presented (Haszprunar, 1988: table 2).

THEORETICAL CONSIDERATIONS

Character analysis is the basis of any phylogenetic analysis. Typically plesiomorphic versus apomorphic states are estimated by application of the rules of Hennig (1966) such as outgroup-comparison, data on fossils, ontogenetic sequences, and the like. Often, however, there is no clear outgroup available

(e.g. Houbrick, 1988; Reid, 1989), and the use of fossils and ontogenetic data has been criticized (Alberch, 1985).

The problem of homology, i.e. the problem of the frequency of change from plesiomorphic to apomorphic character state during phylogeny, seems to be overcome by application of a "maximum-parsimony" analysis, whether by hand or by computer. The working hypothesis of parsimony minimizes the number of analogies (homoplasies) and can produce one (or many) "most parsimonious" tree(s). Colless (1983) has pointed out that the principle of parsimony, which is an operational concept rather than an empirical fact of evolution, does work with negligible rates of failure only if the probability of change in each character-state is very low. As outlined by Gosliner & Ghiselin (1984) for primitive opisthobranchs and identified by Davis (1989) in the Hydrobiidae and in my work on the streptoneurans, however, there is a very large degree of convergence, that is, parallelism, in the data. With an increase in the number of taxa the degree of homoplasy increases (Sanderson & Donoghue, 1989), moreover, suggesting a more or less constant rate of homoplasy among taxa. Indeed, the necessity of a parsimony analysis implies that the basic data matrix is controversial with respect to its proposed synapomorphies. Accordingly, the problem of homology cannot be overcome by parsimony analysis.

The recent cladistic study (done with PAUP) of the Littorinidae by Reid (1989) also shows many cases of homoplasy. Indeed, "59.2% of the character state changes could be ascribed to homoplasy" (Reid, 1989: 59), and this is logically a minimal ("most parsimonious") estimate. Significantly, a final cladogram that differs in certain points from the consenus tree is preferred because "some character-state reconstructions are more likely than others" (Reid, 1989: 63). As stated (Haszprunar 1988: 399), the main problem of any phylogenetic study is that of homology.

As reviewed by Riedl (1975, 1978), Ruppert (1982) and Neff (1986), *a priori* criteria for inference of homology have been provided by Remane (1952, 1954). More recently, Rieger & Tyler (1979, 1985; see also Westheide & Rieger, 1987; Tyler, 1988) have formulated criteria for the counter-version, i.e. the estimation of convergence. Both sets of criteria should be applied to any analysis (see below).

I want to stress that both types of character analysis (homology *versus* analogy, apomorphy *versus* plesiomorphy) must be done prior to construction of the tree, and that both are principially inductive by application of the criteria of Remane (1952) and Hennig (1966) among others. Accordingly, each proposed synapomorphy includes a two-fold degree of probability, one with respect to apomorphy ("-apo-"), and one with respect to homology ("syn-") (Haszprunar, 1989). In the case of character-states, even two analyses of homology are necessary: first, whether all the states belong to the same (homologous) character; secondly, with respect to the homology of the advanced state. For example, in an analysis of the gills of gastropod groups and in particular the (plicate) gill of primitive opisthobranchs, two questions of homology must be answered (for detailed discussion, see Haszprunar, 1985: 20–21; Haszprunar, 1988: 382): (1) Is the opisthobranch gill a homologue of the prosobranch gill (i.e. a ctenidium)? (2) If so, is the plicatid gill homologous in all opisthobranchs?

I believe that these probabilities must be used to "weight" the characters used in the analysis. In other words, the "weight" is not a feature of the character itself, but the degree of likelihood in the present analysis (cf. also Bryant, 1989).

There is no escape from the weighting of characters. Also, the usual analysis involving maximal parsimony weights characters by selecting them (characters not selected lack weight) and by giving each selected character equal weight. Insofar as the degree of homoplasy is great, differentiated weighting of selected characters becomes essential, however. Although Remane (1952) has indicated the way to infer distinct probabilities for a proposed homology, there is still no clear procedure for quantitative *a priori* weighting of characters (e.g. Neff, 1986; Westheide & Rieger, 1987; Bryant, 1989). In using computer algorithms, one possibility would be to include in the analysis only characters with high significance; another is to establish a system of differential weighting (e.g. 1/3/5 corresponding "low/ medium/ high" significance).

These considerations shed light on data presentation as well. For instance, the frequency and circumstances of transformation of coiled shells into asymmetrical limpet-like ones are unimportant; the statement "many" shows that the significance of this character is very low in this phylogenetic analysis. (Its significance might be high in another one, however.)

PRACTICAL CONSEQUENCES

General Remarks

In this section I wish to show by examples the way in which the character analysis and the construction of the cladogram were done in the original paper. For character analysis, I have selected two examples, the number of gills and the conditions of the anterior nerve ring, the significance of which differ considerably. These significances are estimated prior to construction of any cladogram by application of the rules of Remane (1952), Rieger & Tyler (1979, 1985), Neff (1986), Westheide & Rieger (1987) and Tyler (1988). Two groups, Neritimorpha and Pyramidelloidea have been selected to demonstrate the construction of the cladogram.

It was assumed *a priori* that the taxa used in the study all were holophyletic (i.e. monophyletic *sensu* Hennig, 1966), implying that changes within a taxon are secondary phenomena. This approach also concerned the Euthyneura the holophyly of which has been shown earlier (Haszprunar, 1985a,b). It will be shown that in one case (Allogastropoda) this assumption did not work and necessitated the consideration of the subtaxa (see below).

Number of Ctenidia

The question of ctenidial homology throughout the gastropods has been discussed at length by Haszprunar (1985a: 20–22; 1988: 377–383). Whereas the gills of Cocculiniformia, of Valvatoidea, of the allogastropod groups and the Euthyneura were considered to be secondary structures, the gills of the remaining streptoneuran groups were assumed to represent homologues.

Outgroup comparison (Cephalopoda, Tryblidiida) makes it nearly certain that the presence of paired pallial organs is the primitive condition among gastropods. This conclusion is supported by the facts that even gastropods with two gills often have reduced the right one, and that in the Trochoidea and Lepetodriloidea the blood supply of the right gill is retained although the gill itself has been lost. The probability for the hypothesis "plesiomorphy: two ctenidia; apomorphy: one (left) ctenidium" is therefore very high.

Next the probability was considered whether the change from two ctenidia to one occurred once or often in gastropod evolution. Two functional gills are present only in vetigastropod groups ("zeugobranchs"), and even within this group two subgroups have lost the right ctenidium. Anatomical features in Neritimorpha, in which most species have a diotocardian heart and certain species even have a gill-rudiment (Fretter, 1965) and Docoglossa—Patellidae (with two osphradia) likewise suggest an original condition of two ctenidia in these taxa.

Functional morphology shows that a change from two to one ctenidium results in advantages for the animal with respect to water currents in the mantle cavity (Yonge, 1947). Indeed, the presence of two ctenidia necessitates a slit or hole(s) in the shell for passage of waste. Finally, because in zeugobranch gastropods, such as *Haliotis,* the left ctenidium is formed first in ontogeny (Crofts, 1937), a heterochronic process might easily result in a loss of the right ctenidium.

On the whole, I concluded that the change from two to one (left) ctenidium probably occurred several times in gastropod evolution. Thus the probability of the respective syn—apomorphy, i.e. the probability of the homology of the change from plesiomorphic to apomorphic condition, is low.

Anterior Nervous System

The homology of the main ganglia of the anterior nerve ring in gastropods is well established by identical relative positions and interconnections and by identical fields of innervation.

Among the Streptoneura, two conditions of the anterior nerve ring with respect to the relative position of the ganglia can be distinguished: the pleural ganglion might be close to the pedal one (hypoathroid condition) or close to the cerebral one (epiathroid condition). Outgroup comparison is unsatisfactory, because the Tryblidiida lack pleural ganglia and the Cephalopoda have a highly concentrated nervous system. Ingroup comparison reveals, however, that the hypoathroid condition is generally correlated with other plesiomorphic characters, such as presence of nacre, paired pallial and excretory organs, or external fertilization. The hypothesis "plesiomorphic: hypoathroid condition—apomorphic: epiathroid condition" therefore appears well founded.

Again it is now necessary to estimate the number of changes from the hypo- to the epiathroid condition. There is not a single strep-

toneuran taxon in which a mixture of the two conditions occurs (for Viviparidae cf. Haszprunar, 1988: 395). In addition, the distribution of both character states is largely correlated with the ability to produce planktotrophic larvae (exception: certain Neritoidea). On the other hand, a selection pressure that could force such a change is unknown. Moreover, both conditions are uneffected by concentration of the nervous system. Summarizing the argument, I assumed the syn—apomorphy "epiathroid nerve ring" to be of very high significance for streptoneuran phylogeny.

Position of Neritimorpha

Based on the results of the character analysis, estimation of the systematic position of the Neritimorpha starts with consideration of the characters with the highest significance, such as the hypoathroid nervous system.

This step alone reduces drastically the number of possible trees. Starting the analysis with 28 taxa (Haszprunar, 1988: fig. 5) 1.6 $\times$ 10^{35} trees are possible. Accepting "epiathroid nervous system" as a synapomorphy leaves 18 taxa and thus 6.3 $\times$ 10^{18} possible trees [$\times$ = $(2n-3)!/2^{(n-2)}(n-2)!$; in which n is the number of taxa].

Among those "Archaeo-" gastropods, there are two sequences of radular types, each of them again with high significance (stereoglossate—flexoglossate; rhipidoglossate—taenioglossate; Haszprunar, 1988: 390–391). This places the Docoglossa (= Patellogastropoda) and hot-vent group C below and the architaenioglossate groups above the Neritimorpha. The number of possible trees involving the Neritimorpha is further reduced to 3.2 $\times$ 10^{11} (13 taxa remain). Upon consideration of the distribution of ctenidial skeletal support (Haszprunar, 1988: 377–381), *Neomphalus,* the Vetigastropoda and the Seguenzioidea are placed above the neritimorph clade. The number of possible trees is now 15 (4 taxa remain). The Cocculiniformia share many plesiomorphic characters with the Docoglossa, including the primary limpet shell (Haszprunar, 1988: 370–372); thus they are grouped below the Neritimorpha. Finally, *Melanodrymia* shares several characters, such as radula type and protoconch features, with *Neomphalus* and the Vetigastropoda, and is therefore placed above the neritimorph offshoot.

This solution agrees with several character sequences of high significance. The assumption that the Neritimorpha belong among the higher gastropods is based, however, on character stages each of which is correlated with reproductive biology, namely internal fertilization and planktotrophic veligers. The probability of convergent evolution of the features of neritimorph reproductive biology is very high: first, details of the respective characters differ considerably between Neritimorpha and higher groups (genital system, sperm structure, protoconch features); and second, there are numerous examples of internal fertilization within other archaeogastropod clades, and larval planktotrophy has been established through parallel evolution among the Bivalvia.

Position of Pyramidelloidea

Again, the analysis begins with consideration of neural conditions. Earlier the Pyramidelloidea were placed together with the Architectonicoidea in a clade called Allogastropoda (Haszprunar, 1985a). The epiathroid condition of the anterior nerve ring placed the Allogastropoda among the "Apo-"gastropoda, the lack of parietal ganglia and the retention of (at least osphradial) streptoneury (Haszprunar, 1988: 394) suggest a grouping of the Allogastropoda below the euthyneuran level of organization.

On the other hand, the Pyramidelloidea and the Euthyneura share synapomorphies of high significance, such as giant nerve cells, a rhinophoral and a lateral nerve and characters of the sperm (Haszprunar, 1988: 396–397; Healy, 1988a,b). Such proposed synapomorphies were in direct contrast to the originally assumed synapomorphies of the Allogastropoda, namely a shared gill position to the right of the dorsal ciliary tract, an acrembolic proboscis of distinct type (shifted position of buccal ganglia) and spermatophores (Haszprunar, 1985a). Meanwhile, however, pyramidelloids with a different position of the gills (Amathinidae; Ponder, 1987) and a mathildid with the usual placement of buccal ganglia (*Geganyia;* Haszprunar, 1985b) were described. This leaves the spermatophores with very low significance.

As a conclusion, I corrected my earlier opinion and regard the *Allogastropoda* now as a distinct grade rather than a clade. Within this grade, the Pyramidelloidea are placed closest to the Euthyneura, and both taxa represent a sister-group relationship.

CLASSIFICATION

In my approach, the final cladogram is a theorem of probability with very different degrees of likelihood in the various stem-lines of taxa. It is essential to note that a **reconstruction of phylogeny** should be translated into a classification, and not **the phylogeny** itself. In an attempt to base the classification on the same principle as the analysis (probabilities), the central taxa should reflect the highest degrees of certainty in the analysis. A similar point of view was made by Wiley (1979, 1981) in claiming to retain "important" taxa, which very often reflect stem-lines with high probabilities.

Evolutionary systematists often claimed the inclusion of the "anagenetic component" into the classification (e.g. Mayr, 1981). Taxa of high rank are interpreted as an expression of major evolutionary gaps. This array can be real if caused by fast adaptive radiations and a lack of intermediate forms. I interpret taxa of high rank as reflecting stem lines with very likely monophyly. This interpretation equals the distinction between apomorphy and plesiomorphy and gaps between character states (in a reconstruction). In this way, clado- and anagenesis are considered by correlating each with some probability.

Whereas many authors prefer Wiley's (1979, 1981) sequential method of classification, other cladists still use the dichotomic Hennigian way (e.g. Ax, 1984, 1987; Berthold & Engeser, 1987). I prefer the former, and regard my own proposal as a modification of Wiley's (1981) methodology.

Gauthier (1986) has proposed marking so-called "metataxa" (i.e. taxa, the holo- or paraphyletic status of which cannot be given at present) by an asterisk (taxon*). In combining my original mode of marking grades as "taxa" (Haszprunar, 1986) with Gauthier's (1986) ideas, I have more recently proposed to mark grades by asterisks (*taxa*) and to mark metataxa (e.g. *Architaenioglossa*, *Cerithiimorpha*) by a combination of asterisks and *sedis mutabilis* in the subtaxa (Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988). This enables a better conversation of a metataxon into an para- or holophyletic taxon upon addition of new data. At the time the study was finished, the Cerithioidea was an example of a metataxon. I regard Bieler's (1990) solution of omitting the Cerithioidea from the classification as less acceptable than my proposal of marking the taxon unequivocally.

PRESERVATION OF TRADITIONAL NAMES

In the earliest phase of my phylogenetic work (Haszprunar, 1985a,b), I frequently created new taxa of high rank. However, "nobody can hinder me to become wiser," and several of my friends (see Acknowledgements) have convinced me that preservation of traditional names is a better way. As outlined in Haszprunar (1988: 370), certain new taxa still appear necessary to present phylogeny unequivocally or to reflect taxa with high propabilities. I consider the Archaeogastropoda in its traditional, paraphyletic (orthophyletic) sense still useful in systematics, because in many cases only shells (and radulae) are available, which do not allow for a more specific classification. Thiele's Mesogastropoda is a paraphyletic group—it independently gives rise to both the Stenoglossa and Euthyneura—and therefore has been abandoned. I also regard the Neotaenioglossa (again paraphyletic) as a provisional construct which should be abandoned in the future.

CONCLUSION

I have responded Bieler's (1990) critique on the mode of my phylogenetic analysis on streptoneuran gastropods as follows:

(a) I have provided arguments against doing a maximum-parsimony analysis with equal weighting of characters. (b) I have presented examples of the character analysis and of placement of taxa to demonstrate the method used in the analysis. Proposed synapomorphies are considered as two-fold hypotheses with distinct degrees of likelihood. Accordingly the cladogram is regarded as a theorem of probability, and taxa of high rank are thought to reflect stem-lines of high certainty. (c) I have explained the use of certain taxa in the proposed classification.

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APPENDIX

Corrections of Haszprunar (1988)

(1) p. 377: replace "McLean, 1987" by "McLean, 1988".

(2) p. 378/legend Fig. 1: Replace "Ponder, 1987" by "Ponder, 1988a".

(3) p. 381: So far as is known Truncatelloidea—Vitrinellidae have monopectinate gills (e.g. Bieler & Mikkelsen, 1988).

(4) p. 389, p. 400/Table 2, p. 416: As recently outlined by Houbrick (1989), I have misinterpreted his earlier data on *Campanile symbolicum,* listing "eggs connected by chalazae" for this taxon. In fact, campanilid eggmass connections resemble those found in the Epitoniidae. True chalazae are present in the Valvatidae, however.

(5) p. 400/Table 2: A loss of teleoconch occurs also in numerous euthyneuran taxa.

(6) p. 401/Table 2: Tubular salivary glands with ducts occur in patelloid Docoglossa (Patellogastropoda), but not in Lepetelloidea.

(7) p. 401/Table 2: A cord-like visceral loop throughout its length is restricted to the Patelloidea and Nacelloidea (Neolepetopsidae?).

(8) p. 401/Table 2: Eyes with a lens also occur in the Fissurellidae and Scissurellidae.

(9) p. 413: Replace "Haszprunar, 1988" by "Haszprunar, 1989".

(10) p. 420: Bieler (1988) found some more diagnostic differences between Architectonicidae and Mathildidae.

(11) p. 424/Fig. 5: Points 41 and 42 should be interchanged.

(12) p. 428/Table 5a: The arrangement and subordination of "Superfamily Hot-Vent group A (*Melanodrymia*)" and "Superfamily Neomphaloidea" might appear to include them in the Neritimorpha. Judged from text (pp. 412–414) and phylogram (p. 424/Fig. 5), it should be clear that this is not the case, however.

(13) p. 428/Table 5a: Change "Nacelloidea Lindberg, 1988" to "Nacelloidea Thiele, 1891"; "Helicinoidea Thompson, 1980" to "Helicinoidea Férrusac, 1822"; and

"Scissurelloidea McLean & Haszprunar, 1988" to "Scissurelloidea Gray, 1847." According to Ponder and Warén (1988) it should be "Ampullarioidea Gray, 1824"; "Janthinoidea Lamarck, 1810"; "Littorinoidea Gray, 1840"; "Tonnoidea Suter, 1913"; and "Pterotrachoidea Férrusac, 1821" should be replaced by "Carinarioidea Blainville, 1818."

(14) p. 430/Table 5d: The wrong (printer's error) ranking should be corrected so that N. N. ("Helicoida") becomes superior to Neritimorpha and N. N. ("Euhelicoida").

(15) p. 436: Mackie (1984) was missing in the reference list.

(16) The symposium-volume, *"Prosobranch phylogeny,"* was published in late 1988, and there are differences between the published papers and the manuscripts and abstracts that were made available to me prior to publication (Bieler, 1988; Healy, 1988b; Houbrick, 1988; Lindberg, 1988; Ponder, 1988; Ponder & Warén, 1988). For example, Ponder's (1988) "Cingulopsoidea Fretter & Patil, 1958" was not included in my classification, for nomenclatorial corrections; see (13).

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EVOLUTIONARY BIOLOGY OF OPISTHOBRANCHS

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EDITOR'S NOTE

I accepted these papers for publication on 2 January 1991. Due to problems beyond the control of UNITAS this symposium was in danger of not being published. As the result of the concerted efforts of Malcolm Edmunds and Chris Todd in the fall of 1990, the manuscripts were provided to Malacologia on computer disc.

In order to expedite the publication of this symposium and to better serve UNITAS in a timely fashion, the publication of this symposium has not been delayed. Accordingly, limited attempt has been made to make all procedures for this publication conform exactly to Malacologia specifications. Our sympathy is with the authors and UNITAS.

George M. Davis
Editor-in-Chief
Malacologia

MALACOLOGIA, 1991, 32(2): 205–207

INTRODUCTION

Malcolm Edmunds

Department of Applied Biology, Lancashire Polytechnic, Preston

In suggesting the title for this Symposium 'Evolutionary Biology of Opisthobranchs' I was aware of the wealth of recent studies on taxonomy, comparative morphology, neurophysiology, zoogeography, faunistics and ecology; but while comparative morphology papers usually have an evolutionary theme, papers on zoogeography and neurophysiology rarely do. I was also aware that some talks (e.g. very specialized or narrowly taxonomic papers) can be tedious to listen to unless one is just as badly bitten with the same enthusiasm bug as the speaker. I therefore decided to encourage papers from as wide a field of study as possible but united by an evolutionary theme. I hoped that this would make the Symposium of interest to the non-specialist biologist as well as to opisthobranch *aficionados,* and I hoped too that it might stimulate new approaches to those fields of study that have hitherto lacked an evolutionary approach.

Did this strategy succeed? It is hardly for me to judge, but there are certainly some gaps in the range of subjects covered. There is nothing on neurophysiology, for example, but there are papers on comparative morphology, development and ecology. Most papers concentrate on the ever popular Nudibranchia and Ascoglossa, but there are others which deal with the Bullomorpha and the Aplysiomorpha, and there is even one which reviews current knowledge of a very little-known group, the Rhodopidae.

The names used for the major taxa of opisthobranchs are still very far from being agreed by all workers. There is still controversy over the most appropriate names for several of the orders: Bullomorpha or Cephalaspidea, Aplysiomorpha or Anaspidea, and Ascoglossa or Sacoglossa. Possible confusion with chordate class names together with the advantage of a name that relates to a typical genus in the group suggest that use of Bullomorpha and Aplysiomorpha should be encouraged. But Ascoglossa versus Sacoglossa is more of a problem: both names relate to the radular sac or ascus. Having used Sacoglossa for a quarter of a century the word Ascoglossa still sticks in my gullet (or perhaps in my ascus like a discarded radular tooth), but since most of the recognized authorities on the group now prefer Ascoglossa, I guess I must discard my old preference into my ascus and accept the change.

A century ago comparative morphology was the central plank of zoology. It was also used as an aid to devising a systematic arrangement, but there was rarely any discussion of evolution. Today comparative morphology is much more functional in its approach. It is still important, but primarily for the light it sheds on evolution, and only secondarily for the help it gives with classification. Classification today is an exercise in trying to devise a system that reflects the evolution of the group, while recognizing the limitations imposed by a rigid hierarchy of taxa which can never adequately take account of the realities of the different evolutionary rates of different species. Similarly classical zoogeography was really little more than putting dots on maps whereas today one looks for *causes* of the geographical range of a particular species. These causes can be found in the animal's physiology, ecology or development (Clark, 1975; Edmunds, 1977), while a more detailed study gives insight into the process of speciation (Edmunds, 1982). Evolution occurs by means of natural selection, and the forces of natural selection have been studied extensively by observing changes in morph frequency in terrestrial gastropods such as *Cepaea nemoralis* (reviewed by Jones et al., 1977; Clark et al., 1978; and Cain, 1983), and also in some marine gastropods such as *Littorina* spp. (reviewed by Berger, 1983; and Raffaelli, 1982). No such studies have been made on opisthobranchs. Two reasons for this are the lack of a hard shell with easily quantifiable characters, and the difficulty of monitoring individuals and populations of such small animals in the sea. Yet such studies are now possible: many opisthobranch workers are expert SCUBA divers,

and several polymorphic species of opisthobranch are now known which are ideal for such a study, for example the widespread European aeolid *Eubranchus farrani* (Forbes & Goodsir) (Edmunds & Kress, 1969), and the Indo-Pacific *Phestilla minor* Rudman (Rudman, 1981).

This Symposium includes papers that cover a variety of different aspects of the evolutionary biology of opisthobranchs. First there are three papers on food and feeding habits. Each major taxon of opisthobranchs is associated with a particular type of food: sponges for dorids, coelenterates for aeolids and dendronotaceans, and green algae for sacoglossans (sorry, *asco*glossans). While some species of opisthobranch are euryphagous in their choice of food, others are stenophagous to the extreme of eating just a single species of prey. Jensen's paper is essentially a comparative morphology study of the evolution of feeding structures in the Ascoglossa. While the fine details of feeding structures are closely linked to specific foods, Jensen is able to tease out those anatomical characters that indicate evolutionary relationships and which can also be used in classification. The second paper, by Cattaneo Vietti and Balduzzi, reviews the food and radular characteristics of the Mediterranean genera of dorids. It then applies a method of correspondence analysis to the data set and attempts to relate food to radular structure. A clear correlation is found between radula width and diet, but the relationship between finer details of radular tooth shape and diet is not so evident. The third paper in this section by Picton examines food and feeding habits from yet a third viewpoint. It describes the feeding habits of a single species, the aberrant aeolid *Cumanotus beaumonti,* and relates this to its behaviour and ecology.

The next group of papers relate to defence. The molluscan shell probably evolved as a defensive adaptation in a sluggish, benthic animal that would otherwise have been vulnerable to faster moving, jawed predators (Edmunds, 1974). But the shell also has its disadvantages: it is cumbersome to carry around, its formation requires a lot of energy (which could perhaps be better expended in reproduction), it locks up a lot of calcium so that the animal can only live where there is a supply of this mineral, and it has a regularity of shape such that it is difficult to camouflage from predators. With all these disadvantages it is hardly surprising that some representatives of all three gastropod subclasses have reduced and lost the shell. But it is in the opisthobranchs that shell reduction has occurred most often and been so outstandingly successful as judged by the diversity of form and number of species that are extant. Shell reduction and loss can *only* occur provided that an animal has other means of defence including bodily appendages, coloration and glandular secretions (Edmunds, 1966). The paper by Poulicek, Voss-Foucart and Jeuniaux presents the results of a detailed analysis of the chemical constitution of shells from a variety of opisthobranchs, some with well-developed shells, and others with reduced shells. It attempts to draw functional conclusions relating chemical constitution to the development (or reduction) of the shell, but precisely why one shell should have more chitin or lysine than another remains unknown. The second paper in this section by García-Gómez, Medina and Coveñas describes the histology of the large mantle 'glands' of chromodorids. These are widespread in the family and their precise location has been used as a taxonomic character (Rudman, 1984). But this careful study shows that, far from being typical defensive glands opening on the dorsal mantle surface, they do not open to the exterior at all, hence the authors call them 'mantle dermal formations' rather than glands. Nevertheless they must surely have a defensive function (as evidenced by their location), but whether they can only affect a predator that tears open the mantle, or whether appropriate stimulation causes the contents to burst out in the same way that nematocysts burst out of the cnidosac of an aeolid even though it initially has no opening, is not known. The final paper in this section by Edmunds examines the evidence for the occurrence of warning coloration in nudibranchs. It concludes that some species probably are aposematic, it predicts likely consequences of aposematism which could be tested experimentally and it discusses how aposematism may have evolved in nudibranchs.

The third section of the Symposium covers embryological development and larval ecology. Soliman reviews the patterns of development of opisthobranchs with particular reference to those from the Red Sea, and compares these with the developmental patterns of prosobranchs. Todd reviews data on the development and larval ecology of *Onchi-*

doris bilamellata, and shows that the metamorphosed juveniles spend several weeks feeding on detritus before they are large enough to attack the definitive adult prey (barnacles). The evolution of different modes of larval development is reviewed in the light of larval and adult feeding habits and prey availability.

The fourth section of the Symposium comprises a single ecological faunistic paper by Cattaneo Vietti and Chemello on the opisthobranch fauna of one particular habitat. Besides giving a list of the species found in one Mediterranean lagoon, this paper also reviews the species recorded from other lagoons in the Mediterranean. While the data are inevitably very incomplete, this is the sort of habitat that would be ideal to select for an investigation into the origin of an entire fauna. With knowledge of preferred foods, developmental pattern, salinity tolerances and other physiological factors of the various species in the neighbouring sea, it should be possible to explain why some species are commonly found in lagoons while others are absent.

The final section of the Symposium contains two papers on comparative morphology. The first, by Salvini-Plawen, is in classical mould using every available piece of anatomical information to build up a picture of the evolutionary relationships of a very little-known group of molluscs, the Rhodopidae. A new genus, *Helminthope,* is described which has several differences from *Rhodope.* It is now possible to argue the phylogenetic relationships of this group with much more confidence than has been possible in the past, but, perhaps surprisingly, their systematic position still remains obscure. The final paper by Gosliner reviews the numerous examples of parallel evolution in opisthobranchs but here the comparative approach follows the phylogenetic cladistic method advocated by Hennig (1966) of uniting groups on the basis of shared derived (apomorphic) characters. Arguments concerning the relative merits of traditional evolutionary classification and of phylogenetic cladistic methods are summarized by Ridley (1986). The conclusions reached on the basis of Gosliner's analysis do not agree with those of all recent authors, some of whom link groups into taxa on the basis of shared ancestral (plesiomorphic) characters.

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COMPARISON OF ALIMENTARY SYSTEMS IN SHELLED AND NON-SHELLED SACOGLOSSA (= ASCOGLOSSA) (GASTROPODA: OPISTHOBRANCHIA)

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ABSTRACT

The Sacoglossa comprise a "complete" evolutionary series from species with a large shell into which the animal can withdraw completely, over species with a reduced shell covering only the visceral mass, to shell-less ("nudibranchiate") forms some of which have lateral wing-like extensions, parapodia, others bearing leaf-like or cylindrical dorsal appendages, cerata. Phylogeny has been based on the morphology of the central nervous system and, in part, the reproductive system. It is surprising that the organ system most characteristic of the Sacoglossa, the alimentary system, has never been used when attempting to deduce phylogenetic relationships within the group. The Sacoglossa are all specialized suctorial feeders, and almost all are stenophagous herbivores. Hence, many anatomical adaptations to a particular food occur in the alimentary system. However, a number of characters seem to reflect phylogenetic relationships as well. The present study compares the alimentary system of 17 species of Sacoglossa.

The characters which have phylogenetic importance are: Pharyngeal pouches (presence/absence, size and shape), mode of attachment of the descending limb of the radula and its surrounding ascus-muscle, shape of radular teeth, branching pattern of digestive gland, and position of anus. Pharyngeal pouches occur in all genera of shelled Sacoglossa. Pharyngeal pouches also occur in all genera of the non-shelled Polybranchiidae (= Caliphyllidae), in some, but not all, species of *Bosellia* and *Costasiella,* and in *Plakobranchus.* Very few species of the family Elysiidae have pharyngeal pouches, and they are completely absent in the Stiligeridae and Hermaeidae. In these families the descending limb of the radula and its surrounding ascus-muscle is only attached to the pharynx anteriorly. In other sacoglossans the ascus-muscle is attached throughout its length.

Three basic types of radular teeth occur in the Sacoglossa: Teeth with a ventral concavity and lateral denticles, blade-shaped teeth with or without denticles on the median cutting edge, and sabot-shaped teeth with a scoop-like cusp and a dorsal keel over which the preceding tooth fits. The first type of tooth resembles the central tooth of some cephalaspideans, hence must be plesiomorphic. Blade-shaped teeth occur in some shelled species as well as most non-shelled families, hence may have evolved more than once. Sabot-shaped teeth occur only in hermaeids and stiligerids.

From the original solid digestive gland found in the shelled Sacoglossa and in the non-shelled *Cyerce,* forms evolved with two lateral main ducts. In the shelled genera *Volvatella* and *Berthelinia* some digestive gland tubules extend into the mantle. In the cerata-bearing genera the digestive gland is composed of long, wide main tubules, sending lateral branches into the cerata, dorsal body surface and head region. In the Elysiidae, *Plakobranchus* and *Bosellia* the digestive gland consists of short main ducts sending a dense network of narrow branches throughout the body, including the head and parapodia.

In the shelled Sacoglossa the anus is located in the posterior part of the mantle cavity. In the majority of unshelled species the anus is located at the anterior right corner of the pericardium. In some polybranchiids the anus is located laterally, below the anterior rows of cerata, and many hermaeids and stiligerids have an anal spout on top of the pericardium.

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RELATIONSHIP BETWEEN RADULAR MORPHOLOGY AND FOOD IN THE DORIDINA (MOLLUSCA: NUDIBRANCHIA)

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ABSTRACT

The diet of nudibranchs has been the subject of numerous reports and it is well known that different suborders select different types of prey. In the case of the Doridina, these are usually sponges, bryozoans and ascidians.

The relationship between morphological characteristics of the prey and the functional morphology of radular structure has been studied in 28 genera of Doridina. These were put into 12 groups according to different radular models. These groups were identified by the combination of three different characteristics: number of teeth per half-row, shape of the teeth and their uniformity in each row. Employing literature data and original reports, it was possible to relate these 12 radular models with 136 species of prey, re-grouped under 23 different taxa, using correspondence analysis.

First, the analysis discriminated the broad-radula groups, sponge eaters, from the narrow- and very narrow-radula groups, which have a more catholic diet. The narrow radular groups feed mainly on softer food (Ctenostomata Carnosa and Cheilostomata Anasca), while the groups with a very narrow radula feed more on harder organisms (Cheilostomata Ascophora, Cirripedia and solitary ascidians).

The relationship of tooth shape to diet is less clear, while other anatomical characteristics, such as the presence of a suctorial apparatus or a caecate gut, are more clearly related to specific foods.

INTRODUCTION

The predator-prey relationship of doridaceans has been studied from a variety of viewpoints. Thompson (1958) demonstrated the role of food availability for dorid metamorphosis, while Miller (1961) and Bouchet & Tardy (1976) showed the importance of the prey in species distribution. Yoshioka (1982) described one prey's response to predation while Harvell (1984) considered nudibranchs to be 'prudent predators' of bryozoan colonies. Elvin (1976) studied the role of chemotaxis, while several authors (Ros, 1974; Nybakken & Eastman, 1977; Bloom, 1981; Chadwick & Thorpe, 1981) analysed the interspecific competition for food among sympatric species. Ros (1979, 1980) also gave evidence that doridacean stenophagy can be related to their K-selected ecological strategy.

The radula may be a species-specific tool adapted to the animal's particular prey. Feeding regimes for most species are quite narrow and the shapes of radulae correspond well to food preference (Nybakken & McDonald, 1981). Todd (1981), in his review of nudibranch ecology, distinguished four trophic groups: sponge-grazers (dorids), bryozoan-grazers (mainly dorids), hydroid-grazers (aeolids) and 'miscellaneous' groups (including representatives of all nudibranch suborders). Generally the radula of a dorid which eats sponges differs markedly from that of a dorid feeding on sessile acorn barnacles or encrusting bryozoans, but difficulties arise when trying to find the relationships between radular morphology and prey within these two groups.

In this paper an attempt is made to point out the relationship between morphological characters of the prey and functional morphological aspects of radular structure in 28 genera of Doridina.

MATERIALS AND METHODS

Data available in literature were used together with original data collected by one of us (R.C.V.). We have used mainly the data reported by Miller (1961), Swennen (1961), Thompson (1964), McBeth (1971), Clark (1975), Ros (1975, 1978), Barletta (1976), Bloom (1976), Ryland (1976), McDonald & Nybakken (1978, 1980), Behrens (1980), Chadwick & Thorpe (1981), Todd (1981), Garcia & Bobo (1984), Thompson & Brown

(1984), Millen (1985) and Millen & Gosliner (1985). In all, 28 genera of *Doridina* which occur in the Mediterranean Sea were used in the analysis, together with 136 species of prey from all over the world. The dorid genera have been divided according to their radular structure (Table 1).

We have discriminated, first of all, broad (B), narrow (N) and very narrow (V) radulae, with >30, 4–30 and <4 teeth per half-row respectively. It is known that there are intraspecific and ontogenetic radular variations (Bertsch, 1976; Nybakken & McDonald, 1981) and that the number of teeth per row is statistically related to the specimen's weight (Bloom & Bloom, 1977), but in the genera considered here the number of teeth per half-row has a quite narrow range of variation. Moreover the differences in food between adult and young specimens were not taken into consideration.

Secondly we have discriminated the tooth shape, considering separately simple hooked teeth (S), complex hooked teeth (C) and other teeth (O). In this last category we put all types of teeth difficult to catalogue as, for example, the long serrated ones of *Aldisa,* the flat ones of *Ancula* and those of *Crimora.* According to Bloom (1976) the curvature of the hook seems to be important in predation. In this work it is not considered because we have often seen variation in the hooks in the same row.

Finally the similarity (A) or dissimilarity (D) in the shape of the teeth in the same row was considered.

The prey data for each radular group of genera were first studied qualitatively as presence or absence of a particular prey in the diet of each radular group. These data were then quantified to give a weighted predation value (V) for each prey, on the basis of the frequency of reports on diet of each nudibranch species in the literature, according to the following formula:

$$V_{i,k} = \frac{N_{i,k}}{N_k}$$

where $V_{i,k}$ = weighted predation value by the k-th radular group on the i-th prey;

$N_{i,k}$ = number of bibliographic records of predation by the k-th radular group on the i-th prey;

N_k = total number of bibliographic records of predation by the k-th radular group on the whole prey set.

Both qualitative and weighted data were used for statistical analysis by a method of factorial analysis (correspondence analysis, Benzécri et al., 1973) which allows one to evaluate at the same time both the diet differences between radular groups and the relationship between these groups and different kinds of prey.

Following the first analysis which treated all the prey species separately, further analyses were carried out after re-grouping these species into 23 different taxa (generally orders) (Table 2), to reduce the noise of errors or disagreements in the prey determinations at a specific level.

RESULTS

Fig. 1a gives the results of a correspondence analysis of the presence/absence of particular prey in the diet of each radular group, keeping separated the data on all 136 prey species. It shows the expected discrimination between dorids with broad radulae (B) and a sponge diet, and those with narrow (N) or very narrow radulae (V) and a more catholic diet. This discrimination is very evident along the first axis, while along the 2nd, 3rd and 4th axes (these last two not represented in the figure) only three radular groups (NSA, VCA and NOD) are dispersed, all with a very specialized diet.

The variances yielded by the first four axes are, however, low (11.5% for each axis): in fact the heterogeneity of the data and the already mentioned problems of specific determination of prey make the significance of this analysis doubtful.

The results of the second group of analyses, carried out on the prey records put into 23 systematic groups and utilizing the weighted data, confirm many of the preceding observations. Three well-defined clusters are formed (Fig. 1b): the B cluster, with broad radulae feeding nearly exclusively on demosponges; the N-V cluster, with narrow radulae and a non-sponge diet, and the NSA cluster, with narrow radulae feeding on calcareous sponges. The two radular groups VCA and NOD, which in the first analysis remained discriminate along different axes, in this case fall together in the N-V cluster: in fact, their diet is very unusual only at a specific level. It is clear that in this second analysis there is no discrimination between the finer differences of radula and diet within both the B cluster and

TABLE 1. Diet and anatomy in the Doridina. For details of radular models, see text. For each prey group the number of species present in the diet of every radular model is reported in parentheses. The other anatomical characters are: A = acaecate; C = caecate; NS = non-suctorian; S = suctorian. In the final columns: N = total number of single bibliographic records, and V = weighted value for each prey group (see text for derivation).

Radular models	Dorid genera	Other anatomical characters	Prey groups (number of species)	N	V
BSA	*Doris, Archidoris, Discodoris* (= *Anisodoris*), *Peltodoris, Jorunna, Platydoris, Carminodoris*	C, A	Porifera Calcarea (1)	1	.01
			Porifera Choristida (1)	1	.01
			Porifera Hadromerida (4)	5	.06
			Porifera Halichondrida (6)	34	.47
			Porifera Poecilosclerida (6)	11	.15
			Porifera Spirophorida (1)	1	.01
			Porifera Haplosclerida (5)	15	.20
			Porifera Dictyoceratida (1)	1	.01
			Bryozoa Cheilostomata Ascophora (3)	3	.04
BCA	*Cadlina, Chromodoris, Hypselodoris*		Porifera Homosclerophorida (1)	1	.02
			Porifera Choristida (1)	4	.08
			Porifera Halichondrida (3)	4	.08
			Porifera Poecilosclerida (3)	4	.08
			Porifera Axinellida (1)	2	.04
			Porifera Haplosclerida (2)	8	.17
			Porifera Dictyoceratida (8)	15	.33
			Porifera Dendroceratida (2)	7	.15
BCD	*Rostanga*	A	Porifera Halichondrida (2)	2	.12
			Porifera Poecilosclerida (11)	12	.75
			Porifera Haplosclerida (2)	2	.12
BOA	*Aldisa*	A	Porifera Halichondrida (1)	1	.12
			Porifera Poecilosclerida (5)	7	.87
NSA	*Aegires*	NS	Porifera Calcarea (3)	4	1
NSD	*Polycera, Greilada, Palio, Limacia, Thecacera*	NS	Cnidaria Anthozoa Gorgonacea (1)	1	.02
			Bryozoa Ctenostomata Stolonifera (3)	5	.14
			Bryozoa Cheilostomata Anasca (12)	21	.60
			Bryozoa Cheilostomata Gymnocystidea (1)	1	.02
			Bryozoa Cheilostomata Ascophora (5)	6	.17
			Bryozoa Cyclostomata (1)	1	.02
NCD	*Acanthodoris, Adalaria*	S	Bryozoa Ctenostomata Carnosa (6)	15	.57
			Bryozoa Cheilostomata Anasca (4)	6	.23
			Bryozoa Cheilostomata Ascophora (4)	5	.19
NOD	*Crimora*	NS	Bryozoa Cheilostomata Anasca (3)	3	1
VSA	*Polycerella*	NS	Bryozoa Ctenostomata Stolonifera (4)	4	.80
			Bryozoa Cheilostomata Anasca (1)	1	.20
VCA	*Trapania*	S	Entoprocta (1)	1	1
VCD	*Onchidoris, Goniodoris, Okenia, Diaphorodoris*	S	Bryozoa Ctenostomata Stolonifera (1)	2	.02
			Bryozoa Ctenostomata Carnosa (4)	5	.07
			Bryozoa Cheilostomata Anasca (9)	11	.16
			Bryozoa Cheilostomata Cribrimorpha (1)	1	.01
			Bryozoa Cheilostomata Gymnocystidea (2)	2	.02
			Bryozoa Cheilostomata Ascophora (14)	23	.34
			Bryozoa Cyclostomata (2)	2	.02
			Crustacea Cirripedia (4)	5	.07
			Ascidiacea (solitary ascidians) (6)	7	.10
			Ascidiacea (colonial ascidians) (5)	9	.13
VOD	*Ancula*	S	Entoprocta (1)	2	.33
			Bryozoa Ctenostomata Stolonifera (1)	1	.16
			Ascidiacea (colonial ascidians) (3)	3	.50

TABLE 2. List of systematic groups of prey which have been regrouped for some analyses.

	Prey groups	Number of species
1	Porifera Calcarea	4
2	Porifera Homosclerophorida	1
3	Porifera Choristida	2
4	Porifera Hadromerida	4
5	Porifera Halichondrida	6
6	Porifera Poecilosclerida	22
7	Porifera Axinellida	1
8	Porifera Spirophorida	1
9	Porifera Haplosclerida	9
10	Porifera Dictyoceratida	8
11	Porifera Dendroceratida	2
12	Cnidaria Gorgonacea	1
13	Entoprocta	2
14	Bryozoa Ctenostomata Stolonifera	6
15	Bryozoa Ctenostomata Carnosa	7
16	Bryozoa Cheilostomata Anasca	21
17	Bryozoa Cheilostomata Cribrimorpha	1
18	Bryozoa Cheilostomata Gymnocystidea	2
19	Bryozoa Cheilostomata Ascophora	18
20	Bryozoa Cyclostomata	3
21	Crustacea Cirripedia	4
22	Tunicata (solitary ascidians)	6
23	Tunicata (colonial ascidians)	5
Total number of species		136

the N-V cluster. Further analyses were therefore carried out for these groups.

From the analysis carried out on B groups only (Fig. 1c), it is now possible to discriminate three of the four broad-radular models along the first axis (which is the only very significant one in this analysis). BCA radulae, feeding mainly on horny demosponges (Dictyoceratida and Dendroceratida), form a distinct cluster at one extreme of the diagram. BCD and BOA radulae, linked to Poecilosclerida, form a second very discrete cluster at the other extreme. BSA radulae, with a more generalized diet, form an intermediate group dispersed along the second axis. The prey point of ascophoran bryozoans (no. 19) falls in this last cluster too, as the supposed diet of Platydoris argo is the bryozoan Sertella.

Fig. 1d presents the analysis carried out on the radular groups of the non-sponge eating genera. Radular groups VCA (*Trapania*) and VOD (*Ancula*) are clearly separated from the main group of genera: both include entoprocts in their diet. *Trapania* has no other food, while *Ancula* also feeds on colonial ascidians and bryozoans. VSA and NCD groups, both eating principally ctenostomatous bryozoans, are also well separated, showing a good relationship with Stolonifera and Carnosa respectively. The remaining radular groups form two clusters with just two intermediate points. The first cluster (VCD) shows a close relationship with ascophoran bryozoans, barnacles and solitary ascidians, and the second (NOD and NSD) with gorgonaceans and anascan bryozoans.

DISCUSSION

The study of the relationship between radular morphology and food in the Doridina still has many unresolved problems. Literature reports sometimes indicate as prey the organism on which the nudibranch was crawling when it was collected: this makes some of the data unreliable. On the other hand widely distributed nudibranchs may have different preferences in different geographical locations (McDonald & Nybakken, 1978): for example *Goniodoris nodosa* feeds on the ascidian *Dendrodoa grossularia* along the Atlantic French coast (Bouchet & Tardy, 1976), yet in England (Thompson & Brown, 1984) it feeds on fleshy ctenostomes.

Other data appear surprising: for example, as mentioned above, *Platydoris argo* in the Mediterranean Sea (Ros & Gili, 1984) feeds on the bryozoan *Sertella,* but has a typical sponge-eating radula; *Polycera atra* grazes on the gorgonian *Lophogorgia chilensis* (Lewbel & Lance, 1975), but other members of this genus feed exclusively on bryozoans. Moreover, according to Ryland (1976), some doridaceans associated with bryozoans are not necessarily predators: sometimes they can feed on bacterial films and detritus.

The investigation of gut contents can also create errors: while grazing on a sponge, a nudibranch can ingest other casual food such as polychaete larvae, copepods and algal filaments (Aboul-Ela, 1959). These prey are sometimes given a greater importance than the sponge itself.

It is also surprising that some very common species, such as bryozoans of the genera *Flustra, Chartella* and *Sertella* or the sponge *Petrosia ficiformis,* have only one predator: this is probably due to scarcity of data.

