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A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda)

S. A. Ridgway^{1,2}, D. G. Reid¹, J. D. Taylor¹, G. M. Branch³ and A. N. Hodgson⁴

¹*Mollusca Research Group, Department of Zoology, The Natural History Museum, London SW7 5BD, UK*

²*Queen Mary and Westfield College, University of London, London E1 4NS, UK*

³*Zoology Department, University of Cape Town, Rondebosch 7700, South Africa*

⁴*Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa*

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A phylogenetic hypothesis for the patellid limpets is reconstructed by cladistic analysis of morphological characters from 37 species, representing all but one of the living members of the family. Characters included in the analysis are derived from shell shape and microstructure, headfoot and pallial complex, radula and sperm. The species fall into four clades, providing the basis for a new phylogenetic classification into four monophyletic genera: *Helcion* (four species; southern Africa), *Cymbula* (eight species; southern Africa, eastern Atlantic, southern Indian Ocean), *Scutellastra* (17 species; southern and south-western Africa, Australia, Indo-West Pacific, Eastern Pacific) and *Patella* (nine species; northeastern Atlantic and Mediterranean). The analysis suggests sister-group relationships between *Helcion* and *Cymbula*, and between *Scutellastra* and *Patella*. In combination with present-day patterns of geographical distribution, this phylogenetic hypothesis is used to discuss the historical biogeography of the Patellidae. *Scutellastra* may have originated in southern Africa and dispersed across the Pacific, or alternatively may be a primitively Tethyan group. Both *Helcion* and *Cymbula* appear to have originated in southern Africa, but three *Cymbula* species have dispersed respectively to northwest Africa, St Helena and the southern Indian Ocean. The patellids of the northeastern Atlantic form a single clade, *Patella* (including *P. pellucida*), which may have arrived by northward dispersal of an ancestor from southern Africa, or possibly by vicariance of a widespread ancestral Tethyan distribution. The known fossil record of patellids is too fragmentary to permit choice between these alternatives.

Keywords: *Patella*; mineralogy; radula; sperm; biogeography

1. INTRODUCTION

The true limpets, belonging to the order Patellogastropoda, differ from other gastropods in fundamental features of their shell geometry, shell microstructure, radular form and in the morphology of the gills, alimentary system and other anatomical characters.

Consequently, they are now recognized as the basal branch of the extant gastropods (Golikov & Starobogatov 1975; Lindberg 1988a; Haszprunar 1988; Ponder & Lindberg 1997), and are of particular evolutionary interest. Patellogastropods are also of ecological significance. The family Patellidae contains most of the common limpets on the temperate rocky shores of

Europe, where they have a marked influence on community structure (Southward 1964; Hawkins 1981*a,b*; Hawkins *et al.* 1992). Patellid limpets are also ecologically important on the shores of southern Africa, where they reach their greatest diversity; here they exhibit complex behavioural and ecological traits, including territoriality and gardening of algal resources (Branch 1971, 1975, 1976, 1981). As a consequence of their abundance, accessibility and ecological significance, many aspects of the biology of patellid limpets, including behaviour, diet, life history and physiology, have been thoroughly studied (reviews by Branch 1981, 1985*a,b*; Fretter & Graham 1976, 1994). In some regions patellids are gathered for food. Conservation of declining stocks of *Patella candei* and *P. aspera* has become a concern on the Atlantic islands (Hawkins *et al.* 1990); in the Mediterranean *P. ferruginea* is endangered (Cretella *et al.* 1994); and in the eastern Pacific *P. mexicana* may be locally extinct on parts of the mainland coast of Mexico.

Although much is known about the biology of the Patellidae, the systematics of the group have been relatively neglected. Most systematic work has concentrated on the description and discrimination of species, but the taxonomy is not yet completely resolved. Historically, the external form of the shell was the principal character used in the species-level taxonomy of patellids, but in many species this is highly variable, leading to taxonomic confusion. It has long been recognized that the radula is also a useful character for discrimination between species (Thiele 1891; Fischer-Piette 1935; Evans 1947; Koch 1949; Fischer-Piette & Gaillard 1959). The two most recent worldwide taxonomic monographs, by Powell (1973) and Christiaens (1973, 1974*a,b*), both used a combination of shell morphology and radular characters in their diagnoses, but nevertheless show numerous disagreements. Other characters that have been successfully used to discriminate between species include coloration of the foot and pallial tentacles (Evans 1947; Fretter & Graham 1976; Bowman 1981; Cretella *et al.* 1990), sperm ultrastructure (Hodgson & Bernard 1988; Jamieson *et al.* 1991; Hodgson *et al.* 1996), configuration of the loops of the gut (Ridgway 1994) and chromosome number (Cervella *et al.* 1988). Allozyme electrophoresis has also been employed to discriminate between sympatric species (Gaffney 1980; Côte-Real 1992; Sella *et al.* 1993; Côte-Real *et al.* 1996*a,b*). However, there remain uncertainties about the number of species that should be recognized in the family.

The evolutionary relationships of patellogastropods are also poorly understood. Overtly phylogenetic studies are a relatively recent development, and the ideas of the earlier authors on the relationships of patellids must largely be deduced from their classification schemes. From the first, great emphasis was placed on the arrangement of the ctenidial and pallial gills for the definition of families and genera of patellogastropods (Adams & Adams 1854; Gray 1857; Dall 1871*a,b*). Radular characters were also used, particularly at generic and subgeneric level within the Patellidae (Dall 1871*a,b*; Pilsbry 1891), culminating in the systematic study of the docoglossan radula by Thiele (1891). Shell morphology was generally regarded as of subsidiary importance, although some authors defined genera with cap-shaped, pyriform or

stellate shells (Adams & Adams 1854; Gray 1857), and others mentioned the internal texture and appearance of shells (Pilsbry 1891). During the 20th century the most influential schemes for the classification of patellids have continued to rely on this limited set of characters (Thiele 1929; Wenz 1938; Keen 1960; Powell 1973; Christiaens 1973, 1974*a*). Following the descriptive studies of Thiem (1917) and Bøggild (1930), MacClintock (1967) introduced a new suite of characters in a detailed examination of shell microstructure, from which he defined five groups of patellids, and speculated on their evolutionary relationships. Another source of phylogenetically informative characters has been the ultrastructural description of spermatozoa, now available for most patellid species (Hodgson & Bernard 1988; Jamieson *et al.* 1991; Hodgson *et al.* 1996) and some other patellogastropod taxa (Hodgson & Bernard 1989; Hodgson & Chia 1993; Hodgson & Morton 1998). Indeed, the first cladistic analysis of patellids was carried out using data from the sperm morphology of southern African species (Jamieson *et al.* 1991). In a wide-ranging review of patellogastropods and their relationships, Lindberg (1988*a*) emphasized the importance of including all available character sets in phylogenetic analyses, because many individual characters show convergence in unrelated taxa. His review mainly concerned the family-level relationships, with emphasis on the Lottiidae and Acmaeidae, and no detailed consideration of patellid taxa. These views on the higher-level phylogeny of patellogastropods have been reaffirmed more recently (Lindberg & Hedegaard 1996; Lindberg 1998). The first attempt to incorporate all available data from anatomy and shell ultrastructure in a cladistic analysis of patellids was that of Ridgway (1994). This work, however, was largely concerned with the northern Atlantic species. Some information on genetic relationships is now available from allozyme studies, but so far these studies have been restricted to small numbers of species, often of sympatric distribution, having largely been designed to investigate taxonomic problems and population differentiation (Sella *et al.* 1993; Cretella *et al.* 1994; Côte-Real *et al.* 1996*a,b*; Weber *et al.* 1998).

It is clear that these many previous attempts to classify the species of Patellidae and to define phylogenetic groupings within the family have all relied on restricted sets of characters, or have included only a limited selection of species. In this study we aim to re-examine the informative morphological characters in all available species of the family and to combine them in a phylogenetic analysis.

It is now widely recognized that an understanding of phylogenetic relationships provides an essential evolutionary framework for comparative biology (for reviews of methodology and applications see Wiley (1981, 1988), Brooks & McLennan (1991), Forey *et al.* (1992)). Phylogenetic trees can be used as the basis for phylogenetic classifications, with enhanced predictive power about distribution of characters among taxa. In this paper we propose a revised generic classification of the Patellidae. By tracing characters and selective regimes on phylogenetic trees, hypotheses of adaptive function can be developed; with the wealth of ecological, dietary and behavioural data available on patellids, this should be possible in future studies of the group. Here, we use the

phylogeny as a basis for discussion of historical biogeography. The worldwide distribution of patellids is of particular interest as about half of the known species are restricted to southern Africa, a second area of high diversity is found in the northeastern Atlantic and relatively few species are present in the Indian and Pacific Oceans. The origins and relationships of the two principal radiations have been debated, with suggestions of recent trans-equatorial migration in the Atlantic (Vermeij 1992) or older Tethyan distributions (Powell 1973).

2. REVIEW OF THE RELATIONSHIPS OF THE PATELLIDAE AND THEIR SPECIES-LEVEL TAXONOMY

Before carrying out the cladistic analysis, it is necessary to summarize current ideas about the relationships of the Patellidae with other patellogastropods in order to justify the definition of the family and our selection of outgroup taxa. In the older classifications based principally on characters of the gills and radulae, patellogastropods were divided into three families: Lepetidae (gills absent; fused central tooth), Acmaeidae (single ctenidial gill; with or without pallial gills; two pairs of lateral teeth; marginal teeth reduced or absent) and Patellidae (ctenidial gill absent; pallial gills present; two or three pairs of lateral teeth; two or three pairs of marginal teeth) (Dall 1871*a,b*; Pilsbry 1891; Thiele 1929; Wenz 1938; Keen 1960; Powell 1973). Within the Patellidae as thus defined, two sub-families were generally recognized: Patellinae (three pairs of lateral teeth) and Nacellinae (two pairs of lateral teeth) (Thiele 1929; Wenz 1938; Keen 1960; Powell 1973; Christiaens 1974*a*). On the basis of unspecified shell and anatomical differences, the Nacellidae were raised to family rank by Golikov & Starobogatov (1975). In his review of relationships in the Patellogastropoda, Lindberg (1988*a*) proposed a new division into two suborders, Patellina and Nacellina. The former contained the single family Patellidae, and was characterized by the presence of calcitic crossed-foliated outer shell layers. Its sister-taxon, Nacellina, has been variously defined by a chromosomal character, characters of the salivary glands, oesophagus and nervous system, and by reduction of the number of radular teeth (Lindberg 1988*a*, 1998; Lindberg & Hedergaard 1996). Although these suborders have been claimed to be monophyletic, it has not been established that their diagnostic characters are synapomorphic, and there are discrepancies among the definitions offered. The suborder Nacellina originally contained four families—Nacellidae, Lepetidae, Acmaeidae and Lottiidae—defined by reductions of shell layers and simplifications of gills and radulae (Lindberg 1988*a*). In the present study we use Patellidae in the sense of Lindberg (1988*a*). The affinities of Nacellidae (*Cellana* and *Nacella*) remain controversial, but for the purposes of the cladistic analysis we have used representatives of *Cellana*, *Nacella*, *Acmaea* and *Lottia* as outgroup taxa.

It is also necessary to review briefly the confused species-level taxonomy of the Patellidae, to explain the inclusion of taxa in our ingroup. Since Thiele (1929; also Wenz 1938; Keen 1960; Powell 1973), it has been common to classify these species in just two genera, *Patella* (conical shell, pallial gill cordon complete) and *Helcion* (cap-

shaped shell, pallial gill cordon interrupted above head). However, for simplicity and because our aim is to examine the phylogenetic relationships of these species afresh, the genus *Patella* in its broadest sense will be used throughout this section (as indeed has been the practice of many previous authors). Authorities for all recognized species are given in table 1. In several cases there are disputes about valid specific names; here we have used the most familiar names, and have avoided making nomenclatural judgements.

The family is most diverse in southern Africa, and in this region many of the species are well characterized. We follow both Powell (1973) and Christiaens (1973, 1974*a,b*) in recognizing the following 11 southern African species: *P. argenvillei*, *P. barbara*, *P. cochlear*, *P. compressa*, *P. concolor* (as *P. fischeri* Christiaens, 1973, in Christiaens (1974*a,b*)), *P. granatina*, *P. granularis*, *P. longicosta*, *P. miniata*, *P. oculus* (as *P. oculushirci* da Costa, 1771, in Christiaens (1973, 1974*a*)) and *P. tabularis*. We have excluded a possible additional species, *P. sanguinans* Reeve, 1854, because it is identical to *P. miniata* and *P. adansonii* in the morphological characters examined in this study, and appears to differ mainly in the size and coloration of the shell. It is possible that *P. miniata* and *P. compressa* may prove to be ecomorphs (living on rocks and on kelp, respectively) of a single species (Pilsbry 1891), but we have provisionally included both. Since the works of Powell and Christiaens, two additional species have been recognized in Natal, *P. aphanes* and *P. oblecta* (Robson 1986). Three other species in southern Africa, *P. dunkeri*, *P. pectuncululus* and *P. pruinusosus*, have frequently been placed the genus *Helcion* (Thiele 1929; Tomlin & Stephenson 1942; Powell 1973), and were therefore not mentioned by Christiaens (1973, 1974*a*). There has apparently been some taxonomic confusion between *P. dunkeri* and *P. concolor*; records of the former from Natal are misidentifications of mussel-dwelling ecomorphs of juvenile *P. concolor* which strongly resemble *P. dunkeri* (G. M. Branch, unpublished observations).

The patellids of southwestern and western Africa are poorly known. In broad agreement with Powell (1973), we recognize *P. adansonii* from Angola and Namibia (a synonym of *P. safiana* = *nigra* in Christiaens (1974*a*); closely related to, and conceivably conspecific with *P. miniata* from South Africa), *P. canescens* from St Helena (as *P. cyanea* Lesson, 1830, in Christiaens (1973, 1974*a*)) and *P. safiana* from Namibia to Algeria (in the sense of Christiaens (1974*a*), who used the name *P. nigra* da Costa, 1771; Hodgson *et al.* 1996). In addition, we include *P. miliaris* from Angola (not mentioned by Powell (1973); as *P. nigrosquamosa* Dunker, 1846, in Christiaens (1973, 1974*a*)).

The taxonomy of patellids in the Indo-West Pacific province is also problematic. Following Powell (1973) and Christiaens (1986) we employ the name *P. exusta* for a species (or species complex) occurring in the tropical western Indian Ocean (Seychelles, Mascarene Islands, Madagascar, Natal); this was named *P. pica* Reeve, 1854, by Christiaens (1973, 1974*a*). Differences exist between the southern African and Madagascan individuals compared with those further north and west in the Indian Ocean, with the former possessing a much smaller rachidian tooth and paler shells. Similar in shell features is

Table 1. *List of recognized species of Patellidae (after Powell 1973; Christiaens 1973, 1974a,b, 1986; Ridgway 1994; see §2), with generic classification revised according to the phylogenetic analysis (see §§5, 6a), and localities from which anatomical material was examined in the present study*

(Localities: 1, Dunoon, Scotland; 2, Eastbourne, England; 3, Dancing Ledge, Dorset, England; 4, Peveril Point, Dorset, England; 5, Peel, Isle of Man; 6, Black Head, Co. Clare, Ireland; 7, Goleen, Co. Cork, Ireland; 8, Camp Bay, Gibraltar; 9, Rosia, Gibraltar; 10, North Mole, Gibraltar; 11, Ceuta, Spanish Morocco; 12, Magaluf, Mallorca; 13, San Telmo, Mallorca; 14, La Rapida, Mallorca; 15, Santa Teresa di Gallura, Sassari, Sardinia; 16, Capo Plaia, Sicily; 17, Alojera, Gomera, Canary Is; 18, Mitiline, Lesbos, Greece; 19, Tarhzoute, near Agadir, Morocco; 20, Cape Rhir, Morocco; 21, Ponta Delgada, Madeira; 22, El Golfo, Lanzarote, Canary Is; 23, Punta Pechiquera, Lanzarote, Canary Is; 24, Playa Blanca, Lanzarote, Canary Is; 25, Playa Quemada, Lanzarote, Canary Is; 26, Dakar, Senegal; 27, Cape Verde Is; 28, Dixcove Shore, Ghana; 29, Winnerba, Ghana; 30, Thompson's Valley Bay, St Helena; 31, Brand se Baai, Namaqualand; 32, Namib, Angola; 33, Wanda, Angola; 34, Moullie Point, Cape Town, S. Africa; 35, Dalebrook Marine Reserve, Cape Town, S. Africa; 36, Scarborough, Cape Town, S. Africa; 37, Sea Point, Cape Town, S. Africa; 38, Kommetjie, Cape Town, S. Africa; 39, Silwerstroomstrand, Cape Town, S. Africa; 40, West Bank, East London, S. Africa; 41, Esplanade, East London, S. Africa; 42, Port Edward, Natal, S. Africa; 43, Port Nolloth, Natal, S. Africa; 44, Lwandili Transki, S. Africa; 45, Mtwalume, Natal, S. Africa; 46, Durban, Natal, S. Africa; 47, Cape Vidal, Natal, S. Africa; 48, Inhaca I., Moçambique; 49, Salalah, Oman; 50, Kermadec Is; 51, Ulladulla, NSW, Australia; 52, Gerringong, NSW, Australia; 53, Rottneest I., WA, Australia; 54, Tres Marias Is, Mexico; 55, Port Elizabeth, S. Africa; 56, Mauritius.)

