

THE ORIGIN AND EVOLUTION OF THE NEOGASTROPODA

W. F. Ponder

*The Australian Museum
Sydney, Australia*

ABSTRACT

The order Neogastropoda probably evolved from the Archaeogastropoda or from a very primitive mesogastropod type, and not from the higher mesogastropods as is generally believed. It is suggested that the unique features of the neogastropod alimentary canal could be derived from existing structures in the archaeogastropods. The Neogastropoda appear to have evolved into 3 groups, which are regarded here as superfamilies, the Muriceae, Conaceae and Cancellariaceae.

The evolution of the various organ systems within the Neogastropoda is outlined and the tendency to modify structures in a parallel fashion is noted. The relationships of each family in the Muriceae is discussed. With 2 exceptions, it appears that within this group, there are no natural higher groupings, probably because all of the families evolved from a common ancestral form more or less simultaneously. Thus various structures are distributed in an almost random fashion throughout the superfamily according to the way in which each family has evolved. The Marginellidae and Volutomitridae may have arisen independently, whereas the Buccinidae, Melongenidae, Nassariidae and Fasciolaridae are so closely related that they could possibly be regarded as subfamilies.

INTRODUCTION

The order Neogastropoda or Stenoglossa is generally regarded as containing the most highly advanced prosobranch gastropods. They are characterized by the elongate siphonal canal of the shell and rachiglossate or toxoglossate radula. The order is a large one, having at least 1119 Recent and fossil genera and subgenera (Taylor & Sohl, 1962). This number is similar to that of the Archaeogastropoda, but is exceeded by the Mesogastropoda (as defined by Thiele, 1929 and Wenz, 1938-1943).

The large number of species and genera speaks for the success of the Neogastropoda. Although they are not known to have invaded the land, and few have penetrated into freshwater, they have adapted to almost every marine environment, commencing with an explosive radiation during the Cretaceous Period.

The order Neogastropoda is usually divided into 2 suborders, the Toxoglossa and the Rachiglossa. Thiele (1929) and Wenz (1938) divided the Rachiglossa into

3 superfamilies (Stirps), the Muriceae, Buccinaceae and Volutaceae. These divisions have been accepted by the majority of later authors. The use of these groupings is here considered open to question and they have been abandoned for the purpose of the following discussions. Instead the name Rachiglossa will be used to cover all 3 of them.

The object of this paper is to attempt to: (1) clarify the origin of the Neogastropoda and therefore its relationship to the Mesogastropoda, (2) briefly examine the various organ systems within the group, and the evolution of the group and (3) review the distinctive features of the families of the rachiglossate neogastropods and to arrange them in meaningful higher categories.

Recommendation 29A of the International Commission on Zoological Nomenclature (ICZN) in 1961 recommends the superfamily ending—oidea, but this is not used in this paper because the ending—acea has been used consistently by most molluscan workers and this en-

ding is used in the *Treatise on Invertebrate Paleontology*, a work which will be a major reference source for students of the Mollusca for a long time.

Some of the facts presented here are based on the writer's unpublished observations. They are noted by the inclusion of the writer's initials in parenthesis following such information.

The following account is divided into 3 parts; a discussion of the origins of the neogastropods, the evolution of the main organ systems and the higher classification of the order.

PART I. THE ORIGIN OF THE NEOGASTROPODA

Most authors have indicated that the neogastropods evolved from probosciferous mesogastropods, such as the Tonnacea. This belief has been expressed by workers who have looked at several different organ systems, including Amaudrut (1898), Bouvier (1887), Trochel (1865-1875), Perrier (1889), Graham (1941), and Wilsmann (1942). Morton (1963) expressed the belief that there is little difference between the higher Mesogastropoda and the Neogastropoda and this view was also held by Risbec (1955). Cox (1960) combined the Mesogastropoda and the Neogastropoda, calling them the Caenogastropoda. He suggested that the Caenogastropoda were polyphyletic, being derived from various archaeogastropod taxa, which may have even been distinct suborders, and that they have no more in common than that they have advanced to a certain stage along more-or-less parallel lines of gastropod evolution. One group, the Heterogastropoda, was later separated from the Mesogastropoda (Kosuge, 1966).

Knight, et al. (1954) have given the most detailed scheme to be advanced recently on the evolution of the Gastropoda. They indicated that the Neogastropoda were probably derived from the extinct Subulitacea in the Mesozoic, that this superfamily divided into the Muricea, Buccinea and the extinct Nerineacea,

and that the latter gave rise to the Volutacea and Conacea.

The 4 Recent superfamilies existed in the early Cretaceous, all arising more-or-less simultaneously, and all were clearly recognizable and surprisingly modern in appearance by the middle Cretaceous (Sohl, 1964).

Patterson (1969) has shown that the chromosome numbers of the Mesogastropoda and Neogastropoda are very different. The haploid number varies from 28-36 in the Neogastropoda, 7-20 in the Mesogastropoda and 9-21 in the Archaeogastropoda. There is therefore little relationship in the chromosome numbers of the neogastropods to those of the other 2 orders, although the Neogastropoda could have arisen by polyploidy from either.

The evidence given below suggests that the Neogastropoda are a group derived independently from an archaeogastropod or a very primitive mesogastropod ancestral form. They have followed certain general gastropod evolutionary trends which have resulted in their superficial similarity to other groups, such as the carnivorous mesogastropod superfamily Tonnacea. These lines of evolution include the formation of a proboscis, the reduction of the tenidia to a single, monopectinate gill, and the enlargement of the left osphradium and marked increase in its sensory surface by the formation of lateral leaflets. The enlargement of the osphradium was probably coupled with the formation of an anterior siphon. A siphon was probably present in the Subulitacea as members of this group had a well-developed anterior notch in the aperture. The osphradium functions as an efficient chemoreceptive organ in the neogastropods (Kohn, 1961b), the anterior siphon giving it directional significance.

Fig. 1 indicates how the foregut of the Neogastropoda may have evolved. The salivary glands (sg) in the early archaeogastropods (Fig. 1, A) are simple glandular sacs attached to the buccal cavity. They lie just behind the nerve ring (nr) in many archaeogastropods, and probably

the salivary ducts of the ancestral neogastropod were pulled, by the elongation of the snout, through the nerve ring at this primitive stage of development (Fig. 1, B-D) as Graham (1941) suggested.

Two pairs of histologically different salivary glands are found in the Acmaeidae (Thiem, 1917) and also in some Neritidae. In the latter family, in *Theodoxus* (Whitaker, 1951) and *Septaria* (Bourne, 1908), the 2nd pair of salivary glands are blind, glandular tubules which open into a short, ventral extension of the buccal cavity below the odontophore. In structure and position these glands resemble the accessory salivary glands (asg) in the Neogastropoda. The 2nd pair of salivary glands found in some Archaeogastropoda were probably present in the group that give rise to the Neogastropoda, although it is highly unlikely that the Neritacea or the Patellacea were this group.

The structure of the mid-oesophagus is of particular interest in the neogastropods because it is this part of the alimentary canal, together with the radula, which provides the most distinctive and reliable means of separating the group from the remainder of the Prosobranchia.

Amaudrut's (1898) and Graham's (1941) hypothesis for the derivation of the gland of Leiblein (or "unpaired foregut gland") from an oesophageal gland is in keeping with the hypothesis advanced here for an archaeogastropod origin for the Neogastropoda, although these authors believed the group to have originated from the highly evolved mesogastropod group, the Tonnacea.

The valve (or pharynx) of Leiblein (vl) (=oesophageal bulb of Hyman, 1967) is always composed of a glandular pad lying around a ciliated cone or fold (v) which acts as an oesophageal valve (Graham, 1941). Apparently the only function of the glandular pad is to bind together food particles. There is not complete agreement over the derivation of the valve of Leiblein. Graham (1941) suggested that it represents an enlargement of the oesophageal dorsal folds. Amaudrut (1898) supposed that this structure, together with

the glandular mid-oesophageal folds, is homologous with the oesophageal pouches of the mesogastropods. Graham (1941) rejected the idea because the oesophageal pouches in mesogastropods, unlike the dorsal folds, are ventral structures.

It does, however, seem possible that the valve of Leiblein is homologous with the buccal (or oesophageal) pouches (bp) of primitive archaeogastropods (Fig. 1, A) such as *Haliotis* and other Zeugobranchia, the Trochidae, and the Patellacea. These pouches, at least in *Haliotis*, are lined with tall, glandular cells which stain with acid dyes (Crofts, 1929). Just behind the buccal pouches in *Haliotis* are dorsal and ventral ciliated valves and immediately behind lies the glandular mid-oesophagus. The oesophageal gland is confluent with the mid-oesophagus over all of its length and gradually revolves from a ventral to a dorsal position (Fig. 1, A; og). The homology of the oesophageal pouches and the stenoglossan valve of Leiblein is implied by Hyman (1967) who refers to this structure in the oesophagus of all prosobranchs as the "oesophageal bulb."

The anterior oesophagus of the rachiglossan neogastropods probably represents an elongation, coupled with a ventral closure, of the roof of the buccal cavity in front of the buccal pouches. This idea is supported by the presence of dorsal folds and the absence of ventral folds in the rachiglossan anterior oesophagus. In addition, the dorsal folds generally lie laterally or ventro-laterally. In the more advanced archaeogastropods and in the mesogastropods, the anterior oesophagus appears to have been derived by elongation behind the buccal pouches and valve (Fig. 1, H, I) and, consequently, sometimes has a pair of ventral folds. Thus the anterior oesophagus in the Rachiglossa and Mesogastropoda have different origins. The buccal pouches and valves in the Rachiglossa would thus be separated from the buccal mass (Fig. 1, D) and, after being pulled through the nerve ring by the general elongation of the anterior gut, would lie in the correct morphological position for the valve of Leiblein (Fig. 1,

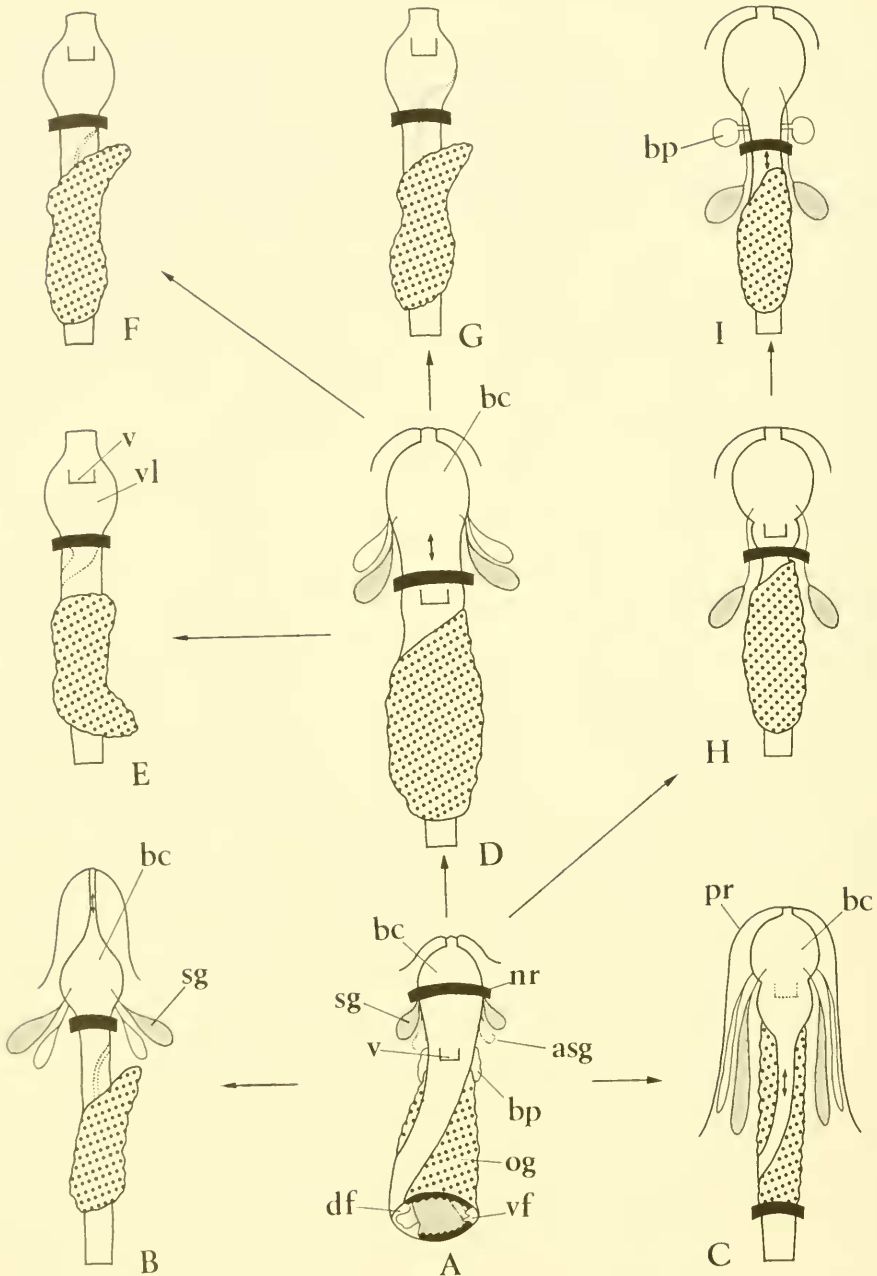


FIG. 1. Hypothetical evolution of the anterior and mid-gut of the ancestral types of the main groups of the Neogastropoda. The oesophageal gland and salivary glands are stippled and the nerve ring is shown in solid black. The dotted line in B, F, and G indicate the scar left by the removal of the oesophageal gland; in E it represents the dorsal food channel. The double-headed arrows indicate the area of elongation of the oesophagus. A, Hypothetical archaegastropod forerunner; B, conacean; C, cancellariacean; and D, muricacean ancestral types. E, Hypothetical fore-runner of marginellid-volutomitrid group. F, Families showing torsion within or behind nerve ring; G, Families showing torsion within valve of Leiblein. H, I, Mesogastropoda.

asg, accessory salivary glands; bc, buccal cavity; bp, buccal pouch; df, dorsal folds; nr, nerve ring; og, oesophageal gland; pr, proboscis; sg, salivary gland; v, oesophageal valve; vl, ventral folds; vl, valve of Leiblein.

E, F, G). The glandular parts of the buccal pouches must have spread around the oesophageal wall and thus form the glandular part of the valve of Leiblein. The oesophageal valves would be homologous with the ciliated cone overlying this pad.

The salivary ducts, which in other prosobranchs enter the buccal wall, are often embedded in the anterior oesophageal wall (usually lying beneath the dorsal folds) in rachiglossans, thus providing further evidence of the buccal derivation of the anterior oesophagus in the Rachiglossa.

The buccal pouches are variable in position in the archaeogastropods, lying alongside the buccal cavity in *Haliotis*, but behind (as in Fig. 1, A) in *Nacella* (Haller, 1894) and in some lower mesogastropods (Fig. 1, I) such as *Littorina* (Fretter & Graham, 1962). The ancestral neogastropod possibly had the glandular buccal pouches lying on either side of the anterior end of the mid-oesophageal gland because the valve of Leiblein sometimes lies at the site of torsion.

The buccal ganglia lie beneath the valve of Leiblein, perhaps indicating the valve's buccal origin. In the Cancellariidae (Graham, 1966) and in probosciferous mesogastropods, the buccal ganglia are situated just behind the buccal mass and have very long connectives, which pass through the proboscis. Graham (1966) showed that the mid-oesophagus lies in front of the nerve ring in *Cancellaria* (Fig. 1, C) and that the valve of Leiblein is just behind the buccal cavity. The mid-oesophageal gland is probably represented by a zone of glandular tissue lying below the dorsal folds of the oesophagus. Thus, in *Cancellaria*, the mid-oesophagus has been pulled through the nerve ring and the ventral valve of Leiblein (buccal pouches) has not departed from its primitive position.

In the toxoglossans the valve of Leiblein has been lost (Smith, 1967) and may never have evolved past the oesophageal pouch stage. The mid-oesophagus presumably commences immediately behind the buc-

cal cavity. This is suggested by the salivary ducts entering the buccal cavity without being attached to the oesophageal walls and by the relative position of the nerve ring. The development of a poison gland by the stripping off of the glandular, mid-oesophageal dorsal folds (Ponder, 1970a), probably took place before the separation of the Terebridae and Conidae from the Turridae.

Graham (1941) stated that *Nucella* and *Buccinum* must have evolved from different groups because they exhibit different positions of torsion in the mid-oesophagus. If this were the case then the Vexillidae (Ponder, 1972b), Marginellidae (Ponder, 1970a) and the Olividae (W.F.P.) must have evolved from a 3rd group, because in all of these families torsion occurs just behind the nerve ring (Fig. 1, F). In the Muricidae, Turbinellidae (Ponder, 1973b), Volutidae (Ponder, 1970b) and possibly the Mitridae (Ponder, 1972b) torsion of the gut occurs within the valve of Leiblein (Fig. 1, G), but in *Buccinum* there is a gradual rotation throughout the mid-oesophagus. There is a similar variability in the position of torsion in the Archaeogastropoda (Fretter & Graham, 1962). The variations in the neogastropods might have resulted from similar variations in the archaeogastropod ancestor that were in evidence before the valve of Leiblein was pulled through the nerve ring. In the Volutomitridae (Fig. 1, E) the oesophageal gland appears to have retreated from the anterior part of the mid-oesophagus and has become stripped off from behind forwards (Ponder, 1972b).

