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The limpet form in gastropods: evolution, distribution, and implications for the comparative study of history

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The limpet form – a cap-shaped or slipper-shaped univalved shell – convergently evolved in many gastropod lineages, but questions remain about when, how often, and under which circumstances it originated. Except for some predation-resistant limpets in shallow-water marine environments, limpets are not well adapted to intense competition and predation, leading to the prediction that they originated in refugial habitats where exposure to predators and competitors is low. A survey of fossil and living limpets indicates that the limpet form evolved independently in at least 54 lineages, with particularly frequent origins in early-diverging gastropod clades, as well as in Neritimorpha and Heterobranchia. There are at least 14 origins in freshwater and 10 in the deep sea, with known times ranging from the Cambrian to the Neogene. Shallow-water limpets are most diverse at mid-latitudes; predation-resistant taxa are rare in cold water and absent in freshwater. These patterns contrast with the mainly Late Cretaceous and Caenozoic warm-water origins of features such as the labral tooth, enveloped shell, varices, and burrowing-enhancing sculpture that confer defensive and competitive benefits on molluscs. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2017, 120, 22–37.

KEYWORDS: biogeography – defence – gastropoda – geological history – phylogeny – refuges.

INTRODUCTION

One of the most frequently encountered shell types among univalved molluscs is the limpet, a cap-shaped or slipper-shaped shell with little or no coiled portion and with an aperture whose rim surrounds the entire base (Fig. 1). Although the limpet form could be close to the ancestral condition in molluscs (Morris, 1990; Hesz *et al.*, 2008; Parkhaev, 2008; Vinther *et al.*, 2012), anatomical and other data indicate that all living limpet-like gastropods are derived from spirally coiled ancestors (Bandel, 1982, 2000; Haszprunar, 1988; Warén & Bouchet, 1993, 2001; Ponder & Lindberg, 1997; Lindberg, 2008), and that the transition to the limpet form has occurred repeatedly and independently in many clades (Baker, 1925; Harry, 1964; Lindberg & Ponder, 2001; Kano, Chiba & Kase, 2002; Walther *et al.*, 2006). Despite this general consensus, a comprehensive account of limpet evolution has not previously appeared. Most available accounts are for particular clades, with a strong emphasis on living members. As a result,

general underlying patterns, as well as causal mechanisms and comparisons among limpet clades, have remained largely uninvestigated. In particular, questions remain about when, how often, and under which circumstances the limpet form evolved.

Besides its value as yet another example of convergence to a common form, such an account of limpets takes on additional significance when it is placed in the broader context of other cases of convergence in independent lineages. In molluscs, well-studied cases for comparison with limpets are available for such frequent innovations as the labral tooth, which speeds predation by gastropods on shell-bearing prey (Vermeij, 2001); shell envelopment and internalization, which is associated with faster locomotion and chemical defence (Vermeij, 2005); the siphonal canal in gastropods, which is associated with olfactory sensation at a distance (Vermeij, 2007); varices, which enhance armour against shell-crushing in gastropods (N. Webster & G. J. Vermeij, unpubl. data); photosymbiosis in bivalves, which enables faster growth and greater competitive ability (Vermeij, 2013a); burrowing-enhancing sculpture in bivalves (Checa & Jiménez-Jiménez, 2003); rigid calcareous opercula in

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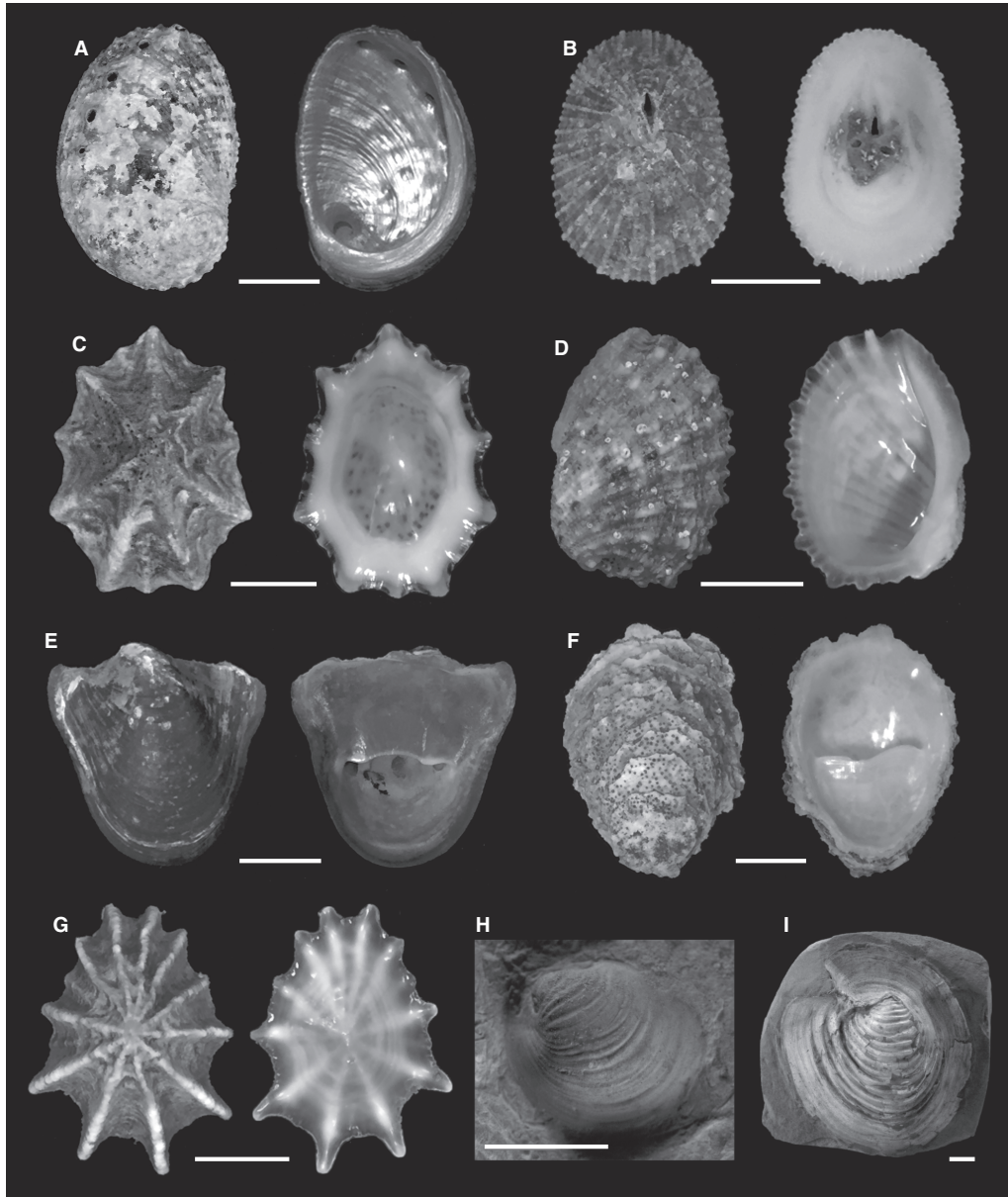


