

REVIEW ARTICLE

RECENT ADVANCES IN MOLECULAR PHYLOGENY, SYSTEMATICS AND EVOLUTION OF PATELLOGASTROPOD LIMPETS

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ABSTRACT

With the advent of molecular phylogenetics, the systematics and taxonomy of Patellogastropoda have been greatly improved. Eight families and 36 genera are currently recognized in the order. We review recent published papers that have used molecular data, discuss the resulting advances in systematics and evolution of Patellogastropoda and suggest directions of future research.

INTRODUCTION

Patellogastropod limpets are abundant and familiar inhabitants of intertidal rocky shores throughout the global oceans from tropical to polar regions, and they play important roles in littoral marine ecosystems (Branch, 1985a, b). They have also colonized other marine habitats and can be found on macrophytes (*Lottia*: Lindberg, 1981; Carlton *et al.*, 1991; *Discurria*: Lindberg, 1988; *Naccula* and *Asteracmea*: Hickman, 2005; *Notoacmea*: Powell, 1979; Nakano & Spencer, 2007), on limestone in the splash zone (*Eoacmaea*: Lindberg & Vermeij, 1985; Kirkendale & Meyer, 2004), on coralline algae (*Yayoiacmea*: Sasaki & Okutani, 1993a), on sunken wood (*Pectinodonta*: Marshall, 1985), on whale bone (*Paralepetopsis* and *Neolepetosis*: McLean, 2008), in brackish water (*Potamacmaea*: Lindberg, 1990), on the shells of other molluscs (*Patelloida*: Nakano & Ozawa, 2005; *Notoacmea*: Nakano *et al.*, 2009a) and in association with vents and seeps (*Bathyaacmaea*: Sasaki, Okutani & Fujikura, 2005; Neolepetopsidae; McLean, 1990) (Fig. 1). Therefore, they have been widely used as subjects in ecological and evolutionary studies.

Taxonomically, they were treated as the three families Acmaeidae, Patellidae and Lepetidae by earlier workers (e.g. Powell, 1973), in part owing to their relatively featureless simple conical limpet shells. Despite numerous morphological studies, the evolutionary relationships of patellogastropods remained poorly known. In the 1990s cladistic analyses based on morphological characters (e.g. Lindberg, 1988; Jamieson, Hodgson & Bernard, 1991; Ridgway *et al.*, 1998; Sasaki, 1998) were conducted and as a result the patellogastropod limpets were reclassified into six families: Patellidae, Nacellidae, Lepetidae, Acmaeidae, Lottiidae and Neolepetopsidae. However, many morphological characters were found to show convergence. Molecular phylogenetics have since been used to elucidate the phylogenetic relationships within Patellogastropoda and to determine objectively the species boundaries in these often morphologically variable limpets. This has led to significant advances in the systematics and taxonomy of Patellogastropoda from the level of family to species (e.g. Koufopanou *et al.*, 1999; Simison & Lindberg, 2003; Nakano & Ozawa, 2007; González-Wevar *et al.*, 2010). At least seven families (Eoacmaeidae, Patellidae, Nacellidae, Pectinodontidae, Lepetidae, Neolepetopsidae and Lottiidae) are currently

recognized in the order (Table 1). The Acmaeidae have been synonymized with the Lottiidae, and the Pectinodontinae have been elevated to familial rank. The family Eoacmaeidae includes the *Patelloida profunda* group formerly assigned to the Lottiidae. Although more than 3,237 sequences of 193 species of patellogastropod limpets have been deposited in GenBank to date (until 30 November 2010), most of them are from intertidal Patellidae, Nacellidae and Lottiidae. Deep-water limpets belonging to Pectinodontidae, Lepetidae and vent- or seep-associated Neolepetopsidae have only rarely been included in molecular phylogenies.

At the specific level, molecular studies have revealed that intraspecific variation in shell morphology and colour are much more common than previously thought (e.g. Nakano & Spencer, 2007; Nakano, Sasaki & Kase, 2010). On the other hand, cryptic species have also been reported in this morphologically simple group (e.g. Simison & Lindberg, 2003; Crummett & Eernisse, 2007; Nakano & Spencer, 2007).

The order Patellogastropoda has been reviewed several times in recent years (Lindberg, 1988, 1998, 2008). In this review, we attempt to give an overview of the latest findings on aspects of phylogeny and evolution of Patellogastropoda based on molecular data.

ORDER PATELLOGASTROPODA AND ITS RELATIONSHIPS

Patellogastropoda have been recognized as the most 'primitive' group of living Gastropoda (Golikov & Starobogatov, 1975; Wingstrand, 1985; Haszprunar, 1988; Lindberg, 1988) (Fig. 2). The monophyly of the group is supported by a number of characters including a divided shell muscle, retractile circumpallial tentacles, several sets of odontophoral muscles, a jaw with anterior wings, odontophoral cartilages, a septate mid-oesophagus, a muscular bulbous aorta, a ventrally positioned gonad and labial ganglia (Ponder & Lindberg, 1997; Sasaki, 1998).

Although morphological analyses have placed patellogastropods in a basal position in phylogenetic trees, i.e. as sister group to all other gastropods (Golikov & Strobogatov, 1975; Haszprunar, 1988; Ponder & Lindberg, 1996, 1997), the placement of the group has been variable in molecular analyses (Tillier *et al.*, 1994; Harasewych *et al.*, 1997; Colgan, Ponder &