Thus it would appear that the divergence of the various rachiglossan families commenced before the main elongation of the proboscis and the associated changes in the foregut and, therefore, before the site of torsion of the gut in each group became a stabilized feature. If these suppositions are correct, similarity in the position of torsion in 2 or more groups would not necessarily indicate a close relationship, as it would probably have been evolved independently.

There are thus 3 basic patterns of organization of the foregut in the Neogastropoda. It is maintained here that each has evolved quite separately and that all were probably derived from an early neogastropod forerunner before the elongation of the snout to form a proboscis. These groupings are: (1) The rachiglossan group in which the dorsal wall of the buccal cavity provided elongation of the oesophagus during the formation of the proboscis; (2) The cancellariids in which the mid-oesophagus is the site of elongation after being pulled through the nerve ring; and (3) The toxoglossan families in which the buccal mass has remained in its primitive position immediately in front of the nerve ring, the formation of a proboscis being brought about by the elongation of a tube connecting the buccal cavity with the mouth (Fig. 1, B).

The 3 types of organization referred to above form 3 natural groups within the living Neogastropoda and will be referred to in the following discussion in parts 1 and 2 as the Conacea, Cancellariacea and Rachiglossa respectively. In part 3 it is suggested that the name Muricea be used for the whole of the Rachiglossa but this usage is avoided at this stage because of the confusion that is likely to arise between the restricted and extended interpretations of the Muricea.

The origin of the rachiglossan and toxoglossan radulae has generally been regarded as a natural progression from the taenioglossan type. However, both the taenioglossan and the stenoglossan radula could have been produced from a reduced rhipidoglossan type. A convenient ancestral stenoglossan radula would have a multienspid central tooth, a pair of large lateral teeth and a pair or more of marginal teeth in each row (Fig. 2, No. 8). Such a radula could have given rise to the stenoglossan and taenioglossan types. A similar radula with only one pair of marginal teeth is seen in some members of the Clavinae (Turridae). From this type of radula, the rachiglossan and toxoglossan types may have been derived. With the loss of the

lateral teeth and the central tooth the normal toxoglossan radula would result. Maes (1971) believes that many turrid radulae have 4 marginal teeth in each transverse row. If this is the case the primitive toxoglossan radula would have had 2 marginal teeth and may have closely resembled the taenioglossan type. The cancellariid type consists of a single row of peculiar, elongated teeth (see Olsson, 1970), which are probably homologous with the central teeth of the remainder of the Neogastropoda.

Graham (1941) advanced the hypothesis that the oesophageal gland in the Rachiglossa was stripped from the mid-oesophagus, during the elongation of the proboscis, when the valve of Leiblein was dragged forward through the nerve ring (Fig. 1, F, G). The removal of this bulky oesophageal gland left a scar, which shows its original line of attachment. The gland then opens by a narrow duct into the posterior end of the mid-oesophagus. This is a much more satisfactory arrangement in a carnivorous gastropod than the widely open connection seen in most mesogastropods and archaeogastropods. A narrow duct to the oesophageal gland has evolved independently in the Triphoridae (Fretter, 1951). Possibly the advantages of the possession of a narrow duct precipitated its evolution in the Rachiglossa, rather than the mechanical explanation offered by Graham.

The stomach of some neogastropods retains a gastric shield and recognizable style sac (Smith, 1967a), and thus resembles those of generalized archaeogastropods, such as *Monodonta* (Graham, 1949). A pronounced posterior caecum is found in many neogastropod species, which may, in some cases, be a secondary structure, although in others it is probably the remnant of a sorting caecum. Graham (1949) summarized the advances of the neogastropod stomach as including (1) the loss of the caecum and therefore the abbreviation of the major typhlosole and intestinal groove, (2) the anterior migration of the opening of the oesophagus coupled with its opening into the main gastric cavi-

ty. (3) the loss of the sorting areas, and the disappearance of the gastric shield. These simplifications, Graham concluded, are due to the carnivorous diet of the neogastropods. These features were observed by Graham (1949) in the Muricidae, but *Nassarius reticulatus* (Linnaeus) was shown to have a gastric shield, a long posterior caecum and a remnant of a posterior sorting area. Morton (1960) and Brown (1969) recorded a crystalline style in 2 species of the Nassariidae, and Ponder (1972b) noted a prominent gastric shield in the Microvolutidae. Thus some of the features of the archaeogastropod stomach are present in some groups of neogastropods, whereas in others it has become simplified, or, as in *Alcithoe arabica* (Gmelin) (Ponder, 1970b), secondarily complex.

An anal (rectal) gland, such as that occurring in many Neogastropoda has not been definitely encountered in any Mesogastropoda (Fretter & Graham, 1962, p 233). Simple types do occur in the Archaeogastropoda, in some members of the Trochidae and Scissurellidae (Fretter & Graham, 1962, p 233), where they are actually an enlargement of the intestinal groove or a pouch on the side of the end of the rectum. They apparently have a lubricating function, but it is conceivable that a gland derived in this way could take over an excretory function like that shown for the neogastropod anal gland (Fretter, 1946).

The possession of a gonopericardial canal in the male genital system of a few neogastropods is a very primitive feature and this is not shared by any mesogastropod, although some show traces of such a duct (Fretter & Graham, 1962). The development of an ingesting gland from a median sperm pouch must also have been an early development for at least 2 of the superfamilies (Muricea, Conacea; as here recognized) have this structure.

Other evolutionary trends in the neogastropods run largely parallel to those in the mesogastropods. The coiled shell causes a loss of the right auricle, right renal

organ and right pallial complex. The right renal organ remains only as an element in the organization of the genital ducts, whereas the pallial glandular parts of the genital ducts may have been derived from the right hypobranchial gland. The reduction and loss of the organs on the right side has allowed the expansion of the left ctenidium, osphradium and hypobranchial gland, and also the migration of the rectum to the right side of the pallial cavity. Associated with these changes, the rectum no longer penetrates the ventricle as it does in many archaeogastropods and both structures come to lie on opposite sides of the body. The shell has lost its nacreous layer and the operculum its spiral form.

Many of the above changes also took place in the early mesogastropods, so that it is probable that the 2 orders may have been derived from the same archaeogastropod group which was beginning to show these tendencies. Separation must, however, have been at a very early stage if this were the case.

In summary it is suggested that the neogastropods arose from an archaeogastropod, or very primitive mesogastropod, for the following reasons: 1. Neogastropods have some organs not found in mesogastropods but known in some archaeogastropods. These include 2 types of salivary glands, a rectal pouch (anal gland of neogastropods) and a gonopericardial duct in the male reproductive system. 2. The anterior alimentary canal in the mesogastropods and neogastropods differs in the following ways. (a) The salivary ducts pass through the circumoesophageal nerve ring in mesogastropods and do not in the neogastropods. (b) The valve of Leiblein seems to be derived from the oesophageal pouches of an archaeogastropod because in mesogastropods these lie ventrally and the oesophageal valve is lost. (c) The site of elongation of the oesophagus is different in the mesogastropods and in the 3 groups of neogastropods.

The Subulitacea have all of the shell features required in an ancestral neogastropod. As well as the loss of the

nacreous layer and development of an anterior notch, they have lost the primitive median sinus and many have a columellar fold. Knight, et al. (1960) suggested that this group originated in the Loxonematacea.

The adoption of a carnivorous mode of life set the ancestral neogastropods apart from their microphagous forebears. They probably commenced feeding on encrusting and other colonial animals, a habit seen in some modern archaeogastropods, and still found in some neogastropods. The Magilidae, for example, may have been at first predatory grazers on corals and have now become suctorial, whereas the primitive vexillid genus, *Austromitra*, is still found to feed on ascidians (Ponder, 1972b).

The adoption of a carnivorous habit resulted in a complex radiation, in which nearly every marine environment was penetrated. Rapid specialization followed in feeding habits, habitat preferences and morphology, so that the various family groups appear more-or-less simultaneously in the fossil record.

The rapid rise in the importance of the neogastropods is paralleled by a similar, but even more diversified, radiation in the mesogastropods (Sohl, 1964).

PART 2. EVOLUTIONARY TRENDS IN THE NEOGASTROPODA

One of the most significant factors of neogastropod evolution is the well-marked tendency towards parallel evolution of the various organ systems. Each family, equipped as it was with a fundamental neogastropod structure, has shown, despite some degree of adaptive radiation, an independent evolutionary tendency towards a similar modification of the internal organs. Their internal structure is, on the whole, rather uniform, but it is suggested that the head-foot, shell and radula underwent early adaptive modifications which, from the outset, stamped a distinctive pattern on each major group and on the separate families within them.

The Shell, Head-foot and Pallial Cavity

These 3 parts of the animal will be treated together, as they deal with the external environment and are often the first structures to be modified by it. The basic structure of the pallial cavity and head-foot is shown in Fig. 5.

The shell in most neogastropods is large, usually fusiform, rather heavy, has a long or short anterior siphonal canal, and usually the animal can withdraw into it completely.

The great variability in shell form is found within the Buccinidae and the families allied to it that are included in Thiele's Buccinacea (Fascioliariidae, Nassariidae, Galeodidae, Turbinellidae, Colubrariidae and Pyrenidae). The members of these families are capable of living on hard and soft substrata and their foot is usually of moderate proportions, but in those species found on hard substrata the foot is often small (e.g., *Buccinum* (Buccinidae) and many Fascioliariida) and they generally have a short anterior siphon. The Nassariidae live mainly on soft substrata and have a larger foot, which reaches a considerable size in *Bullia* (H. & A. Adams, 1853; Quoy & Gaimard, 1833), and a long siphon. The shell and foot are sometimes well adapted for burrowing (e.g., *Cyclope*; Morton, 1960). Versatility in ecology is the keynote to the success of these families.

The Turbinellidae and some Fascioliariidae have developed columellar plaits as a means of providing additional surface for the attachment of the columellar muscle.

The pallial cavity in all of the above families opens in front and on the right side of the animal, but it is not placed as far back on the right as in some of the other families that are modified for burrowing. An exception is seen in the Pyrenidae in which the aperture is often elongate.

Although the hypobranchial gland produces copious quantities of mucus and other pale-coloured secretions, no purple fluid is produced in any of the families listed above.

The foot usually bears an operculum, although this is lost in some Pyrenidae, possibly because of their elongate constricted apertures. The Nassariidae have 2 short tentacles on the posterior end of the foot and the operculum is usually small. The opercular nucleus in all of the above families is usually terminal in position.

In contrast with the above families, the Muricidae have solid, strongly ornamented shells which often bear varices, although parallel examples are occasionally encountered in the Buccinidae (e.g., *Phos*, *Hindsia*). The muricids generally live on hard surfaces so that the foot is usually small. *Concholepas peruviana* (Lamarck) is limpet-shaped, being the end product of a trend in the "thaid" group to enlarge the aperture and foot as an adaptation to life on wave-swept shores.

The pallial cavity in the Muricidae is unspecialized and is probably the closest to the primitive neogastropod type that exists in the modern neogastropods. A purple hypobranchial secretion is produced by most muricids and has been shown by several workers to contain a poisonous component (reviewed by Halstead, 1965).

The siphon rarely projects much beyond the end of the siphonal canal of the shell, although the canal itself, as in some species of *Murex*, is occasionally very long. The operculum is usually large and has a terminal, subterminal or lateral nucleus. On the sole of the foot there is an accessory boring organ that secretes an acid and possibly a calcase enzyme which aids in the boring of shells, a feature for which this family is well known (Fretter, 1946; Carriker, 1961, 1967; Smarsh, et al., 1969).

The Columbariidae have a small foot and a very long anterior canal projects from the small, round aperture of the shell. The shell often bears 1 or 2 rows of spines; the operculum is large and has a terminal nucleus. Little is known of their habits except that they mostly occur in deep water.

One of the most bizarre neogastropod groups is the Magilidae. This family contains genera whose shells resemble those of the Muricidae (e.g., *Coralliophila*, *Tolema*), and others in which the shells

have become limpet-shaped (e.g., *Quoyula*) or are embedded in coral and become vermiform (e.g., *Magilus*). The pallial cavity of the Magilidae is similar to that of the muricids, but the osphradium is small (Gohar & Soliman, 1963). The foot in sedentary forms functions as a sucker, aiding in boring the holes in which the animals live (Gohar & Soliman, 1963). In *Tolema*, which is presumably a free moving member of the family, the foot is similar in size to that of members of the Muricidae (W.F.P.). An operculum with a lateral nucleus is present in members of this family.

Thiele's Stirps Volutacea contains an assemblage of unrelated families, most of which are modified, to some degree, for burrowing in soft substrata. These families are the Mitridae, Vexillidae, Volutomitridae, Harpidae, Volutidae, Marginellidae and Olividae. The first 4 families are the least modified, although their shells have long, often narrow apertures, an adaptation which culminates in displacing the right angle (exhalant aperture) of the pallial cavity far towards the posterior end of the shell. This allows the pallial cavity to function efficiently while the animal is burrowing. The shells of the first 3 families are sometimes elaborately ornamented and are never covered by the mantle or parts of the foot, and the foot is of moderate size only. Some of the genera in the Mitridae and Marginellidae have become adapted to hard substrata but it seems likely that they have been derived from a burrowing ancestral form. In the other families the shell is sometimes sculptured, but rarely elaborately, and is usually smooth.

By contrast with the earlier families, most Marginellidae and a few Volutidae have the mantle edges overlapping the shell. In these 2 families the pallial cavity has swung completely to the right, the siphon lying immediately above the head and the exhalant aperture opening on the posterior edge of the long body whorl. In most Volutidae the shield-shaped head is formed from the fusion of the tentacle bases, over the rhynchostome. There is

usually a pair of siphonal lappets, which aid in blocking off the anterior end of the pallial opening.

In the Olividae the foot has reached its greatest development. Lateral and anterior flaps from the foot are developed which sometimes enclose the shell completely (e.g., *Ancilla*, *Amalda*). Pallial tentacles are sometimes developed, but it appears that the mantle never covers the shell in the Olividae. The eyes are reduced or absent in the Olividae and small in most Volutidae. The foot in the Olividae is usually divided into an anterior segment (propodium) and a large posterior portion (metapodium). Wilson (1969) has shown how the propodium is used as a swimming organ in *Ancillista cingulata* (Sowerby). D'Orbigny (1841) recorded swimming activity effected by movement of the metapodial flaps in *Oliva tehuelhana* (d'Orbigny), and Olsson (1956) and Marcus & Marcus (1959) reported the same type of swimming in *Olivella* species.

The Harpidae have a very large foot which has a distinct propodium, as in the Olividae, but the shell is not covered by the animal (Quoy & Gaimard, 1833).

The columellae of all of the families in this burrowing group of families, except the Harpidae and Olividae, usually have strong plicae, whereas the latter 2 have weak plaits. Usually the foot is large in the Volutidae, Olividae, Harpidae and Marginellidae and the operculum lost, although this is retained in some Olividae and a few Volutidae. A purple hypobranchial secretion occurs in at least some mitrids and volutes.

The enlargement of the foot, and particularly its encroachment on the shell in the Olividae, has resulted in loss of the versatility of movement seen in the Buccinidae and its allies.

The Cancellariidae have neither the foot nor the mantle cavity particularly modified. They have all lost the operculum and the shell is sculptured, ovate, and usually has columellar folds. Little is known about the habits of this family.

The conacean families have only 1 overall distinctive feature of the shell, and that

is the presence of a posterior sinus in the aperture. The shell of the Turridae is often spindle-shaped, with a long or short anterior canal. The turrids appear to match the Buccinidae in versatility of habitat but, although there are a great number of species, they are rarely individually abundant, and in particular are lacking in the intertidal zone. The Conidae, on the other hand, are often abundant as individuals and also live on both hard and soft substrata. Their shells are cone-shaped, usually smooth, and the spire is usually very short. In the sand burrowing Terebridae the shell has a long, slender spire, and it is smooth or weakly sculptured. The foot in the majority of conacean species is small, and the head in the Conidae and Turridae bears prominent eyes, which are often situated near the tips of the tentacles. The eyes and tentacles are usually reduced or lost in the Terebridae and at least some species in this family produce a purple hypobranchial secretion.

The parallel evolution of shell features has often resulted in a confused taxonomy. Several families have developed members that have a superficial resemblance to genera in other families. Some examples are the overall resemblance of the Mitridae, Vexillidae and Volutomitridae, the similarity of some Muricidae (e.g., *Uttleya*) to the Buccinidae and the resemblance of genera such as *Phyllocoma* (Muricidae) and *Colubraria* (Colubrariidae) to the Cymatiidae (Tonnaea).

The Alimentary Canal

The basic lay-out of the rachiglossan alimentary canal is shown in Fig. 5. The feeding habits of the majority of groups are not discussed here, but a detailed summary is given by Pouchon (1968).