Figure 1 . A, external and internal views of *Haliotis varia* (Linnaeus, 1758) (Haliotidae), Kinabohutan, north-east Sulawesi, Indonesia; Vermeij collection. B, external and internal views of *Cranopsis* Dall, 1914 (Fissurellidae), off Iceberg Point, Lopez Island, Washington State, USA; Vermeij collection. C, external and internal views of *Patelloidea saccharina* (Linnaeus, 1758) (Lottiidae), Ngerdis Cove, Arakabesan, Palau; Vermeij collection. Note the strong radial ribs that extend beyond the shell margin. D, external and internal views of *Concholepas concholepas* (Lamarck, 1801) (Muri-cidae: Ralpaninaek), Montemar, Chile; Vermeij collection. E, external and internal views of *Theodoxus vespertinus* (Sowerby, 1849) (Neritidae), near the mouth of Wainiha River, Kauai, Hawaii; Vermeij collection. Note the internal septum and the wing-like sides of the limpet-like shell. F, external and internal views of *Crepidula lessonii* (Broderip, 1834) (Calyptreaeidae), Playa Venado, Pacific coast of Panama; Vermeij collection. Note the internal septum, and the external sculpture of imbricated lamellae. G, external and internal views of *Siphonaria gigas* (Sowerby, 1825) (Siphonariidae), Playa de Panamá, Pacific coast of Costa Rica; Vermeij collection. Note the convergence with *Patelloidea saccharina*. H, external view of *Delminiella soklici* Kochansky-Devidé & Slišković, 1972, Vučipolje near Tomislavgrad, Bosnia and Herzegovina, late early Miocene. Holotype, stored in the National Museum of Bosnia and Herzegovina, Sarajevo (MG3631). Figured from Harzhauser *et al.* (2016), fig. 3A). Photograph provided by T. A. Neubauer. I, *Valenciennius reussi* (Neumayr in Neumayr & Paul, 1875), Tirol (=Königsgnad), Romania, late Miocene (Pannonian). Specimen stored in the Natural History Museum Vienna (NHMW 1900/0009/0005). Photograph provided by T. A. Neubauer.

molluscs, which deter predators from entering the aperture (Checa & Jiménez-Jiménez, 1998; Williams, Karube & Ozawa, 2008; Vermeij, 2015); overlapping shell margins, enabling bivalves to resist predatory attacks (Vermeij, 1987, 2013b); and cementation and exceptional shell thickness in oyster-like bivalves (Vermeij, 1987, 2014).

Limpets provide an interesting contrast to these other convergences. Although some limpets achieve effective protection by combining a stiff shell with tenacious clamping, most molluscs with limpet-shaped shells are highly vulnerable to attack once they are dislodged from their substrate. As a consequence, most live in situations that can be described as refuges from predation or as ancient environments in which intense predation has not yet evolved. Convergence to the limpet form should therefore be observed in a very wide variety of habitat types and at many different times in the Phanerozoic, in contrast to the more concentrated distribution of the other convergences during the Mesozoic and Cenozoic eras. To test these predictions, it is important to choose phenotypes that can be recognized in fossil taxa, and to study clades that have a good fossil record and whose phylogeny has been worked out in some detail. Molluscs are ideal for these purposes.

Here, I present a synthesis of historical, phylogenetic, ecological, biogeographical, and functional data on limpets. I ask how often and in which major clades the limpet form evolved, under which circumstances the limpet shape might be favoured (or might not be a disadvantage), and how the distribution of limpets in space and time compared with that of other cases of convergence in form.

MATERIAL AND METHODS

I compiled a list of fossil and living limpet-like gastropods by conducting a thorough search of the taxonomic literature. No database of taxa is adequate for this purpose. Instead, I relied on my analysis of thousands of papers on gastropod taxonomy and systematics. The relevant taxa were placed in a phylogenetic context on the basis of molecular phylogenetic studies and, in the case of Palaeozoic fossils, phylogenetic inferences from morphological evidence (Ponder & Lindberg, 1997; Wagner, 1999).

In order to document the geographical distribution of living limpets, I analysed accounts of regional molluscan faunas in the literature. In the case of several tropical faunas for which no adequate published account is available, I relied on my research collection of shallow-water gastropods.

To evaluate the incidence of predation-resistant limpet species in living faunas, I surveyed all limpet-

like gastropods from each of several well-sampled shallow-water assemblages represented in my research collection. Traits conferring resistance are a distinctly thickened shell margin, high radial ribs projecting beyond the shell edge, and spines on the shell surface.

