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Shell features associated with the sand-burying habit in gastropods

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ABSTRACT

The relationship between shell form and mode of life in gastropods is important to the interpretation of fossils, but has been little explored owing, in part, to the great diversity of gastropod shells. Infaunal gastropods that actively bury in sand must conform to the demands of moving efficiently and noiselessly through a dense granular medium, but which shell characters reflect these demands and how infaunal gastropods differ from surface-dwelling (epifaunal) species remain incompletely answered questions. Here, I survey infaunal and epifaunal Indo-West Pacific members of four families (Cerithiidae, Mitridae, Costellariidae and Conidae) and consider more broadly the distribution of shell traits that confer streamlining and other potential benefits to infaunal species. Sand-burying cerithiids, mitrids and costellariids (but not conids) have on average slenderer shells than their epifaunal counterparts. The only shell features unique to sand-burying gastropods are terraced axial ribs, spiral cords or sutures, in each of which the trailing edge is steeper than the leading edge in the direction of movement; but not all infaunal gastropods have such features. An angular profile, wide umbilicus, high-relief shell sculpture and limpet-like shell is exclusive to surface-dwelling species. Specializations to the infaunal habit are more common and better expressed in the Indo-West Pacific than in tropical America.

INTRODUCTION

An enduring question in the study of fossils is how ancient organisms lived. The only way to answer this question is to establish a causal connection between form and function in living counterparts. This approach has proved to be highly successful in many groups of plants and animals. In the case of molluscs, it has been especially effective for bivalves (Stanley, 1970), where a distinction among deep-burrowers, shallow burrowers, semi-infaunal species and surface-dwelling epifauna is straightforward and mostly unambiguous.

Perhaps because of their very great diversity of form, gastropods have been more resistant to the establishment of simple relationships between form and mode of life. Part of this resistance stems from the fact that surprisingly few details have been published about how and where gastropods live. Far more is known about the taxonomy and phylogeny of gastropods than about how these animals make a living. In particular, although some work exists characterizing gastropods that bury in sand, direct comparisons between actively burying and surface-dwelling species have not been made.

Effective burial in a dense granular medium like sand requires either a powerful engine—a foot, proboscis, head-shield or other muscular propulsive organ capable of moving or loosening sand—or a streamlined body that reduces frictional and pressure drag, limits back-slippage during digging steps, prevents entrainment of sand particles and limits vibrational noise that potential enemies might detect. Streamlining is especially important for species with a small propulsive organ. Compared with epifaunal species moving on a firm surface, sand-burying species should therefore have narrower shells (a smaller diameter in the direction of burial) and shell features that facilitate movement of sand particles from front to back with minimal disturbance. Shells should be smooth or, if sculpture is present, these sculptural elements should be low in relief. To prevent back-slippage, sculptural features such as spiral cords, collabral ribs and sutures between adjoining whorls should be terraced or ratcheted, with the leading edges less steep than the trailing edges. Shell flanks should be straight or gently rounded without angulations and the spire, if high, should taper gently with the sutures flush or nearly so with the whorl sides. An umbilicus in the direction of digging should be absent or closed with a callus deposit. For burrowers with a siphonal canal, continued contact by the animal with the water above for detecting food and enemies can be maintained with a dorsally or obliquely deflected siphonal canal and often in addition with a distinct adapical (anal) notch or channel. The functions of these attributes in sand-burying gastropods have been documented by measurements of burrowing performance and by observing the method of burying in various species (Trueman, 1968; Signor, 1982a, b, c, 1983, 1993; Vermeij & Zipser, 1986; Savazzi, 1988, 1989, 1994; Dudley & Vermeij, 1989; Trueman & Brown, 1989, 1992a, b; Savazzi & Pan, 1994; Sälgeback & Savazzi, 2006; Vanagt, Vincx & Degraer, 2008).

Not all sand-burying gastropods conform to these expectations in all respects. In order to establish criteria by which the sand-burying habit can be inferred in fossil gastropods, it is therefore important to document the taxonomic and geographic distribution of burying-related traits in gastropods for which the mode of life is known and to compare these traits with those of related surface-dwelling taxa.

In this paper, I compare shapes and external features of shells in sand-burying and surface-dwelling gastropods in the living tropical Indo-West Pacific (IWP) fauna in each of four families. In addition, I examine the distribution of burying-related traits in other families, and document differences in expression of these traits in the IWP and tropical America.

MATERIAL AND METHODS

In order to compare the shell traits of sand-burying and related epifaunal species, I measured with calipers the maximum height (H) and maximum diameter (D) of shells for 660 specimens representing 161 shallow-water IWP species in my research collection. These belong to four families: Cerithiidae, Costellariidae, Mitridae and Conidae. Shell slenderness, expressed as mean H/D for each species, was used as the basis for comparing all sand-burying and all epifaunal species by applying a simple *t*-test. For each species, I also noted whether sculpture is ratcheted and sutures are terraced. Geographical comparisons between the IWP and tropical America were made for families or superfamilies with sufficient numbers of sand-burying species in each region: Strombidae, Conidae, Nassariidae, Olivoidea and Terebridae.

All specimens studied here are in my research collection and all observations of mode of life were made by me in the course of collecting. IWP specimens were obtained at wading depth from 1968 to 1993 in Guam, Palau, Majuro (Marshall Islands), Fiji, Hawaii, French Polynesia, Papua New Guinea, eastern Indonesia, the southern Philippines, Kenya, northern Madagascar and the northern Red Sea. Measured specimens were all adult as indicated by unique apertural modifications associated with determinate growth.

Comparisons with tropical America were based on specimens I observed and collected on the Pacific coasts of Panama, Costa Rica and Mexico, as well as in the western Atlantic in Jamaica, the Netherlands Antilles, Venezuela and Florida. Other more general observations are based on additional material in my research collection.