The Proboscis: The proboscis in the Rachiglossa is always of the pleurembolic type and this form is also found in the Cancellariaacea (Graham, 1966). The proboscis is usually relatively short and broad in the small species of every family, but in the larger species noticeable differences occur. Those families which

specialize in grasping the prey with the foot (Olividae, Volutidae) and the Muricidae (which must use the pedal accessory boring organ in conjunction with the buccal mass in order to drill the shell of their prey) have a short proboscis. The Buccinidae, Nassariidae, Galeodidae and Fascioliidae usually have a long proboscis and the walls of the proboscis sac are normally capable of almost complete introversion. This also applies to *Vasum* in the Turbinellidae, but in *Turbinella* the very long, slender proboscis is coiled in a wide, thin walled sac which is not capable of introversion (Ponder, 1973b). A similar sac with an even longer proboscis is found in *Columbarium* spp. and *Coluzea* spp. in the Columbariidae (W.F.P.), whereas an intermediate type is seen in *Ratifusus reticulatus* (A. Adams) (= *mestayerae* Iredale), in the Colubrariidae (Ponder, 1968) and in some Mitridae (Ponder, 1972b). The species with a long proboscis can "feed at a distance" and are thus capable of preying on animals that live in crevices, narrow holes and tunnels. If additional length is required in a proboscis that is already packed into the cephalic cavity, the sheath must become a wide sac to accommodate the longer, and of necessity, narrower proboscis.

The 2 specialized types of proboscis in the Turridae that were described by Smith (1967) can be derived from a more basic type which also occurs within the family. In the primitive subfamilies that extend back into the Paleocene, the Turrinae, Borsoniinae and the Clavinae, and the even earlier Turriculinae (Powell, 1966) (the Conorbiinae has not been examined by the writer) there is a simple intraembolic proboscis within a wide rhynchodeum (proboscis sac). The long tube, characteristic of the Conacea, traverses the proboscis from the buccal cavity at its base. In *Splendrillia debilis* Finlay (Clavinae), *Comitas onokeana vivens* Dell (Turriculinae) and *Epidirona gabensis* (Hedley) (Turrinae) the proboscis is of moderate size compared with the rhynchodeum, but in *Borsonia* sp. and

Scrinium neozelanicum (Suter) (Borsoniinae) it is more elongate (W.F.P.). This type also occurs in the Conidae (Alpers, 1931; Shaw, 1915) and in *Terebra cancellata* (Q. & G.) (Risbec, 1953) and it presumably gave rise to the advanced type of intraembolic proboscis (Smith, 1967) by the invagination of the distal end seen in *Parabathyoma luhdorffi* (Lischke) in the Borsoniinae (W.F.P.). Many species of Mangeliinae have the advanced, intraembolic type of proboscis (Robinson, 1960; Smith, 1967; W.F.P.) and some Conidae have also developed it (Amaudrut, 1898). It is characterized by a method of proboscis retraction not found in the other 2 neogastropod superfamilies.

Another development from the primitive toxoglossan proboscis resulted in the reduction of the proboscis and an increased emphasis on the development of the mobile lips of the rhynchostome. Intermediate stages in the development of the polyembolic (Smith, 1967) type of proboscis can be seen in some turrids, in which the relatively small original proboscis fills only half of the rhynchodeum in the contracted state. A very powerful sphincter surrounds the long, narrow rhynchostomal opening which is often produced into a snout. This condition is seen in some advanced Clavatulinae (*Phenatoma rosea* (Quoy & Gaimard) and *Maoritomella albula* (Hutton) (W.F.P.)) and in *Pontiothauma* spp., in the Daphnellinae (Pace, 1903). The final stage of this development, in which the rhynchostome forms a pseudoproboscis (Rudman, 1969) which can be inverted, is generally associated with the shortening of the original proboscis. In some species however, the 2 structures, both of moderate length, coexist (*Philbertia purpurea* (Montagu) (= *boothi* Wood); Smith, 1967; and *Hastula cinerea* (Born); Marcus & Marcus, 1960). Species in which the original proboscis has become atrophied include *Philbertia leufroyi* (Michaud) (Mangeliinae); *Cenodagreutes* spp. (Smith, 1967), *Daphnella cancellata* (Hutton) (W.F.P.) (Daphnellinae), *Terebra maculata* (Linnaeus) and certain other

species of the Terebridae (Rudman, 1969). *Terebra maculata* has the pseudoproboscis greatly developed, so that it is folded into the rhynchodeum.

The pseudoproboscis or polyembolic proboscis is thus a new structure developed from the rhynchostome and is not homologous with the original neogastropod proboscis. Whereas the original proboscis was developed by the elongation of the archaegastropod snout, in the Conacea a new elongation of the "pseudosnout" has resulted in a "pseudoproboscis."

Since the above was written Miller (1971) has produced a preliminary report on his work on the feeding mechanisms of the Terebridae. He shows that there are 3 main types of feeding mechanism in this family. Type 1 has a pseudoproboscis, salivary glands and a short proboscis. There is no poison gland or radula. Type 2 are typically toxoglossan having a long proboscis, a poison gland and a radula. Type 3 has a peculiar accessory feeding organ consisting of a "long posterior glandular and muscular stalk, terminating anteriorly in a series of muscular papillae." This type does not have a radula or poison glands and many have lost the salivary glands and buccal tube as well.

Rudman (1969) has described a 4th type in *Pervicacia tristis* (Deshayes) which is similar to Miller's 1st type but differs in the possession of a radula with an odontophore.

The loss of salivary glands, poison gland and radula is sometimes associated with the development of the polyembolic type of proboscis or pseudoproboscis (*Terebra maculata* (Rudman, 1969), *Cenodagreutes* spp. (Smith, 1967)).

The Buccal Cavity and Salivary Glands: The buccal cavity, although showing a general uniformity throughout the Neogastropoda, has been modified in some families. The mouth opens directly into the buccal cavity in most families, but is surrounded by a peristomial rim in the Muricidae (Carriker, 1943) and Mitridae (Ponder, 1972b). There is a long oral tube in the Vexillidae (Ponder, 1972b), and the

Cancellariidae (Graham, 1966). No true jaws are found in the Neogastropoda, but members of the Muricidae have a median, dorsal, jaw-like sclerite (Carriker, 1943; Wu, 1965).

In the Magilidae the buccal cavity appears to extend to the base of the proboscis and the odontophore and radula have disappeared. In this family the buccal cavity is used as a pump in feeding on the coelenterate prey (Ward, 1965). A minute buccal apparatus is found in some Colubrariidae (Ponder, 1968), the Harpidae (Bergh, 1901), and *Vitularia* in the Muricidae (W.F.P.), and *Coluzea* in the Columbariidae (W.F.P.). The conacean families have a long tube leading from the buccal cavity which lies at the base of the proboscis but not at its distal end as in the Rachiglossa. In this group many species lose the muscular odontophore and, although this is retained in several primitive genera (W.F.P.), it seems unlikely that it is ever protruded from the mouth, as in rachiglossans.

The duct of the unpaired foregut gland in the Rachiglossa and its toxoglossan homologue, the poison gland, opens into the buccal cavity in the Conacea and in some Marginellidae (Graham, 1966; Ponder, 1970a). A few terebrids (Troschel, 1856-1893; Bouvier, 1887; Risbec, 1953) and turrids (Smith, 1967), have lost the radula, salivary glands and poison gland.

Many neogastropods possess 2 types of salivary gland (see Fig. 1) or buccal glands (Hyman, 1967).

One type is homologous with the "normal" salivary glands (sg) of most other gastropods. These are white, usually paired, often irregular, bodies composed of masses of minute tubules made up of cuboidal secreting cells. Their ducts usually open laterally into the buccal cavity. These glands will be referred to in the following discussion as "salivary glands."

The 2nd type of salivary gland, often termed accessory salivary gland (asg), usually consists of a pair of elongate vesicles containing the secretion produced by glandular tissue adhering to their outsides. They open by way of a very

narrow duct at the anterior end of the buccal cavity.

Nearly all neogastropods have salivary glands. These glands are usually massive in the Muricidae and Mitridae, as well as in the Buccinidae and its allied families. In these groups there are usually 2 types of cells making up the glandular epithelium (Dakin, 1912 (*Buccinum*); Fretter & Graham, 1962 (*Nassarius*); Ponder, 1972b (*Strigatella*); W.F.P. (*Taron*, *Cominella*) and Wu, 1965 (*Drupa*, *Morula*)). They are also large in the Turbinellidae (Ponder, 1973b) but their histology has not been examined. The salivary glands of the Volutidae (Ponder, 1970b), the Marginellidae (Ponder, 1970a), the Microvolutidae, the Vexillidae (Ponder, 1972b) and the Olividae (Marcus & Marcus, 1959) are composed of more-or-less discrete tubules, in which there is only 1 type of secretory cell, and the entire gland is often small.

The salivary glands of the Conacea are frequently rather small, and sometimes are reduced to a single gland with only 1 duct (which may be 2 fused ducts), as in *Conus lividus* (Brüg.) (Alpers, 1931). There is only 1 type of gland cell present and in *Conus* it is tall and vacuolate (Alpers, 1931), but in the Turridae it is like the normal neogastropod salivary cell (W.F.P.).

The cancellariids have long, narrow salivary glands that lie within the proboscis (Bouvier, 1887; Amaudrut, 1898; Graham, 1966).

The salivary ducts often lie beneath the dorsal folds in the oesophageal wall, but are free in some Buccinidae, Nassariidae, Mitridae and Olividae and in the Conacea and Cancellariacea. They usually open into the posterior end of the buccal cavity above the opening to the radular sac, but in the Pyrenidae (Marcus & Marcus, 1962a) and Conacea (Smith, 1967) they open into this sac. In the Pyrenidae the salivary ducts sometimes form a small vesicle just before they open. In the Volutomitridae and Vexillidae (Ponder, 1972b) the ducts migrate ventrally to open on the buccal floor and in the Mitridae (Ponder, 1972b) they are pro-

jected in front of the mouth by an epiproboscis. In *Olivella* (Marcus & Marcus, 1959) the salivary ducts open at the anterior end of the buccal cavity and in *Coralliophila abbreviata* (Lamarck) they unite dorsally before entering the buccal cavity (Ward, 1965).

The accessory salivary glands consist of a vesicle lined with columnar epithelium in the Muricidae (Bouvier, 1888; Fretter & Graham, 1962; Wu, 1965) and squamous epithelium in the Olividae (Küttler, 1913) and the Volutidae (Ponder, 1970b). This epithelium is surrounded by a layer of circular and some longitudinal muscles, and these are penetrated by the ducts of gland cells lying outside the muscles. The glandular layer consists of 1 or more layers of irregular, subepithelial cells and the secretion fills the vesicle of the gland.

Paired accessory salivary glands have been recorded in the above families and in the Vexillidae (Risbec, 1928; Ponder, 1972b) and the Cancellariidae (Amaudrut, 1898; Graham, 1966), but are not found in the Mitridae (Risbec, 1928; Ponder, 1972b), Harpidae (Bergh, 1901), Terebridae (Risbec, 1953; Marcus & Marcus, 1960) and most Turridae (Smith, 1967; W. F. P.), although the writer has located them in 2 species of the Borsoniinae. None of the families that are generally regarded as related to the Buccinidae possess them (Dakin, 1912; Thiele, 1929), including the Pyrenidae (Risbec, 1954; Marcus & Marcus, 1962a), Galeodidae (Pierce, 1950; W.F.P.), Nassariidae (Bouvier, 1888; Risbec, 1952; Graham, 1941), Fasciolaridae (Marcus & Marcus, 1962) and the Colubrariidae (Ponder, 1968). The Columbariidae (W.F.P.), Turbinellidae (Moses, 1923; Ponder, 1973b) and the Magilidae (Bouvier, 1888; Ward, 1965; W.F.P.) also lack them, whereas in the Volutomitridae (Ponder, 1972b) and the Marginellidae (Ponder, 1970a) a single gland is present, though it is sometimes absent in the latter family.

The function of the accessory salivary glands is still obscure. Bouvier (1888) found it in all of the Muricidae that he

examined, it being very minute in *Murex trunculus* (Linnaeus), larger but embedded in the normal salivary glands in *Trophon philippianus* Dunker and very large in *Ocenebra erinaceus* (Linnaeus) and *Nucella lapillus* (Linnaeus). The ability to bore into shells is best developed in *Nucella* and *Ocenebra* and so, in this family, its size may be correlated with the animal's feeding habits. Wu (1973) has shown that at least 2 muricids lack these glands. However none of the other families that possess it have so far been shown to have the ability to bore into shells, but the structure of the gland is nearly identical in all, except for the difference in the internal epithelium in the Muricidae mentioned above.

Several workers have tested the secretion of the accessory salivary gland and have failed to find anything significant. The salivary glands of some Muricidae contain proteolytic enzymes (Mansour-Bek, 1934) and a toxic secretion has been recorded in some Buccinidae (Welsh, 1956; Fänge, 1960).

The Radula: There is an overall tendency toward reduction of the number of radular teeth and their cusps in most of the families of the Neogastropoda, as also occurs in the Opisthobranchia. Examples indicating this trend are shown in Fig. 2. The inner circle shows a hypothetical ancestral type of radula. The next zone (A) includes examples of multicuspate radulae, showing the maximum number of teeth present in each family. The maximum number found in all the Rachioglossa is 3 teeth in each row, but some of the Clavinae (Turridae) in the Conacea have 5 teeth in each row (No. 20). Some families are not represented in this zone (A), but this does not necessarily indicate that the radular teeth in families such as the Muricidae are any more specialized than those included in the inner zone. The diagram indicates trends and is not necessarily of phylogenetic significance.

Zone B includes those radular teeth that show some simplification or modification from a more basic pattern. Some are

assumed to be secondarily multicuspid such as *Olivella* (No. 16), and *Vexilla* (No. 32). The Olivellinae (Olividae) (No. 16) and the Nassariidae (Nos. 43, 45) often develop accessory plates between the central and lateral teeth. These are probably independently evolved, new structures because they occur in all stages of development in both groups.

The variation in radular pattern in the Buccinidae, and the general similarity in the teeth of all of the families included in Thiele's Buccinacea, should be noted.

The radular teeth shown in zone C are those in which the number of teeth has become reduced. In the Mitridae, Volutidae, Marginellidae, Volutomitridae and Cancellariidae the lateral teeth have been lost, but in the Buccinidae, Pyrenidae and the toxoglossan families the central tooth has disappeared. The lateral teeth in some Harpidae (Peile, 1939) and Volutidae (Pace, 1902) are vestigial, whereas in the Pyrenidae the large lateral teeth may function as tweezers (Marcus & Marcus, 1962a).

The marginal teeth of advanced toxoglossan genera (Nos. 25-27) are hollow and capable of being charged with poison. They are used as harpoons in the capture of active prey (Kohn, 1959; Pearce, 1966) which is then swallowed whole. Some Conacea have more primitive radulae that probably function in tearing the prey (Nos. 21, 28), while the "prototypic" type in the Clavinae (No. 20) is probably capable of combining a food tearing and a spearing function. There are undoubtedly other methods of employing the varied types of radula (Nos. 22, 23) within the Turridae. The Cancellariidae have a single row of elongated, blade-like teeth (Barnard, 1958; Graham, 1966), each an aggregate of "rectangular tubes which form a canal system which transverse the whole length of the radular filaments" (Olsson, 1970).

Several families have lost the radula altogether, these being indicated in the outermost zone (D). Only the Magilidae have no known members with a radula. Some of these "aglossate" forms are probably suctorial feeders (Magilidae,

Marginellidae), whereas others (Terebridae, Turridae) probably engulf their prey whole. It is not known how the Cancellariidae feed, although Olsson (1970) suggests that they may feed on micro-organisms, these being transported down the minute tubes that make up each tooth.

The Mid-oesophagus and Gland of Leiblein: The evolution of the mid-oesophagus (mo) in the Rachiglossa follows 2 main trends, which run parallel in several families. These are (1) the stripping off of the gland of Leiblein and oesophageal dorsal folds from the oesophagus to form a "poison gland" and (2) the loss of the original, glandular oesophageal dorsal folds. Both of these trends have ultimately resulted in genera that have lost all of the glandular structures associated with the mid-oesophagus.

The oesophageal gland attached by a narrow duct is usually referred to as the "gland of Leiblein." Hyman (1967) uses the name "unpaired foregut gland." In order that the following discussion be clarified the use of these terms will be strictly defined. The *unpaired foregut gland* can be used for the unpaired gland which enters the oesophagus by way of a narrow duct. This can include the poison gland of the conaceans, as I have recently shown (Ponder, 1970a) that it is probably homologous to the unpaired foregut gland of the rachiglossans. The *gland of Leiblein* can be used for that part of the unpaired foregut gland that was derived from the oesophageal gland. In some species the unpaired foregut gland consists solely of the gland of Leiblein but in others it involves other parts of the oesophagus, as is shown below.

Fig. 3 shows the evolution of the rachiglossan mid-oesophagus. A and B show a generalized type of mid-oesophagus (although not necessarily the most primitive) which is encountered in several families as the least specialized type. The unpaired foregut gland consists only of the small gland of Leiblein (gl). The mid-oesophagus (mo) is moderately

long (A), or short (B) and has glandular dorsal folds and a prominent valve of Leiblein (vl).

