

AN OUTLINE OF CASSOIDEAN PHYLOGENY (MOLLUSCA, GASTROPODA)

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The phylogeny of cassoidean gastropods is reviewed, incorporating most of the biological and palaeontological data from the literature. Several characters have been checked personally and some new data are presented and included in the cladistic analysis. The Laubierinioidea, Calyptraeidea and Capuloidea are used as outgroups. Twenty-three apomorphies are discussed and used to define cassoidean relations at the subfamily level. A classification is presented in which only three families are recognised. The Ranellidae contains the subfamilies Bursinae, Cymatiinae and Ranellinae. The Pisanianurinae is removed from the Ranellidae and attributed to the Laubierinioidea. The Cassidae include the Cassinae, Oocorythinae, Phaliinae and Tonninae. The Ranellinae and Oocorythinae are both paraphyletic taxa and are considered to represent the stem-groups of their families. The third family, the Personidae, cannot be subdivided into subfamilies and for anatomical reasons probably evolved from the same Early Cretaceous gastropod ancestor as the Ranellidae. The Cassidae (Oocorythinae) appears to have branched off from the Ranellidae (Ranellinae) during the Late Cretaceous. The first significant radiation of the Ranellidae/Cassidae branch took place in the Eocene. The Tonninae represents the youngest branch of the phylogenetic tree.

Key words — Neomesogastropoda, Cassoidea, ecology, morphology, fossil evidence, systematics.

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superfamily, some of them presenting a complete classification. Modern prosobranch classification schemes (e.g. Ponder & Warén, 1988; Vaught, 1989) recognise five cassoidean families: Bursidae, Cassidae, Ficidae, Ranellidae and Tonnidae. Beu (1988a; see also Beu & Maxwell, 1990) convincingly showed that *Distorsio* and its allies, which previously had been attributed to the Ranellidae, represent a distinct family. This is strongly supported here and was adopted in the latest comprehensive publication on the Cassoidea by Warén & Bouchet (1990), who also introduced the Laubierinidae as a new cassoidean family. The classification has been subsequently revised by Riedel (1994), who removed the Ficidae from the Cassoidea and by Bandel & Riedel (1994), who excluded the Laubierinidae. The remaining five families are the subject of this paper, which is an attempt at a clearly defined phylogenetic analysis on which a classification can be based.

INTRODUCTION

The Cassoidea (= Doliacea = Tonnoidea), containing such spectacular gastropods as the tritons and helmet-shells, have been the subject of research for a long time. Many authors have contributed to the knowledge of the

MATERIAL AND METHODS

Living animals were observed and collected by the author

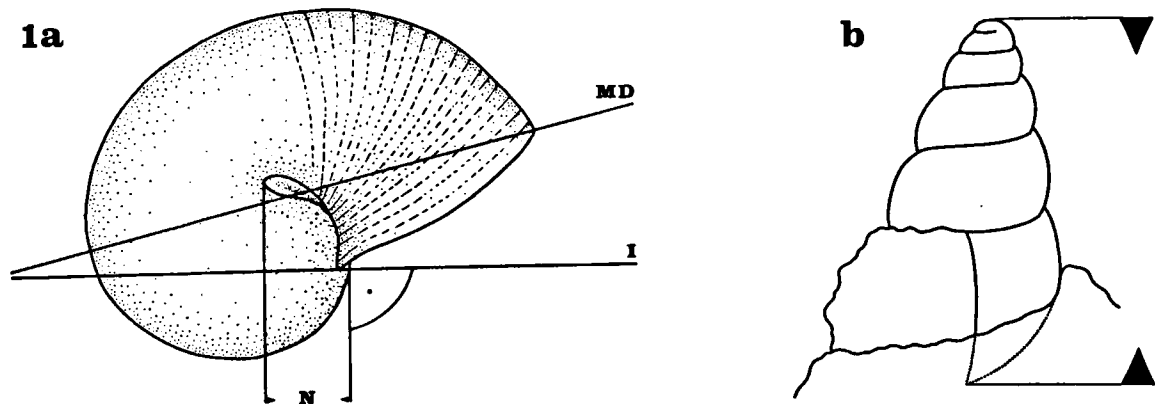


Fig. 1. A: Initial whorl of shell with indication how to measure the maximum diameter (MD) and method of counting whorls; N - nonspiral of shell, I - initial axis defining zero point. B: height of the last protoconch whorl has to be correlated to get a better understanding of height/width ratio.

(by snorkeling, diving and dredging) at several places in New Zealand (including Leigh Laboratory, Portobello Marine Station), Australia (Long Reef/Sydney, Heron Island, Lizard Island) and Bali (Indonesia). The snails usually were relaxed using a magnesium chloride solution isotonic with seawater (3.5 %) and then fixed in 70 % ethanol or 5 to 10 % formalin.

Klaus Bandel (Hamburg, Germany) provided shells of Recent cassoids from the Caribbean, the Mediterranean and the Red Sea. Alan Beu (Lower Hutt, New Zealand) and Bob Penniket (deceased, formerly Warkworth, New Zealand) generously donated several juvenile specimens with preserved protoconchs for further comparison. Additional dry and wet material was borrowed from the Australian Museum (Sydney), the Institut für Hydrobiologie und Fischereiwissenschaft (Hamburg), the Musée royal de l'Afrique Centrale (Tervuren), the National Museum of New Zealand (Wellington) and the Zoologisches Institut und Museum (Hamburg).

Fossil material originating from the Campanian of Mississippi (Coon Creek) and the Paleocene of Alabama (Matthews Landing) was collected by Klaus Bandel in co-operation with David T. Dockery (Jackson). Klaus Bandel and colleagues provided Eocene gastropods from the Brazos River (Texas) and Oligocene gastropods from Glimmerode (northern Germany) among which cassoids with well-preserved protoconchs were examined. Several excellently preserved gastropod faunas from various European Paleocene, Eocene and Miocene localities were borrowed from the Institut royal des Sciences naturelles de Belgique (Brussels), the Nationaal Natuurhistorisch Museum (Leiden) and the Naturhistorisches Museum (Vienna).

Protoconchs, shells of juveniles and radulae were mounted on stubs, coated with gold and examined with the aid of an electron microscope (CamScan). Larger

specimens were photographed using a reflex camera. The method of counting whorls and measuring dimensions of protoconchs is illustrated in Fig. 1.

CLASSIFICATION

The arrangement of the taxa is of course based on phylogenetic considerations. However, in contrast to the phylogenetic cladogram, it appears preferable to introduce the classification as understood by the author, before the characters of certain taxa are discussed. This procedure will hopefully avoid possible nomenclatural confusion. The main changes or rearrangements, compared to other classifications (*e.g.* Thiele, 1929; D.W. Taylor & Sohl, 1962; Golikov & Starobogatov, 1975; Beu, 1981, 1985, 1988a; Ponder & Warén, 1988; Beu & Maxwell, 1990; Warén & Bouchet, 1990) are briefly introduced, but will be discussed in more detail elsewhere in the present paper.

The Ficidae Meek, 1864 have already been removed from the Cassoidea and been recognised as a superfamily (Riedel, 1994). The inclusion of the Laubierinidae Warén & Bouchet, 1990 and Pisanianurinae Warén & Bouchet, 1990 in the Cassoidea presents difficulties on account of the absence of a larval pallial appendage, which unites the other families (compare Bandel & Riedel, 1994). No secondary periostracum on the larval shells is documented in the literature (Warén & Bouchet, 1990). Moreover, the Laubierinidae and Pisanianurinae do not show the episodic growth of the teleoconch which is characteristic for cassoids. It is difficult to imagine that this character was lost. Many other gaps in knowledge have to be bridged and other anatomical features are of uncertain interpretation, *e.g.* the monopectinate osphradium in the Laubierinidae or the asymmetrical osphradium in the

Pisanianurinae have not been recorded in the Cassoidea. The Laubierinidae had already been removed from the Cassoidea (Bandel & Riedel, 1994) and the Pisanianurinae, which, in addition to conchological characters also show anatomical features which are very similar to those of laubierinids, should be provisionally placed within the superfamily Laubierinioidea. Alan Beu (pers. comm.) concurs with this view.

The tun-shells (*Tonna* and its relatives) are recognised as a subfamily of the Cassidae and the frog-shells (*Bursa* and its relatives) possibly represent the sister group of the Cymatiinae. *Sassia* and *Charonia* have been removed from the Cymatiinae and are attributed to the Ranellinae but perhaps represent an independent ranellid branch (subfamily). *Dalium*, *Galeodea* and *Sconsia* have usually been assigned to the Cassinae, but are here considered to be better placed in the Oocorythinae. Subgenera and extinct taxa are not included in the classification presented below. *Personopsis* currently contains but a single Recent species, which, however, will be reassigned by Beu (pers. comm.) to a new personid genus. This means that *Personopsis* will have to be removed from the list of Recent genera when that new name is coined.

Subclass	Caenogastropoda Cox, 1959
Order	Neomesogastropoda Bandel, 1991
Suborder	Troschelina Bandel & Riedel, 1994
Superfamily	Cassoidea Latreille, 1825
1 - Family	Personidae Gray, 1854 <i>Distorsio</i> Röding, 1798 <i>Distorsionella</i> Beu, 1978 ? <i>Personopsis</i> Beu, 1988
2 - Family	Ranellidae Gray, 1854
2a - Subfamily	Bursinae Thiele, 1925 <i>Bufonaria</i> Schumacher, 1817 <i>Bursa</i> Röding, 1798 <i>Crossata</i> Jousseau, 1881 <i>Tutufa</i> Jousseau, 1881
2b - Subfamily	Cymatiinae Iredale, 1913 <i>Cabestana</i> Röding, 1798 <i>Cymatium</i> Röding, 1798
2c - Subfamily	Ranellinae Gray, 1854 <i>Argobuccinum</i> Herrmannsen, 1846 ? <i>Charonia</i> Gistel, 1848 <i>Fusitriton</i> Cossmann, 1903 <i>Gyrineum</i> Link, 1807 <i>Ranella</i> Lamarck, 1816 ? <i>Sassia</i> Bellardi, 1872
3 - Family	Cassidae Latreille, 1825

3a - Subfamily	Cassinae Latreille, 1825 <i>Cassis</i> Scopoli, 1777 <i>Cypraecassis</i> Stutchbury, 1837
3b - Subfamily	Oocorythinae Fischer, 1885 <i>Dalium</i> Dall, 1889 <i>Galeodea</i> Link, 1807 <i>Oocorys</i> Fischer, 1883 <i>Sconsia</i> Gray, 1847
3c - Subfamily	Phaliinae Beu, 1981 <i>Casmaria</i> H. & A. Adams, 1853 <i>Phalium</i> Link, 1807 <i>Semicassis</i> Mörch, 1852
3d - Subfamily	Tonninae Suter, 1913 <i>Eudolium</i> Dall, 1889 <i>Malea</i> Valenciennes, 1883 <i>Tonna</i> Brünnich, 1772

DISTRIBUTION, HABITAT AND DIET

Personidae live in most warm oceans and are mainly represented by the genus *Distorsio* (compare Clench & Turner, 1957; Lewis, 1972; Beu, 1985). *Personopsis* (?) is known exclusively from the West Pacific (Beu, 1985) and *Distorsionella* appears to be restricted to the southern West Pacific (Beu, 1978b, 1985).

Common species such as *Distorsio anus* (Linné, 1758) and *Distorsio reticulata* Röding, 1798, can be found in shallow-water habitats (Orr Maes, 1967; Cernohorsky, 1971; Lewis, 1972), usually under coral rubble (Cernohorsky, 1971). *Distorsio kurzi* Petuch & Harasewych, 1980 was reported from 120-130 m depth in the Sulu Sea (Petuch & Harasewych, 1980), which however is easily surpassed by *Distorsionella lewisi* Beu, 1978, which was dredged in more than 600 m depth (Beu, 1978b). Shasky (1992) reported *Personopsis* (?) *pusilla* (Pease, 1861) from about 10-30 m depth living on stones and pieces of corals.

There are no observations on the feeding strategy of the Personidae. However, J.D. Taylor (1980) found remains of a chaetopteric (Polychaeta) in the alimentary tract of *Distorsio reticulata*. Personal examination of the stomach of *Distorsio* sp. has revealed the cuticle of a 'worm'.

Ranellidae are distributed worldwide and at present are missing only from Arctic and Antarctic seas. Some species occur at many places across the world, e.g. *Cymatium parthenopeum* (von Salis, 1793), which was recorded (see Beu, 1985) from the western Atlantic (Bermudas to Uruguay), the eastern Atlantic (Spain to Angola), the Mediterranean, South Africa, the northern Indian Ocean, Japan, Hawaii, Australia and New Zealand

(Laxton, 1968; Beu, 1970c). Other species of *Cymatium* usually do not exceed these latitudes. *Cabestana* has been reported as far north as Great Britain (Fretter & Graham, 1981; Graham, 1988) and as far south as New Zealand (Powell, 1979) and Argentina but does not occur in the tropics (Beu, 1985). *Charonia*, with the two species *C. tritonis* (Linné, 1758) and *C. lampas* (Linné, 1758), has a similarly wide distribution as does *Cymatium* (Laxton, 1968; Beu, 1970a, 1985; Fretter & Graham, 1981; Graham, 1988). *Ranella*, also with two species attributed to it, occurs from the western Atlantic (via the Indian Ocean) to New Zealand (Dell & Dance, 1963; Arnaud & Beurois, 1972; Beu, 1985). *Fusitriton* has been reported from the temperate and cool waters of the northern hemisphere (J.T. Smith, 1970; Stickle & Mrozek, 1973; Somerton, 1981; Beu, 1985) as well as from the southern hemisphere (J.T. Smith, 1970; Penchaszadeh & De Mahieu, 1975; Beu, 1978a, 1985) but not from the tropics (see discussion). *Argobuccinum* is restricted to the southern hemisphere, being absent from the tropics (J.T. Smith, 1970; Beu, 1985). *Sassia* is a predominantly Indo-Pacific genus with the exception of a single Caribbean species (*Sassia lewisi* Harasewych & Petuch, 1980). *Gyrineum* has a 'worldwide' distribution, mainly in tropical, but also in temperate seas (Beu, 1985). The Bursinae occur mainly in the Indo-Pacific (Beu, 1981, 1985) but also in the Atlantic Ocean, including the Mediterranean (Sabelli & Spada, 1982). The group is unknown from cool waters at high latitudes.

The species of *Cymatium* can be found most commonly in calm (Bandel & Wedler, 1987) and shallow waters, usually under stones, broken platform corals, etc. (Orr Maes, 1967; Houbriek & Fretter, 1969; Bandel, 1976a; pers. obs.). Some species, such as *C. nicobaricum* (Röding, 1798), enter open (unsheltered) areas relatively often. *Cymatium pileare* (Linné, 1758) prefers the seaward side of reefs where currents are strong (J.D. Taylor, 1978), while *C. parthenopeum* is known to dig into soft substrates (Kilburn, 1970). *Cymatium (Linatella) caudatum* (Gmelin, 1791) has been reported from coral rubble and sandy bottoms in fairly deep water (Cernohorsky, 1971; Morton, 1990) but also occurs commonly on intertidal rocks in Hong Kong (Morton, 1990). The genus *Cabestana*, with *C. spengleri* (Perry, 1811), is known from intertidal rocky areas (Riedel, 1992) and *C. cutacea* (Linné, 1767) from soft bottoms (Fretter & Graham, 1981; Graham, 1988). The Ranellinae contain genera or even single species which usually live in a wide range of water depth and because of this can also be found on different substrates. A good example is *Fusitriton magellanicus* (Röding, 1798), which is known from 20 m (pers. obs.) down to 1,500 m depth (Beu, 1978a), living on sandy or muddy bottoms, but also on

hard substrates (Beu, 1978a). *Fusitriton aurora* Hedley, 1916 was reported from 3,300 m (Hedley, 1916), which would have been the greatest depth on record for the ranellids, but this species is a buccinid (compare Dell, 1972). *Sassia kampyla* (Watson, 1855) can be found associated with *F. magellanicus* and is reported from as deep as 900 m (Beu, 1978a). *Argobuccinum pustulosum* (Lightfoot, 1786) was (personally) found at depths between 40 to 100 m but also occurs on intertidal rocks in southern New Zealand (Beu, pers. comm.). *Charonia*, in fairly shallow water, lives on rocky bottoms, but also on sand amongst seaweeds (Laxton, 1968; Bandel, 1976a). The two species of *Charonia* can both be found in deeper water (Beu, 1970a; Fretter & Graham, 1981; Graham, 1988), which probably is the more common habitat for the genus. Most Bursinae live in shallow or fairly deep water. They prefer hard substrates of coral reefs and surrounding areas (Orr Maes, 1967; Cernohorsky, 1971; Bandel, 1976a; Bandel & Wedler, 1987; pers. obs.).