In this paper I concentrate on limpets in the phylum Mollusca, and do not consider convergence to the limpet form in other phyla. It is worth noting, however, that the limpet form has been approached in balanomorph barnacles, craniid inarticulate brachiopods, anomiid bivalves, echinoid sea urchins, and planktonic chondrophorine cnidarians. In fact, several Early Palaeozoic shells, originally described as monoplacophorans or gastropods, have justifiably been reinterpreted as the plates of chondrophorines (Yochelson & Stanley, 1981; Yochelson & Gil, 1984). Within Mollusca, I have not considered internal plate-like or limpet-like shells such as those of aplysiids, *Sinum* (Naticidae), and terrestrial semislugs of the family Testacellidae. I also have not considered polyplacophorans (chitons), which are limpet-like molluscs with multiple shell plates.

LIMITS OF THE LIMPET FORM

Cap-shaped and slipper-shaped shells are, for the most part, unambiguously recognizable, but a few taxa that I include among limpets deserve comment. Most of these fall into the group of slipper-shaped (or crepiduliform) limpets, which have a plate-like or cup-shaped septum instead of a spirally wound columella. Members of crepiduliform groups, such as Calyptraeidae, Phenacolepadidae, *Septaria* (Neritidae), and *Galeropsis* (Muricidae), either lack an operculum or have a nonfunctional one, and are therefore undoubtedly limpets. *Concholepas* (Muricidae) has a small operculum that does not close the aperture fully and is therefore also not effective in defence. The only taxon that I consider a limpet with a fully functional operculum is the crepiduliform *Theodoxus vespertinus* (Sowerby, 1849), a species endemic to streams in the Hawaiian Islands. Its wing-like extensions of the apertural rim on either side of the apical region make this species more limpet-like than other freshwater neritids assigned to *Neritina*, *Theodoxus*, *Clypeolum*, and related genera with coiled shells.

TAXONOMIC ASSIGNMENTS AND TIMES OF ORIGIN

Three taxa of limpets are of uncertain affinity. The Palaeozoic Pragoscutulidae are caenogastropods on the basis of the protoconch (Frýda, 1998b), but further

taxonomic refinement is impossible at this time. The placement of the Early Devonian *Ladamarekiidae* also remains uncertain (Fryda, 1998a); I tentatively consider them as gastropods here. The fossil freshwater North American *Payettiidae* superficially resemble the neritid *Septaria*, and therefore might be assigned to the Neritimorpha (Taylor, 1966), but a relationship with the Latiidae, a Neogene to Recent clade of freshwater pulmonate limpets from New Zealand that is probably derived from the southern-hemisphere Eocene to Recent family *Chiliniidae*, seems more likely (Taylor & Sohl, 1962). I tentatively follow Taylor & Sohl (1962) in this assignment, but consider *Payettia* (the only genus in the family) a separate instance of transition to the limpet form because of the temporal and geographical distance between *Payettia* and *Latia*.

Two Palaeozoic clades that have been considered as gastropods by some workers are here considered to belong to the Monoplacophora. These are the Patelliconidae (see Horný, 2009) and the Ordovician genus *Florapatella* (Lindberg, 2008).

I have treated the Hipponicidae as belonging to the same limpet clade as Calyptraeidae following Bandel & Riedel (1994) and Simone (2002), but this conclusion is not secure. There are also questions about the time of origin of limpets in this clade. Kaim (2004) regarded the Middle Jurassic (Bathonian) genus *Gnaszynium* as an early hipponicid, but there is a very long time gap (to the Late Cretaceous) until the next oldest hipponicids and calyptraeids are recognized (Bandel & Riedel, 1994; Saul & Squires, 2008). In the case of calyptraeids, a highly plausible transition from a coiled ancestor has been recognized in the genus *Lysis* (Saul & Squires, 2008).

There is also uncertainty about the origin of Fissurellidae. This clade (Aktipis, Boehm & Giribet, 2011) is usually considered to have Late Triassic origins (McLean, 1984a; Bandel, 1998), with planispiral bellerophonitids as possible ancestors (McLean, 1984a). Mazaev (1998), however, described the genus *Retshitsella* from the Late Carboniferous of the Moscow Basin as the earliest emarginuline fissurellid. Pending additional discoveries, I regard the Fissurellidae as having a single origin in the Late Triassic, and leave open the possibility that *Retshitsella* is an independent limpet taxon.

Finally, the Patellogastropoda are unambiguously recognized from the Late Triassic onward on the basis of shell microstructure (Lindberg, 2008). However, Mazaev (2015) makes a case for Palaeozoic patellogastropods, and D. R. Lindberg (pers. comm.) believes that this major clade of limpets has origins during the Ordovician. A euomphaloidean ancestor has been suggested for the group (Lindberg & Ponder, 2001; Lindberg, 2008).

FUNCTIONAL ASPECTS

Before placing the evolution of limpets in a phylogenetic context, it is important to review functional aspects of the limpet form. Limpets vary widely in shape and habit, ranging in shell length from 0.92 mm in the Antarctic monoplacophoran, *Micropilina arntzi* (Warén & Hain, 1992), to 350 mm in the tropical eastern Pacific patellid, *Scutellastra mexicana* (Broderip & Sowerby, 1829) (see Powell, 1973), and to 400 mm in the Late Cretaceous (Campanian) *Gigantocapulus giganteus* (Schmidt, 1874) (see Hayami & Kanie, 1980), a species that Beu (2007) tentatively assigns to the Monoplacophora. Depending on the species, limpets can be herbivores, indiscriminate scrapers, parasites, suspension-feeders, predators, and hosts of chemosymbiotic microbes. Species range in habitat from the uppermost reaches of the intertidal zone to a depth of 8595 m (the cocculinid *Macleaniella moskalevi* Leal & Harasewych, 1999) and from freshwater lakes and streams to hydrothermal vents and even the pelagic zone. *Latia* from freshwater streams on North Island, New Zealand, is even bioluminescent, the only freshwater animal known to have this capacity (Ohmiya *et al.*, 2005).