genus (type species)	species	distribution	localities
<i>Cymbula</i> H. & A. Adams, 1854 (<i>P. compressa</i> L., 1758)	<i>C. adansonii</i> (Dunker, 1853)	S. Africa, Namibia, Angola	31
	<i>C. canescens</i> (Gmelin, 1791)	St Helena	30
	<i>C. compressa</i> (L., 1758)	S. Africa	34, 38
	<i>C. depsta</i> (Reeve, 1855)	St Paul & Amsterdam Is	
	<i>C. granatina</i> (L., 1758)	S. Africa, Namibia	34, 38
	<i>C. miniata</i> (Born, 1778)	S. Africa	35, 38, 40, 55
	<i>C. oculus</i> (Born, 1778)	S. Africa	35, 38, 40, 55
	<i>C. safiana</i> (Lamarck, 1819)	Algeria to Namibia	8, 19, 20, 28, 29
<i>Helcion</i> Montfort, 1810 (<i>P. pectunculus</i> Gmelin, 1791)	<i>H. concolor</i> (Krauss, 1848)	S. Africa	40, 44, 45
	<i>H. dunkeri</i> (Krauss, 1848)	S. Africa	34, 35, 36, 39, 40
	<i>H. pectunculus</i> (Gmelin, 1791)	S. Africa	34, 35, 38, 40, 43
	<i>H. pruinosis</i> (Krauss, 1848)	S. Africa	34, 35, 38, 39, 40
<i>Scutellastra</i> H. & A. Adams, 1854 (<i>P. plicata</i> Born, 1778 = <i>P. barbara</i> L.)	<i>S. aphanes</i> (Robson, 1986)	east coast S. Africa	42, 46
	<i>S. argenvillei</i> (Krauss, 1848)	S. Africa	36, 37, 38, 40
	<i>S. barbara</i> (L., 1758)	S. Africa	34, 36, 38, 55
	<i>S. chapmani</i> (Tenison-Woods, 1875)	S. E. Australia	51
	<i>S. cochlear</i> (Born, 1778)	S. Africa	34, 38, 40, 55
	<i>S. exusta</i> (Reeve, 1854)	Natal, W. Indian Ocean	46, 47, 48, 56
	<i>S. flexuosa</i> (Quoy & Gaimard, 1834)	Indo-West Pacific	47, 49
	<i>S. granularis</i> (L., 1758)	S. Africa, Namibia	34, 38, 40, 55
	<i>S. kermadecensis</i> (Pilsbry, 1894)	Kermadec Is	50
	<i>S. laticostata</i> (Blainville, 1825)	S. W. Australia	53
	<i>S. longicosta</i> (Lamarck, 1819)	S. Africa	35, 38, 40, 55
	<i>S. mexicana</i> (Broderip & Sowerby, 1829)	W. Mexico to Peru	54
	<i>S. miliaris</i> (Philippi, 1848)	Angola	32, 33
	<i>S. obtecta</i> (Krauss, 1849)	east coast S. Africa	44, 45, 46
<i>Patella</i> L., 1758 (<i>P. vulgata</i> L., 1758)	<i>P. aspera</i> Röding, 1798	Europe, Macaronesian Is	3, 8, 16, 19, 36
	<i>P. caerulea</i> L., 1758	Mediterranean	8, 12, 13, 16, 18
	<i>P. candei</i> d'Orbigny, 1839	Macaronesian Is	17, 21, 22, 24, 25
	<i>P. depressa</i> Pennant, 1777	Britain to Senegal	3, 4, 19, 20, 26
	<i>P. ferruginea</i> Gmelin, 1791	Mediterranean	8, 9, 10, 11, 16
	<i>P. lugubris</i> Gmelin, 1791	Cape Verde Is	27
	<i>P. pellucida</i> L., 1758	N. E. Atlantic	3, 4, 6
	<i>P. rustica</i> L., 1758	Mediterranean, Macaronesian Is	3, 14, 17, 21, 23
	<i>P. vulgata</i> L., 1758	N. Europe to Portugal	1, 2, 4, 5, 7

P. flexuosa, now believed to occur not only throughout the western Pacific (Powell 1973), but also in the Indian Ocean (Christiaens 1986) and south to Natal (Herbert 1991); in the monograph of Christiaens (1973, 1974a,b) this species was recorded as *P. moreli* Deshayes, 1863, and *P. stellaeformis* Reeve, 1842. Recently, it has been suggested

that the Japanese *P. optima* Pilsbry, 1907, might be a distinct species related to *P. flexuosa* (Sasaki *et al.* 1994). More mysterious is the large *P. tucopiana* (Powell 1925), known only from two shells from Tucopia, Melanesia (Powell 1973); these are distinctive, but confirmation of its status awaits the discovery of living specimens.

Again following the monographs of Powell (1973) and Christiaens (1973, 1974a,b), other species in the Pacific and Indian Oceans are more clearly defined. There are three species in temperate Australia, *P. chapmani*, *P. laticostata* (as *P. neglecta* Gray, 1827, in Christiaens (1973, 1974a,b)) and *P. peronii*. In the tropical eastern Pacific there is the single species *P. mexicana* and in the Kermadec Islands *P. kermadecensis*. In the southern Indian Ocean *P. depsta* occurs on the islands of St Paul and Amsterdam.

There has been considerable disagreement about the taxonomy of patellids in the northeastern Atlantic and Mediterranean. Here, we largely accept the species definitions of Christiaens (1974a), as modified in a recent revision by Ridgway (1994). The three northern European species *P. aspera* (as *P. ulyssiponensis* Gmelin, 1791, in Christians (1973, 1974a,b)), *P. depressa* (as *P. intermedia* Murray, 1857, in Christiaens (1973, 1974a)) and *P. vulgata*, are now relatively well characterized (Fischer-Piette 1935; Evans 1953, 1958; Fretter & Graham 1976; Gaffney 1980). Five species occur in the Mediterranean, *P. aspera*, *P. caerulea*, *P. ferruginea*, *P. rustica* and *P. safiana* (Cretella *et al.* 1990, 1994). The classification of patellids on the Macaronesian Islands has been controversial; for example, Powell (1973) accepted eight species, whereas Nordsieck (1982) recognized 15. Recent work (Hernández-Dorta 1992) has supported Christiaens's view that there are only three species in Macaronesia; these we name *P. aspera*, *P. candei* and *P. rustica*. The last-named species was divided into *P. rustica* from the Canary Islands and Madeira, and *P. piperata* Gould, 1846, from the Mediterranean, by Christiaens (1973, 1974a), but we believe these to be conspecific, as supported by both morphological (Ridgway 1994) and genetic similarity (Côrte-Real *et al.* 1996a). Allozyme variation suggests that *P. candei* from the Azores may be specifically distinct from the species in Madeira and the Canary Islands (Côrte-Real *et al.* 1996b), but in the absence of anatomical differentiation we have treated them as a single taxon. There is a single species found on the Cape Verde Islands, *P. lugubris*. The final northeastern Atlantic species, *P. pellucida*, is easily recognized, but has generally been placed in another genus, either *Patina* (Dall 1871a,b; Fretter & Graham 1976) or *Helcion* (Thiele 1891; Powell 1973).

No living patellids have been reliably reported from the western Atlantic. However, there is an unsubstantiated record of a small *Patella*-like animal from the Sargasso Sea, described as *Patina tella* by Bergh (1871; translation by Pilsbry (1891)).

3. MATERIAL AND METHODS

The 38 patellid species recognized from the preceding taxonomic review are listed in table 1. As a result of the cladistic analysis, we have revised the generic classification of the Patellidae (table 1); these new generic allocations (and their abbreviations) are used throughout the remainder of the text. Anatomical material of 36 patellid species was examined during this study; this was obtained from the localities listed in table 1. No specimens were seen of *Scutellastra tucoipiana*. Shells alone were available for *Cymbula depsta*, and its radular characters were taken from Christiaens (1974a). Although animals of *S. kermadecensis*

and *S. mexicana* were examined, these were insufficiently well preserved for extraction of sperm. All voucher material is deposited in the Natural History Museum, London. Except where noted, all descriptions refer to character states found in adult animals.

For the outgroup in the cladistic analysis, we chose to use exemplars as representatives of their genera, rather than using composite generic taxa. The outgroup consisted of *Nacella concinna* (Strebel, 1908), *Cellana radiata capensis* (Gmelin, 1791) and *Cellana tramoserica* (Holten, 1802) (together representing the Nacellidae), and *Acmaea mitra* (Rathke, 1833) and *Lottia digitalis* (Rathke, 1833) (representing the Acmaeidae and Lottiidae, respectively). Localities for the outgroup taxa were as follows: *Nacella concinna* (Signy Island, Antarctica), *Cellana radiata capensis* (East London, South Africa), *Cellana tramoserica* (Gerringong, NSW, Australia), *Acmaea mitra* (Seldovia, Alaska; Santa Cruz, California, for sperm), *Lottia digitalis* (Friday Harbor, Washington, USA). No sperm sample was available from *Nacella concinna*, and the characters given are those of *N. delesserti* (Philippi, 1849) (Hodgson & Bernard 1989).

Live-collected animals were relaxed in 7.5% (w/v) solution of hydrated magnesium chloride in tap water for several hours, fixed in 10% seawater formalin buffered with excess borax, and finally rinsed in tapwater before storage in 80% ethanol.

Characters of the headfoot, pallial complex and gut loops were examined by dissection. Radulae were removed and the first ten rows of worn teeth discarded. They were then cleaned by soaking in dilute hypochlorite bleach solution at room temperature, thoroughly rinsed in distilled water, mounted on a thin layer of polyvinyl acetate glue on glass coverslips attached to aluminium stubs, and coated with gold/palladium, before examination in a scanning electron microscope.

The ultrastructure of spermatozoa was examined by transmission electron microscopy. Where living material was available, pieces of testis were fixed for 2 h in a 2.5% solution of glutaraldehyde in phosphate buffer; otherwise, museum collections fixed in formalin were used. Fixed tissue was rinsed in phosphate buffer for 12 h, post-fixed in 1% osmium tetroxide for 1 h, dehydrated in an acetone series and embedded in Spurr's resin. Thin sections (50–80 nm) were cut with a microtome, stained in 3–4% uranyl acetate for 30 min, followed by 8 min in lead citrate. Further details of the preparation procedure are given in Ridgway (1994). Additional material was examined by A.N.H. following the protocol of Hodgson & Bernard (1988). Many of our observations on sperm have been published in full elsewhere (Hodgson & Bernard 1988, 1989; Hodgson & Chia 1993; Hodgson *et al.* 1996).

Shell microstructure was investigated using acetate peels of sectioned shells and scanning electron microscopy (SEM) of shell sections. The method of preparation of acetate peels was adapted from Kennish *et al.* (1980). Shells were sectioned through the apex, across the width of the animal, and the posterior section was polished with F320, F500 and F800 grade (29, 13 and 7 grain size) carborundum powder (Allman & Lawrence 1972). The polished sections were then cleaned in an ultrasonic bath and etched in 10% HCl for 5–10 s (Taylor *et al.* 1969). The etched shells were rinsed in distilled water, dried at

Table 2. *List of characters and character states used in cladistic analysis of Patellidae*

character	state	description
1. position of apex	0	anterior
	1	central
2. outer crossed-foliated shell layer	0	radial
	1	concentric
3. orientation of m+1 shell layer	2	absent
	0	radial
4. width of m+1 shell layer	1	concentric
	0	wide
5. calcitic m-2 inner shell layer	1	narrow
	2	absent
6. lateral glandular groove	0	absent
	1	crossed-foliated
	2	irregularly-foliated
7. subpallial sensory streak	0	present
	1	absent
	2	extends into mantle cavity
8. coiling of radula	0	does not reach mantle cavity
	1	absent
	2	below visceral mass and gonad
9. rachidian tooth	0	between visceral mass and gonad
	1	penetrates visceral mass, not visible from dorsum
	2	penetrates visceral mass, visible from dorsum
10. number and arrangement of teeth	3	cusplless or absent
	0	small
	1	large
11. pluricuspid cusp 1	0	mineralized teeth in a V-shape
	1	stepped arrangement of mineralized teeth
	2	only four mineralized teeth
12. pluricuspid cusp 4	0	fully formed
	1	reduced
	2	absent
13. marginal teeth	0	fully formed
	1	reduced
	2	absent
14. anterior thickening of acrosome	0	three each side, lying adjacent
	1	two each side
	2	one each side
15. acrosomal lobe	3	three each side, innermost anterior to adjacent one
	0	not thickened
	1	elongate, laterally thickened
16. basal thickening of acrosome	2	rounded terminal thickening
	3	conical terminal thickening
	4	elongate terminal thickening
17. shape and size of nucleus	0	absent
	1	lobe with homogeneous contents
	2	lobe with anterior differentiation
	3	lobe reduced or absent, internal lobulation
	4	lobe with electron-lucent space
18. shape and size of nucleus	5	lobe elongate, rod-like
	0	absent
	1	thickened
19. shape and size of nucleus	2	strongly thickened
	0	barrel or cylindrical, < 3 µm
	1	elongate, cylindrical, > 3 µm
20. shape and size of nucleus	2	elongate, tapering, > 3 µm

60 °C, dipped in acetone and pressed on to acetate paper. After a few minutes the shell could be removed from the acetate, leaving an imprint of the shell microstructure. The acetate papers were then mounted between slides and viewed using a compound microscope. SEM was used to confirm that acetate peels were adequate for the

identification of the microstructure types. Shells were polished, etched and cleaned as described above, mounted on SEM stubs and coated with gold/palladium before viewing. X-ray diffraction (Ridgway 1994) was used to confirm our recognition of calcitic and aragonitic structures in the acetate peels. The extent of certain shell

Table 3. Character states for the cladistic analysis of Patellidae

(See table 2 for explanation of character numbers and states.)

species	character																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Lottia digitalis</i>	1	2	1	0	0	1	2	2	0	2	?	?	2	4	1	0	0
<i>Acmaea mitra</i>	1	2	1	0	0	1	2	2	0	2	?	?	2	3	1	0	1
<i>Cellana capensis</i>	1	2	0	1	0	1	0	0	0	2	?	?	0	4	5	0	2
<i>Cellana tramoserica</i>	1	2	0	1	0	1	0	0	0	2	?	?	0	4	5	0	2
<i>Nacella concinna</i>	1	2	?	2	2	0	0	2	0	2	?	?	0	4	5	0	2
<i>Cymbula adansonii</i>	1	1	0	1	1	0	0	2	1	0	1	2	0	2	3	2	0
<i>Cymbula canescens</i>	1	1	0	1	0	0	0	2	1	0	1	1	0	2	2	1	0
<i>Cymbula compressa</i>	0	1	0	1	1	0	0	2	1	0	1	2	0	2	3	2	0
<i>Cymbula depsta</i>	1	1	0	1	1	?	?	?	1	0	1	?	0	?	?	?	?
<i>Cymbula granatina</i>	1	1	0	1	1	0	0	2	1	0	1	2	0	2	2	1	0
<i>Cymbula miniata</i>	1	1	0	1	1	0	0	2	1	0	1	2	0	2	3	2	0
<i>Cymbula oculus</i>	1	1	0	1	0	0	0	2	1	0	1	2	0	2	2	1	0
<i>Cymbula safiana</i>	1	1	0	1	0	0	0	2	1	0	1	1	0	2	2	1	0
<i>Helcion concolor</i>	1	1	0	1	1	0	0	3	0	1	1	1	0	2	1	1	0
<i>Helcion dunkeri</i>	0	1	0	1	0	0	1	3	0	1	1	2	?	2	4	1	0
<i>Helcion pectunculus</i>	0	1	0	1	0	0	1	3	0	1	1	2	1	3	4	0	1
<i>Helcion pruinus</i>	0	1	0	1	0	0	1	3	0	1	1	2	1	4	4	0	1
<i>Scutellastra aphanes</i>	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0
<i>Scutellastra argenvillei</i>	1	1	1	0	1	1	0	2	1	1	0	1	0	0	0	0	0
<i>Scutellastra barbara</i>	1	0	1	0	1	1	0	2	1	1	0	1	0	0	0	0	0
<i>Scutellastra chapmani</i>	1	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0
<i>Scutellastra cochlear</i>	1	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	1
<i>Scutellastra exusta</i>	1	0	1	0	0	1	0	1	2	1	0	0	0	2	1	0	0
<i>Scutellastra flexuosa</i>	1	0	1	0	0	1	0	1	1	1	0	0	0	2	1	0	0
<i>Scutellastra granularis</i>	1	1	1	0	1	1	0	2	1	1	1	1	0	1	0	0	2
<i>Scutellastra kermadecensis</i>	1	0	1	0	0	?	0	1	1	1	0	1	0	?	?	?	?
<i>Scutellastra laticostata</i>	1	0	1	0	0	?	0	1	2	1	0	1	0	0	0	0	0
<i>Scutellastra longicosta</i>	1	0	1	0	0	1	0	2	1	1	0	1	0	0	0	0	1
<i>Scutellastra mexicana</i>	1	0	1	0	0	1	0	2	2	1	0	1	0	?	?	?	2
<i>Scutellastra miliaris</i>	1	?	1	0	1	1	0	2	1	1	1	1	0	1	0	0	2
<i>Scutellastra obtecta</i>	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0
<i>Scutellastra peronii</i>	1	0	1	0	0	1	0	1	1	1	0	1	0	3	0	0	2
<i>Scutellastra tabularis</i>	1	0	1	0	0	1	0	2	1	1	0	1	0	0	0	0	0
<i>Patella aspera</i>	1	1	1	1	1	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella caerulea</i>	1	1	1	1	1	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella candei</i>	1	1	1	1	0	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella depressa</i>	1	1	1	1	1	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella ferruginea</i>	1	1	1	1	0	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella lugubris</i>	1	1	1	1	0	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella pellucida</i>	0	1	1	1	1	0	0	0	0	1	2	1	1	2	0	0	0
<i>Patella rustica</i>	1	1	1	1	1	1	0	0	0	1	2	1	3	3	0	0	1
<i>Patella vulgata</i>	1	1	1	1	1	1	0	0	0	1	2	1	3	3	0	0	1

layers could be observed by inspection of ventral growth surfaces of intact shells using a binocular microscope, permitting larger numbers of specimens to be examined.