The diet of ranellids consists of living or dead animals representing a wide range of taxa. Several genera have been observed to prey on echinoderms, which habit is otherwise exclusively known from Cassidae. *Cymatium nicobaricum* has been found to hunt other gastropods, including *Conus* (see Kohn, 1959), bivalves, 'worms' and barnacles (Houbriek & Fretter, 1969; Bandel, 1976a). *Cymatium parthenopeum* probably secretes a relaxing substance, which induces bivalve prey to open their valves (Loch, 1982a). *Cymatium pileare* has been observed to prey on mangrove oysters (Littlewood, 1989). *C. (Linatella) caudatum* has 'a catholic diet' (Morton, 1990, p. 478), preying on gastropods, cirripedes and ascidians and is a major pest of oyster farms in southern India (Beu, pers. comm.). *Cabestana spengleri* seems to prefer ascidians (Tunicata) (Laxton, 1968; Riedel, 1992), but was also observed feeding on polychaetes (Laxton, 1968). The genus *Charonia* became famous through Copland (1966), who reported that the triton preyed on the reef coral-killing asteroid *Acanthaster planci* (Linné, 1758). *Charonia* has since been observed to feed on other sea stars, as well as on echinoids and sea cucumbers (Laxton, 1968; Beu, 1970a; Bandel, 1976a, 1984; Bandel & Wedler, 1987), and on bivalves (Percharde, 1972). In the aquarium tanks of the Laboratoire Arago (southern France), a triton was fed for several years on fish and squid alone (Bandel, pers. comm., 1992). Kohn (1983) designated *Fusitriton* as the ranellid with the widest range of food (see discussion). This genus feeds on echinoids, asteroids, ophiuroids, tunicates, gastropods, bivalves, chitons and polychaetes. *Fusitriton* is able to paralyse its prey and possibly uses a substance based on tetramethylammonium (Asano & Itoh, 1960). Day (1969), on

the basis of aquarium experiments, proposed that *Argobuccinum pustulosum* preferred polychaetes. *Gyri-neum natator* (Röding, 1798) was found to consume algae (J.D. Taylor *et al.*, 1980), which habit is unknown in other Cassoidea (except for larvae). Among the Bursinae, several species of *Bursa* have been observed to consume 'starfish' (Orr Maes, 1967), ophiuroids and echinoids (J.D. Taylor, 1978, 1984; Kohn, 1983), annelids and other 'worms' (Houbrick & Fretter, 1969; J.D. Taylor, 1978, 1984; Bandel & Wedler, 1987), molluscs and cirripedes (Bandel, 1976a; Bandel & Wedler, 1987) and even sponges (J.D. Taylor, 1978, 1984). The alimentary tract of *Bufo nana* (Linné, 1758), in addition to ophiuroids and polychaetes, contained remains of fish (J.D. Taylor, 1980). I observed how a specimen of *Tutufa rubeta* (Linné, 1758) swallowed a comparatively large ophiuroid whole.

Species richness in the Cassidae is greatest in tropical seas. Some species, however, range into temperate and cooler waters. The two genera that make up the Cassinae, *Cassis* and *Cypraecassis*, appear to be confined to warm oceans, and probably both genera are longitudinally distributed worldwide. Among the Phaliinae, the genus *Semicassis* predominates, with a near-global distribution. *Semicassis labiata* (Perry, 1811) can be found in the southern hemisphere and like *S. semigranosa* (Lamarck, 1822) occurs in subantarctic seas (Abbott, 1968; Powell, 1979). *Phalium* is restricted to the Indo-Pacific and the third genus, *Casmaria*, occurs in the tropical Indo-Pacific, with the exception of *C. vibexmexicana* (Stearns, 1894), which is found off tropical west America, and of *C. ponderosa* (Gmelin, 1791), which is also known from the Caribbean (Emerson & Old, 1963; Abbott, 1968; Bradner & DuShane, 1982). Among the Oocorythinae the genus *Galeodea* is most widely distributed. Its species occur in the warm and temperate eastern Atlantic (Fretter & Graham, 1981; Graham, 1988), the Mediterranean (Erlanger, 1893; Fioroni, 1966a; Sabelli & Spada, 1978) and in the southwest Pacific (Dell, 1953; Ponder, 1984; pers. obs.). *Oocorys* has been recorded in the literature only from the (sub)tropical Atlantic (Fischer, 1883; Turner, 1948; Quinn, 1980; Warén & Bouchet, 1990; Bouchet & Warén, 1993), but *O. sulcata* Fischer, 1883 is abundant at bathyal depths all around New Zealand (Beu, pers. comm.). Thus the genus may have a similarly wide distribution as *Galeodea*. *Dalium* is known from the Caribbean only and *Sconsia* lives in the western Atlantic (Clench & Abbott, 1943; Clench, 1959). The Tonninae comprises two genera (*Tonna* and *Eudolium*) which can be found in the Atlantic as well as in the Indo-Pacific. *Tonna galea* (Linné, 1758) represents the species with the widest east-west distribution (Turner, 1948; Kiliyas, 1962; Abbott, 1974). The third genus, *Malea*, is known from

eastern Africa to western America (Kiliyas, 1962).

Most Cassidae seem to prefer soft substrates, from shallow to very deep water. However, there are very few records. *Cassis cornuta* (Linné, 1758) is regularly found on sandy bottoms at depths of 5 to 10 m (pers. obs.). Bandel & Wedler (1987) described *C. tuberosa* (Linné, 1758) and *C. madagascariensis* Lamarck, 1822 also from sandy bottoms and observed the juveniles to dig themselves in. This applies also to *Cypraecassis testiculus* (Linné, 1758), but digging is not restricted to early ontogeny (Bandel, 1976a). *Cypraecassis coarctata* (Sowerby, 1825) was observed to move on the vertical sides of rocks (Abbott, 1968). Both species of *Cypraecassis* were found in comparatively shallow water. *Phalium glaucum* (Linné, 1758) prefers sandy areas of the unsheltered seaward side of reefs (Abbott, 1968). *Semicassis labiata* was found in the intertidal, covered by sand (pers. obs.). One species of *Semicassis*, *S. microstoma* (von Martens, 1903) was dredged from soft bottoms in water depths of 200 to c 1,100 m (Abbott, 1968). Members of the Oocorythinae reach the greatest depth amongst representatives of the superfamily. Fischer (1883) recorded *Oocorys* from depth in excess of 3,600 m. *Galeodea rugosa* (Linné, 1771) has been found living on a muddy soft bottom at depths down to about 700 m (Fretter & Graham, 1981; Graham, 1988). *Tonna galea*, when resting, has usually been found subtidally, hidden in sand (Bandel & Wedler, 1987). Riedl (1983) characterised the habitat of the same species as a sublittoral soft bottom which may be largely covered by empty shells. Wilson & Gillet (1971) recorded other species of *Tonna* burying themselves in soft substrates. *Eudolium* has been dredged from soft bottoms, down to 800 m (Turner, 1948; Marshall, 1992). Kiliyas (1962) maintained that *Malea* might occur even in the deep sea. Bandel (pers. comm., 1992) found *Malea pomum* (Linné, 1758) in shallow water, on a sandy bottom.

There are a few reports on cassid diets. Schenck (1926) assumed bivalves to be the main food item. However, several species of *Cassis* obviously prefer regular (Lyman, 1937; D.R. Moore, 1956; Schroeder, 1962; Hughes & Hughes, 1971, 1981) or irregular echinoids (Foster, 1947; D.R. Moore, 1956; pers. obs. for *Cassis cornuta*). Edmunds & Edmunds (1973) observed (under aquarium conditions) *Cassis tuberosa* to feed on asteroids. *Cypraecassis testiculus* has been reported to prey on regular (Hughes & Hughes, 1981) as well as on irregular echinoids (Bandel & Wedler, 1987). Among the Oocorythinae there is one report that (under aquarium conditions) *Galeodea echinophora* (Linné, 1758) preys on the irregular echinoid *Echinocardium cordatum* (Pennant, 1777) (Hughes, 1986a). Quinn (1980), on the basis of the environment, speculated that *Oocorys* could feed on

'worms'. Species of *Phalium* and *Semicassis* have been described eating echinoids (D.R. Moore, 1956; J.D. Taylor, 1980) or bivalves (Abbott, 1968; Day, 1974). The Tonninae are recorded to feed on fish, crustaceans (Cernohorsky, 1972), echinoderms in general (Cernohorsky, 1972; Powell, 1979) and bivalves (Powell, 1979). Weber (1927) found a species of *Natica* in the oesophagus of *Tonna galea*. Species of *Tonna* have several times been observed to swallow holothurians whole (Grange, 1974; Bandel, 1976a, 1984; Sarver, 1977; Kohn, 1983; Morton, 1991; Fig. 2).

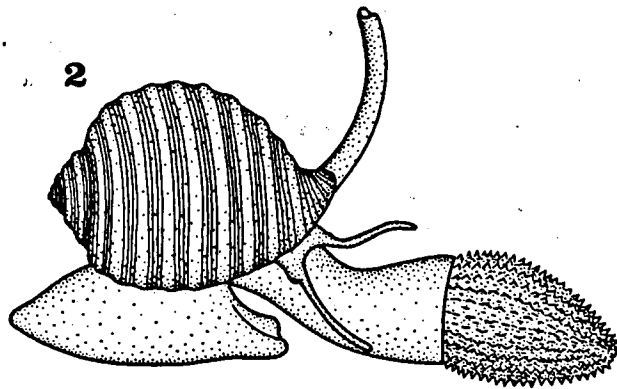


Fig. 2. *Tonna olearia* feeding on a holothurian (after Morton, 1991). Not to scale.

Marshall (1992) found sclerites of a holothurian in the alimentary tract of a *Eudolium* species.

Summarising remarks — naturally, the distribution of the Cassoidea is correlated to their postembryonic development. Below, the almost 'worldwide' occurrence of species such as *Cymatium parthenopeum* is linked to the larval development. The separation of two species of *Fusitriton* by the tropical ocean acting as a barrier appears strange. However, temperature changes of ocean surface waters occurred several times since the evolution of *Fusitriton* (at least since the Oligocene). A temperature decrease of about 5° C during Plio-Pleistocene glaciations (Krömmelbein, 1986) may have been sufficient for the larvae to cross the tropics (compare Beu, 1970d) and a second species of *Fusitriton* may have evolved since then.

Genera reaching great water depths are obviously adapted to cold temperatures. Consequently the same genera, such as *Fusitriton*, can be found closest to the polar oceans. Vice versa, shallow-water species such as most Bursinae, are not known to extend to high latitudes. The substrate preferred by certain cassoids usually can be directly correlated to their potential prey. A wide range of food usually means also a wide range of different substrates to live on.

Feeding experiments under aquarium conditions have clearly demonstrated that a hungry cassid loses its food preference and this may also occur under natural circumstances. However, it is not very convincing to offer only holothurians (see Morton, 1991) as food item and conclude that the genus *Tonna* specialises on these echinoderms. In addition to holothurians, Weber (1927) offered naticids to *Tonna*, and these were preferred (also under aquarium conditions). However, observations under natural conditions and based on examination of stomach contents (see also Bentivegna & Toscano, 1991) indicate that the Cassidae actually have a strong preference for echinoderms and that several genera or species prefer particular groups or species of echinoderms. In contrast, the Ranellidae are not specialised echinoderm feeders, but the fact that they may eat these animals unites them with the Cassidae. It is assumed that the Personidae do not prey on echinoderms, purely on the basis of two negative reports and judging also from the anatomy of these gastropods (see below).

EGG MASSES AND INTRACAPSULAR DEVELOPMENT

Knowledge of the egg masses of the Personidae is based on reports on three different species of *Distorsio* (d'Asaro, 1969a; Cernohorsky, 1971; Kasinathan *et al.*, 1974). The egg capsules are flattened spheres (Fig. 4e), about 1 mm in diameter, each containing 20-40 embryos (d'Asaro, 1969a; Kasinathan *et al.*, 1974). The egg capsules are usually arranged in more-or-less regular arcs; however, with many capsules produced, they form not one but several masses (d'Asaro, 1969a; Cernohorsky, 1971). The largest known spawn (d'Asaro, 1969a) contained about 50,000 embryos. The embryos of *Distorsio clathrata* (Lamarck, 1816) and *D. reticularis* (Linné, 1758) were observed to hatch as free-swimming veligers (d'Asaro, 1969a; Kasinathan *et al.*, 1974). The only detailed embryology was presented by d'Asaro (1969a).

The egg masses of most genera of the Ranellidae have been described in the literature. Among the Cymatiinae the spawn of several species of *Cymatium* (Lamy, 1928; Bouillaire, 1953; Arakawa, 1960; Laxton, 1969; Bandel, 1976a; Ramón, 1991) and *Cabestana* (Simroth, 1907; Lamy, 1928; D.T. Anderson, 1959; Laxton, 1968, 1969; Penchaszadeh & De Mahieu, 1975; Douglas, 1985; Ramón, 1991; Riedel, 1992) have been figured and/or described. The shape of the egg masses is always hemispherical, with a flattened base. The gelatinous hemisphere contains about 80 to 350 egg capsules, arranged in a three-dimensional spiral (Fig. 3).

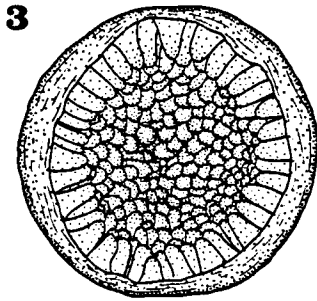


Fig. 3. Apical view of semi-hemispherical egg mass characteristic of Cymatiinae and Bursinae. Not to scale.

The shape of the capsules is more-or-less finger-shaped (Fig. 4d).

The diameters of the egg masses match the maximum width of the teleoconch aperture and sizes of egg masses and capsules are correlated to the sizes of the spawning females. The females were usually found to incubate the egg masses. The embryos of these recorded egg masses hatched as free-swimming veligers (except D.T. Anderson, 1959, but see Riedel, 1992). The number of embryos varies from about 100,000 to 900,000 (pers. obs.) per spawn (see remarks).

The egg capsules in *Fusitriton* are also arranged in a spiral, which is, however, two-dimensional (Philpott, 1925; Howard, 1962; Penchaszadeh & De Mahieu, 1975). *Argobuccinum* (see Kilburn & Rippey, 1982; pers. obs.), *Ranella* (see Laxton, 1968, 1969; Latigan, 1976), *Charonia* (see Lo Bianco, 1888; Bougis, 1950; McCamley, 1965; Berg, 1971; Cross, 1973; Amoroux, 1974; Bandel, 1976a; Marler & Marler, 1982) and *Gyrineum* (see Petit & Risbec, 1929) arrange their egg-capsules in more-or-less regular rows.

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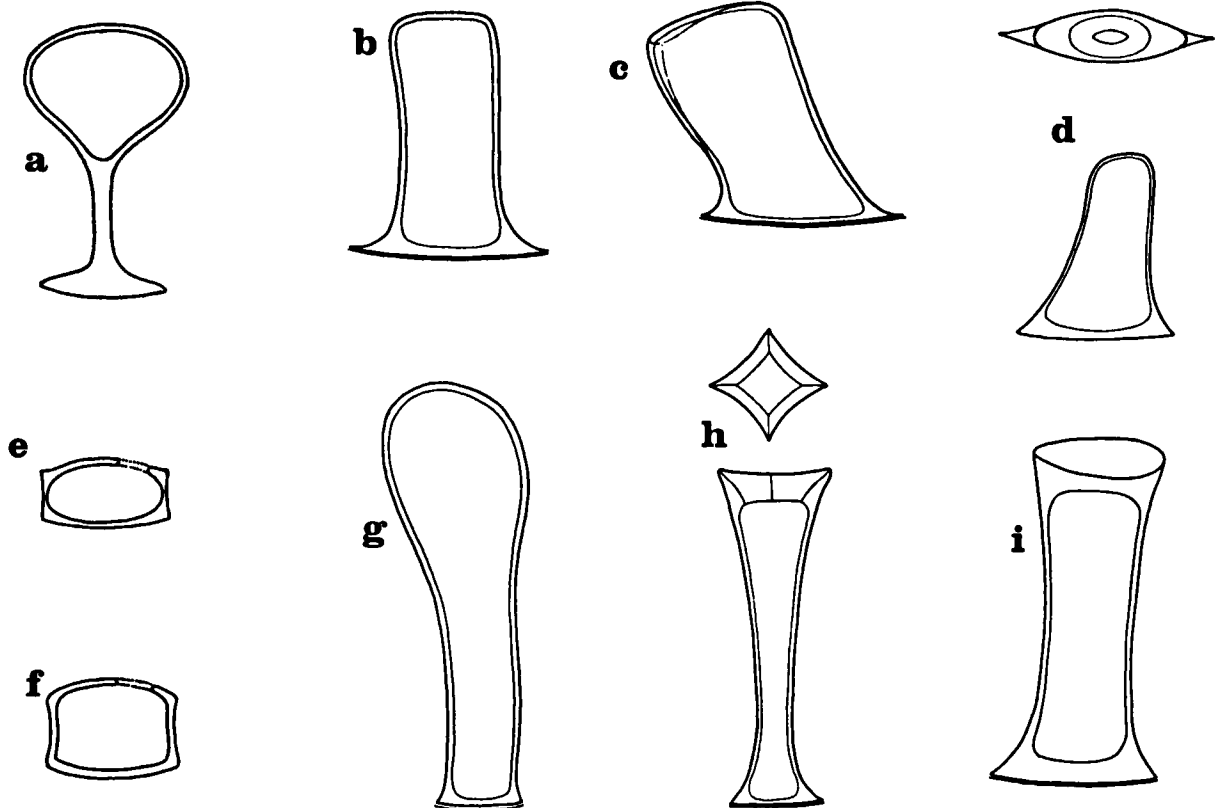


Fig. 4. Egg capsule types of Cassoidea in lateral view and apical view in d and h:

a - *Sassia* (after B.J. Smith *et al.*, 1989); b - *Fusitriton*, *Ranella*; c - *Argobuccinum*; d - Cymatiinae and Bursinae; e - *Distorsio* (after d'Asaro, 1969a); f - *Tonna* (after Bandel, 1976a); g - *Charonia* (after Marler & Marler, 1982); h - *Cassis* (after d'Asaro, 1969b); i - *Cypraecassis* (after Bandel, 1976a). Not to scale.