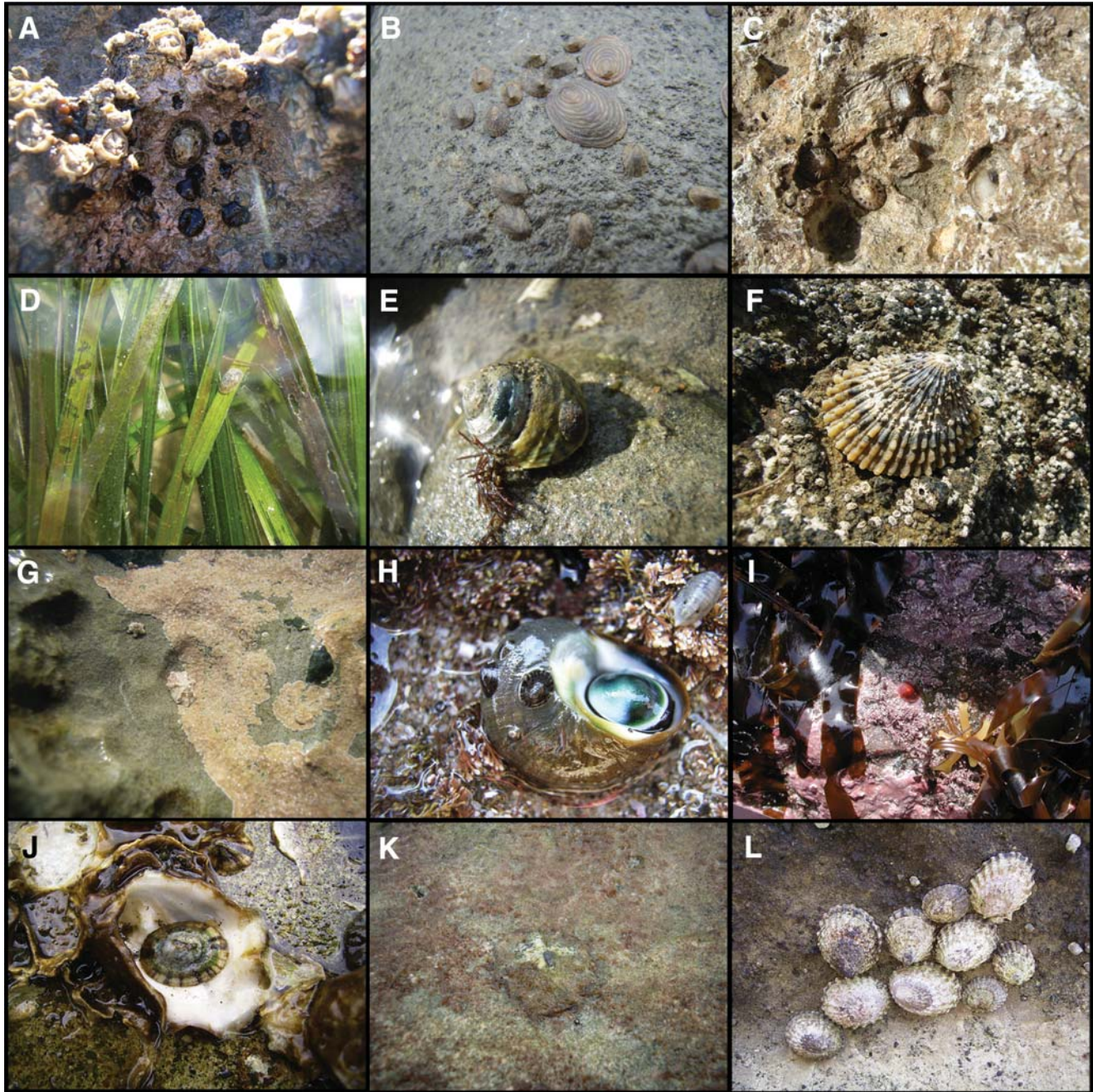


Figure 1. Diversity of Patellogastropoda. **A.** *Notoacmea scopulina* in barnacle zone. **B.** *Atalacmea fragilis* under boulders. **C.** *Eoacmaea chamorroorum* on limestone in splash zone. **D.** *Notoacmea scapha* on leaves of *Zostera*. **E.** *Notoacmea scapha* on topshell. **F.** *Cellana mazatlantica* on rock surface. **G.** *Patelloida cortica* in tide pool. **H.** *Notoacmea turbatrix* on *Lunella*. **I.** *Erginus sybariticus* on coralline algae. **J.** *Patelloida pygmaea* on shell of oyster. **K.** *Scutellastra flexuosa* on rock surface in lower intertidal zone. **L.** Colony of *Lottia dorsuosa* in splash zone.

Eggler, 2000; Colgan *et al.*, 2003; McArthur & Harasewych, 2003; Giribet *et al.*, 2006). Recently, combined analyses based on morphological characters and multiple genes have been conducted by Aktipis *et al.* (2008) (Fig. 2G). The relationships of patellogastropods among Gastropoda have also been unstable under different parameters in these combined analyses. The most recent molecular work using seven genes (18S rRNA, 28S rRNA, histone H3, 16S rRNA, COI, myosin heavy-chain type II and elongation factor-1a (EF-1a)) has suggested that Patellogastropoda are not the basal group within Gastropoda, but sister to Vetigastropoda (Aktipis & Giribet, 2010) (Fig. 2H). Problems in molecular analyses may

be caused by alignments of ribosomal genes and/or long-branch attraction, and both Patellogastropoda and Pleurotomarioidea have long insertions in the ribosomal genes (Harasewych, 2002; Giribet, 2003; Williams & Ozawa, 2006; Nakano & Ozawa, 2007; Aktipis & Giribet, 2010). The higher relationships of the order are therefore still debated.

FAMILIAL RELATIONSHIPS WITHIN PATELLOGASTROPODA

Both morphological and molecular works have attempted to resolve the relationships within Patellogastropoda (e.g. Dall,

Table 1. Classification of Patellogastropoda. Asterisk indicates that type species of genus has been sequenced.

Family	Genus	Estimated number of species
Eoacmaeidae Nakano & Ozawa, 2007	* <i>Eoacmaea</i> Nakano & Ozawa, 2007	15
Patellidae Rafinesque, 1815	* <i>Patella</i> Linnaeus, 1815	9
	* <i>Helcion</i> Monfort, 1810	4
	* <i>Cymbula</i> H. & A. Adams, 1854	9
	* <i>Scutellastra</i> Quoy & Gaimard, 1834	16
	* <i>Cellana</i> H. Adams, 1869	37
Nacellidae Thiele, 1891	* <i>Nacella</i> Schumacher, 1817	15
	<i>Naccula</i> Iredale, 1924	3
	<i>Lepeta</i> Dall, 1869	4
Lepetidae Dall, 1869	<i>Cryptobranchia</i> Middendorff, 1851	2
	<i>Limalepeta</i> Moskalev, 1977	1
	<i>Sagamilepeta</i> Okutani, 1987	1
	<i>Iothia</i> Gray, 1850	5
	<i>Propilidium</i> Forbes & Hanley, 1849	7
	<i>Bathylepeta</i> Moskalev, 1977	1
	<i>Maoricrater</i> Dell, 1956	1
	* <i>Acmaea</i> Eschscholtz in Rathke, 1833	1
	* <i>Niveotectura</i> Habe, 1944	2
	<i>Erginus</i> Jeffreys, 1877	6
'Acmaeidae' Forbes, 1850	* <i>Lottia</i> Gray, 1833	50
	<i>Patelloida</i> Quoy & Gaimard, 1834	30
	* <i>Nipponacmea</i> Sasaki & Okutani, 1993	9
	* <i>Tectura</i> Gray, 1847	1
	* <i>Notoacmea</i> Iredale, 1915	20
	* <i>Scurria</i> Gray, 1847	8
	* <i>Discurria</i> Lindberg, 1988	1
	* <i>Yayoiacmea</i> Sasaki & Okutani, 1993	1
	<i>Potamacmaea</i> Peile, 1922	1
	* <i>Atalacmea</i> Iredale, 1915	2
	<i>Asteracmea</i> Oliver, 1926	6
	<i>Pectinodonta</i> Dall, 1882	10
Pectinodontidae Pilsbry, 1891	<i>Bathyacmaea</i> Okutani, Tsuchida & Fujikura, 1992	5
	<i>Serradonta</i> Okutani, Tsuchida & Fujikura, 1992	2
	<i>Neolepetopsis</i> McLean, 1990	5
Neolepetopsidae McLean, 1990	<i>Eulepetopsis</i> McLean, 1990	1
	<i>Paralepetopsis</i> McLean, 1990	7

1876; Lindberg, 1998; Sasaki, 1998; Harasewych & McArthur, 2000; Nakano & Ozawa, 2004, 2007; Yoon & Kim, 2007). However, there is incongruence between morphological and molecular analyses, and among different authors (Fig. 3). Morphology-based analyses have placed the Lepetidae (Dall, 1876; Sasaki, 1998; Fig. 3A and C) or the Patellidae (Lindberg, 1998; Fig. 3B) in the most basal position. This disagreement may be caused by convergence of the radular, shell morphological and gill characters used. Although recent molecular studies based on the nuclear genes 18S rRNA and 28S rRNA have placed Nacellidae as a paraphyletic grade at the base of patellogastropods (Harasewych & McArthur, 2000; Nakano & Ozawa, 2007; Yoon & Kim, 2007) (Fig. 3E and F), Nacellidae appear as a monophyletic clade related to Patellidae in the analyses based on the mitochondrial genes 12S rRNA and 16S rRNA (Koufopanou *et al.*, 1999; Nakano & Ozawa, 2004) (Fig. 3D). This incongruence may be the result of different evolutionary rates of the nuclear genes used in the analyses within Nacellidae. Therefore, mitochondrial genes are likely to be more informative for relationships within Patellogastropoda as suggested by Harasewych & McArthur (2000) and Nakano & Ozawa (2007).

The molecular phylogeny that included the most extensive sampling of specimens was that of Nakano & Ozawa (2007). This work divided Patellogastropoda into six families: Eoacmaeidae, Patellidae, Nacellidae, Pectinodontidae, Lepetidae and Lottiidae (Fig. 4). The family Eoacmaeidae was newly established for the *Patelloida profunda* group (formerly assigned to Lottiidae), which appeared as the basal branch of Patellogastropoda. Acmaeidae were formerly divided into two subfamilies: Acmaeinae (including only *Acmaea*) and the deep-water group Pectinodontinae. However, in this analysis Acmaeinae did not form a clade with Pectinodontinae, but nested within Lottiidae, whereas Pectinodontinae were related to Lepetidae. Therefore, Acmaeinae were synonymized with Lottiidae, and Pectinodontinae elevated to family rank. However, the mitochondrial ribosomal genes of *Acmaea mitra* sequenced by Nakano & Ozawa (2007) turned out to be contamination from a lottiid species (D. Eernisse, personal communication). Subsequently, a clade of *A. mitra* and *Niveotectura pallida* was supported by COI and histone H3 and is distinct from Lottiidae (Nakano & Warén, 2008). Therefore, the proposal by Nakano & Ozawa (2007) that Acmaeidae is a junior synonym of Lottiidae is herein rejected.