4. SELECTION, DESCRIPTION AND CODING OF CHARACTERS

The characters and character states used in the analysis are summarized in tables 2 and 3. Here we describe and explain our choices.

(a) *Shell morphology and microstructure (characters 1–5)*

The shell morphology of some patellid species is highly variable. In the *Patella* species of northwestern

Europe, shell features sometimes show intergradation between species (Fischer-Piette 1935; Evans 1953), and the microhabitat may have pronounced ecophenotypic effects on shell shape (Moore 1934; Fretter & Graham 1962). Features of shell shape might therefore be considered unreliable for phylogenetic analysis. Nevertheless, in the traditional definitions of the genera *Helcion* and *Patina*, one feature of shell shape has consistently been used, the relatively anterior position of the shell apex (Gray 1857; Dall 1871b; Pilsbry 1891; Thiele 1929; Powell 1973). In *Helcion dunkeri*, *H. pectunculus*, *H. pruinus* and *Patella pellucida*, the apex is situated at approximately one-tenth of the length of the shell behind the anterior edge, so that the shell is cap-shaped rather than conical (**character 1**). This shell shape is also found in *Cymbula*

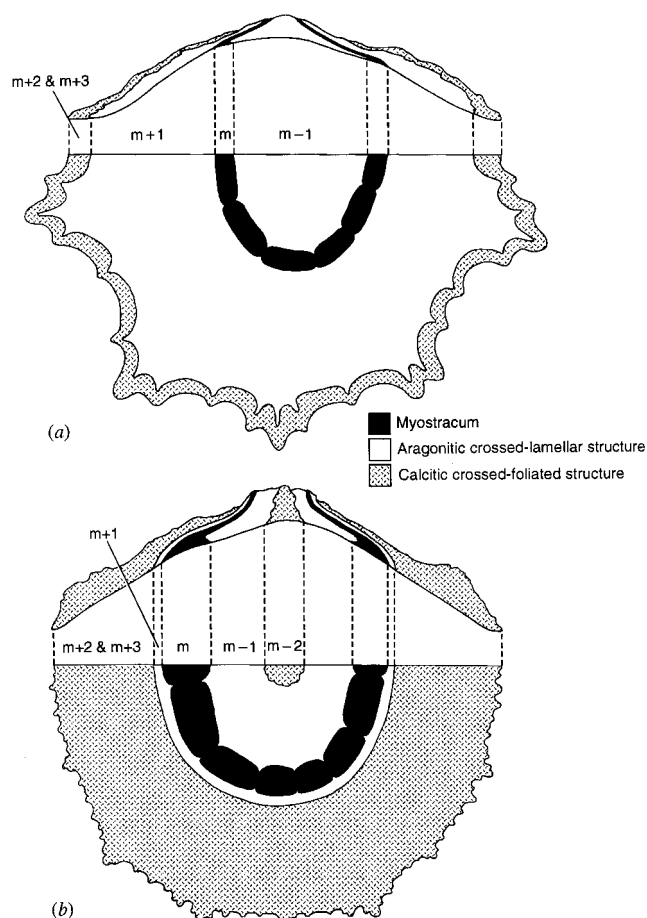


Figure 1. Diagrams of transverse cross-sections, and interior views of posterior halves, of patellid shells. (a) *Scutellastra flexuosa*, showing wide m+1 shell layer (shell diameter 25 mm); (b) *Patella aspera*, showing narrow m+1 shell layer and presence of m-2 layer (shell diameter 30 mm).

compressa. Juveniles of *H. concolor* which occupy mussel beds also have a markedly anterior apex, but this becomes more central in the adult (and the character is coded according to its adult state). The cap-shaped shell is believed to reduce drag in *P. pellucida*, which is exposed to strong currents in its habitat on the fronds and stipe of laminarian algae (Warburton 1976). In the remaining patellid species, and in the members of the outgroup, the apex is at one-third to one-half of the length of the shell. The anteriorly produced, pyriform outline of *Scutellastra cochlear* has often been mentioned and used to support its placement in the monotypic taxon *Olana* (Gray 1857; Powell 1973; Christiaens 1973, 1974a), but this is a unique derived character (autapomorphy) which therefore cannot contribute information about relationships.

The shells of patellogastropods display an extraordinary diversity of microstructure. In the Patellidae there are four to six layers, differing in mineralogy, crystal structure and thickness, which appear as concentric bands on the interior surface (figure 1). Early authors (e.g. Dall 1871b; Pilsbry 1891; Thiele 1929) often mentioned the internal appearance of the shell, whether porcellanous or iridescent, in their definitions of taxa. Nevertheless, the fine structure of the layers was unknown

until the work of Thiem (1917), which was followed by the more detailed descriptions of Bøggild (1930) and MacClintock (1967). Following the convention established by MacClintock (1967), the layers are numbered by reference to the myostracum (m); starting at the outside of the shell, they are designated m+3, m+2, m+1, m, m-1 and m-2. The numbering of the layers on either side of the myostracum refers to the positions of the layers only, and does not imply homology of layers with the same code. The nomenclature used here to describe the crystal microstructures follows that of Bøggild (1930), MacClintock (1967) and Taylor *et al.* (1969).

Although MacClintock (1967) distinguished m+2 and m+3 layers in the shells of patellids, in the present study it was found that these were not clearly separable. This outer layer is characterized by a calcitic crossed-foliated microstructure. Within it, the first-order lamellae are predominantly arranged radially in most members of *Scutellastra*, whereas those of *S. argenvillei*, *S. granularis*, *Helcion*, *Cymbula* and *Patella* are predominantly concentric (**character 2**). In members of the outgroup, a crossed-foliated outer layer is lacking, and a prismatic calcitic layer is outermost. In *Cellana* there is an aragonitic radial crossed-lamellar layer immediately overlying the myostracum, followed by a calcitic foliated layer and an outer complex-prismatic layer. *Nacella* differs from this only in the absence of the innermost (m+1) crossed-lamellar layer. In *Lottia*, the layers external to the myostracum are aragonitic concentric crossed-lamellar, calcitic fibrillar and an outer simple-prismatic calcitic layer. *Acmaea* also shows a concentric crossed-lamellar m+1 layer, but followed by a calcitic foliated layer and an outer layer of complex-prismatic calcite (MacClintock 1967; Lindberg 1988a).

The homologies of the shell layers are difficult to establish, but the aragonitic crossed-lamellar m+1 layer is presumed homologous throughout (although it is absent in *Nacella*). Within the m+1 layer the first-order lamellae of the crossed-lamellar structure are radial in *Cellana*, *Cymbula* and *Helcion*, but concentric in *Scutellastra*, *Patella*, *Lottia* and *Acmaea* (**character 3**). As explained by MacClintock (1967), lamellae are only fully developed in layers more than 10 µm in thickness; thinner layers appear to have a complex crossed-lamellar structure. In adult *Patella* specimens the m+1 layer is indeed sometimes so thin that the lamellae are not fully developed; however, examination of the largest shells confirms that concentric orientation does develop as the layer increases in thickness.

The thickness of the m+1 layer has been included as a separate character (**character 4**). When the intact shell is viewed from below, the m+1 layer is visible as a broad expanse in *Scutellastra*, *Lottia* and *Acmaea*, making up more than half of the width of the combined outer (m+1, m+2, m+3) layers (figure 1). Geographical variation in this character has been described in *S. granularis* by Cohen & Branch (1992), in which the m+1 layer is relatively narrower in specimens from colder environments, although still usually making up more than half of the width of the outer layers. In the remaining patellid species, and in *Cellana*, the m+1 layer is narrow, making up less than half of the width of the outer layers, whereas in *Nacella* it is absent.

The $m-1$ layer is aragonitic and of crossed-lamellar structure in all patellids (as in *Cellana*, *Acmaea* and *Lottia*; it is absent in *Nacella*), and is often the only layer on the inside of the myostracum. In some taxa an $m-2$ layer is present, and the $m-1$ layer may then be thin. This innermost $m-2$ layer is of calcitic crossed-foliated structure (**character 5**); it has been found in five species of *Cymbula*, one of *Helcion*, four of *Scutellastra* and six of *Patella* (figure 1; table 3). The extent of this layer is variable; for example it is wide in *P. vulgata*, but represented only by a small apical patch in *P. depressa*. Within some *Patella* species there is evidence of a geographical trend, the layer being especially well developed in specimens from more northern localities (S. A. Ridgway and J. D. Taylor, unpublished observation); similarly, in *S. granularis* the layer is only present in specimens from the west coast of southern Africa (Cohen & Branch 1992). This calcitic inner layer is absent from all the remaining patellids; this is also true of the outgroup members, *Cellana*, *Acmaea* and *Lottia*, but in *Nacella* there is a calcitic $m-2$ layer of irregularly foliated structure.

(b) Headfoot and pallial complex (characters 6, 7)

A lateral glandular groove is found on either side and running round the back of the foot. It consists of a groove lined with glandular cells, covered by a flap (Davis & Fleure 1903; Thiem 1917), and may prevent desiccation in small limpets by producing mucus (Davis & Fleure 1903), or be connected with resistance to currents (Fretter & Graham 1994). This structure is lost during the ontogeny of most species, but is retained in adult *Helcion*, *Cymbula*, *P. pellucida* (Fretter & Graham 1994, fig. 339) and *Nacella* (**character 6**).

Under the mantle, on either side of the foot, lies the subpallial sensory strip. As described by Thiele (1893), this consists of a ridge innervated by nerves from the pleural and osphradial ganglia. Nevertheless, it is not homologous with the osphradium (as suggested by Thiem (1917)), for its ultrastructure, with ciliated sensory cells surrounded by microvillous supporting cells, is similar to that of the mechanoreceptors of bivalves (Haszprunar 1985). Thiem (1917) found that the length of the sensory strip varied among six species of *Patella* and one of *Nacella*; however, Ridgway (1994) showed that in general the differences in length are not of systematic value. In the Nacellidae and most of the Patellidae the strip extends forwards from the side of the foot, back over the shoulder of the animal and a short distance into the mantle cavity, whereas in three species of *Helcion* it stops short of the shoulder (**character 7**). This organ is absent in *Acmaea* and *Lottia*, as also noted by Haszprunar (1985).

Historically, characters of the gills were among the first anatomical features to be used in the classification of patellogastropods. The true ctenidial gill found in Acmaeidae and Lottiidae is absent in Patellidae and Nacellidae, and has long been used as a principal character for the separation of 'acmaeid' and 'patellid' limpets (Gray 1857; Dall 1871a,b; Pilsbry 1891; Powell 1973). In addition, many patellogastropods possess pallial gills along the mantle edge. These consist of numerous, triangular, ciliated leaflets, as described in detail by Nuwayhid *et al.* (1978). Within the Patellidae, the cordon of pallial gills is usually complete, running all around the mantle

edge. However, in a few species the cordon is interrupted anteriorly, above the head, and many authors have used this character to define the genera *Helcion* and *Patina* (Gray 1857; Dall 1871a,b; Thiele 1929; Christiaens 1973, 1974a). Nevertheless, as first noted by Pilsbry (1891), this character is not consistent. Within *Helcion*, the cordon is incomplete in most individuals, but may become complete in the largest specimens (this may explain Powell's (1973) claim of a complete cordon in *H. pruinosus* and *H. dunkeri*). Among lottiids too there is evidence of intraspecific variation in the development of the anterior part of the pallial gill cordon (Lindberg & McLean 1981). Indeed, Lindberg (1988a) found such evidence of homoplasy in the development of pallial gills among lottiids that he doubted the validity of this character in patellogastropod systematics. Accordingly, we have omitted this traditional character from the analysis. One other gill character has been used in patellid classification. The pallial gill leaflets of *S. mexicana* are arborescent, and Dall (1871a,b) used this character in the diagnosis of a new genus (*Ancistromesus*). The feature appears to be an autapomorphy, perhaps connected with the extremely large size of this species (up to 35 cm).

The mantle edge bears retractile pallial tentacles, which are believed to serve a sensory function (Davis & Fleure 1903; Hodgson *et al.* 1987). Differences between species in the size and arrangement of their pallial tentacles have been claimed (Fretter & Graham 1976; but, see Bowman 1981). However, we found these features to be too variable for use in the analysis.

(c) Radula and alimentary system (characters 8–13)

The patellid radula is long, generally one to two times the length of the shell. It is contained within the radular sac, which is doubled back on itself (Fretter & Graham 1962), and the double strand is then coiled in one of four arrangements (**character 8**). In *Helcion* the radular coil penetrates the visceral mass to such an extent that it is visible from the dorsal surface of the animal when the shell is removed; in *Cymbula*, seven members of *Scutellastra* and in *Nacella*, *Lottia* and *Acmaea*, the radular coil penetrates the visceral mass, but is not visible from the dorsal surface; in *Patella* and *Cellana* the radula coils below the visceral mass and gonad; whereas in nine members of *Scutellastra* the radula lies below the visceral mass but above the gonad.

The ratio of the length of the radula to that of the shell has sometimes been used as a character to distinguish species (Fischer-Piette 1935, 1941; Evans 1953; Christiaens 1974a), but it is now known that this is subject to environmentally induced variation (Brian & Owen 1952). Furthermore, allometric considerations suggest that the use of such ratios is flawed (Paredes & Acuna 1991). Relative radular length was therefore not employed in this study.

Traditionally, features of the radular teeth have been extensively used in the classification of patellogastropods. As an early example, Dall (1871a,b) relied almost entirely on a combination of radular and gill characters to define families and genera. Since then, most systematic studies of the Patellidae have included radular characters, although the emphasis on particular traits has varied. Patellogastropod radulae are of the docoglossate type. In

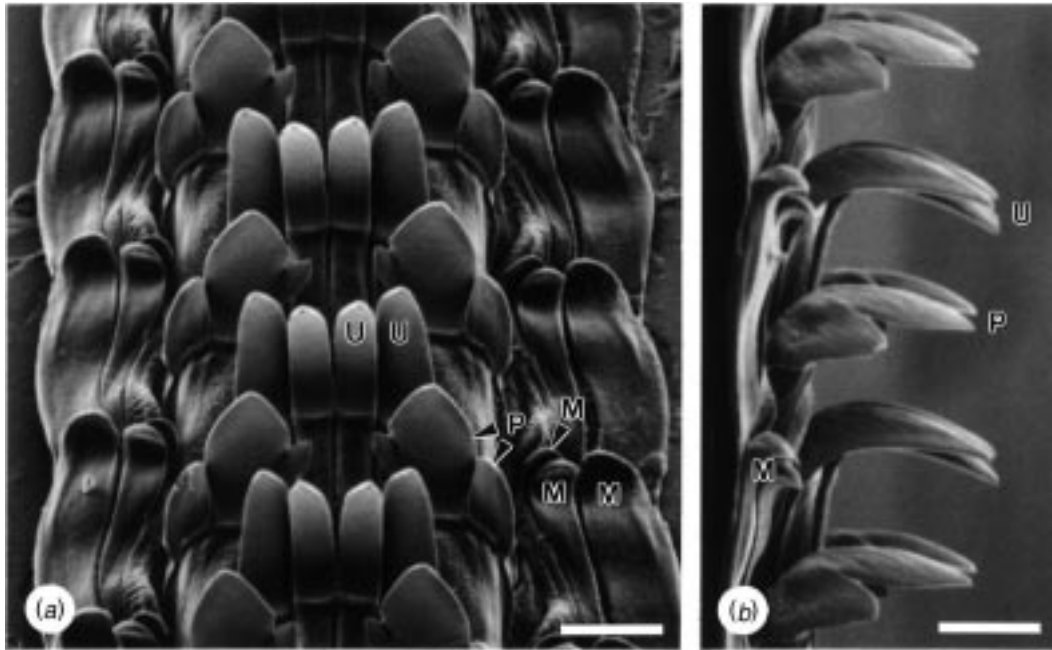


Figure 2. Two views of the radula of *Patella caerulea*: (a) inclined at 45°; (b) side view. The two unicuspid teeth, single pluricuspid tooth and three marginal teeth are labelled on one side of a single tooth row. M, marginal tooth; P, pluricuspid tooth; U, unicuspid tooth. Scale bars, 100 µm.

the Patellidae, a single tooth row consists of four central unicuspid teeth, flanked on each side by a large pluricuspid lateral tooth, and at each outer edge of the row two or three small marginal teeth (uncini) (figure 2). In addition, a single rachidian tooth may be present between the two pairs of unicuspid teeth. The cusps of the unicuspid and pluricuspid teeth, and sometimes of the rachidian, are mineralized with opal and goethite (Runham *et al.* 1969; Mann *et al.* 1986; van der Wal 1989), and are attached to base-plates on the radular ribbon.

