PREY SIZE AND DRILL HOLE STEREOTYPY BY *CONUBER INCEI* (GASTROPODA: NATICIDAE) ATTACKING *PAPHIES ELONGATA* (BIVALVIA: MESODESMATIDAE) ON SURF BEACHES IN QUEENSLAND, AUSTRALIA

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Abstract   On Queensland's ocean beaches on North Stradbroke Island, the naticid gastropod Conuber incei *attacks both juvenile* Donax deltoides *and* Paphies elongata. *This study of prey size and drill hole locations in the latter species from five wave exposed beaches on the island suggests a high degree of stereotypy in contrast to the congeneric* C. conicum *inhabiting a sheltered muddy beach at Monkey Mia in Shark Bay, Western Australia. On this latter beach type, a wide range of prey was attacked at a variety of shell valve locations and with little evidence of stereotypy. In the case of* C. incei, *however, there is close evidence for prey size and drill hole stereotypy possibly arguing for, in such a situation, a greater degree of predator-prey intimacy and, thus, possibly, co-evolution.*

INTRODUCTION

That many representatives of the Naticidae principally attack species of the Bivalvia is well known although other prey can include foraminiferans, gastropods, for example *Umbonium vestiarium* (Linnaeus, 1758) on Malaysian sandy shores (Berry, 1984), and even the egg capsules of the dogfish *Scyliorhinus canicula* (Linnaeus, 1758) (Ansell, 1961) and the bodies of soldier crabs (Mictyridae) (Huelsken, 2011). Scaphopods, for example, *Ditrupa arietina* (O. F. Müller, 1776), have been added to this prey diversity by Morton & Salvador (2009), and this behaviour has, subsequently, also been recorded from the Miocene of the Netherlands (Klompmaker, 2011) and the Upper Cretaceous of Cuba (Villegas-Martín *et al.*, 2016).

To access the resident bivalves that naticids typically share their habitats with, they drill a countersunk borehole through the shell. This is achieved through a combination of mechanical drilling using the radula and chemical etching by secretions from an accessory boring organ (ABO) in the mouth (Ziegelmeier, 1954; Carriker & Williams, 1978; Carriker, 1981; Kabat, 1990). A review of the drilling mechanisms adopted by naticids was provided by Owen (1966). Drill holes are often made on the valve surface, sometimes above the nutritious visceral mass, that is, dorsally (Negus, 1975) or, in the case of some

representatives of the tropical genus *Conuber* (formerly *Polinices*), at the valve margin (Vermeij, 1980; Ansell & Morton, 1985; Mondal *et al.*, 2014).

There is a large literature on naticids and the biology of their predatory behaviours (Kabat, 1990). Intertidal naticids are typical inhabitants of relatively sheltered beaches and attack their prey underground. In sub-tropical Hong Kong such beaches possess a suite of naticids that partition the bivalve resources of their habitat (Ansell & Morton, 1985), typically in relation to shell thickness (Ansell & Morton, 1985). Similarly, Morton & Knapp (2004) showed that in the warm, shallow, waters off Florida, *Naticarius canrena* (Linnaeus, 1758) attacked ten species of bivalve prey at different locations on their valves. It fed principally, however, on *Chione elevata* (Say, 1822), the shells (both valves) of which it mainly drilled posterodorsally. In more temperate waters, resident naticids have a more conservative diet, Wiltse (1980) demonstrating that the larvae of *Polinices duplicatus* (Say, 1822) settle in close proximity to populations of its sole bivalve prey *Gemma gemma* (Totten, 1834).

In general, naticids are not usually regarded as bivalve prey specific. For example, Ansell (1960: fig. 3) demonstrated that, in addition to the examples provided above, *Natica alderi* Forbes, 1838 (=*Euspira nitida* [Donovan, 1804]), as with *N. canrena*, attacked 14 species of bivalves and that the valves of *Venus striatula* da Costa, 1778 (=*Chamelea gallina* [Linnaeus, 1758]), one of its

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principal prey items, were drilled over a wide area mid-ventrally. Conversely, in the deep waters off the Açores, *Timoclea ovata* (Pennant, 1777) was drilled by an unknown naticid, possibly *Natica prietoi* Hidalgo, 1873, at almost random locations all over both valves (Morton, 2009b). Ansell & Morton (1985) demonstrated that in Hong Kong two species of subtidal naticids, *Polinices melanostomus* (=*Mammilla melanostoma* [Gmelin, 1791]) and *Glossaulax* (=*Neverita*) *didyma* (Röding 1798), plus the intertidal *Polinices tumidus* (=*P. mammilla* [Linnaeus, 1758]) attacked a wide variety of bivalve prey some of which were accessed laterally while others were edge drilled at the valve margins. Mondal *et al.* (2014) provided a table of the incidences of bivalve edge, or marginal, shell drilling by naticids.