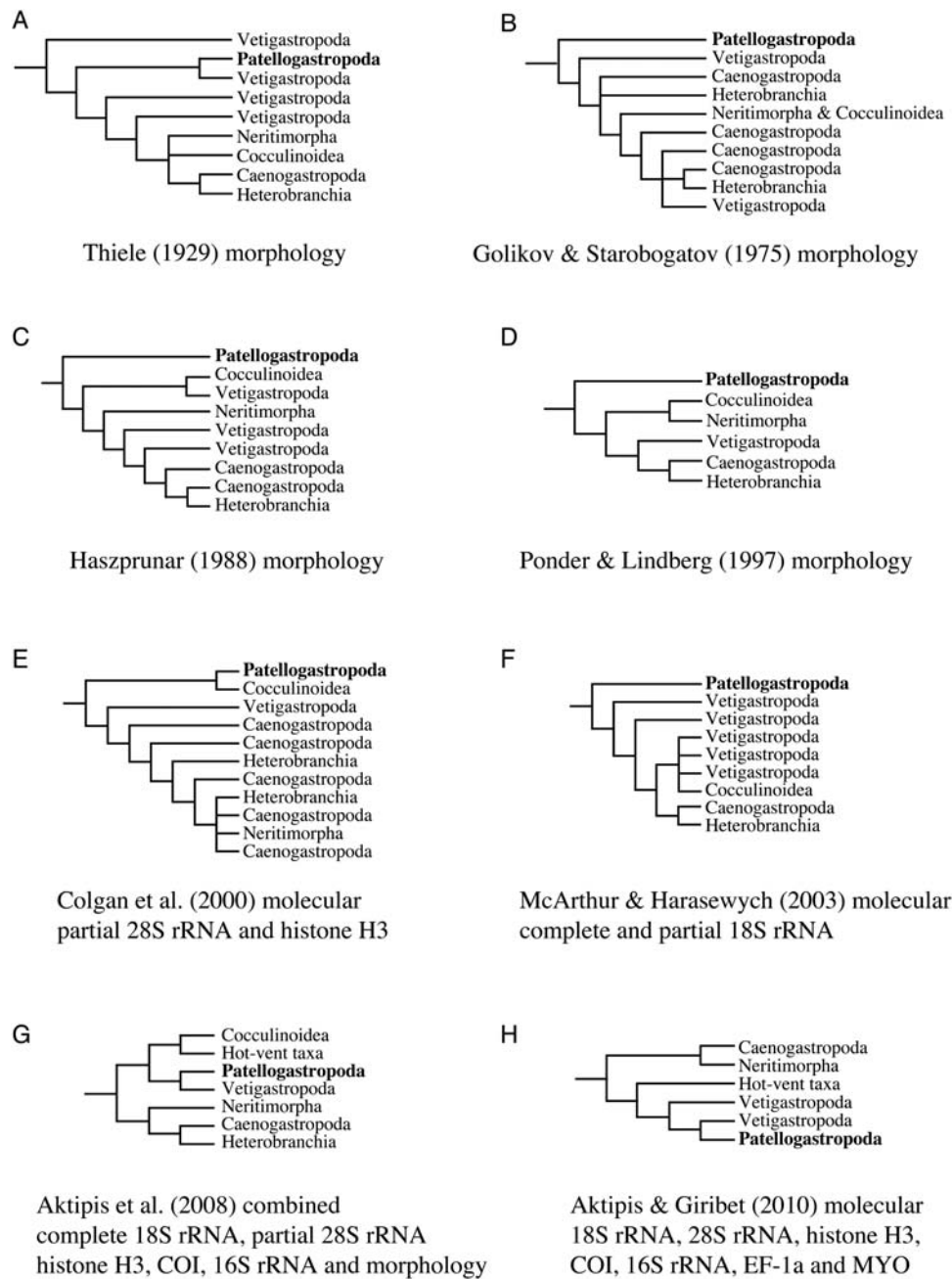


Figure 2. Summary of the placement of Patellogastropoda among Gastropoda by various authors using morphological and molecular data.

Nakano & Warén (2008) have recently sequenced specimens of Neolepetopsidae and shown that they clustered with other deep-water limpets in the Lepetidae (Fig. 3G). Eoacmaeidae and Lottiidae had a close relationship in their analysis. The incongruence between the phylogenetic trees generated by the three mitochondrial genes 12S rRNA, 16S rRNA and COI (Nakano & Ozawa, 2007) and those from COI plus the histone H3 (Nakano & Warén, 2008) may be caused by difficulties of alignments of the ribosomal genes. There are insertions of about 100 and 150 bp in 12S rRNA and 16S rRNA, respectively, in the Lottiidae (Fig. 4). Small indels in multiples of three have also been observed in COI sequences of lottiid species by Nakano & Ozawa (2007) (Fig. 4).

FAMILY EOACMAEIDAE

The separation of this family had not been recognized until its distinct position was revealed by recent molecular phylogenetic analysis. According to Lindberg & Vermeij (1985), the genus *Patelloida* belonging to the family Lottiidae consisted of at least two groups. One group included species characterized by low to medium shell profiles, strong radial ribs or many fine riblets, reduced third lateral teeth, and with habitats including various substrata ranging from exposed shores to sheltered inlets. The other group, called the '*P. profunda* group' by Christiaens (1975) and Lindberg & Vermeij (1985), consisted of species characterized by medium to high shell profiles, many riblets, equal-sized lateral radular teeth, and all species in this group

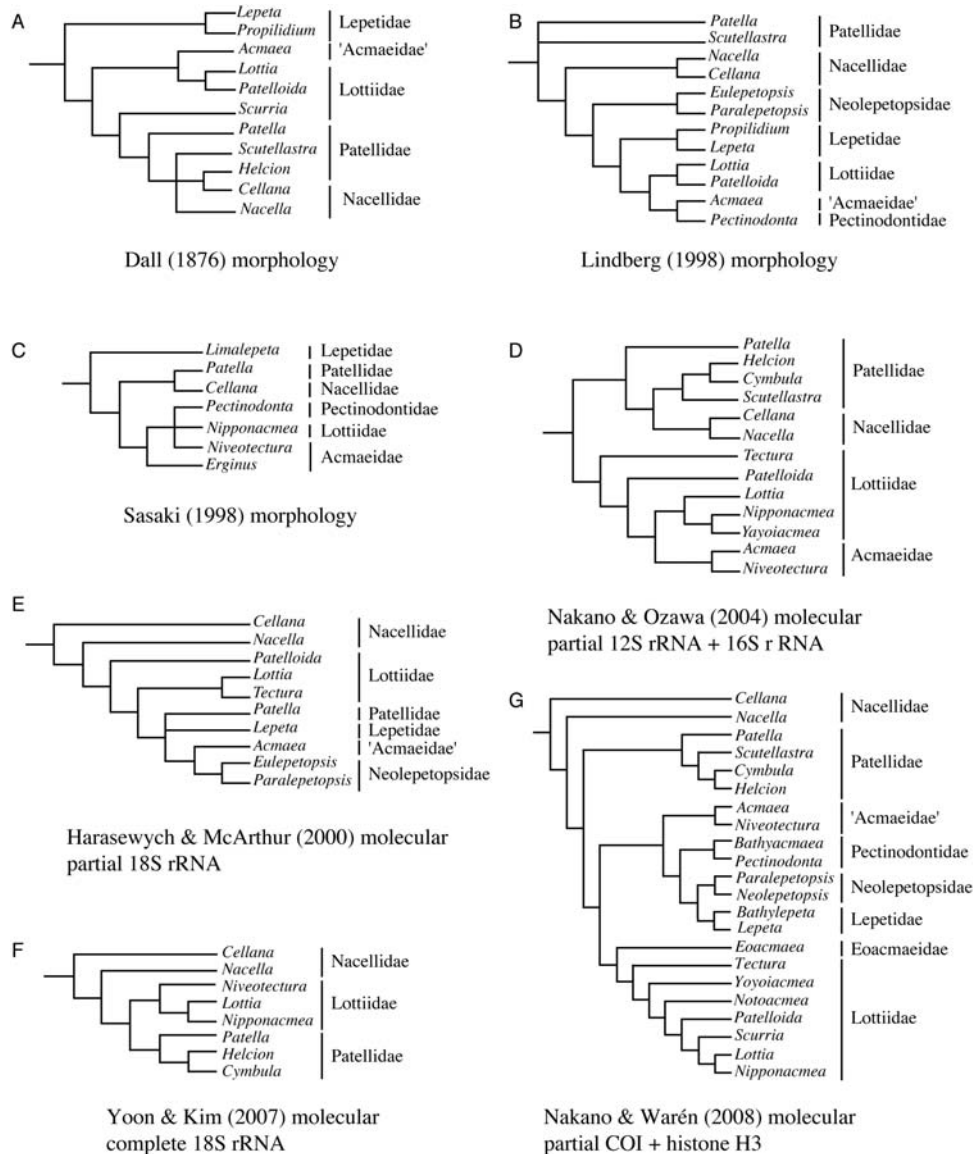


Figure 3. Summary of the relationships within Patellogastropoda by various authors using morphological and molecular data.

are restricted to calcareous substrata in the high intertidal to supratidal zones. Nakano & Ozawa (2007) assigned the *P. profunda* group to a new genus, *Eoacmaea*, because its members differ from other species of *Patelloida* both morphologically and genetically. Furthermore, *Eoacmaea* was found to be distant from other lineages and positioned as the most basal branch within Patellogastropoda. Nakano & Ozawa (2007) therefore proposed a new family Eoacmaeidae for *Eoacmaea*.

