



# Fossil crabs in the Caribbean: taphonomic comparisons as an informed indicator of underexploited occurrences

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## Abstract

The Antilles include over 100 islands, each with a rock record that embraces different slices of the stratigraphic succession; this is probably the most beguiling geological quality of the region. Both authors have been collecting fossil crabs (decapod crustaceans) from these islands for almost 30 years. Experience has demonstrated that, whatever fossil crustaceans have been described from an island, there are undoubtedly more waiting for attention. Marine decapods can commonly be collected in hand specimen. If there are poorly lithified sedimentary rocks, they will likely repay sieving with an abundance of fragments. For many stratigraphic horizons it is only the disarticulated elements such as these that are known, but they are identifiable and can be diverse. We promote three units from the Antilles as being highly likely to produce new and well-preserved faunas of decapod crustaceans: the Yellow Limestone Group (Eocene, Jamaica); the Anguilla Formation (Miocene, Anguilla); and the Rockly Bay Formation (Pliocene, Tobago). Both the Yellow Limestone Group and Anguilla Formation have produced fossil decapods, albeit indifferently preserved. In contrast, both units have yielded a diversity of well-preserved echinoids; the reasons for this contrast remain speculative. The Rockly Bay Formation is the most barnacle-rich unit in the Antilles, yet decapods, another marine arthropod group with a calcareous skeleton, remain undescribed, but are present. These units need to be exploited for fossil decapods and, in so doing, these new data will improve the known palaeobiodiversity of the Antillean region.

**Keywords** Taphonomy · Completeness of the fossil record · Antilles · Echinoids · Barnacles

## Introduction

It is relevant to open this paper with a personal reminiscence by S.K.D., an echinoderm researcher by training. He was offered and accepted a lectureship in the Department of Geology, University of the West Indies, Mona (UWI), in December 1985. At the time, he was attending the Annual

Conference of the Palaeontological Association in Aberystwyth, Wales, and gratefully received intelligence regarding Jamaica's fossil record from informed fellow delegates. One thing that was made clear, by more than one expert, was that the echinoids had already been 'done' by Hawkins (1923, 1924, 1927, 1930) and, particularly, Arnold and Clark (1927, 1934). Once his legs were under the Jamaican table, S.K.D. borrowed copies of some of these publications from the Science Library at UWI and obtained photocopies of others by interlibrary loan. Hawkins described specimens collected by two notable Caribbean geologists and stratigraphers, C.T. Trechmann and C.A. Matley (Donovan 2010b), complete with relevant stratigraphic data. In contrast, Arnold bought fossil echinoids from road menders and sent them to Clark, an echinoderm zoologist (not a geologist), who described them. Thus, geologic detail was minimal in Arnold and Clark's monographs, but, fortunately, locality details enabled S.K.D. to determine, broadly, the stratigraphic position of many species, at least from Arnold and Clark

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(1927). Combining all these data with his own new observations, S.K.D. was able to formulate the first, coarse chart of stratigraphic distribution of Jamaican fossil echinoids. This was a revelation. The echinoids had not been ‘done’ at all; rather, those of the Upper Cretaceous (various rudist limestones) and Eocene (= Yellow Limestone Group) were adequately recorded, but other stratigraphic divisions remained poorly known (Donovan 1988; Table 1 herein). Subsequent research showed that echinoids were locally common throughout the Cenozoic of the island (Donovan 2001, 2004; Donovan et al. 2007).

This result was significant. The palaeontology of Jamaica is one of the best known amongst the Antillean islands (Wright and Robinson 1993; Donovan 2010a), yet there were, and still are, gaping holes in our knowledge of a significant component of the stratigraphic record. It is apparent that, if this is true for Jamaica, then it must be more so for most other islands whose rock records are less well studied.

This paper is one of educated postulations rather than of hard evidence. Each of the authors has been studying decapod crustaceans from the Antillean islands for almost 30 years. We have individually, or in association, visited islands from which decapod crustaceans and echinoids were poorly known or unknown, and yet we have invariably collected further taxa of both groups. Can the presence of one of these groups, or comparison with some other group with a multi-element skeleton such as vertebrates or other arthropods, be used to predict the co-occurrence of the other? We think so, at least at a coarse level; demonstrations have been provided to us by our research in, for example, Carriacou (Donovan et al. 2003) and the ABC islands (Sload et al. 2018). If a unit is known to include common and diverse fossil echinoids (or crabs), might it also include common, yet hitherto undocumented crabs (or echinoids)? We explore the potential of this idea below, as

**Table 1** “Specific diversity of Jamaican fossil echinoids, separated into number of species per major stratigraphic unit” (after Donovan 1988, table 3)

System or series	Species
Pleistocene	6
Pliocene	2
Miocene	5
Oligocene	5
Eocene	74
Paleocene	1
Cretaceous	11
Unknown	24

well as other ideas that are intimately associated, such as style of preservation.

