The biology and functional morphology of the high-energy beach dwelling *Paphies elongata* (Bivalvia: Mactroidea: Mesodesmatidae). Convergence with the surf clams (*Donax*: Tellinoidea: Donacidae)

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**ABSTRACT**

The biology and functional morphology of the Australian endemic *Paphies elongata* (shell length <20 mm) from wave-exposed beaches are described. On Middleton Bay Beach, Albany, Western Australia, the species co-occurs with the smaller (shell length <13 mm) *Donax columbella*. Both make tidally regulated migrations up and down the shore in the swash and backwash of waves, respectively. Emergence from and re-burrowing into the beach sand in concordance with the waves is fast in both taxa (5–10 s). Adaptations to such a life on these high-energy beaches include an anteriorly elongate and posteriorly reduced shell and a mesh of tentacles within the inhalant siphon that screens out sand grains from the mantle cavity but allows entry for particles of detritus that *P. elongata* suspension feeds on when they are raised into the water column with each breaking wave. Internally, relatively large ctenidia, small labial palps, a stomach with many sorting areas and a short intestine equip *P. elongata* for life in such a dynamic habitat. Strong rejectory currents in the mantle cavity keep it clean of sand. *Paphies elongata* is dioecious, as are species of *Donax*, which throughout its Australian range *P. elongata* is sympatric with. These donacid and mesodesmatid taxa have both evolved to exploit the niche and the food resource of detritus held in suspension by breaking waves of high-energy sandy beaches within their respective ranges. Of interest, however, is that the original and sole occupants of such beaches – the Mesozoic Upper Cretaceous Donacidae – have been joined subsequently by representatives of the Mesodesmatidae, such as *P. elongata*, the adoption of this habitat taking place in the Eocene of the Cenozoic, some 50 million years later.

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**Introduction**

Little is known about the natural history of one of the commonest intertidal bivalves in Australia. This is the endemic *Paphies elongata* (Reeve) (Mesodesmatidae), even though it occurs virtually ubiquitously on some of the most dynamic, high-energy beaches in...
Australia, being recorded from every state. There are a few taxonomic papers and anecdotal descriptions of the behaviour (as will be described) of *P. elongata* but the great ecological significance of this intertidal bivalve is largely unappreciated. Its anatomy has not been described either.

In contrast, there are a huge number of research studies, from throughout much of the world, on the Donacidae Fleming and its species of *Donax* Linnaeus that also occupy such high-energy beaches, including those in Australia. Representatives of the Donacidae are not, however, restricted to surf beaches and the euryhaline *Egeria radiata* (= *Galatea paradoxa* [Born]), for example, occupies the lower reaches of rivers in West Africa (Purchon 1963; Adjei-Boateng and Wilson 2013). The majority of species of *Donax*, however, live, sometimes in high concentrations, vertically aligned in the sand on exposed beaches, on tropical and temperate coasts almost worldwide (Ansell 1983). When the waves wash these bivalves out of the sand, they can dig themselves back in again rapidly (Ansell 1983). Over 50 species of *Donax* have been described and the anatomies and behaviours of some of them elucidated in varying degrees of detail, for example, *Donax hanleyanus* Philippi (Narchi 1978), *D. serra* (Röding) and *D. sordidus* Hanley (Ansell 1981), *D. trunculus* Linnaeus (Moueza and Frenkel 1974, 1976; Moueza 1976), *D. gemmula* Morrison (Passos and Domaneschi 2004), *D. gouldi* Dall (Pohlo 1967), *D. venustus* Poli and *D. semistriatus* Poli (Salas-Casanova and Hergueta 1990), *D. striatus* Linnaeus (Wade 1967), *D. denticulatus* Linnaeus (Wade 1969), *D. fossor* Say and *D. variabilis* Say (Simone and Dougherty 2004), and *D. faba* Gmelin, *D. semigranosus* Dunker, *D. cuneatus* Linnaeus and *D. incarnatus* Gmelin (Ansell 1983).

Most donacids are suspension feeders, many species migrating both vertically and horizontally with changes in the tides and degrees of wave action; examples include two of the most well-studied species, *D. variabilis* (Turner and Belding 1957; Ellers 1995) and *D. semigranatus* (= *D. semigranosus*) (Mori 1938, 1950). The large literature on *Donax* was last reviewed by Ansell (1983) but more recent aspects of the biology and anatomy of representatives of this genus on high-energy beaches provide an excellent comparative context within which to consider *P. elongata*.

Yonge and Allen (1985) erected a new superfamily, the Mesodesmatacea (Mesodesmatoidea Gray), on the basis of anatomical evidence related to ligament structure and the degree of siphonal fusion, suggesting that a former affiliation with the Mactroidea Lamarck was incorrect. Most recently, however, Bieler et al. (2010) argued that the Mesodesmatidae does belong to the same superfamily, Mactroidea, as the Mactridae. The modern consensus, therefore, is that the Mactroidea comprises four extant families – the Mactridae, Mesodesmatidae, Anatinellidae Gray and Cardiliidae Fischer (Keen 1969a), a classification accepted, most recently, by Bieler et al. (2010). Of these, the latter two families are poorly studied.

Representatives of the Mactridae are the most well-known mactroids and are currently believed to comprise three subfamilies, the Mactrinae, Lutrariinae Adams and Adams and Pteropsellinae Keen (Keen 1969a). Yonge (1982a) studied the ligament of the mactrids *Spisula subtruncata* (da Costa) and *Lutraria lutraria* (Linnaeus) while Barnes and Morton (1996) examined the anatomy of *Mactrinula reevesii* (Gray) (Mactridae). Yonge (1948a) described aspects of the anatomy of *L. lutraria* (Lutrariinae) while Morton (2010) studied that of the pteropselline *Raeta* (as *Raetellops*) *pulchella* (A. Adams and Reeve).
Keen (1969a) considered that the Mesodesmatidae comprised the subfamilies Mesodesmatinae, Davilinae Dall and Erviliinae Dall, a classification endorsed by Boss (1982). Following a study of the anatomy of the European Ervilia castanea (Montagu) by Morton (1990), however, the genus Ervilia was removed from the Mesodesmatidae and re-located in the Semelidae Stoliczka (Tellinoidea de Blainville) by Morton and Scott (1990). Of the remaining taxa of the Erviliinae, only the anatomy of Caecella chinensis Deshayes has been studied by Narchi (1980) and little has been published on the Davilinae. The anatomies of two mesodesmatids, the North and South American Mesodesma arctatum (Conrad) and Mesodesma mactroides Deshayes, have been studied by Allen (1975) and Narchi (1981), respectively. Representatives of both currently accepted sub-families are near global in distribution and, according to Gofas (2010), the Mesodesmatidae comprises 23 valid species of which eight taxa occur in Australia. Of the eight putative species of Mesodesmatinae assigned to the genus Paphies Lesson, two occur in Australia. These are P. elongata and P. altenai (de Rooij-Schuiling), the former the subject of this study and the latter being restricted to high energy beaches in tropical northern Western Australia and the Northern Territory (Lamprell and Healy 1998). It is, however, worth noting that other species of Paphies have been notionally described from Australia (Macpherson and Gabriel 1962; Roberts and Wells 1981; Wells 1984; Ludbrook and Gowlett-Holmes 1989; Lamprell and Whitehead 1992; Lamprell and Healy 1998; Wells and Bryce 2000), but all are now subsumed under either P. elongata or P. altenai (Gofas 2010) and neither of these have been described anatomically.