Surprisingly, no limpet is yet known to be either fully terrestrial or to house photosymbiotic microbes; and none lives on mangrove trunks and roots or on the bodies of marine vertebrates. Although limpets are not specialized for life on stranded or floating wood, species of *Septaria* have been recorded occasionally from floating logs (Kano *et al.*, 2013). Several limpets (many Cocculinoidea and the patellogastropod genus *Pectinodonta*) live and feed on sunken wood (Hickman, 1983; Haszprunar, 1987; Warén, 1996; Zbinden *et al.*, 2010).

One of the few unifying characteristics of the limpet form is the inability of the soft parts to withdraw into the shell. An important consequence is that the limpet generally cannot right itself when it is dislodged from the substrate and overturned. This inability carries few risks in cluttered environments, such as boulder fields, because the animal will often be within easy reach of a suitable attachment surface. Likewise, the risk is low in the absence of predators that pry the limpet from the substrate. Impediments to the evolution or maintenance of the limpet form are therefore reduced under these conditions, which should prevail in habitats such as the upper shore (at least if predation by land-based animals, such as birds, is rare), the outer and inner surfaces of shells (Mapstone, Underwood & Creese, 1984; Vermeij *et al.*, 1987), on vegetation, and in many deep-sea environments. Predation-poor environments are also more common in freshwater and may have prevailed during much

of the Palaeozoic and Early Mesozoic eras (Vermeij, 2015).

Benefits of the limpet form have been more difficult to identify than the disadvantages, and are likely to vary according to habitat and feeding type. Relative to coiled gastropods, limpets are structurally compact and offer the potential for a large respiratory surface area (Lindberg & Ponder, 2001). Besides accounting for the high frequency of limpets in the oxygen-poor deep sea (and deep fossil lakes), the large surface area for respiratory exchange is also compatible for suspension-feeding in several limpet clades (e.g. Calyptraeidae), which use the ctenidia for both feeding and respiration (Lindberg & Ponder, 2001). A tendency towards superficial external radial symmetry, which could enhance these functions and enable the snail to receive sensory inputs from all sides, is seen in many suspension-feeding calyptraeids and hipponicids and in some members of the herbivorous Patellogastropoda, Haliotidae, Fissurellidae, and Siphonariidae. For intertidal species, the limpet shape could alleviate the potential conflict between gas exchange and tenacious clamping to the substrate while the limpet is at rest, under attack, or exposed to strong currents and waves.

It has long been thought that the limpet form is associated with high tenacity (Davis & Fleure, 1903). There is no doubt that intertidal and freshwater limpets in many clades adhere much more tenaciously to rocks and to other surfaces than do coiled forms (Miller, 1974; Branch & Marsh, 1978; Grenon & Walker, 1981; Lowell, 1986, 1987; Ellem, Furst & Zimmerman, 2002). Strong tenacity coupled with a tendency to home, leads (in a few patellogastropods) to territoriality (Lindberg, 2007). It is important to note, however, that many limpets live in quiet-water environments and that not all species, not even some intertidal siphonariids, are tenacious clampers. Tenacity is therefore not the only, and in many clades perhaps not the most important, benefit of the limpet form.

Intertidal limpets exposed to predators are adapted to them by visually or perhaps chemically cryptic (Fishlin & Phillips, 1980; Frank, 1982; Mercurio, Palmer & Lowell, 1985; Hockey, Bosman & Ryan, 1987); fleeing from slow sea stars or gastropods (Feder, 1963; Margolin, 1964a; Phillips, 1976; Phillips & Chiarappa, 1980; Phillips & Castori, 1982; Branch, 1979; Abe, 1983; Bros, 1986; Espoz & Castilla, 2000; Mahon *et al.*, 2002); being chemically noxious (Rice, 1985; McQuaid, Cretchley & Rayner, 1999; Pinchuck & Hodgson, 2009); raising the shell and extending the mantle over it (Margolin, 1964b; Branch, 1979); clamping firmly, sometimes in a home depression (Branch, 1981; Cook, 1980; Garrity & Levings, 1983; Kunz & Connor, 1986; Lowell, 1986; Lindberg,

Warheit & Estes, 1987; Hahn & Denny, 1989; Denny, 2000; Cedeño, Voltzow & Fetcher, 1996; Vermeij, 1998a); and resisting by means of a robust shell with thickened margins or with stiffening radial ribs that often project beyond the shell margin (Lowell, 1987). Some limpets are aggressive toward predators and toward limpet-like competitors (Branch, 1979; Lindberg, 2007). Projecting ribs are developed in species that clamp to the substrate and that do not flee from predators. Although Tyler, Leighton, Kowalewski (2014) suggest that such ribs do not protect limpets against predations by crabs, ribs could be effective against fishes and especially birds that must push or hammer limpets loose. Species that escape from slow predators or that live in refuges from predation are either smooth or have fine, closely spaced riblets, and clamp less firmly when at rest (Lowell, 1987).

None of the freshwater limpet taxa has any of these defences. Instead, it has been suggested that a flexible shell margin associated with a rim of periostracum could enable many freshwater limpets to clamp more effectively to hard substrates (Albrecht *et al.*, 2004). Several deep-sea limpets likewise have a shell margin that can conform to the substrate by virtue of a periostracal rim. Except for some species of the hipponicid genus *Pilosabia*, which have a fringe of periostracum extending beyond the shell margin, intertidal limpets have a rigid shell edge and achieve a tight fit either by excavating a home depression or by muscle-enhanced adhesion (see also Grenon & Walker, 1981; Cedeño, Voltzow & Fetcher, 1996).

