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TERRESTRIAL HERMIT CRABS (ANOMURA: COENOBITIDAE) AS TAPHONOMIC AGENTS IN CIRCUM-TROPICAL COASTAL SITES

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Abstract

Hermit crabs are ever alert for more suitable shells to inhabit, but what this may mean for coastal shell middens has rarely been considered. Here, the impact of the most landward-based of hermit crab families, the tropical Coenobitidae, upon archaeological shell-bearing deposits is assessed using a case-study: the Neolithic Ugaga site from Fiji. At Ugaga, hermit crabs were found to have removed the majority of shells from the midden and had deposited their old, worn shells in return. The behavioural ecology of genus Coenobita suggests a mutualistic interaction whereby humans make available shell and food resources to hermit crabs, which in turn provide a site cleaning service by consuming human and domestic waste. Diagnostic indicators of terrestrial hermit crab wear patterns on gastropod shells are outlined and the conditions under which extensive 'hermitting' of shell midden deposits may occur are investigated. The ability to recognise hermit crab modification of shells is considered not only important for archaeomalacologists analysing tropical shell deposits, but also for field archaeologists wishing to select suitable shell samples for radiocarbon dating.

Keywords

Terrestrial hermit crabs, Coenobitidae, shell midden, tropical taphonomy, radiocarbon dating of marine shell

1. Introduction

Marine shell forms a conspicuous and important part of the archaeology of islands in the Asia-Pacific region. In the absence - and sometimes even the presence - of suitable sources of stone in many Island Asia-Pacific locations, shell was frequently utilized as a raw material for artefact manufacture. The ubiquity of shell midden within archaeological sites attests to the significance of shellfish as a food resource. Given the central importance of molluscan remains in Asia-Pacific archaeology, accurate identification, quantification and understanding of taphonomic processes is critical in providing robust interpretations of prehistoric behaviour.

A general range of taphonomic processes capable of modifying, transforming or destroying archaeological shell deposits has been identified in the archaeological literature and signatures of many of these have been recognized in the analysis of Asia-Pacific shell. Impacts of processes such as the dissolution of the calcium carbonate matrix of shell in acidic depositional contexts are widely recognized and have been used to explain the absence of shells in certain deposits in the Pacific (e.g. Green and Anson 2000(1998)). Disturbance of shell deposits by fauna, or 'faunalurbation' (after Claassen 1998:78), is equally well acknowledged, though is infrequently invoked by Pacific archaeologists as a possible explanatory mechanism for post-depositional modifications.

Given that many sites on the various islands of the Asia-Pacific region are in coastal locales, there is a plethora of coastal processes that can and do modify archaeological deposits. In terms of crustaceans as agents of disturbance, the impact of the burrowing activities of crabs has been recognised as affecting the integrity of deposits (e.g. Specht 1968, 1985; Green et al. 1967; Palmer 1965). Indeed they sometimes aiding in site recognition through the tendency of some crabs to redeposit sub-surface material upward to the surface (e.g. Kirch 1983:88). These observations acknowledge crabs' ability to confuse stratigraphy and potentially introduce non-cultural elements that fall into burrows, but members of another superfamily, the hermit crabs (Malacostraca: Paguroidea), are capable of physically removing cultural material from sites. The tropical family Coenobitidae is of particular interest, as the largely terrestrial nature of these species means they frequently occupy the same habitats as humans in the coastal zone.

Hermit crabs as agents of site transformation have not been extensively discussed in the archaeological literature. Carucci (1992) identified hermitted shells in deposits from Palau,

but did not pursue questions such as why the hermitted shells were present and what this meant for interpretation of shell middens. Scudder and Quitmyer (1998) assessed a shell-bearing site from the Cayman Islands, initially deemed archaeological, and posited that terrestrial hermit crabs rather than human meat extraction patterns, were responsible for holes observed in the body whorls of a number of the gastropods.

Despite these mentions, information regarding how to recognise terrestrial hermit crab modifications to shells, which types of shells and deposits are most likely to be affected and the potential ramifications for the interpretation of (putatively) archaeological shell-bearing deposits has not been clearly outlined in the archaeological literature.

This paper thus aims to highlight the deposit-transforming potential of terrestrial hermit crabs. Guidelines for recognising typical damage patterns caused by coenobitid hermit crabs are outlined and an investigation of coenobitid behavioural ecology addresses questions about the relationship between humans and coenobitids. A striking case study is considered: the highly-transformed shell-bearing deposit excavated from the Fijian Neolithic site of Ugaga. Evidence of coenobitid interference with cultural deposits is strong and prompts consideration of the circumstances under which this level of modification could occur and where this leaves archaeological interpretation.