The shapes of the egg masses vary. The egg capsules are roughly finger-shaped in *Charonia*, *Ranella*, *Argobuccinum* and *Fusitriton* (Fig. 4) and may be somewhat angulate (Latigan, 1976; pers. obs.).

The capsules of *Charonia* can be easily distinguished by their circular cross section and the bulbous apex (Fig. 4g). The egg capsules of *Sassia* (*Austrotriton*) *subdistorta* (Lamarck, 1822) have been described as being wine-glass-shaped (cited by Beu, 1988b from Watson, 1971; B.J. Smith *et al.*, 1989; Fig. 4a). *Sassia bassi* (Angas, 1869) produces similar stalked egg capsules (B.J. Smith *et al.*, 1989). The capsules of *Gyrineum gyrinum* (Linné, 1758) are flattened ellipsoids (Petit & Risbec, 1929). Incubation has been reported in *Ranella australasia* (Perry, 1811) (see Laxton, 1969; Latigan, 1976), *Charonia lampas* (see Bandel, 1976a) and *Sassia subdistorta* (see Beu, 1988b). The number of egg capsules per spawn varies greatly, usually from 100 to 300. An egg mass of *Argobuccinum pustulosum* contained 130 capsules, with altogether nearly 500,000 embryos that all hatched as free-swimming veligers (pers. obs.). Free-swimming veligers have also been recorded for *Charonia*, *Ranella* and *Fusitriton*. The spawn of *Gyrineum gyrinum* was figured (Petit & Risbec, 1929) to consist of 18 capsules, containing a total of about 250 embryos (see remarks). The embryos of *Sassia subdistorta* feed on nurse eggs and only a single crawling juvenile emerges from each capsule (Watson, 1971; B.J. Smith *et al.*, 1989). This applies also to *Sassia bassi* (see B.J. Smith *et al.*, 1989).

Many Bursinae have egg masses and capsules which are very similar to those of the Cymatiinae (Figs 3, 4d). A more-or-less hemispherical or cup-shaped spawn was described for *Bursa granularis* (Röding, 1798) (see Risbec, 1931; McGinty, 1962; Orr Maes, 1967; Ganapati & Sastry, 1973; Bandel, 1976a), *Bursa corrugata* (Perry, 1811) (see d'Asaro, 1969a), *Bursa rhodostoma* (Sowerby, 1835) (see Loch, 1982b), *Bufonaria echinata* (Link, 1807) (see Thorson, 1940) and *Tutufa bufo* (Röding, 1798) (see Coleman, 1975). The egg masses were incubated by most species. The finger-shaped capsules vary in number from about 100 to 150 per spawn. According to d'Asaro (1969a) the egg mass of *Bursa corrugata* contains more than 100,000 embryos, which all hatch as free-swimming veligers. Thorson (1940) counted about 50-60 developing embryos in each capsule of *Bufonaria echinata* spawn. There is one report of nurse eggs in *Bursa* (see Fioroni, 1966b, but compare remarks). A complete embryogeny of *Bursa corrugata* was presented by d'Asaro (1969a).

The Cassidae exhibit at least three types of egg masses. Most Cassinae form an irregular, more-or-less two-dimensional spawn, with the egg-capsule bases (in rows) attached to a hard substrate. This holds true for

Cassis (see Anonymous, 1961; d'Asaro, 1969b) as well as for *Cypraecassis* (see Work, 1969; Bandel, 1976a; Hughes & Hughes, 1987). The egg capsules in *Cypraecassis* are column-like (Fig. 4i), with a rounded cross section, and in *Cassis* are vasiform with a more-or-less rectangular cross section (Fig. 4h). The apices of the capsules in both genera are somewhat collar-shaped, the central plate of the apex being surrounded by a gelatinous wall. *Cassis cornuta* has been reported to secrete about 230 capsules per spawn (Anonymous, 1961) and *Cassis madagascariensis* about 260 (d'Asaro, 1969b). *Cypraecassis testiculus* may spawn more than 800 egg capsules (Hughes & Hughes, 1987). Reports on *Cassis* cite about 600,000 embryos per spawn all of which hatch as free-swimming veligers. In *Cypraecassis* more than a million veligers may hatch (see also Bandel, 1976a). Incubation is not known in the Cassinae.

Amongst the Phaliinae, the egg masses of three *Semicassis* species have been described (D.T. Anderson, 1965; Abbott, 1968; Wilson & Gillet, 1971). The egg capsules are connected apically and basally (except for the 'ground floor') to each other (D.T. Anderson, 1965), forming a tower-shaped egg mass. In cases where communal spawning occurs (D.T. Anderson, 1965; Wilson & Gillet, 1971) the direction of capsule secretion is horizontal rather than vertical (see Abbott, 1968). The egg capsules are more-or-less finger-shaped and lack an apical collar. The number of developing embryos is vague, but probably amounts to hundreds of thousands (compare D.T. Anderson, 1965). Hatching of embryos was not observed. Huge egg masses are commonly incubated (D.T. Anderson, 1965; Wilson & Gillet, 1971), smaller ones by single individuals (Abbott, 1968).

Communal spawning is also assumed for large egg masses of *Galeodea* (see Erlanger, 1893). However, incubation has not been observed. The egg capsules are more-or-less irregularly (pea-) shaped, nearly as wide as high (Erlanger, 1893; Fioroni, 1966a; Hughes, 1986a). Erlanger (1893) and Fioroni (1966a) observed nurse eggs in the egg capsules of *Galeodea echinophora*, while Hughes (1986a) reported intracapsular cannibalism. About 10 % of the few hundred eggs per capsule (Erlanger, 1893) finally develop and hatch as crawling juveniles. The early development of *Galeodea rugosa* (see Fioroni, 1966a) is very similar to that of *G. echinophora*. The embryogenies of other Oocorythinae have not been observed.

The knowledge of Tonninae egg masses is restricted to the genus *Tonna*. The egg capsules always form a flat, tongue-shaped (or more-or-less irregular) spawn (Thorson, 1940, 1942; Panikkar & Tampi, 1949; Ostergaard, 1950; Amio, 1963; Gohar & Eisawy, 1967; Bandel, 1976a; Penschaszadeh, 1981). The egg capsules are arranged in

arcs and have the shape of a flattened sphere (Fig. 4f), similar to those of the Personidae. The largest spawn was reported by Bandel (1976a) to have a length of 43 cm and width of 8 cm. The number of egg capsules amounted to about 7,000 in that particular egg mass. The number of eggs in each *Tonna* egg capsule varies from about 20 to 100 (Thorson, 1940; Ostergaard, 1950; Bandel, 1976a). Large egg masses therefore contain several hundred thousand embryos, which usually hatch as free-swimming veligers (Panikkar & Tampi, 1949; Bandel, 1976a). Thorson (1940) and Penschaszadeh (1981) both described egg masses, in which they suspected that two different modes of development (in different capsules) occurred. Except for one report (Gohar & Eisawy, 1967), the egg masses of *Tonna* were all collected from soft bottoms. Incubation is unknown, though Ostergaard (1950) observed individuals of *Tonna* remaining near their spawn, which could imply a kind of protection.

Summarising remarks — the shape of an egg capsule is of course correlated with anatomical features. The shape of the spawn, however, must be viewed in the context of ecology and behaviour. In cases where an individual of the personid *Distorsio* forms several egg masses (which appears to be the rule), it is probably not possible to protect or incubate the spawn. The hemispherical egg mass (Fig. 3), which unites the Cymatiinae and Bursinae, can be protected perfectly, while the two-dimensional spawn of e.g. *Charonia* is too large to be fully incubated and usually several egg capsules at the periphery are eaten by predators (e.g. neogastropods; Bandel, pers. comm.). Communal spawning and incubation in *Ranella* and *Semicassis* have to be seen as convergences. The spawn of *Semicassis* is characteristic and cannot be confused. *Tonna* is the only known genus in the Cassoidea that places the egg mass directly on sand. The flat, broad spawn is well adapted to that habitat. However, camouflage, as in naticids, does not occur.

There are three main types of egg capsules in the Cassoidea (Fig. 4). The more-or-less finger-shaped capsule is typical for most Ranellidae, with the exception of *Sassia* and *Gyrineum*. A similar egg capsule type as in *Sassia* can be found also in the Calyptraeoidae (see Bandel, 1976b) and possibly represents the basal condition in the Cassoidea. An apical collar is found only in the Cassinae. The flattened egg capsules of *Distorsio* and *Tonna* are superficially similar, but differ in details (d'Asaro, 1969a; Bandel, 1976a). This capsule type (comparing the same strategy of development) usually contains significantly fewer embryos than the finger-shaped type. However, *Tonna* secretes many more egg capsules than all other cassoid genera and therefore reaches a similar veliger output as e.g. *Cymatium* or

Cassis, whereas *Distorsio* produces the lowest number of eggs in the superfamily. It must be emphasised that it is important to compare the number of eggs in the early embryogeny, as the number is greatly reduced when nurse egg feeding occurs. The low number of eggs reported from capsules of *Gyrineum gyrinum* (see Petit & Risbec, 1929) probably results from nurse egg feeding or intracapsular cannibalism (compare *Sassia subdistorta*). Fioroni (1966b) reported nurse eggs from *Bursa* egg capsules. However, the capsules are too large for any species of Bursinae known from the Mediterranean. Moreover, the spawn is of a different shape and was probably produced by a neogastropod.

It is commonly accepted, and it will also be shown here, that the protoconchs of species in most cases can be used to distinguish non-planktotrophic (nurse eggs, intracapsular cannibalism, lecithotrophic) from planktotrophic development, without actual observations on the early ontogeny.

Estimated egg contents of capsules in the literature, such as 'a few hundred' or 'several hundred', in some cases need to be checked. Several tests I did demonstrated that the actual number may be ten times the estimated total. Numbers of eggs and capsules have been confused in the literature by Amio (1963), who quoted Arakawa's (1960) count of the number of eggs per capsule in *Cymatium parthenopeum*, which, however, was actually the number of capsules for that egg mass. Kiliias (1962), citing Ostergaard (1950), reported 3,000 eggs in a spawn [*Tonna perdis* (Linné, 1758)], which was actually the number of capsules.

Embryogenies usually have to be observed under aquarium conditions. Tank conditions in some instances (e.g. D.T. Anderson, 1959; Gohar & Eisawy, 1967; Latigan, 1976) may have led to abnormal development. However, it must be taken into consideration that these conditions possibly may also occur under natural circumstances, and therefore such results should be included in discussions on macro-evolution.

A final remark on egg masses might seem trivial, but it was a surprise to me to discover that *Fusitriton oregonensis* (Redfield, 1846), occurring in the northern hemisphere, arranges the egg capsule spiral counter-clockwise, and *Fusitriton magellanicus*, which is restricted to the southern hemisphere, secretes a clockwise spiral (the Caribbean *Bursa granularis*: counter-clockwise; the Tasman Sea *Cabestana spengleri*: clockwise). These gastropods appear to react to the Coriolis force, but more data are needed.

LARVAL DEVELOPMENT

Larval development is here understood to be directly

correlated to planktotrophy. This limitation appears useful in the context of embryonic and larval shell characters (see next section). Intracapsular larval stages are attributed to the embryonic development. Lecitotrophic free-swimming veligers are somewhat intermediate, but a distinct larval shell is not built, which (also in the context of interpretation of fossil shells) is the main point here (see also next section).

Specific attributions of larvae call for careful consideration because in most cases only aspects of the ontogenies are known (compare *e.g.* *Distorsio clathrata* of d'Asaro, 1969a and Laursen, 1981). However, larval features of the Cassoidea are often characteristic at the generic level. Cassoid larvae are usually very large and some of them have even been interpreted as adult gastropods (*e.g.* MacDonald, 1855; Pilsbry, 1945). It is very difficult to rear veligers in an aquarium. Consequently nearly all the literature data reflect only stages of larval life, from which, however, some strategies can be extrapolated. Reports listed below all provide information on at least characteristic periostracum sculptures (which are usually corroded after metamorphosis). Living veligers of the Personidae were observed in the genus *Distorsio*. D'Asaro (1969a) provided information of the early veliger of *D. clathrata*. The veliger uses a pallial tentacle to secrete and form periostracal, carina-like, chambers. The velum is bilobate, but already shows lateral indentations, foreshadowing the quadrilobate stage. Bandel *et al.* (1994) described the 'late' veliger of a species of *Distorsio* from the Red Sea. The larva has a comparatively large foot, there are four long velar lobes and a pallial tentacle is used to secrete and form a periostracal carina (without chambers). Two larval shells of *Distorsio* species were figured by Laursen (1981), both bearing a periostracal carina, which, however, is different in the two specimens. An undetermined larva figured by Lebour (1945) also shows this characteristic periostracal sculpture.

Veligers of the Ranellidae have been observed or examined in the genera *Cymatium* (see Simroth, 1895; Lebour, 1945; Pilsbry, 1945, 1949; Scheltema, 1966; Laursen, 1981; Richter, 1984; Warén & Bouchet, 1990; Bandel, 1991; Bandel *et al.*, 1994), *Cabestana* (see Riedel, 1992), *Argobuccinum* (see Pilkington, 1974; pers. obs.), *Charonia* (see Simroth, 1895; Lebour, 1945; Scheltema, 1966; Laursen, 1981; Warén & Bouchet, 1990), *Fusitriton* (see Pilkington, 1976; Warén & Bouchet, 1990; pers. obs.), *Sassia* (see Pilkington, 1976) and *Bursa* (see d'Asaro 1969a; Scheltema, 1972; Laursen, 1981; Richter, 1984, 1987; Warén & Bouchet, 1990; Bandel *et al.*, 1994).

All larvae have in common that, during a certain larval stage, periostracal spines (some *Cymatium*,

Charonia, *Bursa*) or triangular indentations (*Argobuccinum*, *Fusitriton*, *Sassia*, some *Cymatium* ?) are secreted and potentially fixed on all whorls of the larval shell. This is accomplished by a pallial appendage and has been observed in *Charonia* (see Simroth, 1895; Bandel *et al.*, 1994) and *Cymatium* (Bandel *et al.*, 1994). The mode of secretion and formation of periostracum was described in detail by Bandel *et al.* (1994). Bursine larvae can be differentiated from other ranellids by the periostracum, which remains thin in the late larval stage, or vice versa, the periostracum is usually thicker in the larvae of Cymatiinae and Ranellinae (see Bandel *et al.*, 1994).

In all descriptions the early velum is said to be bilobate (see *e.g.* Riedel, 1992) and the late velum quadrilobate. The foot is usually large. Larval food could be identified in the alimentary tracts of *Cymatium* (see Richter, 1987; Bandel *et al.*, 1994), which contained remains of Radiolaria, Foraminifera, tintinnids, dinoflagellates, unidentified phytoplankton, and of *Bursa* (see d'Asaro, 1969a, Richter, 1987), in which Radiolaria, Foraminifera and dinoflagellates were found.

The larvae of the Cassidae other than Tonninae are scarcely known. Two larval shells of *Cypraecassis* (Laursen, 1981; Warén & Bouchet, 1990) and one of *Semicassis* (see Laursen, 1981) have been figured, which show the characteristic large size, but no special periostracum sculpture.

The veliger of the genus *Tonna* has been figured or described by several authors (MacDonald, 1855; Fischer, 1887; Simroth, 1895; Thorson, 1940; Lebour, 1945; Ostergaard, 1950; Scheltema, 1971; Laursen, 1981; Bandel, 1991; Bandel *et al.*, 1994). The velum of the early veliger is already slightly quadrilobate, and in late veligers the four velar lobes are comparatively very long. A proboscis is already formed in the newly hatched veliger (Thorson, 1940; Ostergaard, 1950). The larvae bear an operculum (Simroth, 1895; Bandel, 1991), which is lost during metamorphosis. The larval shells bear periostracal spines as well as spirally arranged, tiny, triangular indentations, which resemble homogeneous lirae under the light microscope (Bandel *et al.*, 1994). A larval pallial appendage was observed in *Tonna* by Simroth (1895) and Bandel *et al.* (1994).

Among the Cassidae the stomach contents of *Cypraecassis* larvae have been examined (Richter, 1987), which comprised fragments of dinoflagellates.

Scheltema (1971) coined and defined the term 'teleplanic' for long-term veligers. Simroth (1895) was the first to recognise that larvae of the Cassoidea may drift for several months. This was taken up by Scheltema (*e.g.* 1966, 1971, 1972, 1986), who demonstrated that certain veligers may stay in the plankton for up to a year.

Summarising remarks — there is strong evidence that the larval life of the Cassoidea reveals a synapomorphic character, allowing the three families to be united within the same superfamily. In some genera (*Distorsio*, *Cymatium*, *Charonia*, *Tonna*) of all three families, a larval pallial tentacle has actually been observed. Moreover, certain periostracal sculptural elements could not be produced by any means other than the pallial appendage. In this way, the existence of the appendage may be demonstrated without direct observation (for details see Bandel *et al.*, 1994).

