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Back Cover: Dr. H. Leonard Vacher, University of South Florida, Keynote Speaker for the 12th Symposium and author of “Keynote Address – Plato, Archimedes, Ghyben Herzberg, and Mylroie”, this volume , p. ix. Photograph by Don Seale.

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A COMPOSITE TRACE FOSSIL OF DECAPOD AND HYMENOPTERAN ORIGIN IN THE RICE BAY FORMATION (HOLOCENE), SAN SALVADOR, BAHAMAS

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ABSTRACT

Composite trace fossils are the product of two or more species of tracemakers. In many instances, such traces are also caused by different tracemaker behaviors and by tracemakers with different environmental requirements. In this study, composite trace fossils from eolianites of the Holocene Rice Bay Formation, San Salvador, Bahamas are examined. These trace fossils are likely decapod dwelling burrows that were later modified by the addition of hymenopteran brooding chambers. The structures are definable in three ways: 1) large Y-shaped vertical burrows; 2) radiating clusters of small ellipsoidal chambers (cells); and 3) a combination of the two, in which the clusters are connected laterally to the exterior of the Y-shaped burrows by thin tunnels. The size and geometry of the Y-shaped burrows coincide with those of dwelling structures made by modern ghost crabs (*Ocypode quadrata*) and are assignable to the ichnogenus *Psilonichnus*. The size and geometry of the cell clusters are consistent with brooding chambers made by hymenopterans and are likely from halictid bees. The probable ichnogenera for these trace fossils are *Celliforma* and *Cellicalichnus*.

The proposed scenario for the formation of this composite trace is: 1) a sandy area in a beach-dune transition was occupied by burrowing ghost crabs; 2) burrows were left open or partially buried during or after crab occupation; 3) female hymenopterans entered these burrows and constructed tunnels and brooding chambers laterally adjacent to the main crab-burrow shafts; 4) eggs were laid in chambers, which were provisioned and sealed; 5) the broods developed into adults and exited the chambers; and 6) structures were buried and cemented. The paleo-

environmental significance of these composite structures is that insect brooding always takes place above the intertidal zone, thus the ghost crab burrows were isolated from direct marine influence long enough for secondary occupation by hymenopterans, yet also before cementation. They also indicate a more narrow facies range than that suggested by each individual trace fossil.

INTRODUCTION

Composite trace fossils are biogenic structures caused by two or more species of tracemaker (*sensu* Pickerell, 1994). Such trace fossils are ichnologically distinctive because they overlap in space, yet also may be displaced in time and habitat. In other words, a trace fossil formed by one tracemaker may have been modified either concurrently or later by a different tracemaker, and the behaviors that caused the traces may also represent different environmental adaptations. Consequently, recognition of composite trace fossils can provide supplementary information about the behavioral ecology of each tracemaker and clues about environmental changes over time. The likelihood of recognizing composite trace fossils in the geologic record is bolstered by examples of modern tracemakers making such traces (Gingras et al., 2002) or having modern analogues directly comparable to composite trace fossils in the same locality (Gregory et al., 2004).

This study explores the potential usefulness of composite trace fossils by describing and interpreting examples from the Rice Bay Formation (Holocene) on San Salvador, Bahamas. In this case, the two inferred

tracemakers, decapods (*Ocypode quadrata*) and hymenopterans (halictid bees) overlapped in habitats but represent dissimilar ecological adaptations. As a result, these trace fossils can be used to define more narrow paleoenvironmental parameters than those attributable to only one tracemaker, an assertion supported by the San Salvador examples described herein.

LOCATION AND GEOLOGIC OCCURRENCE

The trace fossils in this study are located in a small outcrop in the northeastern part of San Salvador, Bahamas, about 1.0 km due east of the Gerace Research Center (Figure 1) with coordinates of N 24° 07.28' and W 74° 27.27' (obtained from GPS surveys). The outcrop, located on the west side of Queen's Highway, was likely connected to and correlative with more extensive outcrops of the Rice Bay Formation (Holocene), and probably belongs to the North Point Member. Samples of the North Point Member yielded ages of about 5,300 years B.P. for rocks on nearby North Point peninsula (Carew and Mylroie, 1987). Preliminary examinations of North Point outcrops and other exposures of the Rice Bay Formation on San Salvador have not revealed any other occurrences of the composite trace fossils described here, although separate elements of them are present in places.