Obviously, comparing the fossil records of echinoids and decapods is not comparing like with like. There are many similarities: both groups have a calcified, multi-element skeleton (Kier 1977; Bishop 1986); are benthic, and include taxa that are epifaunal and infaunal; and are diverse and widespread, both now and in the past. That they are not a perfect match in terms of biostratigraphic and diagenetic behaviour is undoubted. However, our experience of processing bulk samples of more weakly lithified Cenozoic sedimentary rocks from the region has demonstrated that disarticulated elements of both groups may form a major component of the bioclasts. More complete specimens may also be found of both decapods and echinoids where mainly the latter were known hitherto (for example, the Upper Oligocene Antigua Formation of Antigua; research in progress). Our attitude is that the presence of well-preserved fossil echinoids in any unit is not a predictor of the occurrence of decapods, but it may be an indicator.

A note on sampling; we refer the reader to the timely review by Feldmann and Schweitzer (2017) in which they expound the techniques commonly employed to find and collect macroscopic fossil decapod crustaceans. To this we add the note by Donovan et al. (2017) in which we discussed the positive results that we have gleaned from bulk sampling and micropalaeontological processing (Brasier, 1980) of poorly lithified, Neogene sedimentary rocks in the Antilles. In short, if you are sampling a bed for decapods for the first time, the correct technique to employ, out of many, will only be arrived at by utilising both intelligence and experience.

## Yellow Limestone Group of Jamaica (Eocene)

The diverse litho— (Robinson 1988, Fig. 3) and biofacies of the Yellow Limestone Group (Eocene; approximately mid-Ypresian to mid-Lutetian) contribute to making it one of the most fossiliferous units, certainly in Jamaica and probably the Antilles. The biota ranges from microfossils such as palynomorphs (Graham 1993) and benthic foraminifers (Robinson and Wright 1993), to diverse invertebrates, and a burgeoning suite of fishes and tetrapods (Domning et al. 1997; Domning 2001). Famously, these rocks were miscorrelated with the Pliocene Bowden shell beds on the basis that both were highly fossiliferous (Sawkins 1869; Chubb 2010).

This gives pause for thought, when it is noted that the described fossil crabs have only about 20% of the specific diversity of the echinoids from the same unit. The only published monographic study of the decapods of the Yellow Limestone Group is almost 100 years old. Withers

(1924a) described a collection of crabs made by Dr. C. T. Trechmann. Half of the six taxa are mud shrimps; only one species, *Xanthilites? rathbunae* Withers, has an identifiable carapace, the other five being based on limb material only.

A description of a second fauna of decapods from the Yellow Limestone Group is, as yet, unpublished. Portell et al. (Portell et al. in press; Fig. 1 herein) have described the decapod species collected incidentally during



**Fig. 1** Decapod crustacean remains from the Middle Eocene Litchfield Formation, Yellow Limestone Group at Seven Rivers, parish of St. James, western Jamaica (after Portell et al. in press, pl. 2.).

Specimens in the collection of the Florida Museum of Natural History, Gainesville (prefix UF). **a–d** Callianassid sp. indet., UF 261043. **e–h** Diogenid gen. et sp. nov., UF 167083

excavations for vertebrates at the Seven Rivers site, parish of St. James (Domning 2001; Donovan et al. 2007). Although not chosen for the excellence of its fossil invertebrates, Seven Rivers has nonetheless yielded eight species of decapods, including four of mud shrimp; “*Callianassa*” *trechmanni* was first described by Withers (1924a), but from Spring Mount, parish of St. James. All of the Seven Rivers taxa were described from limb fragments only. Also note that Morris (1993, p. 123) recorded “Indeterminate crab fragments” from three other sites in the Yellow Limestone Group.