2. Background to the Case Study Site

Ugaga is situated on the small (c. 250 m long), waterless Ugaga Island in Beqa lagoon to the south of Fiji's main island Viti Levu (see figure 1). Originally recorded by Crosby (1988), the open earthenware-bearing site of Ugaga was excavated in 1997 by Clark (1999). The site is on a small sand plain, with archaeological deposits being found over an area of approximately 30 m by 35 m. A total of fifty-seven 1x1 m squares was excavated with material being screened through 3 mm and 6 mm sieves. The bulk of the cultural remains (including pottery, shell, bone and charcoal) was found in the upper layer, with the three layers beneath containing only sparse remains or no remains at all (Anderson and Clark 2009). Excavations revealed both Lapita period and post-Lapita ceramics, though the major period of use is thought to fall between 2500 and 1000 BP (Anderson and Clark 1999:33; Clark and Anderson 2009). Radiocarbon determinations reflect the disturbed nature of the site, with disturbances by both human and natural agencies being noted during excavation (Anderson and Clark 1999:33).

The Ugaga site yielded several hundred kilograms of marine shell although no total sample weights were recorded. Due to the size of the sample, it was considered more practical to fully analyse the shell from five of the excavation squares (see figure 2). All shells and shell fragments were identified to the lowest possible taxonomic level, counted (using both MNI and NISP quantification methods) and weighed. During analysis, notes were made on the condition of the shells, including the presence of carnivore borings, evidence of beach rolling, the presence of juvenile and sub-adult specimens, breakage patterns and evidence of hermit crab occupation. Analysis of the shell midden sub-sample excavated from Ugaga reveals a “midden” which is primarily composed of gastropod shells deposited by terrestrial hermit crabs rather than being human subsistence refuse.

3. Identification of hermitted shells

There is presently little in the archaeological literature to guide analysts in the identification of shells associated with hermit crab occupation and behavioural diversity within the hermit crab superfamily Paguroidea makes any comprehensive key challenging. Two broad groupings of hermit crabs can be delineated: the marine hermit crabs (most notably families Diogenidae and Paguridae) and the terrestrial hermit crabs (Coenobitidae). Marine hermit crabs are closely tied to marine environments, whereas species in the Coenobitidae can range considerable distances inland with only gravid females compelled to return to the sea to release their young (Nakasone 2001). Hermit crabs are defined by the behavioural (and anatomical) adaptation that prompts them to inhabit empty objects, usually molluscan shells, as a form of protection against predators. In the case of the coenobitids, the shell is also used as a vessel for carrying water (fresh, brackish or salt depending on species), as shelter against desiccation and in the case of females, for brooding young (Hazlett 1981). Thus, whilst marine hermit crabs are fairly broad in their selection of suitable shells, coenobitids have a range of requirements that means shell suitability is rather restricted. Although less suitable shells (or objects – see figure 3a) may be carried, females in small or ill-fitting shells are far less fecund than their well-fitted counterparts (Osorno et al. 1998; Thacker 1994; Bertness 1981), providing a clear evolutionary imperative for good shell fit.

Members of the Coenobitidae are distributed circum-globally throughout tropical and many subtropical areas. Prominent species in the Western Pacific region include *Coenobita rugosus*, *Coenobita perlatus*, *Coenobita brevimanus* and the coconut or robber crab *Birgus*

latro which only carries a shell as a juvenile (see figure 3). Coconut crab is considered a delicacy throughout much of its range to the point where it is highly endangered in some Pacific locales (Fletcher et al. 1990; Niering 1963), but *Coenobita* spp. are not considered to be a food source.

There are currently no key diagnostic traces that link particular discarded shells found in middens to marine crab occupation, although more generic features such as the presence of barnacles, serpulid worm casts and other epibionts and encrusting organisms within the aperture of the shell can make plain that a live mollusc was not present immediately prior to shell discard (Walker 1995:373-374). However in the case of the coenobitids, there exists a distinctive set of physical modifications to the shell generated by both prolonged use and active modification on the part of the crab.

The archaeological literature has not defined these modifications in any comprehensive way, although Reitz and Wing (1999: 65-66, following Scudder and Quitmyer 1998) mention that the Caribbean terrestrial hermit crab *Coenobita clypeatus* thins the shell and chips the aperture of the shell in which it lives. Diagnostic traces of terrestrial hermit crab occupation span well beyond these features and can be seen to manifest slightly differently both in different types of shells and with different species of *Coenobita*. Drawing on the palaeontological and zoological literature as well as observations from the analysis of midden from Ugaga and other tropical Indo-Pacific archaeological sites, the general spectrum of coenobitid modifications to shells is outlined here.

The major indicators of coenobitid hermit crab occupation of gastropods have been outlined in the paleontological literature by Walker (1994, 1995) and in the zoological literature by Kinoshita and Okajima (1968:296). These include drag marks, reduction or removal of the columella and worn outer lip and keel. This damage is caused by a combination of dragging the shell along the ground and the abrasive action of the carapace of the crab as the animal constantly extends out of and retreats into the shell (Walker 1995:375).