The type shown in diagram A occurs in the Volutidae (*Volutocorbis abyssicola* (Adams & Reeve); Woodward, 1900) and the Vexillidae (*Austromitra rubiginosa* (Hutton); Ponder, 1972b), but in some Olividae (*Oliva sayana* Ravenel and *Olivancillaria (Lintrricula) auricularia* (Lamarck); Marcus & Marcus, 1959) the mid-oesophagus is shorter, as in diagram B.

The unpaired foregut gland increases in bulk in the Muricidae (diagram C) but still usually only consists of the gland of Leiblein. The mid-oesophagus is sometimes short but still contains the glandular dorsal folds (Graham, 1941; Wu, 1965). The "Trophoninae," probably the most primitive of the muricid groupings, has the smallest gland of Leiblein. In the Columbariidae (W.F.P.) and the Magilidae (Ward, 1965; W.F.P.) the dorsal folds are not glandular, but the valve of Leiblein is large (diagram D).

In the families Buccinidae (Dakin, 1912; Graham, 1941), Nassariidae (Graham, 1941; Risbec, 1952), Fasciolaridae (Marcus & Marcus, 1962), Pyrenidae (Risbec, 1954; Marcus & Marcus, 1962a) and Turbinellidae (Ponder, 1973b), the dorsal folds are lost or have become inconspicuous, the valve of Leiblein is sometimes reduced in size, and the unpaired foregut gland (entirely gland of Leiblein) remains small and sometimes becomes very thin walled and saccular (diagram E). *Busycon canaliculatum* (Linnaeus) (Pierce, 1950) and *B. contrarium* Conrad (W.F.P.) in the Galeodidae are organized like the Buccinidae, but some members of the Galeodidae (*Melongena melongena* (Linnaeus) Vanstone, 1894; *M. corona* (Gmelin; W.F.P.) have lost the gland of Leiblein (diagram F). In *Melongena* the valve of Leiblein is much reduced and a caecum-like expansion lies just behind the nerve ring which may be homologous with a similar, short caecum found in the anterior part of the posterior oesophagus in *Buccinum undatum* and

FIG. 2 The evolutionary trends in the neogastropod radula. Levels A to D are explained in the text.

- Mitridae (1) *Cancilla (Domipora)* sp. (Cooke, 1920); (2) *Scabricola desetangsi* (Kiener) (= *variegata* Reeve) (Cooke, 1920); (3) *Pterygia crenulata* (Gmelin) (Thiele, 1929).
- Volutidae (4) *Volutocorbis abyssicola* (Ad. & Rve.) (Thiele, 1929); (5) *Voluta musica* Linnaeus; (6) *Scaphella junonia* Shaw (Clench & Turner, 1964); (7) *Alcithoe arabica* (Gmelin) (original).
- (8) Hypothetical ancestral radula.
- Marginellidae (9) *Diluculum inopinatum* Barnard (Barnard, 1962); (10) *Persicula persicula* (Linnaeus) (Thiele, 1929); (11) *Volcarina (Haluginella) philippinarum* (Redfield) (Troschel, 1868).
- Volutomitridae (12) *Paradmete typica* Strebel (Thiele, 1929); (13) *Microvoluta australis* Angus (Peile, 1922).
- Olividae (14) *Pseudoliva crassa* (Gmelin) (Thiele, 1929); (15) *Liva sayana* Ravenel; (16) *Olivella terrecauxii* (Duclos) (Marcus & Marcus, 1959).
- Harpidae (17) *Harpa amouretta* (Röding) (Peile, 1939).
- Vexillidae (18) *Vexillum* sp.; (19) *Pusia* sp. (original).
- Turridae (20) *Drillia umbilicata* (Gray) (Thiele, 1929); (21) *Hornospira maculosa* (Sowerby) (Powell, 1942); (22) *Aforia goodlei persimilis* (Dall); (23) *Polystira picta* (Reeve); (24) *Inquisitor cf. crenularis* (Lamarck) (Powell, 1966); (25) *Phenatoma rosea* (Quoy & Gaimard) (Thiele, 1929).
- Conidae (26) *Conus (Asprella) mucronatus* Reeve (Thiele, 1929 (after Bergh)).
- Terebridae (27) *Hastula (Impages) coeruleascens* (Lamarck) (Troschel, 1866); (28) *Diplomeriza duplicata* (Linnaeus) (Troschel, 1866).
- Cancellariidae (29) *Cancellaria* sp. (original).
- Columbariidae (30) *Columbarium pagodum* (Lesson) (Habe, 1943).
- Muricidae (31) *Beleva hanleyi* (Angas); (32) *Vexilla taeniata* (Powis) (Thiele, 1929).
- Turbinellidae (33) *Turbinella ovoideus* (Kiener); (34) *Vasum ceramicum* (Linnaeus) (Thiele, 1929).
- Columbellidae (35) *Pseudanachis duclousiana* (Sowerby) (Thiele, 1929); (36) *Pyrene (Strombina) gibberula* (Sowerby) (Troschel, 1869, after Moerch); (37) *Paxula paxillus* (Murdoch) (original).
- Buccinidae (38) *Proneptunea duplicarinata* Powell (Powell, 1951); (39) *Liomesus dalei* (Sowerby) (Thiele, 1929); (40) *Mohnia mohni* Friele (Thiele, 1929 after Kobelt); (41) *Buccinum undatum* Linnaeus (Troschel, 1868); (42) *Metuthria martensi* (Strebel) (Thiele, 1929).
- Nassariidae (43) *Cyclope neritva* (Linnaeus) (Troschel, 1868); (44) *Ilyanassa obsoleta* (Stimpson) (Troschel, 1869); (45) *Cyllene lyrata* (Lamarck) (Thiele, 1929).
- Fasciolariidae (46) *Peristernia australiensis* (Reeve) (Thiele, 1929); (47) *Granulifusus niponicus* (Smith) (Habe, 1945).
- Melongenidae (48) *Semifusus (Pugilina) morio* (Linnaeus) (Thiele, 1929).
- Colubrariidae (49) *Iradalula striata* (Hutton) (Ponder, 1968).

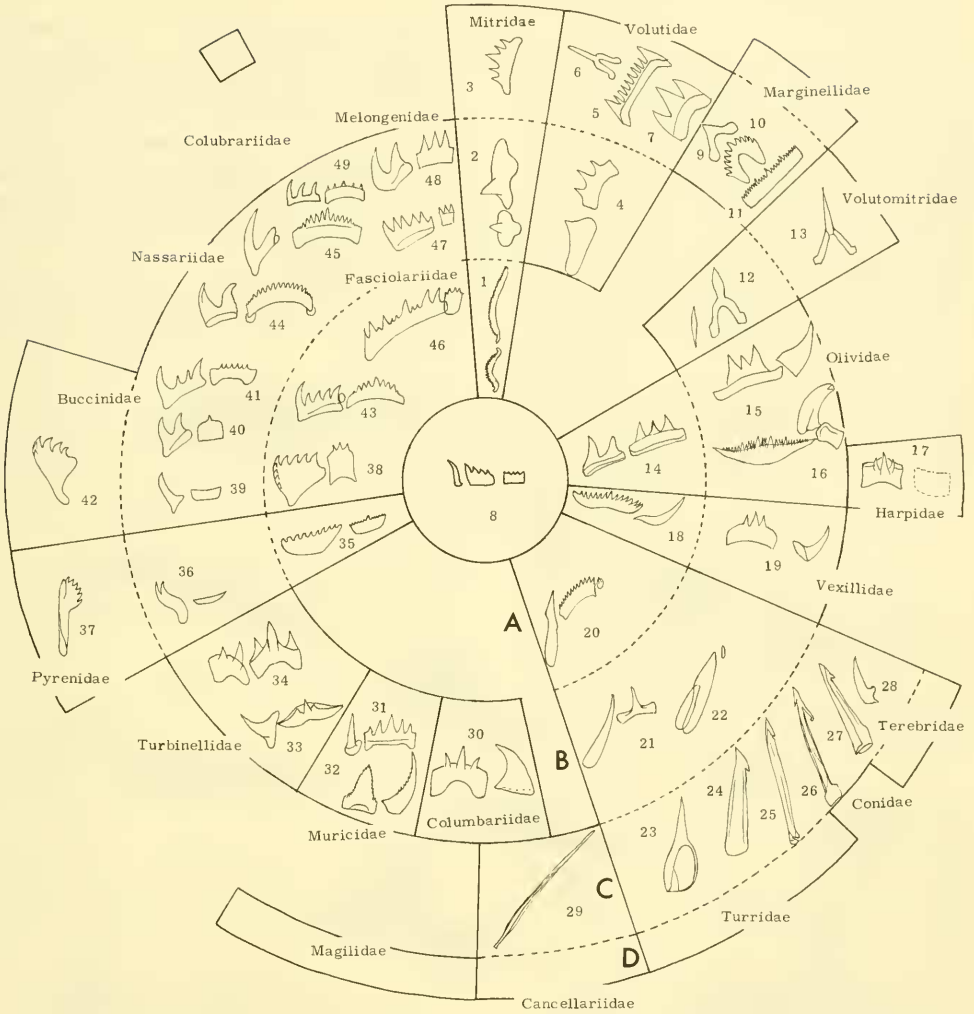
Neptunea antiqua (Linnaeus) (Fretter & Graham, 1962).

The Mitridae (Risbec, 1928; Ponder, 1972b) have no unpaired foregut gland and the valve of Leiblein and dorsal folds are inconspicuous.

In *Harpa* (Bergh, 1901; W.F.P.) the mid-oesophagus has lost all trace of the valve and unpaired foregut gland and of the dorsal folds (diagram P). The mid-oesophagus of the Colubrariidae (Ponder, 1968) has become secondarily elongate and glandular after the loss of the unpaired foregut gland (diagram G).

The mid-oesophagus is very long in the muricid *Poirieria zelandica* (Quoy & Gaimard) (W.F.P.) and the glandular dorsal folds are conspicuous (diagram H). In *Murex tenuispina* Lamarck (= *M. pecten* Lightfoot) (Haller, 1858) and in *Vexillum* spp. (Ponder, 1972b) the dorsal folds have

been partially stripped from the mid-oesophagus (diagram I) by the fusion of their apices. This process has proceeded still further (diagram J) in *Xyruene ambiguus* (Philippi), *Paratrophon quoyi quoyi* (Gray) (Muricidae), *Amalda (Baryspira) australis* (Sowerby) (Olividae) (W.F.P.) and in most Volutidae (Clench & Turner, 1964; Ponder, 1970b). In these species the dorsal folds have been stripped from the mid-oesophagus up to the edge of the nerve ring. The resultant glandular tube lies, as a more-or-less convolute mass, anterior to the gland of Leiblein (*sensu stricto*). The whole structure (the unpaired foregut gland) is usually referred to as the gland of Leiblein, but in fact, the part derived from the dorsal folds (the tubular part) is the main secretory area. The gland of Leiblein itself (the terminal bulbous part) is merely a muscular appendage with



a rather thin epithelium which appears to have hardly any functional significance.

The Volutomitridae (diagram K) appear to have derived the gland of Leiblein from the oesophageal gland in a different fashion from other Rachiglossa (Ponder, 1972b). It appears to have been stripped from the oesophagus forwards, rather than backwards. This family has several features in common with the Marginellidae, and if it is possible that they both had a common origin, the gland of Leiblein in the Marginellidae may have arisen in the same way as in the Volutomitridae. There is, however, no direct evidence to support this assumption

(Ponder, 1970a). In the most primitive marginellid examined (*Diluculum* sp.), the small gland of Leiblein has been stripped from the mid-oesophagus (diagram L), to which it is attached by only a narrow duct (Ponder, 1970a). The following stages in the evolution of the marginellid unpaired foregut gland have been described in detail elsewhere (Ponder, 1970a). Briefly it includes the formation of a pre-torsional tube that bypasses the valve of Leiblein (diagram L) and, following this, the complete stripping off of the dorsal folds along the remainder of the mid (diagrams M, N) and anterior oesophagus (diagram O). Thus a separate tube is formed which

opens directly into the buccal cavity (diagram O).

The formation of a poison gland in the Conacea probably occurred in a similar fashion to that in the marginellids. In the Conacea, however, there is either a very short anterior oesophagus or this is absent altogether, so that the process would be simplified. Evidence in support of the poison gland having formed in this way is provided by the lack of any reports of oesophageal dorsal folds in the Conacea. A

detailed account of the structure of the poison gland of *Conus mediterraneus* (Brüg.) was given by Martoja (1960). The nature of the mid-oesophagus in the cancellariids is described above.

Graham (1941) suggested that because of the different position of the scar indicating the path of torsion in *Buccinum* and *Nucella*, the Muricacea and Buccinacea must have had different origins. The scar in *Buccinum* shows torsion occurring in that part of the oesophagus

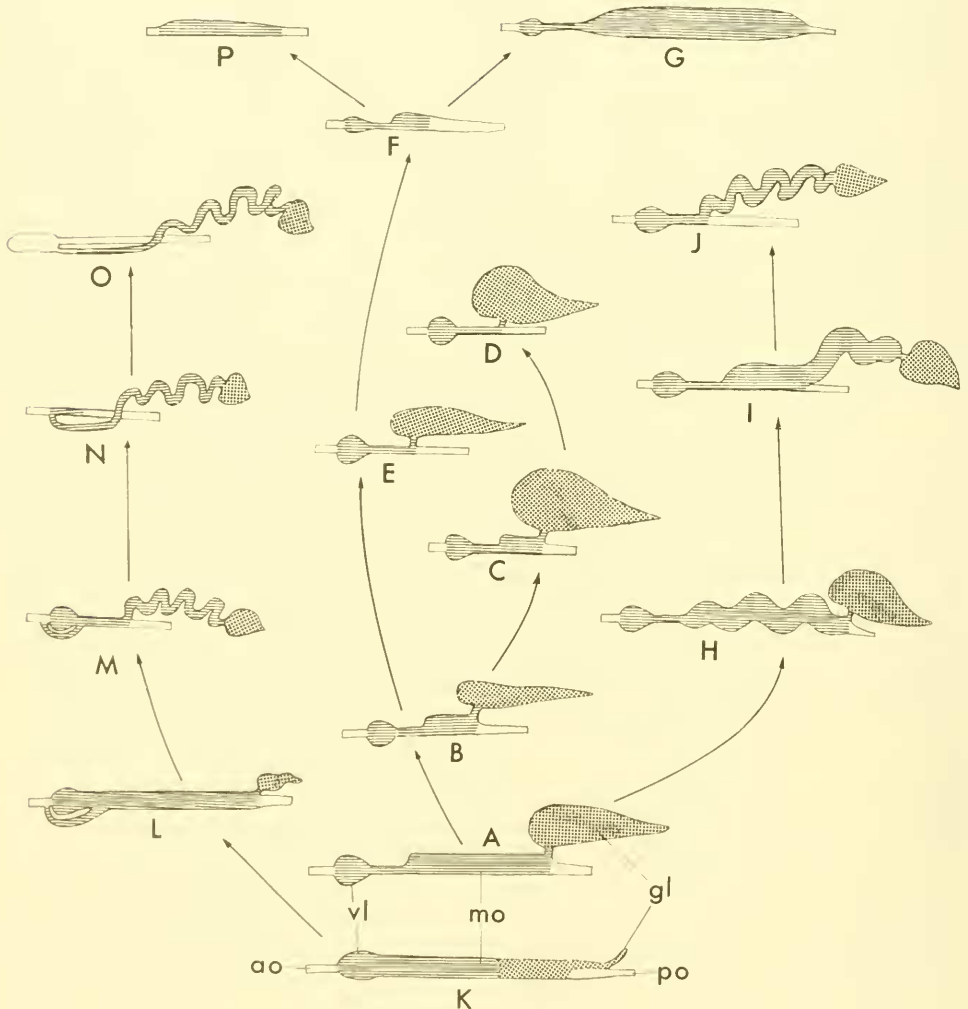


FIG. 3 The evolutionary trends in the mid-oesophagus of the Muricacea. The gland of Leiblein is shown stippled and the mid-oesophagus and the valve of Leiblein are hatched. The valve of Leiblein and the glandular parts of the mid-oesophagus are indicated as broader portions of the mid-oesophagus. For explanation, see text.

which passes through the nerve ring, and Marcus & Marcus (1962) have shown a similar type in the Fasciolariidae. Most Buccinidae, Pyrenidae (Marcus & Marcus, 1962a), Olividae (Marcus & Marcus, 1959) and Nassariidae (Graham, 1941) do not show the path of torsion. The same is true for the Mitridae (Ponder, 1972b), although there is some indirect evidence that it occurs at the site of the valve of Leiblein, as it does in the Muricidae (Graham, 1941), Volutidae (Ponder, 1970b) and Turbinellidae (Ponder, 1973b). A 3rd type which probably represents a modification of that seen in the Buccinidae, shows torsion occurring just behind the nerve ring. This is seen in the Marginellidae (Ponder, 1970a), Vexillidae (Ponder, 1972b) and in the Olividae (*Amalda (Baryspira) australis*, W.F.P.). The Volutomitridae have had the anterior part of the mid-oesophagus pulled through the nerve ring so that the position of torsion now lies a little behind the valve of Leiblein, whereas, originally it probably lay just behind the nerve ring (Ponder, 1972b).