The periostracal spines of small (young) larvae are relatively larger than those of large ones of the same species (compare Simroth, 1895; Laursen, 1981; Bandel *et al.*, 1994). The spines enlarge the diameter of a larval shell, which possibly is a protection from small predators (*e.g.* copepods). A thick periostracum and the spines must be interpreted also as protection from boring organisms or epibionts. Moreover, the periostracal sculptures have effects on the swimming activities (or buoyancy) of the veligers (compare Richter, 1973; Bandel *et al.*, 1994). Short, simple periostracal indentations such as in *Fusitriton magellanicus* and *Sassia kampyla*, are considered to be the more plesiomorphic condition. The possible absence of periostracal appendages in certain species must be considered lost (apomorphy).

Dawydoff (1940) illustrated a veliger that was attributed by Warén & Bouchet (1990) to the genus *Distorsio*. However, apart from a similar periostracal sculpture, this larva has little in common with a personid gastropod, since the eyes are on top of the cephalic tentacles, as in Strombimorpha. The systematic position of this peculiar veliger remains unclear.

PROTOCONCH AND TELEOCONCH

The embryonic shell (or protoconch 1 of authors) is defined here as that part of the conch that precedes a larval or a juvenile/adult shell. This means that the protoconch of all non-planktotrophic species consists of the embryonic shell only, whereas in planktotrophic species the protoconch may be divided into an embryonic and a larval shell (or protoconch 2 of authors). The teleoconch includes all shell material that does not belong to the protoconch.

The embryonic shells of planktotrophic cassoids are usually synonymous with the initial whorl of the conch. The embryonic shells of the Personidae are always (as far as known) smooth, whereas those of the Ranellidae and Cassidae bear a more-or-less regular pattern of tiny hollows with sharp projecting rims (compare Ramón, 1991; Riedel, 1992; Fig. 5). This sculpture is well

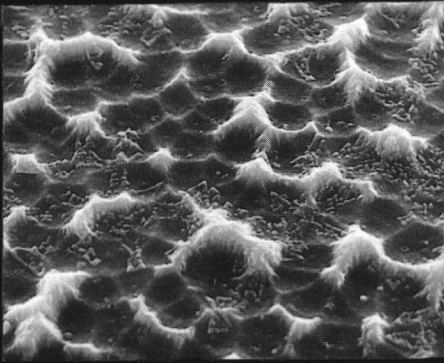
pronounced on comparatively small embryonic shells (*e.g.* in *Cabestana spengleri*), while it is scarcely developed in species with large initial whorls [*e.g.* *Ranella olearia* (Linné, 1758)].

The diameters of embryonic shells (of planktotrophic species) are given here (alphabetically) at the generic level:

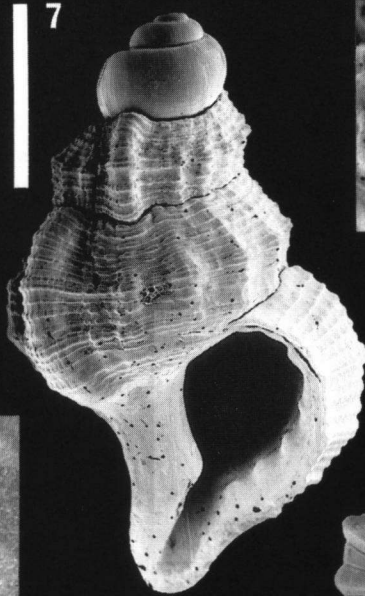
- *Argobuccinum*: 400 μm (pers. obs.)
- *Bufofaria*: 330 μm (Warén & Bouchet, 1990)
- *Bursa*: 150-320 μm (d'Asaro, 1969a; Bandel, 1975; Laursen, 1981; pers. obs.)
- *Cabestana*: 240 μm (Ramón, 1991; Riedel, 1992)
- *Charonia*: 500-850 μm (Berg, 1971; pers. obs.)
- *Cymatium*: 210-430 μm (Arakawa, 1960; Bandel, 1975; Beu, 1986; Ramón, 1991; pers. obs.)
- *Cypraecassis*: 220 μm (Laursen, 1981)
- *Distorsio*: 210-350 μm (d'Asaro, 1969a; Beu, 1986; pers. obs.)
- *Eudolium*: 290-300 μm (Warén & Bouchet, 1990; Marshall, 1992)
- *Fusitriton*: 400 μm (pers. obs.)
- *Gyrineum (Biplex)*: 500 μm (pers. obs.)
- *Malea*: 450 μm (pers. obs.)
- *Oocorys*: 420 μm (Bouchet & Warén, 1993)
- '*Personopsis*': 360 μm (pers. obs.)
- *Ranella*: 540-710 μm (Warén & Bouchet, 1990; pers. obs.)
- *Sassia*: 330-350 μm (pers. obs.)
- *Semicassis*: 330 μm (pers. obs.)
- *Tonna*: 400-560 μm (Thorson, 1940; Ostergaard, 1950; Amio, 1963; Gohar & Eisawy, 1967; Bandel, 1975; pers. obs.)
- *Tutufa*: 330 μm (pers. obs.)

The embryonic shells of non-planktotrophic cassoids usually consist of 1-2 whorls (pers. obs.). However, the diameters are relatively much larger than in planktotrophic species. A few examples: in *Cassis nana* Tenison-Woods, 1874 - 2.7 mm, *Galeodea triganceae* Dell, 1953 - 2 mm, *Gyrineum roseum* (Reeve, 1844) - 1.2 mm (Fig. 6). The typical embryonic shell ornament of planktotrophic species is lost. However, sometimes sculptural elements such as lirae, may be present, but these can be interpreted as having been derived (heterochronically) from the former larval shell sculptural pattern of a hypothetical ancestor.

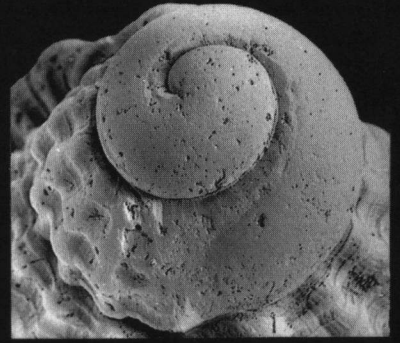
The larval shells of cassoids may reach huge sizes, which cannot be found in many other gastropod taxa. The number of whorls, maximum diameters (D) and heights (H) of larval shells of 86 Recent species have been taken (see Material and methods) from the literature (Cotton,



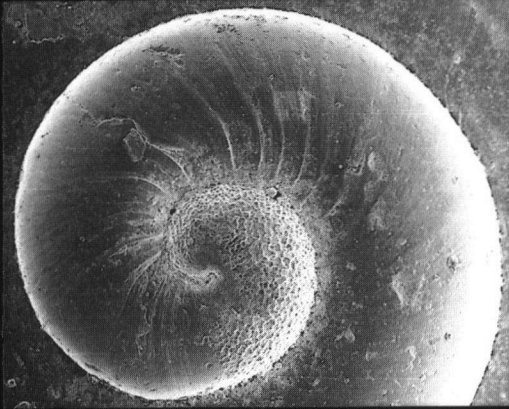
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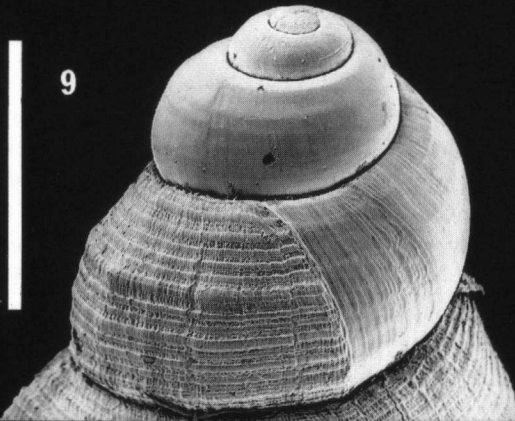
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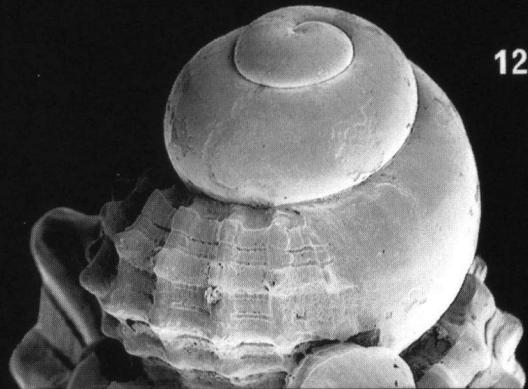
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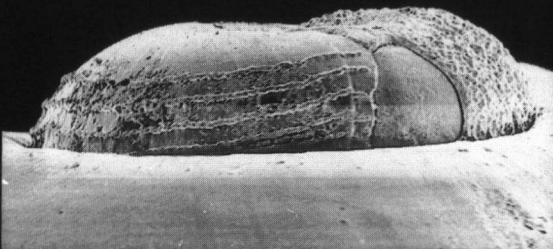
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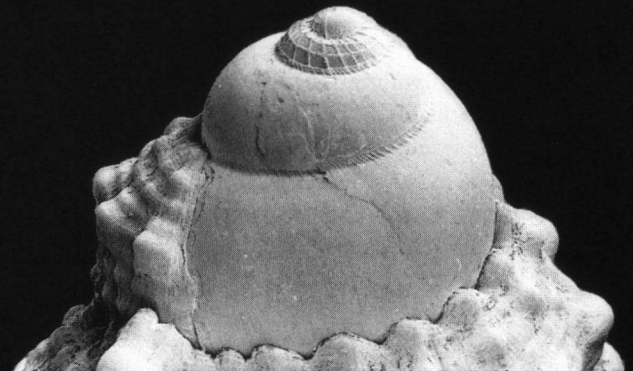
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1945; Clench & Turner, 1957; McGinty, 1962; Barnard, 1963; Abbott, 1968; Lewis, 1972; Beu, 1978a, b, 1986; Finlay, 1978; Petuch & Harasewych, 1980; Gibson-Smith & Gibson-Smith, 1981; Beu & Knudsen, 1987; Beu & Kay, 1988; Warén & Bouchet, 1990; Marshall, 1992; Abbott, 1993; Bouchet & Warén, 1993) or personally measured. The largest larval shell (as far as known) is that of *Tonna allium* (Dillwyn, 1817) with H = 5.7 mm and D = 5.45 mm (compare Bandel *et al.*, 1994). Approaching that size are the larval shells of *Ranella*, *Charonia* and some species of *Cymatium*. The smallest larval shell is found in *Distorsio euconstricta* Beu, 1986 with H = 1.0 mm and D = 1.05 mm. At present, this size defines the lowest limit among cassooid species.

Putting the H and D measurements together leads to the following H/D ratios, and six groups of larval shell shape are defined:

- I globular: H/D = 0.91-1.10: Personidae, Cassidae except for some Phaliinae, some *Bufo*nae, some *Sassia*, *Gyrineum* sp., *Fusitriton magellanicus*.
- II ovoid: H/D = 1.11-1.30: Bursinae except for some *Bufo*nae, *Ranella*, some *Sassia*, *Argobuccinum pustulosum*, some Phaliinae.
- III low conical: H/D = 1.31-1.50: *Cabestana*, *Charonia*, some *Cymatium*.
- IV conical: H/D = 1.51-1.70: some *Cymatium*.
- V high conical: H/D = 1.71-1.90: some *Cymatium*.
- VI turritiform: H/D = 1.91: some *Cymatium*.

The number of larval whorls varies from almost 2 to nearly 6. More than 3.5 whorls are found only in the Ranellidae, the highest numbers occurring in the genus *Cymatium*.

Larval shell ornament consists of axial and spiral lirae (or ribs) forming a reticulate pattern. Reticulation may be reduced to all degrees up to total absence (e.g. in *Sassia parkinsonia* (Perry, 1811) [Figs 7, 8] or species of *Distorsio*). Usually the number of sculptural elements is reduced and/or the reticulation has vanished from parts of the larval whorls (Figs 9-13).

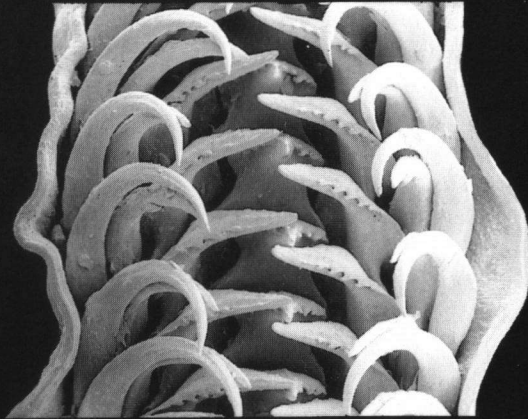
The teleoconchs are not described in detail and readers are referred to the pertinent literature (e.g. Fischer, 1887; Simroth, 1907; Vredenburg, 1919; Thiele, 1929; Clench & Abbott, 1943; Clench, 1944; Wenz, 1944; Turner, 1948; Clench & Turner, 1957; Kiliias, 1962, 1973; Dell, 1963; Cernohorsky, 1967, 1971, 1972; Abbott, 1968, 1974; Beu, 1970a, 1970b, 1970c, 1977, 1978a, b, 1981, 1985, 1986, 1988a, b; Bayer, 1971; Keen, 1971; Wilson & Gillet, 1971; Sabelli & Spada, 1978, 1982; Powell, 1979; Fretter & Graham, 1981; Beu & Cernohorsky, 1986; Beu & Knudsen, 1987; Beu & Kay, 1988; Graham, 1988; Lai, 1990; Warén & Bouchet, 1990; Emerson, 1991; Marshall, 1992; Bouchet & Warén, 1993).

Characters considered to be important for (sub)family phylogeny are the more-or-less distorted teleoconch of all Personidae and among the Ranellidae only the Bursinae (probably all) have an anal canal present in the outer lip at the posterior end of the aperture (Beu, 1981).

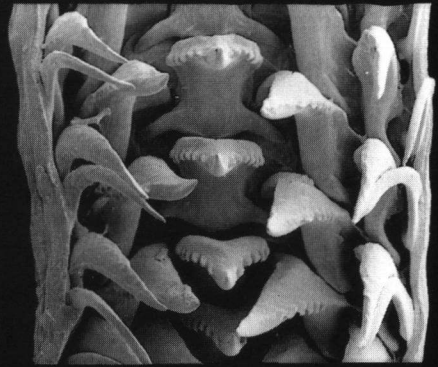
Summarising remarks — Embryonic shell sculpture (Fig. 5) similar to that of the Ranellidae and Cassidae occurs in many other groups, such as Cerithiimorpha and also in other neomesogastropod families (see Bandel, 1975). Therefore, the ornament has to be seen as symplesiomorphic for the Cassoidea, and lost in the Personidae. The typical sculpture of ranellids and cassids is not known from the Neogastropoda (which in other shell characters may be somewhat convergent [?] on certain cassooids), except for a few species such as *Melongena melongena* (Linné, 1758), which, however, has non-planktotrophic development (Bandel, 1975).

Figs 5-13. Photomicrographs illustrating morphology of cassoidean gastropod protoconchs.

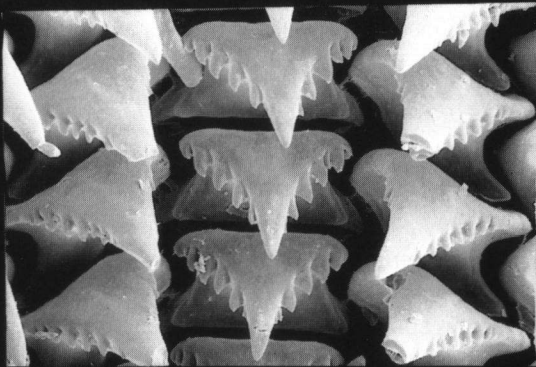
- 5 - Sculptural pattern of embryonic shell (of *Argobuccinum*), which is symplesiomorphic for the Cassoidea. Scale bar equals 10 μ m.
- 6 - Apical whorls of *Gyrineum roseum*, scale bar represents 1 mm.
- 7 - Juvenile shell of *Sassia parkinsonia*, scale bar equals 3 mm.
- 8 - Apical whorls of the same specimen as in Fig. 7, showing diameter and ornament of the embryonic shell and part of larval shell, which is smooth, apart from few remains of axial ribs on the first larval whorl. Scale bar equals 0.3 mm.
- 9 - Apical whorls of *Sassia kampyla*. Scale bar represents 2 mm.
- 10 - The same specimen as in Fig. 9, lateral view of transition from embryonic to first larval whorl, which is partly spirally liriate. Scale bar equals 0.2 mm.
- 11 - Juvenile shell of *Gyrineum (Biplex)* sp., showing the c 180° alignment of varices. Scale bar is 2 mm.
- 12 - Apical whorls of the same specimen as in Fig. 11. Scale bar equals 1 mm.
- 13 - Apical whorls of *Tutufa rubeta*, showing cancellate ornament on first larval whorl. Scale bar represents 2 mm



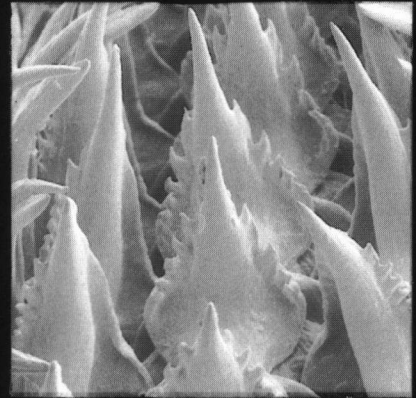
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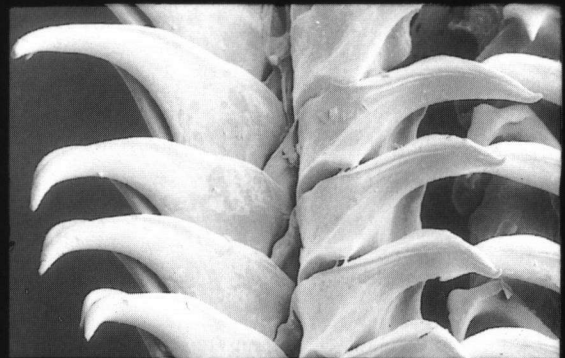
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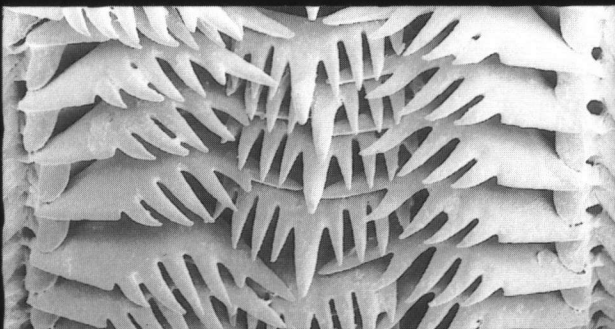
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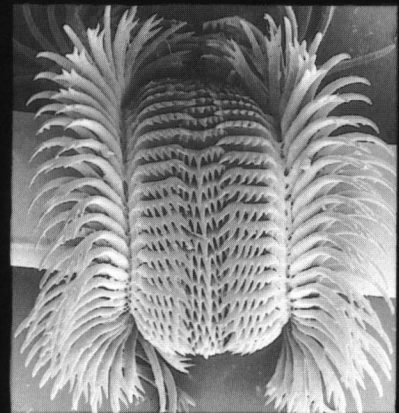
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The embryonic shell sculpture is possibly a useful character to distinguish higher taxa (compare Bandel & Riedel, 1994).