This family includes only the genus *Eoacmaea*. It is distributed in South Africa, the tropical Indo-Pacific, southern Australia and the Caribbean (Christiaens, 1975; Ponder & Creese, 1980; Lindberg & Vermeij, 1985). Kirkendale & Meyer (2004) analysed more than 100 individuals of this group from 13 localities (including 9 of the 14 assigned species), using mitochondrial COI and 16S rRNA genes. They showed that *Eoacmaea* is highly geographically structured (12 reciprocally monophyletic clades reported from 13 localities), and the split between Indian and Pacific basins was estimated as older than 15 Ma. Previous molecular works had suggested that the

divergence between taxa from Indian and Pacific basins was much younger and related to Plio-Pleistocene sea level changes (e.g. Benzie, 1999; Duda & Palumbi, 1999).

This molecular work also revealed that more than five species were undescribed within the genus *Eoacmaea* (Kirkendale & Meyer, 2004). Subsequently, a species from Java was described as *E. javanica* by Nakano, Aswan & Ozawa (2005). Most recently, more undescribed species has been found in Southeastern Asia (Kosuge & Sasaki, 2002; T. Nakano, unpubl.). Further sampling and anatomical work are required to document the diversity of this highly geographically structured group.

FAMILY PATELLIDAE

The family Patellidae is the most studied group among Patellogastropoda. Based on a morphological review of Patellidae (Ridgway *et al.*, 1998), 38 species in four genera were recognized throughout the world. *Patella*, comprising nine species, occurs in the northeastern Atlantic. Nine and four species belonging to *Cymbula* and *Helcion*, respectively, and are

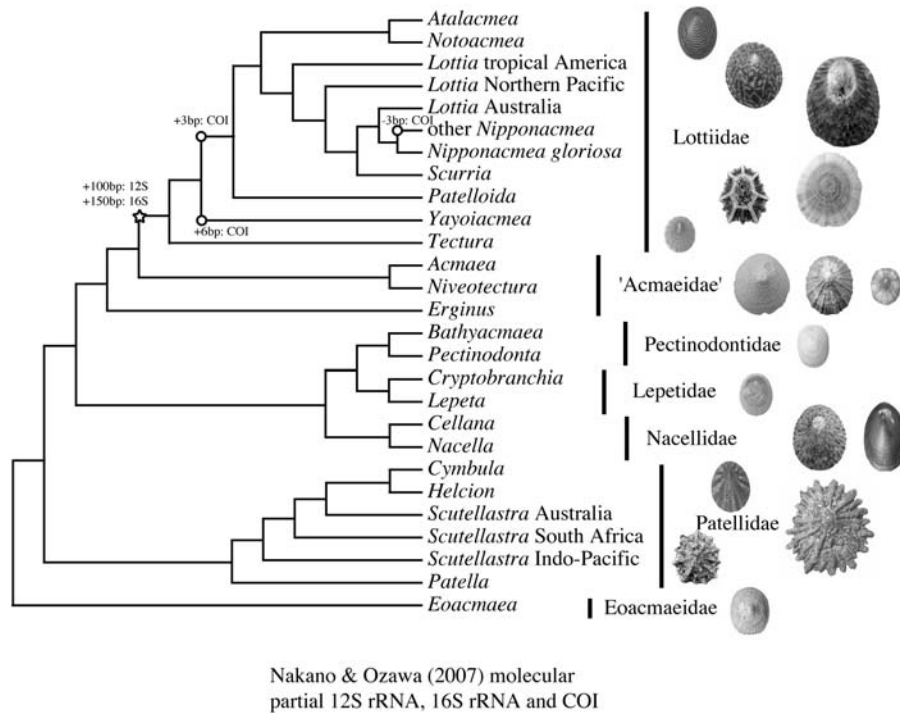


Figure 4. Phylogenetic hypothesis of Patellogastropoda based on three mitochondrial 12S rRNA, 16S rRNA and COI genes, and summary of indels in the partial sequence data (modified from Nakano & Ozawa, 2007: Fig. 4).

endemic to South Africa. A single species, *Cymbula safiana*, is distributed along the West African coast from Namibia to Algeria. The fourth genus, *Scutellastra*, extends across the tropical Indo-Pacific from South Africa to Mexico. Cladistic analyses were made by Jamieson *et al.* (1991) and Ridgway (1994) using morphological characters. Later, Ridgway *et al.* (1998) revised and extended their morphological character set, and included 38 recognized species of Patellidae in a cladistic analysis. As a result they proposed a new classification of Patellidae in four genera.

The first attempt at phylogenetic analyses using mitochondrial genes was conducted by Koufopanou *et al.* (1999). In this work, 33 out of 38 recognized species of the family were analysed using partial mitochondrial 12S rRNA and 16S rRNA sequences. Although the classification of patellids based on molecular data was mostly in agreement with that from morphological studies by Ridgway *et al.* (1998), molecular analysis suggested that *Scutellastra* was a paraphyletic group (Koufopanou *et al.*, 1999). Other molecular works have confirmed the paraphyly of *Scutellastra* (Nakano & Ozawa, 2004, 2007; Lindberg, 2007). *Scutellastra* can be subdivided into three subclades corresponding to geographical distribution in South Africa, South Australia and the Indo-Pacific (Nakano & Ozawa, 2004; Lindberg, 2007) (Fig. 4). These subclades could be recognized at subgeneric or generic rank and further work is needed to evaluate them.

At the specific level, *Scutellastra flexuosa*, widely distributed in the Indo-Pacific region, has been studied genetically. Paulay & Meyer (2002) showed an archipelagic-level differentiation of the species using partial COI data. The species is genetically differentiated even between close archipelagos within French Polynesia (Tuamotu, Society and Cook Islands). With such fine-scale differentiation, the biodiversity of the group could easily be underestimated. This species is the subject of ongoing studies (C. Meyer, personal communication). Lindberg (2007) superimposed the body size and an ecological feature

(migratory or non-migratory) of 12 *Scutellastra* species onto the reanalysed maximum-parsimony tree using the data of Koufopanou *et al.* (1999) and some additional taxa (*Scutellastra flexuosa* and *Cellana* spp.) based on 16S rRNA. As a result he suggested that the non-migratory habit is ancestral in Patellidae, and that there is a close connection between reduced size of the shell and migratory habits.

Many genetic studies have been published on the genus *Patella*, although these have often focused on a small region (e.g. Madeira archipelago; Weber *et al.*, 1998), or on a few species (Côrte-Real, Hawkins & Thorpe, 1992, 1996a, b; Weber & Hawkins, 2002, 2005; Mauro, Arculeo & Parrinello, 2003; Espinosa & Ozawa, 2006). Phylogenetic analyses have been made for *Patella* using 12S rRNA, 16S rRNA and COI data by Sá-Pinto *et al.* (2005), revealing differentiation between Macaronesian and continental populations of *P. ulysiponensis* and *P. rustica*, and the occurrence of three distinct lineages of *P. rustica* within the Mediterranean Sea corresponding to the Atlantic and Western Mediterranean, the Aegean Sea and Eastern Mediterranean, and Mediterranean shores in southeast Turkey. Later, Sá-Pinto *et al.* (2008) analysed COI data from 420 samples of *Patella* including all published data available to investigate gene flow between Macaronesian and continental populations. They demonstrated a genetic disjunction between these regions in both *P. ulysiponensis* and *P. rustica*. *Patella ulysiponensis* shows differences in the radula and shell morphology between continental and Macaronesian populations (Christiaens, 1973) and the name *P. aspera* is available for the latter; these populations are also differentiated genetically (Koufopanou *et al.*, 1999; Weber & Hawkins, 2005). Some authors have pointed out that the Macaronesian form of *P. rustica*, which has previously been proposed as *P. piperata*, should be considered a different species, from a morphological point of view (Christiaens, 1973; Titselaar, 1998). Although Côrte-Real *et al.* (1996a) did not find genetic differences using electrophoretic analyses of isozymes between continental and

Macaronesian population of *P. rustica*, molecular phylogenetic analyses have revealed that the two populations are genetically distinguishable (Koufopanou *et al.*, 1999; Sá-Pinto *et al.*, 2005, 2008). Sá-Pinto *et al.* (2008) have also suggested that *P. candei* is polyphyletic, and can be divided into two groups corresponding to the Canary islands plus Selvagens, and Madeira plus Azores, respectively.