Within the Patellidae the development of the rachidian tooth is variable. Studies by light microscopy (Thiele 1891; Christiaens 1974a) have often claimed that a rachidian tooth is present in all patellids, although frequently reduced. However, studies with the scanning electron microscope have revealed that in some *Patella* species the rachidian is indeed absent, and that its appearance was artefactual in earlier studies (Jones *et al.* 1984). In *P. vulgata*, Ridgway (1994) found a rachidian tooth only in small animals (less than 1 mm in shell length), and in *P. rustica* noted that the rachidian was absent in some adults, but vestigial in others. The absence or state of development of the rachidian has been emphasized in some classifications (Dall 1871a,b; Thiele 1929; Christiaens 1973, 1974a), although other workers have allowed variability in this character within their supraspecific taxa (Pilsbry 1891; Powell 1973). In the present study, the rachidian was found to be absent, or represented only by a reduced base-plate without a mineralized cusp, in adults of *Patella* and *Helcion* (**character 9**). Adult *Cymbula* species have a rachidian tooth with a small mineralized cusp, less than half of the length and width of the cusps of the adjacent unicuspid teeth (figure 3a). In *Scutellastra*, the rachidian tooth is similarly small, with the exceptions of *S. exusta* (material

from Mauritius), *S. laticostata* and *S. mexicana*, in which it is well developed, with a mineralized cusp more than half of the length and width of the adjacent unicuspid teeth (figure 3b). Rachidian teeth are absent in all members of the outgroup.

It has long been recognized that there are two distinctive arrangements of the unicuspid teeth in patellids (Thiele 1891, 1929; Koch 1949; Powell 1973; Christiaens 1973, 1974a). The four unicuspid teeth may lie in a straight line across the radular ribbon, making a stepped arrangement with the pluricuspid teeth (figure 4c), or the inner pair of unicuspid teeth may be a little forward of the outer pair, making a V-shaped arrangement of the mineralized teeth (figure 4b) (**character 10**). The former arrangement is found in all Patellidae with the exception of *Cymbula*, in which the characteristic V shape occurs. In the outgroup families, the number of large, mineralized teeth is reduced. Whereas in Patellidae there are six or seven such teeth in each row (sometimes a rachidian, and on either side two unicuspid and a pluricuspid tooth), in Nacellidae, Lottiidae and Acmaeidae there are just four, with the inner pair lying forward of the outer pair (figure 4a). As the homologies of individual teeth between ingroup and outgroup have not yet been determined, the number and arrangement of the unicuspid teeth were not coded as separate characters. Both Powell (1973) and Christiaens (1973, 1974a) stressed the concave anterior face of the unicuspid teeth of some *Cymbula* species in their subgeneric definitions, but we find that this appearance is an artefact of preparation which produces partial collapse of the cusps, and have therefore not employed this character.

The number and form of the cusps on the pluricuspid tooth have frequently been used as a taxonomic character in patellids, usually to discriminate between species (Fischer-Piette 1935; Evans 1947; Koch 1949;

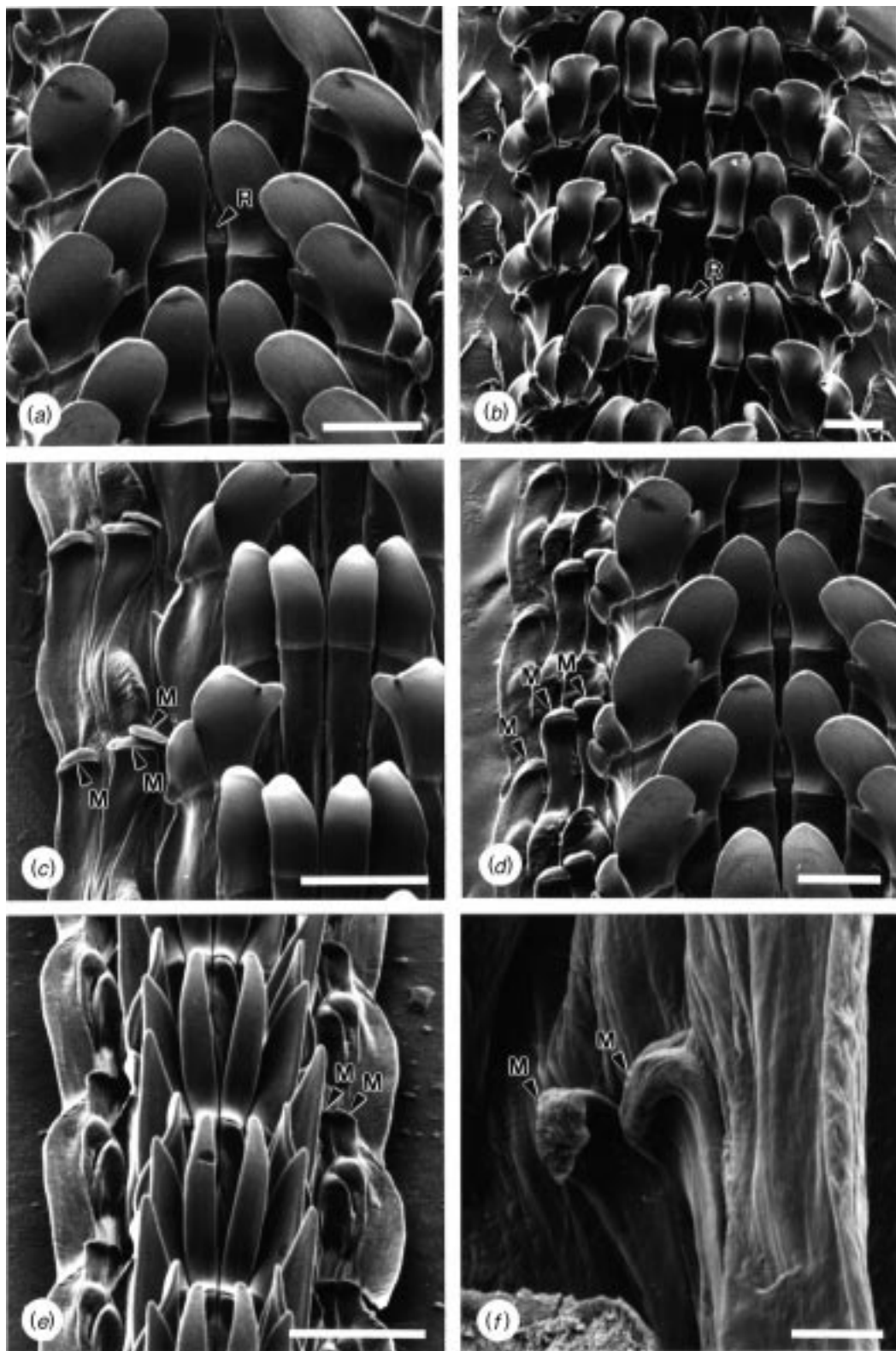


Figure 3. Rachidian and marginal radular teeth of Patellidae. (a) *Cymbula canescens* with small rachidian; (b) *Scutellastra laticostata* with large rachidian; (c) *Patella vulgata* with three marginal teeth, of which the innermost lies anterior to adjacent one; (d) *Cymbula canescens* with three adjacent marginal teeth; (e) *Helcion pectunculus* with two marginal teeth; (f) *Helcion pruinosus* with two marginal teeth. M, marginal tooth cusp; R, rachidian tooth cusp. Scale bars (a) to (e), 100 μ m; (f), 10 μ m.

Fischer-Piette & Gaillard 1959), but also to define supraspecific groups (Christiaens 1973, 1974a). However, as noted by Lindberg (1988a), tooth morphology may be subject to a high degree of convergence and should be

used with caution. For the present study the cusps of the pluricuspid teeth have been numbered 1 to 4 from the margin towards the midline of the radula; of these, cusps 1 and/or 4 may be reduced (figure 4d–f). Cusp 1 (**character 11**) is

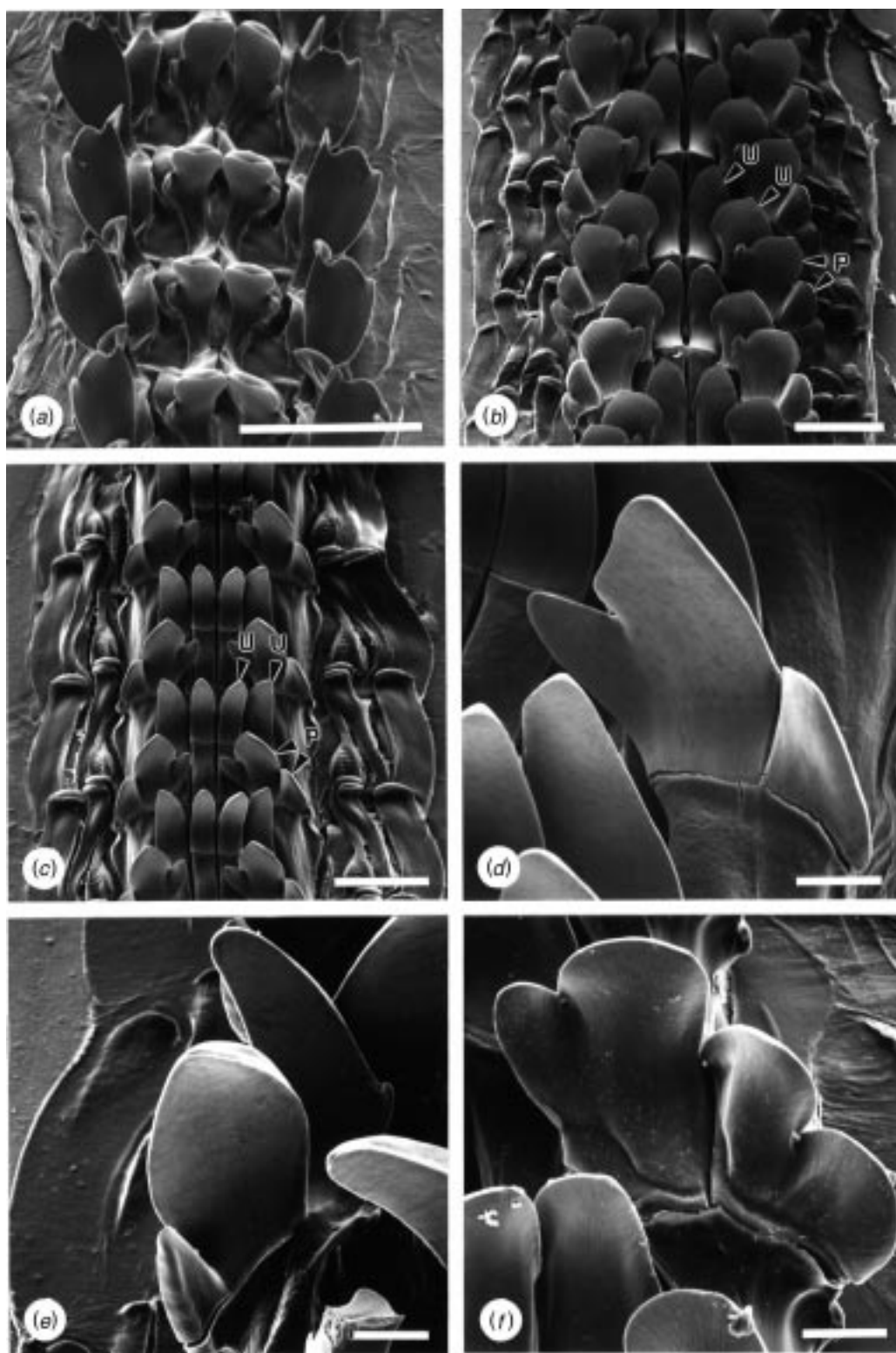


Figure 4. Unicuspid and pluricuspid teeth of Nacellidae and Patellidae. (a) *Nacella concinna* with four mineralized teeth in each row; (b) *Cymbula safiana* with inner pair of unicuspid anterior to outer pair, making V-shaped arrangement of mineralized (unicuspid and pluricuspid) teeth; (c) *Patella ferruginea* with unicuspid teeth in a row across radular ribbon, making a stepped arrangement of mineralized teeth; (d) pluricuspid tooth of *Patella candei* with outermost cusp absent and innermost cusp reduced; (e) pluricuspid tooth of *Cymbula oculus* with outermost cusp reduced and innermost cusp absent; (f) pluricuspid tooth of *Scutellastra laticostata* with all cusps fully developed. P, pluricuspid tooth; U, unicuspid tooth. Scale bars (a) to (c), 200 μm ; (d) to (f), 50 μm .

'absent' (defined as less than 5% of the size of cusp 2) in *Patella*, but 'reduced' (between 25% and 50% of the size of cusp 2) in *Helcion*, *Cymbula*, *S. granularis* and *S. miliaris*. The cusp is fully formed (at least 50% of the size of cusp 2) in the

remaining *Scutellastra* species. Relative to cusp 3, cusp 4 is reduced in *Patella*, 12 members of *Scutellastra*, two of *Cymbula* and in *H. concolor*, absent from the remaining species of *Helcion* and *Cymbula*, and fully formed in the remaining four

species of *Scutellastra* (**character 12**). Some intraspecific variation exists in this character; in *P. rustica* from the Macaronesian Islands, cusp 4 is reduced but distinct, whereas it is vestigial or absent in specimens from the Mediterranean (which led Christiaens (1974a) to regard these populations as distinct species; but, see Ridgway 1994; Côte-Real *et al.* 1996a). Owing to the uncertainties of tooth homology, these characters of the pluricuspid teeth cannot be coded in the outgroup.

In addition to the mineralized teeth, docoglossan radulae may have several small marginal teeth with unmineralized cusps. Their mode of formation and staining reactions suggest that these teeth are in fact modified base-plates, for which the term 'uncini' is more suitable (Dall 1871b; Guralnik & de Maintenon 1997). In the majority of patellids there are three marginal teeth on either side, and these may be arranged in either of two ways (**character 13**). The three marginals may lie side by side diagonally across the width of the ribbon (*Cymbula*, *H. concolor*, *Scutellastra*; figure 3d), or the inner marginal may lie anterior to, and partly concealed beneath, the adjacent marginal (*Patella*, except *P. pellucida*; figure 3c). In a few patellids there are only two cusp-bearing marginals on either side, arranged in line (*H. pectunculus*, *H. pruinus*, *P. pellucida*; figure 3e,f). Using the light microscope, details of the marginal teeth are often poorly visible; in particular it may be difficult to discern whether the reduced marginal base-plates carry cusps or not. This may explain why previous accounts of the radulae of *Helcion* species and of *P. pellucida* have illustrated three marginal teeth (Gray 1857; Thiele 1891). Among the outgroup members, Nacellidae show three marginals in a diagonal line, whereas in *Lottia* and *Acmaea* there is only a single marginal tooth on either side.

The alimentary system of patellogastropods consists of three sections, the foregut, midgut and hindgut, of which the last two are long and thrown into complex coils. Evolutionary trends of decreasing complexity of coiling patterns have been proposed by Fleure (1904), Thiem (1917) and Lindberg (1988a,b), and their ontogenetic development has been studied in Lottiidae (Walker 1968). Ridgway (1994) included the pattern of gut loops in a phylogenetic analysis of patellids. However, with the examination of additional species in the present study, it was found that the character states defined by Ridgway (1994) were not discrete. This character was therefore not included in the analysis.