There is less written about naticid prey and drill hole siting stereotypy, although Kingsley-Smith *et al.* (2003) showed that *Natica pulchellus* Risso, 1826 is size selective in terms of their *Cerastoderma edule* (Linnaeus, 1758) prey, larger predators selecting both a greater and wider range of prey than smaller conspecifics. Notwithstanding, Kelley & Hansen (2003) suggested that, contrary to expectations, based on the hypothesis of escalation (Vermeij, 1987), no temporal trend of increasing stereotypy of drill hole site has occurred over geological time. With regard to extant taxa, however, Negus (1975: fig. 1) was one of the first to show that *Natica* (=*Euspira*) *catena* (da Costa, 1778) typically drilled the shells of its prey *Donax vittatus* (da Costa, 1778) dorsally above the internal location of the digestive diverticulae although some drill holes were located widely over the valve surfaces. Similar to the situation described by Negus (1975), Morton (2008) showed that on one of Queensland's highly wave-exposed beaches, Blue Lake Beach, *Polinces* (=*Conuber*) *incei* (Philippi, 1853), as with *E. catena* and *D. vittatus* above, drilled its prey, juveniles of *Donax deltoides* Lamarck, 1818, close to the shell's umbones.

The aims of this study were thus to determine: (i), at what shell location does *C. incei* drill its bivalve prey *P. elongata*; (ii), prey size preferences if any; (iii), and, therefore, whether only juveniles were being attacked (as with *D. deltoides*) and (iv), to compare the information obtained with that from another study of *Conuber conicum* (Lamarck, 1822) feeding on a wider range of bivalves on a sheltered beach at Monkey Mia in Shark Bay, Western Australia.

MATERIALS AND METHODS

The biology and anatomy of the mesodesmatid bivalve *Paphies elongata* (Reeve, 1854) from Middleton Bay Beach at Albany, Western Australia, has been studied recently by Morton (2016). Here, the species is sympatric with *Donax columbella* Lamarck, 1818 but the naticid *C. incei* is not present due to it being an eastern Australian endemic. In order to gauge the wider impact of *C. incei* on the bivalve inhabitants of Queensland's oceanic beaches, the author undertook a further study of those on North Stradbroke Island and from five of which all the empty shell valves of another resident bivalve, *P. elongata*, both drilled and undrilled (Table 1), were collected for later analysis and which have become the subjects of this paper. In contrast to the few individuals of juvenile *D. deltoides* attacked by *C. incei* (shell width mean: 12.19mm ±0.74, range: 1.6–22.3mm) on North Stradbroke Island's beaches, as described by Morton (2008), this study analyses the much greater numbers of drilled shelled valves of the sympatric mesodesmatid *P. elongata* which this predator also attacks. To achieve this, each beach was searched along its entire length for any shell valves of *P. elongata* and subsequently these were measured along their greatest shell lengths to the nearest 1mm and then separated into left and right undrilled and drilled valves. Significant differences in shell lengths among the drilled and undrilled shells of *P. elongata* from the five beaches were assessed using the Mann Whitney U test (SAS System, Version 9.4). After having verified normal distributions and homogeneity of variances of standardized shell sizes with Shapiro-Wilk's and Levene's tests, respectively, the differences in shell lengths of *P. elongata* between beaches were examined by one-way analysis of variance (ANOVA) for drilled and undrilled samples, independently. Tukey's Studentized Range (HSD) Tests were used for *post hoc* comparisons.

Finally, the locations of any drill holes in the left and right shell valves of *P. elongata* from all five beaches were plotted onto master outlines of them.