The secretion of proteases by the unpaired foregut gland has been investigated in *Murex* (Mansour-Bek, 1934; Hirsch, 1915), *Buccinum* (Brock, 1936) and *Babylonia* (Yamaguchi, et al., 1961). Studies by Kohn, et al. (1960) and Whyte & Edean (1962) have been made on the chemical and pharmacological properties of the venom of *Conus* and a summary of this work, together with some new information, is provided by Halstead (1965).

The pyriform valve of Leiblein is a characteristic feature of the Rachiglossa. A reduction in its size is often associated with a small unpaired foregut gland (as in *Buccinum*) and when this gland is absent the valve is either very small or completely missing (*Melongena*, W.F.P.; *Harpa*, Bergh, 1901; Mitridae, Ponder, 1972b). Alternatively if the oesophagus is bypassed by the unpaired foregut gland, as in the Conacea and in some Marginellidae, the valve of Leiblein is lost (Smith, 1967; Graham, 1966; Ponder, 1970a). Thus the main function of the valve is probably to retain the enzymatic secretion from the

unpaired foregut gland and from the glandular dorsal folds within the mid and posterior oesophagus.

The Stomach: Graham (1949) outlined the features of the neogastropod stomach, which he based on a study of *Nassarius reticulatus* (Linnaeus), *Nucella lapillus* (Linnaeus) and *Ocenebra erinacea* (Linnaeus). Smith (1967a) suggested that 2 evolutionary trends were represented in the stomachs of the neogastropods that he investigated. He found that in the buccinids and the turrids the stomach independently takes on a U-shape. The neogastropod stomach has, in fact, evolved in several different ways. The anterior migration of the oesophagus has occurred in all groups, resulting in a basically U-shaped stomach.

Many neogastropod stomachs (see Fig. 5) have primitive features not found in higher mesogastropods. This is especially noticeable in the Nassariidae (Graham, 1949; Smith, 1967a) and the Pyrenidae (Marcus & Marcus, 1962a), both of these families having species which still retain the gastric shield, style sac and vestiges of a sorting area.

The tendency to form a spacious posterior caecum (c) occurs in several groups, all of which have a distinct style sac area (ss) with recognizable typhlosoles. These include *Neptunea antiqua* (Smith, 1967a) and *Buccinum undatum* (Brock, 1936) in the Buccinidae, and the Nassariidae (Graham, 1949; Morton, 1960; Smith, 1967a), it being especially pronounced in *Nassarius (Alectrion) aoteanus* Finlay (W.F.P.). Morton (1960) has shown that a crystalline style occurs in *Cyclope neritea* (Linnaeus), whereas Jenner (1956) and Brown (1969) have reported one in *Nassarius (Ilyanassa) obsoletus* (Say). *Olixa sayana* Ravenel has a caecum, but in *Olivella verreauxii* (Duclos) this has been transformed into a cuticle lined gizzard (Marcus & Marcus, 1959). A gizzard is also found in the Mitridae (Ponder, 1972b) but in this family it is formed in the oesophageal region of the stomach, there being no caecum. The Vexillidae (Ponder, 1972b) have a broad

caecum, and so does *Peculator hedleyi* (Murdoch) in the Volutomitridae (Ponder, 1972b).

In the above examples having a caecum, the digestive gland apertures open near the entrance of the oesophagus. *Cominella* spp., *Buccinulum* spp., *Austrofusus glans* (Röding) (W.F.P.), and *Penion adustus* (Philippi) (Ponder, 1973a) in the Buccinidae and *Microvoluta biconica* (Murdoch & Suter) in the Volutomitridae (Ponder, 1972b) do not have a caecum. A prominent gastric shield is present in some Nassariidae, some Pyrenidae, and in the Volutomitridae, but certain other families have examples which show remnants of this structure.

A general tendency for the gastric

lumen (i.e., the stomach cavity excluding the style sac) to elongate is seen in *Cominella* (W.F.P.) and *Colus gracilis* (da Costa) (Smith, 1967a) in the Buccinidae and *Taron dubius* (W.F.P.) and *Leucozonia nassa* (Gmelin) (Marcus & Marcus, 1962) in the Fascioliariidae. In these examples the 2 digestive gland apertures have become widely separated and lie at each end of the gastric lumen. This tendency is increased in *Penion* (Ponder, 1973a) and *Buccinulum* (Buccinidae) (W.F.P.) in which the gastric lumen occupies most of the stomach and is, itself, U-shaped.

In the Buccinidae the oesophagus opens into the stomach behind the intestine, but in the Colubrariidae (Ponder, 1968) it

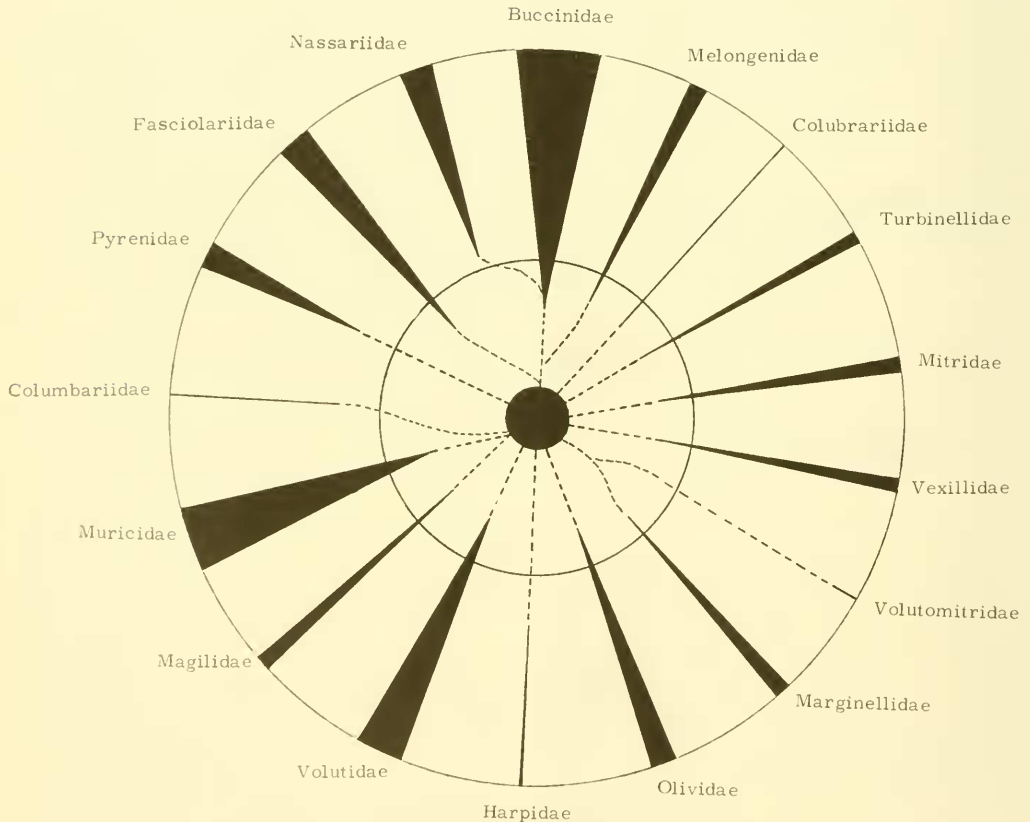


FIG. 4. The evolution of the families of the Muricea. The inner, solid circle represents the lower Mesozoic, ancestral neogastropod group. The middle circle indicates the boundary of the Mesozoic and Tertiary Periods. The relative size of each family at the edge of the outer circle is approximately proportional to the total number of Recent and fossil genera within each group. No attempt has been made to show the proportions of the genera throughout the Tertiary Period.

opens at the anterior end of the very elongate stomach, which has the intestine opening posteriorly and the style sac is lost altogether.

Narrow, superficially U-shaped stomachs have been evolved in the Turridae (Smith, 1967a) and the Terebridae (Marcus & Marcus, 1960), but in these families the wide oesophagus occupies most of the left side of the U, whereas the right side is derived from the style sac. In the Turbinellidae (Ponder, 1973b) the style sac area occupies nearly all of the U.

The muricid stomach has evolved a bag-like, posterior swelling which is, in reality, a wide, short caecum (Graham, 1949; Righi, 1964; Wu, 1965; Smith, 1967a). The marginellid stomach (Ponder, 1970a) has incorporated the digestive gland duct as part of the fundus of the stomach in some species at least, and, as in *Alcithoe arabica* (Gmelin) in the Volutidae (Ponder, 1970b) the style sac, although recognizable, has lost its typhlosoles. The posterior part of the stomach of *Alcithoe*, which is homologous with the gastric lumen in other neogastropods, contains complexly ciliated, leaf-like structures.

The overall trend in the neogastropod stomach is toward a large, relatively simple sac with the walls closely opposed. This allows the available ciliary currents to act to the best advantage in moving waste material, or in keeping food particles in suspension so that they mix with the enzymatic secretion from the digestive gland. Achievement of these conditions is obtained by the elongation of either the style sac or mixing area, or by the formation of a caecum.

The formation of a crop in the posterior oesophagus of many neogastropods serves to store food and, in many cases, it is a site of preliminary digestion. Thus the food can often be broken down before reaching the stomach.

The Anal Gland: An anal (or rectal) gland is found in many neogastropod families. It is possessed by species in all 3 superfamilies and has a similar structure in at least 2 of them (its histology has not

been described in the Cancellariidae). It usually consists of 1 or more branching tubules, that, in the Muricidae (Fretter, 1946), some Magilidae (W.F.P.) and Volutidae (Ponder, 1970b) form a large black mass. Fretter (1946) stated that the gland in *Nucella lapillus* (Linnaeus) has an excretory function, but this has not been demonstrated in any other neogastropod. Smith (1967a) commented on the structure of the gland in the Turridae and the Muricidae.

Other families in which the gland occurs are the Columbariidae (W.F.P.), Olividae (Marcus & Marcus, 1959), Vexillidae, Mitridae, Volutomitridae (Ponder, 1972b), Marginellidae (Ponder, 1970a), Turbinellidae (Ponder, 1973b), Cancellariidae (Graham, 1966), and the Terebridae (Marcus & Marcus, 1960).

In some families normally possessing the anal gland, certain genera appear to have lost it, these including *Vasum* in the Turbinellidae (Ponder, 1973b) and *Diluculum* in the Marginellidae (Ponder, 1970a). In some species it is very small and possibly of little functional importance. Ward (1965) has shown that *Coralliophila abbreviata* (Magilidae) does not possess an anal gland.

None of the families in Thiele's Buccinacea appear to have the gland, nor has the Colubrariidae.

Smith (1967a) pointed out the similarity of the granules in the anal gland of some neogastropods to those in the amoebocytes surrounding the digestive gland. In some instances, however, they do not resemble these latter granules. The refringent granules encountered in renal tissue and often seen in the gland of Leiblein are also similar.

The Male Genital Ducts

In all neogastropods the male genital duct (see Fig. 5) consists of a coiled, upper vas deferens modified to form a sperm storing seminal vesicle (sv) and, in some species, the walls ingest spermatozoa (Fretter, 1941; Smith 1967b). The lower or renal part of the vas deferens is usually straight and it is connected to the pericardium by a renopericardial duct or a strand

of tissue representing it. The Volutomitridae (Ponder, 1972b), the turrid *Oenopota* (= *Lora*) *travelliana* (Turton) (Smith, 1967b) and possibly the turbinellid *Vasum turbinellum* (Linnaeus) (Ponder, 1973b) have a gonopericardial duct. The remnants of this duct have been recorded in some Muricidae, Buccinidae (Fretter, 1941), Fascioliariidae (Marcus & Marcus, 1962) and Turridae (Smith, 1967b). Some others have the renal vas deferens located so close to the pericardial wall that the existence of a vestigial duct cannot be established. A diverticulum of the renal organ approaches the renal vas deferens in the Marginellidae (Ponder, 1970a) and in *Leucozonia* in the Fascioliariidae (Marcus & Marcus, 1962).

In the most primitive condition, the renal vas deferens opens into an open pallial groove lined with prostatic tissue, such as occurs in the Volutomitridae (Ponder, 1972b), Harpidae (Bergh, 1901), and in some volutes (Woodward, 1900; Pace, 1902). In *Alcithoe arabica* in the Volutidae, the sides of this groove become massive, glandular lobes (Ponder, 1970b). A line of fusion showing where the lobes were sealed is found in some muricids (Fretter, 1941) and some turrids (Smith, 1967b), whereas in the Turbinellidae all gradations between open and closed pallial grooves are found (Abbott, 1959; Ponder, 1973b) and Wu (1973) has noted the existence of 3 types of prostate gland in the Muricidae.

It thus appears as though the closed prostate gland (p) developed independently in at least several families. In most families in which a closed prostate gland is found, there is no trace of a line of fusion but they usually have a narrow, posterior, pallial connection, either in the form of a short, ciliated tube or a slit. Such a situation is found in all of the remaining families except the Fascioliariidae which (in *Leucozonia* at least) has lost the posterior opening of the prostate (Marcus & Marcus, 1962).

The penis (pen) is usually of moderately large size, and the duct mostly sealed and embedded in the central part of the penis.

There is, however, an open penial groove in some Turbinellidae (*Tudicula*; Abbott, 1959), Volutidae (*Volutocorbis*; Woodward, 1900) and in the Volutomitridae (Ponder, 1972b). Several forms show a line of fusion representing the edges of an originally open groove such as *Olivancillaria* (Olividae) (Marcus & Marcus, 1959), *Alcithoe* (Volutidae) (Ponder, 1970b) and several genera in the Turbinellidae (Abbott, 1959; Ponder, 1973b).

Prostatic cells occur in the penial ducts of *Buccinum*, *Nassarius* (Fretter, 1941), some Marginellidae (Ponder, 1970a), *Mangelia* (Turridae) (Robinson, 1960), and in the Olividae (Marcus & Marcus, 1959). The Volutomitridae have prostatic tissue lying within the penis and dissociated from the penial groove (Ponder, 1972b).

The Pyrenidae have some unusual modifications in the male genital system (Marcus & Marcus, 1962a). In some, the penis lies within a pouch between the hypobranchial gland and the pallial roof, and some have a seminal vesicle lying either just behind, or in front of, the upper pallial opening of the pallial sperm duct. In 1 species the prostate is divided into 2 separate bodies, but it usually forms a convolute part of the duct. In other species the prostate gland is absent, and in some the penial duct contains prostatic tissue.

Bouvier (1888) and Gohar & Soliman (1963) have shown that the burrowing Magilidae have a penis, however it is sometimes rudimentary. Although copulation cannot take place, spermatozoa are apparently taken in by the inhalant current of the female and fertilization is internal (Gohar & Soliman, 1963).

The Female Genital Ducts

The basic organization of the neogastropod female genital tract is shown in Fig. 6. *Nucella lapillus* and *Ocenebra erinacea* (Fretter, 1941) have a typical structure and have been thoroughly described. The duct in these 2 species consists of a short, upper and renal oviduct (od) leading from the ovary with a gono-

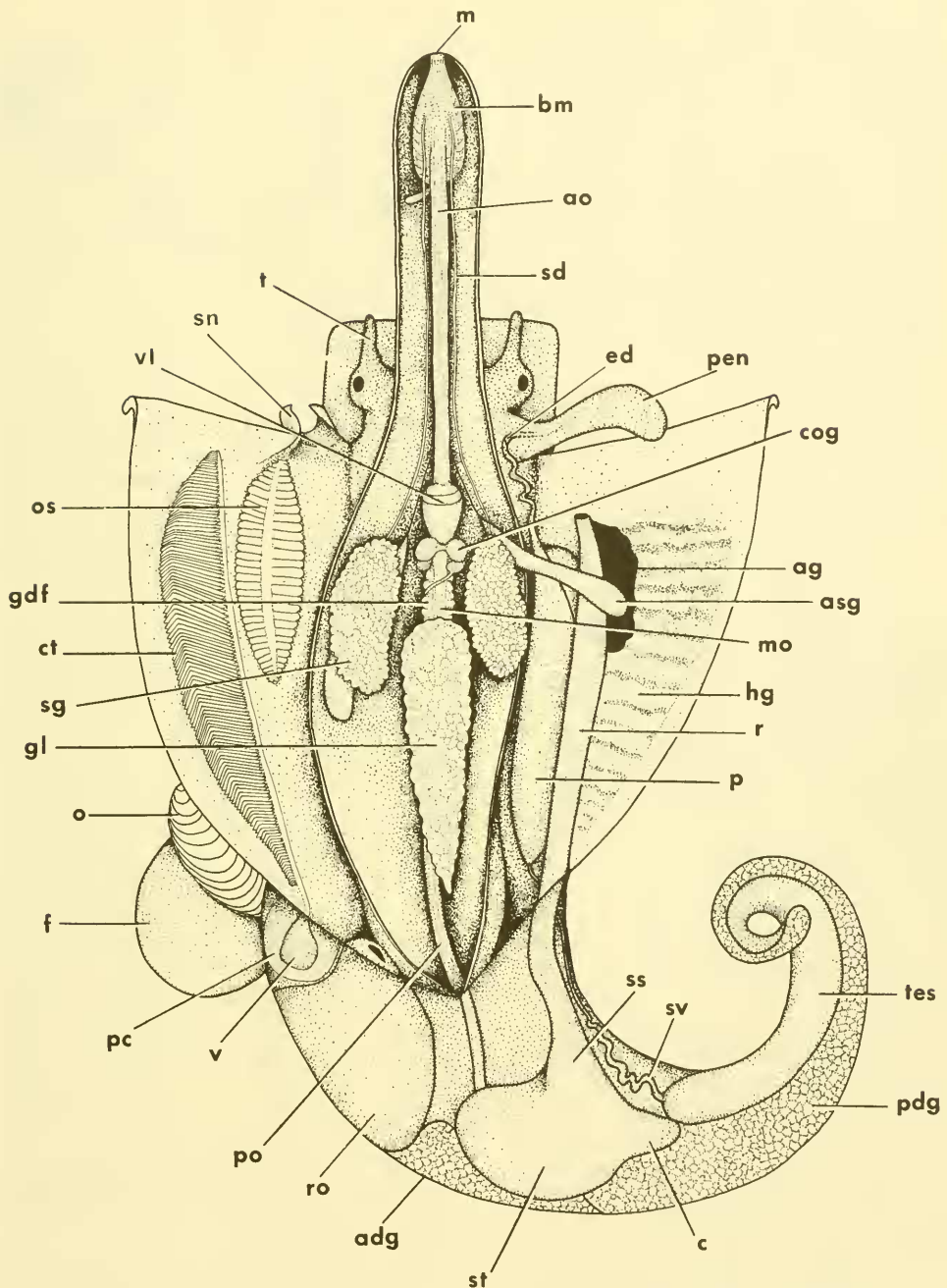


FIG. 5. Generalized muricean neogastropod removed from its shell and viewed dorsally with the pallial cavity and anterior body cavity opened mid-dorsally and the proboscis extended.