The large size of the initial whorl allows the Cassoidea to be differentiated from most other gastropod taxa (*i.e.* their early ontogenetic stages) with similar sculpture of the embryonic shell. The diameter in the Cerithiimorpha for example seldom exceeds 100 μm (Bandel, 1975). Among the Cypraeoidea some species are known (Ostergaard, 1950; Bandel, 1975; Tanaka, 1980; pers. obs.) in which the diameter of the embryonic shell lies within the range of the Bursinae. However, postembryonic stages of the Cypraeoidea certainly cannot be confused with those of any cassoid.

The correlation of embryonic shell size to teleoconch size is difficult. In several cases species with large adult teleoconchs have a large initial whorl, while species with a small adult teleoconch have a comparatively small embryonic shell. However, this cannot be generalised at all, as too many exceptions are known. The size of the embryonic shell must be interpreted in the context of the entire ontogeny of an individual. Comparing two species with a similar teleoconch size and with the same number of larval shell whorls, it can be expected that the embryonic shells are also about equal in diameter. However, if for instance the number of larval whorls is comparatively lower, the embryonic shell is larger in most taxa. This has to be seen as a derived character, because in early ontogenies, where no free larval phase is present, the initial whorl in almost all taxa is largest (with a few exceptions, see *e.g.* Wilson, 1985).

Planktotrophy, and therefore the existence of a larval shell, is a plesiomorphic character for the three cassoid families. A more-or-less globular shape and a comparatively small protoconch size (Personidae and some Ranellinae) are also 'primitive' characters within the Cassoidea (compare Bandel & Riedel, 1994). Conical or even turriform protoconchs occur only in

the Cymatiinae. The larval shells with the highest number of whorls are found in this subfamily. The larval shell sculpture is always based on a pattern of rectangles. However, this can be used as a character at several different taxonomic levels. No larval shells in the Cymatiinae and Bursinae are totally covered by axial and spiral ribs (forming the rectangles). However, complete reticulate ornament occurs in the Ranellinae and Oocorythinae. The Tonninae show a reduced pattern of rectangles, which is characteristic of this subfamily. Loss of sculpture has occurred in all families.

The plesiomorphic teleoconch type in the Cassoidea is assumed to be that of the Ranellinae, for example *Gyrineum* (see Fossil record). The pronounced posterior siphonal canal in the Bursinae represents an apomorphy.

The embryonic, larval and adult shell characters are not repeated in the discussion on the fossil record (see below). The recognition of fossil taxa is of course based on the modern fauna and plesiomorphy or apomorphy of characters is explained further in the context of the chronology of fossils.

ANATOMICAL FEATURES

Among the genera of the Personidae only *Distorsio* has been examined, but most references deal only or mainly with the radula (Troschel, 1863; Clench & Turner, 1957; Cernohorsky, 1967; Beu, 1978b; Bandel, 1984; Warén & Bouchet, 1990). The taenioglossan radula of *Distorsio* is comparatively small. For example, the central teeth of *D. clathrata* are about 60-70 μm wide (see Bandel, 1984; Warén & Bouchet, 1990), and the central teeth of *Distorsionella* are only about 20 μm wide (see Beu, 1978b). The radulae of *Distorsio* and *Distorsionella* show the same characteristic features in having small but strong, serrated, central (with down-curved ends) and lateral teeth and smooth, simple marginal teeth (Fig. 22). The radula of '*Personopsis*' is not known, neither is the animal.

Figs 14-21. Photomicrographs of cassoidean gastropod radulae.

- 14- Section of radula of *Fusitriton magellanicus*. Scale bar equals 0.3 mm.
- 15- *Fusitriton magellanicus*, magnification of central and lateral radular teeth. Scale bar represents 0.2 mm
- 16- Section of radula of *Cabestana spengleri*. Scale bar equals 0.2 mm.
- 17- *Cabestana spengleri*, magnification of central and lateral radular teeth. Scale bar represents 0.1 mm.
- 18- Central radular teeth of *Bursa* sp., showing basal interlocking processes. Scale bar equals 0.2 mm.
- 19- *Bursa* sp., magnification of lateral and marginal radular teeth. Scale bar equals 0.5 mm.
- 20- *Cassis cornuta*, magnification of central and lateral radular teeth. Scale bar represents 0.2 mm.
- 21- Radula of *Semicassis labiata*. Scale bar equals 1 mm.

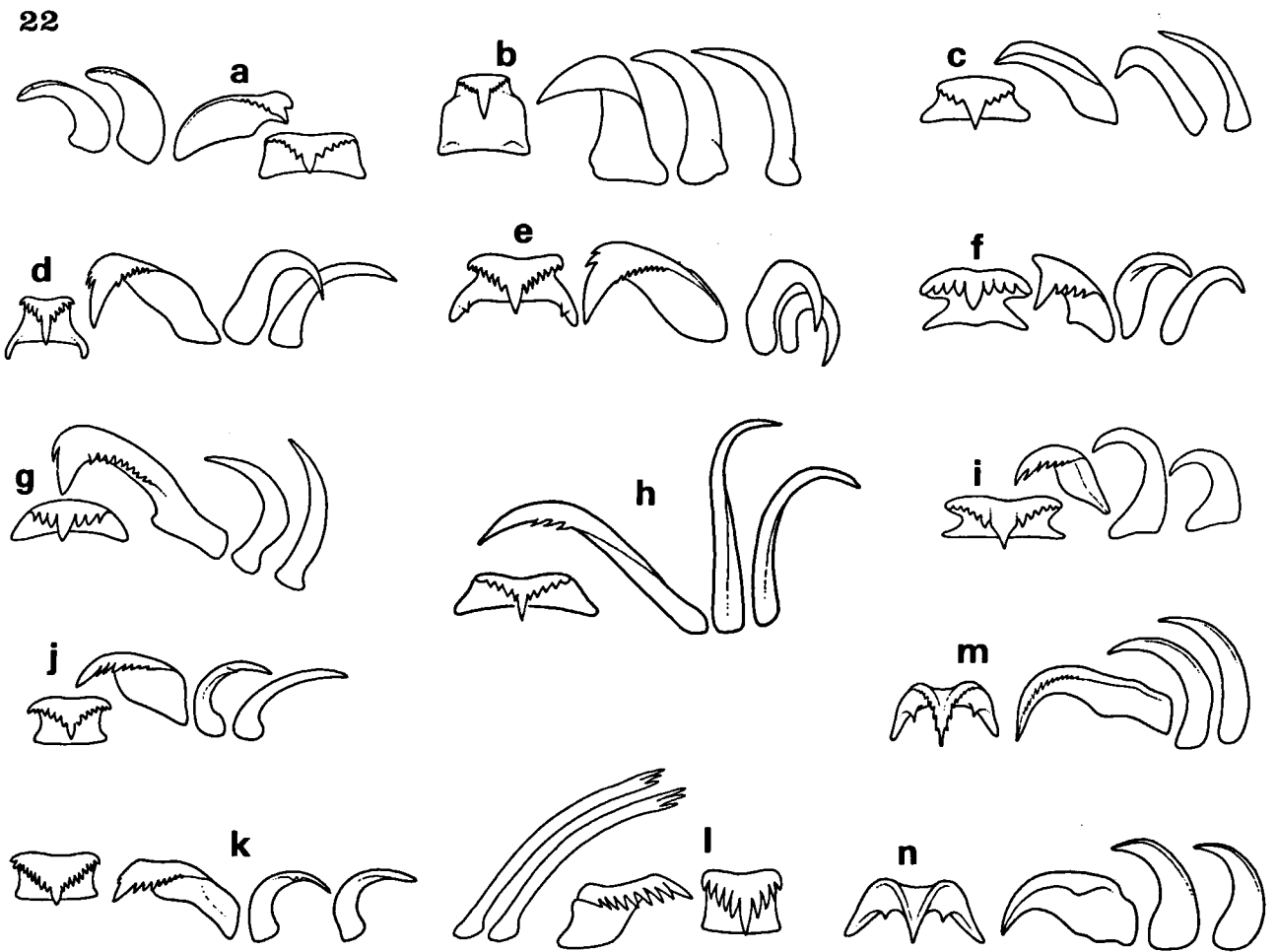


Fig. 22. Radulae (half row) of *Cassoidea* and members of outgroups (not to scale):

- a - *Capulus danieli* (after Orr, 1962);
- b - *Gyrineum gyrinum* (after Cernohorsky, 1967);
- c - *Ranella australasia*;
- d - *Akibumia orientalis* (after Warén & Bouchet, 1990);
- e - *Pisanianura grimaldii* (after Warén & Bouchet, 1990);
- f - *Cymatium muricinum* (after Bandel, 1984);
- g - *Distorsio clathrata* (after Bandel, 1984);
- h - *Charonia lampas*;
- i - *Cymatium (Linatella) caudatum* (after Morton, 1990);
- j - *Oocorys sulcata* (after Bayer, 1971);
- k - *Galeodea maccamleyi* (after Ponder, 1984);
- l - *Casmaria vibexmexicana* (after Bradner & DuShane, 1982);
- m - *Eudolium crosseanum* (after Marshall, 1992);
- n - *Tonna galea* (after Bandel, 1984).

The soft parts of *Distorsio* have been examined by Lewis (1972) and by myself. The animal of *Distorsio* sp. is about 1 cm long (Fig. 25). The foot is medium sized, the operculum typical for the genus. The head is comparatively small. The bases of the cephalic tentacles are thickened to lateral swellings carrying the eyes. Below the base of the right tentacle arises a relatively small penis which is constricted twice to a smaller diameter. The seminal groove is open and runs along the right body wall. The mantle edge is smooth and regular except for the fold of the inhalant siphon. The brownish gill is monopectinate, and rounded anteriorly. The bipectinate osphradium is yellowish. The hypobranchial gland is inconspicuous. The rectum is comparatively short, terminating some distance from the mantle edge.

The body cavity is dominated by the anterior alimentary canal. The proboscis is coiled in several loops when retracted and can be extended to about three times the

length of the animal. The buccal mass, radula and jaws are all relatively small. The oesophageal gland is brown and appears to be homogeneous, but sectioning might reveal a complex of glands. Salivary ducts could not be observed.

Distorsio perdistorta Fulton, 1938 (see Lewis, 1972) is much larger and differs in having a finger-shaped, laterally flattened penis, similar to that of *Fusitriton magellanicus* (Fig. 26). Apart from that the gross anatomy is very similar to that of *Distorsio* sp. Beu (1978b) presented some anatomical features of *Distorsionella lewisi* revealing the same characteristic very elongate anterior alimentary tract.

The gross anatomies of most genera of the Ranellidae have been described in the literature. *Argobuccinum pustulosum*, *Bursa* sp., *Cabestana spengleri*, *Charonia lampas*, *Fusitriton magellanicus*, *Ranella australasia* and *Tutufa rubeta* have been examined personally, but only brief descriptions of some features are given here because most have already been described. General characters of the family or superfamily are pointed out (see also summarising remarks).

The radulae of the Ranellinae (see Troschel, 1863; Clench & Turner, 1957; Barnard, 1963; Dell, 1963; Dell & Dance, 1963; Cernohorsky, 1967, 1970; Arnaud & Beurois, 1972; Kang, 1976; Beu, 1978a; Bandel, 1984; Warén & Bouchet, 1990; Habe, 1992; Figs 14, 15, 22) are all comparatively large, having powerful central and lateral teeth with a varying number of cusps. The marginal teeth are always smooth. The lateral and marginal teeth of *Charonia* are significantly longer compared to those of the other genera of the Ranellinae. The radulae of the Cymatiinae (see Troschel, 1863; Clench & Turner, 1957; Barnard, 1963; Cernohorsky, 1967; Kilburn, 1970; Kang, 1976; Bandel, 1984; Beu & Kay, 1988; Morton, 1990; Warén & Bouchet, 1990) are all very similar, having strong central and lateral teeth set with very sharp cusps. The inner marginal teeth may be indented, and the outer marginal teeth are always smooth (Figs 16, 17, 22). The Bursinae (see Troschel, 1863; Cooke, 1917; Thiele, 1929; Thorson, 1940; Cernohorsky, 1967; Habe, 1973; Melone, 1975; Beu, 1981; Bandel, 1984; Warén & Bouchet, 1990; Figs 18, 19) have radulae that are easily distinguished from those of Ranellinae and Cymatiinae by the presence of two cusps projecting from the base of the central tooth. The central and lateral teeth are powerful and the cutting edges may be set with cusps or not. The inner marginal teeth may bear denticles, the outer marginal teeth are always smooth.

The bodies of two Ranellinae are figured here but only some characteristic features are described briefly in the context of literature data (Bouvier, 1887; Amaudrut, 1898; Barnard, 1963; Dell & Dance, 1963; Cernohorsky, 1967; Laxton, 1968, 1969; Day, 1969; J.T. Smith, 1970).

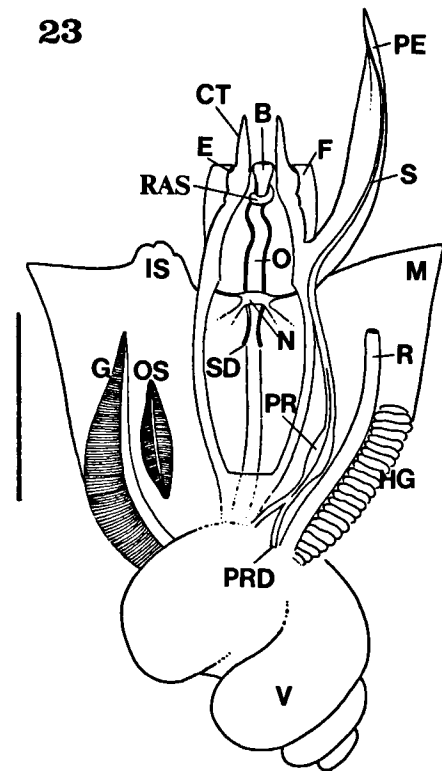


Fig. 23. Gross anatomy of *Argobuccinum pustulosum*. Scale bar equals 2 cm. Abbreviations are as follows (also applicable to Figs 25-32):

B - buccal mass; C - columellar muscle; CT - cephalic tentacle; E - eye; F - foot; G - gill; HG - hypobranchial gland; IS - inhalant siphon; M - mantle; N - nerve collar; O - oesophagus; OG - oesophageal gland; OP - operculum; OS - osphradium; OV - oviduct; P - proboscis; PE - penis; PR - prostate; PRD - prostate duct; R - rectum; RA - radula; RAS - radula sac; S - seminal duct; SD - salivary duct; SG - salivary glands; V - visceral mass.

The animal of *Argobuccinum pustulosum* (Fig. 23) has a comparatively long body cavity, which is widely filled by the glandular complex of the anterior alimentary tract (compare Day, 1969). The salivary ducts pass through the nerve collar, which is the case in all Ranellidae and Cassidae that have been examined anatomically. The seminal groove is open where the prostate is intercalated (and at some distance from it) but closed where it runs along the long, laterally flattened penis, where, however, a seam of adhesion can be recognised. J.T. Smith (1970), however, described a genital duct open over its whole length. A short prostate duct opens into the posterior mantle cavity.