Green (1968) showed that on Crib Island, also in Queensland, the intertidal community of a sheltered estuarine shore was occupied by two naticids – *C. conicum* and *Conuber sordidum* (Swainson, 1821). The same was true for the

Table 1   *Paphies elongata*. Ranges and means of the shell lengths of drilled and undrilled individuals on Blue Lake Beach, Cylinder Beach, Frenchman's Bay, Home Beach and Main Beach, North Stradbroke Island, Queensland, Australia.

Location	Status	n	Mean shell length (mm)	SD	Range of shell length (mm)
Blue Lake Beach	Drilled	50	18.5	3.1	9.6–24.0
	Undrilled	91	18.8	2.6	13.3–25.5
Cylinder Beach	Drilled	65	17.7	2.1	12.3–22.9
	Undrilled	74	18.3	2.5	12.4–24.7
Frenchman's Bay	Drilled	43	19.3	2.7	14.5–25.8
	Undrilled	11	17.6	3.3	12.2–25.0
Home Beach	Drilled	54	18.1	2.3	11.1–22.6
	Undrilled	42	17.6	3.1	10.7–23.0
Main Beach	Drilled	74	18.2	2.8	11.0–26.3
	Undrilled	98	19.1	2.4	12.1–23.7
Means	Drilled	57	18.4	2.6	11.7–24.3
	Undrilled	63	18.3	2.8	11.9–24.4

shores of the sheltered, bay-facing, shores of North Stradbroke Island, for example the beach seaward of Myora Springs but, with limited time available, these two predators could not be studied here. *Conuber conicum* and its bivalve prey had, however, been studied previously from a sheltered sandflat at Monkey Mia, within Shark Bay, Western Australia, during the course of an experimental examination of the feeding behaviour of *Nassarius clarus* (Marratt, 1877). The location of this study beach is illustrated and described in Morton (2003: fig. 1) and, as with the Queensland beaches, the shells of all bivalves drilled by the resident *C. conicum*, again collected by beach walks along the different levels of the shore, were identified to species and the locations of any drill holes plotted onto master outlines of each one. In this location, undrilled and empty valves of all species were never found so that comparisons between drilled and undrilled specimens were impossible. This hitherto unpublished information is used herein as a comparison with the situation of *C. incei* feeding on *P. elongata* on North Stradbroke Island's ocean beaches.

RESULTS

Fig. 1 is a diagrammatic illustration of the right and left valves of individuals of *P. elongata* drilled by *C. incei* from Blue Lake Beach, Cylinder Beach, Frenchman's Bay, Home Beach and Main Beach on North Stradbroke Island. As is evident, most of the drill holes were focused around the umbones in significantly equal numbers for the left and right valves and this was true for all five beaches. Ten drill holes were identified on valves at somewhat greater distances from the umbones. These valves had a mean length of 14.8mm (range 11.2–17.3mm), which is less than the mean lengths of other umbone drilled shells (see below) of *P. elongata*. It seems possible that these smaller valves were drilled by juvenile individuals of *C. incei*, so that as they age their drilling skills are honed around the umbones and, thus, above the most nutritious digestive diverticulae. This may be fortuitous, however, and result from the naticid targeting that area of the shell which is the widest and thereby offering the largest area for applying to it the mouth and accessory boring organ. Furthermore, no incomplete drill holes were encountered suggesting a lack at these sites of intra-specific competion and the absence of interruptions (Hutchings & Herbert, 2013).