adg, anterior lobe of digestive gland; ag, anal gland; ao, anterior oesophagus; asg, accessory salivary gland; bm, buccal mass; c, caecum; cog, circum-oesophageal ganglia; ct, ctenidium; ed, ejaculatory duct; f, foot; hg, hypobranchial gland; gdf, glandular dorsal folds; gl, unpaired foregut gland; m, mouth; mo, mid-oesophagus; o, operculum; os, osphradium; p, prostate gland; pc, pericardium; pdg, posterior lobe of digestive gland; pen, penis; po, posterior oesophagus; r, rectum; ro, renal organ; sd, salivary duct; sg, salivary gland; ss, style sac; st, stomach; sv, seminal vesicle; t, cephalic tentacle; tes, testis; v, ventricle; vl, valve of Leiblein.

pericardial duct (gpd) at the junction of the latter duct with the albumen gland. The albumen gland (ag) is a thickened part of the oviduct itself in *Nucella*, and is humped, with the ventral surface of both halves in contact. A much lobulated ingesting gland (rs) opens by way of a sperm storing duct into the area between the albumen and capsule glands. The capsule gland (cg) forms most of the pallial section of the duct and at its anterior end there is a thin-walled ventral channel (vc) that is a short, muscular vagina (vag). A short, muscular bursa copulatrix (bc) opens into the vestibule, running from which is a thin-walled ventral channel (vs) that is overlain by 2 ciliated folds and a heavy, glandular lobe on the right.

A gonopericardial duct is present in at least some Muricidae, Buccinidae, Nassariidae (Fretter, 1941), Olividae (Marcus & Marcus, 1959), Pyrenidae (Marcus & Marcus, 1962a) and Cancellariidae (Graham, 1966). The renal oviduct of the Volutomitridae sometimes has a connection with the renal organ instead of the pericardium (Ponder, 1972b), and a blind, renal diverticulum lies alongside the renal oviduct in the Marginellidae (Graham, 1966; Ponder, 1970a).

The albumen gland in most Conacea and Rachiglossa is similar to that in *Nucella*, but has often been separated from the oviduct completely, so that it communicates by a separate duct into the region between the capsule and albumen gland into which the ingesting gland and renal oviduct open. This is the case in the Vexillidae and Volutomitridae (Ponder, 1972b), *Vasum* in the Turbinellidae (Ponder, 1973b) and at least some Marginellidae (Ponder, 1970a). There is apparently no albumen gland in *Turbinella* (Ponder, 1973b).

The ingesting gland has tall, brown-coloured cells which ingest spermatozoa and sometimes yolk (Fretter, 1941; Ponder, 1972b). Although Fretter recorded sperm ingestion in *Nassarius reticulatus* (Linnaeus), Johansson (1957) did not observe it in *N. pygmaeus* (Lamarck) or in *N. incrassatus* (Ström.). In at least some

Fascioliariidae (*Leucozonia*, Marcus & Marcus, 1962; *Taron dubius*, W.F.P.) the epithelium of the "ingesting gland" consists of simple, short, columnar cells that do not ingest spermatozoa, but instead the "gland" acts as a seminal receptacle.

Seminal receptacles have been recorded in *Olivella* and *Oliva sayana* Ravenel (Marcus & Marcus, 1959) and in both of these species there is no functional ingesting gland, although there is one in another member of the Olividae, *Olivancillaria (Lintricula) auricularia* (Marcus & Marcus, 1959). Narrow accessory ducts to the ingesting gland in *Alcithoe* (Volutidae) (Ponder, 1970b) store sperm and may be related to the seminal receptacles of the olivids.

The duct of the ingesting gland usually acts as a seminal receptacle, storing orientated spermatozoa. In the species investigated by Fretter (1941) (members of the Buccinidae, Muricidae and Nassariidae), and in the Volutidae (Ponder, 1970b) the ingesting gland duct opens into the ventral part of the gland and is not ciliated. In the Mitridae and Vexillidae (Ponder, 1972b) it is ciliated and opens into the dorsal part of the gland which is, in addition, not as lobed as in the preceding families. Ciliated ducts that do not store sperm are found in the Volutomitridae (Ponder, 1972b) and the Marginellidae (Ponder, 1970a), and the gland in these families is lined with large cuboidal cells that do not ingest spermatozoa. The ingesting gland of some turrids is capable of sperm absorption (Smith, 1967b), but Martoja-Pierson (1958) did not find any evidence for this in *Conus mediterraneus* (Brüg.). There is, apparently, no albumen gland or ingesting gland in *Turbinella pyrum* (Linnaeus) (Ponder, 1973b).

The capsule gland is usually the largest gland in the female oviduct, although in *Alcithoe* (Ponder, 1970b) it is shorter than the albumen gland. Typically it has several zones showing different staining properties and has a ventral channel. This channel is overhung by ciliated folds, usually 2 or 3 in most rachiglossans,

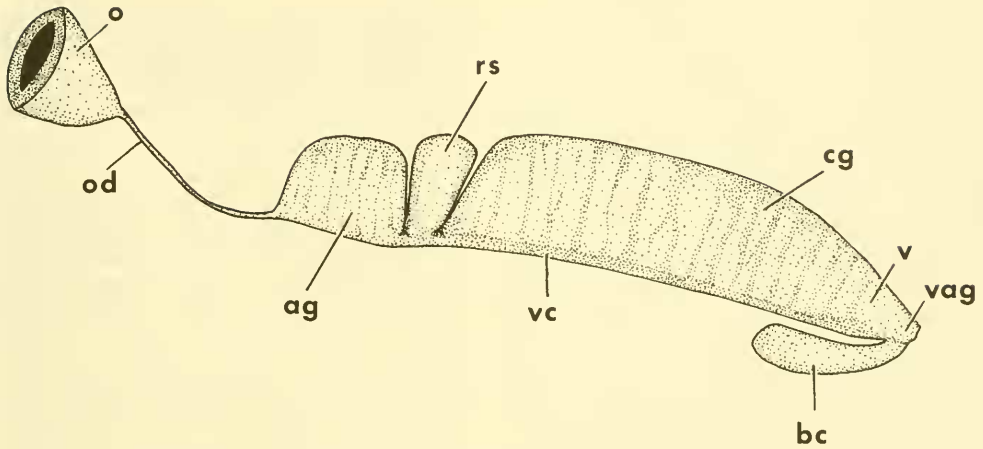


FIG. 6. Generalized neogastropod oviduct viewed laterally from the right side.

ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; o, ovary; od, upper oviduct; rs, seminal receptacle or ingesting gland; v, vestibule; vag, vagina; vc, ventral channel.

but the smaller species are rather anomalous, the Pyrenidae having 0 to 2 (Marcus & Marcus, 1962a) and the Marginellidae being similarly variable (Ponder, 1970a). *Alcithoe arabica* (Volutidae) has 1 ciliated fold on the right (Ponder, 1970b) and *Strigatella pauper-cula* (Linnaeus) in the Mitridae has only the left fold present, but *Imbricaria conularis* (Lamarck) has an additional, small, right fold (Ponder, 1972b).

A glandular lobe on the left side of the capsule gland also overlies the ventral channel in some Muricidae (Fretter, 1941) and in *Alcithoe* (Ponder, 1970b). Wu (1973), however, has shown that there are at least 4 types of organization in the Muricidae. One ciliated fold is present on the right side in *Comus mediterraneus* (Martoja-Pierson, 1958) but *Haedropleura septangularis* (Montagu), a member of the primitive turrid subfamily Clavinae, has a capsule gland like that of *Nucella* (Smith, 1967b). Thus, probably, the loss of the ciliated folds and even of the ventral channel in some other turrids (Smith, 1967b) is a secondary feature.

The bursa copulatrix is a terminal sac for sperm reception, but in some species it has become modified for other purposes. In the majority of the Rachiglossa there is lit-

tle variation in the bursa copulatrix, although it is very large in *Vexillum* spp. (Ponder, 1972b) and in *Oliva sayana* (Marcus & Marcus, 1959). It is often modified for storing orientated sperm as well as catering for temporary sperm storage immediately after copulation. A separate bursa copulatrix is missing in some marginellids (Graham, 1966), *Turbinella pyrum* (Ponder, 1973b) and some turrids (Smith, 1967b).

Some Turridae (Smith, 1967b) have 2 regions in the anterior part of the oviduct, 1 modified for sperm receiving, therefore strictly speaking a bursa copulatrix, and the other for sperm storage. This latter organ is referred to by Smith as a sperm sac, but is almost certainly homologous with the separate bursa copulatrix of other neogastropods and turrids. The "bursa copulatrix" in those species with a sperm sac (and in some without) opens directly into the capsule gland and is thus homologous with the vagina of other Neogastropoda. There is little advantage in changing the names of these structures which have acquired slight alterations (or presumed alterations) in function.

The vestibule and vagina sometimes form a long outgrowth from the capsule gland. In the turrid genus, *Mangelia*

(Robinson, 1960; Smith, 1967) there is an elongated part of the oviduct in front of the short capsule gland and no bursa copulatrix. In the terebrid *Hastula* a similar, but open, structure occurs, as well as a small bursa copulatrix (Marcus & Marcus, 1960). A narrow, tubular vagina runs alongside the massive bursa copulatrix in *Vexillum* spp. (Ponder, 1972b).

Olivella (Marcus & Marcus, 1959) has a bulb lying between the capsule and albumen glands and this is connected by a long, separate duct to the very short vagina. This bulb is lined with tall epithelial cells and contains faecal material with which the egg capsules are covered. It is possible that the long, ciliated duct of this bulb is the pinched-off ventral channel of the capsule gland and that the sperm groove now found in the capsule gland is a new structure. Alternatively it may be a bursa copulatrix as Marcus & Marcus suggest, but there is a small pouch near the genital aperture that could also be homologous with the bursa copulatrix. In *Olivancillaria* (*Lintricula*) (Marcus & Marcus, 1959) the gonopore lies near the junction of the capsule gland and albumen gland where the bursa copulatrix and ingesting gland also open.

The Pyrenidae have several unusual features in the female reproductive system (Marcus & Marcus, 1962a). They fall into 2 groups; 1 having no albumen gland, a gonopericardial duct which, together with the pericardium stores sperm, and a pallial opening from the pericardium. In 1 species sperm is ingested in the gonopericardial duct. The 2nd group has an albumen gland but no gonopericardial duct and does have an anteriorly placed, sperm storage organ (bursa copulatrix) the epithelium of which ingests spermatozoa in some species. The vestibule is, in addition, usually very muscular, with folded walls, and in 1 species there are 2 separate gonopores, 1 to receive the penis and the other for the passage of eggs.

Smith (1967b) has shown that *Propebela* (= *Lora turricula* (Montagu)) is an hermaphrodite.

Many neogastropods have a ventral

pedal gland in the female, which aids in moulding the egg capsule. This appears to be absent in at least some members of the Vexillidae, Volutomitridae (Ponder, 1972b) and the Turridae (Smith, 1967b).

Egg Capsules

The resistant, chitinous, neogastropod egg capsule is a useful taxonomic feature, particularly at the generic and specific level, because the egg capsules have become diagnostic in shape, yet extremely varied in overall pattern. Many neogastropod egg capsules have been described in the literature, but the majority remain unknown. Ankel (1929) and Fretter (1941) have shown how the capsule is moulded by the ventral pedal gland in the female.

Within each major family group there is an evolutionary trend in the shape of the egg capsules. This involves a progressive raising of the primitive, lens-shaped capsule from the substratum and its eventual attachment by a narrow stalk. In many cases the examples and references given below are only a few of those actually available in the literature.

The most primitive type of capsule is the lens-shaped form, which is encountered in the lower mesogastropods (Littorinaeae and Rissoeaeae) and in the archaegastropod Neritaceae. This type is found in most Turridae (Thorson, 1935, 1946; Knudsen, 1950; Lebour, 1934, 1937), some Marginellidae (Knudsen, 1950; Ponder, 1970a) and Olividae (Marcus & Marcus, 1960a), in the "Trophoninae" in the Muricidae (Hedley, 1917; Habe, 1960; Amio, 1957; Dell, 1964; Thorson, 1940b, 1946), and *Sipho* spp. in the Buccinidae (Thorson, 1935, 1949; Lebour, 1937). The lens-shaped type presumably gave rise to the hemispherical type, there being every gradation between these 2 forms. Hemispherical capsules are found in the Volutomitridae (Ponder, 1972b), in some Marginellidae (Knudsen, 1950) and Volutidae (Cooke, et al., 1895; Allan, 1934; Cotton, 1937; Graham, 1941a), in *Austromitra* in the Vexillidae (Ponder, 1972b), and in

Volutopsis norvegicus (Gmelin) in the Buccinidae (Thorson, 1935). A progressive elongation of the capsule, with the eventual formation of a basal stalk, follows in several families. These include the Buccinidae, Pyrenidae, Nassariidae, Muricidae, Marginellidae and Turridae. The latter 2 families and the Pyrenidae have only a few examples with stalked capsules (Knudsen, 1950; Risbec, 1929) but these occur in the majority of the genera in the other 3 families. *Thais* (Muricidae) and allied genera often have parallel-sided capsules (Lebour, 1945; Hedley, 1906). Long chains of capsules on a common stalk occur in the Turbinellidae (*Turbinella*, Hornell, 1922), the Galeodidae (*Busycon*, Abbott, 1954) and the Buccinidae (*Austrofusius glans* (Röding) (W.F.P.). Ball-like clusters of capsules are found in some buccinids (*Buccinum* spp. Thorson, 1935; *Neptunca* spp. Golikov, 1961; and *Penion adustus* (Philippi), Ponder, 1973a).

The Mitridae (Ostergaard, 1950) have vase-shaped capsules, whereas the Conidae (Ostergaard, 1950; Kohn, 1961a) and the Harpidae (Risbec, 1932) have flattened pouches. The Magilidae have thin-walled egg sacs which are retained inside the pallial cavity of the female (Gohar & Soliman, 1963). The capsule of *Cancellaria* sp. described by Knudsen (1950) is scalpel-shaped and attached by a long stalk. Some volutid egg capsules have a calcareous covering, secreted by the pedal gland (Graham, 1941a).

The types of larval development in the neogastropods are reviewed by Anderson (1960).¹ Planktonic development of the veliger larva is retained in many Nassariidae, Pyrenidae, Muricidae, Mitridae, Conidae, some Turridae, Magilidae and Terebridae. Complete development within the egg capsule is found in at least some Buccinidae, Galeodidae, Fasciolaridae, Turbinellidae, Marginellidae, Volutomitridae, Olividae, Volutidae and Vexillidae.

Several families such as the Turridae, Muricidae and Pyrenidae combine both types of development and closely allied genera, or even subgenera, often have different types of life history. Clearly the length of larval life has adaptive significance and the suppression of the free-swimming stage is probably brought about initially by environmental pressures. There is no definite example of the secondary acquisition of a free-swimming larval stage.

In those families exhibiting direct development, usually a large number of "nurse eggs" do not develop, but provide nutriment for those that do (Portmann, 1925; Thorson, 1940a, b). Some, including the Marginellidae (Ponder, 1970a) and Vexillidae (Ponder, 1972b), appear to rely only on yolk contained within the large egg(s), while others use albuminous material secreted by the pallial oviduct (e.g., *Alcithoe arabica*, Ponder, 1970b).