With only one prior study on the anatomy of an exposed sandy beach mesodesmatid, M. mactroides, by Narchi (1981), the present study of P. elongata seems opportune, allowing: (i) comparisons with other representatives of the Mactroidea; (ii) a comparison between the two genera of Paphies and Donax both occupying surf beaches; and (iii) an interpretation of the adaptive convergence expressed by the two taxa.

Materials and methods

Individuals of P. elongata were initially collected from Middleton Bay Beach, Albany, south-western Western Australia, in March 2005. Additional material was obtained from the same beach in October 2013. On both occasions, observations were made on the behaviour of the species on the beach. In addition, the burrowing behaviour of living individuals was examined in basins of seawater and sand from the natal beach in the laboratories of the Western Australian Museum. Following these observations, the ciliary currents of the mantle cavity of a number of individuals were elucidated using carmine powder suspended in seawater. Finally, two individuals were fixed in Bouin’s fluid and decalcified and, following routine histological procedures, sectioned transversely at 4 µm and the resulting slides stained in Ehrlich’s haematoxylin and eosin.

Voucher specimens of P. elongata have been lodged in the collections of the Natural History Museum, London, with the accession number NHMUK 20150021. Voucher specimens of four shell valves of Donax columbella Lamarck, similarly sharing Middleton Bay Beach with P. elongata, and with the same collection data have the registration number NHMUK 20160219.
Results

Biology

Slack-Smith (1990) recorded P. elongata from metahaline waters throughout Shark Bay in north-western Western Australia. The species has also been recorded from south-eastern Australia (and Tasmania) and Queensland by Jansen (1996, 2000). Paphies elongata thus seems to occur throughout Australia and, everywhere it occurs, it is an inhabitant of high-energy surf beaches (Edgar 1997), like species of Donax.

In addition to the two recognized Australian species of Paphies, Roberts (1984) reported on a third putative species, that is, P. cuneata (Lamarck) (but which is now placed in a separate subgenus, Atactodea Dall, by Lamprell and Healy 1998) from the relatively sheltered sandy/mud shores of Princess Royal Harbour at Albany in south-western Western Australia. Here, the species spawns from April to June, that is, in the autumn months of the year. The species also exhibited a uni-modal population structure suggesting that juveniles recorded in June and July mature quickly to reproduce in the following year. No such comparative information exists for P. elongata. What is clear, however, and this is confirmed by the more rounded shell form of Atactodea cuneata, is that it occupies low-energy beaches (for example within Princess Royal Harbour) whereas the wedge-shaped P. elongata occupies much more dynamic sandy shores throughout its range but particularly outside Princess Royal Harbour on Middleton Bay Beach.

Cotton (1961) noted that on such high-energy beaches, P. elongata leaves distinctive burrowing tracks and Allan (1959) described the ability of this species to re-burrow quickly when exhumed from its sandy habitat by strong wave action. Edgar (1997, p. 301) observed that P. elongata ‘uses wave energy to carry it up and down the shore, following the tide’. The same author (Edgar 2001, p. 90) later recorded that P. elongata ‘orients its shell and foot to allow movement up or down a beach with passing waves’. Allan (1959) also recorded that the species is highly susceptible to predation by an unnamed naticid. Such behaviour was elaborated upon by Laws and Laws (1972) who showed that on the sandy Henley Beach near Adelaide, South Australia, Donacilla angusta Reeve (= P. elongata) was heavily predated upon by the shell-drilling Polinices conicus (Lamarck) (= Conuber conicum [Lamarck]) and which individuals attempted to escape from by jumping out of the sand ahead of the advancing gastropod. However, C. conicum is an inhabitant of sheltered muddy shores and the only predator on such eastern Australian exposed beaches is the endemic Conuber incei (Philippi).

Middleton Bay faces south-east-east and is thus exposed to Southern Ocean waves arriving in King George Sound, which it sits at the head of. It is, thus, highly exposed. With a local maximum tidal range of only 1.4 metres, it is clear that the prevailing marine influence on the bay’s beach is wave driven. At the time of the visits to Middleton Bay Beach, salinity values ranged between 29‰ and 30‰, measured with an Atago® handheld refractometer (Cole-Parmer Instrument Co. Ltd., London, UK), the light dilution of the highly oceanic (34‰) King George Sound waters being from freshwater run-off through the dunes behind the beach.

Standing and watching the waves upon Middleton Bay Beach revealed the behaviour of P. elongata. On the rising tide and with each wave’s swash, individuals emerged from the sand and were rolled up the beach. Here they stranded and re-burrowed themselves
rapidly, typically within average-timed observations of 5–10 s, and commenced suspension feeding. When larger waves struck the beach, individuals of *P. elongata* were washed out of the sand and bowled back down the shore in the backwash, where they again re-burrowed. Such behaviour is highly similar to that of representatives of the intertidal, surf-beach species of *Donax*. It is worth noting here, however, that sympatric with *P. elongata* on Middleton Bay Beach is the similarly tidally migrating and wave riding donacid *D. columbella* (this study).

A living individual of *P. elongata* is illustrated in its life position in the sediment in Figure 1 from observations made of basin-held individuals. Each individual burrowed, anteriorly elongate shell face down, within a space of 20–30 s and assumed a vertical position in the sediment with the posteriorly more foreshortened and flatter valve

![Figure 1. Paphies elongata. A living individual in its life position in the sediment. Closed arrow represents the inhalant stream, open arrows the exhalant.](image-url)
margins flush with the sediment surface. The foot is axe-shaped and clearly used to achieve rapid burrowing. When immured vertically in the sediment, the siphons open rapidly and in Figure 1 the closed arrow represents the inhalant stream while the open arrows indicate the exhalant. Figure 1 of *P. elongata* should be compared with the comparable illustration of *M. mactroides* (Narchi 1981, fig. 1) showing the siphons of this species to be much longer – by as much as three times the length of the shell. In this context, as with this study of *P. elongata* in Australia, *M. mactroides* has been recorded by Herrmann et al. (2009) to be sympatric with *D. hanleyanus* on Santa Terasita Breach in northern Argentina.