In spite of these problems this study confirms the relationship between radula and

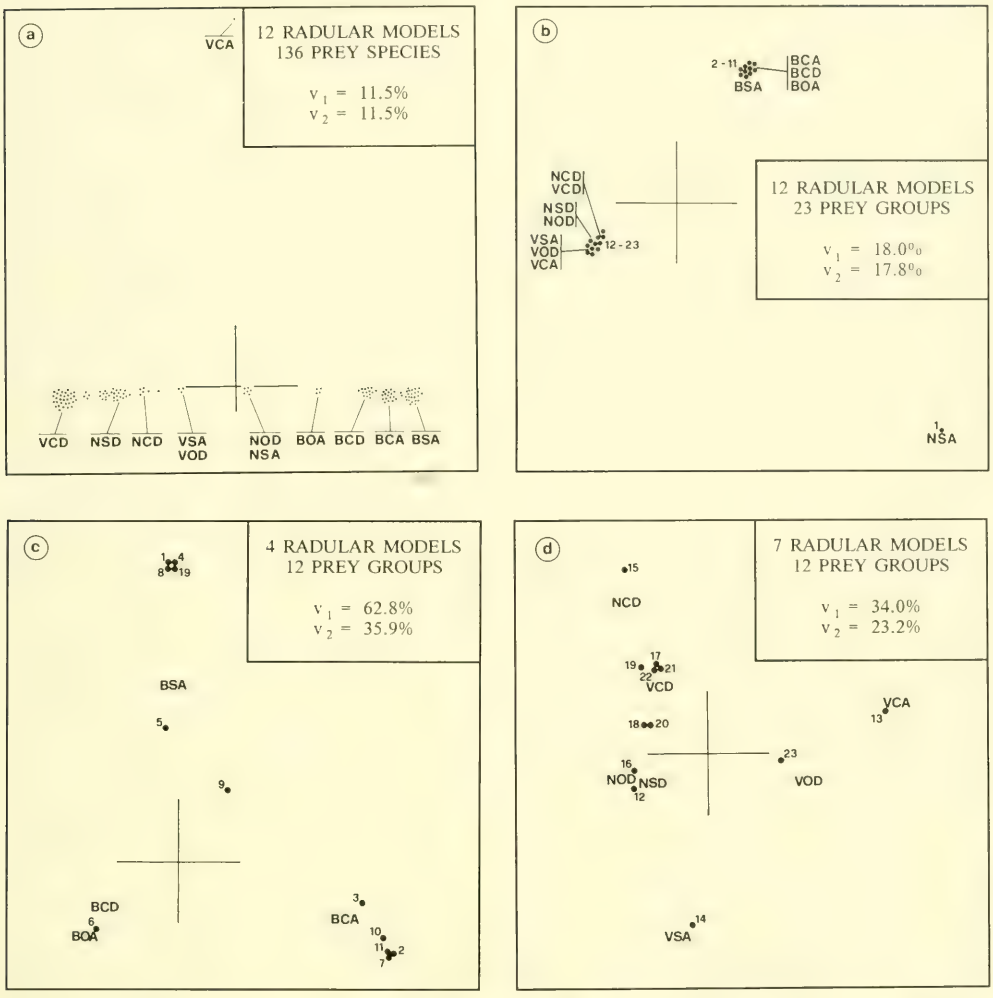

FIG. 1. Diagrams to show the results of the ordination models along the 1st (x) and 2nd (y) axes, using correspondence analysis: a. on all 12 radular models and 136 prey species; b. on all 12 radular models and 23 prey groups; c. on 4 radular models that feed on 12 prey groups (demosponges and bryozoans); d. on 7 radular models that feed on 12 non-sponge prey groups. In each diagram the variance percentages yielded by the axes (v1 and v2 respectively) are reported. Radular model points are indicated by the same abbreviations used in Table 1 (see text for explanation). Prey points are indicated by dots: in diagrams b, c and d numbers refer to the prey groups listed in Table 2.

diet: dorids with broad radulae prey exclusively on sponges while those with narrow and very narrow radulae eat mainly soft (Bryozoa Anasca and Carnosa) and hard prey (Cirripedia, Bryozoa Ascophora, solitary ascidians) respectively. *Aegires,* grazing on Calcarea (Bertsch, 1980), is unusual among sponge-eaters in having a narrow radula, but with more than 20 teeth per row it is really intermediate between the broad- and narrow-radula groups.

The relationship between tooth shape and diet remains unclear: in the most complex group (VCD) it is possible to find species feeding on barnacles (*Onchidoris bilamellata*), on a large variety of bryozoans (*O. muricata*) and on tunicates (*Goniodoris castanea* and *Okenia elegans*). Only in the sponge-eaters can we note that complex hooked teeth (C) are used mainly on horny sponges, while the simple hooked teeth (S) are used on a much wider variety of sponges. This last

type of tooth can also be found both in specialist species (e.g. *Peltodoris atromaculata* which feeds exclusively on *Petrosia ficiformis*) and in more generalist species such as *Archidoris pseudoargus.*

In addition to these correlations between radular teeth and diet there are other anatomical and physiological adaptations to different foods. Among the anadoridaceans there are two types of feeding behaviour, linked to the presence or absence of a suctorial pump connected to the buccal mass. The non-suctorial groups (*Polycera* and allied genera, *Crimora* and *Polycerella*) are rasping feeders and have a diet based mainly on soft bryozoans, while the suctorial ones, such as *Onchidoris* or *Goniodoris,* are sucking feeders, which prey principally on harder organisms such as barnacles, solitary tunicates and strongly calcified bryozoans.

Within the sponge-eating groups the genera *Chromodoris, Hypselodoris* and *Cadlina* graze mainly on horny sponges and have a caecate gut, while *Rostanga* and *Aldisa* feed mainly on the *Poecilosclerida* and have an acaecate gut. Probably this difference is linked to the different nature of the extra-cellular collagen matrix in the various demosponges (Bergquist, 1978) or to differences in the skeletal organization (Bloom, 1981).

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Cumanotus beaumonti (ELIOT, 1906), A NUDIBRANCH ADAPTED FOR LIFE IN A SHALLOW SANDY HABITAT?

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ABSTRACT

Many of the anatomical peculiarities of the family Cumanotidae are possibly explained by the ecology of the species. New observations on the habitat and diet of the species *Cumanotus beaumonti* suggest that the broad foot, long muscular cerata modified for swimming and unusual spawn coil are adaptive features which enable *Cumanotus* to be successful in a shallow sandy environment feeding on the hydroid Corymorpha nutans.

INTRODUCTION

The aeolid nudibranch *Cumanotus beaumonti* has been rather enigmatic since its almost simultaneous discovery in southern England and Norway during the first decade of this century. Recent publications describing the British fauna have relied on the original descriptions of this species, and little was known about its habitat and ecology. The discovery of populations in Northern Ireland during 1985 and direct observations by SCUBA diving have provided new information about this attractive aeolid.

Synonymy

Coryphella beaumonti Eliot, 1906
Cumanotus laticeps Odhner, 1907

Description

The body is 20–25 mm long in mature specimens and the foot is broad, about 8 mm wide. There are prominent propodial tentacles at the front corners of the foot and small oral tentacles on the anterior corners of the head. Two smooth erect rhinophores are placed close together on the top of the head; they are shorter than the surrounding cerata (Fig. 1). The cerata are long and numerous, exceeding three-quarters of the body length; the anterior ones arise in front of the rhinophores. The cerata are arranged in rows, 6 rows of up to 9 cerata arise from the anterior liver ducts and 6–7 single rows of up to 8 cerata arise from the posterior liver. Elongate cnidosacs can be seen at the tips of the cerata. The anal papilla is on the right side of the body, between the cerata arising from the anterior and posterior liver. The coloration of the body is pellucid white, becoming rosy pink in the dorsal and head region. The digestive gland is purple in colour. The dorsal surface and cerata are speckled with gold-coloured pigment, concentrated in the head region.

The reproductive system consists of a coiled ampulla, two bursae, and a coiled vas deferens leading to a large penial sheath containing an extensively coiled penis. There are two distinctive rosettes of tubercles tipped with tiny chitinous hooks alongside the female aperture, as noted by previous authors.

The radula of a 20 mm preserved specimen consisted of 20 rows of teeth of formula 1—1—1. The central tooth is horseshoe-shaped, with a strong central denticle and 11–16 small denticles on either side. The lateral teeth also have strong main denticles and cutting edges of 13–20 small denticles. The radula tapers rapidly from the oldest row with central tooth 50 μm wide to the youngest row, with central tooth 200 μm wide.

Biology

Fifteen specimens were collected in June 1985 in Church Bay and one from Arkill Bay on Rathlin Island, Co Antrim, Northern Ireland. The animals were either crawling on a sea-bed of medium sand in 15 m of water or were at the tops of the stalks of the hydroid *Corymorpha nutans* M Sars, 1835, which was common on the sand. This hydroid consists of a solitary stem, 50–100 mm tall, bearing a single large polyp which measures 15–20 mm across the ring of long, undulating tentacles. Animals on the *Corymorpha* stems were

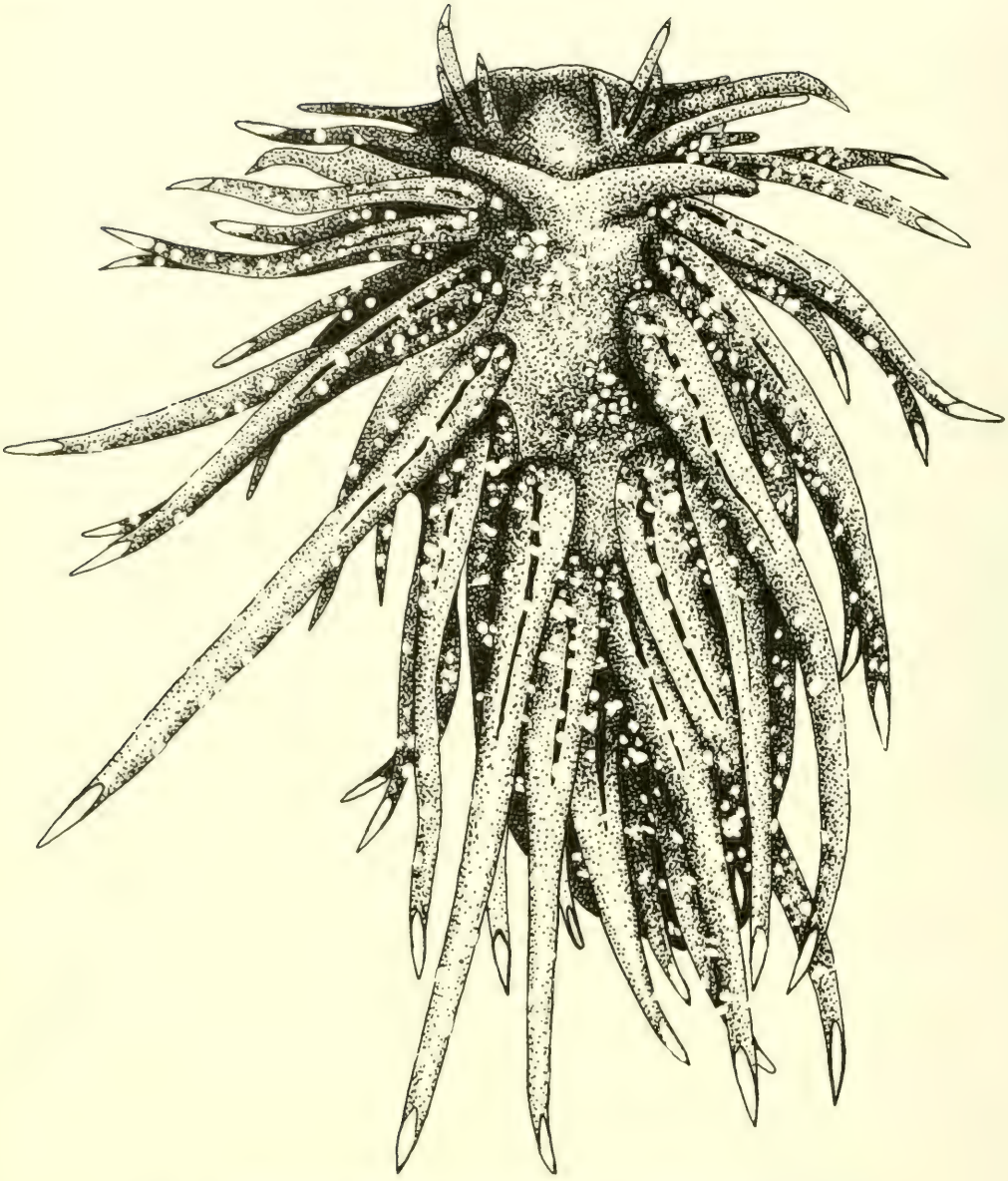

Fig. 1. *Cumanotus beaumonti,* dorsal view of a living specimen (length 20 mm).

in the process of devouring the polyps, and were inconspicuous, with their long, flowing cerata looking very similar to the tentacles of the hydroid. Spawn coils of *Cumanotus* were more numerous than the animals, and consisted of two to four turns of egg-bearing jelly attached to the sand by a long, string-like portion covered with sand grains. Specimens were seen to swim vigorously by moving their cerata in a co-ordinated back and forth motion when collected or disturbed.

DISCUSSION

Two other species of the family Cumanotidae have been described: *Cumanotus cuenoti* Pruvot-Fol, 1936, and *Cumanotus fer-*

naldi Thompson & Brown, 1984. *Cumanotus cuenoti* has recently been redescribed by Tardy & Gantès (1980) and is a smaller animal with no trace of oral tentacles or propodial tentacles and only 5–9 denticles on the central and lateral teeth. It has no surface pigmentation apart from a small orange mark on the head of some individuals. *Cumanotus fernaldi* was proposed as a new name for the species described as *Cumanotus beaumonti* by Hurst (1957) from the Pacific coast of North America. This species is illustrated by Thompson (1976), Thompson & Brown (1976), Behrens (1980) and McDonald & Nybakken (1980). It differs from *C. beaumonti* in colouration, having white apical bands of pigment on the cerata, yellowish-brown digestive gland and none of the gold speckling of *C. beaumonti*. Thompson (1984) reports that the radula is also different, with a slender central cusp flanked by up to 26 denticles on the central tooth and a short cusp on the lateral tooth flanked by 28 denticles.

All known species of Cumanotidae appear to feed on athecate hydroids. The present species feeds on *Corymorpha nutans* as reported above, *C. cuenoti* feeds on *Ectopleura dumortieri* and *Tubularia* according to Tardy & Gantès (1980), and Behrens (1980) reports that *C. fernaldi* feeds on *Tubularia*. *Cumanotus* species have a number of unusual features in which they differ from most other aeolid nudibranchs. Several of these features could be adaptations to life on unstable sedimentary sea-beds, feeding on transitional populations of hydroids. Tardy & Gantès (1980) point out the resemblance between the ceratal morphology, broad foot and spawn coils in *Cumanotus* and *Cerberilla* and suggest that *Cumanotus* may be capable of burrowing. The ability to swim up into the water column was reported for *C. fernaldi* and *C. cuenoti,* and is shared by the *C. beaumonti* populations reported here. Tardy & Gantès speculate on the possibility that this enables *Cumanotus* populations to follow medusae of their reproducing prey to areas down-current where new populations are being established. There is some evidence from the present observations that this may actually happen. On Rathlin Island there was a steady current of 0.5–1 knot and many more spawn coils than seemed possible for the observed population of *Cumanotus*. At sites off Kilkeel, Co Down, in May 1984 numerous spawn coils and stalks of Corymorpha nutans were seen on the muddy sand sea-bed, but no adult animals could be found despite extensive searching. Is it possible that the animals had exhausted their food supply at this site and dispersed en masse in search of new pastures?

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REGRESSIVE SHELL EVOLUTION AMONG OPISTHOBRANCH GASTROPODS

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ABSTRACT

Many opisthobranch molluscs have reduced or lost their shells during evolution. This paper discusses the microstructural and chemical changes associated with shell regression in opisthobranchs. All shells of benthic species examined so far (twelve species belonging to Pyramidellacea, Cephalaspidea and Anaspidea) show the same features: two thick layers of complex crossed-lamellar material below one thin external layer of granular or homogeneous structure. The shells of thecosomatous pteropods (six species with a planktonic mode of life) show an inner helicoidal structure surmounted by a thin granular layer. An intermediate condition is found in the most primitive pteropods (*Limacina*) with a complex crossed-acicular fabric under the granular one. The degree of calcification, chitin content and amino acid composition of both acid-soluble and insoluble fractions of shells of 20 species belonging to Cephalaspidea, Pyramidellacea, Anaspidea, Notaspidea, Sacoglossa and Pteropoda are presented. The degree of calcification shows a marked tendency to decrease and the chitin content to increase from the primitive to the more advanced species. The amino acid content of both protein fractions appears relatively stable in all species, and very similar to that of prosobranchs, although there are some minor variations. All these features can be correlated with the need for suppleness in very thin reduced shells that would otherwise be too brittle. These features are polyphyletic and convergent with shells of other molluscs showing the same tendency to reduce the shell (cephalopods, heteropods, pulmonate slugs, Polyplacophora).

INTRODUCTION

The Opisthobranchia are not defined by a set of features common to all members of the subclass but by certain marked tendencies, one of which is the tendency to lose or to reduce the shell in the course of evolution. Some of them still retain the shell and even the operculum (e.g. the Pyramidellidae and Acteonidae); in others, the shell has become greatly reduced, either remaining external, or internal and covered by two folds of the mantle that may fuse dorsally. In the majority of Opisthobranchia, the shell disappears at the end of larval life. "No doubt some of the early evolutionary experiments along these lines ended in failure, but many more were partially or totally successful and we are fortunate in that modern oceans contain about three thousand species of gastropods which show intermediate stages in the general trend outlined above" (Yonge & Thompson, 1976).

The goal of this paper is to try to describe and understand the process of shell regression at a microstructural and biochemical level. This 'neo-conchological' approach will take into account the principles of Florkin (1966), i.e. that the molecular aspects of adaptation and phylogeny must rely upon relationships established following 'classical' methods (anatomy, embryology, etc.) in order to detect molecular convergences. So we base this paper on the approach of Ghiselin (1966) in which "the comparative and functional anatomy of the reproductive system throughout the subclass is treated critically to provide a sounder basis for phylogenetic studies". We will attempt to outline the ways the shell has changed along some of the main evolutionary lines of the phylogenetic tree proposed by Ghiselin (1966) (Fig. 1). The phylogeny of thecosomatous pteropods adopted here is that of Rampal (1973) (Fig. 2).

The authors wish to dedicate this paper to the memory of Professor C. M. Yonge in recognition of his long-standing interest in, and contribution to, malacology.

MATERIALS AND METHODS

All molluscs studied were collected alive. After removal of the soft parts, the shells were

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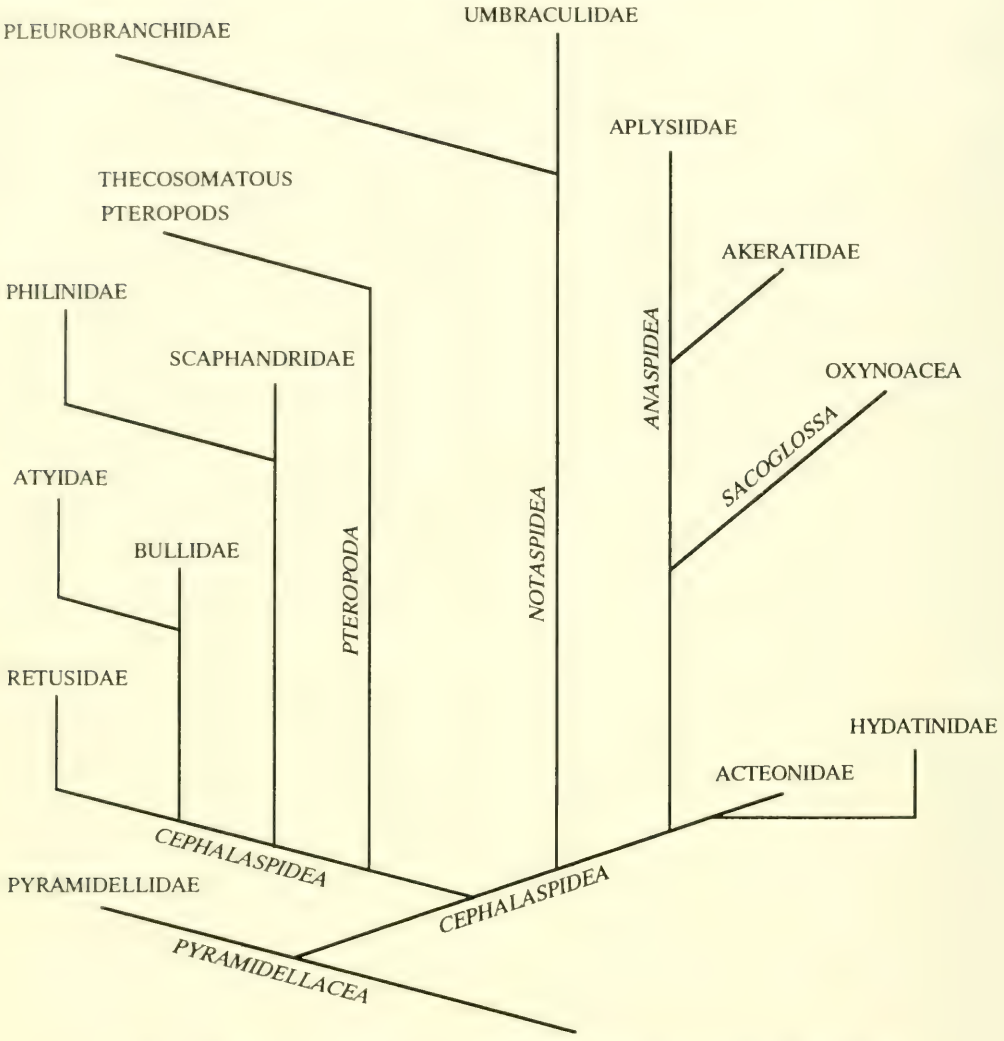

FIG. 1. Phylogeny of opisthobranch gastropods (simplified from Ghiselin, 1966).

cleaned from the periostracal layers with a rotatory metal brush, washed in distilled water and either preserved dried (for SEM) or in 70% ethanol (for biochemical analyses).

Scanning electron microscopy (SEM)

Pieces of shell were cut from the last whorl, some distance away from the aperture and either broken under the dissecting microscope (fracture surfaces) or cut perpendicularly to the growth axis, polished and etched with 0.05N HCl. The material was fixed in 4% glutaraldehyde in 0.2M cacodylate buffer pH 7.4 (2 h), washed and postfixed in OsO_4 (2%) in the same buffer (2 h). After dehydration through graded ethanol series, the dried material was orientated and mounted onto Al-stubs with silver or nickel print, coated with 10nm Au-Pd in a cool-diode sputter coater (Balzers SCD 030). The material was observed with a Cambridge Scientific Instruments Stereoscan or a Siemens ETEC Autoscan electron microscope operated at 20 kV.

Biochemical analyses

The shell material was ground and decalcified with 0.5N HCl at ambient temperature.

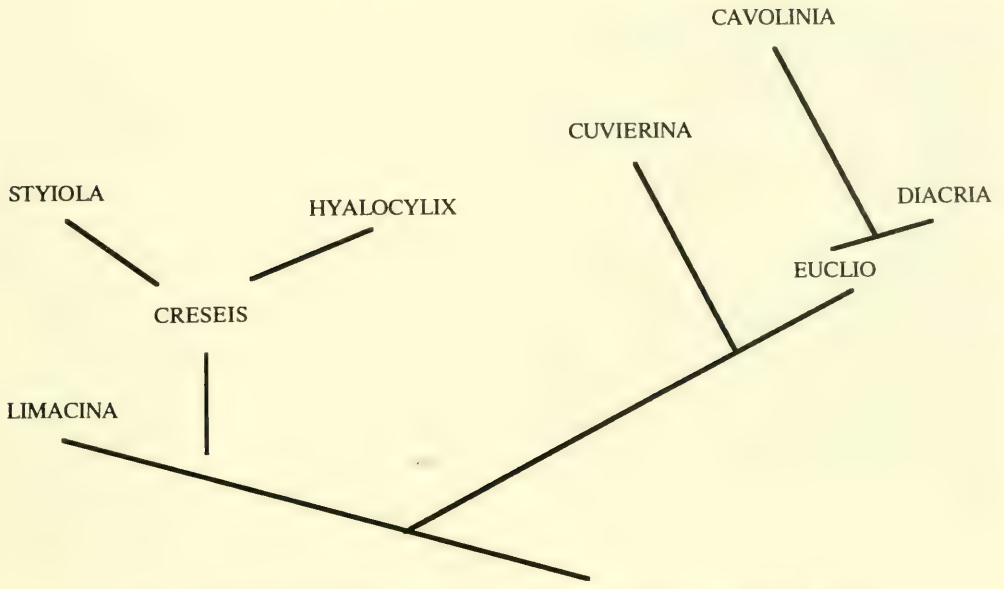

FIG. 2. Phylogeny of thecosomatous pteropods (redrawn from Rampal, 1973).

The organic remains were centrifuged (18,000 rpm), washed and dried to constant weight. The supernatants were dialysed against H2O (min. 1/360 V/V) and the acid-soluble material recovered by evaporation in vacuum in a rotatory evaporator. For amino acid determinations, the material was hydrolysed with 6N HCl for 24 h at 105°C in vacuum. The amino acid patterns were analysed by automatic ion exchange chromatography (single column procedure according to Devenyi (1971)). The method gives reproducible results of better than 1% at the 10−8M level for identical runs (Ghiselin et al., 1967). Chitin was estimated by the specific enzymatic method of Jeuniaux (1965). Its accuracy is better than 4% for chitin weights above 15 μg.

RESULTS

Scanning electron microscopy

Fractures and etched polished surfaces of shells of 18 species belonging to Cephalaspidea (9), Pyramidellacea (1), Anaspidea (2) and Pteropoda (6) were examined with SEM.

The shells of all the twelve benthic species examined (*Pyramidella terebelloides* (A. Adams), *Acteon tornatilis* (L.), *Hydatina physis* (L.), *H. zonata* (Gmelin), *Bulla ampulla* L., *B. punctulata* A. Adams, *Scaphander lignarius* (L.), *Atys cylindricum* Hinds, *Haminoea hydatis* (L.), *Philine aperta* (L.), *Aplysia depilans* Gmelin, *A. punctata* Cuvier) are aragonitic in nature and mainly of crossed-lamellar fabric, typical of more advanced gastropods. The shells of Pyramidellacea and Cephalaspidea are three-layered, with two thick layers of crossed-lamellar structure under a thin layer of homogeneous or granular material. The first order lamellae of the two crossed-lamellar layers are perpendicular to each other. The internal shells of Anaspidea (*Aplysia* spp.) are much less calcified except in the apex area where poorly organized cross-lamellar elements are obvious (Fig. 3).

The shells of the six pelagic species examined so far (*Limacina inflata* (Orbigny), *Creseis acicula* Rang, *Hyalocylis striata* (Rang), *Euclio pyramidata* (L.), *Diacria trispinosa* (Lesueur), *Cavolinia longirostris* (Lesueur)) look quite different. Apart from *Limacina inflata,* the shells are built following the same scheme: under a thin granular layer, there is a crossed-acicular layer progressively becoming helicoidal close to the inner side of the shells (Fig. 4). These observations are consistent with the works of Be et al. (1972) and Bandel (1977) on the shells of *Cuvierina columella* and *Cavolinia tridentata.* The shell of *Limacina inflata* occupies an intermediate po-

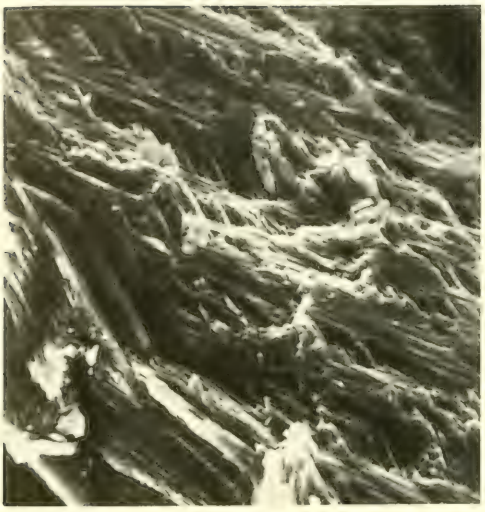

FIG. 3. SEM picture of the crossed-lamellar fabric at the apex of the shell of *Aplysia punctata.* Scale: 10μm.

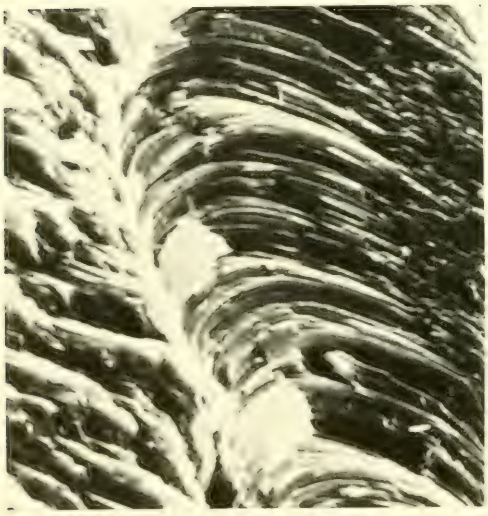

FIG. 4. SEM picture of the helicoidal fabric at the inner side of the shell of *Cavolinia longirostris.* Scale: 10μm.

sition: under a thin granular layer, there are two poorly individualized layers of somewhat disorganized crossed-acicular fabric. This is consistent with the view that the Limacinidae are the most primitive pteropods (Rampal, 1973) (Fig. 2).

Chitin and degree of calcification

We have previously shown that the degree of calcification and the chitin content of mollusc shells can be discussed in an evolutionary perspective (Goffinet & Jeuniaux, 1979; Poulicek, 1982; Poulicek & Kreusch, 1986). We have estimated the degree of calcification and the chitin content of the shells of 20 species of opisthobranchs, some with external shells, others with different degrees of shell reduction. The results are given in Table 1.

Except in the case of *Aplysia, Oxynoe* and the Notaspidea, the organic content of the shells is low (< 1% of the dry calcified weight) as previously shown for other gastropod shells with crossed-lamellar fabric (Poulicek, 1982). The high organic content of *Retusa* is probably due to contamination since it is particularly difficult to get rid of the periostracum in such tiny shells. Nevertheless there is a slight tendency for organic content to increase with shell regression, particularly in the internal shells.

The chitin content data display the same features: low level (<1% of the insoluble organic matter) in the external shells and higher levels of the chitin content in species with smaller internal shells. This tendency is particularly obvious in the internal shells within each of the taxa Cephalaspidea, Anaspidea and Notaspidea: the chitin content is always >1% of the organic matter, close to 8% in *Aplysia, Berthella* and *Berthellina.*

Amino acid composition

Table 2 shows the amino acid composition of the proteins of the insoluble fraction of the shells of eleven species. The patterns are typical of 'conchiolins' with very high acidic amino acid content (Asp and Glu), and much Gly, Ala, Ser and Leu. The sum of these last six amino acids constitutes more than 60% of the total amounts of the residues in the insoluble protein fraction of the shells. There is little Cys in most species and no OH-Pro (except in the case of *Akera* and *Oxynoe* (Degens et al., 1967)).

The variability between the different species is low, probably because they are all fairly closely related. The primitive Pyramidellacea and Cephalaspidea are characterized by high levels of Asp, whereas the shells of the notaspidean *Umbraculum* appear somewhat peculiar with very high Pro content, and

TABLE 1. Organic matter and chitin content in the shells of 20 species of Opisthobranchia.

Opisthobranch species	Type of shell	Calcified weight (mg)	Decalcified weight (mg)	Organic content (%)	Weight of chitin (μg)	Chitin as % of organic matter
PYRAMIDELLACEA						
Pyramidella terebelloides (A. Adams)	external	3361.1	12.1	0.36	46.33	0.38
CEPHALASPIDEA						
Acteon tornatilis (L.)	external	2355.2	17.9	0.76	53.09	0.30
Hydatina zonata (Lightfoot)	external	1658.2	13.1	0.79	21.26	0.16
Retusa obtusa (Montagu)	external	374.0	11.4	3.05	(4.32)	(0.04)
Bulla punctulata A. Adams	external	3882.4	13.2	0.34	37.43	0.28
Scaphander lignarius (L.)	external	1955.9	11.9	0.61	14.57	0.12
Atys cylindricum Hinds	external	2533.3	11.4	0.45	41.16	0.36
Haminoea navicula (da Costa)	external	1200.0	10.8	0.90	51.19	0.47
Philine aperta (L.)	internal	493.2	3.2	0.65	42.80	1.34
ANASPIDEA						
Akera bullata Müller	external	352.9	2.4	0.68	17.52	0.73
Aplysia punctata Cuvier	internal	796.4	121.4	15.24	10234.02	8.43
A. depilans Gmelin(1)	internal	224.4	32.7	14.57	2346.00	7.17
Dolabella auricularia (Lightfoot)	internal	8386.2	9.6	0.11	369.89	3.85
NOTASPIDEA						
Umbraculum mediterraneum (Lamarck)	external	4583.6	71.9	1.57	582.39	0.81
Tylodina citrina Joannis	external	1552.5	29.2	1.88	289.08	0.99
Berthella plumula (Montagu)	internal	1072.7	125.8	11.73	9497.90	7.55
Berthellina citrina Rüppell & Leuckart	internal	361.0	38.0	10.52	3005.82	7.91
SACOGLOSSA						
Oxynoe olivacea Rafinesque	external	325.1	5.7	1.75	41.04	0.72
THECOSOMATA						
Cavolinia longirostris (Lesueur)	external	6307.7	16.4	0.25	56.50	0.34
C. tridentata (Niebuhr)	external	1131.8	5.3	0.47	26.07	0.49

much Leu whereas Iso and Val are less abundant than in other shells.

As far as amino acid composition of shell insoluble proteins is concerned, the evolutionary trends are not obvious. The ratio Gly/Ala appears to increase in the course of evolution: it is 0.95 and 0.93 respectively in the shells of *Pyramidella* and *Acteon,* it reaches 1.31 in *Philine* and *Aplysia* and even 1.57 in *Umbraculum.* At the same time, the Leu and Iso content diminishes slightly with the reduction of the shell, except in *Umbraculum.*

Table 3 shows the amino acid composition of the proteins of the acid-soluble fraction of the shells of nine species. Once again, the typical molluscan shell pattern of soluble proteins is well shown: the sum of Asp, Gly, Ser and Glu residues amounts to 60 to 70% of the total amino acid residues. There is much less basic amino acid (Arg, Leu and His) than in the insoluble fraction. In opisthobranch shells, the relatively low concentration of Asp is compensated for by higher levels of Glu and very high amounts of Ser, which is much more abundant than in the acid-soluble fractions of prosobranch shells.

The variability in the soluble proteins between the different species is higher than in the case of the insoluble fraction. This variability in composition may be related to its heterogeneity (Weiner et al., 1977; Samata et al., 1980; Poulicek, 1982; Poulicek et al., 1986), since it is composed of macromolecular assemblages of several proteins, peptides and glycoproteins which differ from species to species (Krampitz, pers. comm.). This vari-

TABLE 2. Amino acid composition of the organic insoluble fraction of the shells of 11 species of Opisthobranchia compared with that of Prosobranchia (expressed as AA residue/100 residues).

	OPISTHOBRANCHIA											PROSOBRANCHIA(2)
AMINO ACIDS	*P.t.	*A.t.	*B.p.	*B.s.(1)	*P.a.	*A.s.(1)	*A.w.(1)	*U.m.	*O.o.	*C.l.	*C.t.	Mean ± s.d. N = 11	Mean (extreme values) N = 50
ASP	16.51	16.37	15.33	17.10	15.59	12.54	12.83	11.71	13.29	14.78	11.94	14.36 ± 1.96	11.4 (6.9–18.5)
THR	6.31	6.12	6.84	4.73	6.78	3.83	5.61	5.80	5.79	6.07	5.0	5.72 ± 0.90	4.6 (2.86–7.6)
SER	9.73	9.89	8.25	12.25	9.35	11.61	9.04	10.61	9.05	8.09	8.55	9.67 ± 1.34	8.5 (5.8–12.4)
GLU	13.35	13.74	13.49	10.55	13.97	12.12	12.62	10.47	11.75	11.91	9.67	12.15 ± 1.45	8.7 (5.2–14.5)
PRO	2.98	2.78	3.32	6.08	4.21	6.82	4.88	11.29	6.93	3.40	6.65	5.39 ± 2.53	6.1 (3.6–10.2)
GLY	8.45	7.65	10.01	10.22	11.86	11.74	10.70	13.96	9.09	13.21	14.44	11.03 ± 2.23	15.3 (9.9–23.8)
ALA	8.89	8.20	8.20	7.37	9.05	10.05	8.16	8.89	14.32	9.98	7.57	9.15 ± 1.92	8.9 (5.2–15.3)
YS	+	+	+	2.13	+	0.45	0.18	2.11	0.34	+	1.27	0.59 ± 0.84	0.9 (0.4–2.3)
VAL	6.36	6.38	5.92	6.77	6.84	6.89	7.58	2.64	6.02	6.47	5.91	6.16 ± 1.27	4.8 (3.4–6.9)
MET	+ + +	1.09	+ + +	1.16	+ + +	1.19	1.51	5.93	0.71	+ + +	2.75	1.32 ± 1.74	1.4 (0.6–3.1)
ISO	5.38	5.47	4.96	3.83	3.93	4.22	4.62	1.66	4.02	3.51	3.34	4.09 ± 1.07	3.1 (2.0–4.6)
LEU	9.78	9.69	8.96	7.75	7.68	8.10	8.50	10.03	6.32	8.90	5.29	8.27 ± 1.47	7.1 (5.1–10.0)
TYR	0.66	0.96	1.65	1.21	+ + +	1.63	0.89	0.63	1.32	1.67	1.71	1.13 ± 0.53	1.1 (0.5–2.4)
PHE	4.65	4.47	4.14	0.69	4.00	3.47	2.19	1.15	3.97	4.60	2.04	3.22 ± 1.44	2.4 (1.4–4.3)
LYS	2.36	2.43	3.26	4.27	1.86	2.06	2.92	1.54	1.11	3.01	2.75	2.51 ± 0.88	2.6 (1.7–4.1)
HIS	0.47	+ + +	+ + +	0.62	+ + +	0.10	0.36	0.17	0.64	+ + +	0.98	0.33 ± 0.31	0.3 (0.1–1.6)
ARG	4.21	4.92	4.64	3.26	3.34	2.29	7.44	0.44	1.72	4.38	0.14	3.34 ± 2.13	2.2 (0.9–5.2)

*P.t. *Pyramidella terebelloides;* *A.t. *Acteon tornatilis;* *B.p. *Bulla punctata;* *B.s. *Bulla striata;* *P.a. *Philine aperta;* *A.s. *Akera soluta;* *A.w. *Aplysia willcoxi;* *U.m. *Umbraculum mediterraneum;* *O.o. *Oxynoe olivacea;* *C.l. *Cavolinia longirostris;* *C.t. *Cavolinia tridentata.*

(1) Data from Degens & Spencer, 1966.

(2) Compiled from various sources, see Poulicek, 1982

TABLE 3. Amino acid composition of the organic acid-soluble fraction of the shells of 9 species of Opisthobranchia compared with that of Prosobranchia (expressed as A A residue/100 residues)

AMINO ACIDS	OPISTHOBRANCHIA									Mean ± s.d. N = 9	PROSOBRANCHIA(1) Mean ± s.d. N = 9
	*P.t.	*A.t.	*H.z.	*B.p.	*A.n.	*S.l.	*P.a.	*C.l.	*A.p.		
ASP	13.23	6.84	12.01	10.96	7.28	7.05	6.88	9.99	11.81	9.56 ± 2.42	10.77 ± 1.39
THR	5.27	4.89	6.15	5.93	5.01	4.97	4.60	4.33	4.32	5.05 ± 0.61	6.45 ± 1.91
SER	13.68	23.89	15.61	17.62	23.46	23.57	25.94	18.5	18.34	20.07 ± 4.01	8.88 ± 0.79
GLU	17.75	16.84	14.41	15.16	17.47	17.22	16.51	14.27	14.16	16.09 ± 1.36	12.72 ± 0.95
PRO	9.08	6.70	6.60	6.09	4.04	2.98	3.62	6.50	6.32	5.77 ± 1.79	7.33 ± 2.81
GLY	18.45	20.47	16.81	21.30	20.55	21.61	21.86	16.54	18.35	19.55 ± 1.94	15.00 ± 3.03
ALA	10.55	7.89	9.60	9.06	9.06	8.81	8.80	9.35	7.94	9.01 ± 0.77	9.73 ± 1.78
YS	—	—	—	—	—	—	—	—	—	—	—
VAL	4.29	2.45	3.30	3.26	2.91	2.89	2.77	4.59	3.53	3.33 ± 0.67	4.33 ± 0.66
MET	+ + +	+	0.70	+	+	+ + +	+ + +	1.18	—	+ + +	6.63 ± 2.79
ISO	2.10	1.39	1.95	1.73	1.45	1.55	1.63	1.99	2.11	1.77 ± 0.26	2.38 ± 0.29
LEU	4.47	1.96	3.75	3.35	2.10	2.16	2.17	2.79	4.26	3.00 ± 0.86	6.75 ± 0.98
TYR	1.20	0.86	1.05	0.80	1.13	0.96	0.55	0.91	1.29	0.97 ± 0.21	0.72 ± 0.48
PHE	2.73	0.95	1.95	1.23	1.13	1.21	1.29	1.84	2.16	1.61 ± 0.56	2.13 ± 0.59
LYS	2.81	2.08	2.25	1.67	1.77	1.59	1.57	2.11	1.69	1.95 ± 0.38	2.27 ± 0.51
HIS	1.34	2.16	1.80	1.72	2.58	2.85	1.80	2.59	1.42	2.03 ± 0.26	1.02 ± 0.56
ARG	2.99	0.56	1.95	+ + +	+ + +	0.60	+ + + +	2.43	2.28	1.37 ± 0.97	2.53 ± 0.96

(1) Compiled from various sources, see Poulicek, 1982

*P.t. *Pyramidella terebelloides;* A.t. *Acteon tornatilis;* H.z. *Hydatina zonata;* B.p. *Bulla punctulata;* A.n. *Atys naucum;* S.l. *Scaphander lignarius;* P.a. *Philine aperta;* C.l. *Cavolinia longirostris;* A.p. *Aplysia punctata*

ability in amino acid composition is associated with comparable variability in the proteins, peptides and glycoproteins of the different species. The reason why shells should be so variable in composition is probably because each species' shell is adapted to quite specific environmental conditions (temperature, salinity, sand or mud particle size, etc.), but the precise significance of this variation remains unknown or must await further data (Degens & Spencer, 1966; Degens et al., 1967; Ghiselin et al., 1967; Meenakshi et al., 1971; Gregoire, 1972; Poulicek, 1982). The only evolutionary conclusion that can be drawn from Table 3 is that a decrease of the Lys content of the fraction correlates with a reduction in calcification of the shells (Degens et al., 1967).

Some amino sugars other than chitin are present in both fractions. The amount of carbohydrate (mainly glucosamine and galactosamine) varies considerably throughout the phylum (Ghiselin et al., 1967), but in most mollusc classes the relative proportion of carbohydrate to protein seems to have decreased progressively with the evolution of the shells (Poulicek, 1982). This seems to be true also in the Cephalaspidea where those species with well-developed shells have high hexosamine/amino acid ratios and those with reduced shells have low ratios (Table 4). The primitive shelled *Pyramidella* also has a high ratio whereas the more advanced Thecosomata have a low ratio. The Notaspidea, Anaspidea and Sacoglossa are linked by their very high amino sugar content, even if chitin is not taken into account, and irrespective of whether the shell is external or internal. Table 4 also shows that the hexosamine/amino acid ratio is always higher in the insoluble fraction of the organic matrix than in the acid-soluble one.

TABLE 4. Estimate of the ratio (hexosamines/amino acids) x 100 in the acid-soluble and insoluble fractions of the shell organic matrix of 14 species of Opisthobranchia. Chitin was not taken into account in computing the hexosamines of the insoluble fraction.

Opisthobranch species	Acid-soluble fraction	Insoluble fraction (chitin excluded)
PYRAMIDELLACEA		
Pyramidella terebelloides	1.86	4.38
CEPHALASPIDEA		
Acteon tornatilis	1.88	4.20
Hydatina zonata	1.44	—
H. physis (1)	—	3.73
Bulla punctulata	1.38	3.94
B. striata (1)	—	2.93
Philine aperta	0.67	2.81
ANASPIDEA		
Akera soluta (1)	—	5.40
Aplysia punctata	3.48	—
A. willcoxi (1)	—	4.55
NOTASPIDEA		
Umbraculum mediterraneum	—	3.99
SACOGLOSSA		
Oxynoe olivacea	—	3.04
THECOSOMATA		
Cavolinia longirostris	0.22	—
C. tridentata	—	2.12

(1) Computed from data in Degens et al., 1967.
(1) Data from Jeuniaux, 1963; remainder original
(2) Data from Degens & Spencer, 1966.
(3) Compiled from various sources, see Poulicek, 1982

DISCUSSION AND CONCLUSIONS

The Euthyneura are characterized by hermaphroditism, a tendency to lose the effects of torsion, a distinctive type of spermatozoon, a peculiar structure of the pallial complex and a heterostrophic larval shell (Ghiselin et al., 1967). But the most striking external feature of the whole group is a tendency towards shell regression, affecting all evolutionary lines of the opisthobranchs as well as some lines of pulmonates quite independently.

Despite the regressive features altering the shells macroscopically, there is no fundamental reworking of shell structure nor of the chemical composition of its organic matrix. The crossed-lamellar architecture of all shells of benthic opisthobranch species examined is typical of gastropods with a similar level of complexity (i.e. similar to that of mesogastropod and neogastropod prosobranchs) (Poulicek, 1982). Even the most altered internal shells (as in *Aplysia*) exhibit the same kind of crossed-lamellar fabric. The helicoidal microstructure of thecosomatous pteropod shells is presumably adaptive, but can be directly derived from the crossed-lamellar type via some kind of crossed-acicular microstructure. The most primitive Thecosomata (*Limacina*) actually exhibit such intermediate microstructural features. A helicoidal fabric of the same

type is also found in shells of the phylogenetically unrelated heteropods (prosobranchs with a similar planktonic mode of life) (Batten & Dumont, 1976).

The organic matrix isolated from the shells is composed of an insoluble chitin-protein complex and an acid-soluble glycoprotein fraction whose amino acid patterns are typical of 'conchiolins' isolated from shells of crossed-lamellar fabric, whatever the origin of the shell. In both prosobranchs and opisthobranchs it appears that as one goes from primitive to more advanced species, the hexosamine content decreases, the Gly/Ala ratio increases, and the Lys content, which is linked to the degree of calcification, decreases. However, the covariant groups of amino acids described by Degens et al., (1967) are not found here, thus confirming the close relationship of the species. The chitin content and degree of calcification have been shown to be linked in the evolution of mollusc shells (Poulicek, 1982; Poulicek et al., 1986). This relationship is confirmed here: as opisthobranch shells get smaller so their chitin content increases and the degree of calcification decreases. Prosobranchs, by contrast, show a tendency to develop lower chitin content and higher levels of calcification.

This variation in chemical composition of shells must have some adaptive (functional) significance, and where parallel changes in composition occur in unrelated groups it is reasonable to seek for similar causes. In most molluscs, the essential functions of the organic matrix of the shells (contributing to its strength) are carbonate nucleation, shell mineralization and maintenance of shell integrity (Degens et al., 1967; Poulicek, 1982; Poulicek & Voss-Foucart, 1984; Poulicek et al., 1986). While shells may vary in the organic matrix, these key features are retained. In opisthobranchs, however, the shells become thinner and a further decrease in organic content would cause them to become brittle. This brittleness has been avoided by opisthobranchs in three different ways:

1. Incorporation of OH-Pro in the insoluble protein matrices of Anaspidea and Sacoglossa. This probably makes the shell more flexible (Ghiselin et al., 1967), particularly as these shells generally have a high protein content.
2. Increase of the chitin content of the shells in Cephalaspidea, Anaspidea and Notaspidea. Chitin can be considered to form a 'skeleton' of the organic matrix onto which intercrystalline carrier proteins are polymerized (Poulicek et al., 1986). An increase of the chitin content could thus thicken the wall between crystallites and thus provide some suppleness to the structure. An increased chitin content also occurs in other unrelated species with internal reduced shells (Cephalopoda, Polyplacophora, Prosobranchia, Pulmonata) (Poulicek, 1982; Poulicek & Kreusch, 1986; Poulicek et al., 1986).
3. Development of a peculiar helicoidal microstructure in thecosomatous pteropods. The mechanical characteristics of these very light shells allow flexibility and reduce their brittleness. A similar microstructure has evolved in the unrelated heteropods with similar light shells and similar mode of life (Batten & Dumont, 1976).

