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Palaeoecology of the giant Eocene gastropod *Campanile*

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Key words: Eocene, palaeoecology, ichnology, Gastropoda, *Campanile*, *Entobia*

ABSTRACT

The extant Australian gastropod *Campanile symbolicum* Iredale is a subtidal algal feeder, a habit that has been considered to extend to Paleogene members of this Tethyan genus. Support for this extrapolation is provided by a specimen of *Campanile* sp. A from Wait-a-Bit Cave, parish of Trelawny, Jamaica, which is unusually preserved as a cast with a dense infestation of the trace fossil *Entobia* sp. cf. *E. laquea* Bromley & D'Alessandro (= clionid sponge boring). This occurrence is considered analogous to infestations of clionid borings in shells of Recent and Pleistocene *Strombus gigas* Linné in shallow-water, Caribbean environments, suggesting that similar examples of such large, gastropodal 'benthic islands' may be a possible indicator of shallow sublittoral, tropical settings.

ZUSAMMENFSASSUNG

Der australische Gastropode *Campanile symbolicum* Iredale ist ein Algenfresser im subtidalen Bereich. Es wird angenommen, dass diese Lebensweise schon bei den paläogenen Vertretern dieser Tethys-Gattung bestand. Diese Ansicht wird gestützt durch ein Individuum von *Campanile* sp. A aus Wait-a-Bit Cave, Trelawny, Jamaica, das in ungewöhnlicher Weise als Steinkern erhalten ist und einen dichten Befall des Spurenfossils *Entobia* sp. cf. *E. laquea* Bromley & d'Alessandro (= clionider Bohrschwamm) aufweist. Dieses Vorkommen wird mit dem Befall rezenter und pleistozäner Schalen von *Strombus gigas* Linné durch Clioniden in Flachwassergebieten der Karibik verglichen. Dieser ähnliche Fall von angebohrten, grossen Gastropoden gibt einen möglichen Hinweis auf flache, sublittorale, tropische Lebensräume.

1. Introduction

The giant gastropod *Campanile* sp. A of Jung (1987), from the Eocene Chapelton Formation, Yellow Limestone Group, of Jamaica, attained a height of at least 500 mm. However, it is a notable fossil for reasons apart from size. De la Beche (1827) correlated the lower part of his white limestone formation of Jamaica (= Chapelton Formation in modern usage) with the *Calcaire grossier* in France and the London Clay in England, based on the presence of common, giant *Cerithium (= Campanile)* in all three units (Jung, 1987, p. 890; Wright & Robinson, 1993, p. ii). In so doing, De la Beche showed the Chapelton Formation to be Eocene in modern terminology. This was the first biostratigraphic correlation of any Jamaican unit (Donovan, 1996). Indeed, this may have been the first example of Transatlantic biostratigraphic correlation, a notable achievement, and gives Jamaican "*Cerithium*" the distinction of being one of the earliest fossils in the Antillean region (perhaps the first) to have been identified and named, albeit to generic level.

However, despite this impressive pedigree, there is much that is still poorly understood about *Campanile* sp. A. Even though it has been known for over 170 years, it is still to be named with confidence to the level of species, being almost invariably known from incomplete internal moulds (see discussion below). Although classified as *Campanile* cf. *giganteum* (Lamarck) by Trechmann (1923), the Jamaican species was subsequently ascertained to be a distinct taxon (Jung, 1987). Only recently has a partial external mould been discovered and is awaiting description (R.W. Portell, pers. comm.). Campanilid gastropods extend back to the Maastrichtian and were particularly diverse during the Eocene, including some of the largest known gastropods (Houbrick, 1984, p. 234). The only extant species of this genus, *Campanile symbolicum* Iredale from Australia, is a shallow water, algal grazer (Houbrick, 1981, 1984). With a gap of *circa* 50 million years between the Recent and the Eocene species considered herein, it is uncertain if the palaeoecology of the ancient taxon was similar, al-

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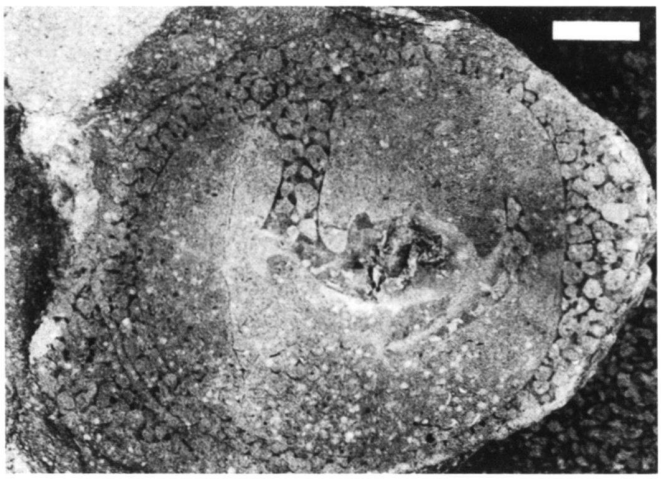