**Anatomy**

**The shell**

The shell of *P. elongata* (Figure 1) reaches a length of 20.2 mm on Middleton Bay Beach, but can reach up to 26 mm on Queensland shores (pers. obs.). The equivalve shell is laterally compressed, anteriorly elongate and posteriorly foreshortened, giving it a sharply inequilateral, subtrigonal form that is, typically, described as donaciform after the species of *Donax* it superficially resembles. Each shell valve has opisthogyrous umbos, is smoothly polished and has a glossy periostracum that confers upon it a yellow coloration except umbonally where the shell can be eroded white slightly. Structurally, the shell is aragonitic and has a microstructure comprising an outer crossed-lamellar layer and an inner complex crossed-lamellar layer, as is typical of all representatives of the Mactroidea (Taylor et al. 1973).

The donaciform shell of *P. elongata* is illustrated in Figure 2(a), as seen from the left side. The small arrow indicates the position of the umbo and a–b represents the dorsoventral axis of the shell. This highlights the anteriorly elongate form of the shell such that the angle between the dorsoventral axis and the posterior shell margin is ~70°. Comparison is here made with the shell of *D. columbella* that *P. elongata* shares Middleton Bay Beach with (Figure 2(c)), and which shows that the posterior face of the latter is slightly more elongate than the former with a dorsoventral axis and posterior shell margin angle of ~80°. The posterior face of the shell of *D. columbella* is also ventrally inset. The difference in the dorsoventral–posterior face angle between of the two species may be related to the fact that, as will be shown and discussed, *P. elongata* has a short internal amphidetic ligament whereas *D. columbella* has a short external opisthodetic ligament – the latter restricting posterior foreshortening. Also illustrated in Figure 2(b) and 2(d) are the shell valves of *P. elongata* and *D. columbella* as seen from the anterior aspect, respectively, and similarly drawn to the same scale. The greatest widths of the two species (x–y) are both slightly dorsal to the mid-point of the dorsoventral axis of the shells and both are laterally compressed. Both, therefore, have the form typical of fast-burrowing taxa and this is also seen in the South American high-energy beach dwelling *M. mactroides* (Narchi 1981).

An internal view of the right shell valve of *P. elongata* is illustrated in Figure 3 showing the hinge plate and muscle scars. The opisthogyrous umbo (U) sits above a posteriorly situated hinge plate to be described in more detail in Figure 4. The musculature as revealed by their scars comprises a divided anterior adductor muscle (AA(1)
and AA(2)), the anteriormost of these being the larger and situated directly above the scar of slightly indented pedal gape (PGS). Internal to the adductor muscles are the scars of the anterior pedal protractor (APP) and anterior pedal retractor (APR) muscles. There is also a posterior adductor muscle (PA) and, internal to this, a posterior pedal retractor muscle (PPR) scar. The pallial line (PL) is indented from the shell margin and has a deep pallial sinus (PS) to accommodate the retracted siphons. The black dot in Figure 3 indicates the position of the only naticid drill hole found in any of the many collected empty shell valves of *P. elongata* on Middleton Beach.

More detailed views of the left (Figure 4(a)) and right (Figure 4(b)) hinge plates of *P. elongata* reveal a somewhat anteriorly aligned amphidetic ligament (L) located between

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**Figure 2.** *Paphies elongata*. (a) Lateral and (b) posterior views of the left shell valve. Also illustrated in (c) and (d) are the same views of *Donax columbella* drawn to approximately the same scale. a–b, the dorsoventral axis of the shell; x–y, the greatest shell width; small arrow indicates the position of the umbones; the angles suggest that the posterior face of the shell of *P. elongata* is slightly more elongate than in *D. columbella*. L, ligament of *D. columbella*. 
an anterior cardinal tooth (ACT) and a bifurcate posterior lateral tooth (PCT) in the left valve, each fitting into sockets (S) and locked in place posteriorly by either another indistinct posterior lateral tooth (PLT?) or a slight enlargement of this region of the shell valve. There is also a long anterior lateral tooth (ALT) in both valves.

A yet more detailed view of the hinge plate of the right valve of *P. elongata* (Figure 5) shows the structure of the amphidetic ligament. This diagram shows that the amphidetic ligament, arising from between the umbonal prodissocoanch (PR), comprises the inner ligament layer (ILL) only and is situated between left and right resilifers (RE). The anterior (AOLL) and posterior (POLL) outer ligament layers extend along the dorsal margin of the hinge plate and are covered by periostracum (P). In more detail too, the bifid nature of the posterior cardinal tooth (PCT) is made clearer as is its location between sockets (S). The anterior cardinal tooth (ACT) and the anterior lateral tooth (ALT) are separated by a narrow socket (S) and extend anteroventrally. As noted above, there is also either a delicate posterior lateral tooth (PLT?) or a slight thickening of the shell valve in this region.

**The siphons**

The siphons of *P. elongata* are illustrated from the posterior aspect in Figure 6(a). They are situated between and enclosed by the papillate margin of the middle mantle folds (MMF). The smaller conical exhalant siphon (ES) is fringed apically by approximately 20 tentacles,
Figure 4. *Paphies elongata*. Internal views of (a) the left and (b) the right hinge plates. ACT, anterior cardinal tooth; ALT, anterior lateral tooth; L, ligament; PCT, posterior cardinal tooth; PLT?, possible posterior lateral tooth; S, socket.

Figure 5. *Paphies elongata*. A more detailed view of the hinge plate of the right valve showing the structure of the ligament. ACT, anterior cardinal tooth; ALT, anterior lateral tooth; AOLL, anterior outer ligament layer; ILL, inner ligament layer; P, periostracum; PCT, posterior cardinal tooth; PLT?, possible posterior lateral tooth; POLL, posterior outer ligament layer; PR, prodissococonch; RE, resilifer; S, socket.
which extend outwards. The more dorsal four of these are longer, the more ventral ones much shorter and, generally, those between them are of intermediate size. The marginal apex of the larger inhalant siphon (IS) is fringed internally and externally by a large number of small papillae but extending inwards, forming a mesh across the siphonal aperture, are eight large, alternately leafed, tentacles. The inhalant and exhalant siphons are shown in lateral aspect in Figure 6(b) and 6(c) (IS, ES), respectively. In this side, view only the inhalant’s apical fringe of papillae are obvious whereas the exhalant’s papillae are shown to arise from beneath the apex of the aperture. It should also be noted that the siphons are transparent white, although the ventral surface of the exhalant is coloured a light pinkish-red. One of the eight largest inhalant siphonal tentacles is illustrated in greater detail in Figure 6(d) and is shown to be basally encircled by the siphon’s marginal papillae and to
comprise an alternately leafed main stem. The much longer siphons of *M. mactroides* have been described and illustrated by Narchi (1981, figs 1 and 3); have been shown to be capable of being regenerated (Nuñez et al. 2010) as, coincidentally, are the siphons of the donacid *D. hanleyanus* (Luzzatto and Penchaszadeh 2001).