Thus the main features characteristic of the regressive evolution of opisthobranch shells can be considered to be adaptive and correlated with the need for suppleness in very thin, calcified shells that otherwise would be too brittle. These features are polyphyletic and convergent with shells of other molluscs showing similar reduction of the shell or the same mode of life.

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STUDY OF THE ANATOMY AND HISTOLOGY OF THE MANTLE DERMAL FORMATIONS (MDFs) OF *CHROMODORIS* AND *HYPSELODORIS* (OPISTHOBRANCHIA: CHROMODORIDIDAE)

José C. García-Gómez[1], Antonio Medina[2] & Rafael Coveñas[3]

ABSTRACT

Mantle dermal formations (MDFs) were studied in 12 European species of *Chromodoris* and *Hypselodoris*. In *Chromodoris* the MDFs are small, numerous and irregular in shape, and are located in a band around the mantle edge. In *Hypselodoris* the MDFs are larger, less numerous and spherical. They are usually located in the anterior and posterior regions, although the anterior, or both anterior and posterior, MDFs may be absent in certain species. Therefore, the presence/absence, location and shape of the MDFs may be of taxonomic importance to separate certain European species, in particular of the genus *Hypselodoris*. The main histological difference between the MDFs of *Chromodoris* and *Hypselodoris* is the presence of a thick, muscular capsule enveloping the MDFs in the latter genus. The strategic location and unpleasant taste of the MDFs suggest that they play a defensive role, but they do not appear to open externally.

INTRODUCTION

The loss of the shell in the Nudibranchia is compensated by the appearance of other defensive mechanisms which are frequently associated with warning coloration. The family Chromodorididae includes many colourful species and, although recent works (see Discussion) show that they possess substances of presumed defensive value, the almost universal presence of dermal formations located in the mantle of the Chromodorididae has received scant attention. Only a few reports deal with such structures (Bergh, 1890; Marcus, 1955; Thompson, 1960, 1972; Edmunds, 1981; Rudman, 1984). The valuable paper of Rudman (1984) thoroughly describes the 'mantle glands' in chromodorid nudibranchs from the Indo-West-Pacific, although from an anatomical and taxonomic viewpoint. In the present paper we study the anatomy and histology of the mantle dermal formations (MDFs) of 12 European species of the nudibranch genera *Chromodoris* and *Hypselodoris,* and compare them with similar formations in other opisthobranchs.

MATERIALS AND METHODS

Most of the specimens studied were collected by SCUBA diving in waters of the Straits of Gibraltar. A few specimens were collected in the intertidal zone of Cadiz (Spain). For the anatomical examination of the MDFs the animals were frozen and subsequently fixed and preserved in 4% formaldehyde.

For the histological study MDFs were removed from specimens of *Chromodoris purpurea, C. luteorosea, C. krohni, Hypselodoris elegans, H. tricolor* and *H. cantabrica.* They were immediately fixed in 2.5% glutaraldehyde in 0.1 M Millonig's buffer (pH 7.3) for 3 h, dehydrated through an ascending series of alcohols or acetones, and embedded in paraffin or Spurr's resin (Spurr, 1969). After fixation in glutaraldehyde, some MDFs were postfixed in 1% osmium tetroxide. Semi-thin sections were cut on an LKB III ultramicrotome and stained with toluidine blue.

Paraffin and semi-thin sections were subjected to histochemical tests for the demonstration of neutral mucosubstances (Periodic Acid-Schiff, PAS), acid mucosubstances (Alcian Blue at pH 2.5, AB) and proteins (Ninhidrin-Schiff, NS) (Pearse, 1968).

RESULTS

Anatomy and location of MDFs in different species:

A. Genus *Chromodoris*

"Single submarginal row of ramifying mantle glands opening dorsally" (in 'diagnosis' of the genus *Chromodoris,* Rudman, 1984).

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In the European species of *Chromodoris* mantle dermal formations (MDFs) are present in all the specimens we have examined. They are distributed along the edge of the mantle, including the cephalic region in some species (Fig. 1A), whereas in others they are absent in front of the inter-rhinophoral plane (Fig. 1B). Their shape and size are quite variable, even in animals of the same species. When the mantle skin is torn with forceps at the level of the MDFs, numerous spherical structures (10–40 μm in diameter) are released. These structures (as revealed by histological examination) correspond to vacuolar cells.

In some species, such as *C. luteorosea, C. luteopunctata* and *C. britoi,* the MDFs are densely packed, which results in an almost uniform distribution along the periphery of the mantle. In others, the MDFs are less dense and sometimes quite isolated (e.g. *C. purpurea, C. krohni*). In these two species the young animals usually have fewer MDFs than the adults.

The MDFs are opaque white, usually clearly visible because of the transparency of the mantle, and unlike the posterior MDFs in *Hypselodoris,* they hardly distort the edge of the mantle.

C. luteorosea (Rapp, 1827) (5 specimens)

The MDFs are located along the whole edge of the mantle, except in front of the rhinophores, forming blurred radial bands. Their vacuolar cells are 30–40 μm in diameter.

C. purpurea (Laurillard, 1831)
(8 specimens)

The MDFs are distributed all along the edge of the mantle. Even the smallest specimens (10–13 mm) show MDFs in front of the rhinophores . The MDFs are usually rounded and the vacuolar cells they contain are normally spherical and quite uniform in size (20 μm), though they are sometimes egg-shaped and measure 30–40 μm.

C. krohni (Vérany, 1846) (12 specimens)

The edge of the mantle is densely packed with MDFs though in small specimens (6–7 mm) they may be absent in front of the rhinophores. The MDFs are usually rounded and the vacuolar cells are very small and usually spherical (10–20 μm).

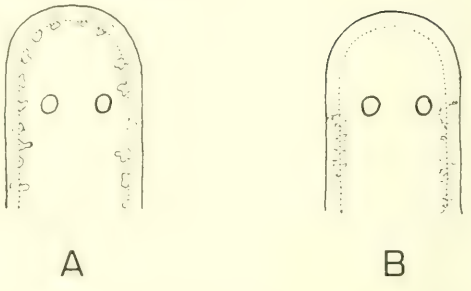

FIG. 1. Diagram to show the location of MDFs in A: *Chromodoris purpurea* and *C. krohni;* B: *C. luteorosea, C. luteopunctata* and *C. britoi.*

C. luteopunctata (Gantès, 1962)
(4 specimens)

MDFs are present along the whole edge of the mantle, except in front of the rhinophores. They form dense white accumulations, which are usually long and irregular in shape. Vacuolar cells, however, have not been distinguished.

C. britoi (Ortea & Pérez, 1983)
(1 specimen)

MDFs are found all along the edge of the mantle, except in front of the rhinophores. They are similar to those in *C. luteorosea,* though the vacuolar cells, also spherical, measure 10–20 μm.

B. Genus *Hypselodoris*

"The mantle glands are single and occur along the edge of the mantle opening at the edge. Posteriorly the glands are greatly enlarged and closely packed and on preservation are partly extruded" (in 'diagnosis' of the genus *Hypselodoris,* Rudman, 1984).

In the European *Hypselodoris*[1] the location of the MDFs varies depending on the species. They may be completely absent (Fig. 2E), present simultaneously at the rear of the mantle and on both sides of the cephalic region (Figs. 2A–C), or confined to the extreme posterior region of the mantle (Fig. 2D).

When anterior and posterior MDFs are present, the posterior MDFs are always larger. However, the smallest posterior MDFs may be similar in size to the largest anterior MDFs. As a general rule, the posterior MDFs increase in size towards the posterior end of

[1]The 'diagnosis' of the mantle glands in *Chromodoris* and *Hypselodoris* by Rudman (1984) is based on species from the Indo-West Pacific.

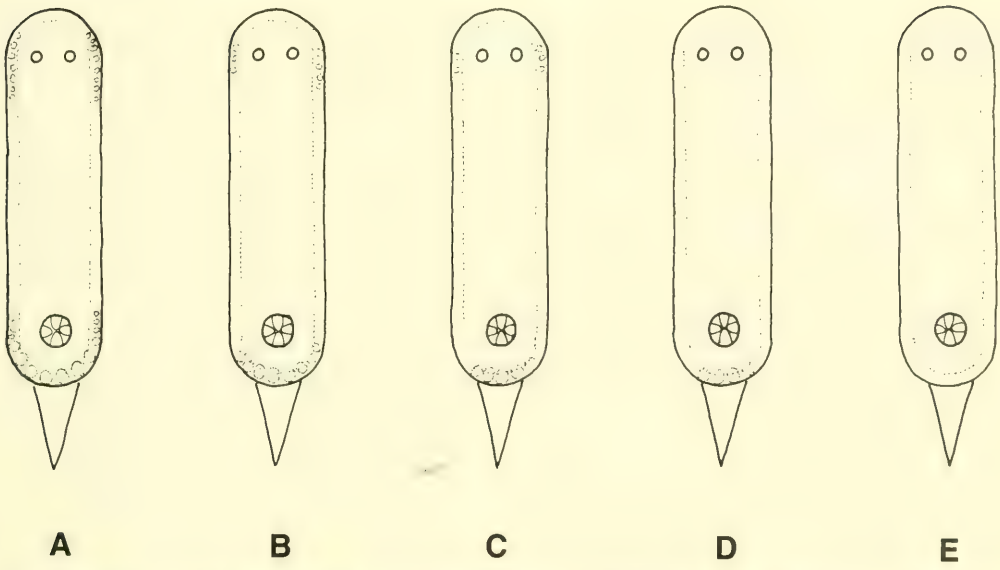

FIG. 2. Diagram to show the location of MDFs in species of *Hypselodoris.* A: *H. elegans;* B: *H. villafranca;* C: *H. bilineata;* D: *H.* cf. *tricolor;* E: *H.* cf. *messinensis.*

the mantle, causing a deformation of its ventral surface (Fig. 3). Although the MDFs are often close together and may appear to be partially fused, each one is a separate, discrete structure.

The MDFs are opaque white in colour, and easily visible because of the transparency of the mantle. The number of MDFs located close to each rhinophore varies: for example a specimen of *H. elegans,* 60 mm in length, possessed four MDFs on the left and 12 on the right. The distribution is more balanced in the posterior MDFs. In young and adult animals belonging to the same species a similar distribution of the MDFs has been observed, though the size and number of them tend to increase with the size of the animal. Occasionally, however, it has been observed that large specimens have fewer MDFs than smaller specimens of the same species.

H. villafranca (Risso, 1818) (26 specimens)

Anterior and posterior MDFs are present. In the smallest specimens observed (4–5 mm) there are one to four MDFs (50 μm) close to each rhinophore, and four (250 μm) in the rear region of the mantle. In the largest specimens (15–25 mm) there are one to four MDFs (300 μm) on each side of the head and four to eight (700 μm) at the caudal end of the mantle (Fig. 2B).

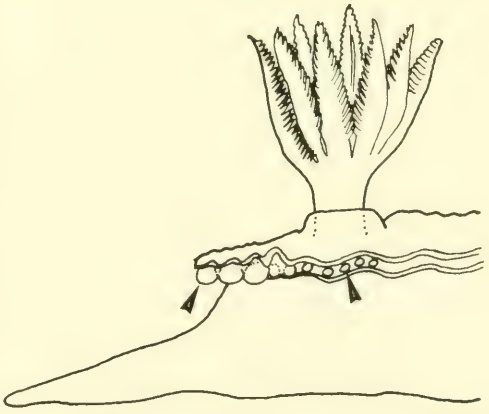

FIG. 3. Caudal region of *Hypselodoris* showing the position of the posterior MDFs (arrowheads). Note the large size of the posterior MDFs which causes deformation of the mantle edge.

H. elegans (Cantraine, 1835) (8 specimens)

Anterior and posterior MDFs are present. In the smallest specimens examined (60–65 mm) 2–12 MDFs (450 μm) are found close to each rhinophore, and 7–24 (1300 μm) in the rear region (Fig. 2A). In the largest specimens (110–130 mm) there are 15–18 MDFs (1000 μm) close to each rhinophore, and 14–20 (2000 μm) in the rear region.

H. cf. *tricolor* (Cantraine, 1835)[2]
(8 specimens)

Only posterior MDFs are present. In the smallest specimens (10 mm) there are two MDFs (500 μm), and in the largest ones (14–20 mm) 4 (900 μm) (Fig. 2D).

H. coelestis (Deshayes, 1866)
(34 specimens)

Only posterior MDFs are found. In the smallest specimens (8–9 mm) 1–5 MDFs (400 μm) are present, while in the largest specimens (13–17 mm) there are 2–5 (500 μm).

H. cf. *messinensis* (Ihering, 1880)
(7 specimens)

There are no MDFs (Fig. 2E).

H. bilineata (Pruvot-Fol, 1953)
(12 specimens)

In the smallest specimens (5–10 mm) there are no anterior MDFs but two to four (180 μm) are present posteriorly. In the largest specimens (13–20 mm) two or three MDFs (200 μm) are present close to each rhinophore, and four or five (450 μm) in the rear region (Fig. 2C).

H. cantabrica (Bouchet & Ortea, 1980)
(5 specimens)

Anterior and posterior MDFs are present. In the smallest specimens (13–25 mm) there are one to three MDFs (300 μm) close to each rhinophore, and three to six (1900 μm) in the rear region. In the largest specimens (40–45 mm) three or four MDFs (600 μm) are located close to each rhinophore, and seven (1400 μm) posteriorly.

Histology of the MDFs

A. Genus *Chromodoris*

For the histological examination of the MDFs in *Chromodoris,* three species have been examined: *C. purpurea, C. krohni* and *C. luteorosea.* The present description is valid for all these species.

The MDFs in *Chromodoris* are small and irregular structures which are embedded in the subepidermal connective tissue. They consist of an outer cell layer enclosing an inner accumulation of vacuolar cells (Fig. 4A). The cytoplasm of the cells in the outer layer appears to contain neutral mucosubstances, since it is strongly stained by the PAS procedure. Curiously, cells with the same histological and histochemical features are present in the epidermis. A thorough microscopic examination of the MDFs shows that their outer layer is continuous and hence they do not appear to discharge into the external medium. Consequently, the term 'gland', which has so far been applied to these formations, could lead to an erroneous interpretation of their functioning, since this terminology suggests an active secretion of substances.

The vacuolar cells show a peripheral cytoplasmic ring surrounding a big central vacuole which occupies nearly the whole cell volume. The nucleus is displaced towards the periphery of the cell. The content of the central vacuole is weakly stained by toluidine blue when the tissue is post-fixed with osmium tetroxide. The histochemical tests used for the demonstration of neutral (PAS) and acid (AB) mucosubstances, and proteins (NS) gave negative results in the vacuolar cells.

On occasions, the cellular organization in the centre of the largest MDFs is lost (Fig. 4A). When the tissue is post-fixed in osmium tetroxide, the central area is weakly stained, so it seems likely that it is filled with substances from the surrounding vacuolar cells.

In the subepidermal connective tissue and between epidermal cells of the mantle of *Chromodoris,* free vacuolar cells, some of which appear to open onto the dorsal surface of the mantle, are present (Fig. 4B).

B. Genus *Hypselodoris*

The histology of the MDFs has been studied in three species of *Hypselodoris: H. elegans, H. cantabrica* and *H. tricolor.* Since the histology of the MDFs in all these species is similar, we shall describe in detail the observations made on *H. elegans,* and then draw attention to significant differences in the other two species.

The MDFs in *H. elegans* are spherical structures consisting of a thick outer capsule which completely surrounds an accumulation of vacuolar cells (Fig. 4C). The capsule is mainly formed by muscle fibres (Fig. 4D) which, as shown by tangential sections, are oriented in all directions. In *H. cantabrica* and

[2]The identification of these three species will be discussed in a paper currently in preparation by Ortea, Bouchet and García-Gómez. It will show that *H. coelestis* is a distinct species, and that the other two are hitherto undescribed species which resemble *H. tricolor* and *H. messinensis.*

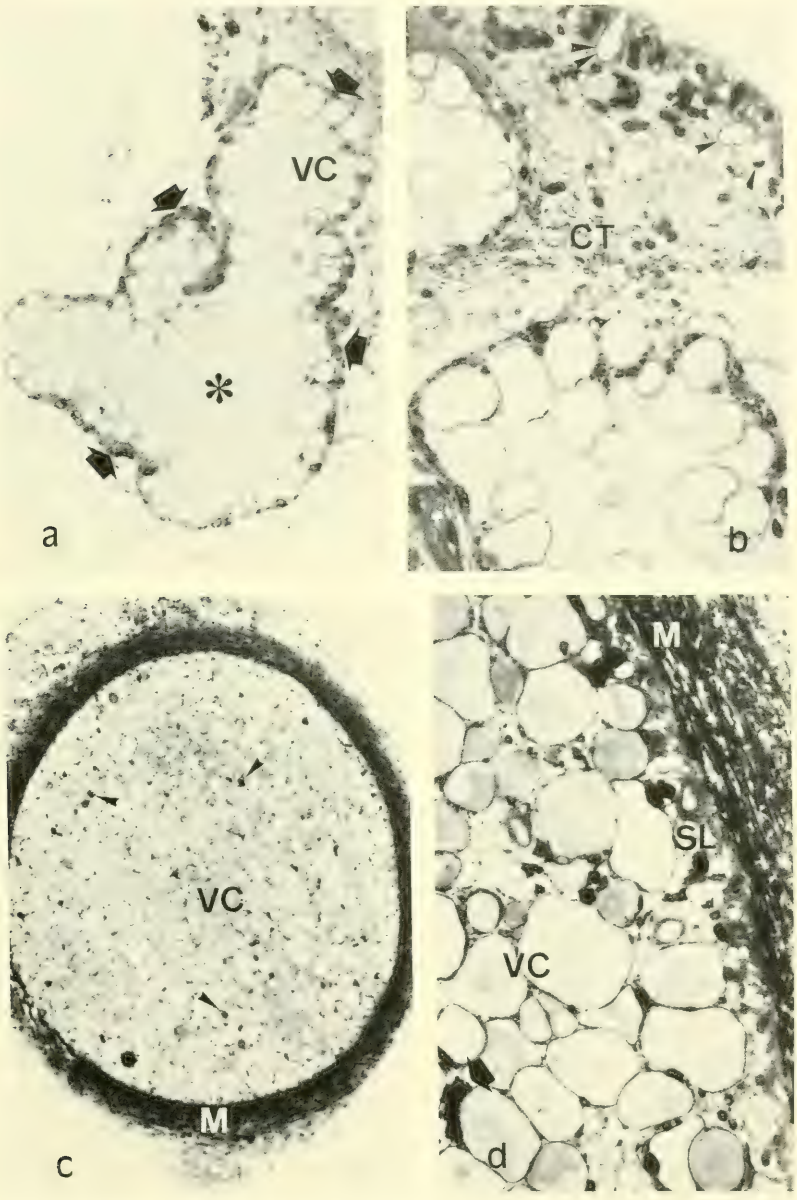

FIG. 4.A: Semi-thin section of MDFs of *Chromodoris purpurea* fixed in glutaraldehyde and stained with toluidine blue. Note the vacuolar cells (VC), the surrounding single cell layer (arrowed), and the central area lacking vacuolar cells (asterisk). x190. B: Section of MDFs and mantle epidermis of *C. purpurea.* Note connective tissue (CT), and vacuolar cells in epidermis (arrowheads), one of which opens onto the dorsal surface of the mantle (double arrowhead). Fixation and staining as for 1a (above). x480. C: Semi-thin section of a MDF of *Hypselodoris elegans* fixed in gluteraldehyde, post-fixed in osmium tetroxide, and stained with toluidine blue. VC, vacuolar cells; M, muscular capsule; arrowheads, granular cells. x75. D: Portion of MDF of *H. elegans* fixed and stained as for 1C (above). Note vacuolar cells (VC) with contents weakly stained by toluidine blue. M, muscular capsule; SL, surrounding cell layer; arrow, granular cell. x480.

H. cf. *tricolor* the capsule is identical in structure, but thinner. Beneath the capsule there is a continuous cell layer (Fig. 4C,D) which appears to be equivalent to the cell layer surrounding the vacuolar cells in *Chromodoris.* In this layer some nuclei are seen, but no definite intercellular limits can be distinguished.

The vacuolar cells are similar to those described in *Chromodoris,* but they are more closely packed. These cells are always clearly identifiable, even in the centre of the largest MDFs. In *H. elegans* and *H. tricolor* some cells containing dense cytoplasmic granules (Fig. 4C,D) are located between the vacuolar cells. This type of cell is not present in H. cantabrica nor in the genus *Chromodoris.*

In all the species of *Hypselodoris* studied, free vacuolar cells are located in the subepidermal connective tissue and in the epidermis.

DISCUSSION

The loss of the shell in opisthobranchs represents an important defensive disadvantage which must be compensated by the acquisition of other methods of defense. In the shell-less opisthobranchs numerous protective mechanisms have evolved (Edmunds, 1966a,b) which vary from defensive behaviour to the presence of protective structures, such as glands or spicules, in the skin.

Many pleurobranchids and dorids secrete acid substances (pH 1 or 2) of possible defensive function when they are molested (Edmunds, 1968; Thompson, 1969,1983; Marbach & Tsurnamal, 1973). The release of these substances has been attributed to epidermal glandular cells (called 'acid' or 'clear' cells) and subepidermal multicellular glands. The epidermal glandular cells are prismatic and show a clear polarity: their nucleus occupies the basal region of the cell and the apical portion is vacuolar (Thompson, 1969). In contrast, the vacuolar cells of the multicellular glands do not show such a polarity, their shape is more spherical and most of their cytoplasm appears clear (Edmunds, 1968). The multicellular glands of *Berthellina* (Thompson & Colman, 1984), *Discodoris* (referred as *Anisodoris* by Edmunds) *stellifera, D. pusae* and *D. tema* (Edmunds, 1968) are similar to the MDFs of *Hypselodoris* in that they are formed by an accumulation of vacuolar cells enveloped by a muscular sheath, but both types of structures differ in that the multicellular glands are scattered all over the mantle, possess a central lumen and open onto the dorsal surface of the mantle.

When some *Hypselodoris* (e.g. *H. villafranca* and *H.* cf. *messinensis*) are molested, the release of an opaque substance from the mantle can be observed. This substance is probably mixed with mucus and thus remains around the body of the animal. This phenomenon was previously suggested to occur in dorids by Potts (1981). The unpleasant taste and neutral pH of the substance secreted are similar to those of the MDFs, so that it is reasonable to suppose that the content of the MDFs and the substance released from the mantle are similar in chemical composition. The distasteful substance is probably responsible for the fact that predatory fish (e.g. some species of *Blennius*) and opisthobranchs (e.g. *Pleurobranchaea meckeli*) reject *Hypselodoris* as food, while other nudibranchs left in the same aquarium are immediately devoured (pers. obs.). Since the MDFs are internal structures and do not open on the surface, they do not appear to be involved in the discharge of the repulsive substance. However, inserted between epidermal cells of *Chromodoris* and *Hypselodoris* are free vacuolar cells. This cell type could thus be responsible for the secretion of the repulsive substance.

Ros (1977) points out that *Chromodoris* and *Hypselodoris* do not release acid substances, but he assumes that they must produce repulsive secretions. In this connection, recent work has shown the presence in these genera of substances which could be obtained from the diet and utilized as chemical defence against potential predators (Hochlowski & Faulkner, 1981; Hochlowski et al., 1982; Faulkner & Ghiselin, 1983; Faulkner, 1984; Okuda & Scheuer, 1985). These studies have not demonstrated the precise location of these substances, so we cannot definitely conclude that they are present in the MDFs.

The strategic location of the MDFs in the cephalic and caudal regions of many *Hypselodoris* species, as well as their unpleasant taste, suggest that they may play a defensive role. Such formations could thus protect the most important external organs (head, rhinophores and gills) from attack by other animals. Although the MDFs of *Chromodoris* are apparently different from those of *Hypselodoris,* the study of both under the mi-

croscope shows that their cells share similar histological features. This does not prove that the MDFs perform the same function in both genera, but the phylogenetic proximity of these genera suggests a similar function for the MDFs.

In *Chromodoris* and *Hypselodoris* the presumed defensive region (the edge of the mantle) is associated with a striking coloured band which contrasts with the general colour of the body. This peripheral band is yellow in the adult of all the species, except *H. coelestis* in which it is white. The band is also white in the young specimens of *C. krohni* and some *Hypselodoris.*

The observations noted above (i.e. the release of repulsive substances by some *Hypselodoris;* the distastefulness of the content of the MDFs and their strategic location; the contrasting coloration associated with the MDFs; the presence of metabolites in numerous *Chromodoris* and *Hypselodoris* species which, according to several authors may act as deterrent substances) lead us to think that, as suggested by Ros (1976)[3], in the European species of *Chromodoris* and *Hypselodoris* aposematic circles, corresponding to a Müllerian mimicry, occur.

The 'diagnosis' of the mantle glands (= MDFs) of *Chromodoris* and *Hypselodoris* given by Rudman (1984) is based on species from the Indo-West Pacific. Our observations on European species of these genera provide additional data which may be used in taxonomy. Thus, in *Hypselodoris* the MDFs may be extruded through the ventral surface of the mantle as the animal dies (1); they may be present simultaneously on both sides of the cephalic region and in the posterior region of the mantle (2), only in the posterior region of the mantle (3), or completely absent (4). Rudman (1984) also reported that "mantle glands appear to be absent around the anterior end", which concurs with our own observations.

The MDFs of *Chromodoris* and *Hypselodoris* are isolated and do not open onto the surface of the mantle. However, in some preserved specimens of both genera whole MDFs appear to be extruded through orifices formed in the skin of the mantle. Rudman (1984) made the same observation on preserved specimens of *Chromodoris* and *Hypselodoris.* Unfortunately, in very few specimens were we able to investigate the possible extrusion of MDFs in living animals, and in no case did we find this phenomenon to occur. Furthermore, the MDFs were not extruded when specimens of some *Hypselodoris* (e.g. *H. gracilis, H. bilineata* and *H. elegans*) were prodded. The extrusion occurs only when the MDFs themselves are pressed, which also justifies the hypothesis that they could be defensive structures. In *Hypselodoris* extrusion was most often observed in the largest MDFs. The MDFs might therefore be storage vessels which would slowly accumulate material and then extrude it when they were full. This explanation of their activity would imply an excretory rather than a defensive function.

Recently, Rudman (1984) discussed the phylogeny of the different genera of Chromodorididae by taking into consideration the distribution of the MDFs. The observations of Rudman and ourselves show that in *Hypselodoris* the MDFs may be completely absent (*H.* cf. *messinensis*), or located along the entire edge of the mantle (*H. bennetti*), with a range of intermediate situations present in other species. Following Rudman's hypothesis (1984), *H.* cf. *messinensis* would represent the final stage in the evolutionary loss of MDFs in the European species of *Hypselodoris.*

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DOES WARNING COLORATION OCCUR IN NUDIBRANCHS?

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ABSTRACT

Direct evidence for the occurrence of aposematic (warning) coloration in nudibranch molluscs is reviewed and is shown to be inconclusive. Many species are conspicuously coloured and are distasteful to possible predators, but there is very little evidence that they are avoided by predators because of their colours or that these colours give better protection than would cryptic colours. Indirect evidence for aposematism can be obtained by assuming that it occurs, predicting the consequences of this assumption, and then testing these predictions. Information to test most of these predictions is either not available or is inconclusive, but the strongest support for aposematism is the widespread occurrence of Batesian and/or Müllerian mimicry. It is concluded that warning coloration does occur in nudibranchs but that there is much scope for further experimental studies.

INTRODUCTION

The occurrence of warning coloration in insects is well established (Cott, 1940), but the possibility of its occurrence in opisthobranch molluscs is more controversial (Thompson, 1960; Harris, 1973; Edmunds, 1974; Todd, 1981). Nearly one hundred years ago Wallace (1889), Garstang (1889, 1890), Herdman (1890) and Herdman & Clubb (1890) suggested that many nudibranchs have warning colours, and further possible examples of warningly coloured species are given by Hecht (1896), Crossland (1911) and by numerous more recent authors (e.g. Harris, 1973). Warning coloration was first given a scientific (Greek) name by Poulton (1890) who defined *aposematic* coloration as: ". . . an appearance which warns off enemies because it denotes something unpleasant or dangerous; or which directs the attention of an enemy to some specially defended, or merely non-vital part; or which warns off other individuals of the same species."

The last two parts of this definition make the concept of aposematic coloration very wide and today most authors restrict it to the first clause. Edmunds (1974), for example, gives the following definition: "Animals which have dangerous or unpleasant attributes, and which advertise this fact by means of characteristic structures, colours or other signals so that some predators avoid attacking them, are said to be *aposematic,* and the phenomenon is called *aposematism.*" Despite the fact that it is nearly a hundred years since it was suggested that nudibranchs have warning colours, there is still considerable uncertainty as to whether any nudibranchs are really aposematic. This is due to lack of evidence. This paper reviews the current state of knowledge, and suggests the type of evidence that needs to be sought in order to establish if a nudibranch is *aposematic.*

Criteria Necessary for Aposematism

If the definition given above is accepted then in order to demonstrate that a particular species is aposematic it is necessary to establish that it fulfils four criteria (Edmunds, 1987):

1. it is sufficiently noxious that some predators will not eat it;
2. it is conspicuously coloured, or advertises itself by means of some other signals;
3. some predators avoid attacking it because of its signals;
4. these conspicuous signals provide better protection to the individual or to its genes than would other (e.g. cryptic) signals.

Only if all these criteria are met will there be selective advantage to an animal in possessing warning colours (Edmunds, 1987). If criterion 4 is not met then an animal would be better protected if it were cryptic and apose-

matic colours could not evolve. Do any nudibranchs fulfil these four criteria?

Criterion 1: *Are any nudibranchs sufficiently noxious that predators will not eat them?*

Many nudibranchs have noxious dermal and epidermal glandular secretions and aeolids retain nematocysts from their food and store them in their cerata; both have a defensive function (Thompson, 1960; Edmunds, 1966). Herdman & Clubb (1890), Crossland (1911), Crozier (1916) and Thompson (1960) have all established that some brightly coloured nudibranchs are unpalatable to fish. The animals were usually dropped into an aquarium or into the sea and were immediately attacked by fish as they fell through the water column. Almost all the nudibranchs survived although they were snapped up and spat out several times before reaching the substrate after which the fish ignored them. Herdman & Clubb (1890) and Thompson (1960) also showed that many cryptically coloured nudibranchs were unpalatable to fish. Harris (1973) obtained similar results with *Phestilla melanobranchia* Bergh, but he found that *P. sibogae* Bergh (= *P. lugubris* Bergh) was usually eaten as it fell through the water. This was because repeated ingestion and spitting out by fish caused it to autotomize all of its cerata so that the "naked" nudibranch was eventually palatable. These simple experiments clearly show that many nudibranchs are unpalatable to some species of predatory fish.

Criterion 2: *Are any nudibranchs conspicuously coloured?*

It has been suggested that the following nudibranchs may have warning colours: *Limacia clavigera* (Müller), *Polycera quadrilineata* (Müller), *Facelina coronata* (Forbes & Goodsir) and *Eubranchus tricolor* Forbes from Europe (Hecht, 1896); *Chromodoris reticulata* (Pease), *C. diardii* (Kelaart) and *Phyllidia varicosa* Lamarck from the Indo-Pacific (Crossland, 1911; Harris, 1973); and *Triopha carpenteri* Stearns and *Diaulula sandiegensis* (Cooper) from the north-west Pacific (Harris, 1973). These are all brightly coloured and so fulfil criterion 2. Perusal of recent monographs with colour illustrations of nudibranchs (Behrens, 1980; Bertsch & Johnson, 1981; Schmekel & Portmann, 1982; Thompson & Brown, 1984; Willan & Coleman, 1984; Just & Edmunds, 1985) indicates that a very large number of nudibranchs are brightly coloured and conspicuous on unnatural backgrounds. Garstang (1890), Hecht (1896) and Thompson (1960), however, have all pointed out that some brightly coloured species are actually cryptic in their natural environment. For example *Rostanga pulchra* McFarland is red but usually lives close to the red sponge *Ophlitaspongia pennata* Lambe (Cook, 1962) while *Catriona gymnota* (Couthouy) is also red but lives almost exclusively on the red hydroid *Tubularia* spp. (Edmunds, 1987).

It is also well known that as light penetrates the sea the red end of the spectrum is absorbed much more quickly than the blue (Hardy, 1956). In consequence many animals that are red actually appear black or brown at the depths they normally inhabit. Dr H. Bertsch (pers. comm.) informs me that *Chromodoris petechialis* (Gould) and *Hexabranchus sanguineus* Rüppell & Leuckart appear brown and cryptic at 18 m depth. But why should these species be red rather than brown or black, since if they were to move into well-lit, shallower waters they could be very conspicuous? The answer to this question may be that it is economically cheaper to evolve red pigment, because red carotenoids are easily sequestered from the animal's food, whereas browns and blacks may have to be synthesized *de novo*.

Criterion 3: *Do any predators avoid attacking nudibranchs because of their colour (or because of some other signal)?*

There is evidence that some fish and some cephalopods can learn to avoid prey that provide aversive stimuli yet still attack other palatable prey which are of different appearance (i.e. have different signals) (summarized in Edmunds, 1974), but only very preliminary experiments along these lines have been carried out with nudibranchs as prey. These showed that grey mullet (*Mugil labrosus*) quickly learned to avoid the red aeolid *Coryphella pellucida* (Alder & Hancock). They also learned to avoid a papillate model coupled with an aversive stimulus while continuing to attack a similar but non-papillate model coupled with food (Edmunds, 1974).

Criterion 4: *Do conspicuous colours provide better protection than cryptic colours?*

Guilford (1990) has recently reviewed the possible ways in which warning colours work. For example, they may be more memor-

able than cryptic colours because they are conspicuous or because they are unfamiliar; they may increase the rate of capture and hence of aversive learning; they may reduce recognition errors in experienced predators; or they may provide frequent reminders of a noxious experience. Gittleman & Harvey (1980) showed that chicks learn more readily to avoid noxious crumbs if these are conspicuous than if they are cryptic, and similar experiments have been carried out by Schuler & Hesse (1985), Sillen-Tullberg (1985) and others (see Guilford, 1990). No comparable experiments have been undertaken using fish or other marine animals as predators. However, if some nudibranchs are aposematic to certain species of fish, then a knowledge of the behaviour of these fish is crucial to our understanding of how the aposematism has evolved. Since different species of predators may respond differently to aposematic prey, the evolution of aposematic nudibranchs may have followed several routes.

The *direct* evidence for aposematism in nudibranchs is thus not conclusive. There is evidence that some nudibranchs fulfil criteria 1 and 2, although further field observations are also required. Much more experimental work needs to be undertaken to see if criteria 3 and 4, which relate to the behaviour of the predator, are applicable. However, it is also possible to look for *indirect* evidence for aposematism in nudibranchs.

Indirect Evidence for Aposematism

The indirect evidence for aposematism in nudibranchs is obtained by assuming that it does occur, predicting the consequences of this assumption and then testing these predictions.

1. Evolution of especially noxious qualities and of ability to survive attacks

Because of its bright colours an aposematic animal is more likely to be found and attacked than is a cryptic animal, and so there will be stronger selection pressure on it favouring more effective noxious qualities and greater resilience to attack. For monarch butterflies (*Danaus plexippus*) this has led to sequestering cardenolides from their food which are emetic to their avian predators, and emesis is a particularly effective way of negatively conditioning a bird (Brower *et al.*, 1968, 1970). For nudibranchs I know of no evidence that the defences of aposematic species are any more effective than those of cryptic ones. Many nudibranchs are resilient to attack with autotomizable papillae and good powers of regeneration, but again I know of no evidence that this resilience is more pronounced in brightly coloured species.

2. Evolution of Batesian and Müllerian mimicry

Aposematic animals may suffer injury or death while predators learn their colour pattern, so selection will favour individuals of different species having the same pattern. Predators need then learn only one pattern for individuals of both species to be protected, and the chances of any one animal being killed will be reduced. This is *Müllerian* mimicry. Selection will also favour the evolution of *Batesian* mimicry, that is of animals with the same colour pattern as the aposematic model, but which are palatable to those predators which avoid the model.

Mimicry is common among nudibranchs; Ros (1976, 1977) lists five mimetic groups from the Mediterranean, including blue and gold chromodorids and orange and white nudibranchs. There are groups of blue and gold chromodorids from the Pacific coast of North America (Bertsch, 1978a,b,c), and numerous colour groups of chromodorids have been described from the Indo-Pacific by Rudman (summarized by Edmunds, 1987). Each mimicry group comprises species belonging to more than one genus, so similarity of colour is not due simply to recent speciation. Some of these mimicry groups are listed in Table 1. Not all mimetic species of a single group occur in any one habitat, for example on the reef off Tema, Ghana, only *Mexichromis tricolor* and *Hypselodoris bilineata* have been found (Edmunds, 1981). The occurrence of mimicry in these species is almost impossible to explain unless some of them are aposematic. It is not known which species in each group are Müllerian and which are Batesian because no experiments involving naturally occurring predators have been carried out, but all of the relevant nudibranchs appear to have glandular or nematocyst defences which could make them unpalatable. Most are therefore probably Müllerian mimics though some could be Batesian, at least towards some predators (Edmunds, 1987). There are, however, some problems. *Eubranchus farrani* (Alder & Hancock) is typically orange and white, conspic-

TABLE 1. Presumed mimetic groups of nudibranchs

Blue and gold group from Mediterranean and east Atlantic (Ros, 1977; Edmunds, 1987)

Chromodoris krohni (Verany)
Hypselodoris bilineata (Pruvot-Fol)
Hypselodoris cantabrica (Bouchet & Ortea)
Hypselodoris messinensis (Ihering)
Hypselodoris tema (Edmunds)
Hypselodoris valenciennesi (Cantraine)
Hypselodoris villafranca (Risso)
Hypselodoris webbi (Orbigny)
Mexichromis tricolor (Cantraine)

Orange and white group from Mediterranean and northern Europe (Ros, 1977; Edmunds, 1987)

Ancula gibbosa Risso
Chromodoris elegantula Philippi
Crimora papillata Alder & Hancock
Diaphorodoris papillata Portmann & Sandmeier
Eubranchus farrani (Alder & Hancock)
Limacia clavigera (Müller)
Polycera faeroensis Lemche
Polycera quadrilineata (Müller)
Trapania maculata Haefelfinger

Blue chromodorids from western America (Bertsch, 1978a,b,c)

Chromodoris mcfarlandi Cockerell
Hypselodoris agassizii (Bergh)
Hypselodoris californiensis (Bergh)
Hypselodoris ghiselini Bertsch
Hypselodoris lapislazuli (Bertsch & Ferreira)
Mexichromis antonii (Bertsch)
Mexichromis porterae (Cockerell)
Mexichromis tura (Marcus & Marcus)

White chromodorids with gold border from Indo-Pacific (Rudman, 1985)

Ardeadoris egretta Rudman
Cadlina nigrobranchiata Rudman
Cadlina willani Miller
Chromodoris aureomarginata Cheeseman
Glossodoris averni Rudman
Glossodoris pallida (Rüppell & Leuckart)
Glossodoris undaurum Rudman
Hypselodoris kulomba (Burn)
Noumea nivalis Baba
Noumea sudanica Rudman
Thorunna africana Rudman
Thorunna furtiva Bergh

uous, and so presumably aposematic, but some populations are polymorphic (Edmunds & Kress, 1969). Polymorphism has clear advantages for cryptic animals, but it is difficult to see any advantage for an aposematic species (Edmunds, 1974, 1987).

3. Evolution of kin selection

The individuals who gain from aposematism can be the ones attacked by the potential predator or they can be other individuals in the vicinity. Where an aposematic animal is *always* killed during the educational experience of the predator, the animals that benefit from the aposematism must share genes with the individual sacrificed: this is *kin selection*. It applies to social Hymenoptera and other gregarious species which live in family groups or in colonies of related individuals. By contrast, where the aposematic animal survives the experience of sampling by a predator, the selective advantage is gained by this individual (*individual selection*), and there is no necessary requirement that it should be gregarious. The question of whether aposematism can only evolve through kin selection or whether it can also evolve through individual selection has generated a series of papers in recent years (e.g. Harvey & Paxton, 1981a, b; Harvey *et al.*, 1982; Jarvi *et al.*, 1981; Sillen-Tullberg & Bryant, 1983; review in Guilford, 1990). In nudibranchs the defensive glands and nematocysts are superficial, some animals have survived being taken into the mouth and spat out by fish, and most species have planktonic larvae so that the probability that two individuals that happen to settle on the same substrate are genetically related is slight. Aposematism is therefore most likely to have evolved because of the selective advantage it gives to the aposematic individuals themselves rather than to their kin. Nevertheless, assuming the same level of predator sampling, kin selection clearly gives greater protection to an individual's genes in terms of inclusive fitness (Hamilton, 1984) than individual selection, so we might predict the existence of kin selection in aposematic nudibranchs.

Is there any evidence of kin selection in aposematic nudibranchs? Kin selection can only occur in aposematic animals if they live in groups of related individuals. In nudibranchs it can only occur in species lacking planktonic larvae because this will enable the young grow up close to the parent. A cryptic animal, on the other hand, is more likely to benefit by having a planktonic larva to ensure wide dispersal so that predators will be less likely to acquire a searching image for its pat-

tern. I therefore predict a higher incidence of non-planktonic development in presumed aposematic than in cryptic nudibranchs.

It should be possible to test this prediction since the developmental pattern of more than 150 species of nudibranch is known. Table 2 summarizes the results, but there are problems with this analysis. First, developmental type has adaptive significance in terms of a species' life cycle and ecological habit (Todd, 1983) which may be of much greater importance than its possible consequences relating to kin selection. Thus the development of two species of arminid is known, but since most of their life is probably spent burrowing it is unlikely that developmental mode is related to colouration. The same argument can be applied to the burrowing aeolid *Cerberilla* and to intersitial acochlidiaceans. These species have been omitted from Table 2.

Second, while planktotrophic larvae clearly have planktonic development and direct developing eggs have non-planktonic development, lecithotrophic larvae include some with planktonic and others with non-planktonic development. It is possible that for some lecithotrophic species the planktonic stage is *obligatory* while for others it is *facultative* so that the larvae usually settle close to the egg ribbon. Such information is rarely published because it is trivial in terms of the development although of crucial importance to the possible occurrence of kin selection. In *Tenellia fuscata* (Gould) the veliger stage may never leave the egg or it may swim for up to a day (Harris *et al.*, 1980). In *Cuthona nana* (Alder & Hancock) and *Tenellia adspersa* (Nordmann) (= *T. pallida* (Alder & Hancock)) the occurrence of planktonic or non-planktonic larvae varies with population or with environmental conditions (Harris *et al.*, 1975; Rivest, 1976; Roginskaya, 1970; Eyster, 1979). These three species have also been omitted from the analysis. Two other species reported by one worker to have planktonic larvae and by another to have non-planktonic development are *Doriopsilla miniata* (Alder & Hancock) and *Cuthona pustulata* (Alder & Hancock) (Shyamasundari & Najbuddin, 1976; Thompson, 1975; Roginskaya, 1962; Gosliner & Millen, 1984). These conflicting reports may be explained by variation in developmental mode, or they may imply that the different workers were actually studying different species. These two species have also been omitted from Table 2, but similar plasticity of developmental mode may occur in some of the other species included in this table. *Moridilla brockii* Bergh and *Favorinus argentimaculatus* Rao have also been omitted from the table because although they have veliger larvae, these metamorphose a few hours after liberation (K.P. Rao, 1965; K.V. Rao, 1970); thus it is not clear if the developmental mode is effectively planktonic or non-plankton.

Finally, while the colour of these animals is known, it is not always easy to decide whether they are cryptic or aposematic. In this table I have assumed that all chromodorids are aposematic while most other doridaceans are cryptic. The decision is even more difficult for some aeolids: red *Coryphella* and *Flabellina* spp. could be cryptic on *Tubularia* or in deep water, or they could be conspicuous and aposematic; and *Aeolidiella* and *Spurilla* spp. could be cryptic or mimetic among sea anemones or they could be conspicuous and aposematic. I have left these species with a '?' in Table 2.

What conclusions can be drawn from Table 2? In the dorids (including chromodorids) there are 45 cryptic and 22 conspicuous species with planktonic development compared with 8 and 7 with non-planktonic development. These figures are not significant ($\chi^2 = 0.51$). However, if the chromodorids are all considered to be conspicuous and are compared with the other doridaceans (most of which are cryptic), we get the following: 53 dorids and 14 chromodorids have planktonic development compared with 8 and 7 with non-planktonic development. This gives a $\chi^2 = 3.03$ which is still not significant, but is close to the 5% level. For aeolids 41 cryptic and 9 aposematic species have planktonic development compared with 4 cryptic and 0 aposematic species without planktonic development. This difference is obviously not significant . Whether we assume that the species whose colour is entered with a '?' are cryptic or conspicuous makes little difference: the figures are still not significantly different. There is therefore no evidence from a study of developmental mode that kin selection occurs in nudibranchs.

Kin selection should also favour aposematic species with non-planktonic development living longer post-reproductively than cryptic species. If a predator learns the colour pattern by killing a senile animal, this will reduce the chances of that individual's offspring or siblings being taken by a predator, and this will increase the chances of the individual's

TABLE 2. Type of development and colour of nudibranchs. Development is classed as with or without planktonic larvae. Colour is assessed as cryptic (C), conspicuous (i.e. aposematic, A), or uncertain (?). Only one reference has been given for each species to economize on space.