Table 1 records the data regarding drilled and undrilled shell lengths of *P. elongata* for the five beaches on North Stradbroke Island. The obtained shell length means suggest that there are no
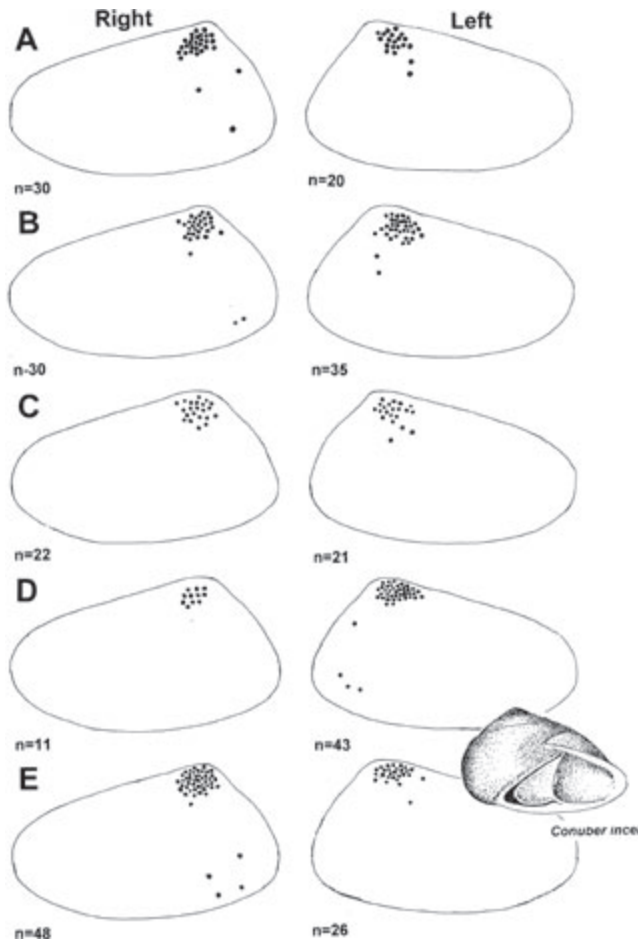
Figure 1 *Paphies elongata* — Diagrammatic illustrations of the right and left valves of individuals drilled by *Conuber incei* from Blue Lake Beach, Cylinder Beach, Frenchman's Bay, Home Beach and Main Beach (A–E, respectively), North Stradbroke Island, Queensland, Australia.

differences between either drilled or undrilled individuals and nor are there any differences in terms of the five sites. To test this further, Fig. 2 represents box and whisker plots of the shell lengths of drilled and undrilled individuals of *P. elongata* from the five Queensland beaches. In Fig. 2, the bottom and top edges of the boxes are drawn at the sample's 25th and 75th percentiles. The central horizontal line in each box is drawn at the 50th percentile, that is, the median value of shell length. The vertical lines, or whiskers, are drawn from each box to the most extreme point within the 1.5 interquartile ranges. Individual shell length values that are outside these ranges are identified by diamonds as statistical outliers. The results of the Mann Whitney U test showed no significant differences in shell length for four

of the Queensland beaches, except for Main Beach ($p < 0.05$) where the median shell length of undrilled shells was significant longer than that of the drilled shells. For undrilled shells, a statistically significant result of ANOVA ($p < 0.05$) was obtained only for Main Beach and Home Beach, which showed significant differences in mean shell length. For drilled shells, a statistically significant ANOVA result ($p < 0.05$) was obtained only for Frenchman's Bay and Cylinder Beach, which were identified as showing a significant difference in terms of mean shell length.

With the above two exceptions, therefore, the over-riding conclusion of this analysis is that *C. incei* is generally selective of its prey *P. elongata* in terms of shell length and, as described earlier, drill hole shell location.

In contrast, at Monkey Mia in Western Australia, *C. conicum* fed on a variety of bivalves (Fig. 3). These included *Pitar citrinus* (Lamarck, 1818), *Anomalodiscus squamosus* (Linnaeus, 1758), *Placamen gravescens* (Menke, 1843), *Circe tumefacta* G.B. Sowerby II, 1851, *Fragum unedo* (Linnaeus, 1758), *Callista chinensis* (Holten, 1802) and *Dosinia sculpta* (Hanley, 1845) (Fig. 3). This figure also suggests, however, that there is a hierarchy of choice, in that *P. citrinus* and *A. squamosus* were most preferred followed by the other bivalves, although this has to be viewed within the context of the fact that I was not permitted to collect living individuals in this World Heritage Site and the herein reported upon material had to be returned to the beach following shell valve measurements and identification of drill hole locations. The obtained information, however, further suggests that the two favoured prey had the greatest incidence of incomplete drill holes, possibly because of shell architecture but maybe, also, due to either intraspecific competition or disturbance.