(d) Spermatozoa (**characters 14–17**)

The sperm of patellogastropods are of the primitive (Franzén 1977) or aquasperm type (Jamieson 1987), consisting of a head, midpiece and tail. The head comprises an acrosome and the nuclear material, the midpiece is composed of mitochondria and two centrioles, and the tail is a flagellum with a 9+2 arrangement of microtubules. The ultrastructure of patellid sperm was first described in *P. rustica* (Azevedo 1981, as *P. lusitanica*) and *P. vulgata* (Maxwell 1983; Smaldon & Duffus 1985). That of the southern African limpets was described by Hodgson & Bernard (1988) and later used in a phylogenetic analysis of the species (Jamieson *et al.* 1991). The remaining species have since been examined and a more complete set of sperm characters has been used to infer

relationships among members of the Patellidae (Ridgway 1994; Hodgson *et al.* 1996). In the following account, information on the ultrastructure of the sperm of *Lottia* is taken from Hodgson & Chia (1993), on *Acmaea* from A. N. Hodgson (unpublished data), on *Cellana* from Hodgson & Bernard (1988), and on *Nacella* from Hodgson & Bernard (1989).

From these earlier accounts it is clear that characters of sperm morphology can prove useful for phylogenetic analysis. However, the interpretation and coding of these characters is often problematic, owing to uncertainties of homology and to differences in the subjective assessment of resemblance. One approach has been to divide the sperm of patellids into five discrete categories (types I–IV and VI; Hodgson & Bernard 1988; Hodgson *et al.* 1996), which show some correlation with traditional schemes of classification of the species. In the first attempt at a cladistic analysis of patellid sperm morphology, Jamieson *et al.* (1991) employed a mixture of qualitative and quantitative morphometric characters. Our approach has been to attempt to identify discrete states of homologous characters, based on an almost complete survey of the sperm of the Patellidae, and in doing so we have reinterpreted some of the earlier findings.

The most complex variation in form occurs in the acrosome, and this has been encoded in three characters. The anterior part of the acrosome (**character 14**) may lack any elaboration or thickening, so that the entire acrosome simply resembles a bell-shaped or conical cap; this state occurs only in *Scutellastra* species (figure 5d,f), with the exception of *S. granularis*, *S. miliaris*, *S. exusta* and *S. flexuosa*. In *S. granularis* and *S. miliaris*, the acrosome is narrowly elongate and appears thickened for the apical half of its length; close examination suggests that this is achieved by thickening of the opposing lateral walls (figure 5g). The acrosome of *Cymbula* species, *H. concolor*, *H. dunkeri*, *S. exusta*, *S. flexuosa* and *P. pellucida* is thickened and rounded at the apex (figure 5e,i–l,n). A different style of thickening is seen in *Patella* species (except *P. pellucida*), *H. pectunculus* and *Acmaea*, in which the tip is pointed, so that the apex is a solid cone (figure 5b,m). A fifth state is recognized in *H. pruinus* which, as in the outgroup members *Lottia*, *Cellana* and *Nacella*, shows a strikingly elongate, thickened, acrosomal apex (figure 5a,c,h). As a second character of the acrosome, there may be a rounded or elongate lobe projecting backwards from the apex into the subacrosomal space (**character 15**). This may appear as a homogenous, electron-dense lobe, as in *Lottia*, *Acmaea*, *H. concolor*, *S. exusta* and *S. flexuosa* (figure 5a,b,e,i). In other cases, various states of differentiation of the contents of the lobe can be seen; there may be anterior differentiation (an electron-dense lobe contrasting with the paler anterior acrosome, as in *C. canescens*, *C. granatina*, *C. oculus* and *C. saffiana*; figure 5l), lobulation (several electron-dense bodies within the acrosome, and a reduction in size or absence of a projecting lobe, as in *C. adansonii*, *C. compressa* and *C. miniata*; figure 5k), or the lobe may itself contain an electron-lucent space and also be elongate or prominent (as in *H. dunkeri*, *H. pectunculus* and *H. pruinus*; figure 5h,j). The acrosome of the Nacellidae has previously been considered quite different from that of the Patellidae, for it was thought to contain an axial rod extending from the acrosome to the nucleus

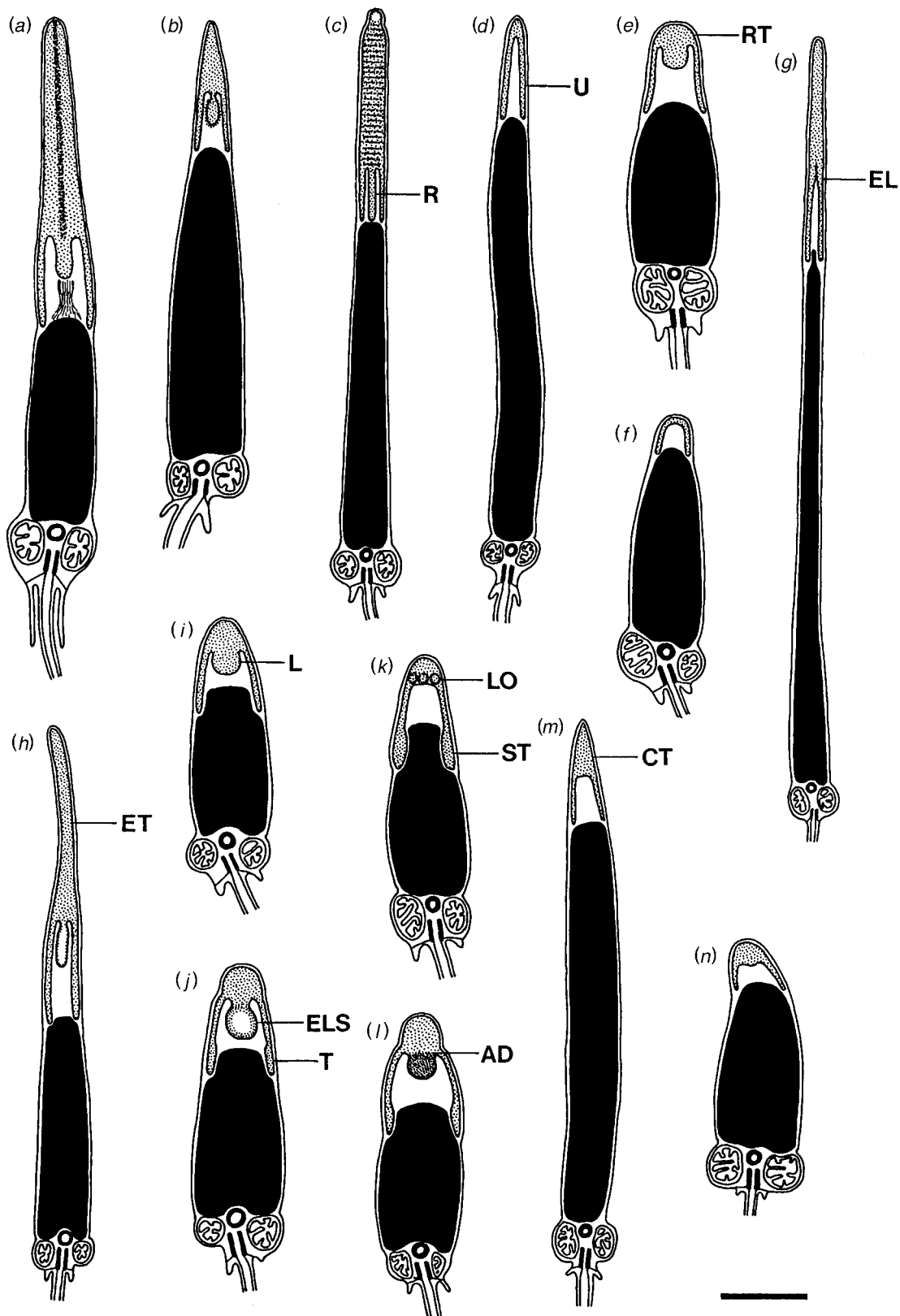


Figure 5. Diagrams of mid-longitudinal sections of the principal types of spermatozoan heads found in patellogastropods, showing characters of nucleus and acrosome, as used in cladistic analysis. (a) *Lottia digitalis*; (b) *Acaea mitra*; (c) *Cellana radiata capensis*; (d) *Scutellastra cochlear*; (e) *S. exusta*; (f) *S. argenvillei*; (g) *S. granularis*; (h) *Helcion pruinosis*; (i) *H. concolor*; (j) *H. dunkeri*; (k) *Cymbula miniata*; (l) *C. oculus*; (m) *Patella aspera*; (n) *P. pellucida*. (a) After Hodgson & Chia (1993); (b) A. N. Hodgson, unpublished data; (c–i, k, l) after Hodgson & Bernard (1988); (j, m, n) after Hodgson *et al.* (1996). Nuclei are shown in black, acrosomes stippled. AD, acrosome with anterior differentiation; CT, acrosome with conical terminal thickening; EL, acrosome with elongate lateral thickening; ELS, acrosomal lobe with electron-lucent space; ET, acrosome with elongate terminal thickening; L, acrosomal lobe with homogeneous contents; LO, acrosome with internal lobulation; R, rod-shaped acrosomal lobe; RT, acrosome with rounded terminal thickening; ST, acrosome with strongly thickened base; T, thickened base of acrosome; U, unthickened acrosome. Scale bar, 1 μ m.

(Hodgson & Bernard 1988, 1989; Jamieson *et al.* 1991). However, after re-examination we consider that the 'axial rod' is in fact a narrow, elongate, cylindrical lobe (figure 5c). In the remaining patellids (most *Scutellastra* and all *Patella* species) the acrosomal lobe is absent. The coding of the sperm of *P. pellucida* presented some difficulty in this scheme (figure 5n). The acrosome in this species is abbreviated, with a rounded and thickened anterior end; despite some resemblance to other *Patella* species, this was coded as a thickened and rounded acrosome. It also shows a very slight bulge into the subacrosomal space, although with no internal differentiation; the acrosomal lobe was nevertheless coded as absent.

Alone among patellids and members of the outgroup, the base of the acrosome in all *Cymbula* species, *H. concolor* and *H. dunkeri* is elaborated into a thickened ring, lying adjacent to the nucleus (figure 5j,l) (**character 16**). Two states of this character are defined, the thickening being distinctly more pronounced in *C. adansonii*, *C. compressa* and *C. miniata* (figure 5k).

All previous comparative accounts of patellid sperm have noted the considerable variation in length of the nucleus (Hodgson & Bernard 1988; Jamieson *et al.* 1991; Ridgway 1994; Hodgson *et al.* 1996). In addition, it has been noted that in some of the species with long nuclei, the shape of the nucleus is tapered ('flask-shaped' or 'triangular' of Hodgson & Bernard (1988)). These descriptions are combined in **character 17**. In the majority of patellid species, and in *Lottia*, the nucleus is short (<3 µm long), barrel-shaped or cylindrical (sometimes 'bottle-shaped', i.e. narrowed at the apex where constricted by the posterior ring of the acrosome, see character 16). Alternatively, the nucleus may be elongate (>3 µm long) and cylindrical (*Acmaea*, *S. cochlear*, *S. longicosta*, *Patella* species except *P. pellucida*; figure 5b,d,m), or elongate and tapered towards the acrosome (*S. granularis*, *S. miliaris*, *S. peronii*, *Cellana*, *Nacella*; figure 5c,g). This latter group probably also includes *S. mexicana*, of which only poorly fixed material has been seen (Hodgson *et al.* 1996).

5. PHYLOGENETIC ANALYSIS

(a) Methods

The 17 characters selected for the analysis are listed in table 2, and their states in 37 patellid taxa, and five outgroup taxa, are given in table 3. No autapomorphic characters were included. Parsimony analysis was performed using the program PAUP, version 3.1.1 (Swofford 1993). The heuristic search option was used, with tree bisection-reconnection (TBR) branch swapping and ten replicates of a random addition sequence. All characters were unordered and unweighted, with the ACCTRAN option used to optimize the character states on the tree. Trees were rooted using the outgroup method. Distribution of character states was further investigated using the program MacClade (Maddison & Maddison 1992).

(b) Results

The analysis of all taxa produced 2442 trees of minimum length (length $l=68$ steps; consistency index $CI=0.559$; rescaled consistency index $RCI=0.487$;

retention index $RI=0.871$), of which the strict consensus is the topology shown in figure 6. This topology is, however, not very stable. More than 3200 trees were found with length less than or equal to 69 steps, and in the consensus of these the clades *Cymbula*, *Scutellastra* and *Patella* (excluding *P. pellucida*) collapsed to polychotomies, while *Cymbula*, *H. concolor* and the remaining *Helcion* species collapsed to a trichotomy. Allowing the tree length to increase by one further step ($l \leq 70$) resulted in complete loss of structure throughout the tree. This instability can be traced to several causes. Clearly, there is a relatively small number of character states (55) available for the phylogenetic reconstruction, and many show homoplasy. More specifically, the states of some characters were either unknown (due to absence or uncertain homology: characters 2, 10, 11, 12) or conflicting (3, 4, 17) in the outgroup, resulting in ambiguous polarization of characters in the ingroup.

In a second analysis, only those ingroup taxa were included for which full anatomical data were available (i.e. excluding *C. depsta*, *S. kermadecensis* and *S. mexicana*). The result was 13 trees of minimum length ($l=66$ steps; $CI=0.576$; $RCI=0.503$; $RI=0.873$), of which the strict consensus was almost identical to that shown in figure 6. The only difference was the improved resolution within the clade *Cymbula*, in which *C. adansonii*, *C. compressa* and *C. miniata* formed a clade, which was the sister-group to *C. granatina*. Once again, complete loss of structure occurred if tree length was allowed to increase by just two steps.

As a result of the analysis, four principal clades of species can be recognized: *Cymbula*, *Patella*, *Helcion* and *Scutellastra*. As these groups correspond in large part with generic or subgeneric groupings used by previous workers, we here name them accordingly, and recognize them at the rank of genus (table 1). (This choice of rank is arbitrary, but see §6.) The topology of the consensus of the minimum-length trees (figure 6) will now be considered in detail, examining the characters that support the structure and interrelationships of the genera, as summarized in table 4.

The genus *Cymbula* is defined by three synapomorphies (indicated in the convention '**character number**: character state', see table 2): the presence of the rachidian tooth in the adult (9:1; shared with *Scutellastra*), the unicuspid teeth arranged in a V shape (10:0; unique synapomorphy), and differentiation of the acrosomal lobe (15:2 or 3; both states unique). Within the clade, characters 5, 12, 15 and 16 showed variation, resulting in phylogenetic structure. Of these characters, only those of the acrosome (lobulation, 15:3; strong basal thickening, 16:2) were unique, clearly defining the three species *C. adansonii*, *C. compressa* and *C. miniata* as a clade in the analysis which excluded *C. depsta* (for which sperm data were unknown).