WITH PLANKTONIC LARVAE

Species	Colour	Reference
Doridacea minus Chromodorididae		
Acanthodoris brunnea MacFarland	C	Hurst, 1967
Acanthodoris nanaimoensis O'Donoghue	C	Hurst, 1967
Acanthodoris pilosa (Müller)	C	Thompson, 1967
Adalaria proxima (Alder & Hancock)	C	Thompson, 1958
Aegires sublaevis Odhner	C	Schmekel & Portmann, 1982
Aegires punctilucens (Orbigny)	C	Thiriot-Quièvreux, 1972
Aldisa cooperi Robilliard & Baba	C	Millen & Gosliner, 1985
Aldisa tara Millen	C	Millen & Gosliner, 1985
Ancula evelinae Marcus	C	Eyster, 1980
Ancula gibbosa (Risso)	A	Thompson & Brown, 1984
Anisodoris prea Marcus & Marcus	C	Eyster, 1980
Archidoris montereyensis (Cooper)	C	McGowan & Pratt, 1954
Archidoris odhneri (MacFarland)	C	Hurst, 1967
Archidoris pseudoargus (Rapp)	C	Thompson, 1967
Asteronotus caespitosus (van Hasselt)	C	Gohar & Soliman, 1967e
Crimora papillata Alder & Hancock	A	Schmekel & Portmann, 1982
Dendrodoris fumata (Rüppell & Leuckart)	C	Gohar & Soliman, 1967a
Dendrodoris krebsi (Mörch)	C	Bandel, 1976
Diaphorodoris lirulatocauda Millen	C	Goddard, 1984
Diaulula sandiegensis (Cooper)	C	Hurst, 1967
Discodoris concinna (Alder & Hancock)	C	Gohar & Soliman, 1967f
Discodoris erythraeensis Vayssière	C	Gohar & Aboul-Ela, 1959
Doridella obscura Verrill	C	Perron & Turner, 1977
Doridella steinbergae (Lance)	C	Bickell & Chia, 1979
Doriopsis aurantiaca (Eliot)	C	Hamatani, 1961b
Doriopsis viridis Pease	C	Hamatani, 1961b
Doris ocelligera Bergh	C	Schmekel & Portmann, 1982
Goniodoris castanea Alder & Hancock	C	Schmekel & Portmann, 1982
Goniodoris nodosa (Montagu)	C	Thompson, 1967
Goniodoris sugashimae Baba	C	Hamatani, 1961a
Gymnodoris bicolor (Alder & Hancock)	A	Hamatani, 1960a
Gymnodoris citrina (Bergh)	A	Young, 1967
Halgerda rubicunda Baba	C	Hamatani, 1960b
Hexabranchus sanguineus Rüppell & Leuckart	C	Gohar & Soliman, 1963
Homoiodoris japonica Bergh	C	Hamatani, 1962
Jorunna tomentosa (Cuvier)	C	Thompson, 1967
Nembrotha limaciformis Eliot	A	Soliman, 1991
Okenia ascidicola Morse	C	Morse, 1972
Okenia impexa Marcus	C	Eyster, 1980
Onchidoris bilamellata (Linnaeus)	C	Thompson, 1967
Onchidoris muricata (Müller)	C	Thompson, 1967
Onchidoris neapolitana (Chiaje)	C	Schmekel & Portmann, 1982
Peltodoris hummelincki Marcus	C	Bandel, 1976
Phyllidia varicosa Lamarck	A	Soliman, 1986
Platydoris scabra (Cuvier)	C	Soliman, 1978
Polycera quadrilineata (Müller)	A	Thompson, 1967
Polycerella emertoni Verrill	C	Franz & Clark, 1972
Rostanga pulchra MacFarland	C	Chia & Koss, 1978
Sebadoris crosslandi (Eliot)	C	Soliman, 1980
Taringa telopia Marcus	C	Bandel, 1976
Thordisa filix Pruvot-Fol	C	Schmekel & Portmann, 1982
Triopha catalinae (Cooper)	A	Hurst, 1967
Trippa areolata (Alder & Hancock)	C	Gohar & Soliman, 1967g

TABLE 2. (*Continued*)

Species	Colour	Reference
Doridacea Chromodorididae		
Chromodoris africana Eliot	A	Gohar & Aboul-Ela, 1959
Chromodoris amoena Chesseman	A	Thompson, 1972a
Chromodoris annulata Eliot	A	Gohar & Aboul-Ela, 1957b
Chromodoris clenchi (Russell)	A	Bandel, 1976
Chromodoris inornata Pease	A	Gohar & Soliman, 1967b
Chromodoris luteopunctata (Gantès)	A	Gantès, 1962
Chromodoris perola Marcus	A	Bandel, 1976
Chromodoris pulchella (Rüppell & Leuckart)	A	Gohar & Aboul-Ela, 1957b
Chromodoris tinctoria (Rüppell & Leuckart)	A	Gohar & Soliman, 1967c
Glossodoris atromarginata (Cuvier)	A	Gohar & Aboul-Ela, 1959
Glossodoris pallida (Rüppell & Leuckart)	A	Soliman, 1991
Hypselodoris bilineata Pruvot-Fol	A	Gantès, 1962
Hypselodoris elegans (Cantraine)	A	Rho, 1888
Hypselodoris kayae Young	A	Young, 1967
Aeolidiacea		
Aeolidia papillosa (Linnaeus)	C	Williams, 1980
Aeolidiella glauca (Alder & Hancock)	C	Hadfield, 1963a
Aeolidiella mannarensis (Rao & Alagarswami)	?	Rao & Alagarswami, 1960
Aeolidiella sanguinea (Norman)	?	Tardy, 1969a
Antonietta luteorufa Schmekel	C	Schmekel & Portmann, 1982
Austraeolis catina (Marcus & Marcus)	C	Clark & Goetzfried, 1978
Berghia benteva (Marcus)	C	Eyster, 1980
Berghia coerulescens (Laurillard)	A	Tardy, 1962c
Berghia verrucicornis (Costa)	A	Tardy, 1962c
Catriona gymnota (Couthouy)	C	Clark, 1975
Coryphella browni Picton	C	Thompson & Brown, 1984
Coryphella fusca O'Donoghue	?	Roginskaya, 1969
Coryphella gracilis (Alder & Hancock)	?	Kuzirian, 1979
Coryphella lineata (Lovén)	?	Thompson, 1967
Coryphella nobilis Verrill	?	Kuzirian, 1977
Coryphella parva Hadfield	C	Hadfield, 1963b
Coryphella pedata (Montagu)	?	Schmekel & Portmann, 1982
Coryphella pellucida (Alder & Hancock)	?	Kuzirian, 1979
Coryphella trilineata O'Donoghue	?	Bridges & Blake, 1972
Coryphella verrucosa (Sars)	?	Kuzirian, 1979
Cratena peregrina (Gmelin)	A	Schmekel & Portmann, 1982
Cratena pilata (Gould)	C	Eyster, 1980
Cumanotus beaumonti (Eliot)	C	Hurst, 1967
Cuthona adyarensis Rao	C	Rao, 1962
Cuthona albocrusta (MacFarland)	C	Hurst, 1967
Cuthona albopunctata (Schmekel)	C	Schmekel & Portmann, 1982
Cuthona coerulea (Montagu)	A	Schmekel & Portmann, 1982
Cuthona futairo Baba	C	Hamatani, 1960b
Cuthona genovae (O'Donoghue)	C	Schmekel & Portmann, 1982
Cuthona ilonae (Schmekel)	C	Schmekel & Portmann, 1982
Cuthona miniostriata (Schmekel)	C	Schmekel & Portmann, 1982
Cuthona ocellata (Schmekel)	C	Schmekel, 1966
Cuthona ornata Baba	A	Hamatani, 1960b
Cuthona pinnifera (Baba)	C	Hamatani, 1960b
Dicata odhneri Schmekel	C	Schmekel & Portmann, 1982
Dondice occidentalis (Engel)	C	Eyster, 1980
Dondice paguerensis Brandon & Cutress	C	Brandon & Cutress, 1985
Embletonia pulchra (Alder & Hancock)	C	Schmekel & Portmann, 1982
Eubranchus cingulatus (Alder & Hancock)	C	Tardy, 1970

(*continued*)

TABLE 2. (*Continued*)

Species	Colour	Reference
Eubranchus doriae (Trinchese)	C	Tardy, 1962a
Eubranchus exiguus (Alder & Hancock)	C	Hadfield, 1963a
Eubranchus farrani (Alder & Hancock)	A	Thompson, 1967
Eubranchus misakiensis Baba	C	Hamatani, 1961b
Eubranchus olivaceus (O'Donoghue)	C	Hurst, 1967
Eubranchus pallidus (Alder & Hancock)	C	Hadfield, 1963a
Facelina annulicornis (Chamisso & Eysenhardt)	C	Thompson & Brown, 1984
Facelina coronata (Forbes & Goodsir)	A	Tardy, 1970
Facelina dubia Pruvot-Fol	C	Schmekel & Portmann, 1982
Facelina fusca Schmekel	C	Schmekel & Portmann, 1982
Favorinus auritulus Marcus	C	Clark & Goetzfried, 1978
Favorinus branchialis (Rathke)	C	Haefelfinger, 1962
Fiona pinnata (Eschscholtz)	C	Holleman, 1972
Flabellina affinis (Gmelin)	?	Schmekel & Portmann, 1982
Flabellina engeli Marcus	?	Bandel, 1976
Hermissenda crassicornis (Eschscholtz)	A	Harrigan & Alkon, 1978
Limenandra nodosa Haefelfinger & Stamm	C	Schmekel & Portmann, 1982
Phestilla lugubris Bergh	C	Harris, 1975
Phestilla melanobranchia Bergh	C	Harris, 1975
Phidiana lynceus Bergh	A	Clark & Goetzfried, 1978
Phyllodesmium xenia Gohar & Aboul-Ela	C	Gohar & Aboul-Ela, 1957a
Piseinotecus sphaeriferus (Schmekel)	C	Schmekel & Portmann, 1982
Pruvotfolia pselliotes (Labbé)	C	Tardy, 1969b
Spurilla japonica (Eliot)	?	Hamatani, 1967
Spurilla neapolitana (Chiaje)	?	Clark & Goetzfried, 1978
Dendronotacea		
Dendronotus albopunctatus Robilliard	C	Robilliard, 1972
Dendronotus frondosus (Ascanius)	C	Miller, 1958
Dendronotus iris Cooper	C	Robilliard, 1970
Dendronotus rufus O'Donoghue	C	Robilliard, 1970
Dendronotus subramosus MacFarland	C	Robilliard, 1970
Doto coronata (Gmelin)	C	Thompson, 1967
Doto doerga Marcus & Marcus	C	Schmekel & Portmann, 1982
Doto fragilis (Forbes)	C	Kress, 1975
Doto japonica Odhner	C	Hamatani, 1963
Doto paulinae Trinchese	C	Schmekel & Portmann, 1982
Doto pinnatifida (Montagu)	C	Kress, 1975
Doto rosea Trinchese	C	Schmekel & Portmann, 1982
Doto yongei Thompson	C	Thompson, 1972b
Hancockia burni Thompson	C	Thompson, 1972b
Hancockia uncinata (Hesse)	C	Schmekel & Portmann, 1982
Lomanotus stauberi Clark & Goetzfried	C	Clark & Goetzfried, 1978
Melibe fimbriata Alder & Hancock	C	Thompson & Crampton, 1984
Melibe leonina (Gould)	C	Bickell & Kempf, 1983
Tritonia cincta Pruvot-Fol	C	Schmekel & Portmann, 1982
Tritonia diomedea Bergh	C	Kempf & Willows, 1977
Tritonia hombergi Cuvier	C	Thompson, 1962
Tritonia plebeia Johnston	C	Thompson, 1967
Arminacea		
Dirona albolineata Cockerell & Eliot	C	Hurst, 1967
Dirona aurantia Hurst	A	Hurst, 1967
Hero formosa (Lovén)	C	Thompson, 1967
Janolus cristatus (Chiaje)	C	Thompson & Brown, 1984

TABLE 2. (*Continued*)

WITHOUT PLANKTONIC LARVAE		
Species	Colour	Reference
Doridacea minus Chromodorididae		
Austrodoris macmurdensis Odhner	C	Gibson et al. 1970
Dendrodoris krebsi (Mörch)	C	Clark & Goetzfried, 1978
Dendrodoris limbata (Cuvier)	C	Si, 1931
Discodoris rosi Ortea	C	Ortea, 1979
Doriopsilla pharpa Marcus	C	Clark & Goetzfried, 1978
Okadaia elegans Baba	C	Baba, 1937
Trippa spongiosa (Kelaart)	C	Gohar & Soliman, 1967g
Vayssieria caledonica (Risbec)	C	Risbec, 1953
Doridacea Chromodorididae		
Cadlina laevis (Linnaeus)	A	Thompson, 1967
Chromodoris loringi (Angas)	A	Thompson, 1972a
Glossodoris obsoleta (Rüppell & Leuckart)	A	Gohar & Soliman, 1967d
Glossodoris sibogae (Bergh)	A	Usuki, 1967
Hypselodoris bennetti (Angas)	A	Thompson, 1972a
Hypselodoris villafranca (Risso)	A	Gantès, 1962
Mexichromis tricolor (Cantraine)	A	Haefelfinger, 1969
Aeolidacea		
Aeolidiella alder (Cocks)	?	Tardy, 1962b
Coryphella salmonacea (Couthouy)	?	Morse, 1971
Cuthona granosa Schmekel	C	Schmekel, 1966
Cuthona poritophages Rudman	C	Rudman, 1979
Embletonia gracilis Risbec	C	Gosliner & Griffiths, 1981
Herviella mietta Marcus & Burch	C	Young, 1967

own genes contributing to the next generation. Conversely if a cryptic animal dies soon after reproducing this will reduce the chances of a predator finding it, acquiring a searching image for its patttern, and then hunting out similarly coloured prey in the vicinity. This argument was first used by Blest (1963) and was supported by evidence from saturniid moths. It should be possible to test this prediction by comparing the times survived after the last oviposition by cryptic and by aposematic nudibranchs with non-planktonic development. Unfortunately although this information is probably available in the files of the many workers who have studied oviposition and development in nudibranchs it has never been published.

4. Evolution of innate responses of predators

Until recently it was assumed that the predators which avoid aposematic prey had to learn through experience to associate unpalatability with colour or with other specific signals, but several predators are now known which have innate aversion responses to specific signals (see Edmunds, 1974). These predators include certain species of birds (Smith, 1975,1977; Caldwell & Rubinoff, 1983) and fish (Rubinoff & Kropach, 1970), but other species of predator which do not experience the specific aposematic signals in their normal environment lack innate aversions (Smith, 1980). An animal is most unlikely to evolve an innate aversion to a stimulus unless there is clear advantage in avoiding that stimulus, otherwise several Batesian mimics would quickly evolve to exploit the situation (Guildford, 1990). Such aversive responses evolved when the predators originally developed learned aversions, but where there was selective advantage in minimizing the time spent, or the danger, in having to learn. It follows from this argument that innate aversive responses imply a long evolutionary history of behaviour in response to a specific aposematic signal.

It is known that some fish have innate aversive responses to sea snakes (Rubinoff & Kropach, 1970), but no such response is known towards any nudibranch, and the experiments of feeding nudibranchs to fish indicate that the aversive responses have to be learned. However, no critical experiments have been undertaken, and where fish appear to ignore nudibranchs crawling around in aquaria it is possible that they actually see and then deliberately avoid them innately.

The Evolution of Aposematism in Nudibranchs

Assuming that a particular nudibranch is aposematic the question arises of which evolved first, unpalatability or warning colours? The first possibility is supported by the fact that many cryptic nudibranchs are unpalatable to fish (Thompson, 1960). In addition, conspicuous colours will only evolve in a palatable animal, or one that is only slightly unpalatable, if they confer some selective advantage which is greater than the liability of attracting predators. Thus they might evolve because they confer an advantage in intraspecific encounters (e.g. sexual, territorial, etc.). However, there is no evidence that colour has such a function in nudibranchs. Colour can also be of value in interspecific contexts (Batesian mimicry, deimatic and flash colours), but these are comparatively rare in nudibranchs (Edmunds, 1987), so I consider it highly improbable that bright colours evolved before unpalatability. I therefore conclude that if aposematic nudibranchs occur, they have evolved through individual selection from initially cryptic but relatively unpalatable species.

CONCLUSIONS

I conclude from this review that aposematism does occur in some nudibranchs and that the evidence for it is particularly strong in those species which are conspicuously coloured in their natural habitat, are unpalatable to some predators, and are part of a mimetic group of species. Clearly there is plenty of scope for more detailed experimental studies of aposematism in nudibranch molluscs, and the purpose of this paper is to raise some of the issues that might usefully be addressed in such an investigation. There are also many anomalies that need further study; one example which I gave recently is *Polycera elegans* (Bergh) which is a brilliantly coloured species that is rare (Edmunds, 1987). Unless an animal is exceptionally noxious and resilient to sampling by a predator, it is difficult to see the selective advantage for a rare species of being conspicuous instead of being cryptic. I hope that this review will stimulate further experimental work on the significance of brilliant colours in nudibranchs.

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A COMPARATIVE REVIEW OF THE SPAWNING, DEVELOPMENT AND METAMORPHOSIS OF PROSOBRANCH AND OPISTHOBRANCH GASTROPODS WITH SPECIAL REFERENCE TO THOSE FROM THE NORTHWESTERN RED SEA

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ABSTRACT

Aspects of spawning, development and metamorphosis of 50 prosobranch and opisthobranch gastropods from the northwestern Red Sea are reviewed. For almost every species, data are given of the breeding season, size and number of eggs laid, and period and type of development. The early embryology, larval structure and behaviour, and post-larval development are summarized. Only the nudibranch *Casella obsoleta* has direct development. In agreement with Thorson's rule, most species have pelagic development, although prosobranchs (neogastropods in particular) show a tendency towards lecithotrophy and rapid metamorphosis. The intrinsic and extrinsic factors affecting the type of development are discussed.

INTRODUCTION

In an attempt to review reproduction in prosobranchs and opisthobranchs, a study of their egg masses has recently been made (Soliman, 1987). The present paper aims to extend the comparative study to other aspects of reproduction, namely egg size and number, early embryology, larval structure and behaviour, and the type of reproduction, and to review the factors which affect development and metamorphosis. This paper also aims to find out to what extent the patterns of molluscan development in the northwestern Red Sea agree with Thorson's rule (1950) and to compare our results with those reported from other areas lying more or less within the same latitudes.

The present study, like the former, is based mainly on new data and on studies made on Red Sea gastropods during the last 30 years (Gohar & Aboul-Ela, 1957, 1959; Gohar & Eisawy, 1963,1967; Gohar & Soliman, 1963, 1967; Eisawy & Sorial, 1968, 1974, 1976; Eisawy, 1970; Soliman, 1977, 1978, 1980, 1983, 1986) together with data from other sources.

SPAWNING, EMBRYOLOGY AND LARVAL DEVELOPMENT

Egg Capsules

Primitively, gastropod eggs are laid singly, uncovered and they are externally fertilized. In most gastropods, however, eggs are enclosed either singly or in groups (up to hundreds) in transparent thin-walled cases, in leathery sacs or hard capsules. Cases may be dispersed freely becoming planktonic. Most often they are embedded in a gelatinous matrix and moulded in thin sheets, ovoid or globular jelly masses (or without a definite shape), cords or ribbons (Soliman, 1987).

In opisthobranchs, egg cases may lie directly in the spawn jelly or, as in many nudibranch egg ribbons, may be primarily enclosed in tubes of thick mucus winding in the spawn matrix in variable fashion. Thus in small ribbons the tubes run in a closely parallel manner (Fig. 1A), but they radiate peripherally in massive undulating ones (Fig. 1B). In some species, each egg case within the tube may be isolated in a thin-walled compartment of various shapes (Fig. 1C,D). The egg string of *Strombus tricornis* (Eisawy & Sorial, 1968) has a similar construction with the egg cases each enclosed in a gelatinous compartment that is finally coated by the egg string (Fig. 1E).

The size limits of opisthobranch egg cases (and the numbers of eggs enclosed) are generally lower than those recorded for prosobranch capsules (Table 1). In the former, cases measure 0.1–0.3 mm on average, but cases up to 0.6 mm across are not uncommon. The largest cases encountered in some masses of the nudibranch *Hexabranchus sanguineus* (2 x 0.6 mm, with more than 100 eggs) (Gohar & Soliman, 1963b) are still far smaller than what exists in certain proso-

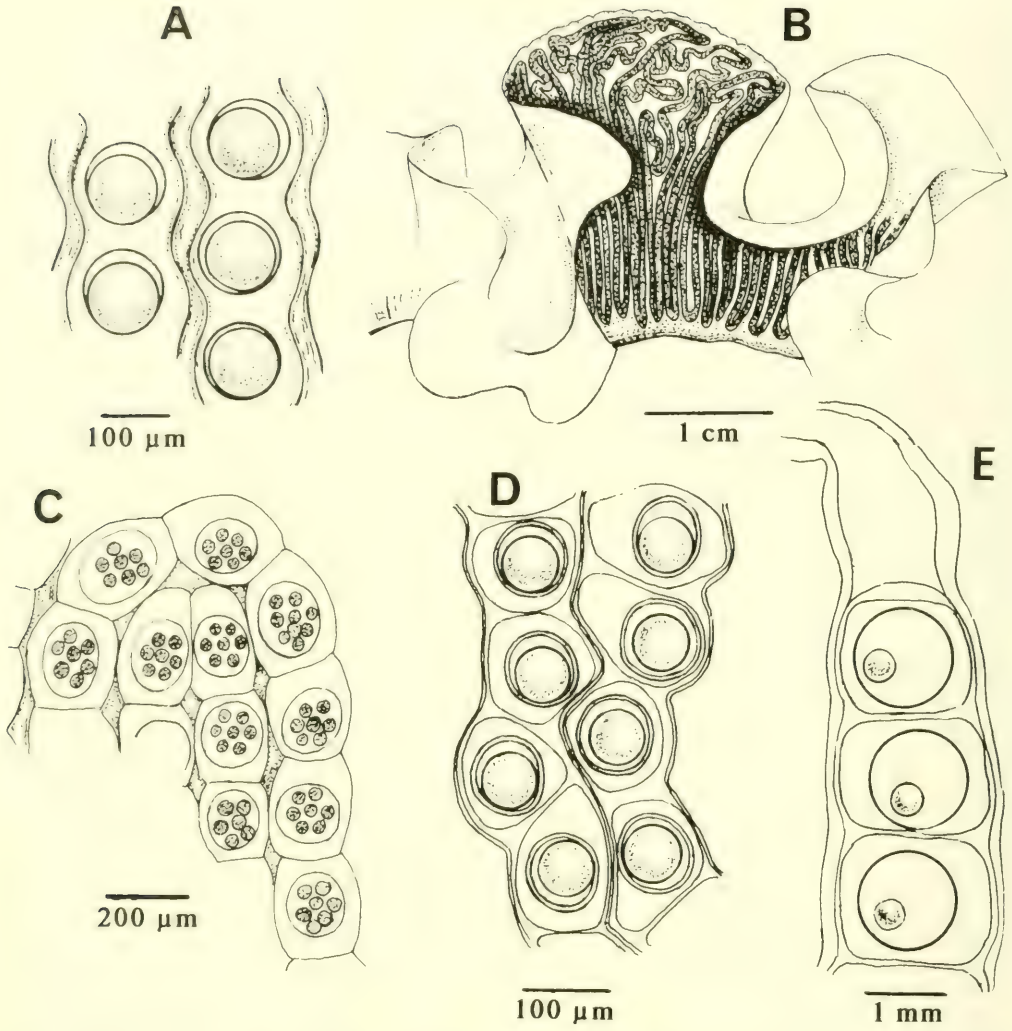

FIG. 1. Patterns of egg case arrangement in the jelly matrix in Red Sea gastropods. A. *Trippa spongiosa:* part of two parallel egg cords in jelly with no compartments (after Gohar & Soliman, 1967g). B. *Discodoris concinna:* enlarged portion of spawn ribbon with cords radiating and winding distally (modified after Gohar & Soliman, 1967f). C. *Asteronotus cespitosus:* segmented egg cord with one case in each segment (after Gohar & Soliman, 1967e). D. *Chromodoris inornata:* egg cases with each enclosed in a separate compartment (after Gohar & Soliman, 1967b). E. *Strombus tricornis:* similar arrangement to D, but eggs are in cords, not in a common jelly (after Eisawy & Sorial, 1968).

branchs (19–35 x 5–9 mm in *Pleuroploca trapezium* with up to 400 eggs, and 8–9 x 3.5 mm in *Nassa francolina* with up to 1678 eggs) (Gohar & Eisawy, 1967b).

Size and number of eggs

The number of eggs laid by a gastropod is inversely proportional to egg size. According to the available data, the maximal size attained in prosobranchs markedly exceeds that in opisthobranchs (up to 0.75 mm in *Conus* (Natarajan, 1957), 0.44 mm in *Strombus tricornis* (Eisawy & Sorial, 1968) and 0.42 mm in *Pleuroploca trapezium* (Gohar & Eisawy, 1967b), against only 0.39 mm in *Cadlina laevis* (Thompson, 1967) and 0.33 mm in *Casella obsoleta* (Gohar & Soliman, 1967d)). As

anticipated, the number of eggs in a spawn deposited by an opisthobranch substantially surpasses what is recorded for prosobranchs (apart from certain archaeogastropods). 148 million eggs were recorded laid by *Aplysia californica* (MacGinitie, 1934) and a little less than 5 million by the nudibranch *Asteronotus cespitosus* (Gohar & Soliman, 1967e).

However, in many prosobranchs (principally neogastropods) the majority of eggs laid act as nurse cells subserving as food for the very small fraction of viable eggs which proceed to full development (15% in *Pleuroploca trapezium,* < 6% in *Chicoreus ramosus* (Gohar & Eisawy, 1967b), 3% in *Fusinus tuberculata* (Eisawy & Sorial, 1976a), 2% in *Chicoreus virgineus* (Gohar & Eisawy, 1967b), and even less in certain other species). According to Thorson (1940) 50,000–100,000 nurse eggs may exist per embryo in *Volutopsius norwegicus.* Nurse cells are not reported to exist in opisthobranchs.

Cleavage and early embryology

In the majority of opisthobranchs, the two initial divisions of the egg invariably bring about the formation of nearly equal macromeres which proceed thereafter in typical spiral cleavage (Fig. 2A). Unequal division is, however, typical of large, yolky prosobranch eggs. Actually such division is mainly dependent on the amount of yolk in the egg irrespective of its size. Thus while the initial division of *Tonna olearium* eggs (0.25 mm in diameter) gives rise to nearly equal macromeres (Gohar & Eisawy, 1967a), similar or even smaller eggs of other species (0.18–0.22 mm, *Chicoreus virgineus;* 0.25 mm, *C. ramosus* (Gohar & Eisawy, 1967b)) exhibit markedly unequal division with the macromeres A-C appearing as if budding from the giant D cell (Fig. 2B). The subsequent divisions do not much affect the relative disparity in the size of the macromeres.

In contrast to the opacity of most gastropod embryos and larvae developing from lecithotrophic eggs, planktonic larvae are relatively transparent. It is not uncommon nevertheless to come across opaque embryos arising from comparatively small eggs (70 μm, *Sebadoris crosslandi* (Soliman, 1980)) or, conversely, lecithotrophic larvae (*Trippa spongiosa,* egg 0.2 mm across (Gohar & Soliman, 1967g)) or veliger and metamorphosing stages of directly developed species (*Acteocina atrata* (Mikkelsen & Mikkelsen, 1984)) with markedly clear structure. Generally, however, as far as the planktotrophic Red Sea gastropods are concerned, the developmental stages of opisthobranchs are much more transparent than are those of prosobranchs. Particularly in *Hexabranchus sanguineus* (Gohar & Soliman, 1963b), with intensely red yolk globules mostly condensed at the vegetative side of the egg, it is possible to follow, in whole live embryos, the formation of the 4d mesoblast and its division into two cells (Fig. 2C), which remain visible even after their migration inwards between the future ectoderm and endoderm. In fact, *H. sanguineus,* because of its abundance, the huge number of eggs it lays, and the clarity of its cells, is ideal material for live study of spiral cleavage, cell lineage and germ layer formation in molluscs.

Among the structures to appear early in opisthobranch embryos are the anal cells. These are initially posteroventral and slightly to the left. Their gradual shifting to the anterior right side (with the future proctodeal invagination and anus) is the only ontogenetic evidence of torsion, which is thus much less than 180°. *Casella obsoleta* exhibits detorsion (Fig. 5D) (Gohar & Soliman, 1967d), with the anal cells and associated organs migrating posteriorly (with the hind gut) during metamorphosis, until they reach their final position in the middle line just in front of the secondary larval kidney. They persist for 7–10 days after hatching and eventually vanish. This differs from Bonar's (1976) report that the anal cells disappear by the time the secondary kidneys develop.

The mouth in some cases forms shortly before the complete closure of the blastopore. In a number of species (*Dendrodoris fumata* (Fig. 4A), *Chromodoris inornata*) the secondary larval kidney develops as early as the anal cells (Gohar & Soliman, 1967a,b). It attains its maximal development structurally and functionally during larval life. It is still encountered in the hatching juvenile of *Casella obsoleta,* but gradually diminishes in size and disappears in three weeks, i.e. after the disappearance of the anal cells.

Hatching and larval behaviour

At hatching, the whole upper wall of the neritid capsule detaches, thus liberating the larvae (Soliman, 1987). In neogastropods in particular (and certain mesogastropods, e.g. *Tonna olearium* (Gohar & Eisawy, 1967a)),

TABLE 1. Breeding season, size, number and type of development of eggs of Red Sea prosobranchs and opisthobranchs.

Species	Breeding season	Dimension(s) of egg-case or capsule (mm)	Number of eggs per case or capsule	Max. number of eggs deposited
PROSOBRANCHS				
Trochus erythraeus	May–Aug	0.124–0.15 x 0.148–0.17	1–2	11,200
Trochus dentatus	Apr–Jul	0.4,0.48 x 0.43 av.	1	—
Turbo radiatus	Feb–May	—	1	—
Nerita forskali	Jan–Oct	2.2–2.5	60–210	—
*Lambis truncata**	Apr–Jul	0.3	1	21,750
Strombus tricornis	May–Aug	1.2–1.3	1	2,800
Strombus gibberulus	—	—	1	—
Strombus fasciatus	—	—	1	157,000
*Polinices mammilla**	Aug–Sep	0.135	1	580,000
*Polinices melanostoma**	—	—	1	61,000
*Tonna olearium**	Aug–Sep	1.4–1.9 x 1–1.5	18–35	—
*Chicoreus virgineus**	Apr–Jul	12–20 x 10–12	1036–2511	625,000
*Chicoreus ramosus**	Apr–May	15–21 x 5–7	300–346	13,450
*Nassa francolina**	Jul–Dec	8–9 x 3.5	1390–1723	1,720
Thais savignyi	Aug–Nov	3.5–3.7 x 2.2–3	250–500	15,000
Leptoconchus cumingii	Feb–Nov	6–9 x 3.7–6.3	600–1600	—
Leptoconchus globosus	Feb–Nov	7–8 x 5–6	700–1800	11,250
Magilopsis lamarckii	Feb–Nov	5–7 x 3.5–4.5	500–1400	—
*Pleuroploca trapezium**	Apr–May	19–35 x 5–9	70–400	70,000
*Fusinus tuberculatus**	Feb–May	11 x 7	—	—
Conus sp.	—	—	—	—
Conus sp.	—	—	—	—
OPISTHOBRANCHS				
Aplysia dactylomela	Apr–Oct	—	4–7	>1,000,000
Dolabella auricularia	Apr–Oct	—	1	>5,000,000
Berthellina citrina	Annual	0.38–0.44	1	23,760
Phyllobranchillus orientalis	Jun–?	0.09	1	117,000
Elysia olivaceus	May–Aug	—	—	—
Nembrotha limaciformis	Jun–Aug	0.09 x 0.075	1	75,600
Gymnodoris sp.	Jun–Sep	0.19 x 0.22 av.	1	61,500
Hexabranchus sanguineus	Annual	0.3–0.7, 0.6–1 x 0.2–0.4 up to 2 x 0.6	4–30 100	4,063,500
Chromodoris quadricolor	Mar–Sep	0.1–0.135	1	68,400
Chromodoris pulchella	Mar–Apr	—	1	48,000
Chromodoris annulata	Jul–?	—	1	108,000
Chromodoris ghardaqana	—	—	1	—
Chromodoris inornata	May–Nov	0.1	1	161,000
Chromodoris tinctoria	Jun–Jul	0.15	1–2	62,000
Chromodoris pallida	Jun–?	—	—	—
Casella atromarginata	Jun–Aug	0.25	1	188,000
Casella obsoleta	May–Sep	0.52–0.58	1	1,900
Asteronotus cespitosus	May–Sep	0.18–0.24	7–10	4,885,650
Platydoris scabra	May–Sep	0.16 x 0.23	1	1,507,520
Discodoris erythraeensis	Feb–Sep	0.24–0.25	1	56,100
Discodoris concinna	May–Sep	0.11–0.126	1	3,796,700
Discodoris sp.	Jul–?	—	1	21,760
Trippa areolata	May–Nov	0.11	1	4,113,500
Trippa spongiosa	Jun–?	0.26–0.3	1	103,600
Sebadoris crosslandi	Jun–Jul	0.12	1	902,000
Dendrodoris fumata	Annual	0.11–0.135	1	165,000
Phyllidia varicosa	Jul–Oct	0.2	1	67,000
Phyllodesmium xeniae	May–Oct	0.13–0.14	1	11,200

*Nomenclature updated.

Egg diameter (μm)	Period to veliger formation (d)	Temperature of culture (°C)	Type of development[†]	Reference
75	3–4	28	P	Gohar & Eisawy, 1963
200–225	24 h	27.5	L	Eisawy, 1970
200	8–9	26	L	Eisawy & Sorial, 1974a
120	—	—	P	Pers. obs.
210–260	7	26	L	Gohar & Eisawy, 1967a
410–440	10–11	28	L	Eisawy & Sorial, 1968
90	3–4	28	P	Eisawy & Sorial, 1976b
130	—	—	P	Eisawy & Sorial, 1976b
—	8	—	P	Gohar & Eisawy, 1967a
—	—	—	P	Gohar & Eisawy, 1967a
240–250	25	25	L	Gohar & Eisawy, 1967a
180–200	40–45	26.5	L	Gohar & Eisawy, 1967b
250	35–38	25	L	Gohar & Eisawy, 1967b
180	30–32	20	P	Gohar & Eisawy, 1967b
185–190	30–60	28–21	L	Eisawy & Sorial, 1974b
200	—	—	P	Gohar & Soliman, 1963a
—	—	—	P	Gohar & Soliman, 1963a
—	—	—	P	Gohar & Soliman, 1963a
400–420	45–47	24	L	Gohar & Eisawy, 1967b
180–200	30–50	22–17	L	Eisawy & Sorial, 1976a
—	—	—	P	Gohar & Eisawy, 1967b
—	—	—	L	Gohar & Eisawy, 1967b
80	7–10	22–30	P	Pers. obs.
92	8–11	22–30	P	Pers. obs.
200–250	7	28.5	L	Gohar & Aboul-Ela, 1957a
60	7½	27	P	Pers. obs.
—	—	—	P	Pers. obs.
65	4½	28	P	Pers. obs.
140	8	26	P	Pers. obs.
110–120	6–12	30–16	P	Gohar & Soliman, 1963b
70–90	12	18	P	Gohar & Aboul-Ela, 1957c
120–170	6	20.5	P	Gohar & Aboul-Ela, 1957c
120–160	6½	29	P	Gohar & Aboul-Ela, 1957c
—	—	—	—	Gohar & Aboul-Ela, 1957c
80	7–9½	30–22	P	Gohar & Soliman, 1967b
100	6–6½	29–27.4	P	Gohar & Soliman, 1967c
—	—	—	P	Pers. obs.
130–140	10	25	P	Gohar & Aboul-Ela, 1959
300–330	13–14	25	D	Gohar & Soliman, 1967d
65–70	4–5½	27.8–24.8	P	Gohar & Soliman, 1967e
90–100	5–5½	27.6	P	Soliman, 1978
140	11½	19	L	Gohar & Aboul-Ela, 1959
75	4½	27.5	P	Gohar & Soliman, 1967f
93	7½	29	P	Pers. obs.
100	4–5¼	27.4–23.9	P	Gohar & Soliman, 1967g
200	7	27	L	Gohar & Soliman, 1967g
70	7	27.6	P	Soliman, 1980
100	5½–17	30–16	P	Gohar & Soliman, 1967a
100	10	27.5	P	Soliman, 1986
95	4	28.5	P	Gohar & Aboul-Ela, 1957b

[†]P, planktotrophic; L, lecithotrophic; D, direct development.

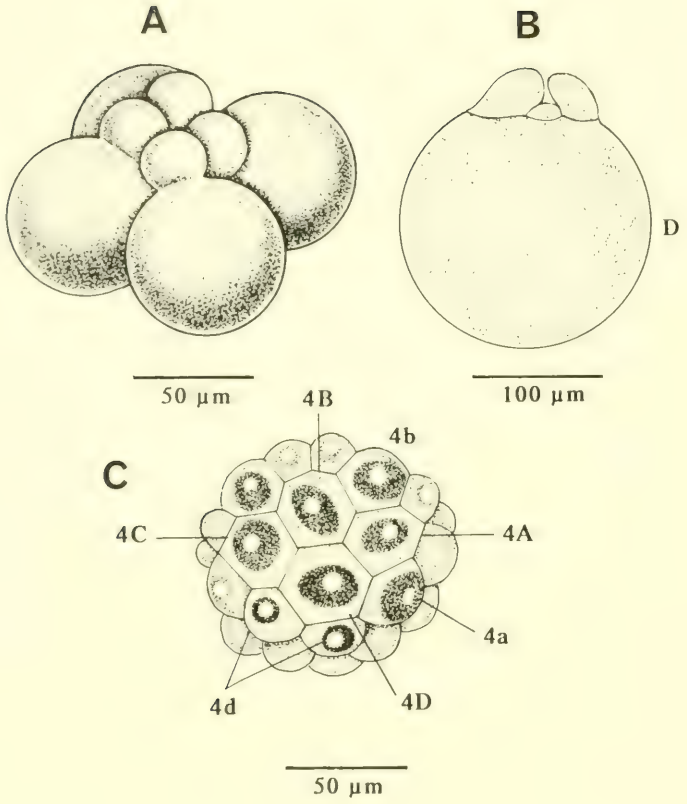

FIG. 2. Early embryology of Red Sea gastropods. A. *Hexabranchus sanguineus:* spiral cleavage, first quartette of micromeres formed (after Gohar & Soliman, 1963b). B. *Chicoreus virgineus:* unequal cleavage of egg in a lecithotrophic prosobranch (after Gohar & Eisawy, 1967b). C. *Hexabranchus sanguineus:* formation of mesoderm mother cell (the mesoblast 4d) (after Gohar & Soliman, 1963b).

the egg capsule has an exit hole with fixed shape and position. The exit hole remains closed throughout development but opens at hatching to permit the release of larvae or succeeding stages. Empty capsules remain intact with firm walls. No comparable exit holes are encountered in opisthobranchs. In the Red Sea opisthobranch species studied, as development proceeds, the embryonic capsules gradually increase in size becoming

turgid with extremely thin walls (apparently due to increased intracapsular osmotic pressure). This allows for an easy penetration by the hatching stages. In only a few cases did the perforated capsules retain their contour. Generally, however, they become collapsed, deformed or entirely ruptured and so can be barely detected in the jelly matrix. This latter in turn may either remain intact, become wrinkled, dissociate into fragments or be converted into thick mucus.

The wide temperature range (16–30°C) and high salinity (around 40‰) of Red Sea waters directly affect the development and larval behaviour of the gastropods studied. In species with extended breeding, the developmental time varies much with temperature (e.g. *Thais savignyi,* 30 d at 28°C, 38 d at 26°C and 45 d at 24.2°C (Eisawy & Sorial, 1974b); *Fusinus tuberculatus,* 30–32 d at 27°C and 45–50 d at 22°C (Eisawy & Sorial, 1976a); *Hexabranchus sanguineus,* 6 d at 27°C and 10 d at 23.5°C (Gohar & Soliman, 1963b); *Dendrodoris fumata,* 5½ d at 28°C and 17 d at 17°C (Gohar & Soliman, 1967a)). The latter species is interesting since the length of the developmental period varies with the slight thermal changes within the same month: 152 h at 26.2°C, 156 h at 25.6°C and 164 h at 25°C. Being a shore species subject to substantial fluctuations in temperature and salinity, its larvae display remarkable tolerance to salinity changes (surviving for several days in 30‰ and for 40 h in 50‰).

At hatching, planktotrophic larvae develop for some time marked positive phototaxis, pursuing phytoplankton for food, and negative geotaxis to effect larval dispersal. Thereafter they become positively geotactic, invariably moving near the bottom but without displaying any tendency to metamorphose for reasons discussed later. Lecithotrophic larvae may remain planktonic for days or hours; they eventually settle and metamorphose. The newly emerging juveniles of *Casella obsoleta,* like the adults, are nocturnal in habit (Gohar & Soliman, 1967d).

Light has a decisive effect on the degree of pigmentation of the veliger shell, and in turn on the general colour of the spawn mass. Even in the same ribbon of *D. fumata,* parts exposed to more light appear darker (Gohar & Soliman, 1967a). Light affects the whole process of development: in the total absence of light it has been shown experimentally that development is retarded or completely inhibited.

Larval Structure

The velum, foot and shell are among the most conspicuous gastropod larval organs which can be of outstanding taxonomic value in prosobranchs.

The enlargement and subdivision of the velum into 4, 6 or more lobes is a common character of large prosobranch larvae (of advanced mesogastropods and neogastropods) which helps them meet their needs for buoyancy and food (Fig. 3A). A large or subdivided velum is not an indication of a long planktonic existence as is sometimes stated (Gohar & Eisawy, 1967a, in the case of *Polinices melanostoma*). Many such larvae have only a short pelagic life, becoming benthic one or two days after hatching; the velar lobes are eventually resorbed (e.g. *Strombus tricornis* (Eisawy & Sorial, 1968), *Chicoreus ramosus* (Fig. 3B, C), *Pleuroploca trapezium* (Gohar & Eisawy, 1967b), *Fusinus tuberculata* (Eisawy & Sorial, 1976a)). A multilobed velum is reported to exist in the larvae of only one opisthobranch, *Philine denticulata* (Horikoshi, 1967). In lecithotrophic and directly-developing opisthobranchs in general, the velum is relatively reduced in size and mobility. During metamorphosis, it may take part in the formation of the juvenile rhinophores (*Casella obsoleta,* Gohar & Soliman, 1967d).

A pedal operculum does not form in directly-developing opisthobranchs. It is lost in early juvenile development in aplysiids (Switzer-Dunlap & Hadfield, 1977), or during metamorphosis in all other opisthobranchs, but in prosobranchs it is only lost in a few non-operculate species.

With only a few exceptions, the larval shell is dextral in prosobranchs, with 1½ to 3 whorls (*Chicoreus ramosus,* Gohar & Eisawy, 1967b). In opisthobranch larvae, it may be cup-shaped, inflated or incipiently sinistrally coiled (hyperstrophic) with ¾–1½ whorls. Anomalous larvae possessing large tubular uncoiled shells are commonly observed in those opisthobranchs laying millions of eggs (*H. sanguineus, Asteronotus cespitosus* (Gohar & Soliman, 1963b, 1967e), *Platydoris scabra* (Soliman, 1978)). While the larval shell is retained in shelled opisthobranchs, it is cast off during metamorphosis in the remaining opisthobranch groups.

Except for *Casella obsoleta* and *Phyllodesmium xeniae* (Gohar & Aboul-Ela, 1957b), the veliger shells of all other Red Sea opisthobranchs studied belong to type B of Vester-

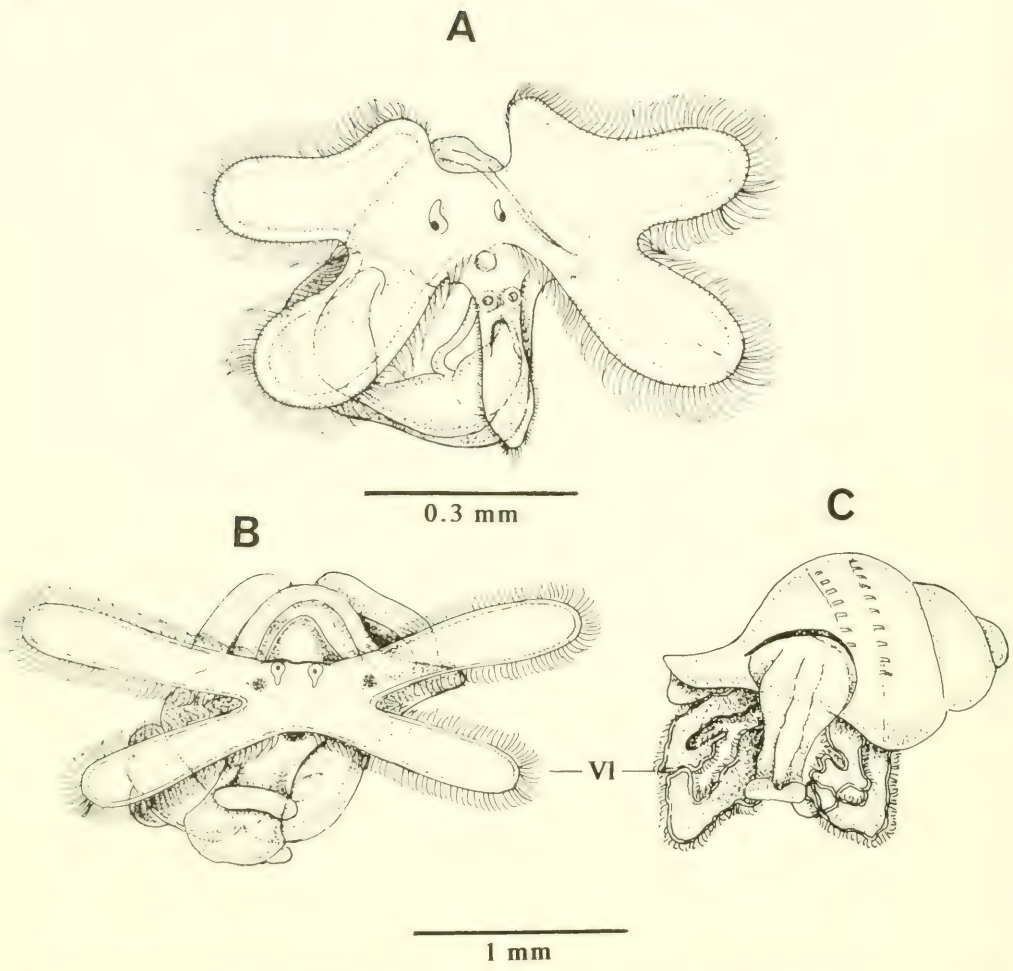

FIG. 3. Larval structure and development of Red Sea prosobranchs. A. *Lambis truncata:* veliger larva with 6-lobed velum (after Gohar & Eisawy, 1967a). B. *Chicoreus ramosus:* newly hatched veliger with 4-lobed velum (after Gohar & Eisawy, 1967b). C. *Chicoreus ramosus:* postlarva showing degeneration of velum during metamorphosis (after Gohar & Eisawy, 1967b). Vl, velum.

gaard & Thorson (1938) and Thorson (1946). While the larval shell type of *P. xeniae* was not reported, that of *C. obsoleta* is of type A. The validity of the latter type was a matter of controversy (Soliman, 1977). It has been rejected by Thompson (1961) on the basis of its possession only by premature abnormal larvae. Its occurrence in the directly developing species *C. obsoleta* and *Glossodoris sibogae* (Usuki, 1967) was considered as evidence for the view that such larval shells are vestigial, pertaining only to capsular development (Hadfield & Switzer-Dunlap, 1984). However, cup-shaped larval shells have been recently reported from planktonic veligers of two lecithotrophic gymnodorid nudibranchs (Boucher, 1986). The still rare occurrence of this type of larval shell and its primitive construction do not preclude its recognition as a valid type.