The Renal Organ

The renal organ (Fig. 5; ro) lies at the base of the pallial cavity. Perrier (1889) divided the neogastropods into 2 groups, the Méronéphridiens and the Pycnonéphridiens, on the basis of the structure of their renal organs. These, he concluded, were 2 natural divisions, the former group having the primary and secondary renal lamellae separated and the latter having them interdigitated. This classification was not used by later authors because of the obvious working disadvantages and, like many classifications that rely on the structure of a single organ, it has little phylogenetic significance. Both of these types of renal organs occur in the Turbinellidae (Ponder, 1973b) and the remainder of the families fall into 1 or the other groups, so far as is known. However, relatively few species have been examined, and with further work the variation within each family group may be found to be greater than our present knowledge in-

¹A detailed summary of patterns of development in neogastropods has recently been given by Radwin, G. E. and Chamberlin, J. L., 1973 (Patterns of larval development in stenoglossan gastropods. *Trans. San Diego Soc. Nat. Hist.*, 17(9): 107-117).

dicates. It is by no means certain which arrangement is the more primitive.

Most Mëronëphridentiens have the primary and secondary lamellae (or filaments) interdigitating to a slight extent. The families with this type of renal organ are the Conidae (Perrier, 1889), the Terebridae (Marcus & Marcus, 1960), the Volutidae (Perrier, 1889; Ponder, 1970b), the Pyrenidae (only partially separated) (Marcus & Marcus, 1962a), the Olividae (Marcus & Marcus, 1959), the Mitridae (Ponder, 1972b) and the Marginellidae (Ponder, 1970a).

The Pëcnonëphridien group includes the Muricidae, Buccinidae (Perrier, 1889), Vexillidae, Volutomitridae (Ponder, 1972b), Fascioliariidae (Marcus & Marcus, 1962) and the Harpidae (Perrier, 1889).

The Nervous System

The nervous system of the Neogastropoda has received relatively little attention. The studies of Haller (1882, 1888), Bouvier (1887) and Marcus & Marcus (1959, 1960, 1962, 1962a) have provided much of the detailed information available.

The nervous system of the Rachiglossa usually shows considerable concentration of all of the circum-oesophageal ganglia and the buccal ganglia are attached by very short connectives to the cerebral ganglia. This type of situation is seen in the Muricidae (Haller, 1882, 1888; Bouvier, 1887), the Buccinidae (Bouvier, 1887; Dakin, 1912), the Pyrenidae (Marcus & Marcus, 1962a), the Fascioliariidae (Haller, 1888; Bouvier, 1887; Marcus & Marcus, 1962), the Marginellidae (Bouvier, 1887), the Mitridae (Bouvier, 1887; Ponder, 1972b), the Vexillidae and the Volutomitridae (Ponder, 1972b), the Harpidae (Bouvier, 1887; Bergh, 1901) and in some Volutidae. A few species in the last family have the supra-oesophageal ganglion separated by a long connective from the right pleural ganglion (details given by Ponder, 1970b).

The cancellariids (Bouvier, 1887; Graham, 1966) have concentrated ganglia, but their buccal ganglia lie just behind the

buccal mass at the distal end of the proboscis, thus having very long connectives. In the Conacea the ganglia are, in all 3 families, much more separated than they are in any rachiglossans, with the exception of the cerebral and pleural ganglia (Bouvier, 1887; Shaw, 1915; Marcus & Marcus, 1960).

There are 2 or 3 visceral ganglia near the base of the pallial cavity, these being well separated from the circum-oesophageal ganglia to which they are connected by the visceral loop.

PART 3 THE CLASSIFICATION OF THE NEOGASTROPODA

The classification of the neogastropods has attracted the attention of many authors, not only because of the many conspicuous groups it contains, but also because the order contains some of the more economically and biologically important gastropods.

It is not intended to give a detailed account of the history of the classification of this order, but a brief examination of some of the more important contributions is necessary in order to understand the derivation of the modern classification.

Contributions to the classification of this group can be divided into 2 groups. Firstly there are those that are reviews of the whole of the gastropods. In these accounts the classification is mainly concerned, out of necessity, with the shell. The other group includes studies on various organ systems, the results of which have been used to modify existing classification.

The work of Adams & Adams (1853) is the earliest comprehensive account of the Mollusca that we need to consider. Their treatment of the families now included in the Neogastropoda differed in a number of cases from the modern interpretation, but nevertheless, the majority of the family groups were much as we know them at present. The names *Stenoglossa*, *Toxoglossa* and *Rachiglossa* were used in Troschel's (1856-1893) classification, based on the radula, which is essentially like that in use today. The classifications of

Perrier (1889) based on the renal organ and Bouvier (1887) on the nervous system mostly supported the familiar classification based on dentition.

Certainly any classification based on a single structure must have its shortcomings, but the radula has the advantages of being readily accessible, as well as easily interpreted and preserved. The radula has indeed proved to be a fairly reliable indicator of the familial position of species in the Neogastropoda, but parallel development of similar types has occurred in distinct families as shown above.

Tryon (1880-1884) and Fischer (1887) produced comprehensive reviews of the families of neogastropods, but their classification differs little from that of Troschel. Thiele (1929) and Wenz (1938-1943) have both provided similar, detailed accounts of gastropod classification and it is these which are generally in use today. The only modern attempts at a critical assessment of gastropod classification are those of Risbec (1955) and Fretter & Graham (1962).

The curious classification of Iredale & McMichael (1962) of the *Rachiglossa* calls for comment. They use, apparently for the first time in several cases, a number of "family" names and include some heterogastropods in this group. Their new families are, without exception, erected without indication or any explanations, and in some cases represent the up-grading of already existing subfamilies.

Since Troschel's (1856-1893) momentous work on the gastropod radula, the Neogastropoda (*Stenoglossa*) have usually been divided into the *Rachiglossa* and the *Toxoglossa*. Apart from the inclusion of the *Mitridae* (e.g., Risbec, 1955) and the *Cancellariidae* (e.g., Troschel, 1856-1893; Keen, 1958), the *Toxoglossa* is equivalent to the *Conacea* discussed above. The main distinguishing characters of the 3 superfamilies given briefly earlier in this paper are outlined in Table 1. The Neogastropoda, can be defined as follows:

Order Neogastropoda

Shell without inner nacreous layer, and with anterior siphonal canal. Operculum,

if present, chitinous, with terminal or lateral nucleus. Radula, if present, with each row consisting of combinations of a central tooth, and a pair of lateral and marginal teeth. Animal with monopectinate ctenidium, bipectinate oesophradium and anterior siphon. Proboscis usually pleurembolic, but may be intra-embolic or polyembolic. Mid-oesophagus usually with oesophageal gland connected by a narrow duct (unpaired foregut gland). Buccal pouches, if present, forming a pad of glandular tissue at anterior end of the mid-oesophagus and surrounding the oesophageal valve to form the valve of Leiblein. Salivary glands with ducts not passing through nerve ring, and accessory salivary glands often present, their ducts opening at the anterior edge of the buccal cavity. Anal gland often present; intestine short and relatively straight. Usually carnivorous. Circum-oesophageal ganglia at least moderately concentrated but visceral connectives rather long. Sexes usually separate, female typically with an ingesting gland (sometimes a seminal receptacle) lying between a pallial albumen and capsule gland, and with a ventral pedal gland which aids in forming the usually horny egg capsules. Male duct with an open or closed pallial portion, and with a penis. Only left auricle and renal organ present, the latter containing 2 types of lamellae and a nephridial gland.

Superfamily Cancellariacea

(Synonym *Nematoglossa* Olsson, 1970)

There are 2 families assigned to this superfamily, the *Cancellariidae* and *Paladmetidae*. The latter family is an extinct group lacking columellar folds, and is discussed in some detail by Sohl (1964).

Olsson (1970) has provided the order *Nematoglossa* for the cancellariids, stating that the radula "is unique and differs so fundamentally from those of other named taxa that a new term based upon radular structure is necessary." In most other respects the *Cancellariidae* falls within the neogastropod group and it is unnecessary, in my opinion, to separate this family at the level of order or suborder.

Table 1. Comparison of the main features of the neogastropod superfamilies

Muricea	Conocea	Concellariacea	
not distinct	usually distinct	not distinct	Posterior sinus of shell
pleurembolic with buccal cavity at its distal end	introembolic or polyembolic with buccal cavity at its proximal end	pleurembolic; with buccal cavity at its distal end	Proboscis
usually present	sometimes present	very elongate	Radula Central teeth Lateral teeth
usually present	rarely present	absent	
absent	present	absent	Marginal teeth
behind nerve ring	behind nerve ring	in front of nerve ring	Position of mid-oesophagus
usually long	absent	absent	Anterior oesophagus
at posterior end of anterior oesophagus, pyriform	absent	immediately behind buccal mass, ventral	Valve of Leiblein
short	short	long	Buccal ganglia connectives
usually concentrated; lie just behind volve of Leiblein	usually loosely connected; lie just behind buccal cavity	usually closely connected; lie near base of proboscis	Circum-oesophageal ganglia
Separated from mid-oesophagus	separated from mid-oesophagus	not separated from from mid-oesophagus (or absent ?)	Unpaired foregut gland (when present)

Superfamily Conacea

(Synonym *Toxoglossa* Troschel, 1848)

The families of the Conacea (Conidae, Turridae, Terebridae and Speightiidae) will not be discussed in detail. Powell's (1942) placing of the extinct Speightiidae in the Conacea is based on the presence of a posterior sinus in the aperture, but otherwise the shells look like fascioliids. Powell (1966) has reviewed the genera and subfamilies of the Turridae and McLean (1971) has proposed 3 additional subfamilies in a review of the higher classification of the Turridae. Rudman (1969) has created a new family, Pervicaciidae, but his basis for its separation from the Terebridae is very slight, particularly in view of Miller's (1971) findings on the variation in the morphology of the terebrids, and its recognition does not appear to be necessary.

Superfamily Muricea

(Synonym *Rachiglossa* Troschel, 1848, and a combination of Thiele's (1929) Muricea, Buccinacea and Volutacea, together with Risbec's (1955) Mitracea and Olsson's (1956) Olivacea.)

Every attempt on the part of the writer to determine detailed patterns of relationship in the families of the Muricea has met with little success. It appears, from the morphological and palaeontological evidence, that most of the muricean families arose independently in the Mesozoic (Fig. 4) and are all more-or-less equally distinct, with the exception of the Buccinidae, Galeodidae, Fascioliidae and Nassariidae. The muricean families are discussed below in an attempt to clarify their relationships to one another. Table 2 summarizes some of the more important features of each family.

The family group names Muricea, Buccinacea and Volutacea all date from Rafinesque, 1815 and were erected in the above order, and Thiele (1929) and Wenz (1938) both use the superfamily names in the same order. For this reason the name

Muricea has been chosen. The name *Rachiglossa* does not suit the requirements for formal use as a superfamily name, as it is not based on a contained genus name (Article 11(e), ICZN, 1961).

Buccinidae, Nassariidae, Fascioliidae, and Galeodidae

Differentiation between these groups is usually possible on shell features and/or radular features. The magnitude of the differences, however, is not great and there are practically no anatomical features which can be used consistently to separate them. The writer has followed the generally accepted practice of retaining these groups as families but, in fact, they show levels of differentiation from one another that could be treated as subfamilial.

The Buccinidae is an extremely large and varied family (as listed by Wenz, 1938) and about 20 family and subfamily names have been based on the genera contained within it. Tryon (1881) included 6 subfamilies, and Fischer (1887) and Cossmann (1901) used 7 within the 1 family.²

Powell (1929) recognized 3 family groups, the Buccinidae, Cominellidae and Neptuniidae, but in 1951 he made the cominellids a subfamily of the Buccinulidae. These groups are based on radular and opercular characters that seem very minor when the total variation within the group is considered, and should not be recognized even as subfamilies. The majority of the other groups erected have been based solely on shell features and, even on this basis, they are hardly separable.

Many Buccinidae pass through their larval stages within the egg capsules, this resulting in a paucispiral protoconch, but the nassariids often have a free swimming larval stage. This difference may, in part, be due to the Buccinidae mainly being in temperate latitudes whereas the majority of nassariids are tropical or subtropical in distribution. This view is reinforced by

²Habe, T. and Sato, J., 1972, (A classification of the family Buccinidae from the north Pacific, *Proc. Jap. Soc. Syst. Zool.*, 8: 1-8) have recognised 6 subfamilies among the larger buccinids of the north Pacific.

Table 2. Comparison of some of the main features of the muricacean families.

Family	Unpaired foregut gland	Radula	Accessory salivary glands	Operculum	Columnellar folds	Kidney (Meronephridien (M) or Pyronephridien (P))	Anal gland
Buccinidae	small gland of Leiblein	1+1+1; rarely 1+0+1			absent		
Nassariidae	small gland of Leiblein	1+1+1			absent		
Fasciolaridae	small gland of Leiblein	1+1+1	none	present	weak if present, usually absent	P	absent
Galeodidae	small gland of Leiblein or lost	1+1+1			absent		
Colubrariidae	lost	1+1+1 or absent	none	present	absent	?	absent
Pyrenidae	small gland of Leiblein	1+1+1 (1+0+1)	none	present or absent	mostly absent, weak if present	M	absent
(Turbinellinae)							
Vosidae (Vosinae)	small gland of Leiblein	1+1+1	none	present	present	M	present
Muricidae	large, most gland of Leiblein	1+1+1	0-2	present	absent	P	absent
Megilidae	large, all gland of Leiblein	absent	none	present	absent	?	present or absent
Columbariidae	large, gland of Leiblein	1+1+1	none	present	absent	?	present
Volutidae	large, most dorsal folds, gland of Leiblein; small	0+1+0; rarely 1+1+1	2	usually absent	present	M	present
Olividae	most gland of Leiblein; sometimes absent	1+1+1	1-2	present or absent	weak or absent	M	present
Harpidae	absent	(1)+1+(1)	none	absent	absent	P	absent
Volutomitridae	small, gland of Leiblein	1+1+1 or 0+1+0	1	rudimentary or absent	present	P	present
Marginellidae	typically most dorsal folds, gland of Leiblein usually small	0+1+0	1 or absent	absent	present	M	usually present
Mitridae	absent	1+1+1 rarely 0+1+0	absent	absent	present	M	present
Vexillidae	gland of Leiblein, usually with dorsal folds	1+1+1	2	absent	present	P	present

Phos and some other tropical/subtropical buccinid genera having multispiral protoconchs. The group including *Phos* and its allies are sometimes separated as a family, Photidae. Risbec (1952) and Bouvier (1888) both show that the Nassariidae and Buccinidae lack any distinctive morphological features that could separate them into 2 groups. The presence of 2 posterior tentacles on the foot does, however, give the nassariids a certain distinctiveness. The radula of the Nassariidae is very similar to that of many Buccinidae, although it often bears an accessory plate, a structure not known in the Buccinidae. The group is a very homogeneous one, although Cossmann (1901) recognizes 3 subfamilies within it. Some Nassariidae have become, secondarily, deposit feeders and have a crystalline style in the stomach (Morton, 1960; Brown, 1969).

The Fascioliariidae differs from the above families and from the Galeodidae in usually having a red-pigmented head-foot. The radula, too, is distinctive, with multicuspid lateral teeth and small central teeth. In the 2 species investigated, the structure in the female pallial genital tract that functions as an ingesting gland in the above 2 families acts as a seminal receptacle only. Typical members of the *Fusinus* group appear to differ from the remainder of the family only in having a long siphonal canal, although they are sometimes separated as a family, the Fusinidae. However, there are many genera difficult to place in 1 group or the other so that the recognition of this group is not recommended.

No members of the Galeodidae (=Melongenidae, Volemidae) have been described in detail, but their anatomy appears to be like that of the Buccinidae (Vanstone, 1894; Kesteven, 1904; Pierce, 1950; W.F.P.) except that species in the genus *Melongenina* have lost the unpaired foregut gland.

The morphological similarity of these 3 families, together with the allied families Pyrenidae and Colubrariidae, might suggest that Thiele's Buccinacea should be used to cover this homogeneous group. If

this were done then the difficulty of placing families such as the Turbinellidae and Mitridae, which also show many "buccinacean" features, would show that the distinctiveness of such a group was, in fact, well below the normal level that one would expect in a superfamily. If one were to retain a division Buccinacea, then most of the other neogastropod families would require different superfamilies.

The similarity of the Pyrenidae to the Buccinidae may be due to parallel evolution, although there are no records of species assigned to this family before the Paleocene, whereas the galeodids, buccinids, and fascioliariids were all present in the Upper Cretaceous (Wenz, 1938; Sohl, 1964).

Colubrariidae (= *Fusidae*)

The features of this family, based on *Ratifusus reticulatus* (A. Adams) (= *mestayerae* (Iredale)) and *Iredalula striata* (Hutton), are outlined by Ponder (1968). This group was probably derived from an early buccinid stock. The protoconch is small and multispiral, so that it is probable that they have a pelagic larval life. The stomach and mid-oesophagus are different from those encountered in the Buccinidae. The shell of *Colubraria* is superficially like that of some members of the Cymatiidae (Tonnacea, Mesogastropoda), but some other genera in the family have a resemblance to certain buccinids.