Sá-Pinto *et al.* (2010) analysed 187 individuals of *P. rustica* using the genetic variability at nine allozyme loci, an intron from the α -amylase gene and mitochondrial COI to examine the gene flow within Mediterranean Sea. They concluded that the eastern Mediterranean clade is highly differentiated and likely to be reproductively isolated. Therefore, it should be treated as an undescribed species. Taxonomic reconsideration is needed in *Patella*, especially for *P. rustica*, *P. aspera* and *P. candei*.

Cymbula safiana is known as an endangered species and has been genetically analysed at the population level (Espinosa *et al.*, 2011), revealing the low genetic diversity and the absence of geographic structure.

FAMILY NACELLIDAE

The family Nacellidae consists of the tropical genus *Cellana*, the cold-water *Nacella* and possibly the Australian endemic *Naccula*. *Cellana* is currently widely distributed in the Indo-West Pacific region and shows greatest diversity in Australasia. On the other hand, *Nacella* is limited to Antarctic and subantarctic waters in high southern latitudes with a center of diversification in the Magellanic Province of southern South America. *Naccula* is restricted to South Australia. The only taxonomic reviews of this family are those published by Pilsbry (1891) and Powell (1973). According to the latter, *Nacella* included only 15 species, whereas *Cellana* contained 37 species and subspecies.

Koufopanou *et al.* (1999) and Nakano & Ozawa (2004) each included five *Cellana* species in for phylogenetic analyses based on 12S rRNA and 16S rRNA. Later, Nakano & Ozawa (2007) included 18 species, using 12S rRNA, 16S rRNA and COI sequences to examine the familial relationships within Patellogastropoda. They suggested that New Zealand and Australian species were the basal group in the genus *Cellana*. This relationship among *Cellana* was supported by the analysis of 23 *Cellana* species using COI and nuclear histone H3 genes (Nakano *et al.*, 2009b; *contra* Goldstien, Gemmell & Schiel, 2006a, see below).

Molecular studies at the specific level in the genus *Cellana* have recently been published by several authors (Goldstien, Gemmell & Schiel, 2006a, b; Bird *et al.*, 2007; Ayre, Minchinton & Perrin, 2009; Nakano *et al.*, 2009a). Goldstien *et al.* (2006a) analysed all recognized species of *Cellana* in New Zealand including subspecies from isolated islands, based on 12S rRNA and 16S rRNA in order to examine the biogeographic origin of New Zealand *Cellana*. They revealed disjunction within the *C. strigilis* complex (*C. s. strigilis* from Campbell Island is different from that on Auckland Island; *C. s. chathamensis* is more closely related to *C. denticulata* than to other subspecies of *C. strigilis*). Later, Goldstien *et al.* (2009) examined genetic structure of *C. strigilis* complex from mainland New Zealand and subantarctic islands using 12S rRNA, 16S rRNA and cytochrome *b* (*cytb*) genes. They found two divergent lineages including *C. s. redimiculum* and *C. s. strigilis* from the mainland and Auckland and Campbell Islands, and *C. s. chathamensis*, *C. s. oliveri* and *C. s. bollonsi* from Chatham, Bounty and Antipodes Islands, but did not resolve the taxonomic status of these lineages. The phylogeography of the three New Zealand endemic species *C. ornata*, *C. radians* and *C. flava* has been examined based on the *cytb* gene (Goldstien *et al.*,

2006b). This study found a genetic break at Cook Strait between the two main islands of New Zealand in each of these three taxa.

Bird *et al.* (2007) focused on Hawaiian endemic limpets. They analysed more than 100 specimens of each of the three species *Cellana exarata*, *C. sandwicensis* and *C. talcosa* based on COI data, to examine their dispersal abilities. Population partitioning at fine spatial scales (less than 200 km) was detected in the three species, suggesting that not only geographic barriers like landmasses but also deep open ocean channels and ocean currents among islands could efficiently prevent gene flow.

Another study at population level using COI gene has been conducted by Ayre *et al.* (2009). They analysed 10 invertebrate species from Australian rocky shores including *C. tramoserica*, to test whether larval type and habitat specificity are predictors of gene flow between biogeographic regions. The genetic disjunction between eastern and southern Australia and a coalescence analysis of sequence differentiation both suggested that a barrier to gene flow has existed at the southeastern corner of Australia since the Pleistocene.

Cellana mazatlantica and *C. radiata enneagona* are endemic to the Ogasawara Islands situated in the centre of the Izu-Mariana Arc in the northwestern Pacific, and their geographic origin has been studied (Nakano *et al.*, 2009a). Molecular analyses using 23 species of this genus from the Indo-Pacific based on COI and histone H3 suggested that *C. mazatlantica* and *C. r. enneagona* in the Ogasawara Islands are the sister species of *C. grata* and *C. toreuma*, respectively, in warm-temperate Japan, and that the two ancestral *Cellana* species may have extended their distribution southwards from the mainland of Japan to reach the Ogasawara Islands using new volcanic islands as stepping stones, followed by isolation as a result of sea-level changes and/or volcanic activity during the Plio-Pleistocene.

Most recently, Nakano & Espinosa (2010) showed that some specimens from Ghana formerly identified as *Cymbula nigra ghansensis* belong to a *Cellana* species, and suggested that this could have been introduced into West Africa from the Indian Ocean. This is the first record of the genus *Cellana* in the Atlantic, and the first example of a long-distance introduction of a patellogastropod.

Although many works have appeared on aspects of the ecology and biology of *Nacella* species (especially *N. concinna* and *N. magellanica*) (e.g. Picken, 1980; Morriconi & Calvo, 1993; Morriconi, 1999; Fraser, Clarke & Peck, 2002; Clarke *et al.*, 2004; de Aranzamendi *et al.*, 2008), the taxonomy of the genus has been confused. A recent morphological study based on shell shape, radular morphology, colour of the mantle and foot by Valdovinos & R uth (2005) found support for the recognition of all but one nominal species previously described from the Magellanic Region. The only exception was *Nacella fuegiensis*, which they considered a junior synonym of *N. magellanica*.

So far only a few *Nacella* species have been included in the molecular phylogenetic studies of evolutionary relationships within Patellogastropoda, using partial 18S rRNA (Harasewych & McArthur, 2000), complete 18S rRNA (Yoon & Kim, 2007), partial 12S rRNA and 16S rRNA (Koufopanou *et al.*, 1999), and 12S rRNA, 16S rRNA and COI genes (Nakano & Ozawa, 2007). Relationships within the genus *Nacella* had been largely unexplored, until Gonz alez-Wevar *et al.* (2010) presented a phylogenetic and biogeographic analysis of 8 out of 15 recognized species of *Nacella* based on mitochondrial COI and *cytb* sequences. Powell (1973) had identified at least four biogeographic regions in the Southern Ocean, and had subdivided *Nacella* into two subgenera based on the apex position, shell thickness and internal coloration of the shell: *Nacella* (*Nacella*) containing

N. mytilina and *N. keruguelensis*, and *Nacella* (*Patinigera*) containing the remaining 13 species. However, the molecular analyses of González-Wevar *et al.* (2010) did not support the monophyly of these subgenera, so that a revision of the systematics and taxonomy of the genus is still needed. At the specific level, they were unable to discriminate the four Magellanic species *N. magellanica*, *N. deaurata*, *N. flammae* and *N. mytilina* based on COI and cytb data, although these are morphologically well separated. Likewise, de Aranzamendi, Gardenal & Martin (2009) found a similar result using only COI and cytb data for three of these Magellanic species (not including *N. flammae*). They were able to resolve these three species successfully using intersimple sequence repeat (ISSR) fingerprint analysis. Their analyses further revealed that *N. delicatissima* is actually a hybrid of *N. magellanica* and *N. deaurata*, and concluded that such ongoing hybridization could reflect the recent speciation of these species.

Because it can reveal high levels of polymorphism, ISSR analysis appears to be a potentially useful method to detect fine-scale population structure in limpets. In another example of the application of this method, de Aranzamendi *et al.* (2008) found that ISSRs could detect genetic differences between two morphological forms of the Antarctic *Nacella concinna* inhabiting the intertidal and subtidal zones.

Naccula consists of three species endemic to southern Australia: the type species *Naccula parva*, *Naccula punctata* and *Naccula compressa* (Lindberg, 1998; Hickman, 2005). The systematic position of the genus is still unresolved. Although Lindberg (1998) placed it in the Nacellidae based on shell microstructure, Hickman (2005) stated that it belongs to Patellidae since the configuration of radular teeth is similar to those of Patellidae. Molecular data are needed to elucidate the phylogenetic position of the genus *Naccula*.

FAMILY LOTTIIDAE

This family is the most diverse within Patellogastropoda, being composed of at least 8 genera and about 130 species, and has an almost worldwide temperate and tropical distribution.