A possible, but unproven, defence in limpets is a spiny surface. This is a surprisingly rare condition, found only in some members of the calyptraeid genera *Bostrycapulus* and *Crucibulum* in tropical America. Conspicuous nodose sculpture occurs in some fissurelline and hemitomine keyhole limpets (Fissurellidae) and in some species of *Haliotis* (Haliotidae).

Still another unusual type of sculpture found in a few limpets comprises concentric elements that are imbricately oriented, with the sharp edge of each lamella pointing toward the shell base. This form of imbrication, whose function has not been investigated, occurs in hipponicids of the genus *Antisabia*, as well as in a few species of *Crepidula*, including the tropical eastern Pacific *Crepidula lessonii* (Broderip, 1834). Peculiarly, it also characterizes some Early Cambrian helcionelloideans.

PHYLOGENETIC DISTRIBUTION

An analysis of phylogenetic studies indicates that the limpet form has evolved independently from coiled forms at least 54 times, not including the plesiomorphic Monoplacophora (Table 1). Transitions to the

Table 1. Limpet clades and their origins

Clade	Habitat	Time range	References
Patellogastropoda	All	Ordovician to Recent	Nakano & Sasaki (2011); Mazaev (2015)
Vetigastropoda			
Haliotidae and <i>Temnotrochus</i>	Shallow marine	Late Triassic to Recent	Bandel & Kiel (2003); Groves & Alderson (2008)
Trochidae, Stomatellinae	Shallow marine	Recent	Hickman & McLean (1990)
Trochidae, Fossarininae	Shallow marine	Recent	Williams <i>et al.</i> (2010)
Chilodontidae, <i>Granata</i>	Shallow marine	Recent	Herbert (2012)
Neomphaloidea, Neomphalidae	Deep sea	Recent	Lindberg & Ponder (2001)
Neomphaloidea, Peltospiridae	Deep sea	Recent	Lindberg & Ponder (2001)
Cocculinoidea	Deep sea	Albian to Recent	Geiger & Thacker (2006); Kiel (2006)
Lepetelloidea	Deep sea	Late Oligocene to Recent	Haszprunar (1988); Schnetler & Beyer (1990)
Temnocrinidae	Deep sea	Recent	Aktipis <i>et al.</i> (2011)
Scissurellidae, Scissurellinae, <i>Incisura</i>	Marine	Recent	Geiger (2003); Geiger & Thacker (2006)
Larochaeidae	Deep sea	Early Eocene to Recent	Lozouet (1998)
Depressizonidae	Deep sea	Recent	Geiger (2003); Geiger & Thacker (2006)
Sutilizonidae	Deep sea	Late Triassic to Recent	Kiel <i>et al.</i> (2010)
Fissurellidae	Marine	Late Carboniferous? Late Triassic to Recent	McLean (1984a); Bandel (1998)
Lepetodriloidae, Symmetrocapulidae	Deep sea, marine	Late Carboniferous? Late Jurassic to Recent	Squires (1989); Mazaev (1998)
Bellerophonitoidea, Bellerophonitidae, Pterothecinae		Middle Ordovician to Late Silurian	Clarkson, Harper & Peel (1995)
Clisospiradae, Progalerinae	Marine	Middle Devonian	Knight <i>et al.</i> (1960)
Neritimorpha			
Phenacolepadidae	Marine	Middle Eocene to Recent	Beck (1989); Landau & Janssen (2015)
Neritilidae, <i>Platynertia</i>	Freshwater	Recent	Kano & Kase (2003)
Pileolidae	Marine	Late Jurassic to Turonian	Bandel (2008)
Orthonychiidae	Marine, parasitic	Silurian to Late Permian	Bandel & Frýda (1999); Bandel (2000)
Pseudorthonychiidae	Marine	Late Triassic	Bandel & Frýda (1999); Bandel (2000)
Neritidae, <i>Septaria</i> and related taxa	Freshwater	Middle Tertiary to Recent	Haynes (2001); Bandel (2008)
Neritidae, <i>Neritonyx</i>	Freshwater	Pliocene	Knight <i>et al.</i> (1960)
Neritidae, <i>Theodoxus verspertinus</i>	Freshwater	Recent	Kay (1979)
Caenogastropoda			
Trichotropidae, <i>Trichamathina</i>	Marine	Middle Miocene to Recent	Habe (1962); Gladenkov & Sinel'nikova (1990)
Capulidae		Campanian to Recent	Warén & Bouchet (1991); Saul & Squires (2008)
Calyptraeoidea, Calyptraeidae and Hipponicidae	Marine	Barthonian? Late Cretaceous to Recent	Bandel & Riedel (1994); Saul & Squires (2008)
Vanikoroidea, Eulimidae, <i>Thyca</i>	Marine parasitic	Capanian to Recent	Warén (1984); Neumann & Wisshak (2009)
Heteropoda, Carinariidae, <i>Carinaria</i> , <i>Brunonia</i>	Planktonic	Early Cretaceous to Recent	Kase (1988)
Ladamarekiidae	Marine	Devonian	Frýda (1998a)