I have chosen not to apply phylogenetic contrasts in these comparisons. This method purportedly controls for history and clade membership as explanations for morphological similarities, but it suffers from the unwarranted assumption that clades are inherently constrained by historical legacies (Vermeij, 2015). In any case, the choice of phylogenetically independent clades with sand-burying species obviates the necessity of resorting to this commonplace but questionable practice.

RESULTS

As expected, sand-burying species tend to have slenderer shells than their surface-dwelling counterparts. This pattern is highly significant for cerithiids, mitrids and costellariids, but not for members of the Conidae (Table 1). Moreover, terraced sculpture and sutures are restricted to sand-burying species. I consider the characteristics of infaunal species for each family below.

Cerithiidae

Most sand-dwelling cerithiids belong to *Rhinoclavis* and related genera (or subgenera) such as *Clavocerithium*, *Longicerithium*, *Ochetoclava* and *Proclava* (Houbrick, 1978). The sand-burying habit seems to have been independently acquired in the IWP *Cerithium salebrosum* Sowerby, 1855 and the tropical eastern Pacific *C. nicaraguense* Pilsbry & Lowe, 1932. Surface-dwelling species belong to many genera, including *Cerithium s. l.*, *Clypeomorus*, *Gourmya*, *Liocerithium* and *Thericium*.

Table 1. Height:length ratios of surface-dwelling and sand-burying gastropods from the Indo-West Pacific.

Family	Surface-dwelling (number of species, mean height:diameter ± SD)	Sand-burying (number of species, mean height:diameter ± SD)	Significance of difference (*t* and *P* values)
Cerithiidae	24, 2.21 ± 0.35	10, 3.23 ± 0.35	9.70, 0.001
Costellariidae	12, 1.87 ± 0.34	33, 2.69 ± 0.38	6.00, 0.01
Mitridae	21, 2.07 ± 0.33	20, 2.56 ± 0.36	4.45, 0.01
Conidae	14, 1.73 ± 0.14	27, 1.82 ± 0.26	1.50, 0.05

The least elongate cerithiids with H/D less than 2.00 are high-shore or open-rock species: *Clypeomorus isselii* (Pagenstecher, 1877) from East Africa and the Red Sea (1.94), *Clypeomorus irrorata* (Gould, 1849) from Singapore (1.83), *Cerithium caeruleum* Sowerby, 1855 from Kenya and the Red Sea (1.90) and *Cerithium mutatum* Sowerby, 1834 from the Mariana Islands and Moorea (1.89).

The five other species of *Clypeomorus*, found on intertidal surfaces, have H/D values of 2.12 or lower: *C. bifasciata* (Sowerby, 1855) (2.07), *C. pellucida* (Hombron & Jacquinot, 1854) on mangroves (2.12), *C. nympha* Houbrick, 1985 (2.03), *C. purpurastoma* Houbrick, 1985 from Madagascar (2.02) and *C. petrosa* (Wood, 1828) (2.09). Coarsely sculptured surface-dwellers with tubercles, nodes and prominent varices range in H/D from 1.89 (*Cerithium mutatum*) to 2.32 (*Cerithium munitum* Sowerby, 1855) and include *Cerithium echinatum* Lamarck, 1822 (2.04), *Cerithium columna* Sowerby, 1855 (2.14), *Cerithium caeruleum* (1.90), *Cerithium nodulosum* Bruguière, 1789 (2.16) and *Cerithium dialeucum* Philippi, 1849 (2.08).

Among surface-dwelling *Cerithium* species, the most slender-shelled live subtidally beneath stones (*C. interstriatum* Sowerby, 1855, H/D = 3.14), on mud (*C. coralium* Kiener, 1843, H/D = 2.45), or on the blades of seagrasses (*C. rostratum* Sowerby, 1855, H/D = 2.91). Another slender species, *C. nesioticum* Pilsbry & Vanatta, 1906 (H/D = 2.81), lives on algae and sometimes also in sand, but it is a slow burrower (Vermeij & Zipser, 1986). Among sand-buriers, the stockiest species live either in small sand pockets on reefs (*Rhinoclavis sinensis* (Gmelin, 1791), H/D 2.50) or in very coarse sand (*Pseudovertagus aluco* (Linnaeus, 1758), H/D = 2.82). Very slender species, such as *R. fasciata* (Bruguière, 1792) (H/D = 3.68) and *R.* (*Proclava*) *sordidula* (Gould, 1849) (H/D = 3.60), are found in extensive areas of fine sand or muddy sand.

All cerithiids have a siphonal canal that is orientated dorsally and to the left. In sand-burying species, the canal extends to or above the level of the upper surface of the last whorl, enabling the animal to maintain contact with the water above the sediment surface even while the bulk of the shell is buried. The canal in all surface-dwelling cerithiids is much shorter and does not reach the level of the body whorl's upper side (see also Houbrick, 1978).

In contrast to surface-dwelling species, sand-burying cerithiids have one or two columellar folds (see also Houbrick, 1978; Signor & Kat, 1984). *Pseudovertagus aluco*, which can bury in coarse sand, is unusual among burying species in lacking folds. The prohibition against columellar folds in epifaunal species does not hold in other cerithioidean families such as Potamididae.

As expected, all sand-dwelling cerithiids have streamlined shells with well rounded last whorls and a gently tapering spire in which the sutures are essentially flush with the whorl flanks. Sutures are not, however, terraced. Sharp angulations at the shoulder or base are absent. The streamlined form of sand-burying species is enhanced in most cases by a distinctly terraced spiral sculpture (Fig. 1). This sculpture is coarsest in *P. aluco*, in which the ratchet effect is produced by backward-pointing nodes, and in *R. sinensis*. *Rhinoclavis vertagus*

(Linnaeus, 1758) has the last whorl and often also the penultimate whorl smooth, so that terraced cords are restricted to the upper spire whorls.