**The mantle**

A transverse section through the right ventral mantle margin of the pedal gape of *P. elongata* is illustrated in Figure 7. The mantle margin comprises the usual three folds identified by Yonge (1957, 1982b); that is, outer (OMF), middle (MMF) and inner (IMF), although the latter are divided into a larger inner component (IMF(1)) and a smaller outer element (IMF(2)). Between the larger outer mantle fold and the outer surface of the middle fold arises the periostracum (P) from the base of the periostracal groove (PG). Identifiable is a small pallial nerve (PN) and the deeply inset pallial retractor muscles (PRM) extend mainly into the inner fold. In this location, i.e. where left and right mantle lobes are not fused at the pedal gape, there is a ciliated rejectory tract (RT) situated between the general mantle surface and the inner surface of the inner component of the inner mantle fold (IMF(1)). The mantle margins seem to lack any glandular structures, typical of many bivalves, although the middle mantle fold (MMF) is papillate as illustrated in Figure 6(a) where it flanks, left and right, the base of the siphons.

The siphons of *P. elongata* are thus formed by fusion of the outer components of the inner mantle folds only, this being type A mantle fusion of Yonge (1957, 1982b), and this is illustrated in Figure 8, which is a transverse section through the fused ventral mantle margin posterior to the pedal gape. The fused outer components of the inner mantle folds (FIMF(2)) are cross-connected by an array of muscle units, creating a solid muscular floor to the infra-branchial chamber of the mantle cavity. There are here basophilic clusters of sub-epithelial secretory cells (SC) – probably producing mucus. Once again the middle mantle folds (MMF) are small and secrete the periostracum (P) against the template of the outer folds (OMF). The pallial retractor muscles (PRM) are united, presumably more firmly, to the inner surface of the shell by transverse muscle connectives (TC). Of most interest, however, is that here at the ventral base of the infra-branchial chamber of the mantle cavity, left and right inner components of the inner mantle folds (IMF(1)) are delicate and overarch to form a cavity that represents the fused rejectory tracts (FRT) that are more widely separated more anteriorly (Figure 7). Such an arrangement has also been demonstrated for the mactrids *M. reevesii* (Gray) by Barnes and Morton (1996) and for *R. pulchella* by Morton (2010).

**The organs of the mantle cavity**

The organs of the mantle cavity of *P. elongata* are illustrated from the left side in Figure 9(a) after removal of the left shell valve and mantle lobe. The lightly plicate ctenidia comprise large, anteriorly directed, inner demibranchs (ID) and smaller, more ventrally directed outer demibranchs (OD). They cover the visceral mass entirely, but the foot (F), when extended, is large and spade-shaped, this form arising from a pointed ‘heel’ (HF) and a similarly pointed dorsal extension (DEF) to the foot. The fused mantle margin (FMM) is seen to extend towards the base of the inhalant siphon (IS) with the exhalant (ES) located above it. Only the anteriormost component of the anterior muscle
Figure 7. *Paphies elongata*. A transverse section through the right ventral mantle margin of the pedal gape. IMF(1), inner mantle fold (inner component); IMF(2), inner mantle fold (outer component); MMF, middle mantle fold; OMF, outer mantle fold; P, periostracum; PN, pallial nerve; PRM, pallial retractor muscle; RT, rejectory tract.
(AA(1)) can be seen although the posterior adductor (PA) and anterior and posterior pedal retractor muscles (APR, PPR) are obvious. The labial palps are small, only the outer (OLP) being visible, the inner situated beneath a somewhat transparent supra-axial extension of the outer demibranch (SAE), as will be illustrated in greater detail in Figure 10. Figure 9(b) is a diagrammatic representation of a transverse section through the left ctenidium showing the ciliary currents. The inner demibranch (ID) has a ventral marginal food groove (VMFG, ●) but there is weak orally directed current (O) in the junction between the ascending lamella of this demibranch and the visceral mass. The ctenidial axis (CA) also has an orally directed ciliary current (●) and this fed by upward currents on the descending lamellae of both inner and outer (OD) demibranchs. The ciliary currents of the ascending lamella of the outer demibranch and its supra-axial extension (SAE) are all downwardly directed, turning upwards towards the ctenidial axis at its ventral margin. This pattern of ctenidial ciliation was identified as Type C(1) by Atkins (1937) and is typical of many representatives of the heterodont Eulamellibranchia.
Figure 10 is a more detailed view of the ciliary currents of the ctenidium and the ctenidial-labial palp junction of \textit{P. elongata}, but this time seen from the right side. The ctenidia are situated between the anteriormost element of the anterior adductor muscle (AA(1)), the reflected outer labial palp (OLP) hiding the smaller inner component, and the larger posterior adductor muscle (PA) and their equivalent pedal retractor muscles (APR, PPR). The ctenidia are connected to the visceral mass (VM) at the ctenidial axis (CA) in which there is an orally directed ciliary tract. The supra-axial extension (SAE) of the outer demibranch is filamentous only posteriorly, the anterior component of it being smooth and possessing only a light ciliation. It connects to the visceral mass at its union with the mantle (PALOD) with what is now seen as a weak orally directed current. The anterior foreshortening of the outer demibranch, also seen in \textit{Clinocardium nuttallii} (Conrad) (Stasek 1963, fig. 1d) creates a ctenidial-labial palp junction of Category II (Stasek 1963) in which only the tips of the filaments of the inner demibranchs (ID) are situated between the bases of the labial palps (ILP, OLP). Figure 10 shows that the main supplier of potential particles of food to the labial palps and, possibly, eventually, to the mouth (M) situated beneath the anterior adductor muscle, are the ciliary currents in the ventral marginal food groove of the inner demibranch (VMFG) and the ctenidial axis (CA). As noted earlier, the labial palps are small, but they still possess ciliary sorting currents on ridges that form their inner surfaces to effect the processes of sorting and selecting for either rejection or acceptance of those particles of potential food that the ctenidia deliver to them.
The musculature

When the ctenidia of *P. elongata* are removed to reveal the visceral mass (VM), the anterodorsal muscle complex is exposed (Figure 11). The two elements of the anterior adductor muscle (AA(1), AA(2)) are shown to abut closely against a small anterior pedal protractor muscle (APP) which, in turn, is similarly closely adjacent to an anterior pedal retractor muscle (APR) – both occurring, of course, as left and right pairs. There is, however, also seen an array of fine fibres of, similarly paired, anterior pedal elevator muscles (APEM) that must fine tune the digging activities and cycles of the foot.