Table 1. Continued

Clade	Habitat	Time range	References
Pragoscutulidae	Marine	Early Devonian to Early Carboniferous	Frýda (1998b); Cook, Nützel & Frýda (2008)
Lamellarioidea, Velutinidae, <i>Capulacmaea</i>	Marine	Early Miocene to Recent	Golikov & Gultbin (1990); Gladenkov & Sinel'nikova (1990)
Muricidae, <i>Concholepas</i>	Marine	Early Miocene to Recent	DeVries, 1995, 2000;
Muricidae, <i>Edithais</i>	Marine	Early to Late Miocene	Vermeij (1998b)
Muricidae, <i>Galeropsis</i>	Marine parasitic	Early Miocene to Recent	Lozouet & Le Renard (1998)
Panpulmonata			
Ellobiidae, Trimusculinae	Marine	Recent	Morton (1955); Romero <i>et al.</i> (2016)
Siphonariidae	Marine	Early Cretaceous to Recent	Kaim (2004); Holznagel, Colgan & Lydeard (2010); Medina <i>et al.</i> (2011); Kocot, Halanych & Krug (2013)
Amathinidae, <i>Amathina</i> , <i>Damesia</i>	Marine	Late Cretaceous to Recent	Ponder (1987); Dockery (1993); Kiel & Krüger (2006)
Amathinidae, <i>Cyclothea</i>	Marine	Recent	Ponder (1987)
Hygrophila			
Lymnaeidae, <i>Delminiella</i>	Freshwater	Early to Late Miocene	Harzhauser <i>et al.</i> (2016)
Lymnaeidae, Valencienniinae	Freshwater	Late Miocene to Pliocene	Marinescu (1969); Harzhauser <i>et al.</i> (2016)
Lymnaeidae, <i>Lanx</i>	Freshwater	Early Cretaceous to Recent	Taylor (1966); Gray (1988)
Latiidae, <i>Latia</i>	Freshwater	Early Miocene to Recent	Marshall (2011)
Planorbidae, Ancyliinae	Freshwater	?	Albrecht, Kuhn & Streit (2007)
Planorbidae, <i>Burnupia</i>	Freshwater	Recent	Albrecht <i>et al.</i> (2004, 2007)
Planorbidae, <i>Protancylus</i>	Freshwater	Recent	Albrecht & Glaubrecht (2006)
Acroloxidae	Freshwater	Palaeocene to Recent	Gray (1988); Mordan & Wade (2008)
Payettiidae	Freshwater	Palaeocene to Recent	Taylor (1966); Gray (1988)
Opisthobranchia			
Cephalaspidea, Haminoeidae, <i>Smaragdinella</i>	Marine	Recent	Rudman, 1972;
Notaspidea, Umbraculidae	Marine	Early Eocene to Recent	Willan (1987); Valdés & Lozouet (2000); Zapata <i>et al.</i> (2014)
Notaspidea, Tylodiniidae	Marine	Early Miocene to Recent	Willan (1987); Valdés & Lozouet (2000)

limpet form have been particularly numerous in early-diverging clades, including Vetigastropoda (17 cases), Neritimorpha (eight cases), and basal pulmonates including the clade Hygrophila (14 cases). By contrast, the large siphonate clade of caenogastropods contains only three cases, all in Muricidae (Vermeij, 1998b; Claremont *et al.*, 2013). No limpets at all are known in the large clades Littorinoidea, Rissooidea + Truncatelloidea, Janthinoidea, Cerithioidea, Triphoroidea, Stromboidea, Buccinoidea, Conoidea, and Stylommatophora. The highly clumped phylogenetic distribution of limpets is typical of convergent states generally (Vermeij, 2005, 2007), and

probably reflects structural predispositions that make a transition to the new state more probable.

At least nine clades that have given rise to limpets also contain slug-like species, in which the ancestral shell has been lost. These transitions to a slug-like form involved a limpet-like intermediate stage in Trimusculinae (Tillier & Ponder, 1992), Fisurellidae (McLean, 1984a,b), Umbraculoidea, and Tylodinoidea (Willan, 1987), and perhaps Lamellarioidea, but probably not in Eulimidae, Neritimorpha, and Cephalaspidea. It is striking that none of the freshwater limpet clades (see below) contains slug-like taxa. The same is true of highly diverse marine

limpet clades such as Patellogastropoda, Scissurelloidea, Haliotidae, Trochoidea, Calyptraeidea, and Siphonariidae. Deep-sea clades with limpet-like representatives also do not contain slugs.

Limpets gave rise to secondarily coiled forms in *Trochita* (Calyptraeidae) (Collin & Cipriani, 2003). Envelopment of limpet shells by the mantle or foot evolved from external limpet shells in at least three clades: *Haliotis asinina* Linnaeus, 1758 (Haliotidae), *Stomatella* (Stomatellinae), and several clades within Fissurellidae (McLean, 1984a,b; Vermeij, 2005).

Among the habitats where limpets have repeatedly evolved, freshwater is particularly notable, with at least 14 independent cases. In addition, the predominantly marine Patellogastropoda gave rise to one freshwater genus (*Potamacmaea*) in South Asia (Lindberg, 1990). Judging from current and former distributions of freshwater limpets, transitions to the limpet form from coiled ancestors occurred in flowing as well as in stagnant water. Ancient lakes in Sulawesi (Indonesia) were apparently the site of origin of the planorbid *Protancylus* (Albrecht & Glaubrecht, 2006), whereas the Miocene and Pliocene lakes of south-eastern Europe witnessed the origin of at least three limpet groups (Valencienniinae, Clivunellidae, and Delminiellidae) from coiled pulmonate ancestors (Harzhauser *et al.*, 2016). No *in situ* origins of limpet-like gastropods are known from the Rift Lakes of East Africa or the great Miocene Pebas inland sea in South America. Many acroloxid limpets occur in Lake Baikal as a result of extensive speciation in that lake, but the group as a whole is widespread in the Old World and probably did not originate in Lake Baikal or in other ancient lakes in Europe and Asia (Shirokaya, 2007; Shirokaya *et al.*, 2012; Stelbrink *et al.*, 2015).