Finally, Fig. 3 shows that for the favoured prey of *C. conicum* although there is the strong suggestion that most drill holes occurred around the umbones there was, overall, a wide range of attack sites all over the various shells and their valves. Unlike the situation with *C. incei* and *P. elongata*, however, not just the greater variety of potentially available prey species is of interest, but that being all less blade-like than the Stradbroke Island mesodesmatid, they are all to greater degrees more rotund and thus offer a greater shell area for attack by *C. conicum*.
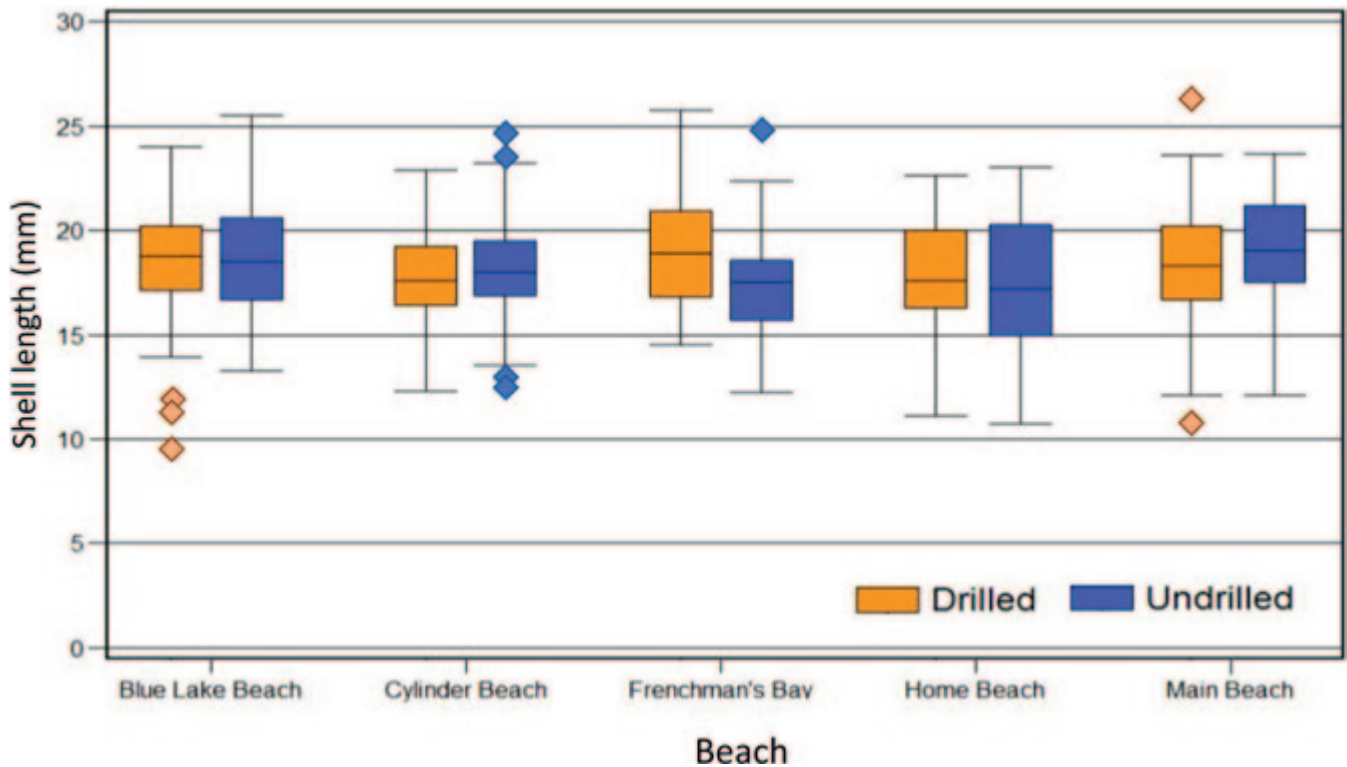
Figure 2 Box and whisker plots of the shell length of drilled and undrilled *Paphies elongata* individuals on Blue Lake Beach, Cylinder Beach, Frenchman's Bay, Home Beach and Main Beach, North Stradbroke Island, Queensland, Australia.