The outcrop is mostly exposed vertically, with only a few bedding-plane exposures, and has a lensoidal cross-section that is thickest (2.3 m) near the middle of its length (23.6 m). It tapers towards the ends (Figure 2A). It is a well-cemented peloidal and bioclastic calcarenite (grainstone) with low-angle trough cross-bedding throughout. Sand-sized peloids, bioclasts, and less common ooids are fine to medium, rounded to subrounded, and well sorted. Cross-bed sets are primarily oriented southeast-northwest. Other than bioclasts, no macroscopic body fossils are evident. However, trace fossils are present, albeit sparsely distributed, and occur most commonly in the middle of the outcrop, 0.3-1.7 m above its base (Figure 2B). One bedding plane also showed

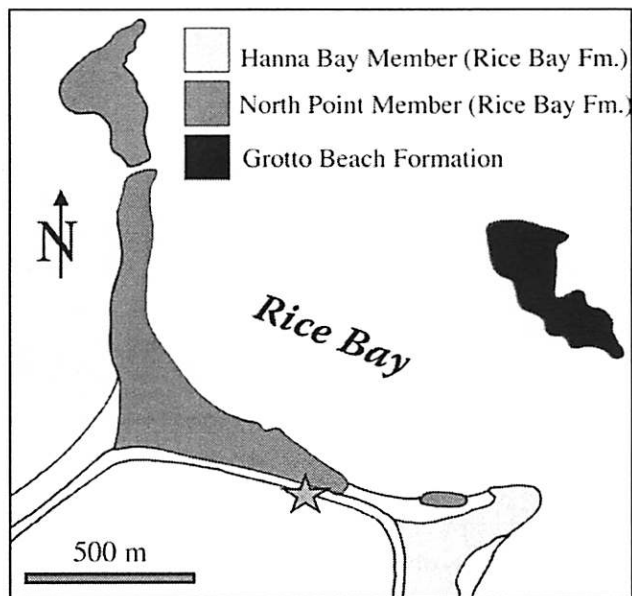


Figure 1. Locality map and general geology of North Point area, San Salvador, Bahamas; star indicates location of studied outcrop. Map adapted from Carew and Mylroie (1995).

faint, low-relief (1-2 mm deep) linear impressions, 1-2 mm wide, either branching or crossing one another. These structures are interpreted as root trace fossils and are the only ones that were found in the outcrop.

The Rice Bay Formation consists of the basal North Point Member overlain by the Hanna Bay Member. Both are interpreted as transgressive eolian deposits that formed as lobate dunes during the latter part of the Holocene (White and Curran, 1988; Carew and Mylroie, 1995, 1997; Curran and White, 1999). The trace fossil assemblage of the Rice Bay Formation supports this interpretation, showing a mixture of insect brooding structures and horizontal root traces (Curran and White, 1987; White and Curran, 1988; 1997a; Curran and White, 1999; Hasiotis, 2003) and less common decapod burrows and trackways (Curran, 1984; Walker et al., 2003).

This assortment of trace fossils attributed to terrestrial and semi-terrestrial organisms occur in dunes that, on this part of San Salvador, overlapped the upper foreshores and backshores (White and Curran, 1988; Curran and White,