The genus *Helcion* is defined by just one unique synapomorphy, the penetration of the radular sac to the dorsal side of the visceral mass (8:3). Three of its species (*H. dunkeri*, *H. pectunculus*, *H. pruinus*) do form a clear group, on the basis of synapomorphies of the anterior shell apex (1:0; shared with *C. compressa* and *P. pellucida*), the short subpallial sensory streak (7:1; unique synapomorphy), the loss of pluricuspid cusp 4 (12:2; shared with

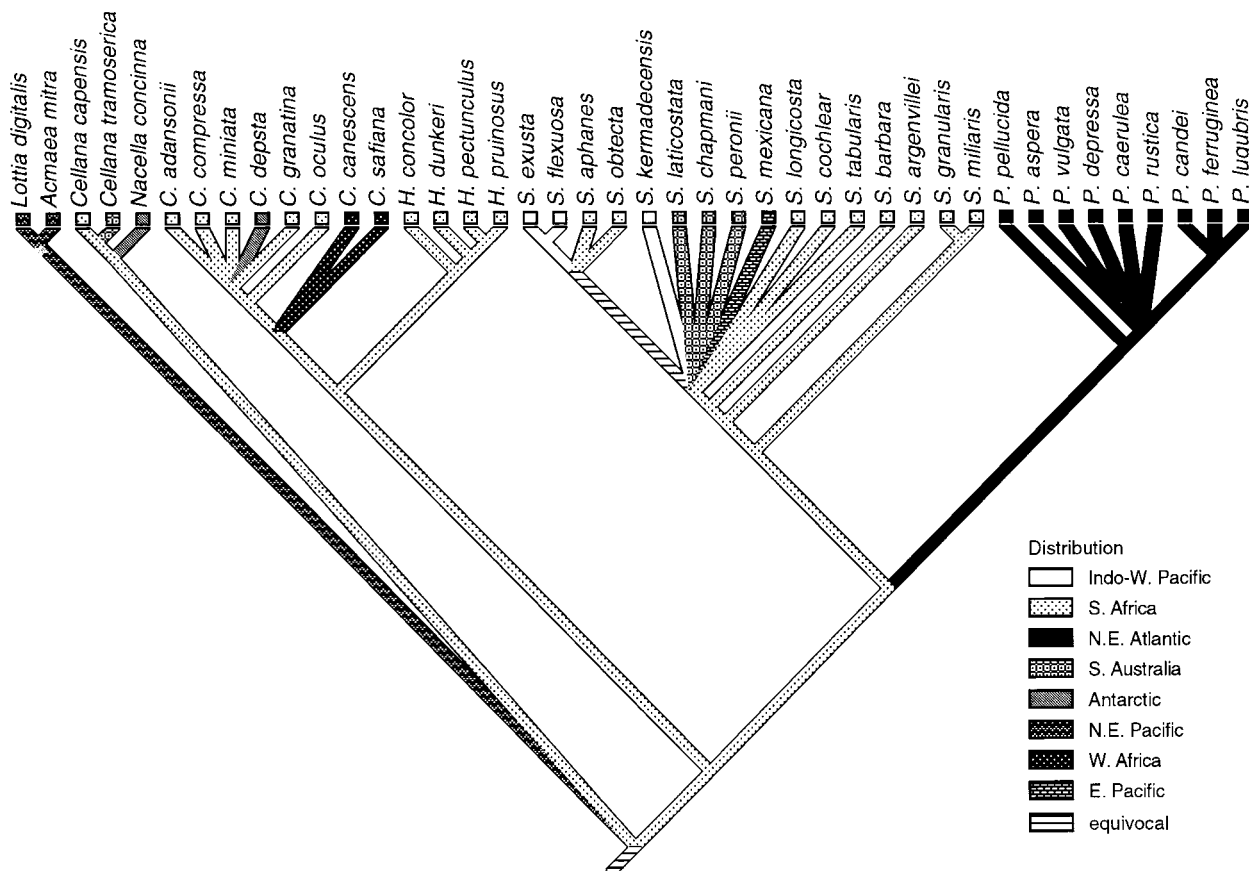


Figure 6. Phylogenetic hypothesis for the Patellidae. The topology is that of a strict consensus tree of the 2442 trees of minimum length ($l=68$ steps) produced by parsimony analysis of all ingroup taxa (see tables 2 and 3). Superimposed on the topology are the geographical distributions of taxa (see table 1), with parsimonious reconstruction of ancestral distributions (assuming a dispersalist biogeographic model). Note that 'S. Africa' includes area from Angola to Natal; 'N.E. Atlantic' extends from N. Norway to the Mediterranean and includes Azores, Madeira, Canary Islands and Cape Verde Islands; 'Antarctic' includes the islands of St Paul and Amsterdam in the S. Indian Ocean; 'W. Africa' includes St Helena. *Cymbula safiana* occurs mainly in W. Africa but extends to the Mediterranean, thus just reaching the N. E. Atlantic region. Note also that distributions shown for the outgroup members (nacellid, acmaeid and lottiid taxa) are those for the species used, and are not representative of the entire clades to which they belong. Generic abbreviations: C. = *Cymbula*; H. = *Helcion*; S. = *Scutellastra*; P. = *Patella*.

five *Cymbula* species) and the acrosomal lobe with an electron-lucent space (15:4; unique). In addition, the reduction of the marginal teeth to 2 (13:1; shared with *P. pellucida*) is a possible synapomorphy of these three species (the state in *H. dunkeri* is unknown).

The largest of the four generic clades is *Scutellastra*, defined by the synapomorphy of the wide $m+1$ shell layer (4:0; unique in the ingroup, but seen also in *Lottia* and *Acmaea*), and by the presence of the rachidian tooth (9:1 or 2; shared with *Cymbula*). In addition, all but three of the members of *Scutellastra* have an unthickened or laterally thickened acrosome (14:0 or 1, except *S. peronii*); both states are synapomorphies, but their reconstruction on the cladogram is equivocal. Within *Scutellastra*, the basal branch is a pair of sister-species, *S. granularis* and *S. miliaris*, which share one unique sperm character (14:1; equivocal synapomorphy) and another shared only with *S. peronii* (17:2; also in *Cellana* and *Nacella*). The remaining species of *Scutellastra* are united by the single, but unique, synapomorphy of the large pluricuspid cusp 1 (11:0). Within this group, all but *S. argenvillei* share a radial

arrangement of the outer crossed-foliated shell layers (2:0), which is also unique. Among the remaining *Scutellastra* species, additional phylogenetic structure is added by characters of the lack of the inner calcitic shell layer (5:0), the coiling of the radula (8:1) and the large pluricuspid cusp 1 (12:0), all of which are unreversed within the genus, and the latter two unique. Of note, is the sister-species pair *S. exusta* and *S. flexuosa*, defined by two synapomorphic sperm characters (14:2; 15:1) (each of which is, however, shared with some *Cymbula* and *Helcion* species).

The fourth generic clade, *Patella*, is defined by two synapomorphies, the coiling of the radula below the visceral mass and gonad (8:0; unique in the ingroup, but shared with *Cellana*), and the lack of pluricuspid cusp 1 (11:2; unique). Within the genus, the first branch is *P. pellucida* (with autapomorphies 1:0, 6:0 and perhaps 13:1). The remaining species show two synapomorphies, the conical terminal thickening of the acrosome (14:3; shared with *S. peronii* and *H. pectunculus*) and the elongate sperm nucleus (17:1; shared with some *Helcion* and

Table 4. Summary of the synapomorphies of the principal clades of Patellidae, from the cladogram of figure 6

(Unless otherwise indicated, all synapomorphies are unequivocal, i.e. reconstruction of character state changes is unambiguous. Character states described as 'unique' are unique within the ingroup. Synapomorphies are abbreviated in the form 'character number: plesiomorphic to apomorphic state'; see table 2 for descriptions of character states.)

clade	synapomorphies	remarks
Patellidae	2:2 to 1 (to 0) 10:2 to 1 (to 0) 14:4 to 2 (to 0,1,3)	unique unique reversed in <i>H. pruinusos</i>
<i>Cymbula</i> , <i>Helcion</i>	3:0 6:1 to 0 16:0 to 1 (to 2)	unique state, equivocal synapomorphy shared with <i>P. pellucida</i> unique, reversed in two <i>Helcion</i>
<i>Cymbula</i>	9:0 to 1 10:1 to 0 15:1 to 2 (to 3)	shared with <i>Scutellastra</i> unique unique
<i>Helcion</i>	8:2 to 3	unique
<i>H. dunkeri</i> , <i>pectunculus</i> , <i>pruinusos</i>	1:1 to 0 7:0 to 1 12:1 to 2 15:1 to 4	shared with <i>C. compressa</i> , <i>P. pellucida</i> unique shared with five <i>Cymbula</i> unique
<i>Scutellastra</i> , <i>Patella</i>	3:1 5:0 to 1 15:1 to 0	unique state, equivocal synapomorphy much homoplasy unique, reversed in <i>S. exusta</i> , <i>S. flexuosa</i>
<i>Scutellastra</i>	4:1 to 0 9:0 to 1 (to 2) 14:2 to 0 or 1	unique shared with <i>Cymbula</i> unique states, reversed in <i>S. peronii</i> , <i>S. exusta</i> , <i>S. flexuosa</i>
<i>S. granularis</i> , <i>miliaris</i>	14:1 17:0 to 2	unique state, equivocal synapomorphy shared with <i>S. peronii</i>
<i>Scutellastra</i> except <i>granularis</i> , <i>miliaris</i>	11:1 to 0	unique
<i>Scutellastra</i> except <i>granularis</i> , <i>miliaris</i> , <i>argenvillei</i>	2:1 to 0	unique
<i>Patella</i>	8:2 to 0 11:1 to 2	unique unique
<i>Patella</i> except <i>pellucida</i>	13:3 14:2 to 3 17:0 to 1	unique state, equivocal synapomorphy shared with <i>S. peronii</i> , <i>H. pectunculus</i> shared with two <i>Helcion</i> , two <i>Scutellastra</i>

Scutellastra). In addition, all species of *Patella* except *P. pellucida* share a unique arrangement of the marginal teeth (13:3), although this is an equivocal synapomorphy owing to ambiguity in the optimization of this character. There is little additional structure to the clade, although *P. ferruginea*, *P. candei* and *P. lugubris* are united by the synapomorphy of the lack of the inner calcitic shell layer (5:1; shared by several members of *Scutellastra*, *Helcion* and *Cymbula*).

The relationships among these four generic clades are less well supported by the analysis (table 4). *Cymbula* and *Helcion* share no unique, unreversed synapomorphies. The radial orientation of shell layer m+1 is a unique state (3:0) of this clade within the ingroup, although only an equivocal synapomorphy owing to the occurrence of both radial and concentric orientation in the outgroup, which results in ambiguous optimization. The presence of the lateral glandular groove (6:0) is a synapomorphy, although shared with *P. pellucida*. The basal thickening of the acrosome (16:1 or 2) is a unique synapomorphy, but this is reversed in *H. pectunculus* and *H. pruinusos*.

Support for the sister-group relationship between *Scutellastra* and *Patella* is no stronger. The concentric orientation of shell layer m+1 is unique in the ingroup (3:1), but again this is an equivocal synapomorphy because of the occurrence of both states in the outgroup. The crossed-foliated calcitic m-2 layer (5:1) is a synapomorphy, but this character shows much homoplasy. A synapomorphy unique to this clade is the loss of the acrosomal lobe (15:0), although this is reversed in *S. exusta* and *S. flexuosa*.

This analysis cannot be a definitive test for the monophyly of the Patellidae as here constituted, for which additional characters and outgroups would be required. However, if the acmaeid and lottiid species alone are defined as the outgroup, and the clade of *Cellana* and *Nacella* (Nacellidae) forms the first branch within the ingroup, then the Patellidae are defined by two unique synapomorphies. These are the presence of outer crossed-foliated layers in the shell (2:1 or 0) and the presence of six or seven teeth (unicuspid, pluricuspid and rachidian) in the centre of the radula (10:1 or 0). A

third synapomorphy, the loss of the elongate terminal thickening of the acrosome (**14:0**, 1, 2 or 3), is reversed only in *H. pruinusos*.

6. DISCUSSION

(a) *Phylogeny and classification of the Patellidae*

As discussed in §1, previous attempts to classify the species of Patellidae, and to define phylogenetic groupings within the family, have all relied on restricted sets of characters and/or species. Our study is the first to employ a range of morphological characters (shell form and microstructure, gross anatomy, radular tooth form, sperm ultrastructure) from all 37 available species, to produce a hypothesis of phylogenetic relationships. This hypothesis is shown in figure 6, and the suggested classification in table 1. For simplicity, these generic and specific names will be used throughout this section, even when quoting authors who have employed different classifications. There are various conventions available for the translation of a cladogram into a formal classification and (if sufficient hierarchical categories are adopted) it is possible to do so without loss of phylogenetic information (e.g. Wiley 1981; Forey *et al.* 1992). In our classification we recognize four monophyletic groups as genera: *Cymbula*, *Helcion*, *Scutellastra* and *Patella*. We have chosen the rank of genus for these four clades, because this is the rank traditionally accorded to *Helcion* (Thiele 1929; Keen 1960; Powell 1973; Christiaens 1974a), which is in fact the least distinctive of the four in our analysis. A few authors have also accorded generic rank to the other groups (e.g. Thiele 1891; Powell 1925; Lindberg 1998). Our suggested classification is the one that we believe best serves the requirements of phylogenetic information content, taxonomic tradition and stability. It may require further modification as the phylogenetic hypothesis is refined by the addition of new information.

The two most recent schemes for a comprehensive classification of living patellids are those of Powell (1973) and Christiaens (1973, 1974a), both of which employed only the traditional characters of gross shell morphology, gills and the radula (as revealed by light microscopy). By making the assumption that their supraspecific taxa are monophyletic, these earlier classifications can be represented as phylograms (figure 8), for ease of comparison with our own phylogeny (figure 6). There are some broad areas of agreement with these and other classifications and phylogenetic schemes, but also some striking differences.

Our genus *Cymbula* is a well-defined clade, with unique synapomorphies of radular and sperm characters (table 4), and has been recognized by many previous workers. The important character of the V-shaped arrangement of the unicuspid teeth (our character **10**: state 0) was first observed by Thiele (1891), who used it to define two genera (*Patellona* and *Cymbula*), which he later combined as a single subgenus of *Patella* (Thiele 1929); curiously, he then also included *S. cochlear*, despite its different radula. In an account of the southern African species, Koch (1949) also described this distinctive radular type. As defined in our study, *Cymbula* comprises two of the subgenera of Powell (1973), who nevertheless recognized their close affinity from their V-

shaped arrangement of unicuspid radular teeth; *P. lugubris* was mistakenly included without knowledge of its radula. Christiaens (1973, 1974a) noted this same radular type, but grouped the *Cymbula* species into two subgenera, on the basis of the pluricuspid cusps. This same character (**12:2**) is likewise used in our analysis to define a clade of five species within *Cymbula*. Previous studies of sperm ultrastructure have also recognized a group corresponding in part to *Cymbula*. Hodgson & Bernard (1988) reported their 'type III' sperm in four of the species here assigned to *Cymbula*, but also included *H. concolor*. To these were added *S. exusta* by Jamieson *et al.* (1991), and three more *Cymbula* species plus *H. dunkeri* by Hodgson *et al.* (1996). The inclusion of species other than members of *Cymbula* arose because the group was defined by nuclear shape and presence of the acrosomal lobe, two characters which have here been refined as thickening of the acrosomal base (**16:1** or **2**; which in turn constricts the nucleus), and differentiation within the acrosome (**15:2** or **3**). In our analysis, the similar acrosomal lobe of *S. exusta* and *S. flexuosa* is a character convergent with *Cymbula*. Hodgson *et al.* (1996) also pointed out the close relationship between *C. adansonii*, *C. compressa* and *C. miniata*, reflected in their grouping as a clade by sperm characters (**15:3**; **16:2**) in our analysis of the reduced set of ingroup taxa. MacClintock (1967) classified patellids into groups on the basis of shell microstructure alone; his 'group 6' was defined by the radial crossed-lamellar structure of layer m+1 (**3:0**; a unique state, but equivocally apomorphic) and corresponds with our clade *Cymbula* plus *Helcion*.

One or more groups corresponding to our *Scutellastra* can also be found in earlier studies. In traditional schemes, the distinguishing features have usually been the porcellanous interior of the shell (the wide m+1 layer, **4:0**) and the presence of a moderate to large rachidian tooth (**9:1** or **2**) (Pilsbry 1891; Thiele 1929; Powell 1973). Overemphasis of the importance of a large rachidian (**9:2**) resulted in an additional section or subgenus (*Ancistromesus*) in some classifications (Pilsbry 1891; Thiele 1891; Powell 1973). *Scutellastra* appears as a clade in our tree (figure 6), and these two characters (**4:0**; **9:1** or **2**) are confirmed as synapomorphies. The peculiarity of *S. granularis* was noticed by Powell (1973; he did not mention *S. miliaris*), who removed it to another subgenus on the basis of shell form, although he remarked that both radulae and shells suggested close relationship to the remaining *Scutellastra* species. Several authors have been misled by the curiously pyriform outline of the shell of *S. cochlear*, for which the monotypic genus or subgenus *Olana* has often been employed (Adams & Adams 1854; Gray 1857; Thiele 1891; Powell 1973; Christiaens 1973, 1974a), although from our analysis this separation is unjustified. Christiaens (1973, 1974a) recognized a subgenus *Ancistromesus*, which corresponds almost exactly with our *Scutellastra*. This he characterized solely by the combination of four pluricuspid cusps (characters **11** and **12**) with aligned unicuspid teeth (**10:1**; a symplesiomorphy). However, this reliance on radular characters led him to include *H. concolor* in the same group. Within this group, he defined sections based on the relative development of the rachidian tooth, shell outline and geographical distribution; none of these is supported by