Discussion

Using laboratory-reared juveniles and under conditions that provided a choice between two potential prey species present in equal densities, Ansell (1984) showed that *E. catena* exhibited a strong preference for one of them. Furthermore, potential prey showed a smooth gradient of mean vulnerability when ranked in relation to the total number of reference prey species, reflecting the role of this naticid as a generalist feeder on bivalves in shallow sandy sediments. This appears to be the case too for *C. conicum* on the beach at Monkey Mia. Incomplete drill holes on bivalve shells are typically regarded as resulting from either the naticid giving up on the drilling process or being interrupted during it (Hutchings & Herbert, 2013). The former situation was most obvious, for example, with *Corbula crassa* (=*ovalina*) (Lamarck, 1818) in Hong Kong where not a single drill hole was completed by its (unknown) naticid predator due to the regular encounters in the drilling process by the proboscis with more inpenetrable conchiolin layers that characterise this species (Morton, 1990a) and

its congeners (Kardon, 1998) and some lucinids (Ishikawa & Kase, 2007).

There is an element of confusion in the literature regarding naticid predation upon *P. elongata* on the open, wave exposed, beaches of Queensland. Laws & Laws (1972) described the escape response of *Donacilla angusta* Reeve, 1854 (=*P. elongata*) in the presence of the naticid *C. sordidum*. These authors illustrated juvenile individuals of *P. elongata* jumping out of the sand at the approach of *C. sordidum*. Firstly, this pattern of escape is the same as that seen in juvenile *D. deltoides* as described by Morton (2008). Secondly, the predator *C. sordidum* is an inhabitant of sheltered, muddy, beaches and not the wave-exposed sand beaches occupied by *P. elongata*. Thirdly, the illustration provided by Laws & Laws (1972: fig. 1) of this interaction shows a buried naticid that does not have the conical shell of *C. sordidum*, but has the disc-like form typical of *C. incei*. Evidence that *C. sordidum* is an inhabitant of sheltered beaches of sandy mud was provided by Booth (1995), who showed that its egg cases were adapted to tolerating low-oxygen level sediments
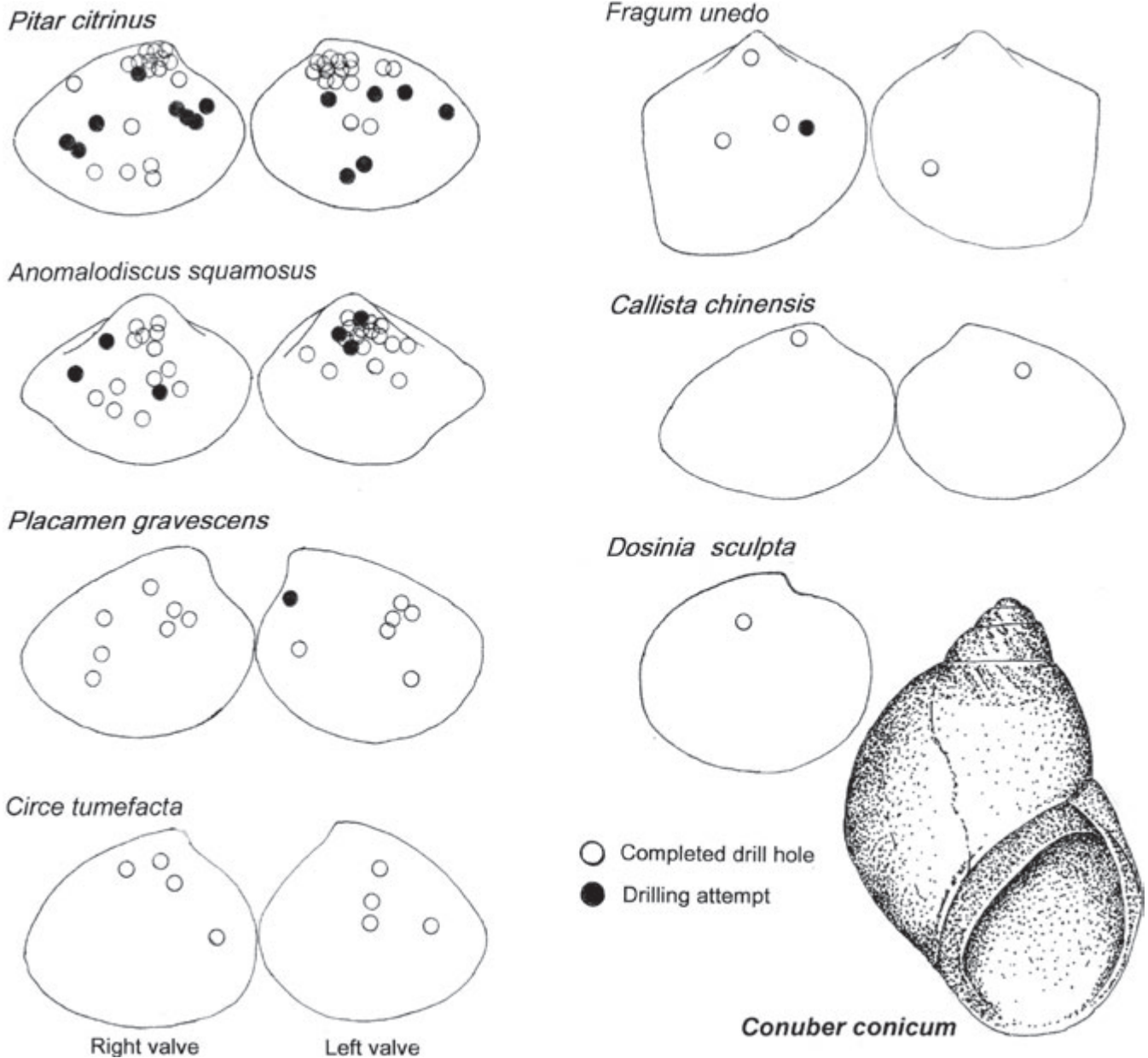
Figure 3 Left and right valves of seven species of bivalves drilled by *Conuber conicum* based on material collected from (and returned to) the beach of the World Heritage Site at Monkey Mia, Shark Bay, Western Australia.