The ciliary currents of the visceral mass and mantle

The ciliary currents of the visceral mass of *P. elongata*, as seen from the left side, are illustrated in Figure 12. The enormous foot (F) of *P. elongata*, with its pointed heel (HF) and similarly pointed dorsal edge (DEF), is dorsally confluent with the visceral mass (VM). The surface is ciliated and these are arranged on both left and right sides to beat in a circular pattern. That is, particles arriving with the inhalant stream are passed anteriorly at the dorsal margin of the visceral mass and beneath where the ascending lamellae of
the inner demibranchs unite with it (Figure 9(b)). Such moving particles of largely unwanted material then circulate downwards in an anti-clockwise direction and ventrally then pass backwards towards the posterior margin of the visceral mass. Here they fall off onto the left and right mantle lobes to be eventually discharged as pseudofaeces.

The ciliary currents of the left mantle lobe of *P. elongata* are complex (Figure 13). Those of the right mantle lobe, like those on the surface of the visceral mass, move in a circular manner. That is, particles entering the mantle cavity with the inhalant stream are in an anterior direction dorsally, beneath the junction of the ascending lamella of the outer demibranch with the mantle where it unites with the visceral mass (Figure 9(b)). These generally unwanted particles are then passed downwards where they are transported in an anti-clockwise direction, picking up any sand grains that may enter the mantle cavity via the pedal gape (PGS) during the burrowing process. Such material is then passed in a posterior direction along the rejectory currents of the fused ventral mantle margin. Here they are, however, enclosed within the sub-chamber created by the over-arching inner components of the inner mantle folds illustrated in transverse section in Figure 8, IMF(1). Finally this unwanted material is rejected from the mantle cavity as pseudofaeces via the inhalant siphon. Figure 14 is an interior view (in part) of the floor of the supra-branchial chamber of

![Diagram](image-url)

**Figure 11.** *Paphies elongata*. A more detailed illustration of the anterior adductor muscle complex. AA(1), anterior adductor muscle (1); AA(2), anterior adductor muscle (2); APEM, anterior pedal elevator muscles; APP, anterior pedal protractor muscle; APR, anterior pedal retractor muscle scar; VM, visceral mass.
Figure 12. *Paphies elongata*. The ciliary currents of the visceral mass as seen from the left side. AA(1), anterior adductor muscle(1); AA(2), anterior adductor muscle(2); APR, anterior pedal retractor muscle; DEF, dorsal extension of the foot; F, foot; HF, heel of the foot; PA, posterior adductor muscle; PPR, posterior pedal retractor muscle; PR, prodissoconch; PS, pallial sinus; VM, visceral mass.

Figure 13. *Paphies elongata*. The ciliary currents of the left mantle lobe. AA(1), anterior adductor muscle(1); AA(2), anterior adductor muscle(2); APR, anterior pedal retractor muscle; PA, posterior adductor muscle; PGS, pedal gape sinus scar; PL, pallial line; PPR, posterior pedal retractor muscle; PR, prodissoconch; PS, pallial sinus.
the mantle cavity. It shows the pedal gape (PGA) anteriorly and the inner components of the inner mantle folds (IMF(1)) over-arching the fused outer components of the inner mantle folds (FIMF(2)) and the inhalant siphon (IS) towards which unwanted particles are being directed for expulsion from the mantle cavity. Figure 14 will be returned to.

The organs of the visceral mass

The course of the intestine in the visceral mass of *P. elongata*, as seen from the right side, is illustrated in Figure 15. The visceral mass is situated between the anterior and posterior adductor muscles (AA(1), PA). As described earlier, the mouth (Figure 10, M) is located beneath the anterior adductor where it abuts the anterior pedal retractor muscle (APR). It opens into a short oesophagus that, in turn, opens into the stomach that is hidden by its surrounding brown digestive diverticulae (DD). The stomach of this species is not described herein because equivalent structures have been described in detail for at least four mesodesmatids and all of which are similar not only to each other but also *P. elongata*. These are the Asian *Atactodea striata* (Gmelin) (personal observations) and *Caecella chinensis* (Deshayes) (Narchi 1980), the West African *Galatea paradox* Purchon (1963), the North American *M. arctatum* (Allen 1975, fig. 4) and the South American surf dwelling *M. mactroides* Narchi (1981, fig. 13). Narchi (1981) showed that the stomach of *M. mactroides* and thus also *P. elongata* was of Type V as defined by Purchon (1960). Such a stomach, including that of *P. elongata* (as herein identified) has a large number of complex sorting areas and numerous openings into the digestive diverticulae. It is clearly functioning to select and transport extremely fine particles of accepted food material from the inhalant stream. The stomachs of representatives of the Donacidae, for example *D. hanleyanus*, also have a stomach of Type V with numerous sorting areas (Narchi 1978), suggesting the same strategy of feeding on fine particles.

As in *M. mactroides* (Narchi 1981), the crystalline style sac (CSS) and an initially expanded region of the mid gut (EMG) of *P. elongata* make separate exits from the stomach. The narrowed mid gut (MG) makes a simple turn in the ventral region of the visceral mass before passing dorsally as the hind gut (HG), looping over the digestive diverticulae and then turning in a posterior direction to penetrate the ventricle of the heart (H) as the rectum (R), passing between the paired posterior pedal retractor muscles (PPR) and over the posterior adductor muscle (PA) to terminate on its posterior face as an anus (AN) situated at the end of a free terminal portion of the rectum. The intestine of *P. elongata* is essentially the same in *M. arctatum* and *M. mactroides* (Allen 1975, fig. 2, Narchi 1981, fig. 12).