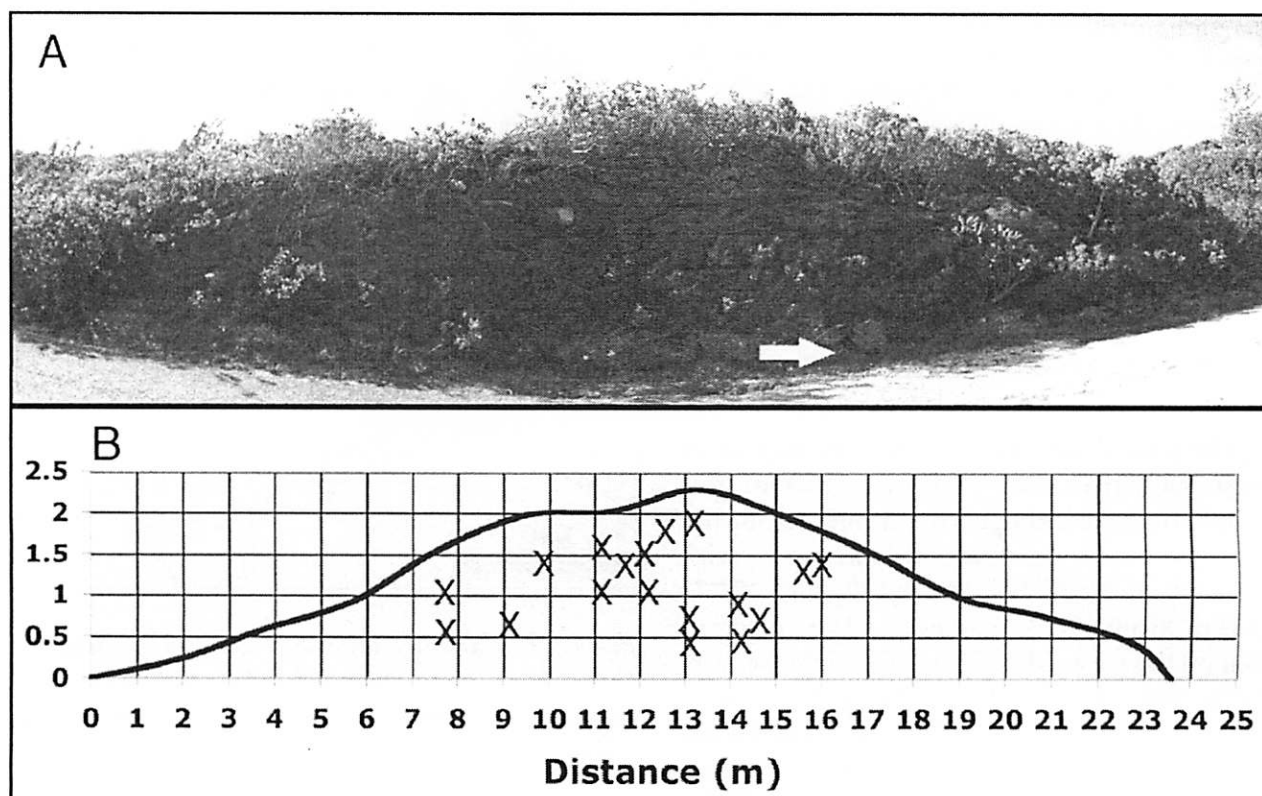


Figure 2. Outcrop of North Point Member examined in this study and distributions of composite trace fossils. A – Panoramic photograph of outcrop showing lensoidal form; backpack for scale (arrow). B – Profile of outcrop with “X” indicating locations of either component of composite trace fossils.

1999). However, the lack of vertically extensive root trace fossils indicates that dunes did not reach the degree of stabilization recognized in eolianites of the Pleistocene Grotto Beach Formation (Carew and Mylroie, 1995; Curran, 1997b; White and Curran, 1997b). In fact, the “unvegetated” eolianites of the Rice Bay Formation at NorthPoint are distinctive from Grotto Beach Formation eolianites on nearby Man Head Cay, in which well-preserved root trace fossils are abundant (Traynham and Martin, 2003).

COMPOSITE TRACE FOSSILS OF RICE BAY FORMATION, NORTH POINT

Description

The trace fossils examined in this study are open structures (full- and semi-relief

endichnia) oriented mostly vertical to oblique with respect to bedding. They are evident as larger-diameter holes and unlined, straight shafts with circular outlines (0.9-3.6 cm) closely associated with or connected directly to clusters of smaller ellipsoids (Figure 3A). The holes are either single or paired, leading correspondingly into single or Y-shaped (branching) shafts. Where Y-shaped, they bifurcate upward, and branches of Y-shaped structures have narrower diameters than lower parts (i.e., they widen below junctions). For example, one structure had upper shaft diameters of 1.4 and 1.9 cm, whereas the lower shaft was 2.9 cm wide. Measurements taken of shaft diameters along the entire outcrop yielded a mean of 1.9 ± 0.8 cm ($n = 46$). Exposed parts of shafts commonly continue into the outcrop; maximum total length of one was 94 cm (43 cm exposed + 51 cm in outcrop).