Combining these data of fossil decapods from the Yellow Limestone Group (Table 2), there are only about 12 taxa, most known from limb fragments and dominated by mud shrimps (callianassids). This is strongly dissimilar to the fossil echinoids of the same unit. Donovan (1993, table 2) listed 65 nominal species of echinoid from the Yellow Limestone Group and most are known from articulated tests, including both infaunal and epifaunal taxa. This is in stark contrast to the single crab from the Yellow Limestone Group known from its carapace. Either well-preserved decapod crustaceans are, indeed, rare in the varied lithofacies of the Yellow Limestone Group or we just have not looked well enough and in the right places.

**Table 2** Localities and nominal decapod crustaceans of the Eocene Yellow Limestone Group of Jamaica (after Withers 1924a; Morris 1993; Portell et al. in press)

<i>Callianassa?</i> <i>gigantea</i> Withers, 1924a	Glasgow
<i>Callianassa?</i> <i>subplana</i> Withers, 1924a	Spring Mount
<i>Callianassa?</i> <i>trechmanni</i> Withers, 1924a	Seven Rivers, Spring Mount
<i>Callianassa?</i> spp.	Seven Rivers, Ulster Spring
<i>Callinectes jamaicensis</i> Withers, 1924a	Glasgow, Spring Mount
<i>Callinectes</i> sp.	Seven Rivers
<i>Eriosachilia bartholomaeensis</i> (Rathbun, 1919)	Glasgow, Seven Rivers
<i>Xanthilites?</i> <i>rathbunae</i> Withers, 1924a	Glasgow, Spring Mount
<i>Varuna?</i> sp.	Spring Mount
diogenid gen. et sp. nov.	Seven Rivers
calappid gen. et sp. nov.	Seven Rivers

Localities: Glasgow, border of parishes of Hanover and Westmoreland (see Donovan 2010c); Seven Rivers, parish of St. James; Spring Mount, parish of St. James; Ulster Spring, parish of Trelawny

**Table 3** Localities and nominal decapod crustaceans of the Lower Miocene Anguilla Formation of Anguilla (after Rathbun, 1919; Withers, 1924b; Schweitzer et al. 2006; Collins et al. 2009)

<i>Callianassa?</i> <i>anguillensis</i> Rathbun, 1919	Cartouche Bay, Crocus Bay
<i>Callianassa?</i> <i>pellucida</i> Rathbun, 1919	Crocus Bay
<i>Calappa earlei</i> Withers, 1924b	Cartouche Bay
<i>Calappa</i> sp.	Cathedral Cave
<i>Lyreidus?</i> <i>fastigatus</i> (Rathbun, 1919)*	Crocus Bay
<i>Parthenope</i> sp.	Cartouche Bay
<i>Psygmodthalmus bifurcatus</i> Collins in Collins et al., 2009	Betty Hill Quarry
<i>Scylla costata</i> Rathbun, 1919	Road Bay
<i>Panopeus</i> sp.	Cartouche Bay

\*Feldmann (1992, p. 944) removed this species from *Lyreidus* sensu stricto; its generic affinity is unknown