Given the great variation seen in gastropod shell morphology and the different ways in which the shell is held and carried by various species of *Coenobita*, typical damage patterns vary between shell taxa. In addition, certain shell taxa are preferentially selected by different hermit crab species to suit variations in habitat, mobility and defence (Barnes 1999). Shells

with round or D-shaped apertures are preferentially used by coenobitids, so narrow-apertured shells such as cowries (Cypraeidae) and cones (Conidae) will be selected against (Barnes 1999; Carucci 1992:166). Barnes (1999) suggests that this is because coenobitids, in particular the most ‘terrestrial’ species *Coenobita rugosus*, need to be able to fully seal the shell to protect against desiccation (see figure 2c), whilst marine hermit crabs, who will often inhabit cowries and cone shells, do not typically face this issue. Thus, turban shells (Turbinidae), nerites (Neritidae), rock shells (subfamily Thaidinae, family Muricidae), dogwhelks (Nassariidae) and moon snails (Naticidae) are most commonly selected for by coenobitid hermit crabs (Barnes 1999; Osorno *et al.* 1998).

Aside from the shape of the aperture, the overall morphology of the shell selected is linked strongly to the general behavioural ecology of the *Coenobita* species in question. Barnes (1999) elucidates differences in shell choice between the burrowing species *Coenobita rugosus*, which prefers low-spined, round-apertured heavy taxa such as species in the Turbinidae and Neritidae and the tree-climbing species *Coenobita cavipes*, which preferentially selects slender, high-spined turriculate shells such as *Terebralia palustris* (Potamididae). Consequently, depending on which particular species of coenobitid is active at the site, a different range of gastropod shells will display damage.

The two most common members of genus *Coenobita* in the tropical Indo-Pacific, *Coenobita rugosus* and *Coenobita perlatus* and both are burrowing species, thus preferring low-spined, robust, rounded-aperture taxa. It should be pointed out that ‘burrowing’ in coenobitids is fairly superficial and unlike many other terrestrial and marine crab taxa, they are not capable of digging any distance down into a substrate. Burrowing behaviour is primarily for the purpose of hiding from the sun during daylight hours. A comparison of reference specimens drawn from the Ugaga archaeological sample enables further articulation of taxon-specific modifications to major shell families.

3.1 Neritidae: Coenobitid damage patterns on neritids are perhaps the most obvious and coenobitid use can often be determined with only a glance. Through repeated movement of the hermit crab in and out of the shell, the hermit crab abrades the columellar pad. This changes the morphology of the aperture from the typical neritid “D-shape” to an aperture that is almost circular in extreme cases. Often denticles present in some species around the inner margin of the aperture (e.g. *Nerita undata*, *N. plicata*, *N. costata*) have been abraded away

completely. Abrasive and/or chemical action also tends to thin the entire shell from the inside out. Thus, although the external sculpture on most areas of the shell may be very much intact, the shell will be noticeably frailer and lighter. In heavily used neritid shells there may also be a wear-patch or hole caused by continuous friction between the shell and the ground. A range of these indicators is illustrated in figure 4.

3.2 Turbinidae: Coenobitid damage patterns are slightly less obvious in the turbinids with damage focused around the aperture and columella. Since the aperture of shells within genus *Turbo* tend to be circular, evidence of abrasion is not as dramatic as in the neritids. However, upon closer inspection turbinids utilised by coenobitids display an enlarged aperture with abrasion being most noticeable along the parietal wall of the aperture. In heavily utilised specimens, the parietal wall may be so abraded that the aperture has connected with the umbilicus. Coenobitids also tend to wear away the columella internally and so, upon looking up into the shell through the aperture, a ‘coenobitized’ (term after Walker 1995:375) turbinid shell will be hollow, or have only a remnant columella. As with neritids, the whole shell will generally feel lighter and frailer than a non-coenobitized specimen. It would appear, from observations during midden analysis, that coenobitids do not only utilise whole turbinids, but also the spire portion of broken turbinids, as these wear patterns can frequently be isolated on broken shells. The coenobitid damage is clearly ‘post-break’ as distinctive abrasion patterns can be seen around the fractured margins of the shell. Figure 5 illustrates coenobitid damage patterns on turbinids.

3.3 Planaxidae and Thaidinae: As with the turbinids, coenobitid wear patterns on these taxa are less obvious than those seen in the neritids. Characteristics follow those for the turbinids with enlarging of the aperture – particularly along the parietal wall – and either full or partial removal of the columella. Examples from these taxa are shown in figure 6.

Using the above descriptions as a guideline, coenobitid damage can also be identified in a range of other shells.

4. Level and nature of hermit crab interference at Ugaga

The molluscan remains from the five analysed test-pits, only two of which were adjoining, totalled 17.26 kg or 2061 shells as per minimum number of individuals (MNI) counts (total NISP = 2925 fragments). One hundred and twenty one molluscan species were represented

although the majority were present only as a single or small number of fragments. Complete results of midden analysis are presented in Szabó (2009a). The vast majority of the sample was composed of four species within two families: *Nerita polita* and *N. albicilla* in the Neritidae and *Turbo chrysostomus* and *T. cinereus* in the Turbinidae (see figure 7). Opercula, or ‘cat’s eyes’ of *Turbo* spp. were present in the sample and although not identified to species, figure 7 shows that the combined total of opercula is much lower than MNI counts for the shells themselves. In keeping with the habitat associations of the four dominant taxa, seventy-five per cent of the shell studied from Ugaga derives from the intertidal reef platform, with smaller numbers deriving from upper to mid-intertidal rocks and the sandy intertidal zone.