By contrast, surface-dwelling cerithiids almost all lack terraced sculpture and often display angulations on the whorls, accentuated by abaxially pointing nodes or tubercles. Exceptions are *C. nesioticum*, in which the very low unterraced spiral cords form no angulations and in which the sutures are flush with the whorl flanks, and the tropical eastern Pacific *Liocerithium judithae* Keen, 1971, a species living beneath stones in the intertidal zone of northwestern Mexico, with a sculpture similar to that of *C. nesioticum*. The only surface-dwelling cerithiid in which I have observed terraced sculpture is *Cerithium traillii* Sowerby, 1855 (H/D = 2.14), a species found on sand and beneath rocks, in which the ventral surface of the last whorl bears weakly ratcheted spiral cords.

Mitridae

In the Mitridae, sand-burying characterizes members of the clades Imbricariinae, Cylindromitrinae and many species of *Mitra*. As in cerithiids, sand-burying mitrids are significantly more slender than surface-dwellers (Table 1). The stockiest sand-buriers are four conical species of *Imbricaria*: *I. conovula* (Quoy & Gaimard, 1833) (H/D = 1.82), *I. conularis* (Lamarck, 1811) (H/D = 2.34), *I. punctata* (Swainson, 1821) (H/D = 1.93) and *I. vanikorensis* (Quoy &

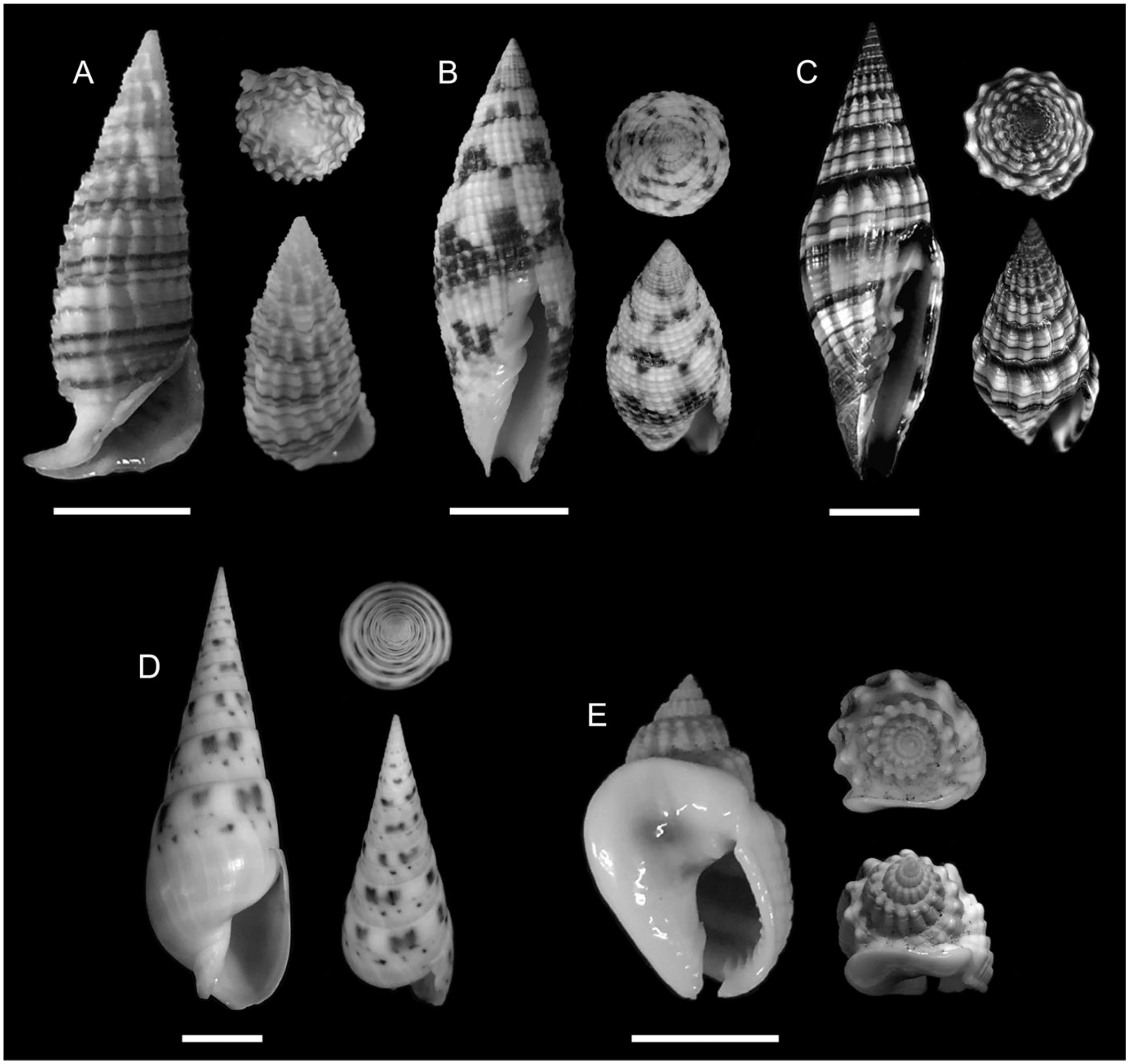

Figure 1. Recent sand-burying gastropods, showing ventral view and close-up of sculptural details. All specimens from the Vermeij collection. **A.** *Rhinoclavis aspera* (Linnaeus, 1758) (Cerithiidae), Piti reef flat, Guam. Note the strongly dorsally recurved siphonal canal and the strongly ratcheted spiral cords. **B.** *Neocancilla clathrus* (Gmelin, 1791) (Mitridae), Piti reef flat, Guam. Note the ratcheted spiral cords and the terraced sutures. **C.** *Vexillum vulpecula* (Linnaeus, 1758) (Costellariidae), Malakal Reef, Palau. Note the terraced suture and the upturned siphonal canal. **D.** *Oxymeris maculata* (Linnaeus, 1758) (Terebridae), Airai Reef, Palau. Note the terraced sutures. **E.** *Nassarius arcularia plicatus* (Röding, 1798) (Nassariidae), Nabeq, Gulf of Aqaba side of Sinai Peninsula, Egypt. Note the large callus pad, the ratcheted anterior spiral cords and last several axial riblets, and the terraced sutures. Scale bars = 1.0 cm.