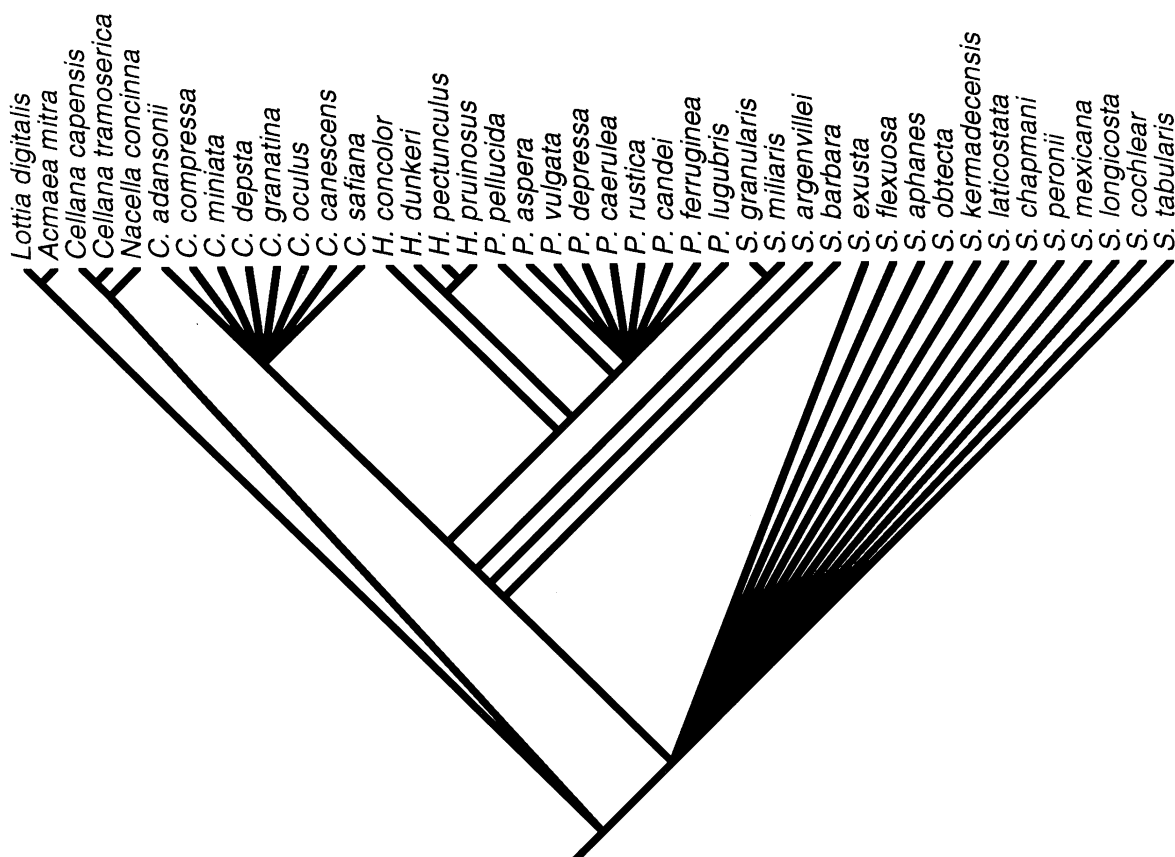


Figure 7. Consensus of a subset of tree topologies of length two steps greater than the most-parsimonious tree (figures 6 and 7), in which *Patella* appears as the sister-group of three *Helcion* species, and *Scutellastra* as a paraphyletic basal group. Some morphological similarities between *P. pellucida* and *Helcion* species, and also the very incomplete fossil record, lend some support to this topology (see §6).

our analysis. The *Scutellastra* group has also been supported by previous studies of sperm ultrastructure; it includes only those species classified as 'type I' and 'type II' by Hodgson & Bernard (1988) and Hodgson *et al.* (1996). The former category describes the simple, unthickened acrosome found in most *Scutellastra* species (14:0, a synapomorphy; 15:0, a symplesiomorphy). The 'type II' category describes the highly distinctive sperm of *S. granularis* and *S. miliaris* (14:1; 17:2; equivocal and synapomorphic, respectively), with the addition of *S. peronii* on the basis of its flask-shaped nucleus (17:2; here shown to be a convergent state). In their cladistic analysis of sperm characters, Jamieson *et al.* (1991) departed from this classification, using a different scheme for the coding of sperm structures; as a result, their supposed clades do not correspond closely with those defined here. In the scheme of MacClintock (1967), based on shell structure, *Scutellastra* species fall mainly into 'group 9', defined by a wide m+1 layer (4:0). He separated *S. argenvillei* and *S. granularis* from these as 'group 8', but united them with some *Patella* species, citing the crossed-foliated m-2 layer (5:1; here showing much homoplasy). Our coding of the predominant orientation of the outer crossed-foliated layer differs from that of MacClintock. In our scheme the predominant radial arrangement (2:0) is the synapomorphy that defines the *Scutellastra* species excepting *S. argenvillei*, *S. granularis* and *S. miliaris*. MacClintock, however, used this character

only to distinguish *S. cochlear* (as 'group 10') from the other *Scutellastra* species. We note that in our tree the sister-species pair *S. granularis* and *S. miliaris* is supported by unique or unusual sperm characters (14:1; 17:2), and that the reduced pluricuspid cusp 1 (11:1) and concentric outer crossed-foliated shell layer (2:1; shared with *S. argenvillei*) make this pair the most basal within *Scutellastra*. Recognition of *S. granularis* and *S. miliaris* as a subgenus might therefore be appropriate, and for this the name *Patellidea* Thiele, 1891, is available. Among other members of *Scutellastra* there is considerable morphological variation in the characters coded for this analysis, reflected in the degree of resolution within this clade.

In our tree, *Patella* appears as a monophyletic group. Once again, some traditional classifications have recognized a similar grouping of exclusively northern Atlantic species, although invariably *P. pellucida* has been excluded. The characters cited have been the iridescent interior (i.e. narrow m+1 layer, 4:1), the linear arrangement of the unicuspid teeth (10:1) and the vestigial or absent rachidian tooth (9:0) (Thiele 1929; Powell 1973). In our tree, these three characters are symplesiomorphic (table 4). Our analysis does, however, provide two synapomorphies of *Patella*, the radula coiled below the visceral mass (8:0) and the loss of pluricuspid cusp 1 (11:2). These synapomorphies unequivocally place *P. pellucida* in this clade, although it has several peculiar features, discussed below. Christiaens (1973, 1974a) defined a similar group,

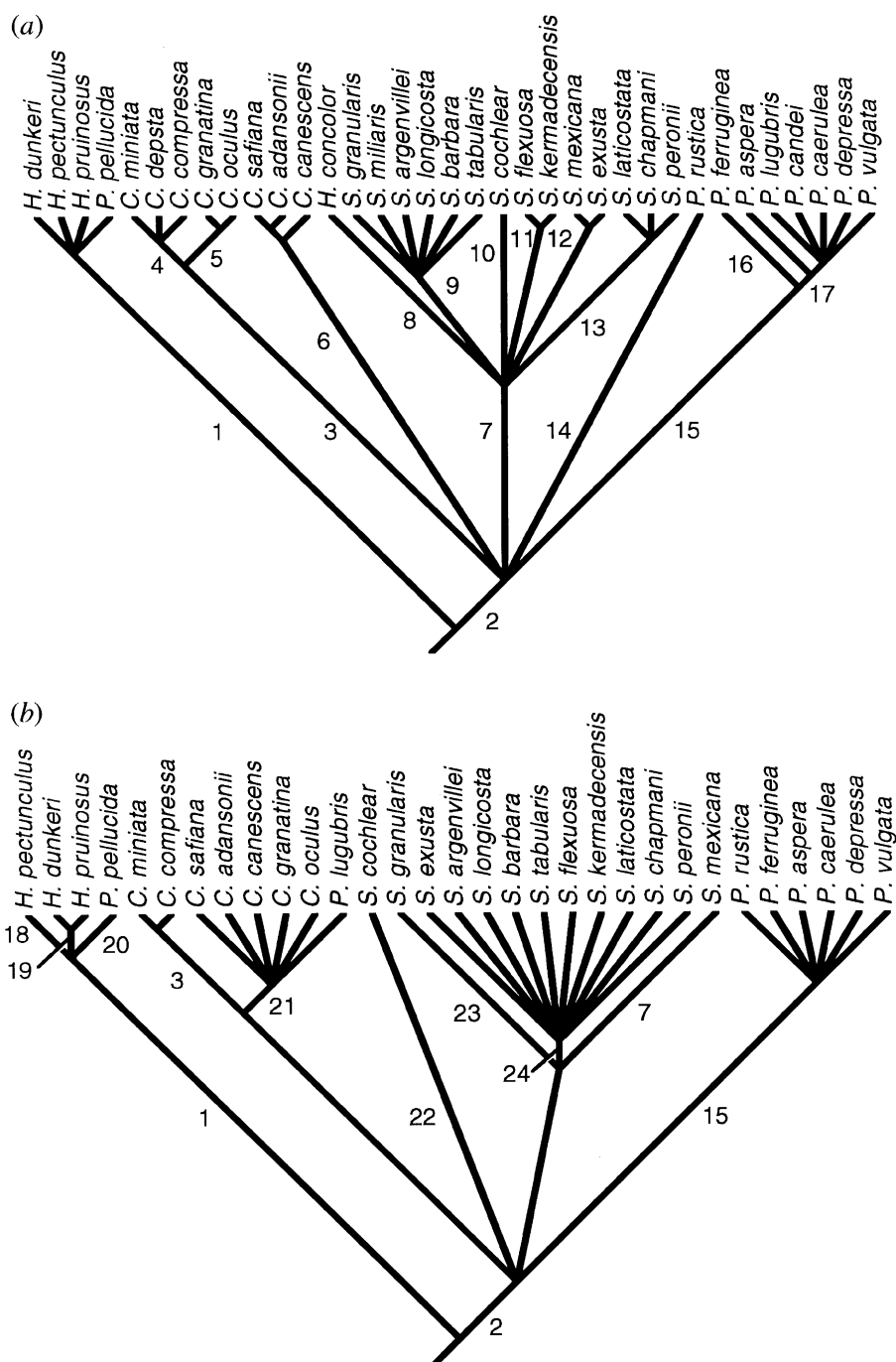


Figure 8. Phylogeny of Patellidae (as defined herein) implied by classifications of the species by previous authors. (a) Christiaens (1973, 1974a). (b) Powell (1973). To facilitate comparison with our phylogenies (figure 6), the species names are those recognized and adopted herein (see §2), with generic allocations as in the revised classification shown in table 1 (generic abbreviations: *C.*, *Cymbula*; *H.*, *Helcion*; *P.*, *Patella*; *S.*, *Scutellastra*). Numbers of clades indicate supraspecific categories as used by Christiaens and Powell (G, genus; SG, subgenus; S, section): 1, G *Helcion*; 2, G *Patella*; 3, SG *Cymbula*; 4, S *Cymbula*; 5, S *Patellona*; 6, SG *Laevipatella*; 7, SG *Ancistromesus*; 8, S *Eliana*; 9, S *Patellidea*; 10, S *Olana*; 11, S *Penepatella*; 12, S *Ancistromesus*; 13, S *Patellanax*; 14, SG *Patellastra*; 15, SG *Patella*; 16, S *Scutellastra*; 17, S *Patella*; 18, SG *Helcion*; 19, SG *Patinastra*; 20, SG *Ansates*; 21, SG *Patellona*; 22, SG *Olana*; 23, SG *Patellidea*; 24, SG *Scutellastra*.

also using the aligned unicuspid teeth, and mentioning the three cusps of the pluricuspid (11:2; a synapomorphy). However, he removed *P. rustica* to a separate subgenus, because of the absence of cusp 4 of the pluricuspid (as discussed earlier, this character is not consistent). Thiele (1891, 1929) likewise separated this species, and one other (*P. ferruginea*), citing the presence of a cusped rachidian tooth. Our clade *Patella* (excluding *P. pellucida*) corre-

sponds exactly with the group of patellids showing sperm of 'type VI' as defined by Hodgson *et al.* (1996), with conical thickening of the acrosome (14:3; a synapomorphy), no acrosomal lobe (15:0; a symplesiomorphy) and an elongate cylindrical nucleus (17:1; a synapomorphy). As mentioned earlier, MacClintock (1967) included three members of *Patella* in his 'group 8', on the basis of the calcitic m-2 layer (5:1; showing much

homoplasy). He separated *P. pellucida* from these as his monotypic 'group 7', although recognizing that the differences (complex crossed-lamellar structure of $m+1$ and $m-1$) were likely to be simply a consequence of the thinness and small size of the shell of this species. We have found members of the clade *Patella* to be morphologically rather uniform (with the exception of *P. pellucida*, discussed below), so that the internal structure of the clade is poorly resolved.

Perhaps the most striking difference between our phylogenetic classification and those of earlier workers is the treatment of the genus *Helcion*. Historically, patellids with thin shells, anterior apex, and in which the cordon of pallial gills is interrupted above the head, have been placed in the genera *Helcion* and *Patina* (Gray 1857; Dall 1871a,b; Thiele 1891). Following Jeffreys (1865), Pilsbry (1891) and Thiele (1929), these have generally been combined under the former name. This simple definition has persisted (Powell 1973; Christiaens 1973, 1974a), reflecting the traditional emphasis on the significance of gills and shell form. To these generic characters, Ridgway (1994) added another, the reduction of the marginal radular teeth to two. In the monograph of Powell (1973) *Helcion* comprised four species: *P. pellucida* from the northeastern Atlantic, and *H. pectunculus*, *H. pruinus* and *H. dunkeri* from southern Africa. In our cladogram the three southern African species are retained in this genus, united as a clade by two unique synapomorphies, the short subpallial sensory streak (7:1) and the elongate acrosomal lobe with electron-lucent space (15:4) (together with other non-unique synapomorphies, table 4). To these we have added *H. concolor*, using the type of radular coiling (8:3, a unique synapomorphy) to define the genus *Helcion*. This generic placement of *H. concolor* has not been suggested previously. It is also supported by the recent observation that shells of '*H. dunkeri*' from Natal are in fact misidentified juveniles of *H. concolor* (G. M. Branch, unpublished observation). Further evidence for the close relationship between *Cymbula* and *Helcion* has previously been available from studies of shell microstructure, since MacClintock (1967) placed their species in the same category, 'group 6'. In addition, Hodgson *et al.* (1996) classified both *H. concolor* and *H. dunkeri* together with the *Cymbula* species in their sperm 'group III'. The sperm of the two remaining *Helcion* species were placed in their own 'group IV' (Hodgson & Bernard 1988; Hodgson *et al.* 1996), because of their complex acrosomes.

The single northeastern Atlantic species hitherto assigned to *Helcion* (Jeffreys 1865; Pilsbry 1891; Powell 1973; Fretter & Graham 1994) or to *Patina* (Gray 1857; Dall 1871a,b; Fretter & Graham 1962, 1976), is here classified as *Patella pellucida*. This is based on the two unique synapomorphies of *Patella* (8:0; 11:2). Although this assignment to *Patella* has not been explicitly proposed by any recent workers, some evidence of the relationship has been available. MacClintock (1967) found no fundamental difference in shell microstructure between *P. pellucida* and other *Patella* species. Lindberg (1988a) remarked that all the patellids of the northeastern Atlantic (including 'marine plant species', i.e. *P. pellucida*) comprised a single endemic radiation, but did not explain why this was so. According to Hodgson *et al.* (1996) the

sperm of *P. pellucida* did not precisely resemble that of *Helcion* species, and did not fit clearly into any of their sperm categories; they suggested a possible affinity with *Cymbula* species and *H. dunkeri*, on the basis of the reportedly differentiated acrosomal contents (not supported by our latest observations). Most recently, a study of allozyme variation has shown that *P. pellucida* is genetically distant from *H. dunkeri*, *H. pectunculus* and *H. pruinus* (Weber *et al.* 1998). Nevertheless, *P. pellucida* shows a number of similarities with members of *Helcion*, which also distinguish it from the remaining *Patella* species. In our most-parsimonious tree topology (figure 6), these appear as autapomorphies of *P. pellucida*, convergent with characters of *Helcion*: the anterior position of the shell apex (1:0), the lateral glandular groove (6:0) and the two marginal teeth (13:1; reconstruction equivocal). Interestingly, among the numerous trees two steps longer there is a subset in which *Patella* is the sister-group of *H. dunkeri*, *H. pectunculus* and *H. pruinus* (*Scutellastra* is then a paraphyletic group at the base of the ingroup in these trees; figure 7). This topology suggests a much closer relationship between *Helcion* and *Patella*, and explains these similarities of *P. pellucida* and *Helcion* as the result of common descent (adding also the rounded, thickened acrosome, 14:2). We also note that the remaining character used by earlier authors to place *P. pellucida* in *Helcion*, the interruption of the pallial gill cordon above the head, is inconsistent. Powell (1973) retained this generic character of *Helcion*, despite his remark that the gill cordon was complete in the subgeneric group comprising *H. pruinus* and *H. dunkeri*. In the present study we have also found a complete gill cordon in large specimens of *H. pectunculus*. Lindberg (1988a) similarly noted variation in the development of the pallial gill within clades, and even within species, and likewise concluded that this is not a reliable character for phylogenetic reconstruction. One possible explanation for the arguably convergent similarities in shell shape, lateral glandular groove, marginal teeth and pallial gill arrangement between *P. pellucida* and some species of *Helcion* is that these might all be examples of paedomorphic characters. Lindberg (1988a,b) has documented a number of paedomorphic trends in other patellogastropods.