Cernohorsky (1971) indicated that the anatomical information presented by Ponder (1968) for *Ratifusus* and *Iredalula* suggested their placement in the Buccinidae, and not that the Colubrariidae is "buccinacean". This view he attempted to substantiate by showing that the type species of *Colubraria*, *C. maculosa* (Gmelin, 1791) (= *muricata* Lightfoot, 1786) does not have a radula whereas *Ratifusus* and *Iredalula* do have a minute radula, which is, however, virtually vestigial. A study of the anatomy of *Colubraria* cf. *sowerbyi* (Reeve) (W.F.P.) has shown that it possesses the same peculiar glandular mid-oesophagus that differentiates *Ratifusus* and *Iredalula* from

the Buccinidae and the other features of the anterior alimentary canal are also similar except that there is no odontophore or radula. It thus appears that some Colubrariidae have lost the radula and that it is relatively small or vestigial in the remainder. It is possible that the whole *Metula-Ratifusus* series discussed by Cernohorsky (1971) belong in the Colubrariidae as they all have similar shell features.

The Upper Cretaceous genus *Fulgerca* Stephenson is possibly a colubrariid, although Sohl (1964) includes it doubtfully in the Buccinidae. Another possible Upper Cretaceous colubrariid is *Plesiostrotion cretaceus* Sohl (Dr. A. G. Beu, pers. comm.). *Colubraria* extends back to the Paleocene (Wenz, 1938).

Turbinellidae (= *Vasidae*, = *Xancidae*)

The features of this family will be discussed elsewhere (Ponder, 1973b). It shows similarity, on the one hand, with the Buccinidae and its allied families, in not having accessory salivary glands and in the possession of a thick, heavy, spindle-shaped shell, large operculum and long proboscis. Discordant features are the radula and anal gland of *Turbinella*, the open or partially fused pallial sperm grooves and the columellar folds. *Vasum* has a radula like that of *Melongena*, and it apparently does not possess an anal gland. The first appearance of this family, like many of the Muricea, is during the Cretaceous (Fig. 4) and it seems likely that most of its features were derived quite independently from, but in a parallel fashion to, the buccinid-nassariid-galeodid-fascioliid complex. The Pyrenidae, too, probably acquired the "buccinean" features of the alimentary canal independently.

The subfamilies Turbinellinae and Vasinae appear to be quite distinct anatomically (Ponder, 1973b).

Pyrenidae (= *Columbellidae*)

The pyrenids exhibit both specialized and primitive features. Risbee (1954) and Marcus & Marcus (1962a) have provided

most of the available information on the anatomy of the family. The alimentary canal is rather uniform and is similar to that of the Buccinidae. The radula shows a tendency towards suppression of the central teeth and the lateral teeth are usually attached by narrow bases. The reproductive system shows considerable diversity and Marcus & Marcus (1962a) suggest that the family could eventually be divided into 2 groups on the basis of the structure of the genital organs. Some pyrenids have become herbivorous (Marcus & Marcus, 1962a). Many species have lost the operculum and their shells usually have long, narrow apertures.

Muricidae (= *Thaididae*, etc.)

Distinctive morphological features of the Muricidae (in the broad sense) include accessory salivary glands, a purple hypo-branchial secretion, a massive gland of Leiblein, a broad caecum in the stomach, an anal gland and a large, closed, prostate gland. The path of torsion is indicated in the conspicuous valve of Leiblein by a narrow groove, and the primary and secondary lamellae of the renal organ are not separated. The small foot has an accessory boring organ on its anterior, ventral surface and the radula has 3 teeth in each transverse row, the central tooth usually having 3 primary cusps. The muricids form a rather homogeneous group in which Cossmann (1903) recognized 5 subfamilies (Ocenebrinae, Muricinae, Trophoninae, Typhinae, and Rapaninae), with the Purpuridae (=Thaididae) as a separate family. The differentiation between the subfamilies is small, although they do appear to form fairly natural groups. The Thaididae is no more distinct than any of the subfamilies contained within the Muricidae and could be regarded as one also. Morphological differentiation between the "subfamilies" is slight, but, judging from the few species that have been examined, the accessory salivary glands show a progressive enlargement and separation from the normal salivary glands through the Muricinae and Trophoninae to the Thaidinae,

Ocenebrinae and Rapaninae. The small radular and shell differences that have been cited between the various groups (e.g., Vokes, 1964) do not appear to be consistent (Ponder, 1972a), although the case for use of several subfamilies has been put strongly by Radwin & D'Attilio (1971) and Vokes (1971). The operculum has often been cited as evidence for the separation of Thaidinae and Ocenebrinae from the remainder of the family because in these groups it has a lateral nucleus. However opercula with both terminal and lateral nuclei occur within the genus *Murex* and other exceptions are known. There appears to be little advantage in retaining these subfamilial groupings until stronger evidence for their distinctiveness is forthcoming.

Wu (1973) has outlined some of the variation of anatomical structures in the Muricidae.

Radwin & D'Attilio (1971) recognize the Rapanidae, Thaididae, and the Muricidae as separate families on the basis of shell, radular and opercular details.

Magilidae (= *Coralliophilidae*, *Rapididae*)

The shells of some members of the family closely resemble those of some Muricidae, but the 2 groups can be separated on the absence of a radula in the Magilidae. The unpaired foregut gland is massive and its interior is divided transversely by conspicuous partitions (Bouvier, 1888; Ward, 1965). This structure was misidentified as the stomach by Gohar & Soliman (1963). The sedentary species that live in burrows within coral appear to possess an anal gland (W.F.P.) whereas the actively mobile *Coralliophila abbreviata* (Lamarck) (Ward, 1965) does not. It is possible that some magilids may be found to possess a vestigial radula and it might be found that, in such species, the Magilidae and Muricidae closely approach one another. The few species of the Magilidae investigated however, have only 1 pair of salivary glands, the ducts of which join to form a common dorsal duct in *Coralliophila abbreviata* (Ward, 1965).

In the sedentary and freely moving

species so far examined the female stores the egg capsules inside the mantle cavity, a habit not seen in any other neogastropod.

These gastropods feed suctorially on coelenterates (Robertson, 1970), although it is not certain how species such as *Magilus* (which are permanently embedded in their coral host with only a tiny external aperture through which the proboscis can emerge) feed.

Columbariidae

The possession of a very long proboscis makes this group distinct from the Muricidae. The radula, too, is rather different from the normal muricid type. The family resembles the Muricidae in having a large unpaired foregut gland and an anal gland, but is similar to the Buccinidae in the lack of any glandular dorsal folds in the mid-oesophagus and in the absence of accessory salivary glands.

Thiele (1929) included *Columbarium* in the Muricidae but Tomlin (1928) separated it, as a family, on shell and opercular features. It was reduced to a subfamily of the Muricidae by Wenz (1938), but Iredale (1936) gave it full family status, which is followed here, based on the anatomy of *Coluzea spiralis* (A. Adams) and *C. mariae* (Powell) (W.F.P.). Iredale placed the family near the "Fusinidae" (Fascioliariidae). This family has recently been reviewed by Darragh (1969).

Volutidae

Distinctive features of the majority of the Volutidae include the broad hood over the rhynchostome, formed by the tentacle bases, the large foot, and the siphonal appendages. Both types of salivary gland are present and there is sometimes a purple hypobranchial secretion. The dorsal folds of the mid-oesophagus are usually incorporated as a duct-like structure in the unpaired foregut gland and the path of torsion is indicated in the valve of Leiblein. The primary and secondary renal lamellae are separated and the pallial, male, genital tract is often an open groove

or prostate gland. Typically the shell has columellar plaits, and there is usually no operculum. The radula nearly always consists of only the central teeth. Development is nearly always complete in the capsule, although some species have small multispiral protoconchs suggesting pelagic larval development.

Cossmann (1899) used 6 subfamilies in the Volutidae, but Wenz (1938) used only 4 (excluding the Volutomitridae). Pilsbry & Olsson (1954) introduced 8 new subfamilies and a number of tribes. Altogether they divided the family into 12 subfamilies and 8 tribes. While this is almost certainly excessive considering the evidence available, there should be no doubt as to the pure composition of each of their groups. It is probable that an assessment of the characters of the male genital system, together with the radula and shell, would derive a more conservative classification that would, at the same time, be natural. Clench & Turner (1964) divided the subfamilies on the basis of the appearance of the salivary glands, the unpaired foregut gland and the shape of the radula. Weaver & duPont (1970), in their monograph of the family, recognize 9 subfamilies among the Recent species.

Olividae

Olsson (1956) created a superfamily for the Olividae in which Marcus & Marcus (1959) included the Harpidae. The morphology of the Olividae has so much in common with that of the rest of the Muricacea that, in the writer's opinion, a separate superfamily is unwarranted.

Olsson (1956) included 4 subfamilies and, doubtfully, a 5th, the Pseudolivinae, which he suggested possibly does not belong in the family in which it is placed by Thiele (1929) and Wenz (1938). Cossmann (1899) included the Pseudolivinae in the Buccinidae.

Marcus & Marcus (1959, 1968) gave a detailed account of the morphology of 5 species of Olividae. *Olivella* stands out sharply in its morphological differentiation.

Marcus & Marcus (1959) suggest that

the Olividae has some features in common with Thiele's Buccinacea and Volutacea and may have been derived from a common ancestor. Perhaps this is so, but the common features they mention such as the large foot and concentrated nervous system were probably derived by parallel evolution, and do not indicate a direct relationship.

The olivids superficially resemble the harpids and volutids, but differ from them in having the sides of the foot extending over the shell. The harpids have no accessory salivary glands, but these are found in most olivids and the region of torsion in the gut of the olives is different from that in the volutes. The radula of *Harpa* is more like that of the Volutidae than the type that is found in most olivids. Both *Harpa* and the olivids have a distinct propodium, a feature not found in any other neogastropods, but this by itself does not necessarily indicate their close relationship. The Olividae and the Harpidae may have both independently developed the muscular propodium of the foot, which is such a useful digging tool. There are several other differences between the 2 families, for example the harpids have a pallial sperm groove (Bergh, 1901), but this is a closed duct in the olivids.

Harpidae

An account of the morphology of this family is given by Bergh (1901) and Quoy & Gaimard (1833). These authors describe how the posterior end of the foot can be automatized. The valve and gland of Leiblein have been lost and there is apparently no anal gland or purple hypobranchial secretion. There is no operculum.

The lack of an anal gland and accessory salivary glands, together with the pycnonéphridien condition of the renal organ, suggest affinity with the Buccinidae. This, however, is rather unlikely considering the other morphological features.

Volutomitridae and Marginellidae

A list of morphological features of these 2 families is given by Ponder (1970a,

1972b). They have several unusual features in common and thus they may have arisen from a common stem. These characters include a single accessory salivary gland; the seminal receptacle lined with large, cuboidal cells; the absence of an ingesting gland; and a narrow diverticulum of the renal organ which approaches or enters the renal genital duct. From the situation in the Volutomitridae, it would appear also that the unpaired foregut gland may have been stripped off the mid-oesophagus forwards instead of backwards.

Both families consist of species with small shells which have columellar plaits. All marginellids and many microvolutids have lost the operculum but some microvolutids have retained it or have it as a rudiment. The lateral radular teeth are absent in the Marginellidae and weak or absent in the Microvolutidae. Differences between the 2 families include the structure of the mid-oesophagus, the male reproductive system, the stomach and the renal organ. Cernohorsky (1970) has reviewed the Volutomitridae.

Wenz (1938) gives an Eocene origin for the Marginellidae, but the Upper Cretaceous genus *Myobarbum* Sohl is possibly an early marginellid.

Mitridae and Vexillidae

The structural differences between these 2 families have been outlined by Ponder (1972b). The 2 groups appear to have evolved quite independently, but show a remarkable parallelism in their shell morphology. Differences in the alimentary canal, including the radula, and in the renal organ, set the 2 families apart. There is a similarity in the reproductive organs, but this is probably part of the general uniformity in these organs throughout the Neogastropoda. Cernohorsky (1970) has reviewed these 2 families (as the Mitridae) in some detail.

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ZUSAMMENFASSUNG

ABSTAMMUNG UND ENTWICKLUNG DER NEOGASTROPODEN

W. F. Ponder

Die Ordnung Neogastropoda entwickelte sich wahrscheinlich aus den Archaeogastropoden und nicht von den höheren Mesogastropoden, wie allgemein angenommen wird. Es wird angenommen, daß die Eigenarten des Verdauungssystems der Neogastropoden von Bildungen abgeleitet werden können, die bei den Archaeogastropoden existieren. Die Neogastropoden haben sich augenscheinlich in 3 Gruppen entwickelt, die hier als Oberfamilien betrachtet werden, die Muricaceae, Conaceae und Cancellariaceae.

Die Entwicklung der verschiedenen Organsysteme bei den Neogastropoda wird skizziert und dabei die Tendenz bemerkt, Strukturen in paralleler Richtung zu modifizieren. Die Beziehungen der einzelnen Familien innerhalb der Muricaceae untereinander werden diskutiert. Es scheint, daß innerhalb dieser Gruppe keine natürlichen höheren Gruppierungen existieren, zwei Fälle ausgenommen, Wahrscheinlich, weil alle diese Familien von der gleichen Stammform mehr oder weniger gleichzeitig abgezweigt sind. So sind verschiedene Strukturen ziemlich zufällig durch die Oberfamilie verteilt, je nach der Weise, wie sich jede Familie weiterentwickelt hat. Die

Marginellidae und Volutomitridae können unabhängig entstanden sein, während die Buccinidae, Melongenidae, Nassariidae und Fasciolariidae so nahe verwandt sind, daß sie möglicherweise als Unterfamilien angesehen werden können.

H.Z.

RESUME

L'ORIGINE ET L'EVOLUTION DES NEOGASTROPODES

W. F. Ponder

L'ordre des Néogastropodes a probablement évolué à partir des Archéogastropodes et non des Mésogastropodes supérieurs, comme on le croit généralement. Il est probable que les caractères uniques du canal alimentaire des néogastropodes aient pu dériver de structures existant chez les archéogastropodes. Les néogastropodes semblent avoir évolué en 3 groupes qui sont ici considérés comme des superfamilles: les Muricacea, Conacea et Cancellariacea.

Dans la présente étude on a tracé à grands traits l'évolution des divers appareils à l'intérieur des néogastropodes et l'on y a noté la tendance à modifier les structures dans des voies parallèles. Les liens de parenté entre chaque famille chez les Muricacea, ont été discutés. A deux exceptions près, il apparaît que dans ce groupe, il n'y a pas de groupements naturels de plus haut niveau, sans doute parce que toutes les familles évoluent à partir d'un ancêtre commun à peu près simultanément. Ainsi les divers types de structures sont distribuées presque au hasard à travers la superfamille, selon la voie dans laquelle chaque famille a évolué. Les Marginellidae et Volutomitridae peuvent être apparues indépendamment, tandis que les Buccinidae, Melongenidae, Nassariidae et Fasciolariidae sont de parenté si proche, qu'elles peuvent être considérées comme des sous-familles.

A.L.

RESUMEN

ORIGEN Y EVOLUCION DE LOS NEOGASTROPODA

W. F. Ponder

El orden Neogastropoda probablemente tuvo descendencia de los Archaeogastropoda y no, como generalmente se cree, de los más evolucionados Mesogastropoda. Se sugiere que las características, únicas, del canal alimenticio en neogastrópodos, pueden haber derivado de estructuras ya existentes en arqueogastrópodos. Parece que, en su evolución los Neogastropoda han producido tres grupos, a los cuales se asigna aquí el rango de superfamilias: Muricacea, Conacea y Cancellariacea.

Se han delineado en forma general los varios sistemas de órganos en Neogastropoda, y se hace notar la tendencia hacia la modificación de estructura en modo paralelo. Se discute también las relaciones entre las familias de los Muricacea. Con un par de excepciones, no parece haber dentro del conjunto grupos naturales de más alta jerarquía, probablemente porque todas las familias se derivan de un antecesor común más o menos simultáneamente. Así, varias estructuras se distribuyen casi al azar en toda la superfamilia, de acuerdo al modo en que cada familia ha evolucionado. Los Marginellidae y los Volutomitridae pueden haber tenido independiente origen, mientras que los Buccinidae, Melongenidae, Nassariidae y Fasciolariidae están tan estrechamente relacionados, que posiblemente podrían considerarse como subfamilias.

J.J.P.

АБСТРАКТ

ПРОИСХОЖДЕНИЕ И ЭВОЛЮЦИЯ NEOGASTROPODA

В. Ф. ПОНДЕР

Отряд *Neogastropoda* развился из *Archaeogastropoda*, а не из высших *Mesogastropoda*, как это обычно считают. Предполагается, что характерные черты строения пищеварительного канала у *Neogastropoda* можно произвести от уже существовавших их структур у *Archaeogastropoda*. *Neogastropoda* видимо должны быть разделены на 3 группы, которые автором рассматриваются как надсемейства - *Muricea*, *Conacea* и *Cancellariacea*.

Рассматривается эволюция систем различных органов внутри отряда *Neogastropoda* и подчеркивается тенденция к параллелизму в модификации их структур. Обозначаются родственные связи каждого семейства в отряде *Muricea*. За двумя исключениями внутри этого отряда видимо нет более высших естественных группировок, может быть потому, что все семейства произошли более или менее одновременно от общего предка. Таким образом, различные структуры встречаются довольно случайно во всем надсемействе, соответственно происхождению каждого входящего в него семейства.

Marginellidae и *Volutomitridae* могли возникнуть независимо друг от друга, в то время, как *Buccinidae*, *Melongenidae*, *Nassariidae* и *Fasciolaridae* имеют такое близкое родство, что их возможно рассматривать как надсемейство.

Z.A.F.