Gaimard, 1833) (H/D = 2.11). The proportions of these small cone-shaped species, as well as those of the more cylindrical *Swainsonia fusca* (Swainson, 1824) (H/D = 2.14) and species of *Pterygia*, are similar to those of sand-burying species of Conidae. The most slender rock-dwelling mitrids in my study are the subtidal *Mitra incompta* (Lightfoot, 1786) (H/D = 2.67) and two species found beneath stones, *M. imperialis* Röding, 1798 (H/D = 2.75) and *Nebularia ferruginea* (Lamarck, 1811) (H/D = 2.61). The least elongate species I examined (H/D less than 2.00) are *N. chrysalis* (Reeve, 1844) (1.53), *N. cucumerina* (Lamarck, 1811) (1.69), *N. doliolum* (Küster, 1839) (1.82), *Strigatella decurtata* (Reeve, 1844) (1.71) and *S. retusa* (Lamarck, 1811) (1.70). At the other end of the spectrum, the most slender sand-burying species (H/D greater than 3.00) are *Mitra mitra* (Linnaeus, 1758) (3.24), *Domiporta praestantissima* (Röding, 1798) (3.36) and *Neocancilla clathrus* (Gmelin, 1791) (3.08).

Terraced spiral sculpture occurs in many but not in all sand-burying mitrids (Fig. 1). It characterizes the IWP genera *Domiporta* and *Neocancilla* as well as many IWP species of *Ziba*, but not *Imbricaria*, *Mitra*, *Pterygia* and *Swainsonia*. All sand-burying mitrids have streamlined shells, although the spire is short in conical species of *Imbricaria*, and the last whorl is posteriorly angulated in those species. Terraced sutures occur in most species of *Pterygia* and *Mitra*, but not in *M. mitra*. Ratcheted spiral sculpture and terraced sutures therefore have complementary distributions in sand-burying mitrids.

Rock-dwelling mitrids do not exhibit terracing either in spiral sculpture or in sutures. Distinctly angulated last whorls are uncommon, but are seen in the final stages of growth in *S. decurtata* and *M. stictica* (Link, 1807) (H/D = 2.01).

Costellariidae

The taxonomy of this family above the species level is in dire need of revision. Rock-dwelling species have generally been assigned to *Pusia*, whereas IWP sand-dwellers are more or less haphazardly placed in *Costellaria* and *Vexillum*.

Costellariids in small sand pockets or in sediments associated with algae cluster at the low end of the range of H/D. These include *Costellaria crocata* (Lamarck, 1811) (H/D = 2.07), *C. pacifica* (Reeve, 1845) (H/D = 2.18), *C. infausta* (Reeve, 1845) (H/D = 2.31) and *C. modesta* (Reeve, 1845) (H/D = 2.31). Slender outliers on harder surfaces with some sand accumulation are *Pusia microzonias* (Lamarck, 1811) (H/D = 2.81) and *P. lauta* (Reeve, 1845) (H/D = 2.06). Very slender costellariids (H/D greater than 3.00) include *C. acuminata* (Gmelin, 1791) (3.36), *C. michaui* (Crosse & Fischer, 1864) (3.12), *C. sanguisuga* (Linnaeus, 1758) (3.05), *C. sculptilis* (Reeve, 1845) (3.03) and *Vexillum vulpecula* (Linnaeus, 1758) (3.18). Ratchet sculpture is developed in only 7 of 33 species examined, occupying the middle range of H/D values: *C. deshayesii* (Reeve, 1844) (2.53), *C. exasperata* (Gmelin, 1791) (2.45), *C. modesta*, *C. pacifica*, *C. sanguisuga*, *C. sculptilis* and *C. virgo* (Linnaeus, 1767) (2.70). All sand-dwellers are well streamlined and high-spired, an effect accentuated by the presence of strong axial ribs. Two species, *V. plicarium* (Linnaeus, 1758) (H/D = 2.42) and *V. rugosum* (Gmelin, 1791) (H/D = 2.47), have relatively stocky shells that exhibit a row of backward-pointing nodes at the shoulder angulation. The dorsal surface of their shells often appears pitted, indicating that the animals might spend considerable time at the sediment surface. Sutural terracing occurs in 20 of the 33 species studied. Three of these (*C. sanguisuga, C. sculptilis* and *C. virgo*) also display ratcheted spiral sculpture. In species without terraced sutures, the sutures are barely perceptible, giving the spire an evenly conical taper, as in all the very slender species and in such small-bodied species as *C. filistriata* (Sowerby, 1874) (2.89), *C. obeliscus* (Reeve, 1844) (2.50), *C. turrigera* (Reeve, 1845) (2.84) and the slightly larger *V. funereum* (Reeve, 1844) (2.83).

Rock-dwelling costellarids never show either terraced sutures or terraced spiral sculpture. Axial sculpture tends to be wider spaced and less prominent than in sand-burying species, but in a few species they form prominent nodes at the shoulder angulation, as in *P. patriarchalis* (Gmelin, 1791).