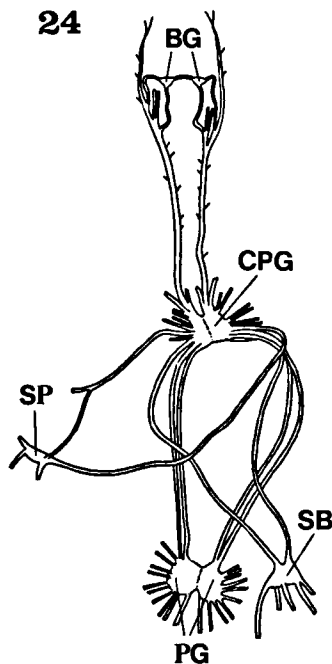


Fig. 24. Nervous system of *Tonna galea* (after Haller, 1893), not to scale. Abbreviations: BG - buccal ganglia; CPG - cerebral and pleural ganglia; PG - pedal ganglia; SB - suboesophageal ganglion; SP - supraoesophageal ganglion.

The hypobranchial gland comprises a row of thick, whitish leaflets. The gill is monopectinate and brown as in all other Cassoidea. The gill tapers to a point, which appears to be the case in all Ranellidae and Cassidae. The osphradium is bipectinate as is usual in the Cassoidea. The body of *Fusitriton magellanicus* differs from that of *Argobuccinum pustulosum* in few characters, mainly the open seminal groove, the lack of an additional prostate duct and the shape and muscular structure of the penis (Fig. 26; compare Beu, 1978a). The animals of the two species of *Ranella* (see Bouvier, 1887; Amaudrut, 1898; Barnard, 1963; Dell & Dance, 1963; Laxton, 1968, 1969; pers. obs.) differ only in details, such as the shape of the penis. The gross anatomy in *Ranella* is very similar to that of *Argobuccinum* and *Fusitriton* species. The seminal duct is open in *Ranella* species. The animal of *Charonia lampas* (Fig. 27) differs in some aspects. Overall differences are the broader head, the hypobranchial gland being formed by numerous lamellae covered by a regular epithelium, and the salivary glands being clearly demarcated both functionally and physically, and distinguished by the orange anterior glands and white posterior glands. The hypobranchial gland of *Charonia tritonis* (see Bouvier, 1887) appears to be similar to that of *Argobuccinum*.

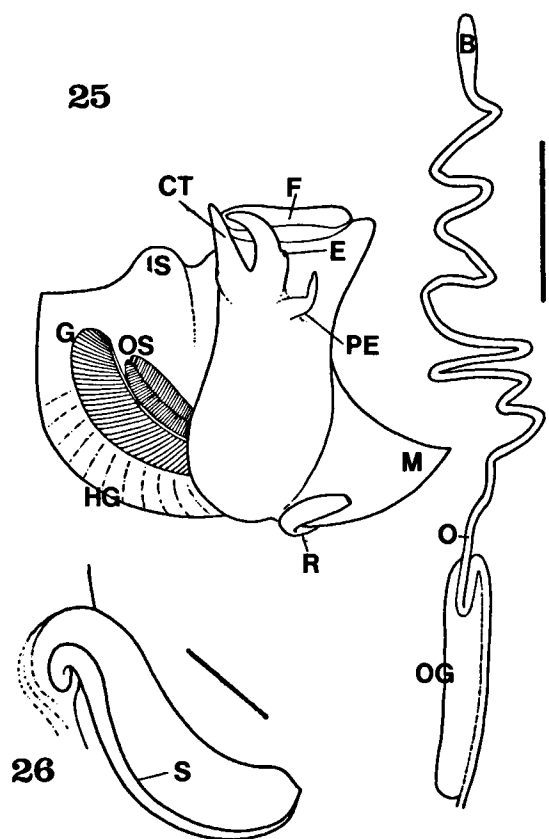


Fig. 25. Gross anatomy of *Distorsio* sp. Scale bar equals 5 mm.

Fig. 26. Penis of *Fusitriton magellanicus*. Scale bar represents 1 cm.

The animals of *Gyrineum* and *Sassia* are poorly known. Cernohorsky (1967) provided a short description of *Gyrineum gyrinum*, in which the 'very thick' proboscis and the 'club-shaped' penis might be of interest. Beu (1978a) figured and briefly described the animal of *Sassia kampyla*, which externally closely resembles that of *Argobuccinum* species.

As an example of Cymatiinae, the animal of *Cabestana spengleri* is figured (Fig. 28) and briefly described here. Conspicuous features are the long gill which terminates close to the mantle edge, the short rectum which terminates far back in the mantle cavity, the simple but comparatively long penis (with an open seminal duct), the stripe-like lamellae of the hypobranchial gland, the salivary ducts fused with the wall of the anterior oesophagus and the salivary glands restricted to the left-hand side of the body cavity. *Cymatium nicobaricum*, described by Houbrick & Fretter (1969), differs mainly with respect to the glandular complex, but is otherwise very similar to *Cabestana spengleri* in most gross anatomical features.

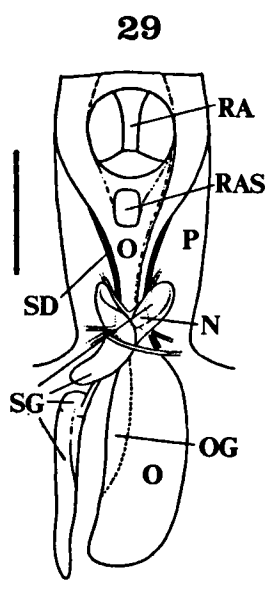
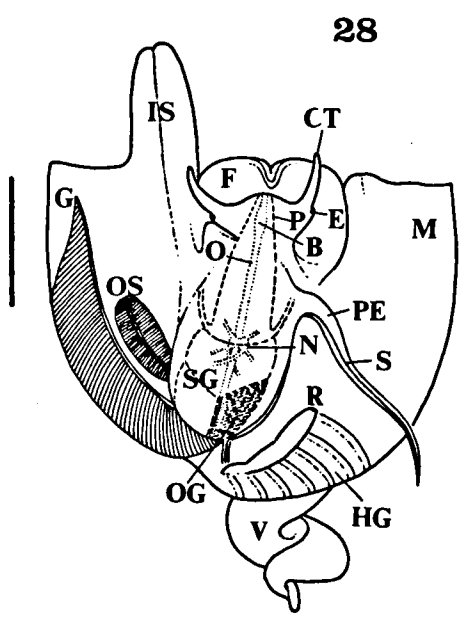
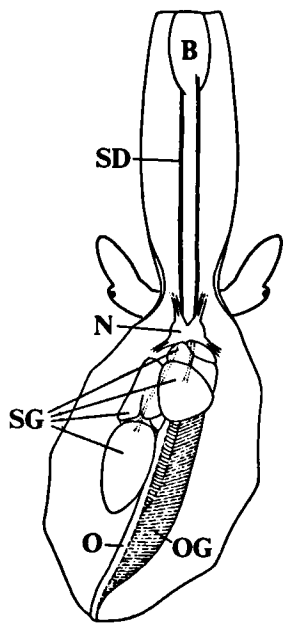
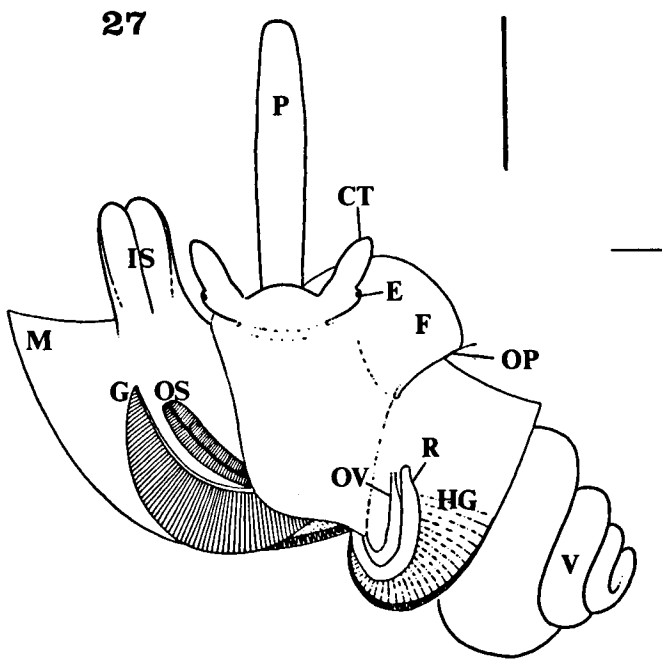


Fig. 27. Gross anatomy of *Charonia lampas*. Scale bar equals 2 cm.

Fig. 28. Gross anatomy of *Cabestana spengleri*. Scale bar equals 1 cm.

Fig. 29. Anterior alimentary tract of *Tutufa rubeta*. Scale bar equals 1 cm.

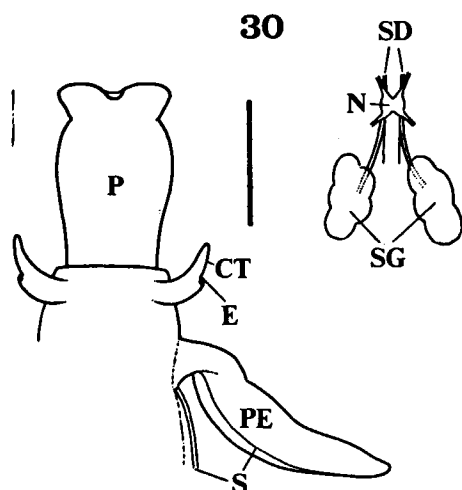


Fig. 30. Anterior body of *Bursa* sp. Scale bar represents 1 cm.

Morton (1990) provided some anatomical data on *Cymatium* (*Linatella*) *caudatum* which justify the attribution of *Linatella* as a subgenus to *Cymatium* (Beu, pers. comm.).

The genera of the Bursinae (Risbec, 1955; Houbriek & Fretter, 1969; Beu, 1981; Figs 29, 30) all have a comparatively broad and short proboscis, a large buccal mass without (minute in *Tutufa*) jaws (see Beu, 1981), and a well-developed mantle fold forming the exhalant siphon. The arrangement of the salivary gland complex varies greatly (inter- and intragenerically; compare Figs 29, 30). The seminal ducts of *Bursa* species are usually open, and in *Tutufa* or *Bufofaria* open genital grooves occur as well as closed ducts (Beu, 1981; pers. obs.).

The radulae of the Cassidae allow the taxa to be grouped in three larger systematic units. The radula type of the Oocorythinae is considered to be basic within the family (Fig. 22). The four genera attributed to this subfamily all have strong central and lateral teeth with a varying number of cusps on the cutting edge (Troschel, 1863; Fischer, 1883; Reynell, 1905; Thiele, 1929; Turner, 1948; Barnard, 1963; Bayer, 1971; Quinn, 1980; Bandel, 1984; Ponder, 1984; Warén & Bouchet, 1990). The marginal teeth are more-or-less hooked and scarcely longer than the laterals. The cutting edge of each inner marginal tooth is serrated in most taxa. Variation in the number of cusps on the central and lateral teeth occurs intraspecifically (Ponder, 1984) as well as interspecifically, which means that using numbers of cusps to distinguish species needs statistical confirmation.

The species of the Cassinae and Phaliinae are united by having significantly longer marginal teeth (Troschel, 1863; Fischer, 1887; Thiele, 1929; Cotton, 1945; Barnard,

1963; Abbott, 1968; Hughes & Hughes, 1981; Bradner & DuShane, 1982; Bandel, 1984; Warén & Bouchet, 1990; Figs 20-22) than in Oocorythinae or Tonninae. The central and lateral teeth closely resemble those of the Oocorythinae. The tip of each marginal tooth is serrated in most taxa. Data on the same species (e.g. Abbott, 1968; Warén & Bouchet, 1990 on *Semicassis granulata*) appear to be contradictory but may indicate considerable intraspecific variation as is the case in *Galeodea* (Oocorythinae).

The Tonninae are well defined by their radular teeth. The radulae of *Tonna*, *Malea* and *Eudolium* species (Troschel, 1863; Fischer, 1887; Turner, 1948; Barnard, 1963; Kang, 1976; Bandel, 1984; Warén & Bouchet, 1990; Marshall, 1992) are closely similar (Fig. 22). The marginal teeth of all three genera are reported to be smooth. The broad central tooth bears two denticles projecting from the left and right flanks of the base in the direction of the main cusp. The cutting edges of the central and lateral teeth of most *Tonna* species are smooth while those of *Malea* and *Eudolium* are serrated. However, the radula of *Tonna maculosa* Dillwyn, 1817 (see Turner, 1948) is intermediate, having few serrations. Turner (1948) and Warén & Bouchet (1990) figured radulae of the veliger of *Tonna* sp., showing serrated central and lateral teeth. This suggests that the smooth condition of the cutting edges is apomorphic within the Tonninae.

There are some descriptions of cassid anatomy in the literature, but only *Tonna galea* has been described in detail (Bouvier, 1887; Haller, 1893; Simroth, 1896-1907; Weber, 1927). Some of the publications focus on the salivary glands (Troschel, 1854; Panceri, 1869; Schönlein, 1898), which produce sulphuric acid. The complex of salivary glands is extremely large, in full contact with the body wall, which by muscular contraction is able to squeeze the glands and force the salivary secretions through the salivary ducts to perform an ejaculation (see Troschel, 1854). The salivary ducts as in all cassooids run through the nerve collar. The nervous system (Fig. 24) has been described by Bouvier (1887) and Haller (1893). The gross anatomy reveals the typical cassoidean arrangement of the organs of the pallial cavity, with a large monopectinate gill and a bipectinate osphradium. The hypobranchial gland is inconspicuous. The rectum terminates close to the mantle edge where a siphonal fold is developed. The seminal duct is open, the penis is approximately finger shaped but laterally flattened. The proboscis is pleurembolic as is the case in all cassooids and characteristic for the suborder Troschelina Bandel & Riedel, 1994. The jaws have developed a terminal hook and are extremely powerful (Weber, 1927; Warén & Bouchet, 1990). A characteristic feature is the large foot lacking an operculum. The foot spreads out very wide

when crawling on a soft substrate, and its anterior edge bears a lateral fleshy hook at each extremity (see e.g. Wilson & Gillet, 1971). Marshall (1992) presented some anatomical features of the genus *Eudolium*, which are not significantly different from *Tonna*. The body of *Malea* has not been described.

Among the Oocorythinae the genus *Galeodea* with the species *G. echinophora* (see Simroth, 1896-1907; Nüske, 1973; Fänge & Lidman, 1976; Hughes, 1986a) and *G. rugosa* (see Reynell, 1905, 1906) has been examined to some extent. The complex of salivary glands is very large. The huge accessory glands have been shown to produce sulphuric acid (Fänge & Lidman, 1976). The nervous system has been described by Reynell (1905, 1906) and is concentrated in a similar style as that of *Tonna*. The gross anatomy does not show any marked differences from the 'bauplan' of *Tonna*. The body in *Oocorys* species (Fischer, 1883; Bayer, 1971; Quinn, 1980; Warén & Bouchet, 1990) is very similar to that of *Tonna* and *Galeodea* species, except for the head, which has developed very long, thick tentacles. The eyes are missing. There are no reports on the anatomy of *Dalium* and *Sconsia*.

The shells of Cassinae have been examined extensively, but there are very few reports on the anatomy (e.g. Amau-drut, 1898; Hughes & Hughes, 1981).

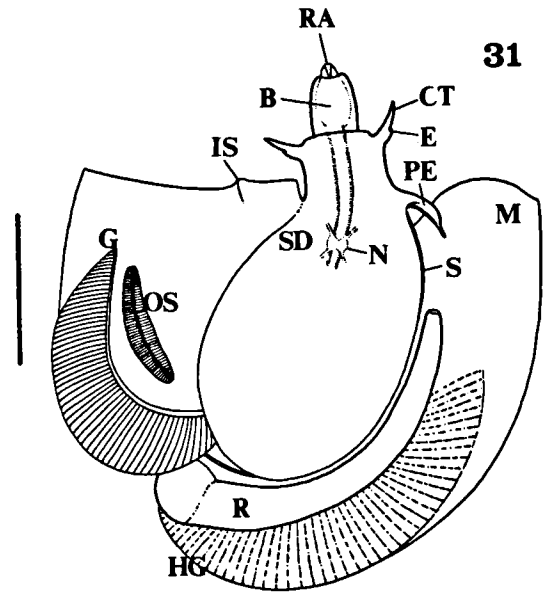


Fig. 31. Gross anatomy of *Cassis cornuta*. Scale bar represents 2 cm.