The variable sculpture and shape of prosobranch larval shells can provide a basis for their identification, but this is not possible with opisthobranch larval shells. Among these, only a few have roughened surfaces and they rarely have characteristic patterns (Hurst, 1967). Colour and exact measurements can nevertheless be reliable characters in certain

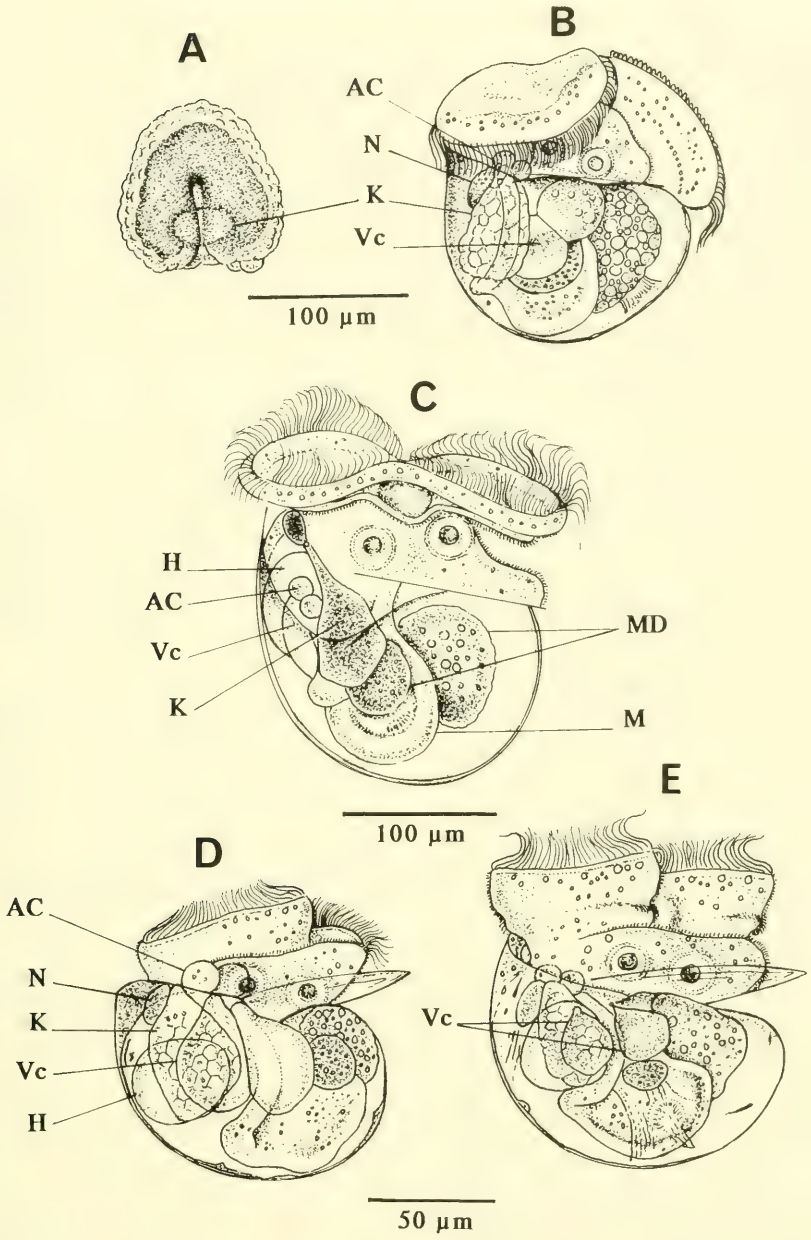

FIG. 4. Embryology and larval development of Red Sea opisthobranchs. A. *Dendrodoris fumata:* early formation of secondary (larval) kidney in gastrula; anal cells in pretorsional position (after Gohar & Soliman, 1967a). B. *Dendrodoris fumata:* 7½ d old embryo. Note excretory structures: nephrocyst, secondary (larval) kidney, and excretory vesicles (after Gohar & Soliman, 1967a). C. *Hexabranchus sanguineus:* newly hatched larva. Note secondary (larval) kidney discharging a large droplet of fluid (modified after Gohar & Soliman, 1963b). D. *Chromodoris inornata:* 7 d old embryo. Note larval kidney and excretory vesicles with attenuated blunt ends (after Gohar & Soliman, 1967b). E. *Chromodoris inornata:* newly hatched veliger with separated excretory vesicles discharging droplets of excretory fluid (after Gohar & Soliman, 1967b). AC, anal cells; H, heart; K, secondary (larval) kidney; M, midgut; MD, midgut diverticula; N, nephrocyst; Vc, excretory vesicle(s).

cases (Gohar & Soliman, 1967g; Soliman, 1978).

As with the early embryological stages, live opisthobranch veligers are ideal material for studying the internal structure of gastropod larvae, e.g. gut, midgut diverticula, retractor muscle, heart, excretory and nervous elements. A heart is said to exist only occasionally in opisthobranch larvae and to have been reported among nudibranchs only for *Adalaria proxima* (Bonar, 1978). In the present material, a pulsatile heart has been described in the nudibranchs *Hexabranchus sanguineus, Dendrodoris fumata, Chromodoris inornata* and *Casella obsoleta* (with 20–21 beats.min-1 in the latter) (Gohar & Soliman, 1963b, 1967a,b,d) (Figs. 4, 5D).

Among the conspicuous larval excretory structures in many nudibranch species are the nephrocysts (symmetrically placed on the anterolateral aspect), the secondary larval kidney, and the large excretory vesicles (located on the right side in the close neighbourhood of the kidney (Fig. 4)). The larval kidney of *H. sanguineus* is highly distinctive by its deep red colour, and clearly has a neck and aperture through which fluid drops are discharged (Fig. 4C). The larval kidney seems to function not only during embryonic and larval life, but also for some time after the juvenile stage is attained (*Casella obsoleta,* Fig. 5D; *Philine denticulata,* Horikoshi, 1967). Very little is known about the excretory vesicles, but the extrusion of hyaline droplets in certain cases (*Chromodoris inornata,* Fig. 4E) suggests they may have an excretory function.

Eyes and tentacles are typical of prosobranch larvae. Their presence in newly hatched opisthobranch planktotrophic veligers is very unusual (Thorson, 1946). They develop 6 days after hatching in *Phyllodesmium xeniae* (pers. obs.), and some time during the larval phase in aplysiids (Switzer-Dunlap & Hadfield, 1977). Some cephalaspids hatch with only the right eye present (*Acteocina canaliculata* (Franz, 1971)), the left eye developing a few days later. Eyes are, however, discernible in the veliger stages of lecithotrophic and directly developing species (*Berthellina citrina, Discodoris erythraeensis* (Gohar & Aboul-Ela, 1957a, 1959), *Trippa spongiosa, Casella obsoleta* (Gohar & Soliman, 1967g,d)) (Fig. 5).

The statocysts develop earlier than the eyes. They are virtually the earliest embryonic nervous elements to develop during gastropod ontogeny and are retained in adult life.

DISCUSSION

Based on the studies of Thorson (1946, 1950), Thompson (1967), Mileikovsky (1971) and Todd (1981) and data of the present study (Table 1), the main types of developmental patterns among gastropods (applicable also to other molluscs) are:

1. Planktotrophic development, with typical veliger larvae feeding during their short or long pelagic existence;
2. Lecithotrophic development, which may be pelagic or non-pelagic; and
3. Direct or capsular development.

Each developmental type is correlated with a specific egg size range. In the present material the egg diameter range for the three types was 60–80 μm, 140–440 μm and 300–330 μm, respectively. This last figure for direct development is, however, based on inadequate data (just a single species, *Casella obsoleta*). Certain factors may, however, intervene allowing relatively small eggs to go through lecithotrophic or direct development, e.g. rich yolk content, rich albumen content of

FIG. 5. Metamorphosis of Red Sea non-planktotrophic opisthobranchs with selected stages of development. A. *Discodoris erythraeensis:* pelagic lecithotrophy in a dorid nudibranch (modified after Gohar & Aboul-Ela, 1959). From left to right: 7 d old embryo; metamorphosing postlarva with reflected mantle fold and no shell; juvenile. B. *Berthellina citrina:* non-pelagic lecithotrophy in a notaspidean (modified after Gohar & Aboul-Ela, 1957a). From left to right: intracapsular veliger stage; newly hatched swimming-crawling stage; pediveliger with absorbed velum and enlarged foot; juvenile with internal shell. C. *Trippa spongiosa:* non-pelagic lecithotrophy in a dorid nudibranch (after Gohar & Soliman, 1967g). From left to right: intracapsular veliger stage; metamorphosing stage; hatching stage deserting its shell; juvenile. D. *Casella obsoleta:* direct development in a dorid nudibranch (after Gohar & Soliman, 1967d). From left to right: intracapsular veliger stage; metamorphosing stage with enlarged foot, subvelar ridge, and reflected mantle fold; embryo, 2 d before hatching, without velum or shell, with anal cells and larval kidney reaching their final detorsional position; juvenile. AC, anal cells; F, foot; H, heart; K, larval kidney; P, reflected mantle fold; R, rhinophore; S, shell; T, tentacle; Vc, excretory vesicle(s); Vl, velum; Vs, subvelum.

A
B
C
D
P
F
S
VI
R
T
200 µm
K
Vc
Vs
AC
H

exceptionally large egg capsules, extracapsular yolk, or presence of nurse cells. Clark & Goetzfried (1978) report even smaller egg diameters of 91.9 μm and 97.7 μm, for the ascoglossans *Elysia papillosa* and *Costasiella lilianae* which develop lecithotrophically and directly, respectively, being provided with extrazygotic food reserves. Extracapsular yolk has been previously described in the spawn ribbons of *Chromodoris tinctoria* (Gohar & Soliman, 1967c). Here, although the egg is 100 μm across, and extracapsular yolk has been shown to be almost depleted before hatching, yet lecithotrophic development was not encountered. Since egg masses were laid in the laboratory only during June and July, animals may proceed to lecithotrophic development at other periods of the year. The development of *Elysia cauze* (Clark & Goetzfried, 1978) is seasonally variable and is apparently controlled by variable utilization of the extracapsular yolk. It is noticeable, however, that in *C. tinctoria,* the newly hatched larvae attained a relatively large size compared with larvae of other species developing from eggs of the same size but having no extrazygotic yolk.

Lecithotrophic development involves a typical veliger stage (which may be the hatching stage) that remains pelagic for a variable period of time, usually not exceeding two weeks (in *Lambis truncata* (Gohar & Eisawy, 1967a) (Fig. 3A); 7 d in *Discodoris erythraeensis* (Gohar & Aboul-Ela, 1959) (Fig. 5A); 4–6 d in *Chicoreus ramosus* (Fig. 3B); 2–3 d in *C. virgineus* (Gohar & Eisawy, 1967b); 2 d in *Strombus tricornis* and 1–2 d in *Fusinus tuberculatus* (Eisawy & Sorial, 1968, 1976a)). During their planktonic existence, which primarily effects their dispersal, the larvae may, but do not necessarily have to, feed. In non-pelagic lecithotrophic development, the veliger stage is passed intracapsularly, and on hatching already metamorphosing swim-crawling or crawling pediveligers are liberated which shortly attain the young stage (*Berthellina citrina, Trippa spongiosa* (Fig. 5B,C); *Cuthona nana* (Rivest, 1978)).

It is not uncommon nevertheless to have pelagic and non-pelagic lecithotrophy occurring in the same species (e.g. *Chicoreus virgineus* (Gohar & Eisawy, 1967b); *Fusinus tuberculatus* (Eisawy & Sorial, 1976a)). In such cases, while the majority of embryos hatch as proper planktonic larvae which start to metamorphose 1–2 d later, a few, having their hatching delayed (possibly due to culture conditions), proceed in development intracapsularly emerging as creeping stages.

In the third type, the whole development and metamorphosis takes place in the embryonic capsule. The veliger stage is either normal, although the velum is not well developed (*Retusa obtusa* (Smith, 1967); *Phyllaplysia taylori* (Bridges, 1975)), or is suppressed to varying degrees (*Casella obsoleta* (Fig. 5D); *Cadlina laevis* (Thompson, 1967)).

Bonar (1978) designates the direct type of development with no proper veliger stage as ametamorphic, exemplified by the dorid *Okadaia elegans* described as having no trace of shell or velum during development (Baba, 1937). This is, however, different from the case of *Casella obsoleta* (included by Bonar among species with ametamorphic development). In this species the veliger stage possesses a reduced but distinct velum, bearing short cilia and a subvelar ridge, and a cup-shaped shell (Fig. 5D). Because metamorphosis does not only affect the locomotory and other external organs, but also (particularly in opisthobranchs) several internal organs including the gut and nervous elements, the use of the term 'ametamorphic' in this context is misleading as it implies that there is no process of metamorphosis. It should appropriately be replaced by 'incomplete' or 'reduced' metamorphosis (i.e. heterometamorphic). Veliger stages with reduced velar lobes, meanwhile, are not restricted to directly developing species, but have also been reported in lecithotrophic species (*Cuthona nana* (Rivest, 1978)) the ontogeny of which could equally be described as involving reduced metamorphosis.

From the above review, the major factors affecting metamorphosis are, in chronological sequence: food conditions, acquiring competence for metamorphosis, and suitable substrata for settlement and metamorphosis. Planktotrophs and pelagic lecithotrophs pass through an obligatory planktonic (precompetent) phase for dispersal and feeding (essential for the former category). Therefore, in laboratory cultures, such larvae should be supplied with suitable food to maintain their survival until after becoming competent to metamorphose. In *Acteocina canaliculata,* only the fed larvae normally metamorphose in culture (Franz, 1971; Mikkelsen & Mikkelsen, 1984). Death of larvae, however, is not only a result of starvation but also of infection by bacteria and ciliates. This has been successfully controlled in laboratories by the use of

selected antibiotics (Bonar & Hadfield, 1974; Hadfield, 1984), ultrafiltration, and/or boiling of sea water before use. Finally, a suitable substratum is essential for metamorphosis in some species. The proximal cue to settlement is probably the presence of specific chemicals which trigger the onset of metamorphosis (Bonar, 1976; Hadfield, 1984), but the advantage of this behaviour is that the settled mollusc has an assured supply of food. Prey organisms of the adult have been frequently reported to be necessary to elicit metamorphosis, while a particular alga must be provided to stimulate settlement and metamorphosis in aplysiids (Switzer-Dunlap & Hadfield, 1977). The specific substratum could also be associated with certain individuals or may provide substances essential for adult life, beside affording optimal conditions for the species. In many species, however, planktotrophic and lecithotrophic larvae, after a period of pelagic existence, normally settle and metamorphose in the absence of a specific substratum (e.g. *Discodoris erythraeensis* (Gohar & Aboul-Ela, 1959); *Acteocina canaliculata* (Franz, 1971); *Pleuroploca trapezium* (Gohar & Eisawy, 1967a), among others).

Other defects in laboratory conditions can possibly also prohibit metamorphosis directly or indirectly. In the present study, rendering the adult's prey or substratum available to the postlarvae of several planktotrophic species (of which many had already become positively geotactic) was unsuccessful in inducing metamorphosis. This involved the use of the definitive coral species bored by the adult in the case of coralliophilids, dead coral pieces for many dorids, the alcyonarian *Sarcophytum* in the case of *Hexabranchus sanguineus* (on which the adults feed, at least in part), and the alcyonarian *Heteroxenia* among whose polyps the aeolid *Phyllodesmium xeniae* lives. Improving laboratory conditions can induce metamorphosis of such larvae developing from large yolked eggs (e.g. *Tonna olearium* (Gohar & Eisawy, 1967a); *Thais savignyi* (Eisawy & Sorial, 1974b)) which otherwise die a few days (6–12) after hatching, and it can help metamorphosing larvae to complete this process successfully (e.g. *Lambis truncata,* whose postlarvae often perish before attaining the young stage (Gohar & Eisawy, 1967a)).

Non-pelagic lecithotrophy and direct development are thus successful modes of molluscan development having advantages over planktotrophy and pelagic lecithotrophy. For the former the dangers of free planktonic existence (e.g. mortality due to predation, starvation, and drifting far from any suitable substratum) are minimized, and no external source of food or a specific substratum for settling and metamorphosing is required. While pelagic lecithotrophic larvae have overcome the food crisis often faced by planktotrophic larvae, they still share with them these other problems. The danger of failing to find a suitable settling ground is even more critical for them than for planktotrophic larvae, because their length of planktonic life is dependent upon their limited yolk supply (Smith, 1967). Non-pelagic lecithotrophs and directly developing species nonetheless have the disadvantages of limited distribution, possible overcrowding and genetic isolation.

The present data agree in general with Thorson's rule (1950) that among benthic invertebrates there is an increase in species with pelagic larvae from the poles towards the tropics and equator. Accordingly, among the 50 species of Red Sea gastropods whose ontogeny has been studied, 35 species (70%) have planktotrophic development, 14 are lecithotrophic and only one (a nudibranch) has direct development. The percentage of pelagic species would appear substantially higher if pelagic lecithotrophic species are taken into consideration. However, within the prosobranchs, the non-planktotrophic species represent a relatively high percentage, i.e. 50% (previously also recorded in the Bahamas (D'Asaro, 1970)), against only 14.3% for opisthobranchs. This may indicate a tendency to planktotrophy among Red Sea opisthobranchs, and to suppress planktonic in favour of non-pelagic development among neogastropods. There are, however, counter views which suggest that ecological conditions in the tropics (Florida, 17–32°C) favour direct development in nudibranchs and Ascoglossa (and probably all opisthobranchs) rather than planktotrophy (Clark & Goetzfried, 1978). While 87% of the nudibranchs studied from our area are planktotrophic, the limited number of species and higher taxa examined do not permit arriving at firm conclusions on this point.

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LARVAL STRATEGIES OF NUDIBRANCH MOLLUSCS: SIMILAR MEANS TO THE SAME END?

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ABSTRACT

Growth, development and metamorphosis of the planktotrophic larvae of *Onchidoris bilamellata* (L.) were followed in the laboratory at a range of culture temperatures and on a variety of microalgal diets. Successful culture of the nudibranch larvae at 5°C (approximating field temperatures) indicated developmental periods in agreement with previous estimations. Thus, predictions of the coincident timing of settlement and metamorphosis of *O. bilamellata* and the prey (*Semibalanus balanoides* (L.)) barnacles in the field are upheld. In this respect Todd & Doyle's (1981) "settlement-timing" hypothesis—as an explanation for the observed larval strategy of *O. bilamellata*—appears tenable. However, juveniles were observed to subsist on detritus for several weeks prior to their ability to prey upon *S. balanoides*. This precludes the validity of inferring a close matching of predator and prey settlement in explaining the specific larval strategy. In the light of other published data on larval/post-larval development, growth and feeding an alternative hypothesis, concerned with selective 'opportunities' in the evolution of nudibranch larval strategies, is outlined.

INTRODUCTION

It is apparent, for a wide variety of marine invertebrate phyla (Strathmann, 1978,1985), that reproduction by means of small eggs giving rise to planktotrophic larvae is the primitive (or ancestral) mode of development, and that pelagic, and thence non-pelagic, lecithotrophy are more advanced evolutionary derivatives. Evolutionary re-acquisition of lost larval feeding structures appears to be comparatively infrequent and we are thus confronted with an essentially uni-directional sequence of events. While there may remain debate over this generalization with respect to particular groups (even the Mollusca as a phylum), there can be little doubt (see Hadfield & Switzer-Dunlap, 1984) that such a trend pertains to the subclass Opisthobranchia. What remain to be ascertained, however, are the selective factors that have dictated a shift away from planktotrophy (which requires a more or less extended period of feeding, growth and development of the pelagic larva prior to metamorphosis), toward lecithotrophy (in which all reserves necessary for the completion of development of the benthic juvenile are provided within the egg by the parent). At present a consensus appears lacking (see Jablonski & Lutz, 1983; Day & McEdward, 1984; Hadfield & Switzer-Dunlap, 1984; Grahame & Branch, 1985; Todd, 1985a for reviews). Indeed, even if it is accepted that non-feeding larval forms have evolved from planktotrophic counterparts, it is likely that the selective regimes for such evolutionary shifts will comprise 'special cases' for many particular species.

In a previous study concerning the reproductive strategy of the Boreo-Arctic dorid nudibranch *Onchidoris bilamellata* (L.) (Todd & Doyle, 1981), emphasis was placed on the possible significance of the differing egg-to-benthic juvenile periods conferred by the three fundamental larval strategies of planktotrophy, pelagic lecithotrophy and non-pelagic lecithotrophy (or 'direct' development). Spawning of this specialist barnacle predator occurs at the coldest time of year and our hypothesis highlighted the approximately 3½-month time gap between peak spawning of the adult nudibranchs (January) and cyprid settlement of *Semibalanus balanoides* (L.) (May), the major prey species. Having a strictly annual and semelparous life-history, these nudibranchs have only the one reproductive opportunity: embryonic and/or larval failure is, therefore, absolute. Of central importance here is the presumably crucial coincidence of newly-metamorphosed molluscs with the establishment of the smallest phase of the barnacle life-cycle, bearing in mind that settlement of barnacles is restricted (but variable) both spatially and temporally. Data then

available suggested that only long-term pelagic planktotrophy could bridge the gap between the empirically predicted optimal time for adults to spawn and the observed optimal time for the veligers to settle and metamorphose. Development data for other British dorids indicated that both the pelagic and non-pelagic lecithotrophic strategies would result in juvenile nudibranchs establishing on the shore some weeks in advance of the availability of post-metamorph barnacle prey. It was perhaps surprising to note that pelagic lecithotrophy resulted in by far the shortest egg-to-juvenile interval, and that non-pelagic development was intermediate in duration.

Our settlement-timing hypothesis was based on a number of assumptions, foremost of which were the prediction of larval developmental periods in the field (from artificial laboratory culture observations at higher temperatures), and the immediate dependence of juvenile *O. bilamellata* upon the smallest post-metamorphic barnacles as prey. Criticisms of the original report (Grant & Williamson, 1985) were defended (Todd, 1985b) on the strength of available information while, independently, yet further specific reservations as to the validity of the principle were also being expressed (e.g. Hadfield & Switzer-Dunlap, 1984; Strathmann et al., 1984). Prior to this, more detailed evaluations of the larval and post-larval development of *O. bilamellata* had been initiated, and it is upon these that I report here. My primary objectives were to determine the duration of the pelagic phase at ambient field temperatures (≈ 5°C), and thereby to obtain further observations of post-larval dependence on barnacle spat. (Previous culturing had resulted in post-metamorph dorids in advance of *S. balanoides* settlement in the field.). I also examined the developmental effects of particular algal dietary species on growth and metamorphosis success in the laboratory. Culture conditions are by definition artificial (especially in terms of algal species and concentrations thereof) and the pitfalls of extrapolation to the field situation are self-evident. Nevertheless, by rearing larvae on a range of monocultures and combinations of phytoplankters ecologically realistic predictions may be made.

I show here that the original hypothesis does not provide an adequate descriptor of the behaviour of the nudibranch, but offer an alternative model for nudibranchs which centres upon larval and post-larval nutrition. It should be emphasized that this hypothesis explains only certain adaptive features of nudibranch reproductive strategies. It does not in itself provide an all-embracing framework of selection for particular larval types, which (if tenable) would also require an appraisal of the bioenergetic constraints and genetic implications of particular life-cycle, life-history and larval strategies (Todd, 1985a, 1987; Havenhand & Todd, 1988a,b,c; Todd & Havenhand, 1988, 1990; Todd et al., 1989).

MATERIALS AND METHODS

Larval culture of *Onchidoris bilamellata* has been undertaken from spawn masses deposited in the laboratory by field-collected adults. Throughout spawning, the nudibranchs were maintained on *Semibalanus balanoides* at ambient field temperatures. Culture methods are outlined elsewhere (Todd & Havenhand, 1984), but the salient features are summarized here. All flagellate larval diets were raised from inocula obtained from the Cambridge Collection of Algae and Protozoa, with the exception of *Isochrysis galbana* Parke, which was supplied by SMBA, Oban. Other algae employed were *Rhodomonas* sp., *Pavlova lutheri* (Droop) and *Tetraselmis* sp. Larvae were reared in glass beakers of 250–1000 ml volume, according to the number of veligers present, at an approximate concentration of 3 larvae.ml-1 and a total algal concentration of 50 cells μl^{-1}. Where mixtures of algal species were provided as the larval diet these were presented in equal numerical proportions. This is particularly pertinent for *Rhodomonas* which, at approximately 15 μm diameter, is much the largest of the species used. Larvae were cultured in 0.22 μm filtered seawater with the antibiotics Streptomycin sulphate and Penicillin G (50 and 60 $\mu g.ml^{-1}$ respectively) added to control any bacterial and ciliate infestations. Cultures were changed every 5 days by concentrating the veligers in a mesh-bottomed filter and pipetting them into freshly prepared beakers. All items of glassware were washed in hot fresh water only, or autoclaved, and at no time were detergents or disinfectants used.

Temperatures of the larval cultures (5, 10, 15 and 18°C) were controlled to within 0.2°C by immersing the vessels in thermostatically controlled water-baths and all were subjected to constant illumination in order to preclude possible complications of variable photope-

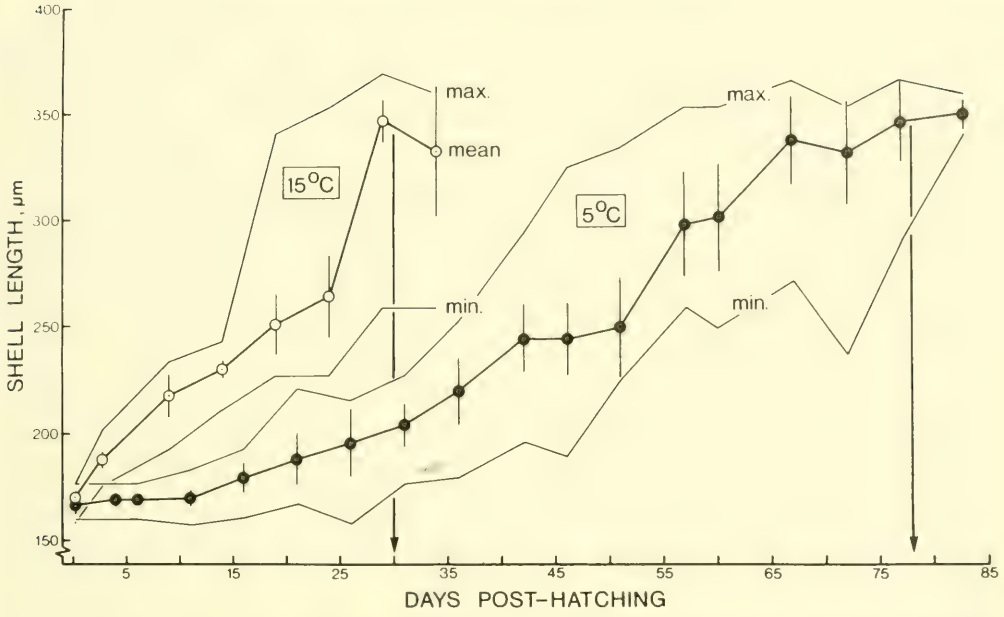

FIG. 1. Growth and development of the planktotrophic larvae of *Onchidoris bilamellata* in laboratory culture on a 1:1:1 mixture of the flagellates *Rhodomonas, Isochrysis* and *Pavlova* at 5°C and 15°C. Mean (with 95% confidence limits), maximum and minimum shell lengths are shown at each change of medium. Occurrence of first metamorphosis is indicated by arrows.

riod. The flagellate diets were, however, all raised at room temperature (≈ 20°C), a factor which may be of some importance to the colder larval cultures (see below).

In view of our previous lack of success in precluding 'rafting' of the larvae in the surface film (Todd, 1981; Todd & Havenhand, 1984), no such preventive steps were taken. Instead, entrapped larvae were resuspended by pipetting small drops of water onto the culture surfaces; this was undertaken at least once daily. 'Rafting' was usually only a problem in the early periods of development, when upward swimming is particularly marked. Periodic measurements of larvae were made to the nearest 3 µm with between 10 and 20 veligers sampled for this purpose. All measurements are of the maximum shell dimension taken from the aperture lip. 'Competence' to metamorphose is visibly assessable from the overall size of the veliger, the presence of eyes, the larval 'heart', a well-formed propodium, and the ability of the larva to crawl across a substratum. Once pediveligers were detected within a culture, subsamples were removed to glass dishes containing live adult *Semibalanus balanoides* (or *S. crenatus* (Bruguière)). If competent, the pediveligers generally commenced metamorphosis within a few hours. Further observations of post-larvae were made by maintaining these at 8°C (12 h light, 12 h dark) in plastic petri-dishes, within which field-collected cyprids of *S. balanoides* had previously been triggered to metamorphose.

The SEM preparations of *S. balanoides* plates were critical-point dried and gold sputter-coated in the standard manner, and were photographed on a JEOL JSM-35CF scanning electron microscope.

RESULTS

The initial success in rearing the larvae of this nudibranch species (Todd, 1981) was obtained in cultures containing a 1:1:1:1 mix of *Isochrysis, Pavlova, Rhodomonas* and *Tetraselmis*. Subsequently only the first three flagellates have been used, either as monocultures or equal mixtures (total concentration 50 cells μl^{-1}). The selected algal concentrations appear to promote maximal growth and metamorphosis success in a range of opisthobranch species (e.g. Chia & Koss, 1978; Bickell & Kempf, 1983). Fig. 1 shows

the growth and development of *O. bilamellata* larvae maintained on 1:1:1 mixtures of *Isochrysis, Pavlova* and *Rhodomonas* at 5°C and 15°C: several striking similarities and contrasts are apparent. First, larvae maintained at both temperatures showed qualitatively similar sigmoid growth curves (a feature probably characteristic of opisthobranchs [see e.g. Perron & Turner, 1977; Bickell & Chia, 1979; Bickell & Kempf, 1983], bearing in mind the geometry of shell growth), and attained similar sizes at metamorphosis. (A cessation of shell, but not tissue, growth is generally noted some days before development of the propodium, and competence to metamorphose.) Second, larvae at the lower temperature (approximating to ambient field conditions (see Todd, 1985b)) developed at a very much slower rate: 79 days at 5°C versus 31 days at 15°C. Third, in both cases there is considerable variation in size at a given age, and hence individual growth rates, within each culture.

Between-culture variation in growth and successful completion of development is inevitable (see e.g. Pechenik & Lima, 1984, and references therein), particularly at lower temperatures where development is so prolonged. But of greater concern, particularly when evaluating the efficacy of differing dietary regimes, is the invariably high within-culture variation. This will be due, in part, to inherent differences amongst the larvae, but the major source of the variance is undoubtedly experimental. Rafting is almost certainly responsible for much of the observed reduction in growth for many larvae. For example, larvae reared on a mixture of *Isochrysis* and *Rhodomonas* show, at any age, marked divergences in overall size and in the colour of the left digestive diverticulum: small slow-growing larvae are invariably green, while the larger fast-growing larvae have dark-red digestive glands. The former are undoubtedly veligers which have persistently become entrapped and which encounter difficulty in obtaining sufficient food. Moreover, *Rhodomonas,* which is a larger, less motile flagellate, tends to precipitate to the bottom of still cultures and is of markedly reduced availability to rafted veligers. Nevertheless *Rhodomonas* alone can promote growth and development equal, or even superior, to that in mixtures (see below). Because development rates are usually expressed in terms of time to first metamorphosis, it is perhaps ecologically valid to compare growth in terms of the fastest growing individuals, rather than the notional 'average individual'. Certainly, it is usual to note a rapid increase in minimum sizes, in the later stages of development, due to the demise of slower-growing individuals and/or those that persistently became entrapped.

Fig. 2 summarizes the successful culture, through to metamorphosis, of *O. bilamellata* at a range of temperatures and on a variety of dietary regimes. It should be emphasized that the majority of cultures were attempted at 5°C and the presented data relate only to those cultures in which growth and development were seen to proceed 'normally'. Data for many other cultures in which survivorship, growth and metamorphosis success were considered unsatisfactory (or were not attained), have not been included. Attention should also be drawn to the extent of the pelagic phase: even assuming no inherent mortality, the fact that only $\approx$ 90% of larvae can be successfully transferred at each change of culture medium results in an 80% loss of veligers over, say, 11 weeks of rearing. Despite the incompleteness of the data sufficient observations are available to make some comment on the effects of both diet and temperature.

Effects of algal diet

In general, mixtures of flagellates, even of only *Rhodomonas* and *Isochrysis,* promoted the highest growth rates and greatest metamorphosis success. Nevertheless, based upon these (and other) cultures it is apparent that *Rhodomonas* alone is almost equally efficacious and, indeed, routine culture of metamorphs is now undertaken on *Rhodomonas* monocultures. Even in mixtures, larvae evidently ingest and digest *Rhodomonas* more than other algae—veligers frequently regurgitate this flagellate when being measured on glass slides, and it colours the digestive diverticula dark red. Whether the above observations arise from differential selection or availability remains unclear, although the former appears more likely. Two other observations are perhaps substantive; first, larvae reared on monocultures of *Pavlova* (at all temperatures) never achieved competence, and second, larvae reared on *Isochrysis* alone were only successfully raised to metamorphosis on one occasion (at 5°C). Larvae on *Pavlova* invariably grew well, but developed very dark concretions in the left digestive diverticulum some time prior to death at a

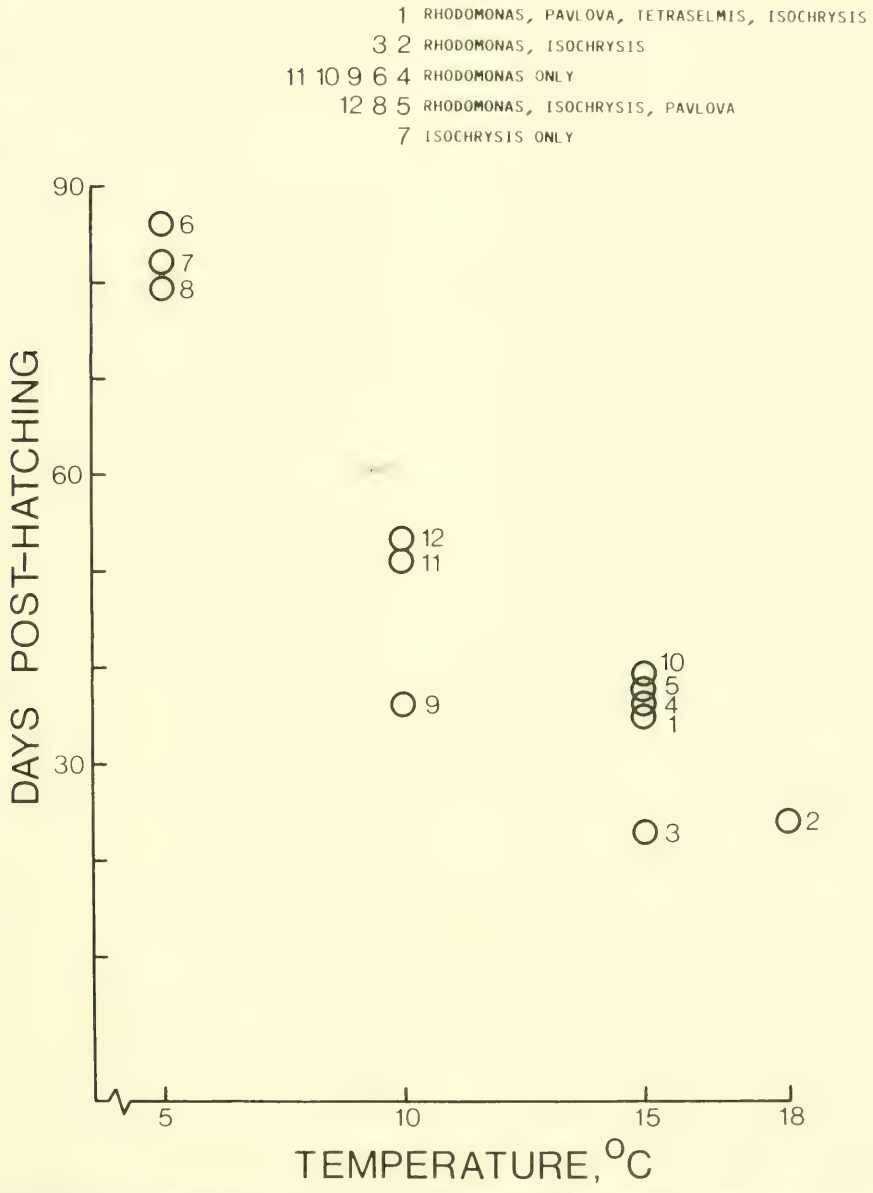

FIG. 2. Time to first metamorphosis of *Onchidoris bilamellata* larvae in culture at a range of temperatures and dietary regimes.

pre-competent stage. Such concretions were also observed in larvae from 'mixed' cultures containing *Pavlova,* and for this reason use of this flagellate was discontinued. The general inadequacy of *Isochrysis* was manifest in survivorship, growth and metamorphosis success. For *Isochrysis* monocultures at 15°C growth and development appeared to proceed normally. Eyed veligers were noted after 25 days of culture, cessation of shell growth between 25 and 30 days, and propodial development after 30 days. Larvae were reared for a further 31 days, during which time they were never observed to crawl and would not metamorphose. Moreover, many larvae (which had completed shell growth) continued

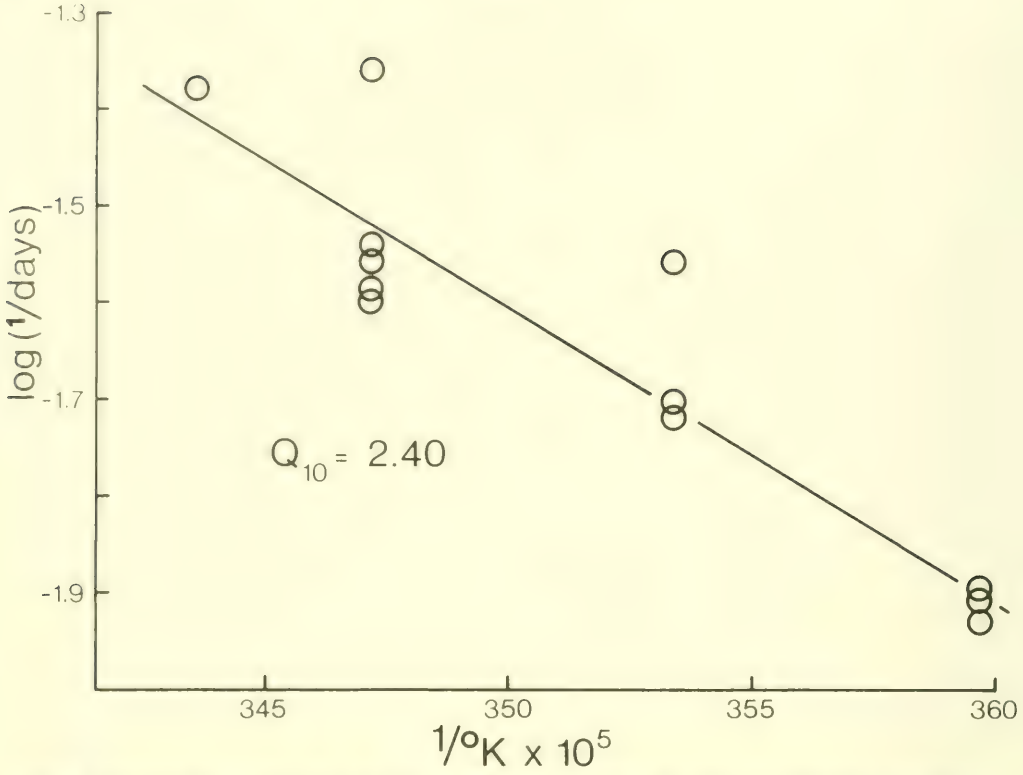

FIG. 3. Arrhenius plot of the data from Fig. 2. The Q_{10} is derived from the fitted regression equation.

to grow somatically, with the tissues finally bulging from the shell. At 10°C, on *Isochrysis* alone, the veligers grew well and rapidly, developed eyes within 26 days, propodia within 29 days and commenced crawling within 36 days. Nevertheless, metamorphosis was never achieved and larvae either died or evacuated the shell spontaneously. It therefore remains possible that *Isochrysis* is an adequate (if not ideal) diet at low temperature, but at higher temperatures its biochemical composition and nutritive value are radically or critically altered.

Effects of temperature

Fig. 3 shows the conventional Arrhenius plot for the data in Fig. 2. Several points require emphasis here: first, no culture at a temperature below 5°C proved successful. Second, only the one culture was attempted at 18°C (a temperature probably at the physiological limit for this species (Todd, 1979a)), and third, there is considerable between-culture variation—even at the same temperature and with the same diet (see, for example, Cultures 9 and 11, Fig. 2). Nevertheless, least squares regression analysis for these data (comprising a range of dietary regimes) shows a very significant relationship ($P < .001$), from which the Q_{10} is derived as 2.40. Undoubtedly a more complete data set is necessary to properly distinguish this quotient, but it is perhaps relevant that the Q_{10} for embryonic development for *O. bilamellata* (upon which basis the pelagic phase duration at field temperatures was previously predicted) was found to be 2.34 (Todd & Doyle, 1981). Despite possible dietary inadequacy, it is clear that at field temperatures ($\approx$ 5°C) the embryonic and larval developmental phases would concur with the predictions made initially (Todd & Doyle, 1981), and that thus far the settlement-timing hypothesis appears at least tenable. That is, with peak spawning in mid-January, embryonic (pre-hatching) and pelagic larval development would require a total of (39 + 73 =) 112 days, resulting in peak larval settlement by early May. Our initial estimation of the larval period in the field (based

on a cultured pelagic phase of 32 days at 15°C, corrected by an observed *embryonic* Q_{10} of 2.34) was 69 days.

Observations of post-larval development

Precise timetables for post-larval ontogeny and development toward the functional predatory juvenile cannot be ascertained; the following is a composite summary of observations of post-larvae reared on various larval diets. At the completion of metamorphosis (when the mantle is fused anteriorly and posteriorly, and the anus has adopted its definitive medial posterior position) the dorsum is both tuberculate and spiculate, but the rhinophores and gills are lacking. Mantle length is ≈ 0.6 mm. The rhinophores are differentiated at 0.85–0.90 mm mantle length, but the gills only become evident at ≈1.7 mm length (approximately one month post-metamorphosis).

Throughout this first month of growth and continued development no predation on barnacle cyprids or spat has been noted. Nevertheless, juveniles were seen to be consistently (if not exclusively) associated with the lateral calcareous plates of juvenile *S. balanoides,* in a manner suggestive of thigmotactic 'refuging' behaviour. Pigmentation of the digestive gland (attributable to the larval dietary flagellates) is progressively lost over the first few weeks of benthic life and is succeeded by a uniform green-brown coloration. This, in turn, becomes less visible as the mantle tissues thicken. Close inspection of the dorids showed that the buccal mass is, in fact, functional from very early on, and that rather than simply refuging against the barnacles the juvenile nudibranchs were actually grazing on diatoms and/or detritus from the plate surfaces. Similar feeding was subsequently observed on field-collected plates of dead adult *S. balanoides*, which are invariably colonized by a considerable microflora. However, metamorphosis will only occur following contact with live barnacles. Figs. 4 and 5 illustrate a portion of the calcareous plates of a laboratory-metamorphosed *S. balanoides,* and here can be seen a radula tooth presumably lost by a juvenile *O. bilamellata* which had been consistently associated with that barnacle.

The dorid *Cadlina laevis* undergoes non-pelagic lecithotrophic development and hatches as a fully-formed juvenile at ≈ 0.8 mm length. 'Growth', by up to 0.2 mm over the first 10 days of benthic life in the absence of feeding, was reported by Thompson (1967). However, *Cadlina* juveniles continue to subsist on stored yolk which is externally visible by its opacity. Indeed, feeding on the definitive poriferan diet (*Halisarca dujardini* (Johnson)) will only proceed after the complete exhaustion of these reserves, perhaps up to 3–4 weeks post-hatching (pers. obs.).

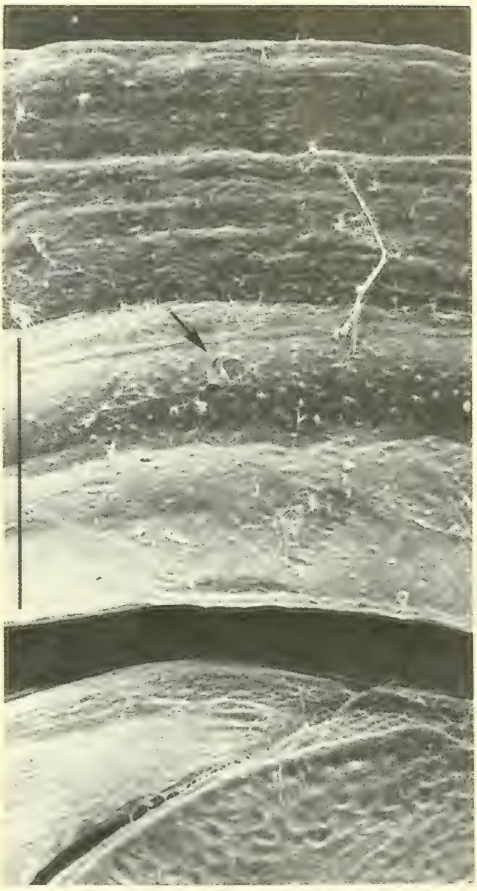

FIG. 4. SEM of the lateral calcareous plates of a metamorphosed *Semibalanus balanoides* (aperture plates to right) with which a juvenile *Onchidoris bilamellata* had been associated. Scale: 100 μm.

The smallest *O. bilamellata* to be seen to penetrate the valve-plates of *S. balanoides* and consume the barnacle tissues measured 1.9 mm (approximately 4–6 weeks post-metamorphosis), and there is no doubt that the juvenile dorids are incapable of tackling live prey up to this time, but choose to graze the surfaces of the calcareous plates. Clearly, therefore, this extended obligatory period of

FIG. 5. SEM detail of radula tooth of *Onchidoris bilamellata* arrowed in Fig. 4. Scale: 10 μm.

detrital grazing—preparatory to stenophagous predation on the definitive barnacle diet—precludes the necessity to infer a close matching of settlement-timing between predator and prey in accounting for the observed ecological association and the predator reproductive strategy. Thus, the settlement-timing hypothesis is inappropriate.

DISCUSSION

Successful laboratory culture of planktotrophic nudibranch veligers has been detailed for 11 species (see Hadfield & Switzer-Dunlap, 1984), but perhaps the most elegant and comprehensive studies of opisthobranch larval biology concern the tropical aeolid *Phestilla sibogae* (Harris, 1973, 1975; Bonar & Hadfield, 1974; Hadfield, 1977, 1978, 1984; Bonar, 1978a,b; Hadfield & Scheuer, 1985; Kempf & Hadfield, 1985; Hirata & Hadfield, 1986; Miller & Hadfield, 1986; Yool et al., 1986). This species hatches as a pelagic lecithotrophic veliger which may metamorphose without feeding within 1–2 days of release from the benthic capsule. Furthermore, larvae of *Phestilla* will ingest and digest flagellates, if available, and this led Kempf & Hadfield (1985) to use the term "facultative planktotrophy" to distinguish this form of larval behaviour from what would be conventionally understood as a truly pelagic (obligatory) lecithotrophic strategy. In this respect *Phestilla sibogae* and the British dorid *Adalaria proxima* are very similar. Both hatch from intermediate-sized eggs, undergo an obligatory 1–2 day ('pre-competent') period, will metamorphose (with or without prior feeding) on contact with the live adult prey, and can delay metamorphosis in the absence of this cue (Thompson, 1958; Kempf & Hadfield, 1985; Kempf & Todd, 1987; Todd et al., 1991).

A survey of the literature shows that remarkably few phytoplankters have been used in the culture of opisthobranch veligers, and that *Isochrysis galbana* (often in combination with another flagellate or a diatom) features particularly prominently. It is clear that different larval diets yield strikingly different developmental outcomes (see e.g. Pilkington & Fretter, 1970; Lucas & Costlow, 1979 for prosobranchs; Switzer-Dunlap & Hadfield, 1977; Chia & Koss, 1978 for opisthobranchs). Interestingly, Switzer-Dunlap & Hadfield (1977) found *Pavlova lutheri* to confer the highest growth and survival in sub-tropical anaspideans, but also noted *Isochrysis galbana* to be quite suitable. Similarly, Chia & Koss (1978) also found *Pavlova* and *Isochrysis* to provide the best results, and encountered success with other (unspecified) organisms. It is relevant, therefore, that for *O. bilamellata, Pavlova* was found to be totally unsuitable and *Isochrysis* of only limited efficacy, with *Rhodomonas* so markedly superior. Care should, therefore, be taken in extrapolating such observations of growth, survivorship or development to the field.