The siphonal canal of Costellariidae is set off from the main part of the last whorl by a concave depression. In most sand-burying species, the dorsally oriented canal extends close to or up to the level of the dorsum of the last whorl. Exceptions occur among the species with ratcheted spiral sculpture, in which the canal is less elevated and the concavity is less apparent. Surface-dwelling costellariids have a short canal, still dorsally oriented, that does not reach the level of the last whorl's dorsal surface.

Conidae

Shallow-water IWP species of Conidae exhibit a narrow range of H/D ratios, from 1.48 in the rock-dwelling *Virroconus chaldaeus* (Röding, 1798) to 2.50 in *Gastridium obscurum* (Sowerby, 1833), a species living in sand beneath stones. No species comes close to the slenderness of many sand-burying mitrids and costellariids.

Although the presence of spiral threads near the base of the shell is almost universal in Conidae, only two species among the 27 sand-burying IWP species I examined have these threads weakly terraced: *Puncticulus arenatus* (Hwass in Bruguière, 1792) (H/D = 1.78) and *P. pulicarius* (Hwass in Bruguière, 1792) (H/D = 1.62). In the case of *P. arenatus*, these threads can extend over the whole last whorl. None of the species shows terraced sutures. Although some sand-dwellers have a gently rounded last whorl indicating streamlining, as in the two species of *Puncticulus*, many others have a straight-sided last whorl and a pronounced shoulder angulation with a tuberculated spire, as in *Conus marmoreus* Linnaeus, 1758 (H/D = 1.81), *Tessuliconus eburneus* (Hwass in Bruguière, 1792) (H/D = 1.69), *T. tessulatus* (Born, 1778) (H/D = 1.76) and the sand-pocket-dwelling *V. abbreviatus* (Reeve, 1843) (H/D = 1.52).

Rock-dwelling species lack terracing of any kind and usually have a straight-sided last whorl and a short, tuberculated spire. Unlike sand-burying species, they are often heavily encrusted with coralline algae, testifying to a mode of life on open surfaces exposed to light.

Strombidae

Although most strombids live on soft substrata and a few even graze on hard surfaces (e.g. species of *Canarium*, *Lambis* and *Harpago*), active sand burial occurs in a small minority of species, all from the IWP. The taxa involved—*Tridentarius dentatus* (Linnaeus, 1758), *Laevistrombus*, some species of *Eurptomus* and a species of *Gibberulus*—are more streamlined and less strongly sculptured than their epifaunal counterparts, but none has terraced sculpture or sutures (see also Berg, 1974; Savazzi, 1991). All have a conspicuously dorsally raised siphonal canal, a deep strombid notch and a gently rounded, slender last whorl. Species with a dorsal knob or spine on the last adult whorl, such as some species of *Canarium*, *Lentigo* and the tropical American *Lobatus*, live on sand but do not bury completely in it.

Terebridae

All shallow-water terebrids I have observed are sand-buriers with a high spire and slender shell. Although many species have spiral sculpture, that sculpture is never ratcheted. Instead, the sutures and subsutural groove are terraced in 25 of 40 IWP species and 4 of 13 tropical American species examined (Fig. 1). Species without such terracing belong to three morphological categories: (1) glossy-smooth shells, mainly in the genus *Hastula*; (2) shells with weak spiral sculpture and no axial ribs, such as *Terebra cingulifera* Lamarck, 1822 and *Terebra laevigata* Gray, 1834; and (3) some strongly spirally and axially sculptured deeper-water species such as *Triplostephanus triseriatus* (Gray, 1834). Terracing is also absent in *Terenolla pygmaea* (Hinds, 1844), a species found in small sand patches on reefs.

Olivoidea

All members of the Olividae and Olivellidae are sand-buriers. Their shells are smooth and covered in life by the foot. The streamlined shape of most species is accompanied in all olivids and most olivellids by terraced extensions of the columellar folds and by a terraced anterior fasciole. In addition, the sutures in many olivids are conspicuously terraced. This occurs in six of 16 IWP species (37.5%) and two of 10 tropical American species (20%) I have examined. No terracing of any kind was found in the temperate northeastern Pacific olivellid *Callianax biplicata* (Sowerby, 1825), the southwestern Atlantic *Olivina puelcha* (Duclos, 1835) and *Olivancillaria urceus* (Röding, 1798), the ancillariine olivids *Arnalda hilgendorfi* (von Martens, 1897), *Sparella sarda* (Reeve, 1864) and *Chiloptygma minima* (Thiele, 1929).

Nassariidae

Unlike most of the other sand-burying gastropods considered here, nassariids have a large, powerful foot, enabling them to bury rapidly (Trueman & Brown, 1976, 1989, 1992a, b; Vermeij & Zipser, 1986; Savazzi, 1989, 1994; Trueman & Hodgson, 1990). In keeping with the trade-off between foot size and streamlining, most nassariids are less streamlined than most sand-buriers in the other clades examined (Fig. 1). The mean shell slenderness of 42 IWP nassariines is 1.74 ± 0.22, with a range of 1.40 in *Nassarius globosus* (Quoy & Gaimard, 1833) and *N. callospira* (A. Adams, 1852) to 2.12 in *N. reeveanus* (Dunker, 1847) and 2.13 in *Reticunassa paupera* (Gould, 1850). Species in the Bulliinae are, however, generally higher spired.

Within Nasariinae (as delineated by Galindo *et al.*, 2016), terraced features are very common, usually affecting the sutures, abapical (basal) spiral cords and sometimes also the last three to five axial ribs formed before the terminal adult outer lip (Fig. 1). I have observed terracing in one or more of these features in 34 of 42 IWP nassariines (81%) and in only six of 16 tropical American sand-burying nassariines (37.5%). Ratcheted axial ribs are restricted to IWP species. Several IWP nassariines have conspicuous rounded beads, as in *N. graniferus* (Kiener, 1834), *N. oneratus* (Deshayes, 1863) and *N. echinatus* (A. Adams, 1852); only those of *N. echinatus* and the related *N. quadrasi* (Hidalgo, 1904) exhibit ratcheting, with steeper adapical slopes.