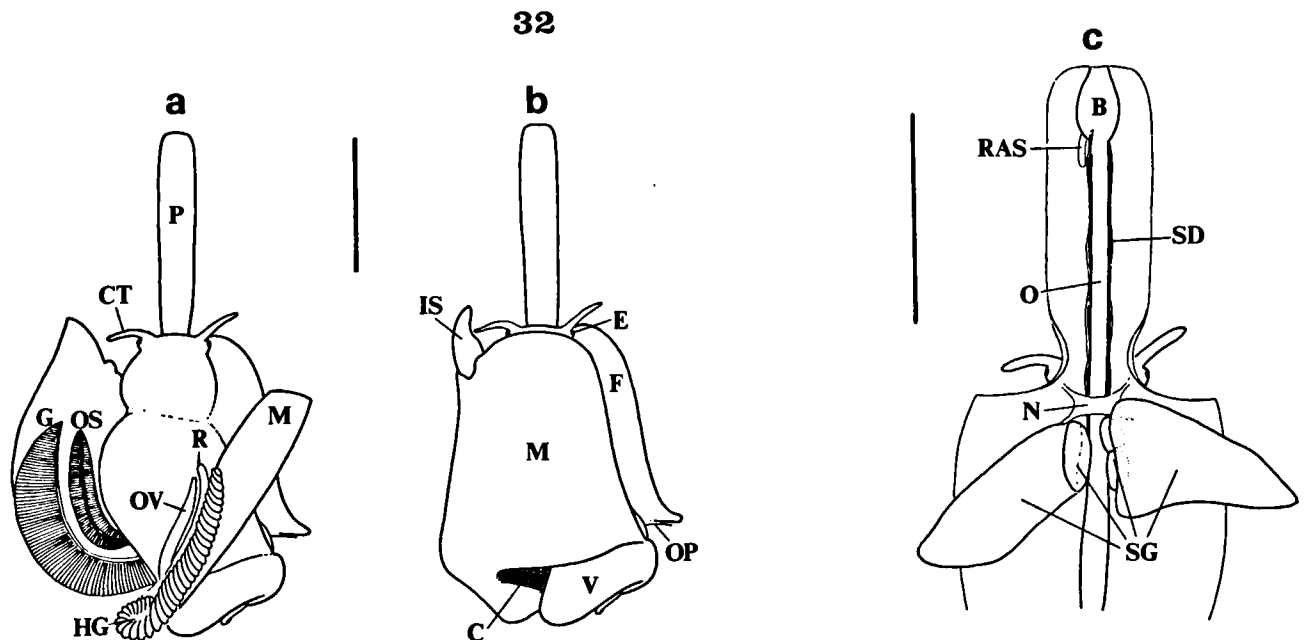


Fig. 32. Gross anatomy of *Semicassis labiata*. The oesophageal gland is not shown. Scale bars equal 2 cm.

A sketchy figure (Fig. 31) of *Cassis cornuta* is provided here to give a rough idea of the spatial arrangement of the body, which is significantly flattened due to the construction of the shell. The important feature is the large complex of salivary glands filling most of the body cavity. The anterior salivary glands are comparatively small, pea-shaped and coloured beige. The two accessory acid glands are huge and slightly greenish. The buccal mass is remarkably large which, however, is also known from some species of other cassoid subfamilies. Among the other organs the penis is conspicuous. It is very small and constricted to form a tiny tip. The seminal groove is open.

Beu (1981) provided anatomical data on the Phaliinae based on *Semicassis pyra* (Lamarck, 1822) (for the penis see also Abbott, 1968), and Hughes (1986b) presented an outline of the anatomy of *S. granulata* (Born, 1778). Gross anatomical features of *S. labiata* are figured here, and a few key characters are commented upon (Fig. 32). The animal is orange except for the visceral mass, which is brown, and the columellar muscle, which is yellowish. Among the organs of the pallial cavity the osphradium is remarkably large and hypobranchial gland is well developed, which is in contrast to the smaller ones in species of the other cassid subfamilies. Again a very large complex of salivary glands is present, with a pair of anterior, beige, small glands and a pair of white accessory (acid-secreting) glands that are relatively as huge as in *Tonna galea*. The salivary ducts are brown, pass through the nerve collar (cerebral and pleural ganglia fused) and run laterally along the oesophagus. However, the left duct joins the buccal cavity dorsally while the right duct terminates ventrally. Apart from two figures of a penis (Abbott, 1968), there is no report on the anatomy of *Casmaria* in the literature.

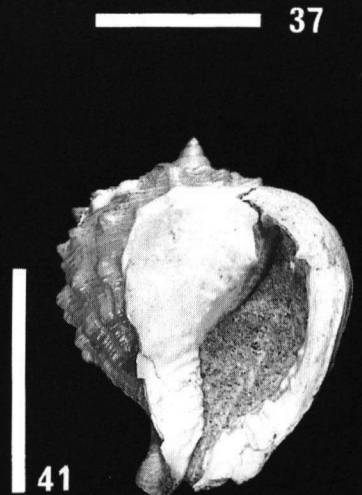
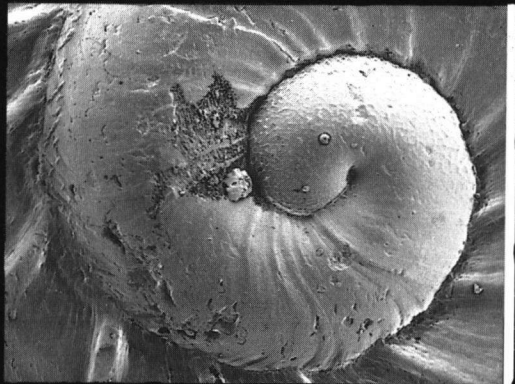
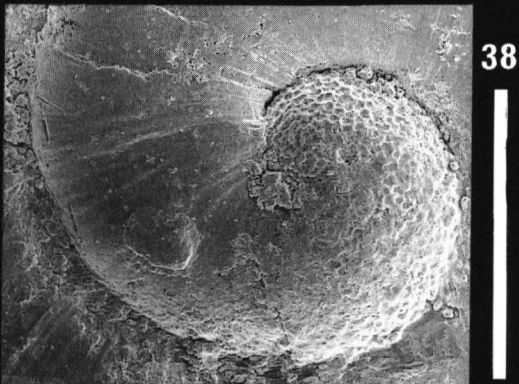
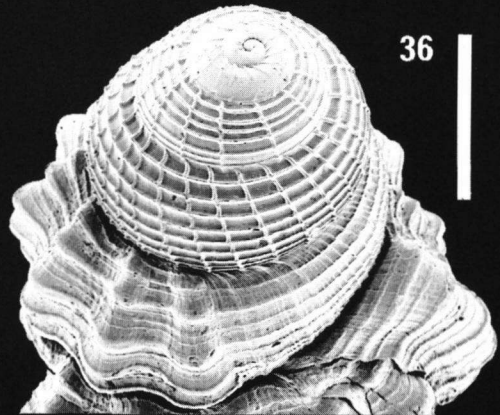
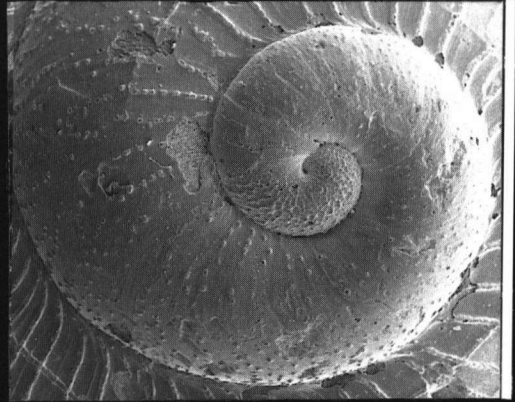
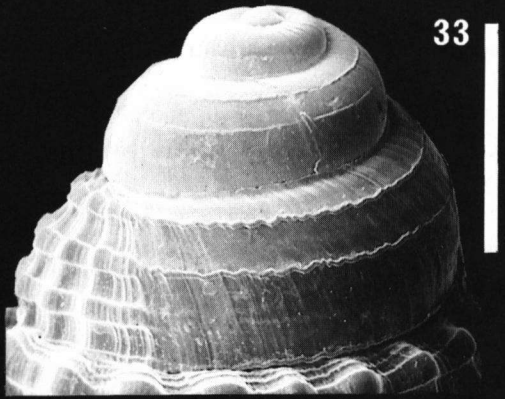
Summarising remarks — Warén & Bouchet (1990, pp. 69, 73) placed emphasis on 'typical salivary glands' ('normal tonnoid type') and indirectly (?) made this anatomical feature the superfamily key character, with the intention of including the Laubierinioidea (see Bandel & Riedel, 1994) within the Cassoidea. Bandel & Riedel (1994) showed that the Laubierinidae Warén & Bouchet, 1990 is best treated as a separate superfamily - to which the Pisanianuridae are added herein - which, however, is close to the Cassoidea. The complex of salivary glands is difficult to interpret in the systematic context of the Neomesogastropoda as the knowledge of the anatomy of the group is very incomplete. Within the Cassoidea, the Personidae have no accessory salivary glands, which refutes the idea as a superfamily key character; the Ranellidae have large accessory salivary glands, but with quite different arrangements (and contents) among the taxa; and the Cassidae have very large accessory salivary glands, which contain sulphuric acid in possibly all taxa. The acid produced by ranellid and cassid species is apparently associated with feeding on echinoderms.

The nervous system of *Tonna* (Fig. 24), with minor differences, is representative of the Cassoidea. Within the Neomesogastropoda a similar concentration of the ganglia can be found e.g. in the Calyptraeioidea, and a more concentrated nervous system occurs in the Lamellarioidea (Bouvier, 1887).

Shape and size of the penis is of limited value in arranging systematic units. In the Ranellidae, however, a long tapering penis predominates, while a finger-shaped, laterally flattened one occurs mainly in the Cassidae. There are several exceptions in each family and the anatomical differences may be greater between species of the same genus than between genera of different families.

Figs 33-41. Photomicrographs (except Fig. 41) of apical whorls of cassoidean gastropods.

- 33- Apical whorls of *Sassia septemdentata* (Eocene, Texas). Scale bar equals 1 mm.
- 34- Initial whorls of *Gyrineum gwinae* (Campanian, Mississippi). Scale bar equals 0.2 mm.
- 35- Apical whorls of *Distorsio tortuosus* (Miocene, The Netherlands). Scale bar represents 1 mm.
- 36- Apical whorls of *Sassia delafosse* (Eocene, Paris Basin). Scale bar represents 1 mm.
- 37- The same specimen as in Fig. 36, magnification of initial shell. Scale bar equals 0.1 mm.
- 38- Embryonic shell of *Sassia* sp. (Paleocene, Alabama). Scale bar represents 0.1 mm.
- 39- The same specimen as in Fig. 38, showing reduction of cancellate ornament of larval shell and first varix of juvenile teleoconch. Scale bar equals 1 mm.
- 40- Early juvenile shell of *Sassia flandrica* (Oligocene, Germany), showing the transition from protoconch to teleoconch. Scale bar represents 1 mm.
- 41- *Galeodea* cf. *echinophora* (Miocene, northern Germany). Scale bar equals 3 cm.



The seminal duct of most cassoid taxa is open and where it is closed (*e.g. Argobuccinum pustulosum*) a seam of adhesion is visible. In comparison with the other superfamilies of the Neomesogastropoda the open genital groove must be the plesiomorphic state.

Other basal neomesogastropod characters include the monopectinate gill, the bipectinate osphradium with large leaflets, and for the Trochelina, the pleurembolic proboscis. A coiled proboscis (when retracted) is found only in the Personidae and represents one good character to justify that family (see Beu, 1988a). The radulae of personid species appear to be reduced in size. However, the down-curved shape of the central teeth is a better character to separate this family from the Ranellidae and Cassidae. In comparison with the outgroups (Lau-bierinioidea, Calyptraeidea, Capuloidea), the basic cassoid radula type occurs in the Ranellinae, *i.e.* in *Sassia* and *Gyrineum* (see discussion on phylogenetic cladogram). The subfamilies of the Ranellidae and Cassidae are each homogeneous in respect to their radulae. The Cassinae and Phaliinae share the same radula type, which is apomorphic to that of the Oocorythinae (simple marginals). The characteristic interlocking processes at the bases of the central radular teeth have developed convergently in the Bursinae and in the Tonninae.

FOSSIL RECORD

The preceding chapters provide the basis for tracing the Cassoidea back through earth history. Convergences exist between adult shells, larval shells or embryonic shells of cassoids and other families of the Neomesogastropoda (*e.g. Trichotropidae*) or Neogastropoda (*e.g. Cancellarioidea*). However, these convergences operate only when comparing the same ontogenetic stage and not when using all different ontogenetic stages as a complex of characters (see protoconch and teleoconch chapter).

In the literature, very few authors provide data on the early ontogenetic shell of cassoids, which only partly results from the diagenesis of fossils. The characters of the protoconchs of only sixteen species could be extracted from the literature and another fourteen protoconchs could be examined personally. This seems to be quite a poor basis to trace back a systematic unit which had its origin sometime during the late Early Cretaceous. However, there are a fair number of descriptions of teleoconchs in the literature and many of them are diagnostic without the reconfirmation of the protoconch characters. Thus very few taxa are difficult to attribute to the next higher taxon and the protoconchs in some cases can resolve these problems. The following is

not a full review of all the literature dealing with fossil cassoids, but a brief summary of important data to produce evidence for the chronological order of at least the subfamily origin.

The Personidae all have a more-or-less distorted teleoconch, which is a character to recognise even in poorly preserved fossils. A species called *Eutritonium praegransum* Cottreau, 1922 from the 'Senonian' (Late Cretaceous) of Madagascar (see Cottreau, 1922) is the oldest known personid. Beu (1988a) attributed this species to the genus *Distorsio* on the basis of its strong teleoconch distortion and coarsely cancellate sculpture. From the Paleocene of Poland, *Personopsis* (= *Eutritonium*) *rutoti* was described (Krach, 1963; compare Beu, 1988a) and Beu (1988a) erected the new genus and species *Kotakaia simplex* from the Paleocene of the Chatham Islands (New Zealand). *Distorsio septemdentata* (Gabb, 1860) (see Pilsbry, 1922; Palmer & Brann, 1966; Maxwell, 1968; Beu, 1978b) was described from the Eocene of Texas (Fig. 33). Beu (1988a) recognised that this species actually belonged to the genus *Sassia* (Ranellidae) and that the slight distorsion of the whorls was due to convergence. A new species of genuine Eocene personid of New Zealand, *Distorsio beui*, was recorded by Maxwell (1968) and attributed by Beu (1988a) to the genus *Personopsis*. From the Oligocene *Distorsio interposita* (Tate, 1894) from Victoria (Australia), *D. crassidens* (Conrad, 1848) from Mississippi (USA) (see MacNeil & Dockery, 1984) and *D. tortuosum subclathrata* (d'Orbigny, 1852) from the Adour Basin (France) (see Lozouet, 1987) have been described.

Descriptions of Miocene material are more numerous and include, among many others, *D. gatunensis* Toulou, 1909 (Panama; Woodring (1959) illustrated the protoconch), *D. tortuosus* (Borson, 1822) (The Netherlands) for which species Janssen (1984) documented the protoconch (Fig. 35), *D. constrictus simillimus* (Sowerby, 1849), a large species from Santo Domingo (see Pilsbry, 1922), and *D. reticularis* from Burma (Dalton, 1908) and India (Dey, 1961).

The oldest documented member of the Ranellidae is probably a specimen from the Aptian (Early Cretaceous) of northern Germany figured by Schröder (1992). The specimen is a damaged juvenile, which, however, shows a densely cancellate larval shell and some postlarval whorls with varices. Other Cretaceous shells which appear to be ranellids come from the Turonian of Utah (USA) (Stanton, 1893, *Tritonium kanabense*; see Beu, 1988a), from the Campanian of Mississippi (USA) (Dockery, 1993: *Sassia carlea*, *Gyrineum gwinae*, with protoconch, Fig. 34), from Lybia (Wanner, 1902, *Triton tuberculosum*); Madagascar (Basse, 1932, *Triton sauryi*) and Tennessee (Wade, 1926, *Tritonium univaricosum*).

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RANELLIDAE

CASSIDAE

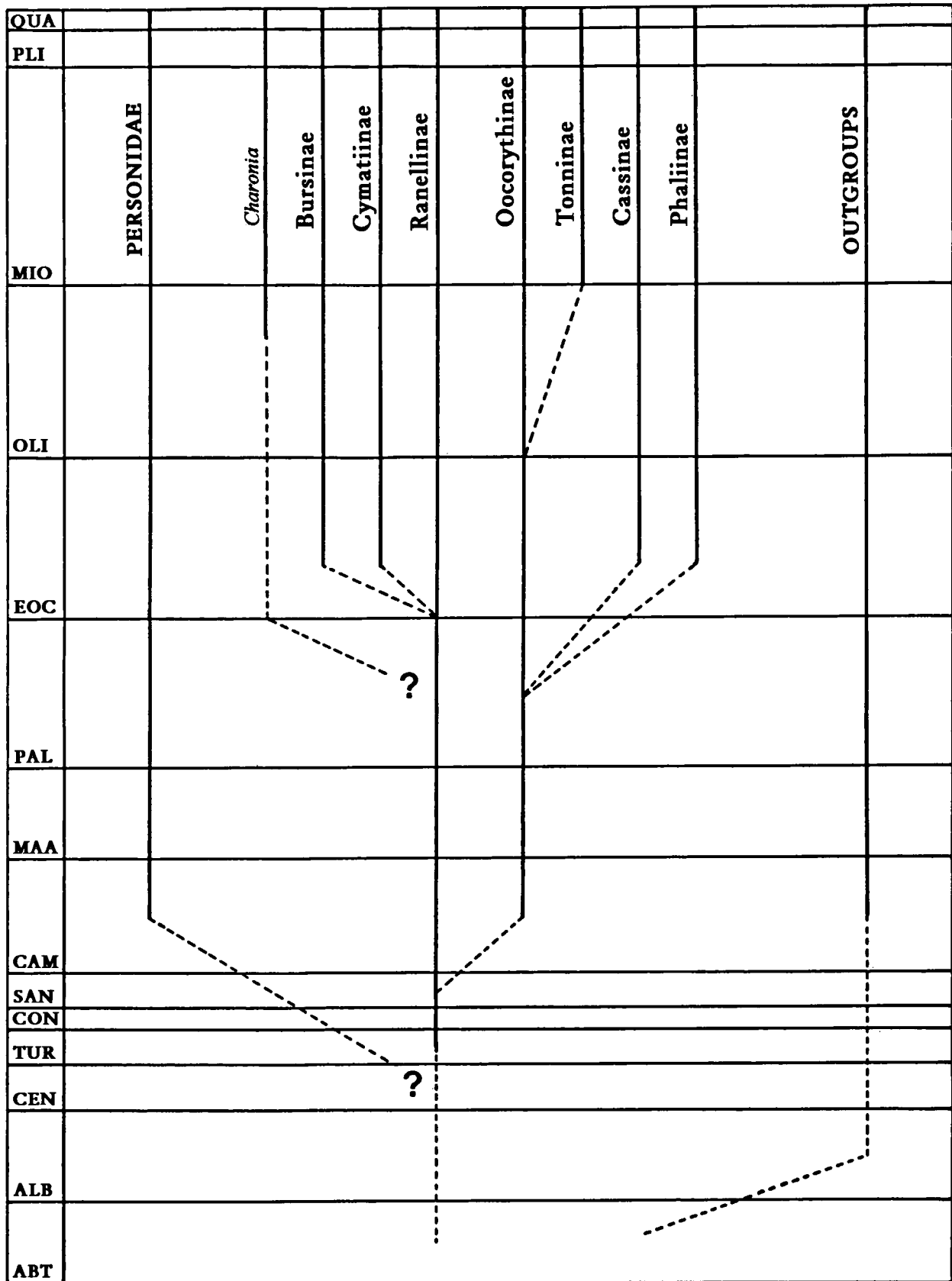


Fig. 42. Chronology of the evolution of Cassoidea at the subfamily level (see text).