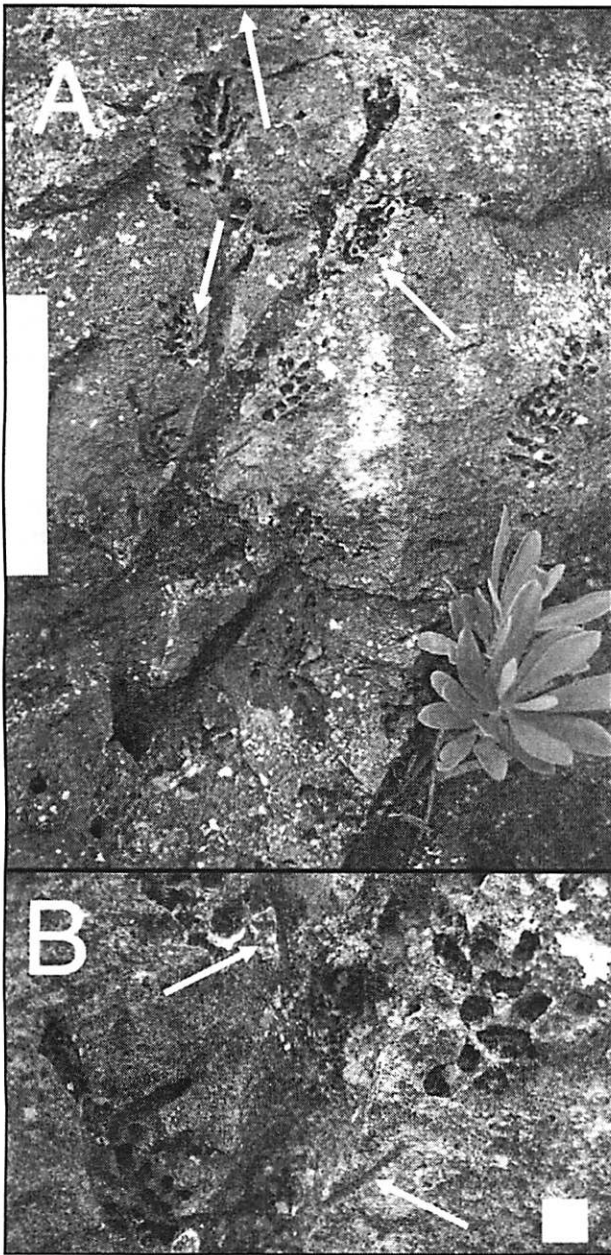


Figure 3. Composite trace fossils in North Point Member. A - Large-diameter Y-shaped shafts with cells clusters directly connected to or on peripheries of shafts; scale bar (left) = 15 cm. B - Close-up of cell clusters (from inset in A) showing tunnels (arrows) directly connecting to large-diameter shaft; square = 1 cm².

Clusters of ellipsoids, herein referred to as “cells”, cover areas as small as 1.5 x 2.0 cm but as much as 3.6 x 4.0 cm. Most clusters are

apparently isolated from the shafts but in nearly all cases are within 20 cm of them. Some clusters show clear connections to the shafts via thinner (about 5-7 mm diameter) and obliquely oriented tunnels or are directly associated with upward terminations (Figure 3B). Clusters consist of 4-16 cells but average 10 (n = 12 clusters). However, cell counts are complicated in instances where two or more clusters may overlap, causing as many as 28 cells in one instance. Individual cells are elongate, flask-shaped (wider at their terminations), smooth-walled, 5 X 7 mm wide, and 14-20 mm (but typically 18 mm) long. Cells seemingly radiate outward from a central point or axis, rendering longitudinal, oblique, and cross sections on vertical surfaces, but also seem aligned in places. Only one bedding plane view of cell clusters was found, which showed distal ends of cells linked with one another and forming a poorly defined radial pattern (Figure 4). In this example, individual cells also display maximum diameters of 6 mm and lengths of 18 mm.