DISCUSSION

The foregoing survey shows that sand-burying gastropods generally differ from surface-dwellers in ways consistent with greater streamlining. Data from Terebridae, Olivoidea and Nassariidae further support the conclusion that sand-burying specializations are more widespread and better expressed among shallow-water gastropods in the IWP than among those in tropical America.

Traits that have been associated with the ability to bury in sand are not, however, found in all clades with sand-burying members. Below I consider the phylogenetic distribution of these traits and comment on their utility as indicators of the sand-burying habit in gastropods.

Shell form

Shell-bearing gastropods that commonly bury in sand conform to nine categories of shell form, none of which is unique to them (Table 2). Each of these types has evolved multiple times among, or been adopted by, infaunal gastropods. As shown above for cerithiids, mitrids and costellariids, terebriform (high-spired) and mitriform gastropods living in sand have slenderer shells than phylogenetically related species from surface habitats. Some parasitic triphorids, cerithiopsids and eulimids have extremely slender

Table 2. Shell-shape categories of sand-burying gastropods: characteristics and taxonomic composition.

Shell shape	Characteristics	Taxa
Terebriforms	High spire (much higher than height of last whorl), short last whorl, ovate to circular siphonate or rarely nonsiphonate aperture whose height:width ratio is 2.0 or less	Cerithiidae, Terebridae, Columbellidae (*Aesopus, Clavistrombina, Mazatlania*), Pyramidellidae (*Pyramidella*), Nassariidae (*Bullia*)
Mitriforms	Relatively high to low spire, cylindrical to fusiform shell, long and often basally constricted last whorl, narrowly elongated siphonate or nonsiphonate aperture with height:width ratio often much greater than 2.0	Costellariidae, Mitridae, Colubrariidae (*Metula, Truncaria*), Pyramidellidae (*Otopleura*), Acteonidae, Seraphsidae (no abapical constriction); Olivellidae and Olividae (often covered by extensions of foot,and not basally constricted), Mangeliidae, Columbellidae (*Graphicomassa*, most members of *Strombina* group), Volutidae
Coniforms	Low spire (usually much less than height of last whorl), last whorl long and evenly abapically tapering, very narrow siphonate aperture with a height:width ratio usually 4.0 or higher	Most Conidae, Mitridae (some *Imbricaria*), Marginellidae (*Prunum*)
Cypraeiforms	Enveloped shell, low or immersed spire, thickened outer lip, narrow aperture, adapical and abapical apertural canals	Some Marginellidae
Bulliforms	Elongate to ovate-cylindrical to fusiform, spire sunken, narrowly elongated aperture widening abapically to the nonsiphonate or rarely weakly notched anterior end	Most Cephalaspidea
Cassiforms	Globose to ovate shell, low to moderately high spire, ovate siphonate aperture, often a callus pad	Many Nassariidae, Cassidae, Harpidae, Costellariidae (*Zierliana*), Olividae (some *Olivancillaria*)
Naticiforms	Ovate to globose, short to very short spire, very large last whorl, rounded nonsiphonate aperture	Naticidae, Ampullinidae, Neritidae (*Linnerita*)
Umboniiforms	Disc-shaped with very low spire, dorsoventrally flattened whorl with median keel or rounded angulation, flattened base, rounded aperture usually without siphonal notch	Umboniinae, Solariellidae, Architectonicidae (*Architectonica*, *Psilaxis*), Nassariidae
Strombiforms	Fusiform shell with relatively high spire, long basally constricted last whorl, narrowly elongate aperture, variably expanded adult outer lip, often glazed inner lip extending onto ventral part	Strombidae

terebriform shells, as do some semi-infaunal turritellids. Among umboniiform (disc-shaped) gastropods, infaunal umboniines and architectonicids have flatter, more distinctly keeled shells than their surface-dwelling counterparts (see also Bieler, 1988). Many categories of shell form are not represented among infaunal species. These include shells that are loosely coiled, planispiral, widely umbilicate, broadly fusiform with an ovate aperture, turbinate, trochoid or limpet-like. Also not represented are shells with long spines, high collabral lamellae, high tubercles, an axially extended long siphonal canal or an angular whorl profile. Multiple high spiral keels and a thick lamellose or hairy periostracum occur only in epifaunal gastropods.

Columellar folds

Columellar folds were thought to be typical of high-spired terebriform or turritelliform sand-burying gastropods, in which they function to limit the lateral displacement of the contracting columellar muscle as the snail digs into the sand (Signor, 1982b; Signor & Kat, 1984). Columellar folds are indeed the norm in high-spired terebrids, pyramidellids and cerithiids, but they are absent in similarly shaped columbellids. Most surface-dwelling high-spired gastropods lack these folds, but some epifaunal potamidids do have them, including species of *Terebralia* and *Telescopium* (Lesport & Cahuzac, 2002; Reid *et al.*, 2008), as do some fossil members of the Campanilidae. Most mitriforms, whether sand-burying or surface-dwellers, have columellar folds, but exceptions occur in columbellids and mangeliids with these habits. Many surface-dwellers of other shapes have a pleated columella, indicating that the presence or absence of folds is not tied to a particular habit or shell shape.