The high frequency of transition from a coiled ancestor to a limpet-like descendant in freshwater contrasts dramatically with the lack of transition in freshwater gastropods, from shell-bearing ancestors to slug-like forms. Slug-like freshwater acochlidioideans are derived from marine slug-like ancestors (Schrödl & Neusser, 2010) and therefore do not violate this generalization. The situation on land is precisely reversed: numerous clades evolved slug-like species from shell-bearing ancestors (Runham & Hunter, 1970; Hausdorf, 2001), but there are no terrestrial limpets.

The absence of terrestrial limpets is puzzling in view of the high diversity of limpets in the intertidal zone, where patellogastropods, siphonariids, and trimusculines are well represented, even at the highest reaches of marine influence. Three or four limpet clades – Siphonariidae, Trimusculinae, Smaragdina (Haminoeidae), and perhaps Fossarininae – probably originated in the intertidal zone. None of these clades made the transition to land, whereas at

least two groups of shell-less gastropods (*Aiteng* and the Onchidiidae, the latter resembling domed limpets in form) are known from both the intertidal zone and terrestrial forests (Dayrat, 2010; Kano *et al.*, 2015).

It is notable that, although the clade Neritimorpha has given rise to limpets at least eight times, these limpets do not occur in the intertidal zone, even though many members of this clade (especially those of the genus *Nerita*) have diversified extensively in intertidal habitats (Frey & Vermeij, 2008). Like strictly intertidal littorinids, which also contain no limpets in their ranks, intertidal neritids have followed adaptive pathways emphasizing hermetic closure of the soft parts in the shell against drying and predation (Vermeij, 1973). Among limpet-like neritids, the operculum, which in intertidal species effectively seals the aperture, has become internal and vestigial (Vermeij, 1969; Fretter, 1984; Haynes, 2001).

Deep-sea and dysoxic shallow-water marine environments, including hydrothermal vents and cold seeps, have been sites of origin of the limpet form in at least 10 clades (Table 1), with additional colonization of these habitats by members of the Monoplacophora, Patellogastropoda, and Fissurellidae. Some fossil freshwater limpets, especially members of the Valencienniinae in the family Lymnaeidae, characterize dysoxic environments in lakes (Harzhauser *et al.*, 2016).

Members of at least six clades are, or were, parasitic limpets: Capulidae on various hosts (Matsukuma, 1978; Schiaparelli, Cattaneo-Vietti & Chiantore, 2000); Platyceratoidea in crinoids (Bowsher, 1955); *Thyca* in the Eulimidae on echinoderms (Elder, 1979; Warén, 1980; Bouillon & Jangoux, 1984; Neumann & Wisshak, 2009); two clades within Amathinidae on molluscs (Ponder, 1987); and *Galeropsis* (Muricidae: Coralliophilinae) on corals (Lozouet & Le Renard, 1998). Commensals living on the shells of molluscs and hermit crabs occur in five clades (Patellogastropoda, Capulidae, Calyptraeidae, Hipponicidae, and some freshwater *Protancylus*) (Vermeij *et al.*, 1987; Vermeij, 1989, 1998a). Some patellogastropods and siphonariids are found on seagrasses and large marine algae. These habitats function as refuges from predation for these limpets relative to adjacent open rock surfaces (Mapstone *et al.*, 1984; Vermeij, 1987; Vermeij *et al.*, 1987).

GEOGRAPHICAL DISTRIBUTION

Within the shallow-water marine realm, substantial regional differences exist in the proportion of local faunas comprised by limpets (Table 2). Limpets make up 40% or more of the faunas of central and southern Chile, 10–25% of faunas in the North

Table 2. Incidence of limpets in Recent marine faunas

Fauna	Location	Number of gastropods	Number of limpets	Percentage	Source
Polar	East Greenland	84	4	4.8	Thorson (1944)
	Arctic Canada	105	5	4.8	Macpherson (1971)
	Kerguelen	139	6	4.3	Cantera & Arnaud, 1984;
Cool-temperate	Southern Chile	30	12	40.0	Reid & Osorio (2000)
	Norway	327	17	5.2	Höisaeter (1986)
	Northern New England	17	4	24.0	Vermeij collection
	Washington State	238	38	16.9	Kozloff (1987)
	Akkeshi Bay, Japan	74	8	10.8	Habe (1958)
Warm-temperate	Central Chile	58	27	47.0	Aldea & Valdovinos (2005)
	Algeciras, Spain	277	15	5.4	van Aartsen, Menkhorst & Gittenberger (1984)
Tropics	New Jersey	22	3	14.0	Vermeij collection
	Sudan	228	9	4.0	Taylor & Reid (1984)
	Western Florida	68	6	8.8	Vermeij collection
	Jamaica	121	16	13.2	Vermeij collection
	Western Panama	240	29	12.0	Vermeij collection
	Palau	300	12	4.0	Vermeij collection
	Guam	482	20	4.2	Vermeij collection
	Hawaiian Islands	800	26	3.0	Kay (1979)
	Easter Island	106	12	11.2	Rehder (1980)
	Enewetak	883	32	3.6	Kay & Johnson (1987)
Vents and seeps	Clipperton	207	14	6.7	Kaiser (2007)
	Japan	39	16	41%	Sasaki, Okutani & Fujikura (2005)

Pacific, and 5–24% of faunas in the North Atlantic. Within the tropics, western Atlantic, and eastern Pacific, the percentages of faunas (9–13%) are all higher than those in the inner Indo-West Pacific (3.0–4.2%), with slightly higher values (6.7% and 11.2%) for the outlying Clipperton and Easter Island, respectively. Polar and subpolar faunas support a very low proportion of limpets (4.3–4.8%). These patterns generally support earlier work by Knox (1963), who observed that limpets reach maximal diversity along temperate shores in Australasia; and my observation (Vermeij, 1978) that, whereas limpets (especially fissurellids) are prominent on tropical Atlantic and eastern Pacific shores, they are scarce or absent in much of the Indo-West Pacific.