The pedal ganglia and statocysts

The pedal ganglia (PEG) of *P. elongata* are illustrated in transverse section in Figure 16(a). The paired pedal ganglia at the junction of the visceral mass and foot make connection with the cerebral ganglia via the cerebro-pleural connective nerves (C-P-CONN). From the pedal ganglia arise left and right pedal nerves (PEN). There are no statocysts, in other bivalve taxa located externally and dorsolaterally to the pedal ganglia, as for example in representatives of the Anomalodesmata and as described by Morton (1985). Rather, there appears to be located within each ganglion, internal to where the cerebro-pleural connectives join with them, a pair of putative statocysts (STA) that contain a single, cell-
Figure 14. *Paphies elongata*. An interior view of the fused ventral mantle margin posterior to the pedal gape and showing the rejectory tract. This figure also illustrates the posterior adductor muscle and the visceral ganglia beneath it. AN, anus; AVG, accessory visceral ganglia; FIMF(2), fused inner mantle folds (outer component); IMF(1), inner mantle fold (inner component); IS, inhalant siphon; PA (1), posterior adductor muscle (anterior component); PA(2), posterior adductor muscle (posterior component); PGA, pedal gape; R, rectum; RT, rejectory tract; SN, siphonal nerve; SRM, siphonal retractor muscles; VG, visceral ganglia; VG-AVG-CONN, visceral ganglia-accessory visceral ganglia connective.
Figure 15. *Paphies elongata*. The course of the intestine in the visceral mass as seen from the right side. AA(1), anterior adductor muscle(1); AN, anus; APR, anterior pedal retractor muscle; CSS, crystalline style sac; DD, digestive diverticulae; DEF, dorsal extension of the foot; EMG, expanded region of the mid gut; F, foot; G, gonad; H, heart; HF, heel of the foot; HG, hind gut; M, mouth; MG, mid gut; PA, posterior adductor muscle; PPR, posterior pedal retractor muscle; R, rectum.

Figure 16. *Paphies elongata*. (a) A transverse section through the pedal ganglia showing the position of two putative statocysts. (b) A single putative statocyst illustrated in greater detail. C-P-CONN, cerebro-pleural-visceral ganglia-connective; PEG, pedal ganglia; PEN, pedal nerve; STA, statolith; STC, statocyst.
like, nucleated statoconia (STC) within a vacuolated chamber. This unusual structure is illustrated in greater detail in Figure 16(b).

The visceral ganglia

Returning to Figure 14: in addition to showing and describing the ventral mantle margin and the ventral mantle rejectory tract of *P. elongata*, it also illustrates an interior view of the posterior adductor muscle and the visceral ganglia. The posterior adductor muscle is actually like the anterior adductor muscle, divided into two elements (*Figure 14, PA(1) and PA(2)*), but this not so obvious except when seen from this perspective. From beneath the posterior arise the siphonal retractor muscles (SRM) that find attachment on the shell valves at the pallial sinus. The inner components of the inner mantle folds (IMF(1)) with their rejectory tracts (RT) also continue, from their mid-ventral base, around the lateroventral margins of the posterior adductor muscle (PA(1)), keeping this area of the supra-branchial chamber free of unwanted material too.

Situated on the floor of the posterior adductor muscle of *P. elongata* are the paired visceral ganglia (VG). Anteriorly, these will connect with the cerebral ganglia. There are, however, on the second component of the posterior adductor muscle (PA(2)), a second pair of accessory visceral ganglia (AVG), which connect with the true ganglia by means of fine nerves (VG-AVG-CONN). These accessory ganglia arise just beneath the point where the rectum (R) separates from the posterior adductor muscle to terminate in its free anus (AN). Siphonal nerves (SN) arise from the true visceral ganglia and other fine nerves arise from the connective between these ganglia and their accessory structures and from the latter themselves and probably also help in co-ordination of the siphonal apparatus. Narchi (1981, fig. 4) described similar structures to the visceral ganglia’s accessory ganglia for *M. mactroides* but called them siphonal hearts. Whether these are same as the structures described herein for *P. elongata* is unknown.

The organs of the pericardium

The organs of the pericardium of *P. elongata*, as seen from the right side, are illustrated in *Figure 17*. The pericardium is located in the embayment under the posterior lateral tooth of the hinge plate and anterior to the posterior pedal retractor (PPR) and posterior adductor (PA) muscles. The pericardium contains the heart, which comprises a single ventricle (V) that is penetrated by the rectum (R). The epithelia of the left and right auricles contain elements of the light brown-pigmented pericardial gland (AU+PE). The paired kidneys (K) are located on the anterior faces of the posterior pedal retractor muscles and the reno-pericardial apertures (R-PA) open into them at the posteroventral edge of the pericardium. The renal apertures (RA) open into the component of the infra-branchial chamber between the ctenidial axis (CA) and the point of attachment of the ascending lamella of the outer demibranch with the visceral mass/mantle (PALOD). The point of attachment on the visceral mass (VM) of the ascending lamella of the inner demibranch (PALID) is marked by tissue remnants following removal of the ctenidium to expose the pericardium.

*Paphies elongata* is dioecious, the paired gonads (G) occupying most of the visceral mass surrounding the intestine and the digestive diverticulae (DD). The paired gonadial
apertures (GA) open into the same component of the supra-branchial chamber as the also paired renal apertures (RA), but just anterior to these.

**Discussion**

Jones et al. (2007) record that there are about 8000 ocean beaches in Australia, and it is likely that all of these will be occupied by either one or more species of *Donax* (Donacidae) and either *P. altenai* or *P. elongata* (Mesodesmatidae) in the tropical north or more temperate south, respectively. *Paphies altenai* and *P. elongata* are endemic to Australia whereas species of *Donax* occur virtually worldwide throughout the tropics and temperate zones, their choice of habitat being determined by particle grain size (De La Huz et al. 2002). Sand is granular and non-cohesive, enabling grains to be moved more easily relative to each other, and macrofaunal burrowers, such as species of *Donax* and, it

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**Figure 17. Paphies elongata.** The organs of the pericardium as seen from the right side. AN, anus; AU, auricle; CA, ctenidial axis; DD, digestive diverticulae; G, gonad; GA, gonadial aperture; K, kidney; PA, posterior adductor muscle; PALID, point of attachment of the ascending lamella of the inner demibranch to the visceral mass; PALOD, point of attachment of the ascending lamella of the outer demibranch to the mantle; PG, pericardial gland; PPR, posterior pedal retractor muscle; PR, prosisococonch; R, rectum; RA, renal aperture; R-PA, reno-pericardial aperture; V, ventricle; VM, visceral mass.
is assumed (as will be discussed), *P. elongata*, use the re-arrangement of such grains in order to burrow rapidly (Dorgan 2015). Further, however, exposed sandy beaches are surface-solid so that fine particles of detritus can settle out upon them as waves recede but are light enough to be put back into suspension with each new wave swash. Morton (2011) showed how on the 80-mile beach at Broome in north-western Western Australia the nassariid gastropod *Nassarius bicallosus* (E.A. Smith) feeds on the fine film of detritus that layers the surface of the shore as waves recede.

When such detritus is put back into, albeit temporary, suspension by each breaking wave, the same habitat, such as Middleton Bay Beach, and its detrital food resources are exploited by species of *Donax* and *P. elongata*. These two taxa have thus evolved to here suspension feed by tidally following the fate of such seston as it changes its location with each wave and each tide.