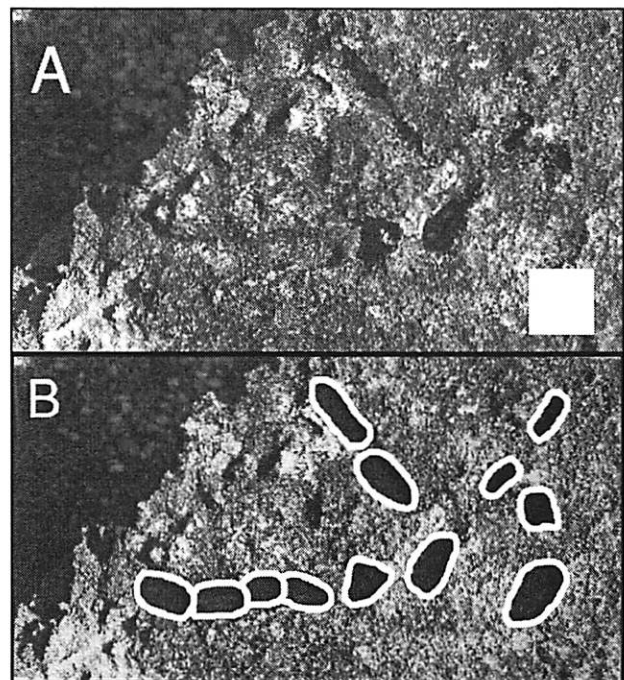


Figure 4. Bedding-plane view of cell clusters. A - Bedding plane showing negative-relief cells forming semi-radial pattern and linking of cells; scale = 1 cm². B - Outlines of cells and associated concavities.

Interpretation

Synopsis Interpretation of Trace Fossils.

The trace fossils in the Queen's Highway outcrop are interpreted as composite trace fossils caused by semi-terrestrial decapods and terrestrial insects, specifically ghost crabs (*Ocypode quadrata*) and halictid bees, respectively. The size, geometry, and facies occurrence of the larger-diameter holes and shafts are consistent with those reported for *Psilonichnus*, which in the Bahamas is interpreted as a dwelling burrow formed by *O. quadrata* tracemakers (Curran, 1984, 1997a; Frey et al., 1984). The size, geometry, and facies occurrence of the cell clusters are consistent with the ichnogenera *Celliforma* or *Cellicalichnus*, both of which are interpreted as hymenopteran brooding and pupation structures, specifically of halictid bees (Genise, 2000). The former ichnogenus was tentatively interpreted from the Rice Bay Formation on San Salvador (Curran, 1997a; Hasiotis, 2003), but the latter has not yet been identified in the Bahamas. Other presumed trace fossils of hymenopteran brooding structures, described by Curran (1997a), Curran and White (1999), and Dustira and Curran (2004), have not been given formal ichnotaxonomic designations.

Diagnosis of Decapod Component.

Psilonichnus and burrows made by modern *O. quadrata* are well documented in the Bahamas, and on San Salvador in particular (Curran, 1984; Frey et al., 1984; Curran and White, 1987; Curran, 1992; Clum, 2003), thus they are readily comparable to the structures described in this study. The Y-shaped branching, smooth unlined walls, burrow diameters, lengths, and other features are consistent with examples of *Psilonichnus* identified in Holocene eolianites by previous workers elsewhere on San Salvador.

However, a common dilemma in ichnology is the happenstance of multiple species of tracemakers making morphologically indistinguishable traces (Frey, 1973, 1975). Consequently, two alternative hypotheses are that the burrows are the handiwork of: 1) the same

tracemaker that made the cell clusters, meaning that these would be classified as compound trace fossils, rather than composite trace fossils (Pickerell, 1994; Rindsberg and Martin, 2003); or 2) a tracemaker other than *O. quadrata* or the maker of the cell clusters. An explanation similar to the former hypothesis was proposed for the informally named "stellate burrows" described from the Hanna Bay Member of the Rice Bay Formation. These trace fossils have central 2.5 cm diameter shafts that connect with smaller (1.0 cm diameter) burrows and cells radiating from the peripheries of the shafts; they are currently interpreted as brooding structures of halictid bees (Curran and White, 1999; Hasiotis, 2003). With regard to the latter hypothesis, trace fossils in the North Point Member described by Curran and White (1987), informally named "cluster burrows" are large-diameter, straight, vertical to obliquely oriented, and intersect upwards in places. As a result of their large diameters, orientations, and occasional (false) branching, they superficially resemble burrow shafts of *Psilonichnus*. These cluster burrows are interpreted as escape burrows of juvenile sphecid wasps (Curran and White, 1987, 1997a; White and Curran, 1993; Hasiotis, 2003). Other possible *Psilonichnus*-like structures made by non-decapod tracemakers are root traces, some of which can also exhibit bifurcations, sizes, and preservational modes comparable to *Psilonichnus* (Curran, 1984).