Notwithstanding the above, the present developmental data uphold the original predictions with respect to the duration of the pelagic phase of *O. bilamellata.* While not overstating the case it is perhaps noteworthy

that the presently derived Q_{10} for the larval stage is remarkably close to that previously determined (Todd & Doyle, 1981) for the intracapsular embryonic phase. This may not be a trivial result, especially if it proved to be characteristic of opisthobranch development. Embryonic development data are not difficult to obtain and, on the strength of only a single successful larval culture on a mixture of flagellates and at a realistic temperature, it may be possible to confidently predict the natural egg-to-juvenile period.

The extended 4–6 week obligatory period of post-metamorphic detrital grazing in *O. bilamellata* clearly confounds the criteria for support of the settlement-timing hypothesis. Indeed, intermediate detrital feeding appears to be widespread—if not actually predominant—amongst those species for which developmental data are available. Thus, *Doridella obscura* obligatorily grazes detritus for up to 5 days, before the juveniles (≈ 1 mm) handle *Membranipora crustulenta,* the definitive anascan bryozoan diet (Perron & Turner, 1977). *D. obscura* attains some 230 μm in length at metamorphosis (Table 1) and it is thus curious that its congener *D. steinbergae* (210 μm) does not apparently feed at all for the first three days post-settling, but thereafter handles the adult diet *Membranipora* spp. (Bickell & Chia, 1979; Bickell et al., 1981). For the small, short-lived aeolid *Tenellia pallida,* Eyster (1979) recorded feeding of juveniles on "debris" from hydroid surfaces, but adults preying directly upon *Eudendrium.*

My own observations at field ambient temperatures include obligatory feeding of post-larval *Onchidoris muricata* (Müller) and *Adalaria proxima* (Alder & Hancock) (Todd & Havenhand, unpublished; cf. Thompson, 1958) on detritus for perhaps 1–3 weeks prior to their being capable of handling *Electra pilosa* zooids. Furthermore, *Archidoris pseudoargus* (Rapp) post-metamorphs also graze detritus and microalgae for an as yet unspecified but certainly prolonged period. Although competent larvae of *Archidoris* may metamorphose (Todd & Havenhand, 1984) in the presence of the adult prey sponge, *Halichondria panicea* (Pallas), recent observations (Todd & Davies, unpublished) show that this sponge is not the metamorphosis trigger. Pediveligers are most reluctant to crawl on, or otherwise associate with, this heavily-spiculate sponge and may well subsist on detritus for an extended period, not dissimilar to *O. bilamellata,* before taking the definitive prey species.

Despite the above findings there are numerous records of post-metamorphs not taking any intermediate dietary material before handling the definitive adult prey (Table 1). Relative sizes at metamorphosis are almost impossible to compare inter-specifically, due to the lack of mass measurements. Length data are, however, available which, albeit imprecisely, permit some contrasts to be drawn. Table 1 shows that there is remarkable similarity of post-larval sizes, but three species are exceptional: *Tritonia diomedea* attains perhaps 440 μm and *O. bilamellata* 470 μm at metamorphosis, while *Cadlina laevis* (non-pelagic lecithotrophic) measures approximately 800 μm at hatching. Moreover, correlations between metamorph size, whether or not intermediate 'detritus' grazing is undertaken, and adult prey type are also apparent. Thus, species in which grazing does not occur prior to specialist predation include cnidarian (*T. diomedea, T. hombergi, P. melanobranchia, P. sibogae, C. salmonacea*), and spiculate (*Rostanga*) or slime (*Cadlina*) sponge associates. *Melibe leonina* juveniles attack ciliates and subsequently microcrustacea (as do adults), but this is a highly specialized species. Those which clearly do graze detritus as an intermediate diet include the bryozoan grazers (*D. obscura, A. proxima, O. muricata*) and the one barnacle predator (*O. bilamellata*). Data for *Archidoris pseudoargus* are clearly at variance with *Rostanga,* as are data for *Tenellia* with *Phestilla* spp. Nevertheless, *Tenellia* is very small (≈ 150 μm) at metamorphosis and *Eudendrium* is probably a well-defended prey item to this small aeolid.

The conclusion from these data is that with the exception of *D. steinbergae,* those species which encounter considerable (perhaps overwhelming) prey-size constraints appear to undertake a more or less extended period of post-larval feeding (and growth) on detritus prior to switching to the definitive prey. Certainly bryozoan zooids and barnacles present few problems to the adult forms, but to the meiofaunal-sized juveniles the size differential is enormous (see e.g. Bickell et al., 1981: their Plate 10, 'inset').

On the strength of the foregoing, and in acknowledging the redundancy of the settlement-timing hypothesis, I offer the following argument to account for the evolutionary 'opportunities' and constraints for selection away from the ancestral state amongst nudibranchs. Fig. 6 provides a schematic summary.

TABLE 1. Summary of ontogenetic and post-larval data for a range of nudibranch species. Only those species for which detailed observations are available have been included.

Species	Pelagic phase	Benthic size	Detrital grazing + period [non-feeding period]	Life-cycle	Definitive prey	Comments	Reference
Adalaria proxima	1–2 d (8–10°C)	≈300 μm	Yes, 1–3 weeks	9–10 mo	Bryozoans, especially *Electra pilosa*	Pelagic lecithotrophic	Thompson, 1958; pers. obs.
Archidoris pseudoargus	37 d (10°C)	≈300 μm	Yes, probably several weeks	2 yr	Poriferan, only *Halichondria panicea*	Egg size 150 μm, large for planktotrophic species	Todd & Havenhand, 1984
Cadlina laevis	—	≈800 μm	No [2–3 weeks on yolk]	4–5 yr	Poriferan, only *Halisarca dujardini*	Non-pelagic lecithotrophic	Thompson, 1967; pers. obs.
Coryphella salmonacea (stimpsoni)	—	No data	No, feeds on hydroids following hatching	No data	Probably hydroids	Non-pelagic lecithotrophic	Morse, 1971
Doridella obscura	9 d (25°C)	≈230 μm	Yes, 5 d	26 d	Bryozoans, especially *Membranipora crustulenta*		Perron & Turner, 1977 Bickell & Chia, 1979
Doridella steinbergae	25–26 d (12–15°C)	≈210 μm	No [3 d]	3-4 wk to maturity	Bryozoans, especially *Membranipora* spp.		

Eubranchus farrani	<1 d (10–12°C)	≈245 μm	No data	Probably subannual	Hydroid *Aglaophenia pluma*	*Obelia geniculata* triggers metamorphosis	Todd, 1981
Melibe leonina	30–48 d (12–14°C)	≈335 μm	No [2–3 d]	No data	Zooplankton, microcrustaceans	Unique oral "hood";	Bickell & Kempf, 1983
Onchidoris bilamellata	70 d (6°C)	≈470 μm	Yes, 4–6 weeks	9–10 mo	Barnacles, especially *Semibalanus*	This paper	Todd, 1981; Todd & Doyle, 1981
Onchidoris muricata	58–59 d (10°C)	≈300 μm	Yes, perhaps 2–3 weeks	9–10 mo	Bryozoans, especially *Electra pilosa*	cf. *Adalaria*	Todd & Havenhand, 1984
Phestilla melanobranchia	8 d (21–25°C)	≈225 μm	No data	4.5 mo	Corals, *Dendrophyllia* spp.	Tropical	Harris, 1973, 1975
Phestilla sibogae	1–2 d (21–25°C)	≈300 μm	No data	4.5 mo	Corals, *Porites* spp.	Tropical	Harris, 1973, 1975
Rostanga pulchra	35–40 d (10–15°C)	≈260 μm	No [not stated]	Annual?	Poriferan, only *Ophlitaspongia pennata*		Chia & Koss, 1978
Tenellia pallida	—	≈150 μm	Yes, extensive feeding on detritus on hydroid	A few weeks	*Eudendrium* sp.	Capsular metamorphic	Eyster, 1979
Tritonia diomedea	34–41 d (≈12°C)	≈440 μm	No [5 d]	Annual?	Various pennatulaceans		Kempf & Willows, 1977
Tritonia hombergi	1–2 d (8–10°C)	≈340 μm	No [not stated]	2 yr	Alcyonarian, only *Alcyonium digitatum*		Thompson, 1962

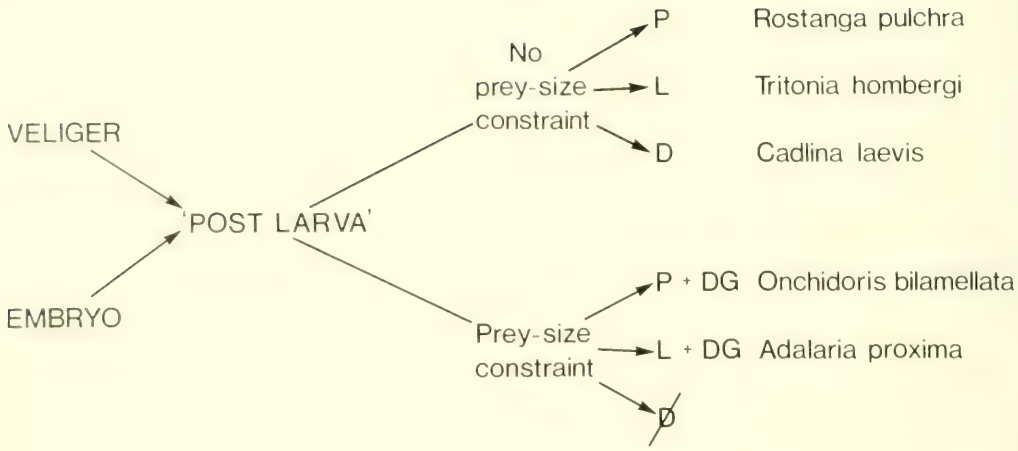

FIG. 6. Schematic summary of the relationship between post-larval prey-size constraints and reproductive strategy 'opportunities' for evolution away from the primitive, or ancestral, status of planktotrophy amongst nudibranchs. It is assumed that the potential for detritus-grazing by post-larval planktotrophs has always remained, but may not be expressed where it is not required.
(P: planktotrophy; L: (pelagic) lecithotrophy; D: direct (non-pelagic) development; D [struck through]: direct development not supportable; +DG: plus detrital grazing).

Assumptions

1. The production of small eggs hatching as pelagic planktotrophic larvae is the primitive or ancestral condition, as is detritivory by the immediate post-metamorph.
2. Pelagic lecithotrophy is a consequential derivative from 1 (above) and is attained essentially by increasing the nutritive (yolk) reserves and protection of the embryo. Pelagic lecithotrophic larvae appear otherwise very similar to competent planktotrophs.
3. Non-pelagic lecithotrophy—whether as capsular metamorphosis (e.g. *Aeolidiella alderi,* Tardy, 1970; *Tenellia pallida,* Eyster, 1979), or truly vestigial, intra-capsular development (e.g. *Cadlina laevis,* Thompson, 1967)—is a derivative of 2., and *C. laevis* represents the extreme of embryogenesis, i.e. opposite to 1. (See Todd, 1981; Hadfield & Switzer-Dunlap, 1984 for qualifying reviews and discussion of the above.)
4. Planktotrophy is a highly conservative mode of development. It is displayed by the overwhelming majority of nudibranch species.
5. There is considerable intra-specific variation in egg-size (see Todd, 1987) and this provides scope for at least the initial stage on the path to establishing lecithotrophy.
6. The primary function of pelagic larvae is not necessarily dispersal (Strathmann, 1978,1985; Todd, 1985a; Todd et al., 1988): rather dispersal, which may or may not be advantageous to particular organisms, should be viewed as an unavoidable consequence of the ancestral larval strategy.
7. Opisthobranch larvae, as opposed to prosobranchs, apparently cease growth on attaining competence (see Kempf, 1981; Pechenik & Lima, 1984) [possibly related to biophysical size constraints in detorting?]: nudibranch metamorphic size potential therefore seems more or less specifically fixed.
8. Nudibranchs of all developmental strategies are characteristically of broadly similar post-larval sizes; even *Cadlina laevis* at 800 μm is small by contrast to, for example, many of the larger muricid prosobranch hatchlings. Almost without exception, nudibranch embryos are provided only with zygotic yolk (but see Boucher, 1983).

Conjecture

A. If no post-metamorphic prey-size constraints apply, the ancestral planktotrophic

pattern may well suffice for establishment of the benthic phase (e.g. *Tritonia diomedea, Phestilla melanobranchia*).

B. If such prey-size constraints do apply, some increase in post-larval size may derive from extended planktotrophy (as shown by *O. bilamellata*), but this alone may be inadequate: in such cases (e.g. *O. muricata*) an intermediate diet is expedient. Nudibranchs are typically specialist predators. If such a putative intermediate diet were another invertebrate this scenario would require two suitable prey species to be consistently and reliably sympatric and adjacent, because post-larvae lack both the reserves and motility to undertake extensive searching. Furthermore, which species (intermediate or definitive?) should comprise the metamorphosis stimulus? Selection ought to favour specific cueing to the definitive prey, and thus detritus perfectly fits the intermediate requirements if only due to its ubiquity and non-specificity.

C. Neither detritivory, nor microalgal grazing, demand morphological or physiological specializations—the larval gut is, after all, adapted for phytoplanktivorous microphagy (Bickell & Chia, 1979; Bickell et al., 1981; Bickell & Kempf, 1983) and, with the present exception of *Melibe*, post-larval stages bear a radula. In essence, post-larval detritivory by planktotrophic forms necessitates only an ontogenetic delay in the reorganization to accommodate the carnivorous status.

Evidence

Here, I confine my argument to those species from the British Isles with which I have previous experience: these embrace the full spectrum of fundamental larval strategies.

1. *Onchidoris muricata.* Following metamorphosis, this species encounters size constraints in handling *Electra pilosa.* Planktotrophy plus post-larval detrital feeding appears to suffice, and the ancestral larval form is retained.
2. *Onchidoris bilamellata.* As outlined and discussed above this species has critical juvenile prey-size constraints. Direct development would not yield hatchlings sufficiently large to handle barnacle spat and, furthermore, that strategy precludes detritivory because a larval gut is not differentiated (see *Cadlina* below). With the possible exception of 'facultative' planktotrophy (see *Adalaria* below) only long-term planktotrophy plus detritivory appears to provide the necessary growth potential. Of all cultured planktotrophic nudibranchs, *O. bilamellata* has the largest post-metamorphic size. In the absence of putative genetic or energetic constraints there appears to be no obvious adaptive advantage to be gained from, or which demands, a shift from the ancestral planktotrophic condition in this species.
3. *Adalaria proxima.* Like *O. muricata,* this dorid is a specialist bryozoan predator which preferentially takes *Electra pilosa.* We have shown that *O. muricata* and *A. proxima* display an extraordinarily high degree of genetic similarity, and that they undoubtedly share a recent common evolutionary ancestry (Havenhand et al., 1986). *Adalaria* is presumed to be the more advanced derivative because of its pelagic lecithotrophy. Selection away from planktotrophy appears to have been dictated by the unpredictability of energy flux divertible toward reproduction by individual adults (see Todd, 1979b, 1987; Todd & Havenhand, 1983; 1988, 1990; Havenhand & Todd, 1988a,b,c). Here, lecithotrophy is viewed as enhancing individual fitness, compared with long-term planktotrophy, by reducing reproductive variance as a result of the higher probabilities of larval survival and metamorphisis. Nonetheless post-larval prey-size constraints persist, as for *O. muricata,* since these two dorids both metamorphose at similar sizes ($\approx$ 300 μm). *Adalaria* larvae can feed (Thompson, 1958), but despite digestion of flagellates in culture it is evident that somatic degrowth occurs, just as it does on starvation (Kempf & Todd, 1989). The question as to why *Adalaria* retains a functional larval gut therefore appears to relate to this species' requirement to undertake post-larval particulate or detrital feeding prior to definitive bryozoan grazing. The retention of an apparently functionless, explicitly larval, structure to perform a strictly post-larval activity is, I believe, a deduction of fundamental importance which supports the hypothesis.
4. *Tritonia hombergi.* This species has lecithotrophic larvae which apparently lack a functional gut (Thompson, 1962), although some larvae in culture clearly in-

gest flagellates (Kempf & Todd, 1989). Current investigations of the biennial life-cycle and reproductive energetics of this dendronotid are not yet complete so it is premature to speculate on why it has become lecithotrophic. However, in contrast to *A. proxima,* no prey-size constraints are encountered by post-larvae, and grazing immediately ensues on the alcyonarian prey ectoderm once the juvenile gut structures become organized.

5. *Cadlina laevis.* Despite undergoing vestigial 'larval' development, embryos still transiently differentiate typical larval gastropod features such as a shell and velum (Thompson, 1967). Juveniles hatch and complete development toward the adult form, but subsist entirely on stored yolk for a few weeks before preying only upon the slime sponge *Halisarca dujardini* (Johnson). Here a functional larval gut is not differentiated, but it is not required because prey-size constraints do not apply. Similarly, *Coryphella salmonacea* commences preying upon hydroids immediately on hatching (Morse, 1971).

If one's perspective of the evolution of nudibranch larval types were confined to the prejuvenile period it would appear intuitively sensible to suggest that the sequence is one of planktotrophy → (non-feeding) lecithotrophy → non-pelagic lecithotrophy. Thus, the retention of a functional larval gut by *Adalaria proxima* (and *Phestilla sibogae*) would be suggestive of only an intermediate step along the path to true lecithotrophy (see Kempf & Hadfield, 1985; Kempf & Todd, 1989). Alternatively, one has to infer an adaptive advantage to such feeding because of the resource demands in differentiation of the larval gut; but this confounds the *a priori* assumption of selection to circumvent the (redundant) larval digestive system in the shift from planktotrophy to true lecithotrophy. The detritus hypothesis obviates this *non sequitur.*

Nevertheless, *Phestilla sibogae* presents an as yet intractable obstacle: fed larvae (in contrast to starved larvae) at least maintain somatic tissues during the facultative pelagic phase, in addition to better retaining competence to metamorphose (Kempf & Hadfield, 1985). Here, some adaptive advantage is deducible, but despite this the undoubtedly high levels of planktonic mortality may still render the (smaller) earlier-settling *P. sibogae* larvae of higher mean fitness. In outlining the detritus-feeding hypothesis I emphasized the improbability of a sympatric intermediate prey organism, but one aeolid species appears to show just such an adaptation. The lecithotrophic veligers of *Eubranchus farrani* would not metamorphose in response to the adult prey hydroid *Aglaophenia pluma,* but did so on encountering *Obelia geniculata* (Todd, 1981). *Obelia,* by contrast to *Aglaophenia,* has a wide aperture to the hydratheca which presents no size constraint to post-metamorphs gaining access to the tissues of individual polyps.

With regard to the reproductive strategy of *Onchidoris bilamellata,* it has proven that Hadfield (1963) showed remarkable foresight in predicting that "small adults may depend entirely on grazing of algae and sessile ciliates until they reach sufficient size to feed on barnacles". In withdrawing the settlement-timing hypothesis I have presented an alternative argument predicting selection in favour of particular larval strategies amongst nudibranchs. But this should not be interpreted as an adaptive explanation of evolutionary shifts along the axis highlighted in Assumptions 1–3. Rather, it defines which larval types are possible under given circumstances. Thus, for example, because there appear to be constrained upper (cf. muricid prosobranchs with nurse eggs) and lower limits to nudibranch post-metamorph/hatchling sizes, this hypothesis would not predict truly direct development in a species which encounters major prey-size constraints following metamorphosis. However, either of planktotrophy or pelagic lecithotrophy would be supportable if detrital grazing potential were retained. It has long been my contention (Todd, 1979a,b, 1981, 1985a, 1986; Todd & Havenhand, 1983, 1988; Havenhand & Todd, 1988a,b,c) that absolute energetic allocations and partitioning within the individual's budget may be important, if not actually uppermost, in determining the scope for such evolutionary shifts. Selection acts on the differential production of offspring among genotypes and this is inevitably some function of energetic capacity and the manner in which this is partitioned. Without wishing specifically to resurrect the settlement-timing hypothesis, one final point should also be stressed. Although planktotrophy and lecithotrophy appear equivalent, in terms of size and level of development at metamorphosis, they do differ markedly in their conferred egg-to-benthic juvenile periods. Both

the temperate and tropical lecithotrophic species discussed above attain their benthic status more rapidly, and so the three fundamental larval strategies cannot be viewed as essentially similar means to the same end. Questions relating to the adaptive significance of this intriguing feature of larval biology remain very much open.

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THE OPISTHOBRANCH FAUNA OF A MEDITERRANEAN LAGOON (STAGNONE DI MARSALA, WESTERN SICILY)

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ABSTRACT

The opisthobranch fauna present in a lagoon (Stagnone di Marsala) near Marsala (western Sicily) is described. There is a rich opisthobranch fauna, with more than 20 species, some of which are very abundant. Bullomorpha, with several species often very common in this particular ecosystem, are well represented, but the species of Sacoglossa and Nudibranchia are quite different from those in other Mediterranean lagoons. Many species, which are usually common in similar environments, are rare or absent, e.g. several aeolids and anadorids, but a rich sponge population supports the presence of several eudoridaceans, including the little-known *Paradoris granulata* and *Doriopsilla rarispina. Elysia timida, Hypselodoris villafranca* and *Dendrodoris limbata* can, perhaps, be considered euryhaline species as they were frequently collected in brackish or lightly polluted waters. Finally, the opisthobranch fauna present in Mediterranean lagoon waters is reviewed.

INTRODUCTION

Brackish water lagoons in the Mediterranean have considerable annual variations in temperature and salinity (Colombo, 1977; Sacchi, 1979; Barnes, 1980; Guelorget & Perthuisot, 1983) and this therefore poses major physiological problems for animals living there. Opisthobranchs from brackish waters in the Mediterranean are known from several studies (see Table 2) but there have been few detailed systematic investigations of opisthobranchs in this habitat.

The purposes of this paper are to present the results of a 3-year study of opisthobranchs in the Marsala Lagoon and to review the opisthobranchs living in this habitat throughout the Mediterranean.

The Marsala Lagoon, which is called 'Stagnone', extends for 2000 ha in western Sicily and has been extensively studied (Cavallaro et al., 1977; Calvo et al. 1982). Information on its malacological fauna has been reported by Cavallaro et al. (1977) and Sparla (1985).

The Marsala Lagoon is morphologically divided into two basins (Fig. 1). The southern basin is connected with the open sea by a large channel, between Punta d'Alga and the Isola Grande. The northern basin, the true 'Stagnone', has markedly more lagoon characteristics such as shallow waters, irregular water movements and variable salinity and temperature. There is, moreover, a progressive silting up because the Birgi River, recently deviated southward, was canalized near the 'Tramontana' mouth, and so discharges its abundant waste into the lagoon.

Sampling Stations

The average depth of the northern basin of the Marsala lagoon is around 0.5–1.0 m, with a maximum of 3 m near Isola Grande. Most of the specimens were collected by snorkeling in different periods of the years 1984–86, near sparse shoots of *Posidonia oceanica* (Stations A,E), in *Cymodocea nodosa* prairies, under or on small hard objects or animals (stones, anchor logs, sponges) and on *Rytiphloea tinctoria* aegagropyla forms near Mozia (Stns A,E,G), Punta Grassellino (Stn C), Punta Palermo (Stns B,F), Saline (Stn D), between Mozia and Punta Palermo (Stns H,I) and near Punta d'Alga (Stn L). The average depth of the samples taken was at 0.5–1.5 m. The species collected and the numbers of specimens are reported in Table 1.

The opisthobranch fauna of the Marsala Lagoon

The opisthobranch fauna in the Marsala lagoon is quite rich (Table 1), with more than 20 species, compared with about 60 species recorded from all other Mediterranean lagoons.

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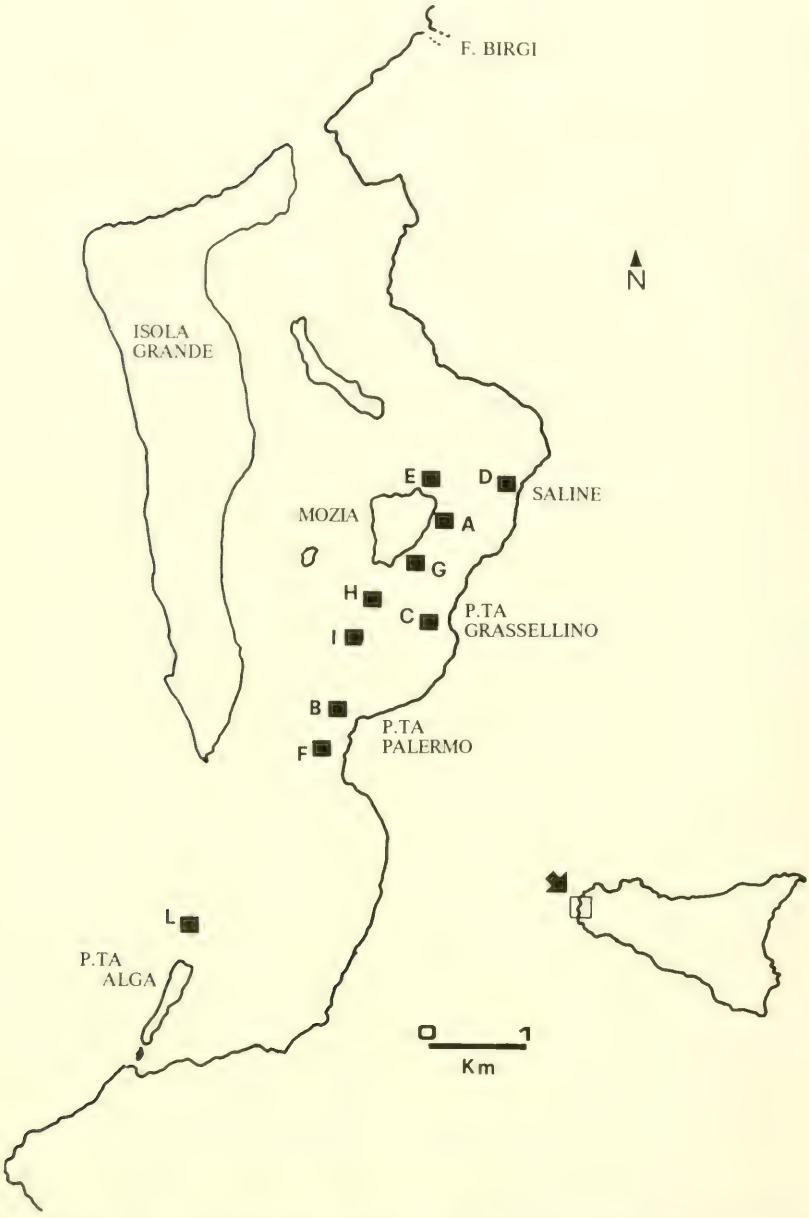

FIG. 1. The Marsala Lagoon (western Sicily). Sampling areas: A, E, G: Mozia Isle; B, F: Punta Palermo; C: Punta Grassellino; D: Saline; H, I: between Mozia Isle and Punta Palermo; L: Punta d'Alga.

This richness could be due to the presence of at least five habitats: *Posidonia* beds, *Cymodocea* prairies, sandy bottoms, the peculiar 'microhabitat' of aegagropyla forms of *Rytiphloea tinctoria* (Sparla & Riggio, 1984; Riggio & Sparla, 1985), and hard substrates made up, above all, of tufaceous outcrops and calcareous red algae (*Lithothamnium fruticulosum, L. calcareum,* and pleustophytic forms of *Mesophyllum lichenoides*).

On the mud beds, Bullomorpha are common with well-known euryhaline species, such as *Mamilloretusa mammillata, Bulla striata* and *Haminoea hydatis,* while *Haminoea*

TABLE 1. Opisthobranch molluscs present in the Marsala Lagoon (western Sicily). For the sampling areas see the legend to Fig. 1.

Species	Sites sampled										
	A	B	C	D	E	F	G	H	I	L	Total
Retusa semisulcata[1]	—	—	—	—	—	—	—	—	—	—	—
Retusa truncatula[1]	—	—	—	—	—	—	—	—	—	—	—
Mamilloretusa mammillata[1]	2	—	2	—	—	1	—	—	—	—	5
Bulla striata[2]	3	—	1	—	1	1	—	—	—	—	6
Haminoea hydatis[1,2]	2	1	3	—	3	—	—	—	—	—	9
Haminoea cymoelium	—	—	1	—	—	—	—	—	—	—	1
Elysia timida	—	—	6+	—	—	—	—	—	—	—	6+
Aplysia fasciata[1]	—	—	—	—	—	—	—	—	—	—	—
Berthella aurantiaca	1	—	—	2	2	2	3	2	4	—	16+
Berthella stellata	—	—	—	—	1	—	—	2	—	—	3
Doris verrucosa[1]	—	—	—	—	—	—	—	—	—	—	—
Doris sp.[1]	—	—	—	—	—	—	—	—	—	—	—
Glossodoris sp.[1]	—	—	—	—	—	—	—	—	—	—	—
Chromodoris sp.	5	—	—	—	—	—	—	—	—	—	5
Hypselodoris villafranca	10+	—	—	—	2	—	—	—	—	—	12+
Hypselodoris elegans	1	—	2	—	—	—	—	—	—	—	3
Hypselodoris messinensis	—	—	10+	—	—	4	—	—	—	—	14+
Paradoris granulata	11+	—	4	—	—	—	—	—	2	—	17+
Platydoris argo	—	—	—	—	—	—	—	—	—	1	1
Dendrodoris limbata	2	—	—	—	—	4	—	1	—	—	7
Dendrodoris grandiflora[2]	1	—	—	—	—	—	—	—	—	—	1
Doriopsilla rarispina	13+	—	2	—	1	—	—	2	—	—	18+
Spurilla neapolitana	1	—	—	—	—	—	—	—	—	—	1
Total number of specimens	52+	1	31+	2	10	12	3	7	6	1	125+

\+ = more specimens were observed than collected
1 = recorded by Cavallaro et al., 1977
2 = recorded by Sparla, 1985 (unpublished data, thesis)

cymoelium should probably be considered a young *H. hydatis.*

The only common notaspidean in the Marsala lagoon is *Berthella aurantiaca.*

The species composition of Sacoglossa and Nudibranchia in this lagoon is quite different from that known from other Mediterranean lagoons. Among the Sacoglossa, *Elysia timida* is very common on hard artificial bottoms at 0.2 m depth, near *Acetabularia acetabulum,* on which it feeds (Ros & Rodriguez, 1985). This easily-recognized white species with red spots (Bouchet, 1984) seems to prefer shallow and euryhaline waters. It has also been found in other brackish waters such as Strea Lagoon (Ionian Sea), Oristano (Sardinia) and S. Marco Cape near Sciacca (Sicily).

A rich sponge population (Corriero, 1984) supports the presence of several eudoridaceans, some of them also of considerable scientific interest. *Doriopsilla rarispina,* a very rare species recently re-described by Perrone (1986) from the Ionian Sea, has been found and there is a large population of *Paradoris granulata.* This beautifully-camouflaged species is easily found inside the sponge *Ircinia variabilis* or in its oscula. There is also what is probably a new, undescribed species of chromodorid in the Marsala Lagoon. It is a few centimetres long and presents a translucid pale white colour with characteristic pale azure-white ocelli surrounded by an opaque white ring. It lives at the base of *Cystoseira barbata* brown algae, on the sponge *Tedania anelans.*

Many young specimens of *Hypselodoris villafranca* and *H. messinensis* were collected among *Rytiphloea tinctoria* aegagropyla forms which seem to be 'nurseries' for these nudibranchs.

On the other hand, some common euryhaline or widely-distributed species (*Polycera quadrilineata, Favorinus branchialis, Coryphella pedata and Cratena peregrina*) are absent, probably due to the sparseness of hard bottoms with few hydroids and bryozoans.

FIG. 2. Mediterranean Sea: brackish waters in which opisthobranchs were found (see Table 2)— SPAIN: 1. Mar Menor; 2. Salinas de Calblanque. FRANCE: 3. Salses; 4. Sigean; 5. Thau (or Sète); 6. Berre; 7. Brusc; ITALY: 8. Orbetello; 9. Oristano; 10. Lungo; 11. Caprolace; 12. Fogliano; 13. Patria; 14. Fusaro; 15. Faro and Ganzirri; 16. Tindari; 17. Stagnone of Marsala; 18. Sciacca; 19. Vendicari; 20. Mar Piccolo of Taranto; 21. Strea of Porto Cesareo; 22. Venezia; 23. Grado and Marano; USSR: 24. Azov Sea; ISRAEL: 25. Dor; 26. Mikhmoret. EGYPT: 27. Bardawil. TUNISIA: 28. Biban; 29. Bizerte; 30. Tunis; MOROCCO: 31. Nador.

The rarity of *Spurilla neapolitana* and the absence of the common euryhaline *Aeolidiella* spp. are surprising since their food, *Parastephanauge pauxii* is very common on *Cymodocea* leaves.

Finally, the common Mediterranean species *Elysia timida, Hypselodoris villafranca* and *Dendrodoris limbata* can be considered euryhaline, because they were frequently seen also in other brackish habitats such as the 'Strea' of Porto Cesareo (Taranto) and Oristano lagoon. According to Perrone (1984), *Dendrodoris limbata* can live in polluted waters and this fact confirms its adaptability to environmental changes.

Review of opisthobranchs in Mediterranean brackish waters

The Opisthobranch fauna present in Mediterranean brackish waters is still not well known (Fig. 2). There are useful reports by Barletta (1980) and Torelli (1982), while Guelorget (1985), in his review of the parhalic domain, considered *Akera bullata* an exclusively brackish species, while *Aplysia depilans* and *Philine aperta* are the most common opisthobranchs present in Mediterranean lagoons. Additional information is available from general studies carried out on the malacological fauna of lagoons, even though nudibranchs were often ignored. A summary of opisthobranch records in Mediterranean lagoons is given in Table 2.

Many opisthobranchs can live in this peculiar habitat which is subject to considerable variation in the main physico-chemical conditions such as salinity, temperature, oxygen saturation, pH, etc. The Bullomorpha, living on soft bottoms, are widespread and include euryhaline species such as *Retusa truncatula, Haminoea navicula, Bulla striata, Philine aperta* and *Akera bullata.*

Many Sacoglossa are present in the lagoon ecosystem but they only inhabit areas where food plants occur. *Oxynoe* and *Lobiger,* for example, are confined to *Caulerpa* prairies (sometimes living in outer zones of the lagoons). The majority of other species are linked to the distribution of the green algae *Bryopsis* and *Cladophora.* Only *Limapontia capitata,* found in the Fusaro Lake (Naples), seems to occur exclusively in brackish waters (Jensen, 1977). The occurrence of *Alderia modesta,* an Atlantic euryhaline species (Adam & Leloup, 1939; Engel et al., 1940), is still uncertain in the Mediterranean Sea.

Algal availability is also important for aplysiomorphs: they are sometimes abundant in the zones where Ulvales flourish while *Bursatella leachii,* in the Mediterranean Sea, was always recorded in still-water areas like lagoons.

TABLE 2. Opisthobranch molluscs present in Mediterranean lagoons.

Species	Locality (Reference)
BULLOMORPHA	
Acteon tornatilis (L.)	France: Berre (Mars, 1966) Italy: Venice (Coen, 1928); Grado, Marano (Zucchi Stolfa, 1977)
Cylichnina girardi (Audouin)	Egypt: Bardawil (Mienis, 1976; Barash & Danin, 1982)
Retusa semisulcata (Philippi)	Italy: Marsala (Cavallaro et al., 1977); Grado, Marano (Zucchi Stolfa, 1977)
R. perstriata (Cerulli Irelli)	Italy: Grado, Marano (Zucchi Stolfa, 1977)
R. truncatula (Bruguière)	France: Salses, Sigean, Thau, Berre (Mars, 1966) Italy: Orbetello (Mari, 1976); Marsala (Cavallaro et al., 1977) Tunisia: Tunis (Zaouali, 1981) Morocco: Nador (Saubade, 1979)
R. umbilicata (Montagu)	France: Berre (Mars, 1966)
Retusa spp.	Egypt: Bardawil (Barash & Danin, 1982)
Mamilloretusa mammillata (Philippi)	Italy: Marsala (Cavallaro et al., 1977); Mar Piccolo (Tortonici & Panetta, 1977)
Ringicula auriculata (Menard de la Groye)	Italian Lagoons (Torelli, 1982)
R. conformis (Monterosato)	Italy: Porto Cesareo (Parenzan, 1970)
Bulla striata Bruguière	France: Berre (Mars, 1966) Italy: Orbetello (Mari, 1976); Caprolace (Ardizzone, 1985); Faro, Ganzirri (Giudice, pers. comm.); Marsala (Sparla, 1985—thesis); Vendicari (Chemello, pers. obs.); Mar Piccolo (Parenzan, 1969; Tortorici & Panetta, 1977) Egypt: Bardawil (Barash & Danin, 1982) Tunisia: Bizerte (Zaouali, 1979) Morocco: Nador (Saubade, 1979)
Atys blainvilliana (Récluz)	Egypt: Bardawil (Barash & Danin, 1982)
Haminoea hydatis (L.)	Spain: Mar Menor (Olmo & Ros, 1984) Italy: Lungo, Caprolace, Fogliano (Ardizzone, 1985); Fusaro (Ferro & Russo, 1981); Faro, Ganzirri (Scordia, 1927; Parenzan, 1979); Tindari (Chemello, pers. obs.); Marsala (Cavallaro et al., 1977; Sparla, 1985—thesis); Venice (Coen, 1933,1938; Vatova, 1940); Grado, Marano (Zucchi Stolfa, 1977) Egypt: Bardawil (Barash & Danin, 1982)
H. navicula (Da Costa)	Spain: Mar Menor (Olmo & Ros, 1984); Salinas de Calblanque (Templado et al., 1983) France: Sigean, Thau, Berre (Mars, 1966) Italy: Orbetello (Mari, 1976); Faro, Ganzirri (Parenzan, 1979); Mar Piccolo (Tortorici & Panetta, 1977); Venice (Coen, 1933;1938) Tunisia: Biban (Zaouali & Baeten, 1985); Bizerte (Zaouali, 1979); Tunis (Zaouali, 1974,1981) Morocco: Nador (Saubade, 1979)
H. orbignyana (Férussac)	Spain: Mar Menor (Murillo & Talavera, 1983; Olmo & Ros, 1984); Salinas de Calblanque (Templado et al., 1983)
Akera bullata Müller	Spain: Salinas de Calblanque (Templado et al., 1983) France: Thau, Berre (Mars, 1966) Italy: Venice (Coen, 1933)
Philine aperta (L.)	Spain: Mar Menor (Olmo & Ros, 1984) France: Thau, Berre (Mars, 1966) Italy: Mar Piccolo (Parenzan, 1969; Tortorici & Panetta, 1977) Tunisia: Bizerte (Zaouali, 1979)
Philine cf. scabra (Müller)	Italy: Grado, Marano (Zucchi Stolfa, 1977)
APLYSIOMORPHA	
Aplysia depilans Gmelin	France: Thau (Mars, 1966) Italy: Venice (Coen, 1938) Tunisia: Bizerte (Zaouali, 1979); Tunis (Zaouali, 1974)

(*continued*)

TABLE 2. (*Continued*)

Species	Locality (Reference)
A. fasciata Poiret	Spain: Salinas de Calblanque (Templado et al., 1983) France: Thau, Berre (Mars, 1966) Italy: Orbetello (Mari, 1976); Patria (Sacchi, 1961); Faro, Ganzirri (S.I.M. comm.); Marsala (Cavallaro et al., 1977); Porto Cesareo (Cattaneo Vietti, pers. obs.)
A. punctata Cuvier	France: Thau, Berre (Mars, 1966) Italy: Venice (Coen, 1933)
Bursatella leachii leachii Blainville	Italy: Venice (Cesari et al., 1986)
B. l. savignyi Audouin	Italy: Mar Piccolo (Tortorici & Panetta, 1977) Israel: Dor, Mikhmoret (Barash & Danin, 1972)
Notarchus punctatus Philippi	Italy: Mar Piccolo (Parenzan, 1969)
NOTASPIDEA	
Pleurobranchaea meckelii Leue	Italy: Mar Piccolo (Parenzan, 1969)
Berthella aurantiaca (Risso)	Tunisia: Bizerte (Zaouali, 1979)
SACOGLOSSA	
Oxynoe olivacea Rafinesque	Italy: Mar Piccolo (Parenzan, 1969,1970; Tortorici & Panetta, 1977)
Lobiger serradifalci (Calcara)	Italy: Orbetello (Mari, 1976); Mar Piccolo (Parenzan, 1969; Tortorici & Panetta, 1977)
Elysia viridis (Montagu)	Spain: Mar Menor (Olmo & Ros, 1984) France: Thau (Mars, 1966) Italy: Fusaro (Schmekel, 1968)
E. timida (Risso)	Spain: Mar Menor (Ros & Rodriguez, 1985) Italy: Oristano (Cattaneo Vietti, pers. obs.); Sciacca (Chemello, pers. obs.); Porto Cesareo (Cattaneo Vietti, pers. obs.)
Calliopaea bellula d'Orbigny	Spain: Salinas de Calblanque (Templado et al., 1983) Italy: Fusaro (Schmekel, 1968)
Placida viridis (Trinchese)	Italy: Fusaro (Schmekel, 1968)
P. dendritica (Alder & Hancock)	Italy: Fusaro (Schmekel, 1968)
Ercolania funerea (Costa)	Italy: Fusaro (Schmekel, 1968)
Limapontia capitata (Müller)	Italy: Fusaro (Schmekel, 1968)
Alderia modesta (Lovén)	— (Pruvot-Fol, 1954)
NUDIBRANCHIA Doridina	
Okenia elegans (Leuckart)	Italy: Fusaro (Toscano, pers. comm.)
Doris verrucosa L.	France: Thau (Mars, 1966) Italy: Orbetello (Mari, 1976); Marsala (Cavallaro et al., 1977) Tunisia: Bizerte (Zaouali, 1979)
D. bicolor (Bergh)	Italy: Venice (Coen, 1938)
Hypselodoris villafranca (Risso)	Italy: Orbetello (Mari, 1976); Porto Cesareo (Cattaneo Vietti, pers. obs.)
Chromodoris krohnii (Verany)	Italy: Orbetello (Mari, 1976)
Polycera quadrilineata (Müller)	France: Canaux de Sète (Mars, 1966) Italy: Orbetello (Mari, 1976); Fusaro (Schmekel, 1968; Toscano, pers. comm.)
P. dubia Sars	Italy: Fusaro (Schmekel, 1968)
Polycerella emertoni Verrill	Italy: Fusaro (Schmekel, 1968)
Limacia clavigera (Müller)	Italy: Fusaro (Toscano, pers. comm.)
Dendrodoris limbata (Cuvier)	Italy: Faro, Ganzirri (Giudice, pers. comm.); Porto Cesareo (Cattaneo Vietti, pers. obs.)

TABLE 2. (*Continued*)

Species	Locality (Reference)
NUDIBRANCHIA Arminina	
Janolus cristatus (Delle Chiaje)	Italy: Orbetello (Mari, 1976); Fusaro (Schmekel, 1968; Toscano, pers. comm.)
NUDIBRANCHIA Aeolidina	
Coryphella pedata (Montagu)	France: Canaux de Sète (Mars, 1966) Italy: Fusaro (Toscano, pers. comm.)
C. lineata (Lovén)	France: Canaux de Sète (Mars, 1966)
Calmella cavolinii (Verany)	Italy: Orbetello (Mari, 1976)
Facelina coronata (Forbes & Goodsir)	France: Thau (Mars, 1966)
F. annulicornis (Chamisso & Eysenhardt)	France: Thau (Mars, 1966)
Cratena peregrina (Gmelin)	France: Canaux de Sète (Mars, 1966) Italy: Orbetello (Mari, 1976)
Favorinus branchialis (Rathke)	France: Brusc (Riva & Vicente, 1976) Italy: Fusaro (Schmekel, 1968)
Eubranchus exiguus (Alder & Hancock)	Italy: Fusaro (Schmekel, 1968)
Cuthona caerulea (Montagu)	France: Canaux de Sète (Mars, 1966)
Tenellia adspersa (Nordmann)	USSR: Azov Sea (Roginskaya, 1970)
Calma glaucoides (Alder & Hancock)	Tunisia: Tunis (Zaouali, 1974)
Aeolidiella alderi (Cocks)	France: Brusc (Riva & Vicente, 1976) Italy: Fusaro (Schmekel & Portmann, 1982); Porto Cesareo (Cattaneo Vietti, pers. obs.)
A. rubra (Cantraine)	France: Thau, Berre (Mars, 1966)
Baeolidia nodosa (Haefelfinger & Stamm)	Spain: Salinas de Calblanque (Templado et al., 1983)
Spurilla neapolitana (Delle Chiaje)	Spain: Salinas de Calblanque (Templado et al., 1983) France: Thau (Mars, 1966); Brusc (Riva & Vicente, 1976) Italy: Caprolace (Ardizzone, 1985); Fusaro (Schmekel, 1968)
Berghia verrucicornis (Costa)	Italy: Orbetello (Mari, 1976)

Many species of nudibranchs occur in the lagoons. Species which are characteristic of shallow water and tide-pools (e.g. *Polycera quadrilineata, Polycerella emertoni, Calmella cavolinii, Doris verrucosa*) can also thrive in brackish waters. When hydroids settle on hard bottoms, aeolids are commonly found on them (e.g. *Coryphella* spp., *Facelina* spp., *Cratena peregrina* and *Cuthona coerulea*). Typical euryhaline species are *Spurilla neapolitana, Aeolidiella* spp., *Favorinus branchialis* and *Tenellia adspersa.* Finally, *Tergipes tergipes* and *Embletonia pulchra,* which are euryhaline species along the Atlantic coasts (Pruvot-Fol, 1954; Thompson & Brown, 1984), have rarely been recorded in the Mediterranean Sea and do not appear to be associated with any particular ecological conditions.

Mediterranean lagoons vary in their species composition of hydroids (Morri & Bianchi, 1983), serpulids (Bianchi et al., 1984; Bianchi, 1985) and prosobranchs (Torelli, 1983), and doubtless similar variation will be found to occur in opisthobranchs. One might expect the North Atlantic type lagoons of the north Adriatic to have a very different fauna from the xero-Mediterranean lagoons of Sicily and north Africa, but data even for the better known Bullomorpha are too poor to enable any such conclusions to be made.

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THE STATUS OF THE RHODOPIDAE (GASTROPODA: EUTHYNEURA)

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ABSTRACT

Based on investigations of *Rhodope veranii, R. transtrosa* sp. nov. and *Helminthope psammobionta* gen. et sp. nov., the organization of the Rhodopidae is reconsidered. *Helminthope* is characterized by a slender body, by typical verrucose rods, by lack of a radula, stomach and dorso-rostral caecum, and especially by five free ganglia on the visceral loop. The animals inhabit the interstitia of subtidal sands. The number of ganglia confirms earlier developmental investigations in *R. veranii* with respect to the pentaganglionate (= euthyneurous) level. The shift of the visceral ganglion to the left side, as well as the lack of special vacuolar bodies in the epidermal cells, argue against a classification of the Rhodopidae within the Anthobranchia (= Doridacea) and the Nudibranchia. The lack of both a paired procerebrum and cerebral gland excludes a direct relationship of the Rhodopidae with the Gymnomorpha (Onchidiacea, Soleolifera) and Pulmonata. Furthermore, the free visceral ganglion in *Helminthope* and the monauly preclude a classification of the Rhodopidae amidst higher tectibranch groups (= Paratectibranchia). Consequently, the Rhodopidae, (including *Helminthope* and five presumed species of *Rhodope*) remain as a taxon Rhodopemorpha, of uncertain systematic rank and affinity, as a specialized off-shoot from the lower opisthobranchs.