Terraced features

The most reliable indication of the sand-burying habit in gastropods is the presence of terraced or ratcheted features, in which the leading edge in the direction of digging is less steep than the trailing edge. Such terracing can deter back-slippage during the digging cycle (Signor, 1982a, b, c, 1983; Vermeij & Zipser, 1986; Savazzi & Pan, 1994). Ratchet-like profiles can affect axial ribs, spiral cords, sutures and even columellar folds that extend onto the ventral side of the last whorl. As shown below, terracing is widespread among sand-burying gastropods, especially in the IWP, but it is not universal among infaunal species.

Terraced axial ribs occur in sand-burying harpids (IWP species of *Harpa* and several species of *Morum*), many IWP species of *Nassarius* in the Nassariidae (usually only the four or five riblets closest to the adult outer lip), young *Cassis* in the Cassidae and in two IWP species of the IWP neritid genus *Linnerita*, the only infaunal members of their family (Vermeij, 1984). Axial elements in infaunal cerithiids, stromboideans, columbellids, colubrariids, mangellids and terebrids are never ratcheted.

The axial lamellae of many epitoniids are conspicuously recurved abaperturally, giving them a distinctly ratcheted appearance. Epitoniids parasitize cnidarians, but some, like the European *Epitonium clathrus* (Linnaeus, 1758) with recurved lamellae, can spend time infaunally in sand. Nothing appears to be known about the mobility of epitoniids when away from their hosts, or about the possible functions of recurved lamellae in these gastropods. The difference between the recurved lamellae of epitoniids and the terraced axial sculpture of nassariids and other infaunal gastropods is that the former tend to be well elevated above the general shell surface, rather than being flattened and adherent.

Terraced spiral cords are common in sand-burying cerithiids, cassids, nassariids (usually only the basal cords), mitrids, costellariids, harpids (some species of *Morum*), acteonids and haminoeids (*Atys* and *Aliculastrum*). Infaunal species of *Architectonica* display a few terraced cords on the flattened base. The only members of the Conidae with terraced spiral sculpture are species of *Puncticulis* from the IWP (see above) and the tropical American *Ximeniconus perplexus* (G. B. Sowerby II, 1857) from the eastern Pacific and *X. puncticulatus* (Hwass in Bruguière, 1792) in the Caribbean, in which the basal cords are weakly ratcheted. Spiral cords or threads are never terraced in infaunal colubrariids (except in *Truncaria*, if that genus is a colubrariid), columbellids, volutids, mangellids, terebrids and stromboideans.

The only epifaunal gastropod with terraced spiral sculpture known to me is the Caribbean high-shore littorinid *Cenchritis muricatus* (Linnaeus, 1758). Its shell has spiral rows of small, adapically steep beads over the entire surface (Vermeij, 1973). Unlike the ratcheted spirals of many sand-burying gastropods, these terraced beads occur everywhere on the shell, including sectors where potential flow of the surrounding medium would be of little benefit. Moreover, the sutures of *C. muricatus* are well impressed, giving the shell a decidedly unstreamlined shape. I speculated that the terracing of the beads could promote reflectivity of the sun's rays when the snail is directly exposed to solar heating, as it commonly is at the upper fringes of marine influence in the West Indies (Vermeij, 1973).

Numerous epifaunal gastropods have backward-pointing tubercles or spines, but these features are very large compared with the ratcheted cords of infaunal gastropods and therefore confer an angular profile to the shell. A crown of backward-pointing spines such as those in *Melo* and *Cymbiola* (Volutidae), some *Angaria* (Angariidae), and *Babelomurex* and *Latiaxis* (Muricidae: Coralliophilinae) could serve to protect against predators attacking from the back.

Terraced sutures, often accompanied by a terraced, subsutural groove, characterize many IWP terebrids, nassariids, mitrids, costellariids and harpids. Many members of the Olivinae also have distinctly terraced sutures, as do some infaunal columbellids (the IWP genus *Graphicomassa* and the western Atlantic *Mazatlania cosentini* (Philippi, 1836), but not the *Strombina* group or the eastern Pacific *M. fulgurata* (Philippi, 1846)). No sutural terracing is known in infaunal cerithiids, ancillariine and most olivelline olivids, stromboideans or conids. Infaunal pyramidellids (*Pyramidella* and *Otopleura*) and mangeliids often do have terraced sutures.

An unusual form of terracing occurs in the IWP marginellid genus *Cryptospira*, the western Atlantic volutid genus *Scaphella* and most Olividae except Ancillariinae. In these taxa, columellar folds emerge as strongly terraced features on the ventral side of the shell in the sector nearest the aperture. In all olivids, including Ancillariinae, the abapical fasciole is also terraced. Whether these features assist in burial is unknown. To my knowledge, the terraced columellar folds of *Scaphella* are unique within Volutidae and serve, among other features, to distinguish this genus from the superficially similar Oligocene to Pliocene eastern Atlantic genus *Euroscaphella*. The latter genus, like almost all other taxa with columellar folds, has erect folds with equally steep abapical and adapical sides. Moreover, these more typical folds do not extend beyond the aperture.

Although I interpret terraced features as adaptations with a genetic basis, it cannot be ruled out that terracing results directly from forces acting on the mantle edge where the feature in question is laid down. Forward and downward motion of the animal during digging could push the shell-secreting sectors of the mantle edge slightly backward, producing the terracing effect. Whether and how this effect might be brought about depends on the role of the shell in digging. The direct influence of the force of digging on shell features could be tested by allowing shells of terraced gastropods to grow under conditions where the gastropod cannot bury itself, or by subjecting normally epifaunal gastropods to a soft-sand substrate into which they could bury. In the former case, one would expect terracing not to develop, whereas in the latter case terraced features might form. Regardless whether terracing is genetically based or the direct result of environmental forces created by the gastropod itself, the presence of terraced features appears to be a reliable indication of active sand burial.