During analysis, all gastropods that showed evidence of hermit crab occupation were noted. Equivocal specimens with possible minimal alteration were not included in the final totals of hermitted shells. As can be seen in figure 8, the vast majority (87 per cent) of specimens of the four major species show signs of hermit crab, rather than human, deposition. Overall, at least 63 per cent of the total analysed midden sample bore traces of coenobitid hermit crab occupation. Species that showed no evidence of hermitting were those with a morphology unsuitable for coenobitid occupation, including bivalves and gastropods such as the ‘false limpet’ *Siphonaria* sp., narrow-apertured *Strombus* spp. and *Conus* spp. and cowries (*Cypraea* spp.). This spread of species utilisation strongly suggests that *Coenobita rugosus* was the dominant species taking and discarding shells at the Ugaga site, with its strong preference for strong, low-spined, round-apertured shells within the Neritidae, Turbinidae and Muricidae, as well as the rejection of shells in the Strombidae (see Barnes 1999).

The presence of large quantities of prehistoric ceramics associated with charcoal, fishbone accumulations and other culturally-deposited materials at Ugaga plainly establish it as an archaeological site. That so much of the associated shell is non-archaeological requires explanation and an investigation of hermit crab behavioural ecology provides a number of insights into midden formation and transformation processes at Ugaga.

5. Coenobitid behavioural ecology – considering the susceptibility of tropical coastal shell middens

Coenobitids are typically found in the supra-littoral zone, though may wander some distance inland with some species climbing to altitudes of over 800m (Walker 1994:403). Although

coenobitids are well adapted to a life on land, their lungs require adequate moisture to function and the animal must either be close to water or carry its own supply in its shell. To help avoid desiccation, coenobitids tend to be either crepuscular or nocturnal and often bury themselves or retreat to shade during the heat of the day. Studies conducted on coenobitid populations in Mozambique would indicate however that these activity patterns are somewhat flexible. Barnes (2001) has investigated the effect of nearby human populations on the timing of activity and feeding patterns of local coenobitids (*Coenobita cavipes* and *Coenobita rugosus*) and found that the normally diurnal coenobitid populations became increasingly nocturnal as the density of human population increased.

As feeding generalists and active scavengers, coenobitids will consume rotting plant and animal matter, fungi and faeces, as well as other coenobitids on occasion (Thacker 1996; Brodie 1998). Experimental studies have shown that coenobitids are attracted to the smell of food that they have not recently consumed and this tendency encourages a broad-spectrum diet, leading to a more balanced intake of food and limiting their exposure to toxins (Thacker 1996). Observational studies of coenobitid food preferences in the wild (Barnes 1997a) indicate that food choices are indeed broad. Of relevance to studies of human-coenobitid interaction, Barnes (1997a) discovered that, when coenobitid populations were in close proximity to human populations, human faeces became the single most important food source for *Coenobita cavipes* and was consumed as much as other major food sources in the case of *Coenobita rugosus*.

Being hermit crabs, availability of shells is very important to the survival and success of a population. Shell availability has been demonstrated to be an important limiting factor in hermit crab populations (Barnes 1997b:133; Hazlett 1970; Kellogg 1976) and in a shell-starved environment, suitable shells can be recycled many times within the coenobitid community (Walker 1994:408). Humans can alter the pattern of available shell distributions markedly through the creation of middens. Shells that may previously have been out of the reach of coenobitids become available and this major constraint on hermit crab population growth is no longer a critical variable (Barnes 2001:245). Hazlett (1981:16) observed that empty shells cast high up the beach by storm surges were “rapidly removed” by coenobitids and the research of Barnes (1999) looking at crab/human interaction demonstrates that the same is true of cultural shell middens. It should further be noted that it has been proven that female coenobitids in better-fitting shells are much more likely to reproduce than females in

ill-fitting shells (Thacker 1994:1478), meaning that increased availability of suitable shells would likely lead to greater reproductive success.

Although little research has been done on the interaction of human and coenobitid populations, a number of observations have been made about potential benefits for both sides relating to shell and food availability on the one hand and hygiene and rubbish disposal on the other.

In recent studies of coenobitids on Quirimba Island, Mozambique, Barnes (2001) has considered the impacts, both positive and negative, of human populations upon coenobitid density and behaviour. Barnes (2001:245-6) noted that humans provided two important resources for local coenobitid populations: food and shells. Shell middens alleviate the problem of shell availability and this in turn promotes population growth (Barnes 2001:245). In addition to a supply of shells, humans also provide food in the form of domestic waste and faeces, thereby also promoting population growth. Being highly general scavengers, as well as gregarious feeders, coenobitids will quickly 'clean up' organic waste discarded around a site. Walker (1999) notes that in the Galapagos Islands local populations of coenobitids (*Coenobita compressus*) would emerge just after sunset to feed on food scraps discarded by tourists. She comments the coenobitids "are indeed important organisms for maintaining the cleanliness of Galapagos beaches with their late night beach-sweeping activities" (Walker 1999). This quick disposal of rotting matter and faeces removes potential breeding grounds for pests and associated diseases (Page and Willason 1983; Barnes 2001:241) and is thus considered beneficial to humans.