INTRODUCTION

At the present time, the Rhodopidae are scientifically known only by the Mediterranean *Rhodope veranii* Kölliker and by the southwest Atlantic *R. marcusi* (see p. 308). Since the original description of *R. veranii* (Kölliker, 1847), few additional specimens have been found. Due to the investigations of Graff (1883), Böhmig (1983), and Riedl (1959,1960), however, we are fairly well informed about the anatomy, histology, biology, and development of this species; Marcus & Marcus (1952) supplemented this knowledge by the description of a closely related form (see p. 308). The central question about *Rhodope* concerns its phylogenetic affinities. After the definitive classification of the species as an euthyneurous gastropod (Riedl, 1960), its affinities within that subclass still remain uncertain (cf. Oberzeller, 1969; Salvini-Plawen, 1970; Tillier, 1984: 359). Further recent findings of *Rhodope veranii, R. transtrosa,* and *Helminthope psammobionta* enlarge our knowledge of the Rhodopidae and permit a re-evaluation of its systematic relationships.

Rhodope veranii Kölliker

Fifteen *Rhodope veranii* were recently found in one of the marine aquaria of the Zoological Institute (Universität Wien) filled with sediment and secondary hard-bottom material from the Northern Adriatic Sea and the Gulf of Naples. In nature, *R. veranii* appears to inhabit shallow subtidal areas with stones and *Ulva* growth (Graff, 1883: p.74; F Starmühlner, pers. comm., for Rovigno/Istria; Salvini-Plawen in Arnaud et al., 1986: p 158). All specimens beyond 1 mm in length are characterised by the more or less distinctly T-shaped dorsal orange-red pigmentation (Riedl, 1960). In contrast to previously found animals with a maximum length of 4 mm (Graff, 1883: p.74; Riedl, 1960: p.297), the present individuals were distinctly larger, ranging up to 8 mm in length. The subepithelial spicules and the inconspicuous eyes are typical. However, there is remarkable variation in the location of the genital opening: Graff (1883: p.79) confused the protonephridiopore with the male gonopore and the anus with the female opening (both located at the right posterior border of the transverse pigment bar, i.e. anterior to the middle of the body). Riedl (1959: his Fig. 2) located the genital opening at the right anterior border of the transverse pigment bar, irrespective of the state of contraction of the animals. Apparently the location of the gonopore varies in different individuals. The examination of six serially sectioned specimens (Riedl's and the present material) revealed that only one specimen possessed the genital

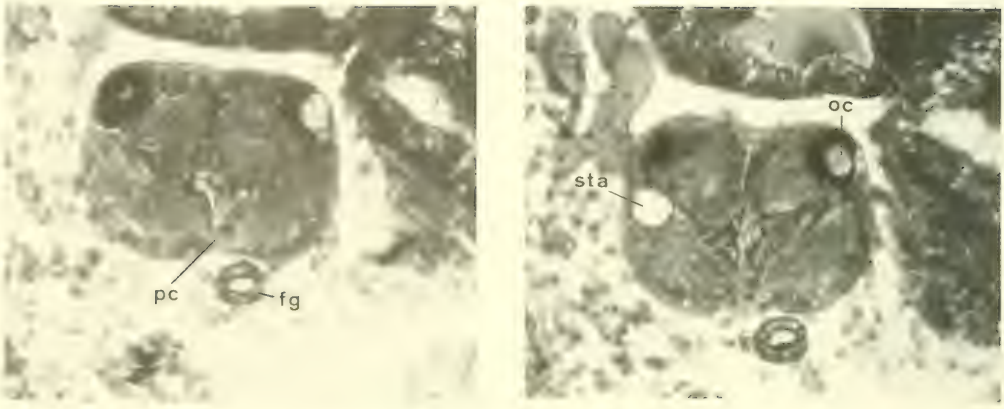

FIG. 1. *Rhodope veranii:* Two successive cross sections through the cerebral nervous ring in a specimen with the foregut (fg) outside the pedal commissure (pc). oc eye, sta statocyst.

opening in the location indicated by Riedl; two animals show the gonopore laterally at the level of the perioesophageal central nervous mass (with embedded eyes visible, see Fig. 1), while three individuals show the genital opening distinctly anterior to the ganglia complex, viz. anterior to the eyes (in one the gonopore is even located at the level of the mouth).

In the concentrated nervous system the closely adjoining cerebro-pleuro-parieto-intestinal ganglia (cf. Riedl, 1960; Oberzeller, 1969) have a short cerebral commissure and the eyes as well as optical ganglia incorporated (Fig. 1); the optical connective itself has its origin in the pleuropedal connective. Besides the buccal connectives, there are three pairs of rostral nerves, the two medial ones with a common (?) root running to the oral region (labial nerves). The most lateral one at each side corresponds to the Hancock's or rhinophoral nerve in other opisthobranchs and has a basal swelling which shows a double root in the cerebral ganglion; there is no head-shield-tentacle nerve (Huber, 1987). In addition, a strong lateral nerve, with bifurcated root in both the (cerebro-) pleural ganglion and the pedal ganglion, runs anterior-laterally to the body flanks; at the right it also innervates the copulatory organ. The two abdominal 'nerves' (right-visceral and left-genital) running ventrally close to the body end are regularly provided with nuclei, thus assuming the aspect of weak medullary cords. A peculiarity was noticed in one of the specimens: instead of being surrounded by the mass of the concentrated ganglia, the oesophagus runs outside (i.e. below) the pedal comissure (Fig. 1).

The midgut shows the usual, somewhat winding, rostral caecum or right midgut gland (Riedl, 1960: p. 284). Close to the junction of the short intestine and the voluminous midgut there is a narrow pouch or small diverticulum. In both Riedl' s and the present material, this pouch is lined with a low, ciliated epithelium that is histologically continuous with the intestinal epithelium. In contrast to Böhmig (1893: p.56 & Fig. 13), however, this pouch is well separated from the adjacent intestine, and, in agreement with Riedl (1960: pp.284–285), it corresponds to the remnant of the true stomach.

The chromosome number of *R. veranii* is 2n = 32 (pers. comm. Claudia R. Schweizer, Wien). The spermatozoa, with a spiralated head, have a characteristic shape and fine structure; in some aspects they appear to be fairly primitive and similar to prosobranch sperm (pers. comm. F. Giusti di Massa, Siena).

Rhodope transtrosa sp. nov.

A single specimen (Fig. 2A) was collected from an aquarium (Ehrmann Zoo, Wien XII) filled with phytal material from the tropical Indo-Pacific (Ceylon/Sri Lanka ?). The living animal measured 1.65 mm x 160 μm maximum. The anterior third of its whitish body is provided with a characteristic dorsal transverse bar *(transtrum)* of orange-reddish pigmentation (about 160 μm in length). The anteriormost section is markedly elongated and

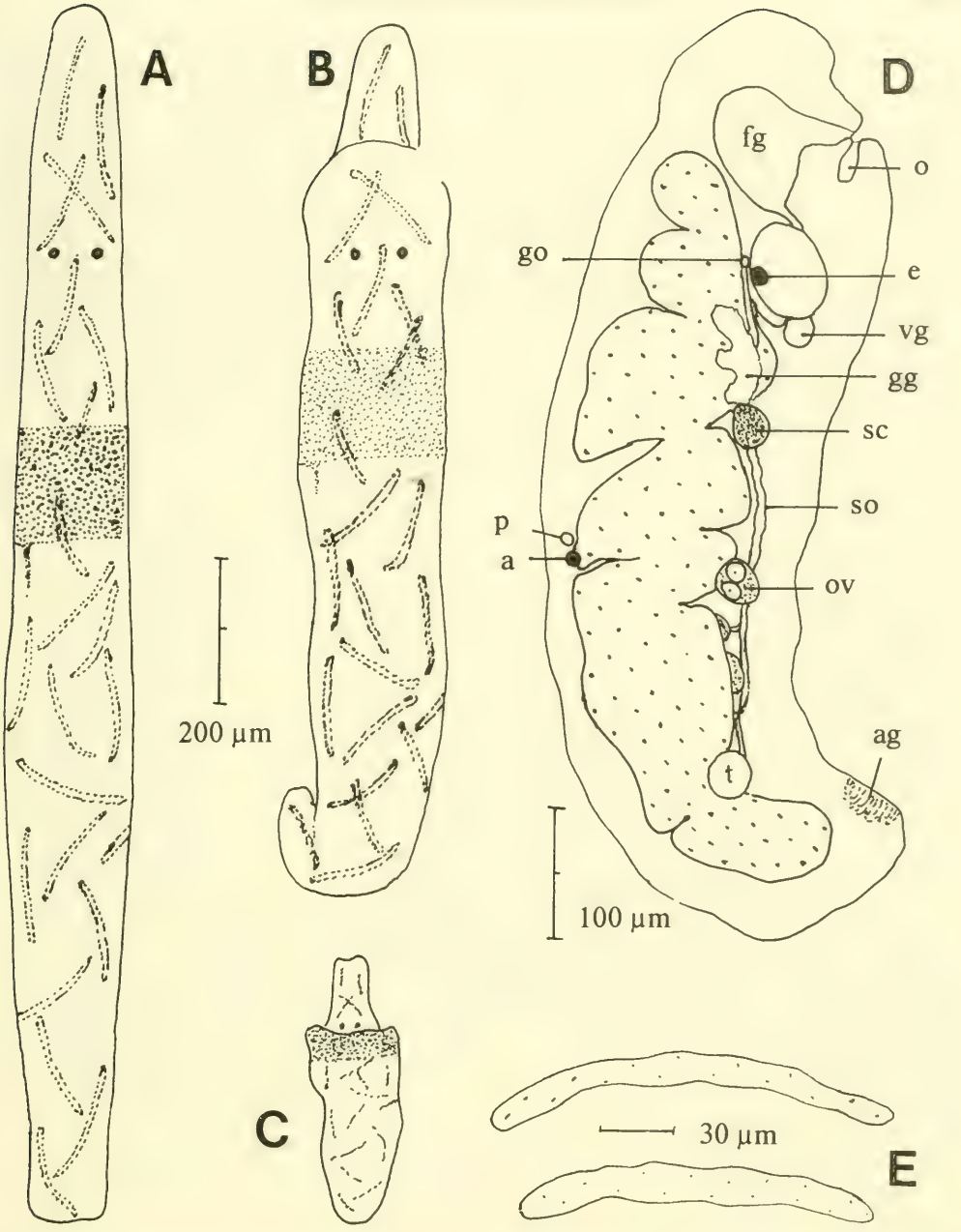

FIG. 2. *Rhodope transtrosa:* A: living animal (1.65 mm); B: semi-preserved animal; C: contracted animal; D: arrangement of organs as seen from the right side in preserved animal; E: spicules. a anus, ag adhesive gland, e eye, fg foregut, gg genital gland, go genital opening, o outlet of oral glands, ov ovarial sac, p protonephridiopore, sc spermatocyst, so hermaphroditic duct, t testicle, vg visceral ganglion.

acts as a highly-bendable snout with subfrontal mouth opening; in the contracted state this snout may be retracted far into the subsequent, still pre-ocular section. The eyes are clearly visible in life. The body is somewhat truncated terminally due to the distinct adhesive organ. The spicules are fairly densely arranged and are slightly curved with a faintly

verrucose surface. They measure 150–170 μm x 14–17 μm (Fig. 2E).

The internal organization closely resembles that of *R. veranii,* but there are some distinct differences. Ventral to the subterminal mouth, a short median sac bearing the peripherally arranged oral glands opens (the glands are arranged as a paired cluster in *R. veranii* and *R. marcusi*). The foregut shows a precerebral enlargement with taller epithelium, but no pharyngeal bulb. This section receives the salivary glands in paired arrangement. Immediately behind the central nervous complex the foregut leads dorsally into the sac-like midgut (midgut-gland). The latter forms an elongated organ extending from above the foregut to the posterior end of the body; in the preserved animal, there are several contraction-folds along its course, but no actual winding. Somewhat behind the mid-length of the body, the short intestine emerges dorsally from the sac-like midgut and runs directly, without any winding, to the right. It opens laterodorsally closely behind the laterodorsal protonephridiopore, both being located (in contrast to *R. veranii* and *R. marcusi*) posterior to the middle of the body (preserved animal). Immediately adjacent, and to the left of the intestine, a small but distinct posteriorly directed pouch or diverticulum is present; this corresponds to the remnant of the true stomach in *R. veranii.*

The nervous system largely resembles that of *R. veranii* with respect to the general arrangement of the ganglia and, on each side, the two proximally joined labial nerves, the double root of the rhinophoral nerve, the bifurcated (pleural and pedal) root of the lateral nerve, and the optical ganglion emerging with its connective from the pleuropedal connective. Differences are evident in the less concentrated state of the ganglia with the discrete statocysts between the cerebro-pleuro-parieto-intestinal ganglia and the pedal ganglia, the discrete optic ganglia, the strong parapedal commissure, the fairly free and median visceral ganglion, as well as the symmetrical origin of the right visceral and left genital medullary nerves (cf. Huber, 1987).

In the hermaphroditic genital system there is a 55 x 45 μm terminal testicle and a much larger testicle (70 x 50 μm) more anteriorly on the left. The median hermaphroditic duct then connects two ovarial sacs on the left, one on the right, and two more on the left (these being located anterior to the anal region of the body). Approximately half way between the intestine and the central ganglia complex the spermoviduct turns to the right and continues in the form of a narrow connection with an enlarged portion filled with sperm. In contrast to *R. veranii* and more similar to *R. marcusi,* this sac represents a distinct elaboration (spermatheca) rather than a simple enlargement of the spermoviduct (as in *R. veranii*). It opens anteriorly into a three-lobed glandular complex (albumen and mucus glands) from which the genital duct runs antero-laterally to open on the right at the level of the cerebral ganglia and eyes. In contrast to *R. veranii* and *R. marcusi,* no copulatory organ is developed in the present specimen.

Helminthope psammobionta gen. et sp. nov.

This mesopsammic species comes from the western North Atlantic. Specimens were collected by R. Rieger (Innsbruck) and W. Sterrer (Bermuda) from Bermuda (North Rock reef and Tobacco Bay, at 8–10 m depth), North Carolina (30 m depth) and Georgia (2 m depth). They inhabit fairly clean, coarse subtidal sands (cf. Rieger & Sterrer, 1975: pp. 263–264 & their Figs. 34–35). The present animals ranged between 1 mm and about 2.5 mm in length (Figs. 3–4) and are circular in cross section (diameter 60–150 μm), but are able to contract by 30–50%. They are whitish with black eyes; in transmitted light they appear transparent-colourless with a darker, somewhat greenish tinge to the midgut. The body openings are almost invisible as two ciliated patches arranged one close behind the other on the right anterior side. These patches indicate the sites of the protonephridiopore and the anus. The genital opening could not be seen. Because of its internal organization (below), the present specimens are defined as *Helminthope psammobionta* gen. et sp. nov. (Figs. 3–4).

All three specimens sectioned were unfortunately poorly preserved for histological examination, so only an outline of the body organization can be given. The entire body is covered by ciliated epidermal cells among which gland cells are interspersed. In no animal could a definite terminal gland be seen (in contrast to *Rhodope veranii, R. marcusi* and *R. transtrosa;* see Fig. 2D). The loosely and irregularly arranged spicules measure between 45 x 5.5 μm and 70 x 7 μm, and they are weakly curved to slightly angled or geniculate in shape (Fig. 4C). Towards their tips the spicular surface is generally roughened,

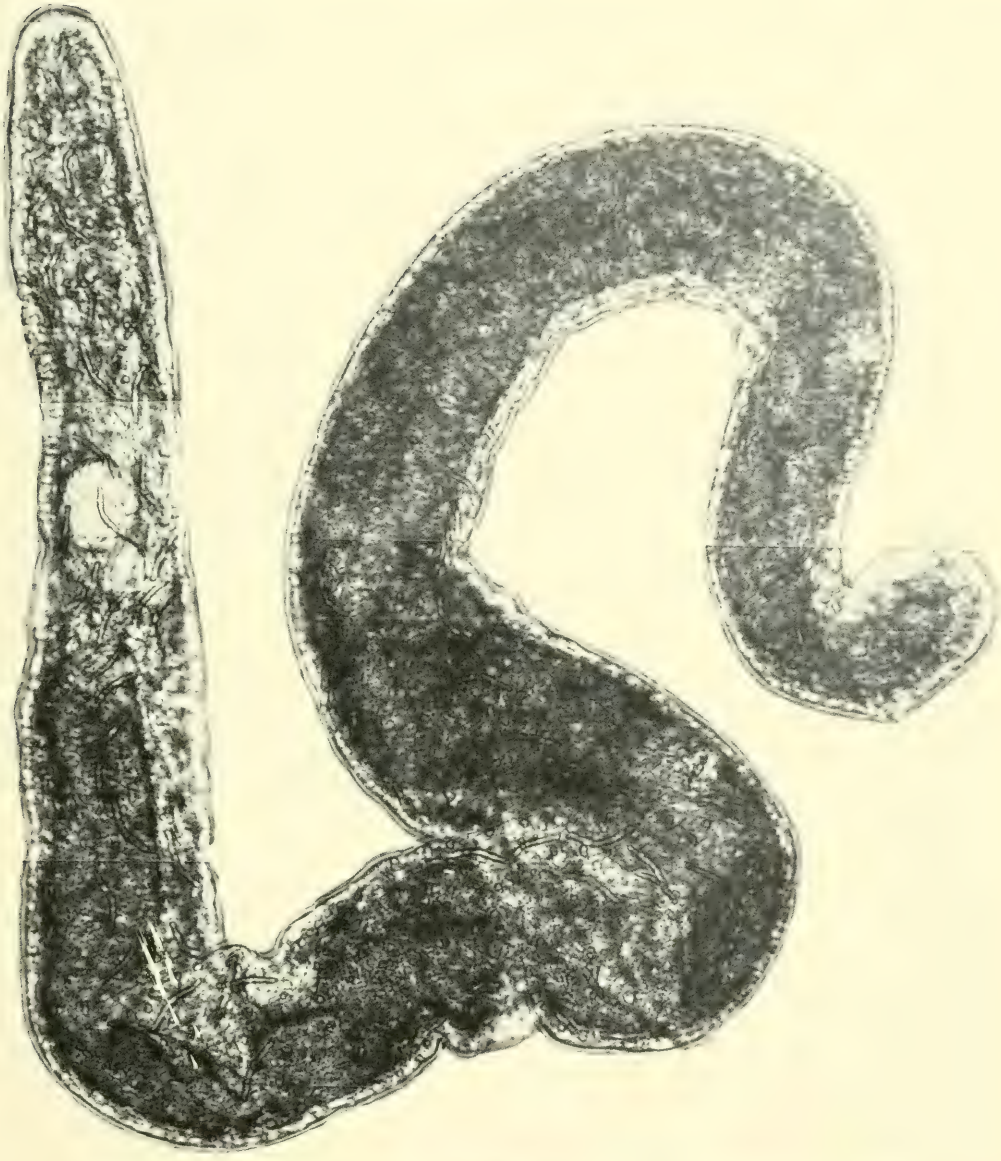

FIG. 3. *Helminthope psammobionta:* living specimen (about 1.5 mm in size) from Bermuda.

and some spicules seem to be hollow (Rieger & Sterrer, 1975: Fig. 34). The spicules are situated in the fibrous connective tissue directly below the epidermis and are surrounded by a spicule-forming cell (Rieger & Sterrer, 1975: Fig. 35). In addition to the elongate spicules (similar to those in *R. veranii* (Graff, 1883: p.75–76) or *R. transtrosa* (Fig. 2E)) very small and platelet-like elements are embedded subepithelially. As indicated by the high contractility of the body, there is a well-defined longitudinal musculature; no regular circular fibres could be seen.

The alimentary canal begins with a subterminal mouth. This leads into a narrow foregut which soon widens and is lined with a tall ciliated epithelium surrounded by circular muscle fibres (pharynx). A pair of ill-defined salivary glands accompany the foregut dorsolaterally. In the region of the cerebral ner-

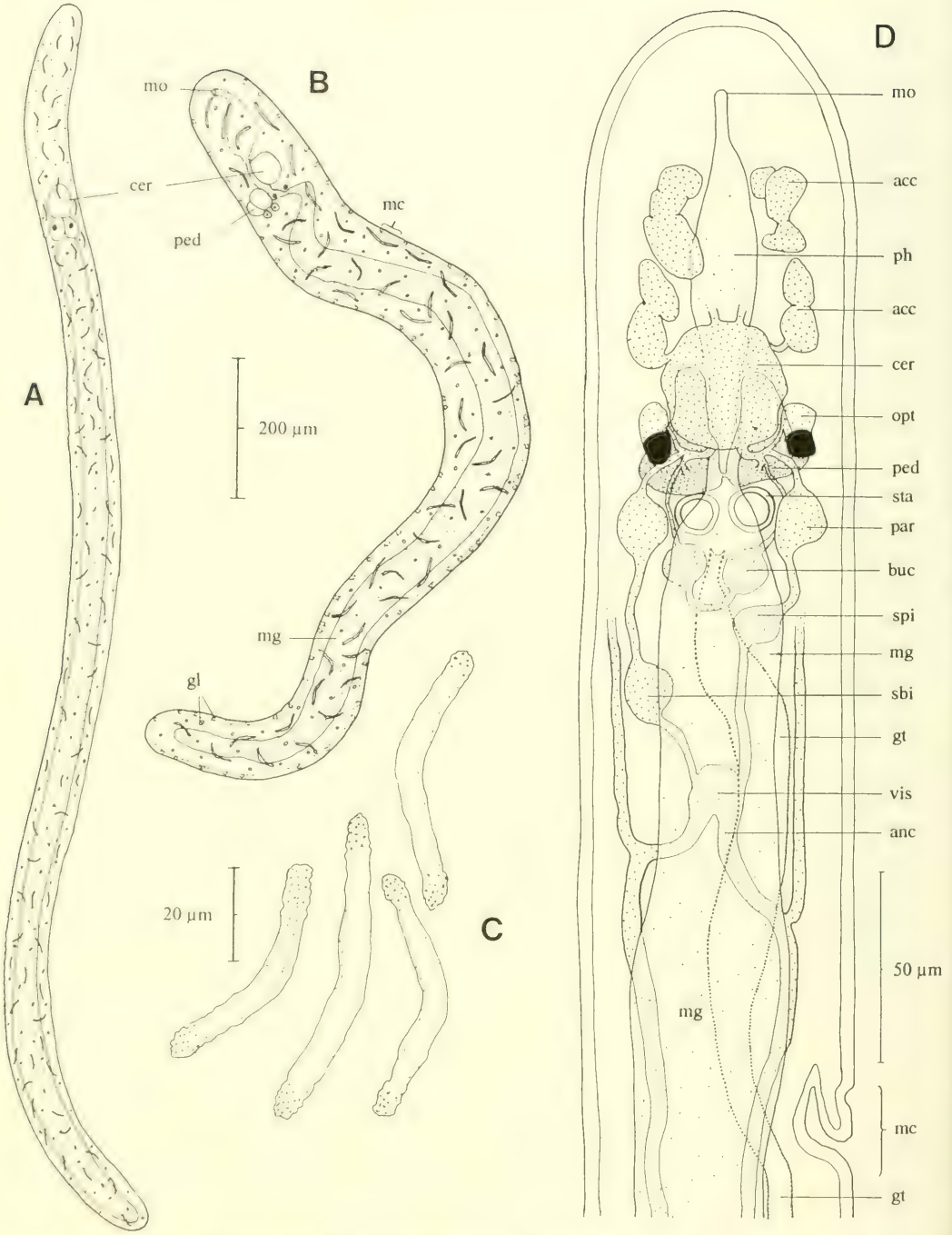

FIG. 4. *Helminthope psammobionta:* specimen from North Carolina gliding (A) and in contracted state below cover glass (B); C: spicules; D: main internal organization. acc accessory ganglia, anc right abdominal nerve cord (— visceral nerve), buc buccal ganglion, cer cerebro-pleural ganglion, gl epidermal glands, gt genital tube (spermoviduct), mc area of (reduced) mantle cavity, mg midgut, mo mouth opening, opt optic ganglion, par parietal ganglion, ped pedal ganglion, ph pharynx, sbi sub-intestinal ganglion, spi supra-intestinal ganglion, sta statocyst, vis visceral ganglion.

vous ring the foregut narrows again. Behind the pedal ganglia the oesophagus connects to the midgut. There is no antero-dorsal caecum (right digestive gland). The midgut represents a homogeneous tube-like organ with high glandular epithelium extending the length of the body. There is no histological break during the course of the midgut except for the almost total disappearance of the lumen in the terminal portion (representing the posterior = left midgut gland?). The lumen is also restricted to a somewhat narrower space posteriorly due to the genital organs. The intestine emerges from the midgut dorsolaterally (approximately 100 μm behind the visceral ganglion) and runs obliquely direct to the lateral anus. Only in one specimen could an organ closely associated with the anus and extending a short distance anteriorly be discerned, probably the protonephridium.

In the nervous system apart from the cerebro-pleural complex all ganglia are separate (Fig. 4D). The fused cerebro-pleural ganglia still show a mid-dorsal incisure and a distinct cerebral commissure; the pleural portion is separated by an accumulation of nuclei. Anteriorly, at least two pairs of cerebral nerves (the labial and the Hancock's/rhinophoral) leave the ganglia. Very characteristic is the presence at each side of two complexes of accessory ganglia. These appear to be incorporated in the course of the cerebral nerves, each complex assuming two to three swellings.

A short connective runs from each cerebral ganglion to the respective pedal ganglion and a strong, terminal cerebropleural connective splits to connect with the optic, the parietal, and the pedal ganglion, as well as the buccal ganglion at each side. The buccal ganglia themselves are well separated and lie behind the statocysts. The small optic ganglia with the embedded eyes are separate from the cerebral ganglia and are located above the pedal ganglia (Figs. 4A,D). Each of the latter is very prominent and shows an anterior lobe. A lateral nerve of the pedal ganglion emerges at each side close to the pleuropedal connective. The statocysts, each with a single statolith, are close by, but they are separate from the ganglia and main nerves. The parietal ganglia are widely separated from the cerebral complex. On the right a strong connection exists to the supra-intestinal ganglion lateroventrally to the midgut, and to the left a much longer connective leads to the (ventro) lateral sub-intestinal ganglion. Both connectives unite in the mid-ventral visceral or abdominal ganglion, which appears to be located at a fairly constant distance of about 135 μm from the beginning of the cerebral ganglia. In histological continuation of the right (supra-intestinal) connective the strong genital 'nerve' emerges from the left portion of the ganglion and runs posteriorly as the left cord, and the left connective continues into the right cord (visceral nerve). Thus, there is a chiasma of fibres in the visceral/abdominal ganglion reflecting the only remaining trace of streptoneury. Furthermore, both abdominal 'nerves' terminate together with the midgut-sac and exhibit a regular coat of nuclei. They thus assume the aspect of medullary cords and each gives off a strong anterior branch (Fig. 4D).

The genital system is absent in one specimen, is represented only by the rudiment of a simple tube extending below the midgut in a second specimen, and is not fully differentiated in the third sectioned individual. In the latter two individuals, the anteriormost part of the genital system is represented by a narrow tube extending posteriorly from between the buccal ganglia; the outer portion and genital opening could not be discerned and still appear to be absent. The genital tube (sperm-oviduct) gradually enlarges posteriorly where it is lined with a high, glandular epithelium without a well-defined lumen (prostate gland?). The tube then continues posteriorly between the midgut and nervous system, its epithelium decreasing again in size toward the anal region. More posteriorly, approximately 850 μm from the anterior tip of the body (about 600 μm behind the visceral ganglion or 500 μm behind the anal region), the simple tube enlarges again to become a weakly ciliated vesicle filled with spermatozoa (spermatheca). This vesicle opens dorsally with its terminal narrowed portion into a voluminous (albumen and mucus) gland, the anterior region of which is lined by densely granulated and ciliated cells which are then replaced posteriorly by large slime cells. A narrow, ciliated duct continues from this gland and appears to become a ramified germ gland. This latter condition could not, however, be ascertained in detail, and only some accumulation of sperm in vesicles (testicles) were observed. Thus, as is *Rhodope veranii* (Riedl, 1960:p.299), the present new species also appears to be protandric (gonochorism is also possible).

Systematic Discussion of the Rhodopidae

In contrast to *Rhodope veranii, R. transtrosa* and *R. marcusi* (see pp. 300, 302), the new type *Helminthope psammobionta* is characterized and defined by the wide nervous system with free ganglia and the differentiation of precerebral (= accessory) ganglia, by the axial connection of the foregut and midgut without anterior caecum, and by the lack of a ventroterminal adhesive gland. These characteristics indicate that it belongs to a distinct genus. It is also characterized by the elongate body without pigmentation, the less verrucose and smaller spicules, the far posterior location of the spermatheca and the presence of the albumen/mucus genital gland behind it, as well as the interstitial habitat. There is, however, no doubt that *Helminthope* is a rhodopid characterized by a pentaganglionate visceral loop with medullary visceral and genital nerves, subepidermal spicules, reduced mantle cavity on the right side (anus and protonephridiopore), lack of a shell, radula, jaws, stomach, heart, and head-shield/tentacles.

The systematic roundabout of the Rhodopidae is summarized in Riedl (1959). With respect to the developmental characters and the pentaganglionate visceral loop, the family definitely belongs to the Pentaganglionata = Euthyneura (Riedl, 1960: pp.303–312; Salvini-Plawen, 1970; Haszprunar, 1985). A more precise classification has assumed a close affinity to the Soleolifera and Onchidiacea with the inclusion of all three groups within a separate euthyneuran subclass Gymnomorpha (cf. Riedl, 1960; Oberzeller, 1959; Salvini-Plawen, 1970; Arnaud et al., 1986). Such a classification cannot, however, be upheld because the present investigations demonstrate that neither *Rhodope* nor *Helminthope* possess a procerebrum and/or cerebral glands. This special neurosecretory/neurohaemal system is characteristic of the Pulmonata and Gymnomorpha (cf. Haszprunar, 1985). In addition, both groups (= clade of Aeropneusta) are characterized by the absence of a postero-lateral cerebral nerve equivalent to the Hancock's or rhinophoral nerve present in Rhodopidae as in all other opisthobranchs (Huber, 1987). Thus, the Rhodopidae cannot be included within one of these two supra-orders (Fig. 5). On the other hand, the slug *Smeagol manneringi* (Climo, 1980), which due to the (inaccurate) original description had been excluded from the Gymnomorpha (Haszprunar, 1985; Arnaud et al., 1986), in fact belongs to the supra-order Gymnomorpha: a re-examination has revealed the presence of a procerebrum and of cerebral glands which, together with other characters, place the species in closer affinity to the Onchidiidae (pers. comm. G Haszprunar; cf. Arnaud et al., 1986: p.175).

An ultrastructural investigation of the integument of *Rhodope veranii* (pers. obs.) and *Helminthope* (Rieger & Sterrer, 1975: their Fig. 35) demonstrates that there are no special vacuolar cells provided with vesicles (amphidisk-like inclusion; cf. Schmekel, 1982,1985) and consequently the Rhodopidae cannot be classified within the Nudibranchia s.s. (= less Doridacea). Because, on the other hand, investigated members of *Pseudovermis* (Aeolidacea: Heteroprocta) possess vacuolar cells (pers. obs.), their lack in Rhodopidae could perhaps be correlated with the diminutive size (as accessory ganglia appear to be) or the special habitat. An identical argument would be valid with respect to the Anthobranchia (= Doridacea or Holohepatica or '(Eu-)Ctenidiacea') which have special vacuolar cells in the rhinophores (cf. Kress, 1981; Schmekel, 1985); because, however, all tentacles are reduced in the Rhodopidae no comparison is possible here.

Up to the present, the configuration of the nervous system provided a valid argument to exclude *Rhodope* from the Anthobranchia (as well as from Pleurobranchomorpha and Nudibranchia s.s.; cf. Salvini-Plawen, 1970). The presence of the visceral/abdominal ganglion in *Rhodope veranii* on the left side, or almost fused with the sub-intestinal ganglion (Riedl, 1960; Oberzeller, 1969), is the opposite of the condition found in the Eleutherobranchia (Pleurobranchomorpha, Anthobranchia and Nudibranchia; cf. Haszprunar, 1985). Against this argument, however, the more conservative configuration in *Helminthope* (Fig. 4) and even in *R. transtrosa* still makes any concentration possible. This is a renewed confirmation that the position of the visceral ganglion on the left side is a convergence. On the other hand, the visceral ganglion in Bullomorpha, Aplysiomorpha = Anaspidea, and Saccoglossa (except the Cylindrobullidae, cf. Burn, 1966), as well as in Umbraculomorpha, Acochlidiomorpha, and Gymnosomata, is already fused to the left side (generally with the sub-intestinal ganglion). Because *R. transtrosa* and *Helminthope* show a well-separated visceral ganglion, no link can be proposed among these more advanced tecti-

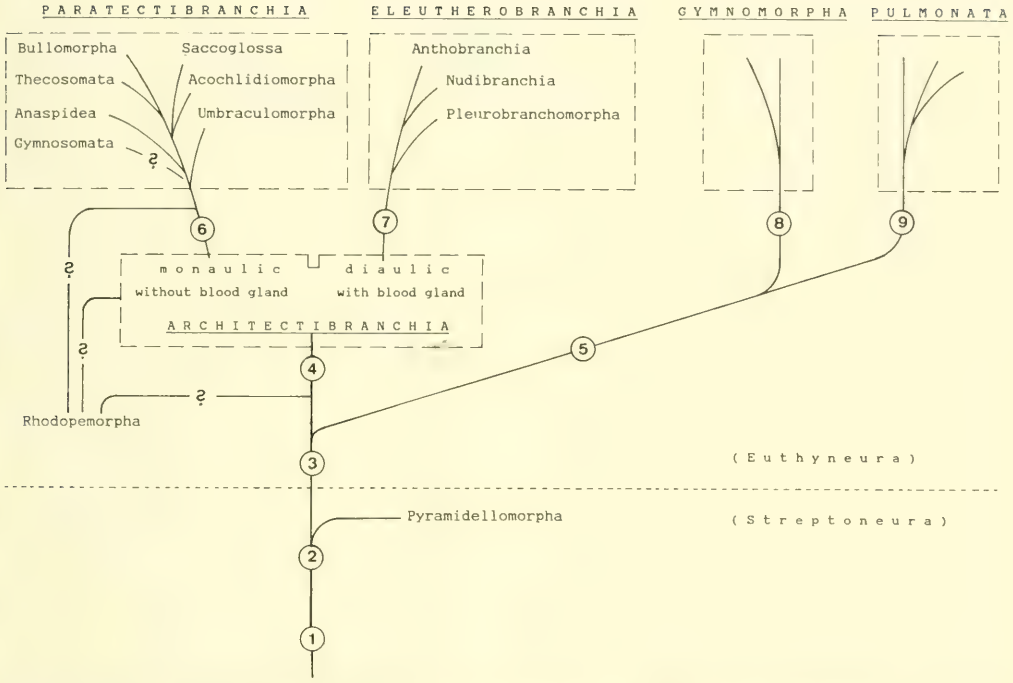

FIG. 5. Relationship of Rhodopemorpha within pentaganglionate (= euthyneurous) gastropods: 1 = Streptoneura with epiathroid nervous system, tentacle nerves bifurcated, parapedal commissure; heterostrophy; mantle cavity with two opposed ciliary tracts and devoid of ctenidia; eggs united by chalazae, spiral type of sperm with glycogen helices within midpiece. 2 = Eyes median of tentacles; cerebral ganglia with giant cells, pedal ganglia with lateral nerve; with paired rhinophoral (= Hancock's) nerve; small animals with reduction of paired oralis nerve. 3 = Elongation of head-pedal complex with parietal ganglia; with pallial caecum and repugnatorial glands. 4 = Opisthobranchia: Head-shield with bifurcated tentacle (= clypeo-capitis) nerves; Hancock's sense organs with external branch of labiotentacularis nerve. 5 = Procerebrum with cerebral glands and dorsal bodies; small animals (= without oralis nerves), anterior shift of female genital opening outside the mantle cavity and restriction of the opening of mantle cavity: Aeropneusta; loss of paired rhinophoral nerve. 6 = Anterior gizzard. 7 = Disintegration of head-shield; visceral ganglion migrates to the right side to fuse primarily with the supra-intestinal ganglion; chromosomes restricted to generally 12–13 pairs. 8 = Mantle cavity reduced to 'cloaca', or lost; loss of shell, pedunculated eyes. 9 = Mantle cavity becomes a 'lung'.

branchs (= Paratectibranchia, below). Finally, the bifurcated lateral nerve in *Rhodope* (see pp. 300 and 302) has a similar origin in several Nudibranchia. However, because it corresponds to the purely latero-pedal nerve in *Helminthope* and other Euthyneura (Huber, 1987; see Fig. 5), this similarity between *Rhodope* and those nudibranchs appears to be convergent due to concentration.

Whereas the structure of the spermatozoa gives little evidence of phylogenetic value (see p. 300), the chromosome number in *Rhodope veranii* with n = 16 appears to be of more interest. The general chromosome numbers in Eleutherobranchia are n = 12 (Pleurobranchomorpha) or n = 13 (Anthobranchia and Nudibranchia), in Saccoglossa n = 17 (except for *Bosellia* : n = 7), and in other Tectibranchia likewise n = 17 (see Burch, 1967; Schmekel, 1985; Vitturi et al., 1985). Exceptions (so far as known) include the cephalaspideans *Scaphander, Hami-*

noea, Philine aperta and two Smaragdinellidae with n = 18, *Philinoglossa* with n = 13, the anthobranch *Platydoris* with n = 12, two *Aplysia* species (Anaspidea) with n = 16, as well as the dendronotacean nudibranch *Tethys leporina* with n = 16 (see Curini-Galetti, 1985; Vitturi et al., 1985). These two latter exceptions, as well as the chromosome number n = 16 in *Veronicella* (Gymnomorpha) and the lower pulmonates *Siphonaria* and *Bakerilymnaea* (cf. Burch, 1967), are of special interest since they demonstrate a polyphyletic decrease of the chromosome number n = 17 along with anagenesis (in higher pulmonates, the number of chromosomes is generally increased; cf. Burch, 1967). Thus, the number n = 16 in *Rhodope* appears to show that the Rhodopidae cannot be directly linked with one of the present orders, but rather it demonstrates the primitive level still reflected in some Anaspidea, Nudibranchia, Gymnomorpha, and lower Pulmonata.

The monauly in the genital apparatus of *Helminthope* as well as of *Rhodope* (though with possible incipient functional diauly in *R. veranii;* cf. Böhmig, 1893: p.81) excludes a closer relationship to the diaulic Eleutherobranchia, Sacoglossa, and Anaspidea (see Fig. 5). In addition, it is interesting to note that the gonad includes separate testicles and ovaria, a condition only known in several Streptoneura.

In conclusion, the pentaganglionate Rhodopidae cannot, on the one hand, be directly linked with Gymnomorpha and Pulmonata, nor, on the other hand, can they be classified within the Eleutherobranchia (Pleurobranchomorpha, Anthobranchia, and Nudibranchia), Saccoglossa, or Anaspidea. The Rhodopidae share only a general level of organization with several tectibranch gastropods. According to a recent analysis by Haszprunar (1985), however, the tectibranchs should be subdivided into the conservative group of Architectibranchia (Diaphanoidea, Ringiculoidea, Acteonoidea) and the other more advanced tectibranchs (Fig. 5); this latter group preferably should be named Paratectibranchia (Salvini-Plawen, 1988), and are monophyletically characterized by a gizzard (if not secondarily reduced). Since the two proximally joined labial nerves on each side in *Rhodope* (according to Huber 1987) correspond to the internal plus external branch of the labiotentacularis nerve, such condition would the Rhodopidae unequivocally classify within the opisthobranchs (i.e. above the level 4 in Fig. 5). At the present time, the characters of the Rhodopidae only permit this family to be classified as a taxon **Rhodopemorpha** nov. of uncertain systematic rank representing a highly specialized offshoot of the lower opisthobranchs (Fig. 5).

Recent Rhodopemorpha, with at present the single family Rhodopidae, include the following three phytal and three interstitial members (cf. Rieger & Sterrer, 1975: p.262–265; Arnaud et al., 1986: p.158,171):

1. *Rhodope veranii* Kölliker, 1847, from the Adriatic Sea and the adjacent Mediterranean, measures 1–8 mm and inhabits shallow subtidal areas with stones and *Ulva*. It is characterized by an orange-red, roughly T-shaped dorsal pigmentation as well as by verrucose and more pointed, slightly bent spicules of 90–200 μm length. Reduced mantle cavity anterior to the middle of the body.

2. *Rhodope marcusi* sp. nov. (= *R. veranyi* Marcus & Marcus, 1952, nec Kölliker, 1847; = *Rhodope* species A in Arnaud et al., 1986: p.158) comes from the Bay of Santos (Brazil, off São Paulo) and lives in the rocky or stony tidal zone among *Sargassum stenophyllum* and *Padina*. In contrast to *R. veranii* Kölliker, and to *R. transtrosa* (below), the *c.* 2 mm long specimens are characterized by the lack of orange-red pigmentation, by the crescent shaped spicules, and by the position of the reduced mantle cavity with anus and protonephridiopore in the mid-length of the body (cf. Marcus & Marcus, 1952).

3. *Rhodope transtrosa* sp. nov. is at present known only by a single specimen from an aquarium filled with phytal material from tropical Indo-Pacific waters. It is characterized by an orange-red transverse bar at the anterior third of the 1.65 mm long and slender body, as well as by scarcely verrucose, slightly curved spicules of 150–170 x 14–17 μm size. The reduced mantle cavity is located somewhat posterior to the middle of the body; differences in the internal characters are as indicated above. Type: Naturhistorisches Museum, Wien, No. 83438.

4. *Rhodope* species D was recorded from coarse shell-sand at 25 m off Bergen, Norway by Karling (1966). This colourless specimen is 1.5 mm long and accordingly should already possess the reddish T-pigmentation if conspecific with *R. veranii.* It is possibly conspecific with the specimens found in shell-sand at 50 m by Swedmark (1958: p.61) and off Madeira by Langerhans (in Graff, 1883: p.74–75). This eastern Atlantic species pos-

sesses slightly curved verrucose rods (65–100 μm) and pointed spicules similar to *R. veranii,* as well as ramified elements (cf. Karling, 1966).

5. *Rhodope* (?) *crucispiculata* sp. nov. (= *Rhodope* ·species C in Arnaud et al., 1986) was collected by Christine Schöpfer-Sterrer from subtidal sand at 14 m from the coast of Tunisia (cf. Rieger & Sterrer, 1975: p.262, 265). Though certainly immature (400 μm in size), this species is defined and easily recognizible by the densely arranged, regularly cross-shaped spicules (25–60 μm) with central hole.

6. *Helminthope psammobionta* gen. et sp. nov. (= *Rhodope* species B in Arnaud et al., 1986). The new genus and species is characterized as described above. Type: Naturhistorisches Museum, Wien, No. 83439.

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MORPHOLOGICAL PARALLELISM IN OPISTHOBRANCH GASTROPODS

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ABSTRACT

Opisthobranch gastropods exhibit parallel evolution in most of their organ systems. Levels of 60–80% parallelism of characters are not uncommon in many opisthobranch taxa. High levels of parallelism have traditionally produced difficulties in the classification of opisthobranchs and persist when modern phenetic and cladistic methods are employed. Examples from many cephalaspidean taxa demonstrate the minimum levels of parallelism present in opisthobranchs when parsimony methods are used. Strict adherence to statistically parsimonious evolution may yield phylogenies that are not parsimonious from a functional or adaptive point of view. Classification of opisthobranchs, at all systematic levels, is profoundly affected by parallelism. Historical difficulties of classifying some Sacoglossa with aeolid nudibranchs is a manifestation of parallel evolution. Cladistic classification of members of several families of cephalaspideans by parsimony methods produces erroneous relationships that reflects grades of organization rather than phylogeny. The subdivision of the aeolid nudibranch family Aeolidiidae into genera is also problematic owing to parallel evolution. On the basis of synapomorphy, the Akeridae must be regarded as anaspideans rather than cephalaspideans. Schmekel's separation of the Umbraculomorpha as a distinct order is unwarranted, and is based upon erroneous assumptions of monophyletic change of the reproductive and central nervous systems within the opisthobranchs.

INTRODUCTION

Recent studies on parallel evolution in opisthobranch gastropods (Gosliner & Ghiselin, 1984; Gosliner, 1985a) have focused on the theoretical aspects of parallelism and their implications to phylogenetic methodology. While these papers provide examples of parallelism in the opisthobranchs, the morphological details of much of this work have yet to be presented. As previously discussed (Gosliner & Ghiselin, 1984), parallelism occurs in most major organ systems within the Opisthobranchia and may occur at all systematic levels. Interpretations of parallelism have led to differing views of the classification and phylogeny of the opisthobranchs. Examples include the Opisthobranchia in general (Ghiselin, 1966; Schmekel, 1985), the Sacoglossa (Russell, 1929) and the aeolidiid nudibranchs (Gosliner, 1985b).

A review of the organ systems within the Opisthobranchia is here provided to demonstrate the morphological diversity present within the subclass and to suggest the extent to which parallel evolution has occurred.

METHODS

In the present study a wide variety of opisthobranch taxa were dissected both to verify published morphological observations and to provide additional data (Table 1). Whenever possible, morphological observations described in the literature were verified. Most major organ systems were examined, including the shell, operculum, mantle complex, digestive system, central nervous system and reproductive system. The variability of structures within and between taxa was compared.

Polarity of some morphological characters in the Opisthobranchia has been previously discussed (Gosliner, 1981a; Schmekel, 1985). In order to further ascertain the polarity of morphological transformation series, outgroup comparison was employed at a variety of systematic levels. The outgroups utilized for the entire Opisthobranchia include the probable sister group of the opisthobranchs, the Pulmonata. Other taxa used as outgroups were the Heterogastropoda and various other mesogastropods. Functional arguments to establish polarity, as advocated by Gosliner & Ghiselin (1984), ontological sequences and palaeontological data were also employed to augment outgroup comparison methods of determining polarity.

RESULTS

The morphological variability of the various organ systems within the Opisthobranchia is

TABLE 1. Summary of taxa studied. [* indicates type species of genus].

Sources of material:

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania.
CAS	California Academy of Sciences, San Francisco, California.
EM	Dr Eveline du Bois Reymond Marcus, University of São Paulo, Brazil.
GCW	Dr Gary C Williams, South African Museum, Cape Town.
HB	Dr Hans Bertsch.
KM	Ms Kaniaulono Meyer, University of Cincinnati, Ohio.
LACM	Los Angeles County Museum, California.
LGH	Dr Larry G Harris, University of New Hampshire, Durham, New Hampshire.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge,Massachusetts.
MLG	Mr Michael L Gosliner, Takoma Park, Maryland.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
RB	Dr Robert Beeman, San Francisco State University, California.
SM	Ms Sandra Millen, University of British Columbia, Vancouver, Canada.
YPM	Peabody Museum, Yale University, New Haven, Connecticut.