Fig. 1. Polished, oblique transverse section (viewed under water) of *Campanile* sp. A of Jung (1987) infested by *Entobia* sp. cf. *E. laquea* Bromley & D'Alessandro, 1984. This view shows the more apical end of the specimen. This is University of the West Indies Geology Museum specimen number UWIGM 1997.17. Scale bar represents 10 mm.

though this has been assumed. Herein, we present new observations that provide significant supporting data regarding the palaeobathymetry of *Campanile* sp. A, based on a uniquely preserved specimen from Jamaica.

2. Locality and Description

The specimen was collected from Wait-a-Bit Cave, south of Green Town, parish of Trelawny, central Jamaica, at Jamaican grid reference 951 769 (1:50,000 (metric edition) topographic sheet 7, "Albert Town-Alexandria"). This is about 18° 14.65' N 77° 31.10' W (R.W. Portell, pers. comm.). The cave exposes a section in the Stettin Member, Chapelton Formation, Yellow Limestone Group, of late early or early middle Eocene age. The geology of this locality was discussed in detail by Miller & Donovan (1996), who also included a locality map and a cave survey. Although collected loose from float, this specimen was probably derived from unit 1 of Miller & Donovan (1996, text-Fig. 3), an unbedded, nodular limestone with silty mudrock partings. Jung (1987, p. 891) also recorded *Campanile* sp. A from this locality.

The specimen (Fig. 1) is a wedge-shaped fragment of a shell of *Campanile* sp. A that retains parts of three whorls and some of the adhering matrix. Both ends were fresh when collected, suggesting it formed part of an originally more complete specimen. The matrix is a grey, orange-weathering bioclastic limestone, rich in benthic foraminifers and molluscan debris. The shell fragment has a maximum diameter of 73 mm and a height of about 74 mm. Unusually, the shell is preserved as a cast rather than an internal mould and has been replaced by calcite spar. This cast encloses a dense infestation of a camerate *Entobia* isp., with the chambers infilled and continuous with the same limestone that forms the enclosing matrix. *Entobia* is readily apparent at both ends of the specimen (which have been polished to facilitate examination; Fig. 1) and laterally, particularly on broken surfaces. Chambers of *Entobia* are closely crowded together, with outlines that are rounded to rounded rectangular to irregular, and are linked by short, usually quite broad necks or apparently coalesced, attaining growth phases C/D of Bromley & D'Alessandro (1984); that is, it is a mature infestation. Maximum chamber dimension is typically in the range 2–4 mm. Apertures are difficult to identify, but occur on both the inner and outer surfaces of the shell. However, delicate structures such as exploratory threads are not apparent, although, even if these were originally present, they may have been destroyed during the recrystallisation of the gastropod shell. The ichnospecies appears to be near to *Entobia ovula* Bromley & D'Alessandro, 1984, or, perhaps more closely, *Entobia laquea* Bromley & D'Alessandro, 1984 (see below). This is the oldest specimen of *Entobia* recorded from the Jamaican fossil record.

3. Discussion

Jung (1987, p. 891) noted that *Campanile* sp. A is commonly preserved as incomplete internal moulds, an assessment with which we readily agree based on 12 years of observations by the senior author. However, Trechmann (1923, p. 353) considered that "Most examples occur not exactly as casts but with the shell crushed or partly destroyed." To test Trechmann's interpretation, we cut transverse sections through four further, incomplete shells of this species, from the Guys Hill Member, Chapelton Formation, of Seven Rivers, parish of St. James (locality of Domning et al., 1997). All were internal moulds with the columella forming a more or less spar-filled cavity and short sections of inner shell whorls preserved as spar; one of these appears to be infested with *Entobia*. The unusually good preservation of the Wait-a-Bit Cave shell is probably the result of early diagenesis, supported by the three-dimensional preservation of plant macrofossils within the nodules of unit 1. This shell is also less deformed than specimens from Seven Rivers.