It is necessary to comment briefly on the nomenclature of the genera. The authorities and type species of each are listed in table 1, and generic synonymies are given by Powell (1973) and Christiaens (1974a). Nomenclatural difficulties arise only in the case of the group for which we employ the familiar name *Scutellastra*. In their original introduction of this generic name for limpets with stellate shells, Adams & Adams (1854) listed three species (from which the type species must be designated): *P. gorgonica* Humphrey (presumably *P. gorgonica* Da Costa, 1771, a *nomen oblitum* for which the name *P. ferruginea* Gmelin, 1791, is now in use; see Christiaens 1974a), *P. pentagona* Born, 1778 (figured by Born (1780), probably the species commonly known as *P. flexuosa* Quoy & Gaimard, 1834), and *P. plicata* Born, 1778 (the figure by Born (1780), is *P. barbara* L.; see also Brauer 1878). Christiaens (1974a) accepted Kobelt's (1879) designation of *P. ferruginea* as the type species, and therefore employed the name *Ancistromesius* Dall, 1871 (type species *P. mexicana*), for the group in question (regardless of the fact that an earlier available

name is *Olana* H. & A. Adams, 1854; type species *P. cochlear* by monotypy). In fact Kobelt's (1879) designation was invalid ('Typus ist *Patella ferruginea* Gmelins. *plicata* Costa nec Born'), since *P. ferruginea* was not one of the three originally included taxa, and *P. plicata* Born is specifically excluded. Subsequently, Fischer (1887) mentioned *P. pentagona* as an example of *Scutellastra*, while Thiele (1929) gave *P. plicata*, but neither constitutes formal designation of a type species. We recognize the explicit designation by Wenz (1938) of *P. plicata* (= *P. barbara*, see above) as the first valid one, and therefore employ the name *Scutellastra* in that sense. Furthermore, this decision conserves a familiar name in its accustomed usage. Following Pilsbry (1891), *Olana* is a junior synonym, although introduced in the same publication (Adams & Adams 1854).

From the foregoing discussion, it is clear that the four generic groups that we propose (*Cymbula*, *Helcion*, *Scutellastra*, *Patella*) are each defined by a few unambiguous morphological characters. These groups correspond in part with those recognized by previous authors, who have usually considered only limited suites of characters. By combining a wide range of characters in a single analysis, we have attempted to resolve existing discrepancies between these earlier classifications. We reiterate that our phylogenetic hypothesis is not very robust, because of the limited number of morphological characters available to us, and because of variable or ambiguous states in the outgroup taxa. As mentioned earlier, the set of trees just two steps longer includes alternatives (e.g. figure 7) strikingly different from that of figure 6. More information is necessary, and this is presently being sought by the sequencing of mitochondrial genes. There has been little previous speculation about, and still less analysis of, phylogenetic relationships among the patellid genera. Various authors have commented on the evolution of the Patellogastropoda, but this has mostly been in relation to trends in particular characters, such as the gills, radula and shell microstructure, and at the level of relationships between the families (reviews by MacClintock 1967; Lindberg 1988a). The hierarchical classification schemes for patellids can be interpreted as indicative of phylogenetic relationships, but only if it is assumed that taxa are monophyletic and their defining characters synapomorphic, because very few early authors made such distinctions. Thus, in many classifications a genus (or subgenus) *Helcion* (and/or *Patina*) has been distinguished from *Patella* (*sensu lato*, including all the remaining patellids as here defined) (Dall 1871a,b; Pilsbry 1891; Thiele 1929; Wenz 1938; Keen 1960; Powell 1973; Christiaens 1974a), implying a phylogenetic division of the family. Our analysis clearly refutes this; *Helcion* (as traditionally defined) is polyphyletic.

There have been just three previous attempts to reconstruct the phylogenetic relationships among a wide range of patellid taxa. From his studies of shell microstructure, MacClintock (1967) defined five types of patellid shells, and sketched two dendritic diagrams of their possible phylogenetic relationships. These are difficult to compare precisely with our cladogram, but (ignoring the groups now classified as Nacellidae, Acmaeidae and Lottiidae) do approximate to the topologies of figure 6 and figure 7,

i.e. either *Patella* and *Scutellastra* are sister-taxa, as are *Cymbula* and *Helcion*; or *Scutellastra* is a basal stem group from which the remaining patellids have been derived (MacClintock's figs 113 and 115, respectively). (It is notable that in the latter case the polarities of the shell characters (3 and 4) are reversed. Thus, in the topology of figure 7, the wide m+1 layer and its concentric orientation in *Scutellastra* are both reconstructed as plesiomorphic, whereas the former, and possibly the latter, is apomorphic in figure 6. This ambiguity arises because for each of these two characters both alternative states occur in the outgroup.) Jamieson *et al.* (1991) attempted a formal cladistic analysis of ultrastructural features of the sperm of 18 species of (mainly southern African) patellids and nacellids. However, their rooting of the cladogram was based on the unjustified assumption that a small, simple sperm was primitive, and the tree can therefore be interpreted only as a dendrogram of phenetic similarity. Few of their groupings correspond with clades in our analysis. The most recent cladistic analysis of the Patellidae was that of Ridgway (1994) which, as in the present study, employed a wide range of morphological characters. The coding of character states was somewhat different, and only 22 species were included. In the resulting cladogram three clades were recognized, *Cymbula*, *Helcion* (including *P. pellucida*) and *Scutellastra* plus *Patella* (in which *Scutellastra* was a basal paraphyletic group). Our study is a refinement of this preliminary analysis.

(b) *Biogeography and the fossil record*

The most striking feature of the distribution of the 38 species of patellid limpets is that they show two centres of diversity. The highest diversity is found in southern Africa, where 18 endemic species occur between Natal and Angola. The second centre is in the northeastern Atlantic, between the British Isles, the islands of Macaronesia and Cape Verde, and the Mediterranean, where the total number of species is ten. Only 11 species can be found elsewhere, distributed in West Africa, St Helena, the southern Indian Ocean, southern Australia, the Indo-West Pacific and the tropical Eastern Pacific (see table 1 for species distributions).

From an ecological perspective, this curious pattern could be explained in terms of competition and exclusion. In southern Africa the actual diversity of sympatric species is lower than the figure above suggests, but nevertheless as many as 13 species can be found together on the highly productive shores in the vicinity of the Cape (Branch 1971, 1981). Among the large and frequently abundant endemic patellids, resource partitioning is well developed, taking the form of differential zonation, dietary specialization and behavioural traits, including algal 'gardening' (Branch 1971, 1975, 1976). The species diversity in southern Africa is further increased by occurrences of Atlantic and Indo-West Pacific species here at the limits of their ranges. In the northeastern Atlantic the number of sympatric species rarely exceeds five (up to seven in the western Mediterranean, S. J. Hawkins, personal communication), and again there is differential zonation (Fretter & Graham 1976), although biomass and abundance are much lower than the highest levels attained in southern Africa, and dietary specializations and behavioural

interactions are less striking. If it is assumed that intertidal limpets belonging to other patellogastropod families occupy similar ecological niches, it is striking that these are rare or absent in southern Africa and the north-eastern Atlantic, but are diverse in other parts of the world. Thus, in the northeastern Pacific, lottiids (*Lottia*, *Tectura*) and acmaeids (*Acmaea*) are abundant on rocky shores; in the western Atlantic only lottiids occur; the limpet fauna of western South America is dominated by the lottiid *Scurria*; the lottiids *Notoacmaea* and *Patelloida*, and the nacellid *Cellana*, are common in the Indo-West Pacific and Australasia; whereas *Nacella* dominates in the Antarctic and southern Chile (see Lindberg 1988a). The areas of maximum diversity of the principal clades of intertidal patellogastropods are therefore to a large extent mutually exclusive and complementary.

However, from a phylogenetic perspective it is of interest to consider how the distribution of patellid limpets has been achieved. Two sources of evidence can be used to reconstruct historical biogeographic patterns. First, areas of endemism can be superimposed on to the phylogeny, and the resulting pattern interpreted in terms of either 'vicariance' (e.g. Wiley 1988) or 'dispersalist' (e.g. Brundin 1988) models. Second, the fossil record provides direct evidence for historical distributions. In figure 6, the geographical distributions of taxa have been superimposed on the phylogeny. The figure shows parsimonious reconstructions of ancestral areas, and therefore assumes a dispersalist interpretation. For marine invertebrates with the potential for widespread larval dispersal, this model may be more appropriate, as originally vicariant patterns may frequently be obscured by subsequent dispersal (Kabat 1996). However, repeated patterns of area relationships can in some cases be explained by large-scale vicariant events in the marine realm (Reid 1990, 1996). In practice, it is often impossible to decide between competing vicariant and dispersalist interpretations of present-day distribution patterns, in the absence of direct evidence from a complete fossil record. All members of the Patellidae broadcast their gametes for external fertilization, and undergo pelagic development (Lindberg 1988a, 1997). Nevertheless, little is known about developmental time and the potential for larval dispersal. In the laboratory, several European *Patella* species develop for about two weeks before metamorphosis (Dodd 1955; Hatch 1977). However, the fact that whereas larvae can be common in inshore waters (Lebour 1937), but are not found in offshore trawls (Fretter & Shale 1973), implies a limited capacity for long-distance larval dispersal. This suggestion is also supported by observations of *P. depressa*, which is rare on the island of Lundy, only 16 km offshore (Hawkins & Hiscock 1983), and has apparently failed to disperse across the Irish Sea (Crisp & Southward 1958). In addition, studies of recruitment in *P. aspera* have shown an exponential decline away from refuges where adults are protected from collection (Hockey & Branch 1994). Studies of population genetics are also in agreement; for example the considerable differentiation between populations of *P. rustica* on the Macaronesian Islands and the African mainland, and between *P. candei* on these islands, suggests low gene flow on this geographical scale (Côte-Real 1992; Côte-Real *et al.* 1996a,b).

The parsimonious area reconstruction in figure 6 is consistent with southern Africa as the centre of origin for all the patellids. The genus *Cymbula*, originally southern African, has dispersed to the isolated islands of St Helena (*C. canescens*) and St Paul and Amsterdam in the southern Indian Ocean (*C. depsta*). Although such distances are probably too great for larval dispersal, it is known that adult *Cymbula* are able to raft on drifting macroalgae, since shells of the southern African algal-dwelling *C. compressa* have been recorded from St Helena (Pilsbry 1891). The rock-dwelling *C. safiana* has a large distribution, from Namibia to the Mediterranean, and appears to have dispersed northwards by colonization of the West African coast. The genus *Helcion* is exclusively southern African in distribution.

The hypothesis of figure 6 implies that *Scutellastra* is also of southern African origin, from whence dispersal has taken place to southern Australia (*S. laticostata*, *S. peronii*, *S. chapmani*), the rest of the Indo-West Pacific (*S. exusta*, *S. flexuosa*, *S. kermadecensis*), and the eastern Pacific (*S. mexicana*). Interestingly, among the alternative topologies two steps longer are some in which the Indo-West Pacific, Australian and Eastern Pacific species are basal. This hints at the possibility of an ancient Tethyan distribution for the genus and (if *Scutellastra* is indeed a basal paraphyletic group) for the family as a whole. The distributions of *S. exusta* and *S. flexuosa* are almost unique among patellids, as they are not only broad, but include relatively isolated oceanic islands. Nothing is known of the development or dispersal of these species, but as neither appears to have the potential for rafting as an adult, this distribution pattern might suggest a longer pelagic life, or greater potential for larval dispersal. The single Eastern Pacific species, *S. mexicana*, is of particular interest. Unfortunately, in the absence of a detailed description of its sperm, its precise relationships are not known, although almost certainly its affinities are with Indo-West Pacific or Australian species (the large rachidian tooth is shared with *S. exusta* and *S. laticostata*; the elongate, tapering sperm nucleus with *S. peronii*). Dispersal from the Western to the Eastern Pacific is unlikely, as this would be in opposition to prevailing currents which, together with the great distance between Polynesia and South America, make 'Ekman's Barrier' almost impenetrable to most shallow-water marine invertebrates of the Western Pacific (Vermeij 1987; Richmond 1990; but, see Emerson 1991). The alternative view is that *S. mexicana* is a relict of a clade of *Scutellastra* with a formerly broad Tethyan distribution (Powell 1973), which was disrupted by tectonic events and extinction.

The most puzzling aspect of the distribution of patellids is the presence in the northern Atlantic of the single clade *Patella*. Biogeographic studies of the northern Atlantic marine fauna and flora have demonstrated the importance of the biotic interchange between the northern Pacific and northern Atlantic that took place following the opening of the Bering Strait during the Pliocene. This interchange involved almost 300 molluscan species, of which the great majority originated in the northern Pacific (Vermeij 1991), and included such common Atlantic genera as *Littorina* (Reid 1990, 1996) and *Nucella* (Collins *et al.* 1996). Another Pacific immigrant was the lottiid limpet *Tectura* (Vermeij 1991). However, patellids

could not have arrived by this route, as neither living nor fossil patellids are known from the far northern Pacific, and a southern African origin has generally been assumed. Lindberg (1988a) indicated that the northern Atlantic patellids were a single radiation with an originally southern African ancestry, but gave no further details. Vermeij (1992) reviewed the limited similarity between the shallow-water temperate biotas of Europe and southern Africa, and concluded that dispersal between the two was most likely during the Early Pliocene, perhaps because of stronger equator-wards (Benguela and Canary) currents at this time. The only patellid example mentioned was the genus *Helcion*, then thought to include a European representative, *P. pellucida*. (It may not, in fact, be necessary to invoke ancient differences in currents, or a narrower tropical zone than at present, to account for trans-equatorial dispersal of patellids in the Atlantic. The distribution of patellids is not exclusively antitropical; the widespread occurrence of *C. safiana* in West Africa, and of *Scutellastra* species in the Indo-West Pacific, shows that patellids can survive in tropical latitudes.) Our phylogenetic tree is consistent with these ideas of a southern African origin for *Patella*. Vicariant hypotheses could, however, also be considered; for example, if *Scutellastra* was originally a widely distributed Tethyan group, the Miocene closure of the Tethys Sea might have isolated its sister genus *Patella* in Europe. The biogeography of Patellidae has also been briefly considered by Hodgson *et al.* (1996). From the geographical occurrence of their sperm categories they suggested separate regional radiations in the northeastern Atlantic (corresponding largely with *Patella* as we define it here), the eastern Atlantic extending to the southeastern coast of South Africa (*Cymbula* and *Helcion*) and the Indo-Pacific with a focal point in South Africa (*Scutellastra*). Within the northeastern Atlantic, it has been suggested that speciation has been promoted by climatic and oceanographic fluctuations during the late Pliocene and Pleistocene, and that differentiation is continuing on the isolated Macaronesian Islands (Côrte-Real *et al.* 1996a,b).

It is unfortunate that the fossil record of patellids is so poorly known. Although numerous fossil species of patellogastropods have been described, their generic or even familial assignment is seldom known with any certainty because there have been few studies of the diagnostic characters of shell microstructure. The oldest known member of the Patellidae is '*Patella*' *costulata* Münster, 1869, from the Triassic St Cassian Formation of northern Italy; this has recently been confirmed as a true patellid by the description of its crossed-foliated outer shell layer (Hedegaard *et al.* 1997), although preservation was too poor for unequivocal generic assignment. Kase & Shigeta (1996) described '*Patella*' *soyaensis* from the Upper Cretaceous of northern Japan, classifying it in MacClintock's (1967) shell structure group 10 (typified by *S. cochlear*); accordingly, this is here included in the genus *Scutellastra*. Intriguingly, this species is believed to have attached to the shells of pelagic ammonites (Kase & Shigeta 1996), recalling the habit of the Recent *S. flexuosa*, which is frequently epizoic on large molluscan shells (D. G. Reid, unpublished observation). Other species from the Middle Miocene and Lower Pliocene of Japan (Kase 1994) can also be assigned to the genus *Scutellastra*

on the basis of their shell microstructure. Two species from New Zealand of a similar age may also belong to *Scutellastra*, although this assignment is based only on overall shell form (Powell 1973). Without the necessary examination of shell structure, such assessments of relationship can be misleading, as shown by the reallocation, to the nacellid genus *Cellana*, of a large Pliocene limpet from Chile ('*Patella*' *fuenzalidai* Herm, 1969), formerly considered to be related to *S. mexicana* (Lindberg & Hickman 1986). Of the fossil records of the other patellid clades that we have defined, still less is known. Vermeij (1992) mentioned southern African species of *Helcion* from the Late Miocene. The late Pliocene *P. hendeyi* described by Kensley & Pether (1986), from the west coast of South Africa, appears to be the oldest known fossil member of *Cymbula*. The fossil record of *Patella* is also obscure. *Patella vulgata* and *P. pellucida* are reliably reported from the Pliocene of Iceland and Europe (Gladenkov *et al.* 1980). However, of the numerous Cenozoic '*Patella*' species that have been described from Europe, shell structure has been investigated in only three from the Eocene of France, which showed lottiid affinities (MacClintock 1967).

Until more information is available, it would be premature to place too much emphasis on the fossil evidence. However, predictions can be made from our phylogenetic hypotheses. If *Patella* and *Scutellastra* are sister-taxa (figure 6), these clades must be of the same age, and it is to be expected that the fossil record of *Patella* will likewise extend back at least to the Upper Cretaceous. If, however, *Scutellastra* is a basal paraphyletic group (figure 7), it is to be expected that it will have the longest fossil record, as indeed is presently the case. The available fossil evidence, although very incomplete, therefore lends some support to the second of these topologies. Morphologically, we have found the Recent species of *Patella* to be relatively uniform, in contrast to the greater diversity within *Scutellastra*. This too hints at the possibility that *Patella* is a relatively young clade, as implied by the topology of figure 7. Detailed study of fossil patellogastropods is clearly required because, as emphasized by Lindberg (1988a), their historical distribution may be very different from that of Recent clades, and may well alter the tentative biogeographic hypotheses that we have proposed.

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