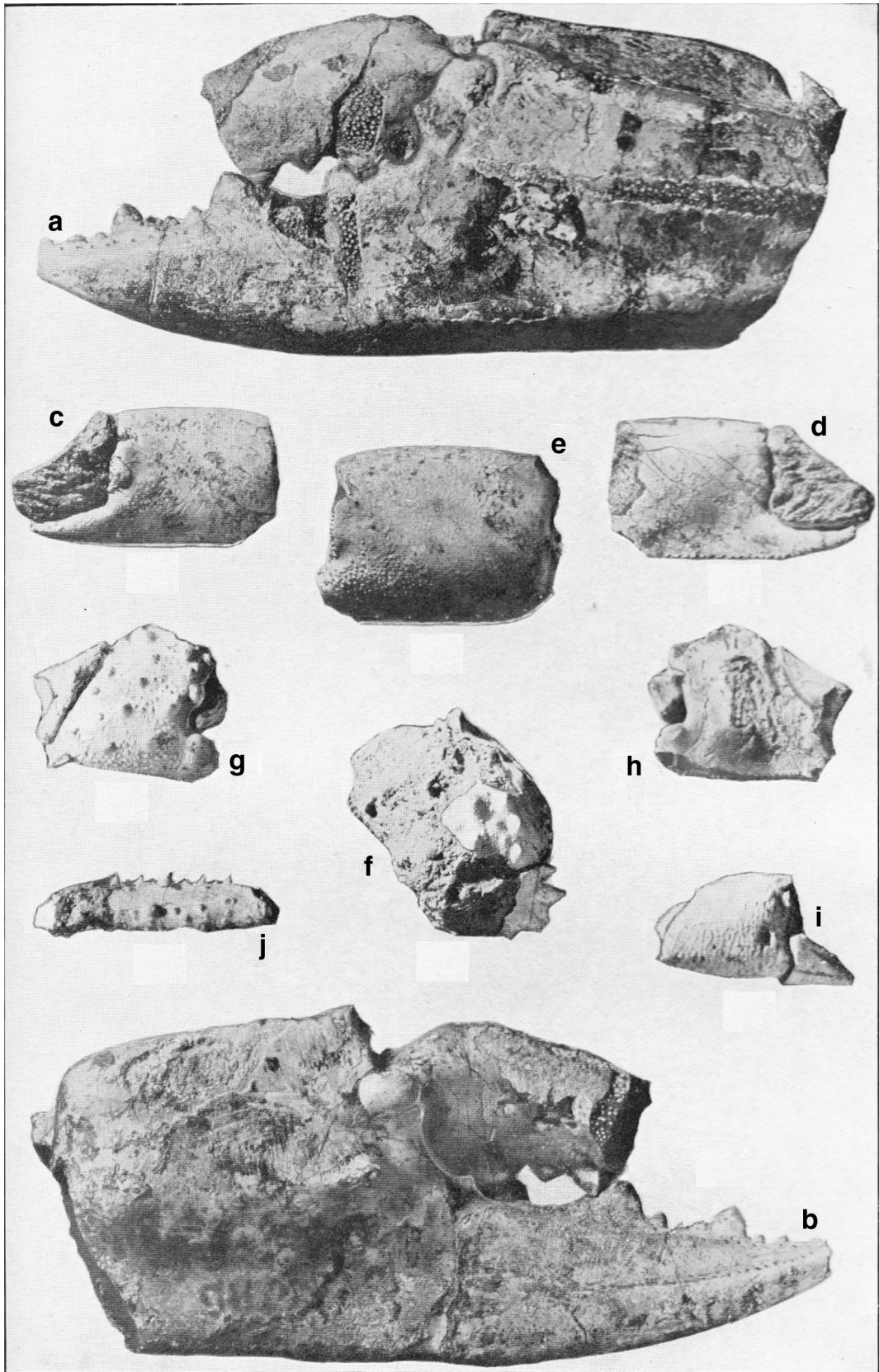
**Fig. 2** Decapod crustacean remains from the Lower Miocene Anguilla Formation of Anguilla (slightly modified after Withers 1924b, pl. 6; for locality information, see Table 3). Original size of plate 165 × 105 mm. Specimens in the collection of the Natural History Museum, London (prefix BMNH). **a, b** *Scylla costata* Rathbun, 1919, BMNH In. 23768, left minor chela, outer (**a**) and inner views (**b**). × 1. **c–e** *Callianassa?* *anguillensis* Rathbun, 1919. **c, d** BMNH In. 23770, left propodus, outer (**c**) and inner view (**d**). × 1. **e** BMNH In. 23771, left propodus, outer view. × 1.5. **f–h** *Calappa earlei* Withers, 1924b. **f** BMNH In. 23785, holotype, right side of carapace, outer view. X 1.5. **g, h** BMNH In. 23786, paratype, right cheliped, outer (**g**) and inner view (**h**). × 1.5. **i** *Panopeus* sp., BMNH In. 23787, right propodus, outer view. × 2. **j** *Parthenope* sp., BMNH In. 23788, merus of right cheliped, inner view. × 1

The latter must be strongly suspected based on the disharmony of the echinoid and decapod datasets.

### Anguilla Formation of Anguilla (Miocene)

Anguilla, at the northern tip of the Limestone Caribees (Wadge 1994, p. 169), is a tiny island compared to Jamaica, only 26 km in length compared to 235 km. Yet Anguilla has palaeontological treasures not found in





Jamaica, namely a large and diverse fauna of Lower Miocene echinoids. Although Jamaica does have Miocene echinoids, only a few are locally common—such as *Clypeaster concavus?* Cotteau, 1875, from the Newport Formation (Donovan 2004, table 1)—but many taxa are only known from fragments, with or without a coating of calcite spar (Donovan et al. 2005).