Despite this apparently beneficial mutualism, certain facets of coenobitid shell selection mean that not all tropical, coastal, human-generated shell middens are prone to hermit crab turnover. Aside from the fact that shells considered suitable for occupation by coenobitids must be present in the midden, results of experimental and observational work within zoology on the nature of shell selection by coenobitids demonstrate further constraints. Firstly, coenobitids will rarely investigate any shell that is partially or fully buried (Barnes 1999: 249). Kinoshita and Okajima (1968) showed that the investigation of potential shells in *Coenobita rugosus* was largely based on visual assessment of size and form, with the important caveat this is not absolute size or form, but filtered through the visual angle of the crab. Thus, a crab in experimental tests could not distinguish between two black balls, one

twice as large as the other but placed twice as far away (Kinosita and Okajima 1968:304). The initial exploration of a potentially suitable shell is through visual assessment, followed by a series of holding and 'dimensional tests' performed with the claws (Kinosita and Okajima 1968). Given the importance of visual cues, if the aperture of the shell is not fully visible to the crab, or accessible for 'claw-fit' tests, then it will not be investigated. At Ugaga, hermitted shell is present in quantities throughout the vertical levels of the deposit, suggesting that coenobitids were constantly replacing shell throughout the process of midden accumulation.

6. Hermitting, shell midden and explanation at Ugaga

As one of twelve shell middens analysed as part of a large project on the prehistory of Fiji, Ugaga was the only deposit that had been significantly altered through the actions of coenobitids (Szabó 2009a). While there are small percentages of coenobitid shell replacement at other sites, there is necessarily a reason why turnover of shell by coenobitids is so great at Ugaga. Many other Fijian middens analysed would provide coenobitids with shells and food and would thus theoretically promote the presence and growth of coenobitid populations. Although reasons for this distinction in levels of hermitting are presently speculative, the fact that Ugaga is situated on a small waterless island with only sporadic human occupation is posited here as a contributing factor. Unlike more established habitation sites on larger islands, coenobitids were unlikely to have been competing with significant populations of other human-associated scavengers such as rats and dogs. While not assessing the relationship between coenobitids and other scavengers in depth, Barnes (1997a:299) states that coenobitids may have to "compete strongly" for higher-quality food, which often eventuates in the procurement of only "low quality food". In saying this, he is implying that coenobitids will often lose better quality food items to other scavengers. Thus, unlike sites on the main island of Viti Levu and other islands more well-resourced than Ugaga, it is likely that the only serious constraints on coenobitid population sizes on Ugaga Island were likely to have been the availability of food and shells.

Given that over 65% of mollusc remains excavated from the Ugaga Lapita site were shown to have been occupied by coenobitid hermit crabs, what can we say about the place of shellfish in human subsistence patterns at Ugaga? It is impossible to say what species and numbers of each species were present in the original Ugaga midden, as we cannot assume that the coenobitids removed a shell of the same species as the one they left behind. However there

are three lines of enquiry to assist in reconstructing a picture of what may have been originally present.

Firstly, there are clearly species of mollusc represented in the midden that would have been of no use or interest to coenobitid hermit crabs. These include the bivalves as well as non-coiled gastropods such as limpets and narrow-apertured gastropods such as the cowries (Cypraeidae) and cones (Conidae). Although these taxa are found in the Ugaga deposits, they form a relatively minor part of the assemblage and thus do not tell us a great deal about shellfish consumption at Ugaga.

Secondly, although most of the turbinids (*Turbo chrysostomus*, *Turbo cinereus* and *Turbo crassus*) present in the deposits have been coenobitized, there are a number of *Turbo* spp. opercula present in deposit which allow us to make some general comments about *Turbo* spp. within the original Ugaga midden. The presence of *Turbo* spp. opercula indicates that at least some *Turbo* spp. shells were brought to the site with the original animal still within the shell. Although the numbers of opercula present in a deposit rarely match actual remains of the shell in terms of minimum numbers (e.g. Gosden and Robertson 1991:32), the presence of opercula at least indicate that a number of *Turbo* spp. shells were present in the original midden.

Thirdly, as discussed above, coenobitids prefer certain shell taxa with some variation between different species of coenobitid based on different behavioural patterns. The pattern of coenobitized shells at Ugaga indicates that they were utilised by a burrowing species, being solid and short-spined, as opposed to climbing coenobitids which prefer lighter, taller shells. The two most preferred families of *Coenobita rugosus* have been observed to be Neritidae and Turbinidae – both the most common and most coenobitid-utilised families within the Ugaga deposits. Since a hermit crab is very unlikely to swap a preferred shell for a less-preferred shell, we can infer that many of the specimens originally taken from the Ugaga midden belonged to families Neritidae and Turbinidae. Exactly which species in these families were originally represented and in what proportions is impossible to say.