Although species-level identification of lottiid limpets has been done using genetic data by many authors (e.g. Murphy, 1978; Simison & Lindberg, 1999, 2003; Nakano & Ozawa, 2005; Crummett & Eernisse, 2007), fewer molecular phylogenetic analyses have been conducted (Koufopanou *et al.*, 1999; Espoz *et al.*, 2004; Nakano & Ozawa, 2004, 2007). Koufopanou *et al.* (1999) included only two lottiids as outgroups, while Espoz *et al.* (2004) focused on the genus *Scurria*. Nakano & Ozawa (2004) analysed many acmaeids and lottiids and supported the monophyly of Lottiidae. Later, Nakano & Ozawa (2007) added more taxa and to produce a more robust phylogeny of Lottiidae. One of the most surprising results of this study was that the genus *Lottia* turned out to be paraphyletic. *Lottia* can be subdivided into three clades corresponding to geographical distribution, a basal tropical American clade, a northern Pacific clade and an Australasian clade. These clades could be treated as different taxa at generic or subgeneric rank.

The genus *Notoacmea* has long been believed to have an anti-tropical distribution, with representatives from temperate waters in both the southern and northern Pacific (Keen, 1971; Abbott, 1974; Habe & Okutani, 1975; Ponder & Creese, 1980). However, Lindberg (1986) transferred all North American species to *Tectura*, and Sasaki & Okutani (1993b) erected the new genus *Nipponacmea* for the Japanese species. Molecular work using 12S rRNA and 16S rRNA (Nakano & Ozawa, 2004) subsequently confirmed the monophyly of *Nipponacmea*, but restricted *Tectura* to one northeastern Atlantic species *Tectura virginea*, and removed the northeastern Pacific

species to *Lottia*. After these revisions, *Notoacmea* was restricted to the species from New Zealand and Australia.

There are other lottiid limpets belonging to *Atalacmea* and *Radiacmea* in New Zealand waters (Powell, 1979). *Atalacmea* formed a clade with *Notoacmea*, and *Radiacmea* was nested within *Notoacmea* in the analysis of Nakano & Ozawa (2007). Therefore, *Radiacmea* was synonymized with *Notoacmea*.

The genus *Collisella* has been synonymized with *Lottia* (Lindberg, 1986) and this has been confirmed in molecular phylogenetic analyses (Nakano & Ozawa, 2004, 2007). However, *Collisella* has commonly been used until recently, probably inappropriately, for the four Brazilian lottiid species (de Carvalho Rios, 2009). The affinities and systematic position of these species remain untested. On the western coast of South America only the lottiid genus *Scurria* occurs, together with one species *Lottia orbigny*. The monophyly of *Scurria* has been confirmed by molecular data (Nakano & Ozawa, 2007), and Espoz *et al.* (2004) have distinguished at least eight species of *Scurria* in the Chilean-Peruvian Province using sequences of 16S rRNA.

Although the genus *Discurria* was proposed by Lindberg (1988) on the basis of a different radular morphology, it was nested within *Lottia* in a phylogenetic tree based on 12S rRNA and 16S rRNA (Nakano & Ozawa, 2007), so its separate generic status can be rejected.

Molecular results have confirmed the integrity of *Patelloida*, which is widely distributed in the Indo-West Pacific region (Nakano & Ozawa, 2004, 2007; see earlier comments about *Patelloida profunda* group, now placed in *Eoacmaea*). *Patelloida* can be divided into two groups: one clade includes species with strong radial ribs and inhabits rocky shores (*Patelloida saccharina* group), while the other is composed of species with rounded shells and occupies various substrata (*Patelloida pygmaea* group) (Nakano & Ozawa, 2004, 2007). *Potamacmaea*, the only patellogastropod inhabiting brackish water, is likely to be positioned between these two groups (T. Sasaki & T. Nakano, unpubl.), so its status as a separate genus remains in question and in general the subdivisions of *Patelloida* require further work.

The genus *Asteracmea* consists of tiny limpets, including at least six species in New Zealand and Australia (Powell, 1979; Lindberg, 1998; Hickman, 2005). Lindberg (1998) suggested that *Asteracmea* has a cosmopolitan distribution ranging from the Red Sea to the Caribbean. Three species, *A. stowae*, *A. roseoradiata* and *A. crebristriata* have been reported from the blades of seagrasses in Australia (Hickman, 2005). Judging from the relatively tall conical shells with curved margin, *A. illibrata*, *A. axiaerata* and *A. roseoradiata* inhabit substrata that are not flat (Hickman, 2005). However, the habits of these species remain unknown. Most of the collections of these species are of shells from sandy sediments. Although Lindberg (1998) and Hickman (2005) placed this genus in Lottiidae, the placement is still unclear since neither detailed anatomy nor genetic data are available.

A minute Japanese lottiid has similarly tall conical shells with curved margins, and is restricted to coralline algae (Sasaki & Okutani, 1993a). The species was originally described as *Collisella oyamai*, and subsequently assigned to the new genus *Yayoiacmea* based on detailed anatomy (Sasaki & Okutani, 1993a). Molecular data have confirmed that this genus belongs to the family Lottiidae, but the relationship between *Yayoiacmea* and *Asteracmea* remains unclear.

Lottia gigantea is the first mollusc of which the full genome has been sequenced (Gonzales, Lindberg & Rokhsar, 2010). This is potentially important as a representative of one of the basal lineages in the Gastropoda.

FAMILY ACMAEIDAE

The definition of the family Acmaeidae had changed drastically in the past (e.g. Lindberg, 1986), and the family is currently composed of three genera: *Acmaea*, *Niveotectura* and *Erginus*, as proposed by Nakano & Ozawa (2007). Originally the name Acmaeidae was widely applied for many lottiid genera and species (e.g. Pilsbry, 1891). This scheme was totally revised by Lindberg (1986), based mainly on the shell structure groups of MacClintock (1967). The genus *Acmaea* was restricted to its type species *Acmaea mitra*, and the rest of the former acmaeids were transferred to the Lottiidae (Lindberg, 1986).

All species of *Acmaea*, *Niveotectura* and *Erginus* are distributed in cold-water regions in the northern Pacific. These three genera have similar ecological preferences on subtidal calcareous algae (Lindberg & Marincovich, 1988). *Acmaea mitra*, the sole member of its genus, occurred in Japan in the Miocene (Kurihara & Kase, 2008), but now survives only in California.

The genus *Niveotectura* consists of two species having white shells with prominent radial ribs and conical profile (*N. pallida* and *N. funiculata*; Lindberg & Marincovich, 1988). The genus *Erginus* is characterized by a tiny and smooth shell with centrally pointed apex and also by its brooding habit (Golikov & Kussakin, 1972; Lindberg, 1979; Sasaki, 1998; Chernyshev & Chernova, 2002). Molecular phylogenetic analyses have yet to be conducted for the entire genus. There are six nominal species in the Recent fauna, which should be critically revised in future: *E. apicina*, *E. galkini*, *E. moskalevi*, *E. puniceus*, *E. rubella* and *E. sybariticus* (Lindberg, 1987; Chernyshev & Chernova, 2002).

This family is one of the least studied groups for molecular characters within Patellogastropoda. It needs further work to elucidate its status and position within the order, as mentioned above.

FAMILY LEPETIDAE

Lepetidae are strictly subtidal, and are restricted to cold waters. They occur from just below the low-water mark in the Northern Hemisphere, but extend to depths in excess of 5,000 m towards the equator (Moskalev, 1977). According to Sasaki (1998), eight genera are currently recognized within Lepetidae: *Lepeta*, *Propilidium*, *Iothia*, *Cryptobranchia*, *Sagamilepeta*, *Maoricrater*, *Bathylepeta* and *Limalepeta*. Moskalev (1977) reviewed the Lepetidae of world oceans and presented a classification based primarily on radular characters. The anatomy of *Lepeta*, *Iothia* and *Propilidium* was summarized by Angerer & Haszprunar (1996). However, the relationships within Lepetidae are not known and only a few representatives of Lepetidae have been analysed using partial 18S rRNA (Harasewych & McArthur, 2000) and partial 12S rRNA, 16S rRNA and COI (Nakano & Ozawa, 2007). Most recently, Warén, Nakano & Sellanes (2011) have analysed 11 species from six genera including the type species of four of them, *Lepeta caeca*, *Limalepeta lima*, *Sagamilepeta sagamiensis* and *Iothia fulva*, using partial COI and histone H3 genes. They recognized two main clades in the family corresponding to *Iothia* plus *Bathylepeta* and to the remainder of the Lepetidae (*Lepeta*, *Cryptobranchia*, *Limalepeta* and *Sagamilepeta*). In the latter clade, *Lepeta caeca* and *Lepeta caeca pacifica* do not cluster together. Although *L. caeca* is related to *S. sagamiensis*, *L. caeca pacifica* clustered with *L. lima*, so this clade is clearly in need of revision.