Nonetheless, the broad range of burrow diameters described in this study, along with qualitative evidence, belie the hypothesis of a non-decapod tracemaker. For example, burrows made by wasps and bees are quite regular in diameter and oftentimes approximate the adult body diameters of the tracemaker species (Jorge Genise, personal communication, 2004), which is in direct contrast to those seen here. An instance of this size consistency is provided by the aforementioned cluster burrows of the North Point Member, which vary from 1-2 cm in diameter but are mostly 1.2-1.4 cm (White and Curran, 1997a). Indeed, perhaps the most convincing evidence supporting a ghost crab origin for the burrows is the range, average, mode, and variability of

burrow diameters, which match very well with those associated with populations of modern ghost crabs. For the sake of comparison, an equal-sized sample (n = 46) of *O. quadrata* burrow diameters was measured June 6, 2004, on a beach of Grahams Harbor at low tide. The data were then described statistically and plotted on a histogram for visual comparison with the fossil examples. Interestingly, the two histograms (Figure 5) show similar spreads of data, and descriptive statistics yielded near-identical ranges (3.0 cm modern vs. 2.6 cm fossil), means (1.8 cm modern vs. 1.9 cm fossil), medians (1.7 cm vs. 1.6 cm), and coefficients of variation (0.44 vs. 0.42), as well as identical modes (0.9 cm).

Of course, a few caveats should be mentioned: 1) 46 burrow diameters represent a

relatively small sample and therefore may not be reasonably representative of a population of *O. quadrata* burrows (modern or fossil); and 2) Curran (in Frey et al., 1984) made a general observation that *Psilonichnus* diameters tend to be slightly larger than those of modern *O. quadrata* burrows on San Salvador. Nevertheless, the quantitative results presented here provide an illustrative example. When the close resemblance of the overall forms to those associated with known examples of *Psilonichnus* is taken into account, the preponderance of evidence argues more persuasively for an *O. quadrata* origin rather than insects. Moreover, root traces are also unlikely candidates for the structures because of the near-constant diameters maintained along any given shaft and upward branching. Root traces, in contrast, typically narrow distally and have increasing amounts of secondary branching in deeper parts that likewise taper (Gregory et al., 2004).

In the Bahamas and similar semi-tropical or tropical areas, the environmental range for *O. quadrata* is limited to the uppermost foreshore, backshore, and lowermost dune environments. This is narrower than for the same species in more temperate areas, such as the Georgia (USA) coast (Frey et al., 1984; Curran and White, 1987; Curran, 1992). Nevertheless, *O. quadrata* burrows do occur in the lowermost parts of dunes in the Bahamas, although in lesser numbers than in intertidal zones (Curran, 1984; Clum, 2003). As a result, the eolian facies occurrence of the trace fossils described here is consistent with modern *O. quadrata* traces in the Bahamas.