**Ecological significance**

The many studies on species of *Donax* have highlighted the productivity that can be engendered by them on their natal beaches and Laudien et al. (2003) demonstrated that on highly exposed Namibian sandy beaches, *Donax serra* achieves biomasses of between 141–546 ash-free dry mass (AFDM) per m² per year, underlining the importance of these surf clams for the beach-surf ecosystem. As a consequence, predation upon surf clams is from many sources including a variety of other marine organisms and bird life. For example, Luzzatto and Penchaszadeh (2001) showed that on Argentinian wave-exposed beaches *D. hanleyanus* suffered siphon nipping by fishes, but that they could be regenerated. Salas et al. (2001) showed that on the surf beaches of southern Spain, *Donax trunculus* Linnaeus suffered from sub-lethal foot nipping by crabs, notably *Portumnus latipes* (Pennant). Smith (1975) showed that, on Sanilbel Island, Florida, *D. variabilis* is predated extensively by the high-shore ghost crab *Ocypode ceratophthalma* (Pallas). Gulls, oystercatchers and sanderlings are also known to prey on various species of *Donax* (Ansell 1983). And, on Florida and other Gulf of Mexico beaches, *D. variabilis* is also predated upon by ruddy turnstones, *Arenaria interpres* (Linnaeus), and sanderlings, *Calidris alba* (Pallas) – the former picking the valves open, the latter swallowing individuals whole (Loesch 1957; Smith 1975; Schneider 1982).

In contrast to this plethora of information on the many species of *Donax*, there are many fewer publications on the wave-exposed beach species of the Mesodesmatidae. The only study of this aspect of South American beaches is that of Nuñez et al. (2010), showing how siphon nipping by fishes facilitates the lethal predation of *M. mactroides*.

On Australian beaches, Laws and Laws (1972) showed how *Donacilla angusta* (= *P. elongata*) is preyed upon by the shell-drilling naticid *Polinices conicus* (= *Conuber conicum* [Lamarck]) along surf beaches near Adelaide, South Australia. Morton (2008) showed that *P. elongata* was less obvious on the highly exposed Blue Lake Beach on North Stradbroke Island, Queensland. Here, the significant bivalve was the large pipi, *Donax deltoides* Lamarck, juveniles of which were predated upon by the shell-drilling naticid *Polinices incei* (Philippi) – surfing up the beach to catch its prey just like them but in their case to avoid predation. Instead, *P. elongata* was dominant on the somewhat less exposed Frenchman’s Bay, Home Beach, Main Beach and Cylinder...
Beach, close by. On these beaches, as reported by Laws and Laws (1972), it was predated upon by the shell-drilling *Polinices conicum*, but this is more likely to be *C. incei* (pers. obs.). On the similarly slightly more sheltered Middleton Bay Beach, in south-western Western Australia, *P. elongata* shares this habitat with a pipi but here the small (<13.5 mm) *D. collumbella*. From this beach, unlike in South Australia and Queensland where *P. elongata* is said to be heavily predated by *P. conicum*, but actually, *C. incei*, only one example of shell drilling was detected (Figure 3), but by an unknown naticid predator. Wells and Bryce (2000) record 11 naticid species, but the eastern Australian endemic *C. incei* is not one of these and, hence, the perpetrator of the above event and the almost non-existent predation upon these Middleton Bay Beach bivalves remains to be explained.

**Anatomical comparisons**

Table 1 is a compendium of many of the anatomical characteristics of species of Donacidae and Mesodesmatidae with reference in the case of the latter family to those taxa, *Paphies* and *Mesodesma*, which, like *Donax*, occupy wave-exposed beaches in South America and Australia (and New Zealand) and Northern Europe. Allen (1975) and Yonge and Allen (1985), and Narchi (1981) described the anatomies of *M. arctatum* and *M. mactroides* from surf beaches in the north-west Atlantic and Brazil, respectively. Table 1 shows that mesodesmatids and donacids, despite both having aragonitic shell mineralogies, have different structures: two and three layers, respectively. Typically, the former are largely smooth externally, some of the latter (but no means all), are also at least partially radially ribbed. As alluded to earlier and as will be demonstrated further, their shell forms are similar, although mesodematids have an internal ligament, donacids an external one. Their arrangements of the hinge teeth are similar but not identical. Similarly, they both share similar musculatures, this being related to the similar complex digging movements each must make in order to occupy successfully such a dynamic, wave-exposed, habitat. Trueman (1971) showed for *Donax denticulatus* that tactile responses of the foot initiate burrowing, pedal stretch receptors control the duration of each digging cycle, and that the digging cycle is programmed within the nervous system without peripheral feedback. Presumably, given the same complex musculature (this study), the same mechanisms are at work with *P. elongata*.

Being a tellinoidean, species of *Donax* possess cruciform muscles posteroventrally in the mantle margin (Yonge 1949; Keen 1969b) whereas mesodesmatids do not. Nevertheless, both have simple fusions of type A (Yonge 1948b). The siphons are not especially long, commensurate with the shallow-burrowing lifestyle of both donacids and mesodesmatids, although those of *M. mactroides* are especially and unusually long (Narchi 1981, fig. 1). Appropriate for their suspension habits, the ctenidial ciliation of both taxa are of type C(1) (Atkins 1937) and their labial palps are generally small. The ctenidial-labial palp junctions of these donacids and mesodesmatids are subtly different, type II and III, respectively, but this difference is small (Stasek 1963) in reality. Finally, they both have exceedingly short intestines and stomachs that are replete with sorting areas to exploit the finest particles of detritus collected by the inhalant streams (Purchon 1960).
Table 1. A comparison of the anatomical features of the Mesodesmatidae (*Paphies elongata; Mesodesma mactroides*) and the Donacidae (*Donax hanleyanus; D. gemmula*).