Miller & Donovan (1996) inferred that unit 1 at Wait-a-Bit Cave was deposited as lime-rich muds and silts, inhabited by burrowing bivalves and the infaunal spatangoid *Schizaster hexagonalis* Arnold & Clark. The presence of ribs of prorastomid sirenians indicates that the sea floor may have been stabilised by seagrasses (Domning, 1981), thus suggesting a shallow-water environment (<30 m water depth?) within the photic zone, and the fauna of foraminiferans is suggestive of a low energy, lagoonal setting. This is slightly different from the environment of extant *Campanile symbolicum*, which lives subtidally (1–4 m water depth) on sandy substrates, sometimes with associated seagrasses or macroalgae, that occur between exposed limestone on rocky platforms (Houbrick, 1981, 1984). Thus, the presence of *Campanile* sp. A in the Wait-a-Bit Cave succession supports a broad uniformitarian interpretation of

the habitat of this species. The interpretation of Miller & Donovan (1996) is further supported by the dense infestation of *Entobia* found in the figured specimen.

Bromley & D'Alessandro (1984, p. 264) and Bromley & Allouc (1992, p. 49) noted that cross sections are inadequate for the precise identification of *Entobia*. Of the camerate ichnospecies of *Entobia* (see Bromley & D'Alessandro, 1984, 1989; Bromley & Asgaard, 1993), we consider the Wait-a-Bit specimen to most closely approach *E. laquea*, although this identification cannot be made unequivocally. *Entobia* is absent from the littoral zone (Bromley, 1970, p. 76), occurring from shallow water (for example, see Bromley & Asgaard, 1993) to bathyal depths (Bromley & Allouc, 1992). However, Bromley (1970, p. 76) noted that clionid sponges construct their borings (= *Entobia*) most actively in the uppermost 25 m of the sublittoral zone and that "... a rich ichnocoenosis of sponge borings indicates a depth of less than 100 m."

We consider it highly suggestive that the dense infestation of *Entobia* under discussion should occur in a giant gastropod shell. Infestation was undoubtedly post-mortem, as indicated by apertures opening of both the outer and inner surfaces of the shell. It is not the first example of giant fossil *Campanile* to be documented with an infestation of clionids. For example, Fischer (1868, Pl. 24, Fig. 3) illustrated Eocene *Campanile giganteum* (Lamarck) from the *Calcaire grossier* of the Paris Basin that is densely infested with *'Clione cerithiorum'* Fischer, the latter being an unrecognisable entobian (Bromley & D'Alessandro, 1984, Tab. 2); such infestations are common (R. Janssen, written comm.). A modern analogue of this association exists in the late Cenozoic of the Antillean region. The commonest, large extant gastropods found in the shallow water of Jamaica and the Caribbean belong to the strombid *Strombus gigas* Linné. Where dead shells of this species are found accumulated in shallow water (such as where they have been discarded by fishermen in less than 2 m of water), they are invariably infested by clionid borings, although we have not noted these sponges in the shells of any live gastropods of this species. Evidence that this is not a recent phenomenon is provided by the occurrence of similarly bored shells of the same species in the late Pleistocene of the island (Pickerill & Donovan, 1997; Pickerill et al., 1998). In these examples, the borings were identified as camerate *Entobia ovula* Bromley & D'Alessandro and *Entobia* isp. or ispp.

Ancient borings are powerful tools in palaeoecological analysis (Bromley, 1994). Herein we note that the intense infestation of *Entobia* in large gastropod shells is not a new phenomenon in the Caribbean, but extends back at least 50 million years. Large, dead shells on a tropical sea floor provide a hard substrate for infestation by a variety of boring and encrusting organisms that would be otherwise excluded from a 'soft bottom' setting. Hitherto, such associations have been poorly documented, but in the Recent and Pleistocene are known to occur in shallow water environments, which agrees with the observations of Bromley (1970; see above). We suggest that the infestation of Eocene *Campanile* by *Entobia*, documented herein, may be analogous to late Cenozoic associations of *Strombus gigas* and clionids that are known to occur in shallow water settings. This comparison is considered to have a still broader significance, as the strombid gastropods may have been amongst those that competitively replaced the campanilids in the late Cenozoic (Houbrick, 1984, p. 234). Supporting palaeoecological data (Miller & Donovan, 1996) suggests that *Campanile* sp. A in Wait-a-Bit Cave was living in a shallow water, soft bottom environment within the photic zone. This interpretation is apparently supported by the infestation of *Entobia*, which may be a useful tool for determining the broad palaeobathymetry of such occurrences in tropical palaeoenvironments.

In conclusion, we consider dense infestations of *Entobia* borings in giant Tethyan gastropods to be indicative of a shallow water environment, probably within the photic zone. This interpretation in the case of bored *Campanile* sp. A is supported by other faunal and sedimentological evidence, and by comparison with a late Cenozoic analogue, *Strombus gigas*.

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