In the absence of other taphonomic indicators such as beach-rolling and carnivore bore-holes, we can say that the species not preferred by coenobitids fairly represent midden shell. We can also say that *Turbo* spp. shells were represented in the original deposits on the basis of

the presence of *Turbo* spp. opercula. Based on the knowledge that burrowing coenobitids and in particular *Coenobita rugosus*, have a preference for shells of the families Neritidae and Turbinidae and that they are very unlikely to swap a preferred shell for a non-preferred shell, we can surmise that shells taken were of the families Neritidae and Turbinidae.

7. The importance of isolating hermitted shell within archaeological deposits

In the course of midden analysis, it is standard practice for archaeomalacologists to isolate shells that display evidence of post-mortem collection by humans or incorporation into archaeological deposits through a non-human vector. Such indicators generally include abrasion and muting of shell sculpture associated with ‘beach-rolling’, the presence of boreholes from carnivorous gastropods in the Muricidae or Naticidae and the presence of adhering or eroding organisms within the aperture (gastropods) or inner valve surface (bivalves) of the shell. Shells manifesting such traces may have been deliberately brought to a site by humans for use as a raw material in artefact production (e.g. Szabó 2008, 2009b), but by virtue of their taphonomic signatures cannot represent food waste. To this list can be added markers indicating that the shell was inhabited by a coenobitid hermit crab rather than a mollusc. Shells identified thus, especially when present in considerable numbers, are likely to indicate that the original midden shell has been removed by hermit crabs, who have deposited their old shells – of unknown original provenance or age – in return.

This process obviously distorts the results of midden analysis if undetected, but it also has the potential to generate spurious radiocarbon dates if such shells are chosen as samples for radiocarbon dating. There is no guarantee that the shell deposited by the hermit crab correlates in age to the midden shell it removes. Indeed, it can either be dramatically older or dramatically younger. Walker (1994) reports the intensive use of Pleistocene fossil molluscs (*Cittarium pica*) by the Bermudan hermit crab *Coenobita clypeatus*, which she notes has the capacity to confound geological timelines constructed using gastropod assemblages. As well as coenobitids moving old shells around the landscape, any ‘mining’ of fossil or sub-fossil deposits by crabs will presumably often result in a much younger shell being deposited within older exposed shell accumulations such as middens. Thus, in areas where coenobitids occur and where marine shell is a material used for radiocarbon dating, archaeologists should examine any gastropods for evidence of terrestrial hermit crab occupation.

8. Conclusion

Coastal zones are highly dynamic with processes such as wave action, dune migration and various forms of bioturbation capable of greatly modifying archaeological sites and assemblages. Coenobitid hermit crabs form only a small part of this range of potential processes, but as the case from Ugaga has demonstrated, the impact of their actions can be substantial. If the signatures of coenobitid hermitting are not recognized then spurious midden data and radiocarbon dates can result. Thus, the isolation of terrestrial hermit crab interference with shell middens is critical to both constructing a picture of past human shell-gathering practices and the selection of shell for radiocarbon dating in the tropics.

Whilst dogs and rats and well recognised scavengers around human occupation sites, hermit crabs have not drawn much attention as potential vectors of site transformation. Their capacity to not only remove shell midden material from its primary context, but to introduce material of unknown original provenance to the site represents a novel type of biotic transformation: the size of the shell deposit remains relatively constant but the internal composition can be dramatically altered.

Despite the large-scale impact that coenobitids can have on tropical shell middens, a consideration of terrestrial hermit crab behaviour and ecology can help to isolate which types of shells would not have been attractive and are thus likely to represent human refuse. Likewise, an investigation of hermitted shell taxa can assist in projecting what types of mollusc may have been removed. Additionally, the vertical spread of hermitted shells within a deposit can reveal whether shell replacement was happening simultaneously with the creation of the midden or whether it represents later disturbance.

Drawn from investigations of coenobitid behavioural ecology as well as research within palaeontology, the guide to standard shell modifications effected by terrestrial hermit crabs presented in this paper will help analysts isolate cases of coenobitid shell deposition. The length of shell use by hermit crab/s as well as variability in original shell morphology mean that the visibility and exact nature of modifications can vary, but the case study from Ugaga reinforces that quantifying hermitting within shell midden samples may turn out to be of more than cursory interest.

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Figures – Szabó MS

Figure 1: Map of Fiji showing the location of the Ugaga Site

Figure 2: Plan of the Ugaga Site showing the location of the squares selected for shell midden analysis. Site plan adapted from Anderson and Clark (2009) figure 53, p. 112.

Figure 3: Some tropical Western Pacific members of the Coenobitidae; (a) juvenile *Birgus latro* (Coconut or Robber Crab) inhabiting a glass jar, Yona, Guam; (b) *Coenobita rugosus* in a *Volema myristica* (Melongenidae) shell, Bako National Park, Sarawak, East Malaysia; (c) *Coenobita rugosus* retracted into a *Monodonta labio* (Trochidae) shell. Note the tight fit of the appendages within the aperture of the shell. Bako National Park, Sarawak, East Malaysia; (d) *Coenobita rugosus* inhabiting a *Polinices tumidus* (Naticidae) shell. Note the damage around the lip of the aperture and the lack of algal growth on the ventral surface of the shell from constant dragging. Bako National Park, Sarawak, East Malaysia. All photographs by K. Szabó.