In contrast, the latest taxonomic reassessment of the Lower Miocene echinoids of the Anguilla Formation (Poddubiuk and Rose 1985, table 3) listed 20 species, 12 of which are abundant or common. The monograph of Cotteau (1875) illustrated most of these taxa.

Unlike those of the Eocene of the Yellow Limestone Group, the decapod crustaceans of the Anguilla Formation have a diversity almost half that of the echinoids, nine species in seven genera (Collins et al. 2009, p. 58, Table 2; Table 3 herein). Yet, and again, the preservation is inferior to that of the echinoids. For example, of the five species figured by Withers (1924b, pl. 6), all represent fragments of limbs except “Carapace (right side)” (pl. 6, fig. 6) which is the holotype of *Calappa earlei* Withers, 1924b (Fig. 2).

Thus, the patterns of preservation of decapods and echinoids in the Anguilla Formation and Yellow Limestone Group are, at least, superficially similar. The echinoids of both are diverse and commonly well known from multiple, well-preserved tests; decapod crustaceans of both show less variety and inferior preservation. Undoubtedly, the roots of these differences are many, embracing palaeobiodiversity, form, function, palaeoecology, taphonomy and collection bias, amongst others; similar lists could be applied to all the units considered herein. Determining the proportionate contribution of each factor to the fossil record is problematic, however. It may simply be that the echinoids were more species-rich than the decapods at the times of deposition of both units, although that does not explain the differences in styles of preservation.

Yet there are also similarities in these patterns of fossilization. Contrast these ancient echinoids and decapods with a coeval echinoderm group, the Asteroidea, which are only known from disarticulated ossicles in the Yellow Limestone Group (Donovan et al. 1993; Portell and Donovan in press) and are so far unknown from the Anguilla Formation. Yet all three groups are common denizens of the modern Caribbean Sea and, surely, were widely distributed in the past. Each of these groups has their own taphonomic pathways and signatures (Bishop 1986; Donovan 1991). A ‘rule of thumb’ scale of preservation can be recognised—echinoids (high preservation potential) > decapod crustaceans > asteroids (low preservation potential). This does not imply whether or not well-preserved fossils in each of these groups may or may not be found. Rather, it summarises what we know from the field; even if fossil echinoids are common, the decapods and

**Fig. 3 a** Geological map of south-west Tobago (after Donovan 1989, fig. 1, redrawn from Saunders & Muller-Merz 1985, fig. 1). The inset map shows the position of Tobago (arrowed) in the eastern Caribbean. **b** Schematic reconstruction of the palaeoenvironment of the mid-Pliocene *Balanus* Bed, Rockly Bay Formation, of Tobago (after Donovan 1989, fig. 7). Relationships between localities not to scale. Vertical scale approximates both to water depth and bed thickness

asteroids will probably be fragmentary, although a crab carapace is a more likely relic than a multi-plated starfish arm.