FAMILY PECTINODONTIDAE

This family has been considered as a subfamily Pectinodontinae within Acmaeidae, although it was elevated to familial rank since it was clearly unrelated to sequences

erroneously attributed to *Acmaea mitra* based on partial 12S rRNA, 16S rRNA and COI genes (Nakano & Ozawa, 2007). No other molecular test of its relationships to Acmaeidae is yet available. Pectinodontidae includes *Pectinodonta*, *Bathyacmaea* and possibly *Serradonta*. *Pectinodonta* is restricted to substrata of sunken wood in the Pacific, whereas *Bathyacmaea* attaches to rocks or shells of other molluscs in vent and seep sites in the western Pacific and seeps off Costa Rica (Okutani, Tsuchida & Fujikura, 1992; Okutani, Fujikura & Sasaki, 1993; Sasaki *et al.*, 2005; Sasaki, Fujikura & Okutani 2007). *Serradonta* is restricted to the surface of vestimentiferan tubes from seeps in Japan (Okutani *et al.*, 1992; Sasaki *et al.*, 2007). Only *Pectinodonta rhyssa* and *Bathyacmaea nipponica* have been analysed genetically and these two species clustered together in a phylogenetic tree based on 12S rRNA, 16S rRNA and COI (Nakano & Ozawa, 2007). The systematic position of *Serradonta* has not been tested using molecular markers. *Serradonta* and *Bathyacmaea* are very similar in their pale shells with a fine reticulate sculpture but are distinguishable by radular morphology (Sasaki *et al.*, 2010). Sasaki, Okutani & Fujikura (2006) described the anatomy of *B. secunda* and new taxa are still being found at previously unexplored sites. This family is one of the less studied groups within Patellogastropoda.

FAMILY NEOLEPETOPSIDAE

The family Neolepetopsidae was proposed by McLean (1990). It consists of three genera *Neolepetopsis*, *Eulepetopsis* and *Paralepetopsis*. Globally, it is limited to hydrothermal vents and cold-seep sites, except for *Neolepetopsis nicolasensis* and *Paralepetopsis clementensis*, which have been collected from whale carcasses off California (McLean, 2008). Fretter (1990) described the anatomy of some species of Neolepetopsidae and details of their shell structure have been recorded by Hedegaard (1990) and Kiel (2004). Additional species of neolepetopsid limpets have been described by Beck (1996), Warén & Bouchet (2001, 2009) and McLean (2008).

McArthur & Koop (1999) published the first molecular analysis of Neolepetopsidae. They analysed 32 gastropod genera, including *Eulepetopsis vitrea*, using partial 28S rRNA to examine the origin of vent endemic gastropods. Harasewych & McArthur (2000) analysed partial 18S rRNA sequences from representatives of all living families of Patellogastropoda, including *E. vitrea* and *Paralepetopsis floridensis*, together with most other gastropod groups, to confirm the monophyly of Gastropoda and to resolve familial relationships within Patellogastropoda. Nevertheless, the phylogenetic relationships within Neolepetopsidae are still unclear because these two previous studies were based on quite sparse sampling of patellogastropod representatives and otherwise only a few representatives of Neolepetopsidae have been sampled. On morphological grounds, Warén & Bouchet (2001) suggested that the distinction between *Neolepetopsis* and *Paralepetopsis* is not clear. Further work is needed to elucidate the generic status and relationships of groups within Neolepetopsidae.

At the population level, *E. vitrea* has been analysed using partial COI sequences to discuss comparative phylogeography among vent species along the East Pacific Rise (Plouviez *et al.*, 2009). These authors have compared genetic patterns from seven vent species and demonstrated vicariant processes and population expansion.

DISPERSAL ABILITY OF
PATELLOGASTROPOD LIMPETS

Almost all members of Patellogastropoda reproduce by broadcast spawning and have pelagic development with

lecithotrophic larvae (Lindberg, 1998). An exception is *Erginus* (Acmaeidae), which is the only genus known to brood its larvae (Lindberg, 1979; Sasaki, 1998). The developmental time and dispersal ability of larvae are poorly known. In laboratory experiments, patellogastropod larvae have survived for only a few days or up to 10 days (Amio, 1963; Wanninger *et al.*, 1999; Wanninger, Ruthensteiner & Haszprunar, 2000; Kay & Emler, 2002; earlier references therein), suggesting that larvae normally disperse less than is the case for many marine invertebrate larvae, especially those which are planktotrophic.

Consistent with this, larvae can commonly be found in coastal waters (Lebour, 1937), but have not been reported from offshore samples (Fretter & Shale, 1973). Recently, Bird *et al.* (2007) have attempted to estimate dispersal distances of Hawaiian endemic limpets from their phylogeographic patterns. In all the three species of *Cellana*, the analysed population partitioning was observed at scales <200 km, finer than previously thought possible for species with a pelagic larval period. They suggested that deep ocean channels and variable currents among islands could prevent gene flow. Goldstien, Gemmell & Schiel (2006b) observed a genetic disjunction across the Cook Strait in central New Zealand for three New Zealand *Cellana* species, so again a relatively small stretch of open sea acted as a dispersal barrier. The populations of *Patella rustica*, *P. ulysiponensis* and the *P. candei*–*P. lugubris* complex have no shared haplotypes between the Macaronesian archipelagos and continental shores of northeastern Atlantic, also suggesting a limited dispersal ability (Sá-Pinto *et al.*, 2008).

The dispersal ability is determined not only by larval period and geographic distance, but also by habitat specificity (Ayre *et al.*, 2009). These authors showed that there is a phylogeographic break at the southeast corner of Australia for rock specialists with planktonic larvae, whereas species with relaxed habitat specificity show no such genetic differentiation. They suggested that a 300-km sedimentary shore without suitable habitat may present a barrier to gene flow for rocky specialists despite an obligate planktonic larval stage. The Japanese limpet *Cellana nigrolineata* is subdivided into three geographical clades (Nakano *et al.*, 2010). One of these clades is currently isolated by inhospitable sandy shores (<100 km). From all these studies, although based on indirect evidence, it might be concluded that patellogastropod limpets typically disperse <100–200 km during their larval period.

Rafting is a plausible means for long distance dispersal in some species (Donald, Kennedy & Spencer, 2005). South African *Cymbula depsta* and *C. canescens* may have reached the southern Indian Ocean by rafting on algae (Ridgway *et al.*, 1998). Algal-dwelling *Cymbula compressa*, *Nacella edgari* and *N. mytilina* also have the potential for rafting (Pilsbry, 1891; Powell, 1973).

There is an exceptional case suggesting the possibility of dispersal over longer distances. Picken (1980) studied the larval development of *Nacella concinna*, and showed that it achieved settlement after one month under laboratory conditions (0°C). This example indicates that long-distance dispersal of larvae may occur at low temperatures at high latitudes.

CRYPTIC SPECIES

Limpets with low dispersal ability could easily undergo differentiation on isolated islands. Paulay & Meyer (2002) reported archipelagic endemism in *Scutellastra flexuosa* across the Indo-West Pacific region as the first such example within the patellogastropods. Later, the genus *Eoacmaea* (as *Patelloida*) was also found to show endemism on islands ranging from South Africa to the Caribbean (Kirkendale & Meyer, 2004). Both species complexes are difficult to identify based on shell morphology alone. *Patelloida saccharina*, distributed in the

Indo-West Pacific, also includes many phylogenetic species (T. Nakano, unpubl.). In this case, specimens from Singapore to Hong Kong (a stretch of >1,000 km along continental shores) are identical based on COI, whereas there are at least six lineages in the Philippines archipelago. These cryptic species can also be distinguished by a combination of the colour of the side of the foot and shell morphology.

Nakano & Spencer (2007) found five biological species under the single species *Notacmea helmsi*. There is some habitat differentiation or distinctness by light-avoiding behaviour. Nakano *et al.* (2009a) revealed a further example of cryptic species in the pair *N. elongata* and *N. daedala*, between which they could find neither conchological nor ecological differences.

Cellana radiata is also a species complex (Nakano & Ozawa, 2007). According to Powell (1973), *C. radiata* consists of four subspecies, *C. radiata radiata*, *C. radiata capensis*, *C. radiata ennea-gona* and *C. radiata orientalis*. Molecular analyses have resolved six genetically distinct clades, corresponding to the four nominal subspecies and another two unnamed clades (Nakano & Ozawa, 2007; Nakano *et al.*, 2009b). Further work and extensive sampling are needed to clarify the taxonomy of this widely distributed Indo-Pacific group.