Actively burying gastropods in several clades are capable of swimming or of sailing with incoming waves on sandy beaches. They include several species in the Nassariidae (genus *Bullia*), Olivoidea, Seraphsidae (*Terebellum*), Solariellidae, Umboniinae and Terebridae (*Hastula* and related genera) (Okutani, 1961; Farmer, 1970; Miller, 1979; Herbert, 1987, 1992; Trueman & Brown, 1989; Savazzi, 1991; Hickman, 2003; Vanagt *et al*., 2008). Burying snails that can also swim or sail always have smooth, narrowly elongated or compressed disc-shaped, thin-walled shells with a relatively wide aperture and lacking terracing.

No terracing of any kind is known in sand-burying Stromboidea, Naticidae, umboniine Trochidae and the ampullinid *Cernina*. Most of these taxa have smooth shells, although sand-burying members of the strombid genus *Euprotomus* have spiral cords and small rounded nodes.

Glossy surfaces

Among infaunal gastropods, a glossy-smooth shell is associated with rapid burial (Vermeij & Zipser, 1986). Slippery-smooth shells characterize *Terebellum* in the stromboidean family Seraphsidae, *Bullia*, some species of *Nassarius* and the southern European nassariid *Cyclope neritea* (Linnaeus, 1758). It is also found in *Imbricaria olivaeformis* (Swainson, 1821) in the Mitridae; *Hastula* and related genera in the Terebridae; *Plicoliva* in the Volutidae; a few Naticidae; and most Olividae and Marginellidae. The genus *Melanella* (Eulimidae) also has a glossy-smooth shell and is often found in sand when away from its holothurian hosts, but is presumably a slow burrower. Although sand-burying conids do not have a glossy-smooth shell surface, they achieve slipperiness in life by a thin periostracum. A thin film of mucus on the shell has a similar effect in sand-burying haminoeids. Shells with a slippery surface are by no means restricted to sand-burying species; they are the rule in Cypraeoidea as well as in the rissoid genus *Zebina*, some columbellids (*Nitidella*), and nonburying marginellids and cystiscids, all of which are surface-dwellers.

Apertural canals

Most sand-burying gastropods have both an anterior siphonal canal and a posterior ('anal') notch or channel. When present, a siphonal canal or notch is invariably oriented dorsally, often dramatically so as in cerithiids, cassids, costellariids, nassariids, volutids, terebrids and strombids. The only infaunal gastropods without a siphonal canal are umboniine trochids, solariellids, ampullinids and naticids. An adapical notch or extension occurs in most infaunal gastropods, but is absent in umboniines, solariellids and pyramidellids. Neither abapical nor adapical channels are restricted to infaunal gastropods. but axially elongate and completely sealed tubular siphonal canals occur only in epifaunal species (Vermeij, 2007).

Large propulsive organ

Fast-burying gastropods typically have a large foot, which can be hydraulically expanded and contracted. Shell features associated with such a large structure are a large, broadly ovate to circular aperture and/or a well-developed callus pad located ventrally to the left of the aperture (in dextral species). In extreme cases (Olividae, Harpidae, Naticidae and some Nassariidae), part or all of the shell can be enveloped by the expanded lobes of the foot (Vermeij, 2005). A distinct callus pad is common in sand-burying nassariids, especially in the IWP; Strombidae, again in the IWP (*Eurpotomus*, *Laevistrombus*); and cassids. Surface-dwelling adult personids, cassids and some muricids also have much of the ventral side of the shell covered with a thick callus pad or shield, but in most cases this feature is accompanied by a crenulated outer lip that clamps to hard surfaces (Vermeij, 2014).

CONCLUSIONS

Despite the functional demands of active burial in the dense granular medium of sand, infaunal gastropods display a considerable variety of shell types, reflecting the multiple ways of achieving functional adequacy in mobile infaunal animals. Nevertheless, sand-burying gastropods differ from their surface-dwelling counterparts by generally having a more streamlined shell. Unique to many infaunal gastropods is the presence of terraced features (axial ribs, spiral cords or sutures), in which the sides facing the direction of forward and downward motion are less steep than the opposite sides. These specializations not only make movement through sand energetically more efficient but, perhaps more importantly, they reduce vibrational cues to potential predators. The role of predators in shaping the burying-related adaptations of gastropods can also be inferred from the peculiar circumstance that many infaunal gastropods have a small or narrow aperture and therefore potentially a small propulsive foot. The restricted aperture is an effective deterrent against predators, including infaunal crabs, and could in many cases limit digging performance. This limitation is partially overcome in olivids, whose shell has a narrow aperture, but whose foot can be expanded to envelop all or part of it. Thus, both the demands of streamlining (reducing noise) and resistance to predators place limits on the speed of burial in most infaunal gastropods.

Dudley & Vermeij (1989) previously noted that sand-burying specializations are better developed in the IWP than in tropical America, but they were unable to detect a significant difference in gastropod burying performance between these two regions, as measured by a burrowing-rate index. The reasons for the morphological contrast, which is also documented here, are not well understood, but shallow-water IWP faunas generally display better-expressed defence-related adaptations, more specialized relationships between commensals or parasites and their hosts, and greater degrees of habitat specialization than in tropical America (Vermeij, 1989, 1993). In this connection, it is interesting to note that the clades with particularly large numbers of sand-burying species in the IWP—Mitridae, Costellariidae, Olividae, Nassariidae and Cerithiidae—are also the ones in which terraced burying-related features are most common and best expressed. These clades diversified much less in tropical America. When and how these differences arose remains an open question of considerable importance to the interpretation of the history of tropical marine biotas.

These biogeographic and historical considerations will be the subject of a separate paper. Meanwhile, it is important to point out that an adequate account of functional performance—sand-burying in gastropods in this case—requires knowledge not only of the focal function, but also of other selective agencies against which form and function must be measured.

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