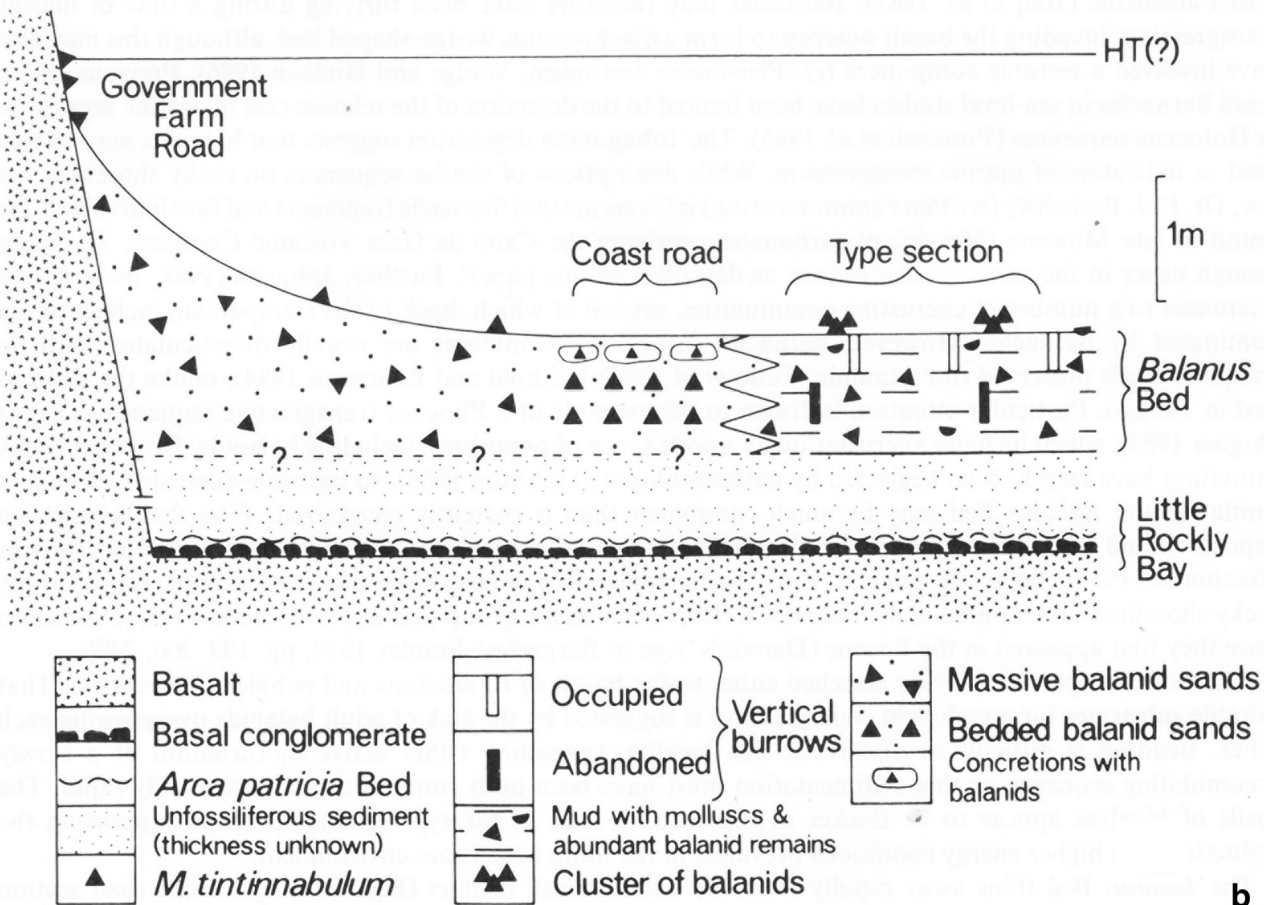
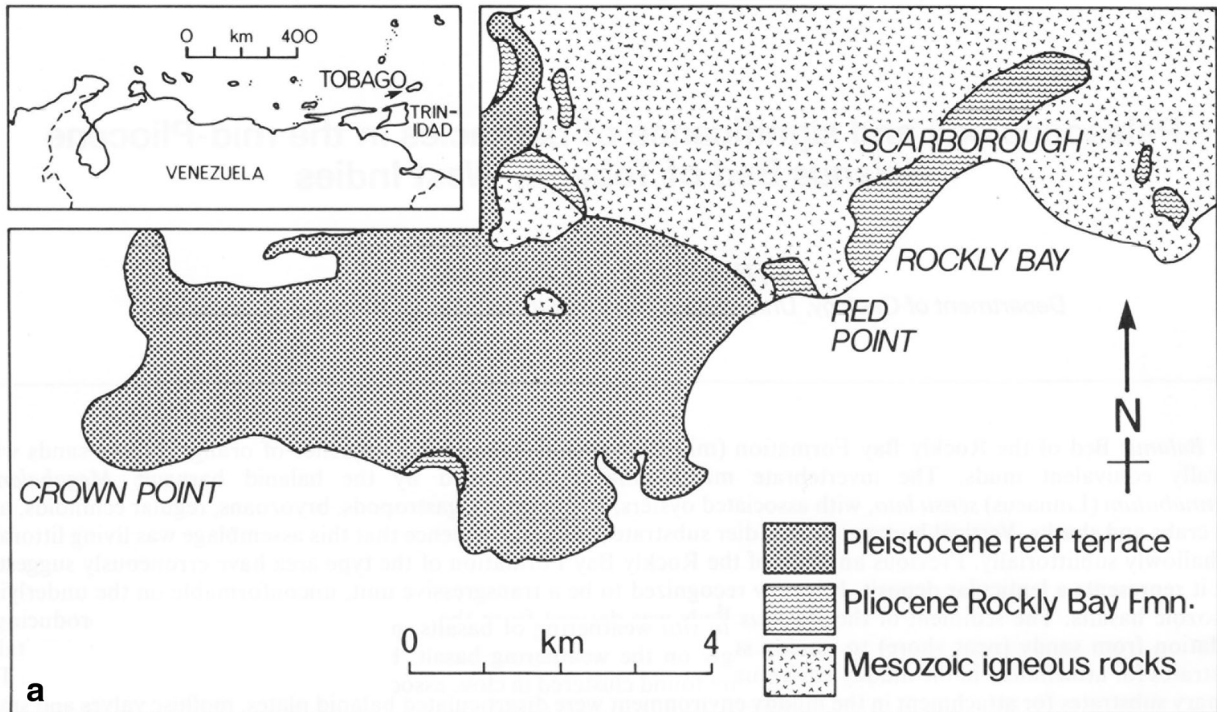
### Rockly Bay Formation of Tobago (Pliocene)