| Character                        | Mesodesmatidae                          | Donacidae                          | References                        |
|----------------------------------|-----------------------------------------|------------------------------------|-----------------------------------|
| Fossil record                    | Cenozoic: Eocene (34–56 mya)            | Mesozoic: Upper Cretaceous (65–100 mya) | Keen (1969a, 1969b)               |
| Distribution                     | Near global, tropical/temperate         | Near global, tropical/temperate     | This study; Ansell (1983)          |
| Habitat                          | Intertidal, exposed sandy beaches       | Intertidal and shallow subtidal of exposed sandy beaches | This study, Ansell (1983)          |
| Lifestyle                        | Intertidally migrating suspension feeders | Intertidally migrating suspension feeders | This study, Ansell (1983)          |
| Shell mineralogy                 | Aragonitic                              | Aragonitic                         | Taylor et al. (1973)              |
| Shell microstructure             | Two layers                              | Three layers                       | Taylor et al. (1973)              |
| Outer layer, crossed lamellar    | Inner layer, complex crossed lamellar   |                                    |                                   |
| Inner layer, complex crossed lamellar |                                  |                                    |                                   |
| Outer shell surface              | Smooth, never marginally denticulate/crenulate | Smooth or radial sculpture, characteristically wedge-shaped in intertidal species; more streamlined equitable in subtidal species, often marginally denticulate | This study, Narchi (1981), Ansell (1983) |
| Shell form                       | Subtrigonal, anteriorly elongate, posteriorly squared | Subtrigonal, anteriorly elongate, posteriorly squared | This study, Narchi (1981), Passos and Domaneschi (2004) |
| Ligament                         | Inner ligament layer internal, amphidetic | External, parivincular, posteriorly opisthodetic | This study, Narchi (1981), Passos and Domaneschi (2004) |
| Hinge teeth                      | Two cardinals teeth, single posterior lateral tooth | Two cardinal teeth, anterior and posterior lateral teeth | This study, Narchi (1981), Passos and Domaneschi (2004) |
| Musculature                      | Both adductor muscles divided; anterior and posterior pedal retractor muscles; anterior pedal elevator muscles; anterior pedal protractor muscles present | Both adductor muscles not divided; anterior and posterior pedal retractor muscles; anterior pedal elevator muscles; anterior pedal protractor muscles present | This study, Yonge (1949), Pohl (1967), Wade (1967, 1969), Narchi (1978, 1981), Moueza and Frenkel (1974), Passos and Domaneschi (2004), Ansell (1981, 1985) |
| Mantle margins                   | Inner folds duplicated Cruciform muscles absent | Inner fold (or alternatively interpreted as middle folds) duplicated Cruciform muscles present | This study, Narchi (1981), Passos and Domaneschi (2004), Ansell (1981, 1985) |
| Mantle fusions                   | Outer components of the inner folds only (Type A) Separate: relatively short (Mesodesma) | Inner folds only (Type A) Separate: relatively short | Yonge (1957, 1982b); This study, Ansell (1981, 1985) |
| Siphons                          | Ctenidial category                      | Ctenidial category                 | This study, Narchi (1981), Passos and Domaneschi (2004), Atkins (1937), Ansell (1981, 1985) |
| Cenidial labial palp junction    | Type II                                 | Type III                           | Stasek (1963)                     |
| Labial palps                     | Small                                   | Small                              | This study, Narchi (1981), Passos and Domaneschi (2004), Ansell (1981, 1985) |
| Intestine                        | Separate style sac and mid gut          | Separate style sac and mid gut     | This study, Narchi (1981), Passos and Domaneschi (2004), Ansell (1981, 1985) |
| Stomach type                     | Type V                                  | Type IV or V                       | Purchon (1963)                    |
| Sexual strategy                  | Dioecious                               | Dioecious                          | Ansell (1983)                     |
Convergence

Biologists often distinguish between parallel and convergent evolution. This distinction generally assumes that when a given phenotype evolves, the underlying genetic mechanisms are different in closely related and distantly related species, respectively (Arendt and Reznick 2008). Another term, repeated evolution, has been used when similar behaviours and physiologies are encountered between closely related taxa, that is, it is similar to parallel evolution (Ord and Summers (2015). Notwithstanding this genetic and terminological debate, Arendt and Reznick (2008) concluded that all instances of the independent evolution of a given phenotype can be described using a single term, convergence, and this term is used herein with respect to P. elongata (Mesodesmatidae) and species of Donax (Donacidae) in the following discussion.

The Donacidae evolved in the Upper Cretaceous of the Mesozoic and the Mesodesmatidae in the Eocene of the Cenozoic (Keen 1969a, 1969b). Their origins are thus some 50 million years apart. Although as shown herein for species of Donax and P. elongata their shells are remarkably similar in overall form, the different structures of the hinge plates easily distinguish them in the fossil record. This allowed Stanley (1977, table 11) to confirm Keen’s ancestral dates for the two families. More modern fossils of both taxa, for example D. serra from the Miocene to early Pliocene (~5 mya) of South Africa (Kensley and Pether 1986; Le Roux 1993), and Mesodesma donacium (Lamarck) from the Holocene and Middle Pleistocene (<1.8 mya) of Chile (Riascos et al. 2009), confuse the issue because these records relate to relatively modern changes in the distribution of the beaches themselves and, thus, secondarily, the fauna that colonizes them over time.

Representatives of both families have thus evolved both temporally and spatially to exploit the niche of high-energy beaches virtually worldwide and, thereby, to access a singular food resource of fine particles of detritus held in suspension by crashing waves. This convergence is illustrated diagrammatically in Figure 18, which provides a comparison of the basic anatomy of P. elongata (Figure 18(a) and 18(b)) compared with that of D. hanleyanus (Figure 18(c) and 18(d)). Figure 18(a) and 18(c) are views of the apertures of the inhalant siphons showing how they both have an incurved dense array of tentacles and papillae that allow entry into the mantle cavity of fine particles but exclude sand grains. Figure 18(b) and 18(d) reveal the organization of the internal organs of the mantle cavity showing how the visceral mass and foot, the musculature, the orientation of the ctenidia (lightly plicate in P. elongata: deeply plicate in D. hanleyanus) and labial palps (smaller in P. elongata) are highly similar in both taxa (see earlier illustrations for labelling). Similarly, both species possess stomachs which are modified for the sorting and digestion of fine particles and belong to Type V (Purchon 1960). There are differences between the two taxa of course. Donax hanleyanus is clearly a slightly deeper burrower than P. elongata and this is reflected in the comparative depths of the pallial sinuses and lengths of the siphons. But, in my view, it is these differences that reinforce the similarities.

Species of Australian Hemidonax (Mörch) (Hemidonacidae Scarlato & Starobogatov) (Ponder et al. 1981), despite the evocative name, are unlike Donax (Donacidae) and P. elongata (Mesodesmatidae) in that constituent taxa occupy deeper, calmer waters and stable sands. The remarkable convergence seen in Donax and Paphies (and some other Atlantic mesodesmatid cousins) to life on wave-exposed sand beaches, however, attests
to the plasticity of the bivalve form, the morphological adaptability of this sub-class of Mollusca, and helps explain its success.

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Figure 18. The anatomy of *Paphies elongata* (a and b) compared with that of *Donax hanleyanus* (c and d), both drawn to the same relative scale (for actual scales see the earlier illustrations). (a) and (c) are views of the apertures of the inhalant siphons; (b) and (d) are the internal organs of the mantle cavity showing the visceral mass and foot, the musculature, the orientation of the ctenidia and labial palps and the simplified intestine. (c) is re-drawn after Luzzatto and Penchaszadeh (2001, fig. 1); (d) is a compendium of re-drawn figures from Narchi (1978). (See previous illustrations for interpretations of structure).
Disclosure statement

No potential conflict of interest was reported by the author.

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