As would be expected from the fact that most limpet species live in refuges from predation, limpets with predation-resistant morphologies (e.g. conspicuously thickened shell margin, and prominent projecting radial ribs), constitute a minority of shallow-water limpet faunas (Table 3).

The incidences are lowest in cold-temperate faunas (0–20%) and somewhat higher in the warm-temperate zones (30–39%) and tropics (24–38%). Limpets with excavated home depressions are restricted to

warm-temperate and tropical species in the Patellogastropoda, Hipponicidae, Calyptraeidae, and Siphonariidae.

GENERAL DISCUSSION

The pattern of evolution and distribution of limpet-like gastropods contrasts strongly with that of gastropods whose shells converge on morphologies conferring high predation resistance, rapid locomotion, and more effective subjugation of prey. Features including varices, a labral tooth, an enveloped shell, and sculpture that enhances burrowing in sand are overwhelmingly tropical and warm-temperate in distribution and originated mainly during or after the Late Cretaceous (Vermeij, 2001, 2005, 2015; Checa & Jiménez-Jiménez, 2003). Long-distance chemoreception, as indicated by the presence of a siphonal canal, is spatially and temporally more widespread (Vermeij, 2007), as are molluscan photosymbioses (Vermeij, 2013a), calcified opercula (Williams *et al.*, 2008; Vermeij, 2015), and cementation and thick shells in oyster-like bivalves (Vermeij, 2014). Limpets, however, are far more widely distributed and their origins are temporally more

Table 3. Incidence of predation-resistant limpets in Recent marine limpet assemblages based on the Vermeij collection

Fauna	Location	Number of gastropods	Number of limpets	Percentage
Cold-temperate	Aleutians	16	3	19.0
	Northern New England	5	0	0.0
	Washington State	15	3	20.0
Warm-temperate	Central California	20	6	30.0
	South-Central Chile	18	7	39.0
Tropics	Jamaica	16	6	38.0
	Western Panama	29	7	24.0
	Palau	13	4	31.0
	Guam	20	5	25.0

spread out than any other shell types that have evolved repeatedly.

I attribute this difference to the refugial status of the habitats where limpets are most successful and where many clades made the transition to the limpet form. Predation-resistant limpets, which conform in time and space to other shell types associated with high performance against predators during the escape and resistance phases of attack, appear to be phylogenetically derived relative to more vulnerable morphologies, as inferred from analyses of Fissurelloidea (Aktipis *et al.*, 2011) and Siphonariidae (Dayrat, Goulding & White, 2014). Spiny calyptraeids and depression-excavating, radially strongly ribbed hipponicids of the genus *Sabia* originated in the Early Miocene (Vermeij, 1998a), well after the Cretaceous origins of these limpet clades.

TIMES OF ORIGIN

Transitions to the limpet form have occurred throughout the Phanerozoic from the Early Cambrian to the Neogene (Table 1). Considering only those transitions for which there is fossil evidence, limpets arose three times in the Early Palaeozoic, six times in the Middle and Late Palaeozoic, five or six times in the pre-Cretaceous Mesozoic, seven or eight times during the Cretaceous, and 21 times during the Caenozoic. Although these raw numbers show an increase in the number of origins over time, so does molluscan diversity overall. It is therefore not obvious that limpet origins have risen as a proportion of standing diversity over time.

The fact that 14 or 15 origins predate the Cretaceous (32–36% of the 42–44 known times of origin) indicates that, by contrast to convergent traits associated with adaptation to predators, limpets arose over a very wide time interval. For example, shell envelopment originated just twice before the Cretaceous, out of approximately 50 independent cases (4.0%) (Vermeij, 2005). The labral tooth evolved

approximately 60 times, all from the Late Cretaceous onward (Vermeij, 2001). The same temporal concentration is seen in burrowing-enhancing sculpture in bivalves, which evolved once in the Cretaceous and several times during the Caenozoic (Checa & Jiménez-Jiménez, 2003). The siphonal canal, which in gastropods is associated with long-distance chemoreception, is the only well-studied innovation that evolved predominantly before the Cretaceous (22 of 23 cases; see Vermeij, 2007). In the case of molluscan photosymbioses, nine of 17 cases in shell-bearing groups (nine of 17 origins, 53%) occurred before the Cretaceous (Vermeij, 2013a). Cementation evolved in several brachiopod and bivalve clades during the Palaeozoic and Early Mesozoic, but exceptionally thick oyster-like bivalves have a Cretaceous to Recent history (Vermeij, 2014). These data thus indicate that traits associated with passivity evolved convergently throughout the Phanerozoic, whereas those denoting greater activity have a more recent record of multiple independent origins.

CONCLUSION

The study of evolutionary convergence, as exemplified in this paper by limpets, offers an approach to what might be called comparative history. Although history is often pejoratively portrayed as ‘one damn thing after another’, different actors and relationships at different times and in different places follow independent pathways, which can be compared and analysed for such phenomena as historical directionality, contingency (the effect of initial conditions and the particulars of time and place), and dynamics (the rates at which processes and events occur). Such an approach is essential for uncovering general properties of historical narratives, a major goal of palaeobiology, evolutionary biology, and the study of human history. A comparative account demands knowledge of the present, which in the case of organisms requires experiments and observations about how living things

work and interact. It cannot simply be gleaned from names of taxa, phylogenies of clades, and distributions alone. Although obviously important, these properties mean little in the absence of function. History, whether human or in the more general realm of life, is fundamentally about relationships and interactions, not about entities in isolation.

Approaches like the one taken here can be applied profitably to other traits and features in other groups for which a good fossil record and a detailed understanding of historical sequences (including phylogenies) exist. Only by exploiting the relative independence of events and actors can we transform the study of history as particular narrative to a real science of comparative history.

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