Our third potential decapod crustacean locality, the Pliocene Rockly Bay Formation of Tobago, presents a different problem from our first two examples. The Rockly Bay Formation (Jackson and Donovan 1994) is well known as the most barnacle-rich unit in the Cenozoic of the Antilles (Donovan 1989) (Fig. 3). Trechmann (1934) referred to this formation as the Tobago Crag, in comparison to the fossiliferous and flat-lying ‘craggs’ of East Anglia. Rare echinoids do occur, but only two species are known, of which one is only found as spines (Lewis and Donovan 1991). Yet the occurrence of many hundreds of articulated balanid barnacle shells in a sedimentary succession in which the dominant bioclasts (Maxwell 1948, p. 843; Rowley 1979, p. 68; Donovan 1989, p. 244) are their disarticulated plates argues incontrovertibly that the palaeoenvironment favoured preservation of arthropod calcite.

Donovan (1989, p. 244; also Jackson and Donovan 1994, table 11.2) recorded “rare ...crab remains” from the type section. That the type section in the low cliffs of Rockly Bay should be the most likely spot for collecting decapod remains is suggested by its position removed from the unconformity with the Cretaceous basalts (Fig. 3). That is, this is the most ‘open water’ site exposed and is also a mudrock lithology with the bedding picked out by barnacle plates; complete *Megabalanus tintinnabulum* (Linné) shells form in situ, fist-sized ‘reefs’ of barnacles. Of all the units discussed herein, the type section of the Rockly Bay Formation would be the most easily exploited by techniques of bulk sampling.

### Discussion

Papers in more theoretical aspects of palaeontology commonly interrogate and analyse big numerical databases to reveal patterns and drive theories. We have no magic database to scrutinize, but have pooled *circa* 60 years field



experience in discussing recognisable patterns and their extrapolation to potential future field campaigns.

There are three principal imperatives propelling this theoretical contribution. One is time, perhaps better called age. It is a truism that it is easier to collect fossil specimens than to invest the time necessary to identify and describe them. In consequence, museums and universities abound with important collections that remain unpublished. The authors are aware that they are custodians of the many collections that they have already accumulated and need to describe while they still can (for example, S.K.D. will retire in 2021). Although we still have ideas for exciting fieldwork, we realise that it may not be used in the field.

There is also Antillean palaeobiodiversity, which remains patchily and poorly known. Part of this is due to real gaps, but there are also gaps in knowledge for which the data are available, but unexploited. When mention is made of the so-called incompleteness of the fossil record, we can envisage with equal facility the influence of our incomplete knowledge of the fossil record. Herein, we take the decapods as our 'model' group. Their exoskeleton is calcified with a good preservation potential and at each ecdysis each individual can contribute fragments to the fossil record (Bishop, 1986). But fragments can be difficult to identify or name and even experienced palaeontologists may ignore parts of limbs or misidentify a carapace for a poorly preserved bivalve.

There is also the decline in numbers of active systematists and systematic expertise generally. This is true of all groups of organisms and is a decrease that we have watched over the past 40 years. One way to encourage new systematists is to show them the problems and show them the fossils. We maintain that decapod crustaceans are among the most attractive and scientifically challenging of the invertebrate macrofossils.

What is a fact is that the fossil records of both the Anguilla Formation and Yellow Limestone Group have yielded decapod crustaceans; the preservation of the echinoids in both units is superior. The Rockly Bay Formation is unusually rich in barnacles that suggests it should also preserve remains of other, marine, calcareous arthropods such as crabs. It is informed speculation to suggest that more focussed collecting of all three units will lead to discovery of superior decapod crustacean fossils.

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