and by Huelsken (2011) who suggested that it also fed on soldier crabs (Mictyridae) on such beaches.

Regardless, on the five Queensland beaches herein discussed, it was *C. incei* that was feeding on *P. elongata* in addition to juveniles of *D. deltoides* on Blue Lake Beach. In this context, Kitching & Pearson (1981) suggested that *C. incei* detects its bivalve prey by receiving 'sound' signals from them. Such a stimulus would more likely be vibrations as the prey items attempt to escape their predator as demonstrated by Laws

& Laws (1972) and Morton (2008) for *P. elongata* and *D. deltoides*, respectively.

This study reveals, however, a high degree of stereotypy exhibited by *C. incei*. This was first demonstrated for a few preyed-upon individuals of *D. deltoides* (Morton, 2008) but much more significantly, as demonstrated herein for *P. elongata*. Firstly, this study shows that on every one of the five beaches (Fig. 1), *C. incei* attacked *P. elongata* at the umbones (Morton, 2016: fig. 17) below the thickened hinge plate of the bivalve. Furthermore, the presumably average-sized *C.*

incei attacked left and right valves in equal proportions on all five beaches but it also generally chose virtually the same sized prey to attack on three of the five beaches. A similar situation has been encountered in the Açores where the shallow subtidal inhabitant of exposed beaches, *Ervilia castanea* (Montagu, 1803), was attacked in a stereotypical manner by *Natica* (=*Euspira*) *intricata* (Donovan, 1804) (Morton, 1990b) but at the postero-ventral region of both valves equally and, as here seen with regard to *P. elongata* and *C. incei*, with no incomplete drill holes.

It has been suggested by Hutchings & Herbert (2013) that naticid intraspecific competition leads to incomplete drill holes. As with the examples of *E. intricata* and *E. castanea* above, this is not the case with *C. incei*, however, as no incomplete drill holes in the *P. elongata* shells were ever encountered. This suggests a lack of either inter- or intra-specific competition with but a few *C. incei* free to attack the average-sized prey *P. elongata* of their choice.

Thus, although predatory naticids have followed the same general rules with regard to prey choice and size since the Mesozoic (Kitchell, 1985), with a direct relationship between cost-size benefits (Das *et al*., 2015), this study puts into focus the differences between those naticids inhabiting bivalve diverse, more muddy, sheltered habitats and those occupying, virtually exclusively, exposed sandy beaches inhabited by, in the case of Queensland, but two bivalves *D. deltoides* and *P. elongata*. On the former beach type, a wide variety of prey is attacked at a variety of shell locations and with little evidence of stereotypy. On the latter, however, there is close evidence for prey size and drill hole stereotypy arguing for, in such a situation, a greater degree of predator-prey intimacy and, possibly, co-evolution (DeAngelis *et al*., 1985).

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