Figure 4: Coenobitid damage patterns as seen in neritids. *Nerita costata*: (a) undamaged specimen; (b) hermitted specimen; (c) schematic of hermitted specimen showing (i) abraded drag-mark; (ii) abrasion and reshaping of columellar pad; (iii) abraded patch on the inner shell surface caused by movement of the crab's carapace; and (iv) abrasion of the palatal edge of the aperture. *Nerita polita*: (a) undamaged specimen; (b) hermitted specimen; (c) schematic of hermitted specimen showing (i) extensive bioerosional damage to shell surface; (ii) abrasion and reshaping of columellar pad; (iii) hole formed from inner surface of shell through constant movement of the crab's carapace; and (iv) abrasion of the palatal edge of the aperture.

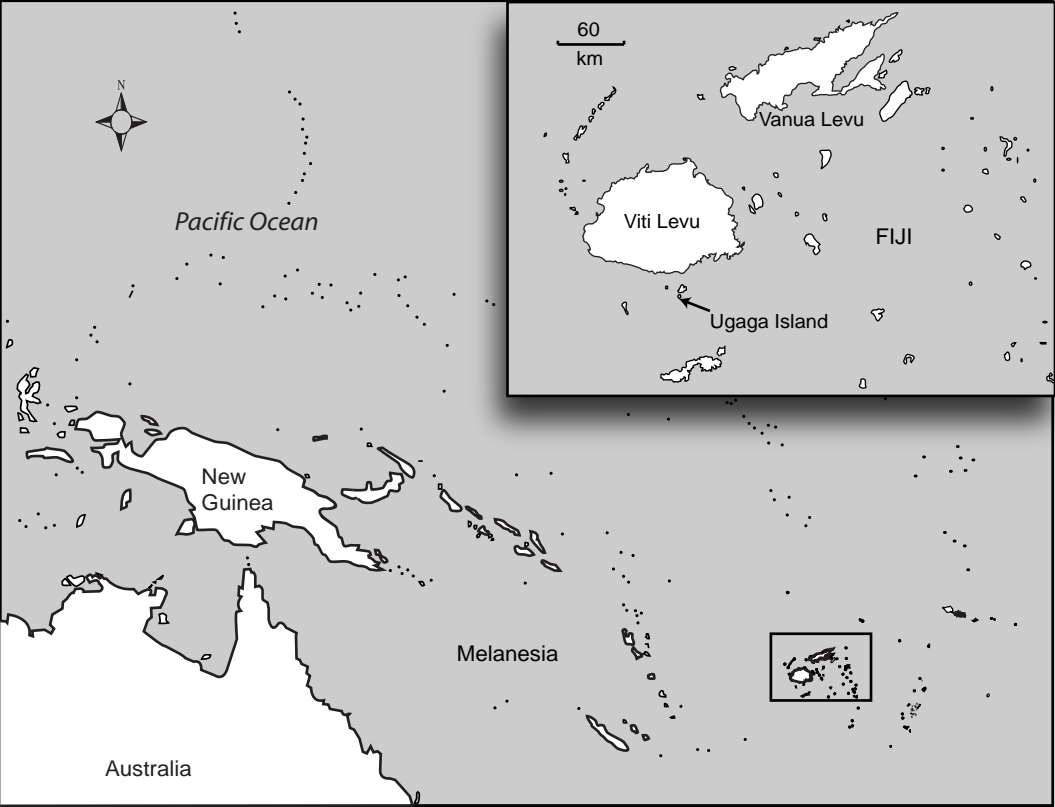
Figure 5: Coenobitid damage patterns as seen in turbinids. *Turbo cinereus*: (a) undamaged specimen showing axis of the undamaged columella; (b) moderately hermitted specimen; (c) schematic of previous showing (i) abrasion of parietal edge of aperture resulting in the fusing of the aperture and umbilicus; and (ii) chipping and abrasion at the anterior of the aperture; (d) heavily hermitted specimen; and (e) schematic of previous showing (i) abraded drag-mark; (ii) abrasion and distortion of the parietal edge of the aperture and umbilicus; (iii) abrasion and reshaping of anterior surface of aperture; and (iv) chipping and abrasion at the anterior of the aperture. *Turbo chrysostomus*: (f) undamaged specimen showing axis of columella; (g) heavily hermitted specimen; (h) schematic of previous showing (i) abraded drag-mark; (ii) abrasion of parietal edge of aperture connecting it to the umbilicus; note also the absence of the columella; and (iii) abrasion of the palatal edge of the aperture; (i) heavily hermitted partial shell; (j) schematic of previous showing (i) abraded drag-mark; (ii) position of absent columella; and (iii) abraded surface of broken shell.