Taxon	Locality	Source of Material
Order CEPHALASPIDEA		
Family Ringiculidae		
Ringicula nitida Verrill, 1872	N. Atlantic	MCZ
Family Acteonidae		
Acteon hebes Verrill, 1885	N. Atlantic	MCZ
**Rictaxis punctocaelatus* (Carpenter, 1864)	California	LGH, TMG
Pupa nitidula (Lamarck, 1816)	Seychelles	ANSP
P. sp. I	Seychelles	ANSP
P. sp. II	Seychelles	ANSP
Family Hydatinidae		
**Hydatina physis* (Linnaeus, 1758)	Madagascar, Seychelles	ANSP, GCW, MLG
H. zonata (Lightfoot, 1786)	Okinawa	ANSP
**Micromelo undata* (Bruguière, 1792)	Florida	TMG
**Parvamplustrum tenerum* Powell, 1961	N. Atlantic	MCZ
Family Scaphandridae		
**Scaphander lignarius* (Linnaeus, 1758)	Scotland	MCZ, MNHN
S. punctostriatus (Mighels, 1841)	N. Atlantic	MNHN, YPM
S. mundus Watson, 1883	Atlantic, S. Africa	MCZ, MNHN
S. gracilis Watson, 1883	N. Atlantic	MNHN
S. nobilis Verrill, 1884	N. Atlantic	MNHN
Acteocina bidentata (Orbigny, 1841)	Brazil	EM
A. canaliculata (Say, 1826)	New York—Nova Scotia	ANSP, KM, LGH, TMG
A. inculta (Gould, 1856)	California	TMG
A. cerealis (Gould, 1852)	California, British Columbia	SM, TMG
A. culcitella (Gould, 1852)	California	LACM
A. oryza (Totten, 1835)	Connecticut	KM
Cylichna alba (Brown, 1827)	New Hampshire, Maine	TMG
C. attonsa (Carpenter, 1864)	British Columbia	SM
**Mamillocylichna richardi* (Dautzenberg, 1889)	N. Atlantic	MCZ
Cylichnium africanum (Locard, 1897)	N. Atlantic	MNHN
'Bulla' semilaevis Seguenza, 1880	N. Atlantic	MCZ
'Bulla' simplex Locard, 1897	N. Atlantic	MNHN
Family Philinidae		
Philine alba Mattox, 1958	California	CAS, GCW
P. bakeri Dall, 1919	California	CAS
P. finmarchica Sars, 1858	New Hampshire	MCZ, TMG

TABLE 1. (*Continued*)

Taxon	Locality	Source of material
P. infundibulum Dall, 1889	N. Atlantic	MCZ
P. lima (Brown, 1825)	New Hampshire	TMG
P. quadrata (Wood, 1839)	N. Atlantic	MCZ
P. sp.	Hawaii	TMG
Family Aglajidae		
**Aglaja tricolorata* Renier, 1807	Italy	CAS
A. ocelligera (Bergh, 1894)	California	TMG
A. orientalis Baba, 1949	Hawaii	TMG
A. regiscorona Bertsch, 1972	Gulf of California	CAS
A. unsa? Marcus & Marcus, 1969	Brazil	EM
A. sp.	Florida	YPM
**Chelidonura hirundinina* (Quoy & Gaimard, 1832)	Hawaii	TMG
C. fulvipunctata Baba, 1938	Hawaii	TMG
C. inornata Baba, 1949	Madagascar	ANSP
C. pallida Risbec, 1951	Palau, Malaysia	CAS, LGH
C. sp.	Madagascar	ANSP
**Melanochlamys cylindrica* Cheeseman, 1881	Hawaii	TMG
M. diomedea (Bergh, 1893)	California	TMG
**Navanax inermis* (Cooper, 1862)	California	TMG
N. aenigmaticus (Bergh, 1894)	tropical Americas	ANSP, HB, LACM, KM, TMG
N. polyalphos (Gosliner & Williams, 1972)	Gulf of California	LACM
**Philinopsis speciosa* Pease, 1860	Hawaii	TMG
P. cyanea (Martens, 1879)	Australia	LGH
P. depicta (Renier, 1807)	Italy	MCZ
P. pilsbryi (Eliot, 1900)	Hawaii	TMG
P. cf. pelsunca	Italy	CAS
Family Gastropteridae		
Gastropteron pacificum Bergh, 1894	California, Washington	CAS, TMG
Siphopteron michaeli (Gosliner & Williams, 1988)	Réunion Island	GCW, MLG
Family Retusidae		
**Retusa obtusa* (Montagu, 1807)	New Hampshire—Maine	TMG
Volvulella cylindrica (Carpenter, 1864)	British Columbia	SM
Family Bullidae		
**Bulla ampulla* Linnaeus, 1758	Zanzibar	MCZ
B. striata Bruguière, 1792	Florida	TMG
B. gouldiana Pilsbry, 1895	California	CAS
Family Haminoeidae		
Atys cylindrica (Helbling,1779)	Seychelles	ANSP
A. sp.	Zanzibar	MCZ
Haminoea vesicula Gould, 1855	California	CAS, TMG
H. virescens (Sowerby, 1833)	California	CAS, TMG
H. strongi Baker & Hanna, 1927	Gulf of California	CAS
H. solitaria (Say, 1822)	Connecticut—Massachusetts, Nova Scotia	KM, TMG
H. elegans (Gray, 1825)	Yucatan Peninsula	TMG
**Roxania utriculus* (Brocchi, 1814)	N. Atlantic	MCZ
Phanerophthalmus sp.	Madagascar	ANSP
Haminoeidae sp.	Hawaii	TMG
Family Diaphanidae		
**Diaphana minuta* (Brown, 1827)	New Hampshire	TMG
D. californica Dall, 1919	California	TMG

(*continued*)

TABLE 1. (*Continued*)

Taxon	Locality	Source of material
D. sp. I	N. Atlantic	MCZ
D. sp. II	N. Atlantic	MCZ
Order THECOSOMATA		
Family Limacinidae		
Limacina retroversa (Fleming, 1823)	New Hampshire	TMG
Family Cavoliniidae		
Cavolinia tridentata (Niebuhr, 1775)	N. Atlantic	YPM
Order SACOGLOSSA		
Family Cylindrobullidae		
**Ascobulla ulla* (Marcus & Marcus, 1970)	Brazil	EM
A. californica Hamatani, 1971	Gulf of California	CAS
Volvatella sp.	Hawaii	TMG
Order ANASPIDEA		
Family Akeridae		
**Akera bullata* Müller, 1776	England	RB
A. sp. I	Enewetak Atoll	ANSP
A. sp. II	Madagascar	ANSP
Order NOTASPIDEA		
Family Umbraculidae		
**Umbraculum sinicum* (Gmelin, 1791)	Hawaii, Zanzibar	MCZ, TMG
Tylodina fungina Gabb, 1865	California	CAS, TMG

presented with a discussion of the phylogenetic relevance of this variability.

Shell

The shell in opisthobranchs is exceedingly variable (Fig. 1). In its least derived form it is thickly calcified with a well-elevated apex. It may be modified into a variety of forms within the holoplanktonic Thecosomata (Spoel, 1967) but exhibits less variability within the remainder of the subclass. In most opisthobranchs, where a shell is present in the adult, either it is bulloid with an involuted spire or else it is an internal flattened plate. In the majority of opisthobranch species the shell is entirely lost at metamorphosis from a planktonic to benthic existence. Bulloid shells are derived from shells with an elevated spire and, similarly, internal flattened plates probably represent modifications of bulloid shells. The transformation of these shells into more derived structures has occurred many times within separate clades of opisthobranchs (Table 2). A bulloid shell has evolved from a shell with an elevated spire at least six different times. In each of these cases, both the ancestral and derived character states occur within members of distinct clades, and in *Retusa* and *Acteocina* within single genera. Reduction and internalization of the shell has similarly occurred a minimum of six times within the Opisthobranchia.

These same trends in shell reduction and loss also occur in parallel within the sister group of the opisthobranchs, the Pulmonata. Prosobranch gastropods of the Cypraeacea, Lamellariacea and Naticidae also have representatives with bulloid shells and reduced internal shell plates.

A shell is entirely absent in the adults of many derived opisthobranchs, including all members of the Gymnosomata and Nudibranchia. The presence of a shell and its subsequent loss within distinct clades (Table 3) indicates that this has occurred independently at least five times within the Opisthobranchia.

Operculum

A chitinous operculum is present in virtually all members of the Prosobranchia, but is absent in most opisthobranchs and all but one pulmonate (Hubendick, 1945). All opistho-

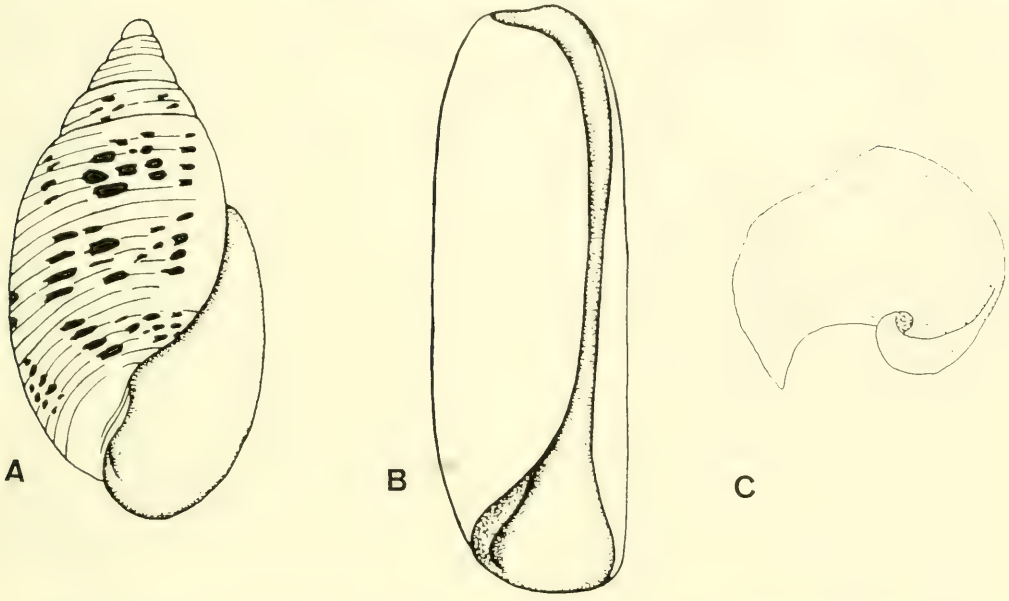

FIG. 1. Shell variation in opisthobranch gastropods. A: *Japonateon* sp.; B: *Cylichna tubulosa* Gould, 1859; C: *Melanochlamys* sp.

TABLE 2. Variation in shell morphology in representative opisthobranchs.

Taxon	Elevated spire	Reduced external shell	Internal flattened plate
Acteonacea	*Acteon, Pupa*	*Hydatina, Micromelo*	—
Acteocina	*A. inculta, A. canaliculata*	*A. oryza, A. bidentata*	—
Philinacea	*Meloscaphander*	*Cylichna, Scaphander*	*Philine,* Gastropteridae, Aglajidae
Diaphanidae	*Toledonia*	*Diaphana*	*Colpodaspis*
Haminoeidae-Runcinidae	—	*Haminoea, Atys*	*Phanerophthalmus,* Runcinidae
Retusidae	*Retusa obtusa*	*R. truncatula*	—
Anaspidea	—	*Akera*	*Aplysia, Petalifera*
Thecosomata	*Limacina*	*Cuvierina*	—
Sacoglossa	—	*Cylindrobulla, Ascobulla*	*Lophopleurella*
Notaspidea	—	*Tylodina, Umbraculum*	*Berthella, Pleurobranchus*

TABLE 3. Shell loss in opisthobranchs.

Taxon	Present	Absent
Cephalaspidea	*Gastropteron rubrum*	*Siphopteron citrinum*
Notaspidea	Umbraculidae, Pleurobranchidae	*Pleurobranchaea, Euselenops*
Philinoglossidae	*Pluscula*	*Sapha, Philinoglossa*
Acochlidiacea	—	all members
Sacoglossa	Cylindrobullidae, Oxynoidae	Elysiidae, Hermaeidae
Anaspidea	Akeridae, most aplysiids	*Stylocheilus,* some *Phyllaplysia*
Nudibranchia	—	all members
Gymnosomata	—	all members

TABLE 4. Presence of operculum in opisthobranchs.

Taxon	Present	Absent
Acteonacea	most Acteonidae, Bullinidae	*Rictaxis,* Hydatinidae
Retusidae	*Retusa operculata*	*R. obtusa*
Scaphandridae	*'Bulla' semilaevis*	most Scaphandridae
Thecosomata	Limacinidae	Cavoliniidae, Peraclidae

branchs with shelled larvae possess an operculum at this stage, but only a few primitive forms retain it as adults (Table 4).

Distribution of the presence and loss of the operculum within distinct clades indicates that within the opisthobranchs it has been lost independently at least four times.

Mantle complex

Within the opisthobranchs a partial or complete detorsion of the mantle complex commonly occurs (Gosliner, 1981a; Gosliner & Ghiselin, 1984). In a few cephalaspidean opisthobranchs the mantle cavity is directed anteriorly, but in most of them it is placed on the right side of the body. In the more highly derived Runcinidae, the mantle cavity has undergone complete detorsion and is situated at the posterior end of the animal. From the distribution of this transformation series in opisthobranchs (Table 5) it is apparent that these changes have occurred several times in distinct clades.

In other opisthobranch taxa, the mantle cavity has been altered in a variety of different ways. In the Anaspidea the position of the mantle cavity, on the right side of the body, remains essentially unchanged, despite the radical transformation of the body form from the Akeridae to the Aplysiacea. In the cephalaspidean family Gastropteridae and Notaspidea the ctenidium is situated on the right side of the body, but is not enclosed within a mantle cavity.

The form of the ctenidium varies considerably within the Opisthobranchia. Fretter & Graham (1962) and Brace (1977) have suggested that in opisthobranchs the ctenidium is primitively absent and a gill has evolved secondarily in some clades. This has been discounted by Hoffmann (1940) and Gosliner (1981a), who both suggested that the presence of a gill is plesiomorphic in opisthobranchs and that the opisthobranch gill is homologous to that of prosobranchs. A secondarily bipectinate ctenidium is found in opisthobranchs such as *Navanax* and the Notaspidea. This merely represents an elaboration of the plicate condition found in less-derived cephalaspideans. Gills are entirely absent in a variety of derived opisthobranchs and gas exchange occurs through the body surface. While gill loss is often associated with reduced body size, as in the dorid nudibranch *Okadaia* (Baba, 1931), some taxa with large representatives also lack gills. These include some members of the Sacoglossa, Arminacea and Aeolidacea. It is apparent that loss of the ctenidium has occurred in several different lineages of opisthobranchs.

Buccal mass

The presence of paired jaws and a radula are the plesiomorphic states within the Opisthobranchia. The configuration of the radula varies greatly within and between clades of opisthobranchs and does not characterize major monophyletic groups as it does within the Prosobranchia. For example, within the Acteonidae the radula may be exceedingly broad with numerous simple teeth or there may be few highly-specialized teeth (Fig. 2). In this case, it is exceedingly difficult to establish which condition is plesiomorphic. Similarly, there is too much variability in radular morphology among extant primitive opisthobranchs to suggest an ancestral condition.

Within a few major clades such as the Sacoglossa and the aeolidacean nudibranchs the radula is less variable and has a characteristic morphology. Within the Aeolidacea one can suggest plesiomorphic and apomorphic states. The presence of lateral teeth in the more primitive representatives of the two major clades of aeolids (Table 6), and their subsequent loss, provides an example of parallel reduction in radular teeth within the opisthobranchs.

Within several lineages of opisthobranchs the radula has been entirely lost. This has occurred within the Retusidae, the Aglajidae and the dendrodorid, phyllidiid and tethyid nudibranchs.

An increase in the number of radular teeth by addition of both number of radular rows

TABLE 5. Placement of the mantle cavity in various opisthobranchs.

Taxon	Anterior	Right	Posterior
Acteonacea	Acteonidae	Hydatinidae	—
Ringiculidae	*Ringicula nitida*	*R. buccinea, R. conformis*	—
Philinacea	*'Bulla' semilaevis*	*Acteocina, Scaphander*	Philinidae, Aglajidae
Bullacea	—	*Atys, Haminoea*	*Phanerophthalmus, Runcina*

and number of teeth per row is likely to be a derived feature within the Notaspidea and perhaps also in cryptobranch dorid nudibranchs.

Gizzard plates

In many opisthobranchs the esophagus is expanded into a highly muscularized region which contains chitinous triturating plates. Gosliner (1981a) stated that opisthobranchs probably lacked gizzard plates ancestrally, although many primitive opisthobranchs do in fact possess them. This suggestion was based largely on the facts that none of the outgroups of opisthobranchs contain any chitinous structures within the oesophagus, and some primitive opisthobranchs, such as the Ringiculidae and Acteonidae, lack gizzard plates. What is unclear is whether the lineages that do possess gizzard plates represent a monophyletic group or whether gizzard plates have evolved within the opisthobranchs on more than one occasion. The fact that *'Bulla' semilaevis,* which is a primitive member of the Philinacea, lacks gizzard plates, but retains an operculum suggests that absence of a gizzard may be a plesiomorphic condition within the Philinacea. If this is indeed the case, then gizzard plates have evolved at least twice within the Opisthobranchia. The issue is further complicated by the fact that several lineages of opisthobranchs have secondarily lost the gizzard. This has occurred in the Philinidae and Aglajidae, both of which contain some species with a gizzard and some without. In other cases, such as in the Gastropteridae, it is impossible to suggest whether absence of a gizzard is plesiomorphic or apomorphic, since all members of the taxon lack a gizzard.

The morphology of gizzard plates within various clades of opisthobranchs has undergone some evolutionary transformations that have increased the efficiency of mastication of prey. The ancestral condition of the gizzard in opisthobranchs may be a series of numerous randomly-placed plates of various sizes, as is found in the Akeridae and the remainder of the Anaspidea. Alternatively, the ancestral gizzard may have consisted of three simple plates of equal size. This configuration is found in the Bullidae, Haminoeidae and some members of the Retusidae and Philinacea. Within the Thecosomata and the Runcinidae there are four rather than three gizzard plates. This is considered to be derived from the plesiomorphic, three-plate condition, and appears to have occurred independently within the two taxa. In the Runcinidae the plates are highly ridged as in the Haminoeidae, while the thecosome gizzard plates have a high dorsal keel, which appears to be a unique innovation within that taxon.

The greatest variation in the morphology of the gizzard plates occurs in the Philinacea (Rudman, 1978; Gosliner, 1980). From a configuration of three simply-rounded plates of equal size, several parallel changes have occurred that are directly related to feeding specializations. This plesiomorphic condition is found in *Cylichna, Cylichnium, Mamillocylichna, Philine alba, P. gibba* and *P. falklandica.* Most members of this order feed on hard-shelled mollusks and Foraminifera. In order to crush the shells of their prey, many philinaceans have increased the relative size and strength of the gizzard plates. This has led to the development of elaborately ridged plates of several different forms. In several species there are pores present in the plates. In some taxa the plates have become differentiated and are no longer equal in size. This has occurred independently in *Scaphander, Acteocina* and in some species of *Philine.* In the Retusidae the gizzard plates are tuberculate.

In herbivorous taxa such as the Bullidae, Haminoeidae and Runcinidae, the gizzard plates have serrated ridges which facilitate the breakdown of algal tissue.

Stomach

As in the case of the gizzard of opisthobranchs, the stomach may become highly

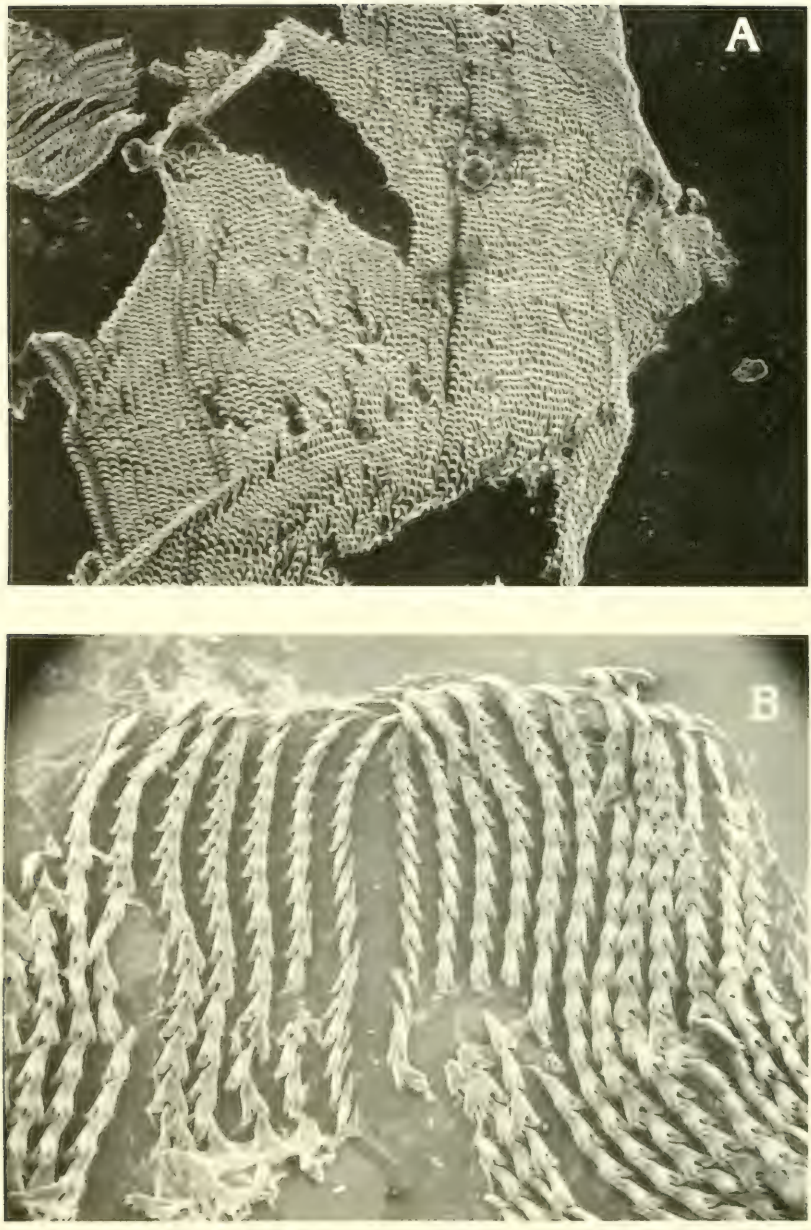

FIG. 2. Scanning electron micrographs of acteonid radulae. A: *Acteon traski* Stearns, 1897; B: *Hydatina physis* (Linnaeus, 1758).

muscularized and may contain chitinous structures. This has occurred in the Ringiculidae (Fretter, 1960) and in several genera of dendronotacean nudibranchs (Odhner, 1936). Odhner believed that the presence of cuticular plates in the stomach represented a derived condition within the Dendronotacea. However, a chitinous lining of the stomach with large conical plates is present in some members of most families of the suborder, and is therefore considered to represent the plesiomorphic state. Within the Dendronotacea, both plesiomorphic and apomorphic states are present in different families. In the

TABLE 6. Loss of lateral teeth in aeolid nudibranchs.

Taxon	Several laterals	Single pair of laterals	No laterals
Notaeolidiidae	*Notaeolidia*	—	—
Flabellinidae	*Flabellina islandica*	remainder of family	—
Eubranchidae-Tergipedidae	—	Eubranchidae	Tergipedidae

Tritoniidae and Tethyidae large chitinous plates are present in some species, but are entirely absent in others. It appears that loss of stomach plates has occurred independently in different dendronotacean lineages.

Digestive gland

Within opisthobranchs, the digestive gland may be elaborated with branches entering epidermal structures called cerata. Cerata have evolved independently in four lineages of opisthobranchs: the Sacoglossa, the aeolidacean, dendronotacean and arminacean nudibranchs. In the Janolidae the ancestral condition is present in *Bonisa,* but is apomorphic in the remainder of the genera (Gosliner, 1981b).

Streptoneury/Euthyneury

Primitively, the lateral nerve cords are twisted and cross each other, resulting in a streptoneurous arrangement of the central nervous system. As a result of detorsion, the cords become untwisted and are then considered to be euthyneurous (Gosliner, 1981a; Gosliner & Ghiselin, 1984). Euthyneury has evolved from streptoneury on numerous occasions within the opisthobranchs (Table 7). Similarly, euthyneury has evolved independently in the cypraeid and triviid prosobranchs (Gosliner & Liltved, 1985) and in the Pulmonata (Marker, 1913).

Cephalization

Independent of the changes in the configuration of the central nervous system, caused by detorsion, is the trend towards the concentration of the central nervous system and fusion of ganglia. Both concentration and fusion are parts of the process of cephalization. One of the most obvious changes that occurs is the shortening of the visceral loop. In the plesiomorphic state the visceral loop is elongate and the visceral, subintestinal, supraintestinal and genital ganglia are situated at the posterior end of the body cavity. In derived opisthobranchs there is a shortening of the visceral loop, such that all the ganglia are situated in the circumoesophageal nerve ring. Both the ancestral and derived states are present in members of at least four distinct clades (Table 8).

Several trends occur in the movement and fusion of ganglia (Fig. 3). In many taxa, one of the first transformations that takes place following development of euthyneury is the movement of the supraintestinal ganglion anteriorly until it is adjacent to the right pleural ganglion. This has occurred independently in several lineages of opisthobranchs, including the Philinidae and Haminoeidae. In *Philine,* the plesiomorphic condition is present in *P. lima, P. quadrata, P. alba, P. falklandica* and *P. gibba,* while the apomorphic state is present in *P. finmarchica, P. aperta, P. auriformis* and *P. powelli* (Rudman, 1972a; present study). In the Haminoeidae the ancestral state is present in *Atys* and *Haminoea* and the derived state is present in *Phaneropthalmus* and *Smaragdinella* (Rudman, 1972b; present study).

Similarly, the genital ganglion may be distinct or it may be fused with the visceral ganglion. Again, this change has occurred independently in several lineages. The plesiomorphic state is present in *Philine auriformis, P. angasi* and *P. aperta* but the ganglia are fused in the remainder of the species studied (Rudman, 1972a; present study). Fusion of the genital ganglion with the visceral ganglion also has occurred at least twice within the Aglajidae, where both the plesiomorphic and apomorphic states are present in members of the genera *Melanochlamys* and *Chelidonura* (Gosliner, 1980). This same fusion of ganglia has occurred in the Haminoeidae, where the plesiomorphic state is present in *Atys, Haminoea* and *Smaragdinella* and the apomorphic state is present in *Phanerophthalmus* (Rudman, 1972b; present study).

In many different clades of opisthobranchs there has been a partial or complete fusion of the cerebral and pleural ganglia (Table 9).

TABLE 7. Evolution of euthyneury in opisthobranch clades.

Taxon	Streptoneurous	Euthyneurous
Acteocina	most of genus	*A. oryza*
Scaphander	*S. punctostriatus, S. lignarius*	*S. mundus, S. nobilis*
Retusa	*R. operculata* (Minichev, 1967)	*R. obtusa, Volvulella*
Haminoeidae	*Atys, Haminoea*	*Smaragdinella, Phanerophthalmus*
Anaspidea	Akeridae	Aplysiidae
Ringiculidae	Ringicula	*Ringiculoides* (Minichev, 1967)

TABLE 8. Shortening of the visceral loop in opisthobranchs.

Taxon	Visceral loop long	Visceral loop short
Philinacea	Scaphandridae, Philinidae, Aglajidae	Gastropteridae
Bullacea	Bullidae, Haminoeidae	Runcinidae
Sacoglossa	Cylindrobullidae	remainder of order
Anaspidea	Akeridae, Aplysiinae	Dolabriferinae

This has occurred independently at least five times.

Separation of Genital ducts

Ghiselin (1966) described the functional advantage of various configurations of the hermaphroditic reproductive system of opisthobranchs and discussed the phylogeny of the subclass. He concluded that the plesiomorphic state was a monaulic system, where all exogenous and endogenous gametes are transported through a single genital duct. From this configuration oodiaulic and androdiaulic systems developed. A triaulic system represents a further modification of an androdiaulic arrangement. Rudman (1978) maintained that an oodiaulic system is plesiomorphic in the Opisthobranchia, but this has been discounted by Gosliner (1980,1981a) and Schmekel (1985).

In discussions of the phylogeny of the Philinacea, Rudman (1978) placed considerable phylogenetic weight on whether the hermaphroditic duct branches to the female glands prior to entering the genital atrium. He termed this an oodiaulic arrangement. Within the Philinacea there is considerable variation in the branching of the hermaphroditic duct (Gosliner, 1980; present study). An unbranched duct is considered to be plesiomorphic because of its functional simplicity. Presence of both the ancestral and derived states within the Philinidae and Aglajidae indicate that a branched duct has evolved from an unbranched one more than once within the Philinacea. The branched duct of the anaspideans, where oodiauly is more pronounced, appears to be yet another instance of independent acquisition of the derived condition.

An androdiaulic arrangement of reproductive organs occurs in a variety of opisthobranch taxa and it appears to have evolved independently on several occasions. Within the Ringiculidae, monaulic and androdiaulic configurations are present.

The Acteonidae, Bullinidae and Hydatinidae are exclusively androdiaulic, but differ fundamentally from all other opisthobranchs in that the non-protrusible penis is located at the opening of the mantle cavity rather than on the right anterior portion of the head. This appears to be a morphologically and evolutionarily unique form of an androdiaulic configuration within the Opisthobranchia.

In the Sacoglossa, all extant representatives are either androdiaulic or triaulic. Within the Cylindrobullidae, however, a vestigial sperm groove is present even though the tubular vas deferens is internal (Marcus & Marcus, 1970; present study). This suggests that sacoglossans evolved from a monaulic ancestor rather than one which was already androdiaulic.

Within the Notaspidea there is considerable variation in the anatomy of the reproductive system. In the Tylodinidae the reproductive system is monaulic and is the most plesiomorphic condition among extant opisthobranchs (Gosliner, 1981; Schmekel, 1985). In the Berthellinae and Pleurobranchaeidae the reproductive system is androdiaulic, while it is triaulic in the Pleurobranchinae (Marcus &

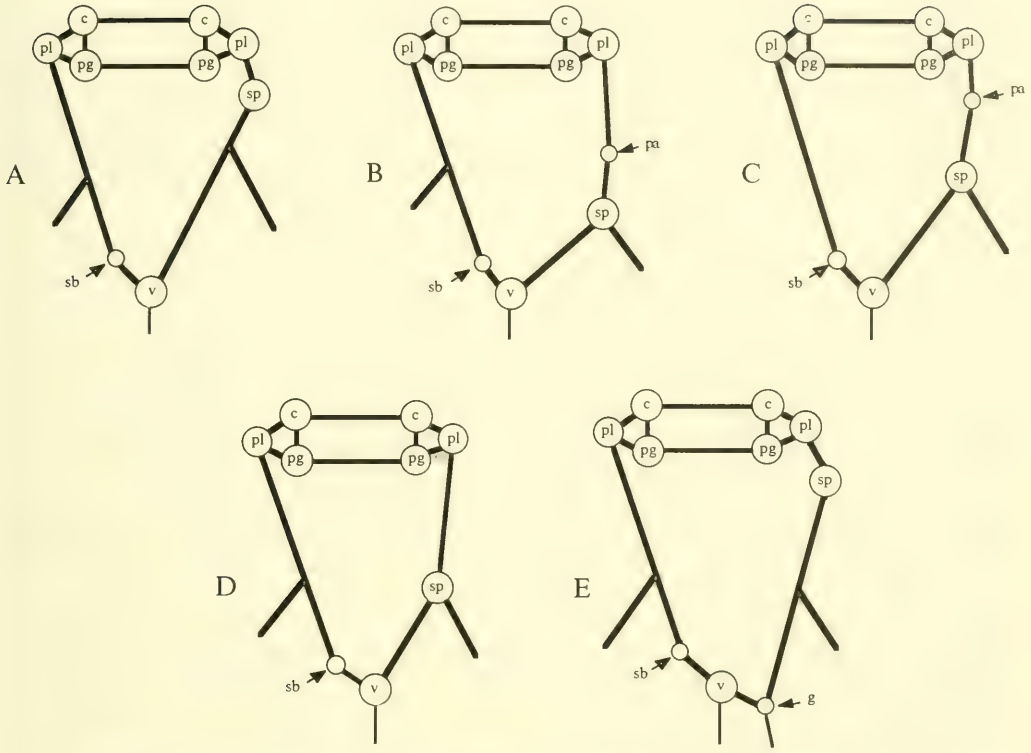

FIG. 3. Variation in the central nervous system of *Philine*. A: *P. finmarchica* Sars, 1858, *P. infundibulum* Dall, 1889; B: *P. lima* (Brown, 1825); C: *P. quadrata* (Wood, 1830); D: *P. alba* Mattox, 1958; E: *Philine sp.* c cerebral ganglia, pa parietal ganglion, pg pedal ganglia, pl pleural ganglia, sb subintestinal ganglion, sp supraintestinal ganglion, v visceral ganglion.

Gosliner, 1984). Thus it appears that the androdiaulic arrangement of reproductive organs has evolved at least four times within the Opisthobranchia.

Similarly, it appears that a triaulic arrangement has evolved from an androdiaulic configuration at least three times, since representatives of the Sacoglossa, Notaspidea and Nudibranchia possess both the ancestral and derived form.

Position of Receptaculum seminis and Bursa copulatrix

Ghiselin (1966) and Gosliner (1981) have suggested that the presence of a proximal receptaculum seminis and a distal bursa copulatrix represents the plesiomorphic state within the Opisthobranchia. In many instances one of these sperm receptacles may be absent (Table 10). The distribution of the ancestral and derived conditions within various clades of opisthobranchs suggests that the receptaculum seminis and the bursa copulatrix have been lost on numerous occasions within independent lineages of opisthobranchs.

DISCUSSION

The widespread nature of parallelism in opisthobranchs has been well documented (Ghiselin, 1966; Gosliner, 1981; Gosliner & Ghiselin, 1984), but its extent within every organ system has not been precisely established.

What has not received adequate attention is the question of how differing interpretations of which characters have undergone independent change and which are truly monophyletic may alter dramatically one's perception of phylogeny and systematics. Gosliner & Ghiselin (1984) described two historical examples

TABLE 9. Fusion of cerebral and pleural ganglia in opisthobranch clades.

Taxon	Separate	Fused
Ringiculidae	*Ringicula*	*Ringiculoides* (Minichev, 1967)
Retusidae	*Retusa obtusa*	*R. operculata* (Minichev, 1967)
Haminoeidae	remainder of family	*Phanerophthalmus*
Notaspidea	Umbraculidae	Pleurobranchidae
Janolidae	*Janolus cristatus, J. longidentatus*	*J. capensis, J. australis*

of conflicting scenarios of opisthobranch phylogeny. The placement of cerata-bearing sacoglossans and aeolid nudibranchs in the same taxon by early workers was disputed by Russell (1929) because there are significant differences in the arrangement of ganglia between sacoglossans and nudibranchs, despite the fact that they are at approximately the same level of cephalization. In sacoglossans the visceral ganglion is located on the left side of the circumoesophageal nerve ring, while it is on the right side in nudibranchs.

The second example involved Boettger's (1954) study of the phylogeny of the Euthyneura (opisthobranchs and pulmonates). By placing organisms at the same level of organization in the same clades, he produced a classification scheme that contained polyphyletic grades rather than clades.

More recently, Gosliner (1985b) addressed problems in the classification of the nudibranch family Aeolidiidae. Differences in the systematics of the family are related to divergent opinions as to whether rhinophoral structure or ceratal arrangement is monophyletic within the family. The two characters produce contradictory affinities of the genus *Berghia* to either *Spurilla* or *Baeolidia*.

Schmekel (1985) recently discussed the anatomy and phylogeny of the opisthobranch taxa. She provided much new synthetic material, particularly relating to our knowledge of the Nudibranchia and Sacoglossa. Her conclusions differ significantly from the scenarios presented by Ghiselin (1966) and Gosliner (1981a). This is a direct result of the fact that her conclusions are based on different assumptions about the monophyletic or polyphyletic evolution of various characters within the Opisthobranchia and uniting taxa based on symplesiomorphy rather than apomorphy.

The systematic placement of the Akeridae has been the subject of controversy for almost a century. Several workers (Thiele, 1931; Franc, 1968; Marcus, 1970; Thompson, 1976; Schmekel, 1985) have considered *Akera* as belonging to the Cephalaspidea, while others (Guiart, 1901; Boettger, 1954; Ghiselin, 1966; Morton, 1972; Beeman, 1977) suggested that it was better placed in the Anaspidea. Ghiselin (1966: p.369–370) stated that "the placement of the Akeratidae among the Anaspidea (Guiart, 1901) is well supported by the structure of the reproductive system, as well as by numerous other similarities, and is no longer disputed". While I believe that Ghiselin was correct in ascribing the Akeridae to the Anaspidea, he was incorrect in assuming that the controversy had been resolved. Thompson (1976: p.129) stated that "in some ways, notably in features of the alimentary canal, the spermatozoa, and the defensive glands, *Akera* exhibits aplysiomorph characters, but on balance it seems best to retain the akerids as a bullomorph family, by virtue of their possession of a large external shell, parapodia continuous with the pedal sole, a non-tentaculate spatulate cephalic shield, organs of Hancock, posterior pallial lobe and long visceral connectives". Schmekel (1985) made similar arguments in suggesting that *Akera* is not an anaspidean. Thompson and Schmekel placed *Akera* in the Cephalaspidea solely because it shares numerous symplesiomorphies with that group. None of the characters suggested by either of these workers are apomorphic. Schmekel erroneously ascribed an androdiaulic reproductive system to *Akera* and suggested that this was apomorphic with some cephalaspideans. When one examines the morphology of *Akera* and anaspideans (Guiart, 1901; Beeman, 1977; present study) there are numerous synapomorphies in common: similar defensive glands, jaws with elongate rod-like elements, a broad radula with multidentate rachidian tooth and denticulate laterals, a gizzard composed of numerous conical teeth, a central nervous system with the pleural ganglia situated closer to the pedal ganglia than to the cerebral ganglia, an oodiaulic reproductive system, a distinct genital atrial gland (reservoir seminal of Guiart), a cephalic penis armed with chitinous spines and spermatozoa

TABLE 10. Configuration of bursa copulatrix and receptaculum seminis in the Opisthobranchia.

Taxon	Bursa and receptaculum present	Receptaculum absent	Bursa absent
Acteonidae	*Pupa*	*Acteon, Rictaxis*	—
Diaphanidae	*Toledonia*	*Diaphana*	—
Facelinidae	*Hermosita*	—	*Facelina*
Flabellinidae	*Flabellina bicolor*	*F. iodinea*	*F. babai*
Tergipedidae	*Cuthona divae, C. concinna*	rest of family	—
Pleurobranchaeidae	most species	*Pleurobranchaea californica*	—
Janolus	*J. longidentatus*	*J. hyalinus*	—
Hancockia	*H. californica*	*H. uncinata*	—

with an elongate helical nucleus (Franzén, 1955; Thompson, 1973). Many of these derived features are unique to *Akera* and other anaspideans. If one subscribes to Hennig's (1966) philosophy that derived features are the only ones which can phylogenetically link taxa, and that taxa should be monophyletic rather than paraphyletic, there is no alternative but to consider the Akeridae as anaspideans.

Schmekel (1985) based most of her hypotheses about the phylogeny of the opisthobranchs on the argument that there are two basic lineages. There is one lineage derived from monaulic cephalaspideans that have remained monaulic or have developed oodiauly. Within this lineage the cerebral and pleural ganglia have remained separate. The second lineage arose from androdiaulic cephalaspideans and includes all androdiaulic and triaulic taxa. In this clade the cerebral and pleural ganglia have been fused. Implicit to this scenario of opisthobranch phylogeny are the assumptions that androdiauly and fusion of the cerebral and pleural ganglia have evolved only once within the opisthobranchs.

As described above there are difficulties with these assumptions. First of all, it appears that androdiauly has evolved at least four separate times within the opisthobranchs, within the Ringiculidae, Acteonidae, Sacoglossa and notaspidean-nudibranch clade. There are distinct morphological differences between the various androdiaulic forms. For example, the pallial penis in the Acteonacea differs markedly from the cephalic penis found in the Sacoglossa and the Ringiculidae. The fact that the diaulic Cylindrobullidae retain an external sperm groove suggests that they arose from monaulic ancestors, rather than from an androdiaulic form such as an acteonacean. Secondly, it does not appear that fusion of the cerebral and pleural ganglia is monophyletic within the Opisthobranchia (Table 9). Presence of both ancestral and derived states within such clearly monophyletic taxa as the Haminoeidae and the Janolidae demonstrates polyphyly of this character. Similarly, janolids, which may have either separate or fused cerebral and pleural ganglia, are members of the lineage which is presumed to possess only fused ganglia.

The phylogenetic hypotheses presented by Schmekel are not consistent with the traditional systematic placement of the Umbraculacea within the Notaspidea. Members of this taxon have a monaulic reproductive system and separate cerebral and pleural ganglia, while the remainder of the Notaspidea are androdiaulic or triaulic and have fused ganglia. To resolve this inconsistency Schmekel removed the Umbraculacea from the Notaspidea and placed them in their own order, the Umbraculomorpha. Schmekel stated that the characters uniting the Umbraculacea with the Notaspidea are all plesiomorphic. However, there are several features which are shared by members of these taxa which appear to be apomorphic. The gill in both taxa is pinnate and is not enclosed by a mantle cavity. The labial cuticle is chitinous and possesses polygonal elements, although these are poorly developed in most umbraculaceans. The association of the visceral ganglion with the right side of the body is characteristic of members of the notaspidean-nudibranch clade. These synapomorphies link the Umbraculacea to the remainder of the notaspideans. While considerable phenetic distance separates the Umbraculacea from the Pleurobranchacea, together with the Nudibranchia, they form a cladistically monophyletic taxon and should be united with these taxa, following Willan (1987).

Discussions of parallel evolution in opisthobranchs led one cladist colleague to suggest

that if the opisthobranchs really do possess that much parallel evolution, then it might be more prudent to work on another group of organisms! While the preponderance of parallelism in all organ systems of opisthobranchs presents problems in dealing with their phylogeny and systematics, the situation is not as hopeless as it might appear. Though most of the organ systems do exhibit polyphyly within the Opisthobranchia as a whole, one must attempt to determine at what level these changes are monophyletic and employ those synapomorphies as a basis for construction of phylogenetic hypotheses. By combining this methodology with placing greater qualitative weight to uniquely derived and divergent features, as advocated by Gosliner and Ghiselin (1984) one can successfully produce phylogenies of opisthobranchs that can be further tested. As virtually all of these parallel changes are responses to similar selection pressures it is also fruitful to ascertain the possible adaptive significance of these morphological transformation series. This is not only useful in determining the polarity of these changes, but also places the major changes in a hypothetical evolutionary perspective that is consistent with the data.

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Taxa in **bold** are new; page numbers in **bold** indicate pages on which new taxa are described; pages in *italics* indicate page numbers on which appear figured taxa.

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(Continued on inside back cover)

ERRATUM

Due to an error, Fig. 5 of the article by Roger Seapy entitled, 'The Pelagic Family Atlantidae (Gostropoda: Heteropoda) from Hawaiian waters: A faunistic survey' was not produced in color on p. 115 of Malacologia 32(1). I apologize for this error and have had the figure printed here in color.

The Editor

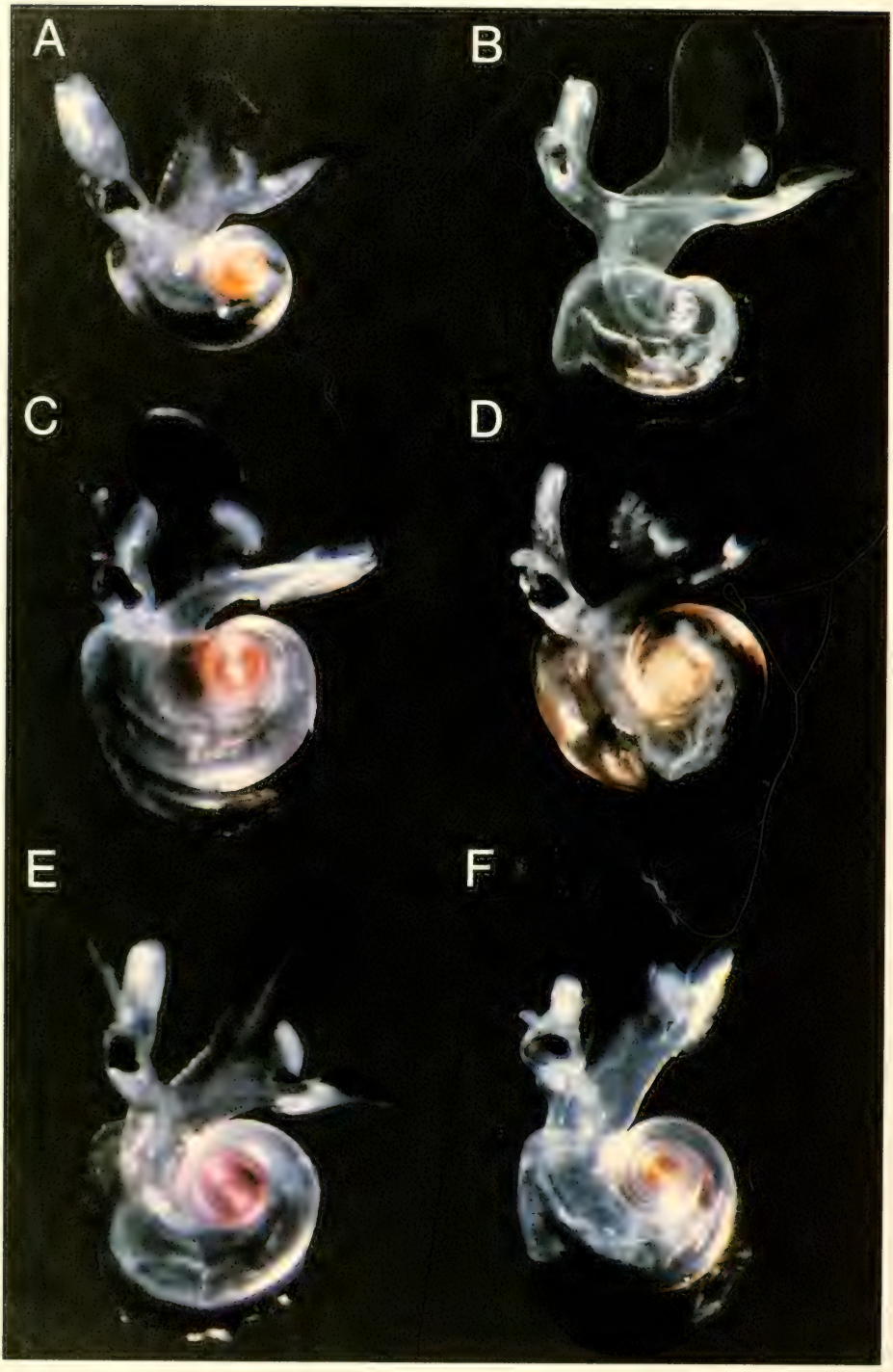

FIG. 5. Laboratory photographs of five allantids collected from southwest side of Oahu May 1987. A. *Protatlanta souleyeti* (0.8 mm) B. *Atlanta lesucuti* (1.2 mm). C. *A. torriculata* (0.9 mm). D. *tokiokai* (1.5 mm). E. *echinogyra* (1.0 mm). F. *A. intiata* (0.9 mm).

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UNITAS MALACOLOGICA
9th International Malacological Congress Symposium
EVOLUTIONARY BIOLOGY OF OPISTHOBRANCHS

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