As discussed above, several members of the genus *Patella* also appear to consist of cryptic or morphologically similar species (e.g. Sá-Pinto *et al.*, 2008, 2010).

INTRASPECIFIC VARIATION AND SPECIES BOUNDARIES

Molecular techniques have revealed that intraspecific variation is much more common than previously thought. Simison & Lindberg (1999) were the first to demonstrate intraspecific variation in radular morphology in *Lottia* (as *Notoacmea*) *fascicularis* using COI data. *Patelloida pygmaea* and *P. ryukyensis* also show variation in radular morphology (Nakano & Ozawa, 2005).

The New Zealand lottiid *Notoacmea turbatrix* shows complex variation in colour and shell morphology (Nakano *et al.*, 2009a). Individuals inhabiting rocks or other gastropod shells have a smaller shell with narrower outline, whereas those in tide pool have larger depressed shells with white or black colour, which resemble two other congeners *N. badia* and *N. parvicornioidea*, respectively. The variation of colour and shell forms is discussed further below.

Shell height variation has been observed in many limpet species, and is believed to be an ecophenotypic effect. For example, the ratio of height to length in specimens from higher tidal levels is greater than in those from lower levels in the nacellid limpet *Cellana toreuma* (Ino, 1935). This has been explained by a response to desiccation stress at higher levels (Vermeij, 1973; Branch, 1975) or to water turbulence (Simpson, 1985). Recent molecular work has not found any genetic differences between the two shell forms of European *Patella ferruginea* (Espinosa & Ozawa, 2005). However, other recent work has detected genetic differences between the intertidal and subtidal populations of *Nacella concinna* in Antarctica, suggesting that the two forms are likely to be genetically distinct populations maintained by low levels of gene flow (De Aranzamendi *et al.*, 2008). This is the first work to show genetic differentiation between intertidal and subtidal populations in limpet species.

The accuracy of ecological work is dependent on correct species identification, but it is often difficult to define species boundaries of ecologically important patellogastropod limpets due to their highly variable shell morphologies and colour

patterns. Molecular approaches have helped to resolve these questions.

The species identification of seagrass-associated forms of limpets is a longstanding issue. *Lottia alveus* has a laterally compressed shell that had been thought to represent an ecotype of *L. testudinalis*, but has more recently been regarded as a distinct species with an obligate association living on eelgrass. This specialized species became extinct after drastic decline of the eelgrass beds (Carlton *et al.*, 1991). In an analogous case, phylogenetic analyses of two genes (mitochondrial COI and nuclear ITS1) revealed that the laterally compressed shell of *Notoacmea scapha* is an ecophenotypic response to living on the blade of the seagrass *Zostera*, and such forms are genetically identical to those individuals living on hard substrata which have larger and more rounded shells (Nakano & Spencer, 2007). Similar phenomena have been described in multiple lottiid species (e.g. Lindberg, 2007) based on morphology, and these have been supported by recent molecular studies (D. Eernisse, unpubl.). The ecophenotypic plasticity exhibited by *N. scapha* would repay study to determine if the ability to respond to substrate is retained throughout life or not.

Nakano & Ozawa (2005) have recognized four species in the *Patelloida pygmaea* complex which had been treated as one species with two ecological forms, using COI and 16S rRNA genes. The four species correspond to *P. pygmaea* on the shell of *Crassostrea gigas* or rocks, *P. conulus* on the shell of the gastropod *Batillaria*, *P. heroldi* on rocks and *P. ryukyuensis* on the shell of *Saccostrea* or rocks, and each species shows strict habitat specificity. The ecologically interesting question is how they recognize their host before settlement.

Colour variation of the patellogastropod limpets is also debated. The cause of shell colour polymorphism is generally believed to be ecophenotypic. For example, the North American *Lottia digitalis* displays two colour morphs: individuals living among colonies of barnacles have a light colour, whereas those on rocks have a darker colour (Giesel, 1970). Nakano *et al.* (2009a) reported a similar phenomenon in the New Zealand lottiid *Notoacmea parviconoidea*. In these cases, the differences of shell colour were caused by difference of food resources (especially algae) (Lindberg & Pearse, 1990), and/or selection by visual predators (Hockey, Bosman & Ryan, 1987; Giesel, 1970; Sorensen & Lindberg, 1991). Physical agents such as desiccation and temperature can exert selection on colour forms of intertidal molluscs (Sokolova & Berger, 2000). In the case of *Cellana nigrolineata*, there are two colour forms, the 'radial form' with a radially striated pattern and the 'concentric form' with a concentrically wavy pattern. This dimorphism might be controlled genetically rather than being a result of ecological and phenotypic responses (Nakano *et al.*, 2010). There is also potential for colour polymorphism to be maintained by a balance between selection and gene flow (e.g. Cain & Sheppard, 1950; Cain & Currey, 1968). Variability of environments may exert different selective pressures within a species with a wide geographic range. Molecular work in connection with ecological work is needed to understand the colour polymorphism of variable patellogastropods.

Correct identification of biological species can stimulate further ecological work, because ecological characteristics can enforce reproductive isolation. Three Japanese species *Lottia kogamogai*, *L. tenuisculpta* and *L. lindbergi* are considered to be isolated by their breeding season, and therefore to be biological species (Sasaki & Okutani, 1994). The Japanese *Patelloida pygmaea*, *P. conulus* and *P. heroldi* are distinguished by differences of microhabitats as described above (Nakano & Ozawa, 2005). In New Zealand, the lottiid *Notoacmea rapida* has distinctive light-avoiding behaviour, the first example of behavioural separation of sibling species in molluscs (Nakano *et al.*, 2009a). Dong & Williams (in press) have examined the variation in

physiological responses to thermal stress in two naecellids in Hong Kong, *Cellana toreuma* and *C. grata*, and have shown that *C. toreuma* is more sensitive to increase of temperature than is *C. grata*. Later, it was shown that *C. toreuma* from Hong Kong and the Japanese mainland are genetically identical and represent a warm-temperate species, whereas *C. grata* in Hong Kong turned out to be a tropical species genetically distinct from supposed conspecifics in Japan (Nakano & Espinosa, 2010; T. Nakano, unpubl.). Taxonomic and ecological work should be undertaken together in the future.

FUTURE STUDIES

As shown in this review, the classification and phylogeny of the Patellogastropoda have been greatly improved by recent advances in molecular phylogeny and more detailed morphological and anatomical studies. However, much more work is needed to obtain a robust phylogeny of the entire order, with increased taxonomic sampling and multi-locus gene analysis. Intertidal taxa have been extensively collected and analysed to date, but the deep-water species (e.g. Lepetidae and Neolepetopsidae) are less studied. New deep-water species continue to be found (Sasaki *et al.*, 2010). At the generic level, *Asteracmea*, *Rhohdopetala* and *Naccula* should be collected for molecular work to elucidate their status and phylogenetic relationships. Brazilian '*Collisella*' are in need of systematic revision.

The most pressing phylogenetic problems involve the perceived incongruence between molecular and morphological data, although these two classes of data are consistent in many cases. The reliability of molecular data can be increased by multigene analyses, whole mitochondrial genomes or nuclear single-copy protein-coding genes. However, it is difficult to know which morphological characters show convergence. If the phylogenetic trees based on morphological and molecular data are too different, combined analyses based on both datasets will produce inaccurate phylogenetic trees. The phylogenetic position of Patellogastropoda among Gastropoda and the relationships within the order remain inconsistent based on morphological and molecular data. At present we recommend evaluation of each dataset separately.

Population-level genetic analysis is required in order to understand phylogeographic and microevolutionary processes, because patellogastropod limpets have limited dispersal ability and therefore show small-scale differentiation. Such analysis can also reveal cryptic species. DNA barcoding is useful for the unequivocal identification of patellogastropod limpets with variable shell morphology. However, barcoding is not so useful for incompletely sampled groups (Meyer & Paulay, 2005). We need comprehensive sampling not only of traditionally recognized species, but also of closely allied species. The development of microsatellite markers would be helpful in this context. A literature search has revealed reports of microsatellite markers for only six species *Patella depressa*, *P. rustica*, *P. ferruginea* (Pérez *et al.*, 2007; Machordom *et al.*, 2010), *Cellana grata* (Ng *et al.*, 2009) and *Lottia gigantea* (Fenberg *et al.*, 2010).

New taxonomic discoveries frequently raise interesting evolutionary questions. Closer collaboration between systematists and ecologists is recommended to enhance the understanding of the evolution and adaptation of patellogastropod limpets.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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