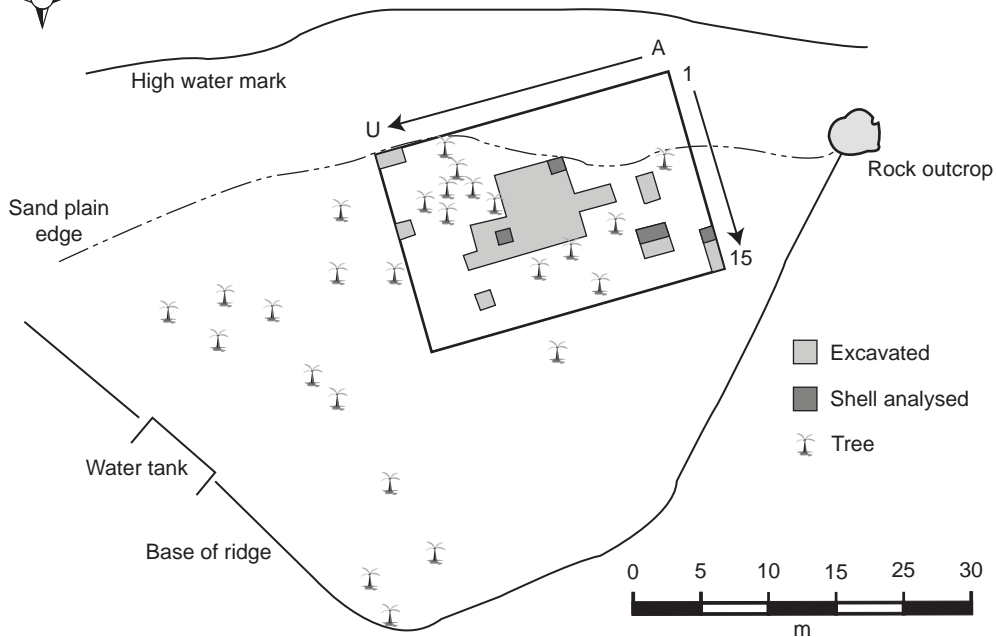
Figure 6: Coenobitid damage patterns as seen in genus *Thais* and family Planaxidae. *Thais* spp.: (a) undamaged *Thais tuberosa*; (b) hermitted *Thais armigera*; (c) schematic of previous showing (i) abrasion of columella; (d) heavily hermitted *Thais tuberosa*; (e) schematic of

previous showing (i) abraded drag-mark; (ii) position of absent columella; and (iii) abraded palatal edge of aperture. *Planaxis sulcatus*: (f) undamaged specimen; (g) hermitted specimen; (h) schematic of previous showing (i) abraded drag-mark; (ii) abrasion of columella; and (iii) abrasion of inner surface of aperture and removal of lirae.

Figure 7: Graph to show molluscan taxa represented by ten or more individuals (MNI) within the analysed Ugaga shell midden sample. Remainder of sample represented by less than ten individuals totalled 260 MNI.

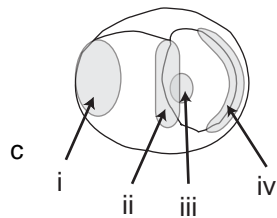
Figure 8: Graph to show the extent of hermit crab replacement of the major shell taxa within the Ugaga shell midden sample.



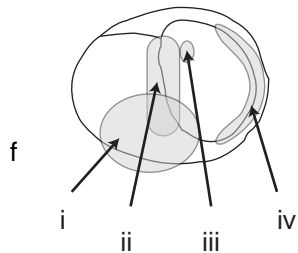




Nerita costata



Nerita polita

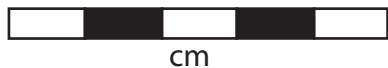


cm

Turbo cinereus

a

position of columella



b

d

c

i

ii

e

i

ii

iii

iv

Turbo chrysostomus

f

position of columella

g

i

h

i

ii

iii

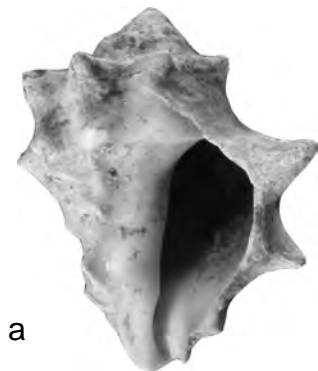
j

i

ii

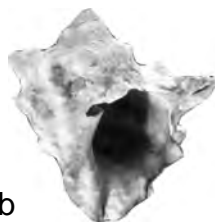
iii

***Thais* spp.**



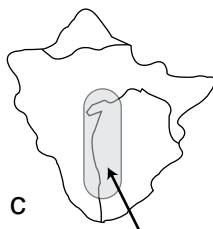
a

Thais tuberosa



b

Thais armigera



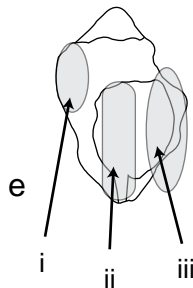
c

i



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Thais tuberosa



e

i

ii

iii

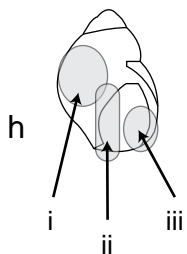
Planaxis sulcatus



f



g



h

i

ii

iii



cm