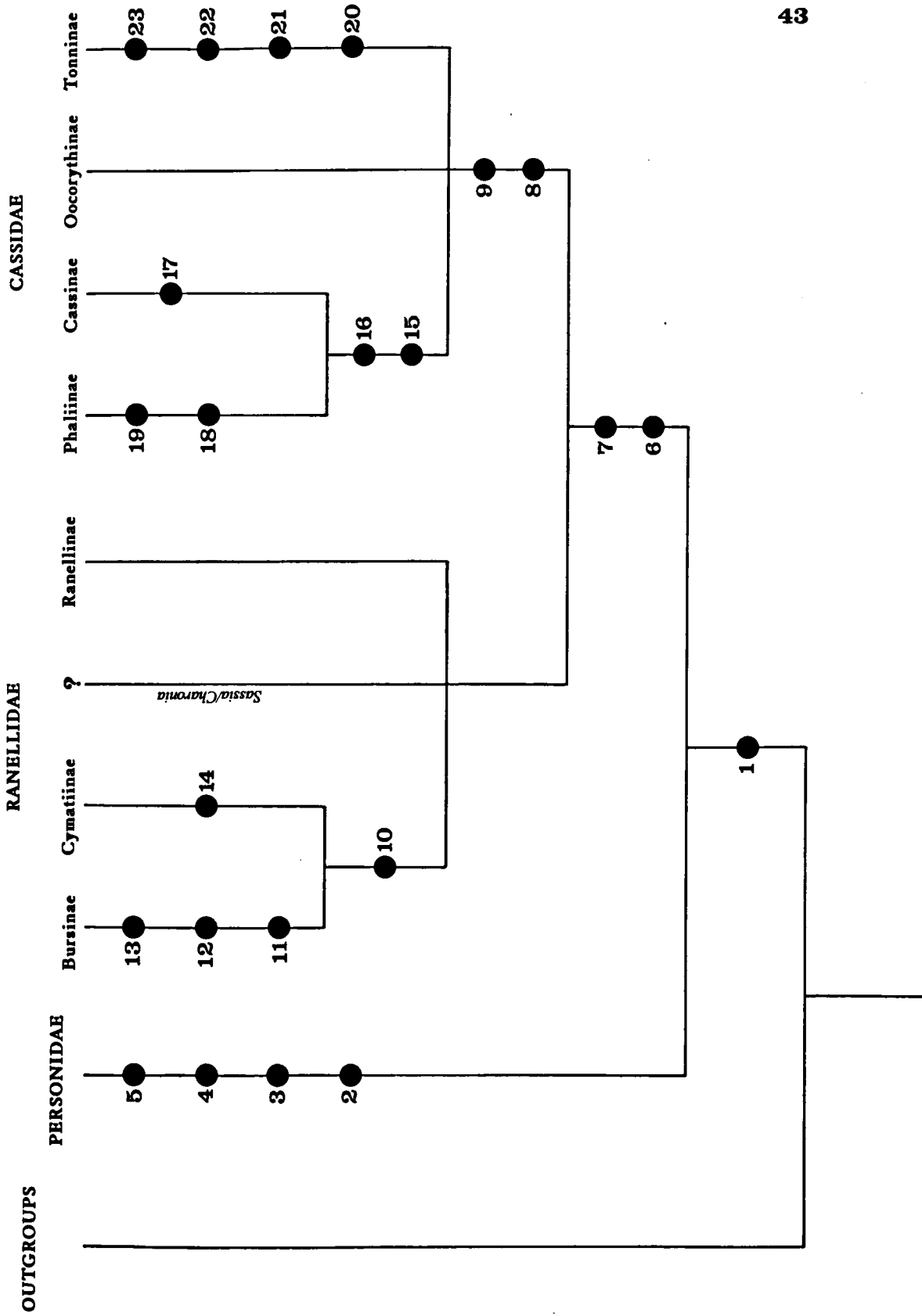


Fig. 43. Phylogenetic cladogram of the Cassoidea (see text).

In the Paleocene of Belgium occur species which Glibert (1973) assigned to the genus *Charonia*, subgenus *Sassia* (see remarks). Kollmann & Peel (1983) recorded a ranellid from the Paleocene of Greenland, while Zinsmeister (1983, *Gyrineum judithi*) and Beu (1988a, *Ranella louellae*) from California and Traub (1979) described some ranellids from the Paleocene of Austria. All these gastropods are best referred to the subfamily Ranellinae. A protoconch of a species of *Sassia* from the Paleocene of Matthew's Landing (Alabama) is illustrated here (Figs 38, 39).

In the Eocene, the ranellid fossil record increases in quantity as well as in quality (Figs 36, 37) and the Bursinae and the Cymatiinae can be recognised to branch off and diverge (see Cossmann, 1903; Weaver, 1912; Olsson, 1930; Squires, 1983; Beu, 1988a). Several protoconchs have been documented by Beu (1988a) and teleoconchs have become more characteristic (see chapter on protoconch and teleoconch). The radiation of the three ranellid subfamilies is very well reflected in the fossil record of the Oligocene (see Beyrich, 1854; von Koenen, 1866; Speyer, 1866; Ravn, 1907; Hickman, 1969; J.T. Smith, 1970; Kuster-Wendenburg, 1973; Gürs, 1983; MacNeil & Dockery, 1984; Lozouet, 1987; Fig. 40) and Miocene (see Cossmann, 1903; Dall, 1909; Pilsbry, 1922; Cossmann & Peyrot, 1923; Sorgenfrei, 1958; Woodring, 1959; Dey, 1961; Beu, 1970c; Jung, 1971; Beets, 1984; Janssen, 1984).

The origin of the Cassidae has been discussed, amongst other authors, by Cossmann (1903), Schenck (1926) and Abbott (1968). Cossmann and Abbott proposed an Eocene origin while Schenck assumed the origin to be in the Late Cretaceous. Schenck's view (1926) is accepted here based on the record of a few fossils of Late Cretaceous age (Wanner, 1902, *Cassidaria* sp.; F.M. Anderson, 1958, *Haydenia impressa*; Poyarkova & Dzhililov, 1985, *Cassidaria* sp.; Abdel-Gawad, 1986, *Cassidaria truncata*) appear to be close to the genus *Galeodea* and represent members of the Oocorythinae. A Paleocene *Galeodea* species from New Zealand was recorded by Beu & Maxwell (1990). The Cassidae radiated during the Eocene, which is well documented in a number of papers (see among others Deshayes, 1866; Cossmann, 1903; Oppenheim, 1906; Clark & Woodford, 1927; Wrigley, 1934), and in addition to the Oocorythinae, the subfamilies Cassinae and Phaliinae can be recognised. Cassids from Oligocene deposits have been described by (among others) Beyrich (1854), Speyer (1862, 1866), Cossmann (1903), Ravn (1907), Kuster-Wendenburg (1973), MacNeil & Dockery (1984) and Beu & Maxwell (1990).

Miocene strata yield the first shells attributable to the Tonninae (Dalton, 1908, *Dolium* sp.; Toula, 1909, *Malea camura* [see also Woodring, 1959; Jung, 1971]; Pilsbry,

1922, *Malea* sp.; Cossmann & Peyrot, 1923, *Malea orbiculatum* Vokes, 1986, *Eudolium subfasciatum*). The other three subfamilies of the Cassidae have radiated worldwide (see Ravn, 1907; Dall, 1909; Cossmann & Peyrot, 1923; Gardner, 1948; Parker, 1948; Woodring, 1959; Dey, 1961; E.J. Moore, 1963; Jung, 1971; Kanno, 1973; Janssen, 1984; Beu & Maxwell, 1990) and their relation with the modern faunas is obvious (Fig. 41).

Summarising remarks — the evolution of Personidae and Ranellidae has been analysed and discussed by Beu in numerous papers (see References) and there is no need for a revision. However, some additional remarks have to be made in the context of a partly new classification of the Ranellidae and the story of the Cassidae needs some reevaluation. The author fully supports Beu's (e.g. 1988a) assignment of fossils to certain genera, though *Sassia* (see classification) is now placed in the Ranellinae (but see final discussion), which means that this subfamily has the longest fossil record and represents the stem-group of the Ranellidae and also of the superfamily (Fig. 42). The Ranellinae possibly originated during the Aptian (Schröder, 1992) and are definitely recognised from the Turonian onwards (Beu, 1988a).

Personidae (see final discussion) and Cassidae branched off during the Campanian at the latest. In the context of the phylogenetic analysis (see following section), the Personidae must have branched off earlier than the Cassidae. A significant radiation of the Ranellidae and Cassidae occurred at the Paleocene-Eocene boundary. The subfamilies Bursinae and Cymatiinae are easily recognised in several Eocene faunas. Kase (1984) attributed *Hainabursa aquilana* (Parona, 1909) from the late Early Cretaceous of Japan to the Bursinae. This species is not a cassoid but closely resembles certain cerithioidean gastropods (e.g. *Cerithium columba* Sowerby, 1834).

The oldest cassid fossils have to be attributed to the Oocorythinae, which represent the stem-group of the family (Fig. 42). A radiation of the Cassidae occurred at the start of the Eocene where the subfamilies Cassinae and Phaliinae can be differentiated. The Tonninae cannot be recognised with certainty prior to the Early Miocene, and they represent the youngest branch of the Cassoidea. As for the Bursinae, there is a single record (see Wenz, 1938-44) of a Cretaceous specimen. The genus *Protodolium* Wilckens, 1922 is comparatively small, has a very thick shell, no siphonal canal, no columellar plait and the inner lip of the aperture is pronounced. Stilwell (1994) has recently re-assigned this genus to the Neritopsidae (Neritimorpha).

The fossil record of the Cassoidea in the context of the Neomesogastropoda has recently been discussed by Bandel & Riedel (1994). Cassoid outgroups such as the Calyptraeoida and Capuloidea can be traced back to the

Mesozoic and probably evolved during the Early Cretaceous.

PHYLOGENETIC CLADOGRAM AND DISCUSSION

Neomesogastropod phylogeny has been discussed by Bandel & Riedel (1994), with the introduction of two new suborders, Simrothina (comprising the superfamilies Naticoidea, Cypraeoidea and Lamellarioidea), and Trochelina (comprising superfamilies Cassoidea, Laubierinoidea, Calyptroidea and Capuloidea). The characters used to define these systematic units are not repeated here apart from those of the cassoid branch, which are presented in a more detailed phylogenetic tree (Fig. 43). The following characters have already been introduced in the preceding chapters and therefore are only summarised here.

The Cassoidea have developed a larval pallial tentacle (1) which allows the veliger to secrete, form, fix and dissolve periostracal sculptural elements. It represents a special adaptation to a long-term planktonic life (see Bandel *et al.*, 1994) and the only synapomorphy for the Cassoidea that could be found among the available data on this superfamily. Alan Beu (pers. comm., 1994) is of the opinion that episodic growth of the teleoconch is another synapomorphy for the Cassoidea.

In subdividing the Cassoidea into families, the Personidae can be defined by at least four apomorphies. The whorls of the teleoconch are distorted (2), the larval periostracal sculpture forms a carina (3), the egg capsules are more-or-less globular (4) and the proboscis is extremely long and has to be coiled when retracted (5). The Ranellidae and Cassidae both include echinoderms in their diet (6) and are also united by the possession of large accessory salivary glands (7) containing acid. The Cassidae can be separated from the Ranellidae by two features: they are specialised for feeding on echinoderms (8) and the accessory salivary glands are extremely enlarged (9), allowing the body wall to exert pressure by muscular contraction.

The Ranellidae show the plesiomorphic conditions and cannot be defined by an apomorphy. The Ranellinae represent the basal line from which the other two subfamilies have branched off. The genera *Charonia* and *Sassia* are placed in the Ranellinae on the basis of their radulae, egg capsules and protoconchs, although the shape of the larval shell of *Charonia* is similar to those of some Cymatiinae. *Sassia* and *Gyrineum* are probably the oldest genera of the Ranellidae and *Sassia* may have derived from *Gyrineum*. The alignment of teleoconch varices is about 180° in *Gyrineum* and about 270° in *Sassia* (compare Beu, 1981, 1985), 180° being considered plesio-

morphic. *Sassia* is not only closely related to *Gyrineum*, but also to *Charonia* and *Cabestana* (Beu, pers. comm.). *Sassia* and *Charonia* are somewhat intermediate between Ranellinae *sensu* Beu (*e.g.* 1988a) from which they originated and Cymatiinae/Bursinae to which they gave rise. *Sassia* and *Charonia* should be considered to constitute an independent subfamily.

The Cymatiinae and Bursinae both have semi-globular egg masses with the egg capsules arranged in a three-dimensional spiral (10). The Bursinae have developed a prominent posterior siphonal canal (11), the central radular teeth bear basal interlocking processes (12) and the whorls of the larval shell do not have an open suture and are covered only by a comparatively thin periostracum (13). The Cymatiinae have developed conical to turritiform protoconchs (14).

The stem-group of the Cassidae is represented by the Oocorythinae, which shows the plesiomorphic conditions (teleoconch, protoconch, radula, egg capsules, etc.) within the family. The Cassinae and Phaliinae are united by two synapomorphies: the cancellation of the larval shell is lost (15) and the marginal radular teeth are extended, while the central and lateral teeth are widened (16). Despite these two synapomorphies other characters support Beu's (1981) introduction of the subfamily Phaliinae. The egg capsules of the Cassinae have collar-like apices (17), while the Phaliinae retain a basal egg capsule type and produce a tower-like egg mass (18), which usually is brooded (19).

The fourth subfamily of the Cassidae, the Tonninae, is very well defined by at least four apomorphies: the operculum is lost during metamorphosis (20), the egg capsules are flattened spheres forming a solid tongue-shaped mass (21), the ornament of the larval shell is largely reduced (22) and the bases of the central radular teeth bear interlocking processes (23), as in the Bursinae.

In the past there have been some classificatory problems with the tun-shells, the helmet-shells and *Oocorys* and relatives. Fischer (1887) introduced the family Oocorythidae, while Dall (1909) placed *Oocorys* in the Cassidae, Thiele (1929) and Turner (1948) in the Tonnidae. Quinn (1980) again recognised a family Oocorythidae. Warén & Bouchet (1990) preferred assignment of the Oocorythinae to the Cassidae. Beu (pers. comm.) synonymises the Oocorythinae with the Cassinae, which together with the Phaliinae constitute the Cassidae. The Tonnidae are considered to be closely related to Cassidae. The classification presented here collects these taxa at the subfamily level within a single family and therefore incorporates former proposals, which initially appeared to be controversial, but in fact combined observations on different taxonomic levels.

The Ranellinae and Oocorythinae are both paraphyletic taxa which, however, is a good indication of

stem-groups. The chronology of the fossil record coincides largely with the cladistic analysis and therefore appears to be reliable. The Tonninae cannot be older than the Oocorythinae, the Cassinae and Phaliinae are monophyletic and must have evolved at the same time, the Personidae do not have large accessory salivary glands and therefore must have branched off from the stem-line earlier than the Cassidae, etc. The latter, however, implies that all ranellids and cassids are descended from a single species, which had developed accessory salivary glands. This would mean that the other early Ranellinae without such glands became extinct. A second possibility could be the loss of accessory salivary glands in the Personidae. In my opinion it is more likely that the Personidae are as old as the Ranellidae and did not branch off from the Ranellinae, both taxa having evolved from a common ancestor. In this case the fossil record must be interpreted as incomplete and the Personidae must have evolved during the Aptian at the latest.

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