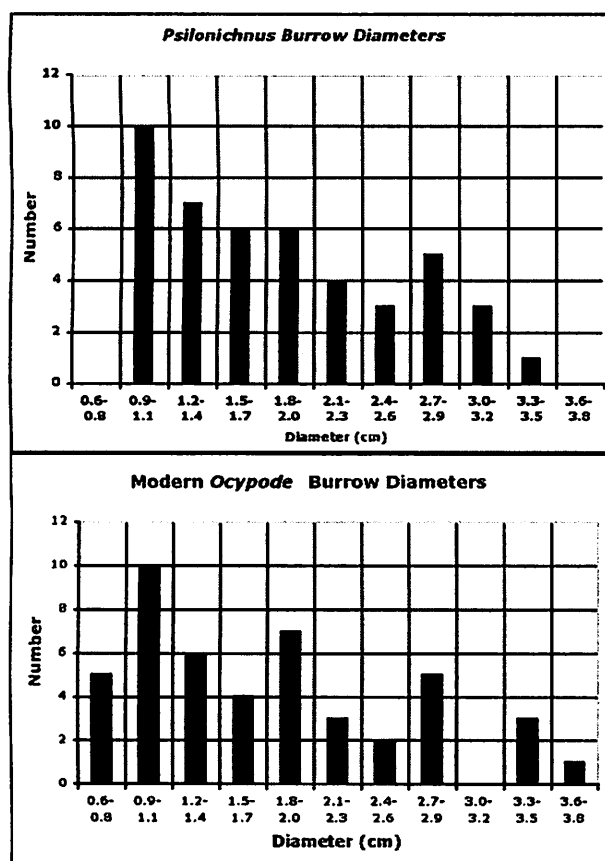


Figure 5. Size-frequency distributions between *Psilonichnus* burrow diameters (top) and modern *Ocyopode quadrata* burrow diameters, Grahams Harbor, June 6, 2004 (bottom).

Diagnosis of Hymenopteran Component. The hymenopteran-related components of the structures are akin to *Celliforma* or *Cellicalichnus*, which are trace fossils attributed to halictid bees (Genise, 2000; Hasiotis, 2003). Trace fossils related to bees and wasps on San Salvador are documented, although the results of this study demonstrate that they deserve more intensive study. Sphecid wasps and halictid bees are the suspected makers of the insect-related trace fossils described thus far on San Salvador, and most of these are interpreted as reproductive

structures, consisting of burrow shafts, brooding chambers, and juveniles exit burrows (Curran and White, 1987, 1991, 1999; Hasiotis, 2003). However, attempts to link these trace fossils with extant genera or species of hymenopteran tracemakers has met with little success. But to better assess the probable makers of the cell clusters described in this study, I will briefly explore them here.

Burrowing wasps and bees on San Salvador include sphecids wasps such as *Sphex jamaicensis*, *Cerceris watlingensis*, and *Stictia signata*, as well as halictid bees, such as *Agapostemon columbi* (Elliott, 1984; Elliott, 1992, 1993; Elliott et al., 1986, 2003). Of these species, *Sphex jamaicensis* is the most common. However, their adults are slightly longer (24 mm) than lengths of brooding cells measured in this study (Elliott, 1993). *Stictia signata* can be gregarious in sandy areas, but again the adults are a little larger (22 mm) than the cells described here (Elliott, 1993). A consideration other than size is the configuration of the brooding burrows and chambers, which in both sphecids are rather simple, consisting of single shafts leading to single cells (Matthews et al., 1981). At the time of this writing, detailed information about the architecture of *Cerceris watlingensis* burrows and brooding structures was not available, but those of other species of *Cerceris* are well documented. Like *S. signata*, they are typically burrows with single or several cells on the ends of short tunnels (Mueller et al., 1992).

Wasp and bee brooding cells, which usually serve as pupation chambers, differ morphologically in several ways: 1) bee cells are smooth-walled, often flask-shaped, and sealed with a spiral cap, whereas wasp cells are rough-walled, capsule-shaped, and lack a cap; 2) bee cells form clusters connected to tunnels, but wasp cells are more often solitary and attached by short tunnels off main burrow shafts or at the ends of shafts (Michener, 2000; Hasiotis, 2003). An important behavioral difference between bee and wasp nest construction is in provisioning. Most burrowing bees use non-animal food sources, such as pollen balls, whereas most burrowing wasps are predators or parasitoids. As is typical for

predators, many wasp species display fierce competition for ecospace. For example, some species of *Cerceris* tend to nest in large aggregations. Originally this was interpreted as parasocial behavior (Wilmer, 1985). However, subsequent studies showed that this sociality masked fierce competition for individual burrows. Usurpation of previously made burrows and provisions in species of *Cerceris* is quite common (Elliott et al., 1986; Elliott and Elliott, 1987; Mueller et al., 1992; Field, 1994; Field and Foster, 1995).

Based on this information, the best explanation for the structures described here is that they are from halictid bees. *Celliforma* is the ichnogenus most often applied to suspected fossil halictid brooding chambers, although a full consideration of associated burrow architectures reveals that this designation is too broad (Genise, 2000). On San Salvador, Curran (1997a) and Hasiotis (2003, in figure 12E-F) tentatively compared the stellate burrows in the Hanna Bay Member to *Celliforma*. However, the architecture of these structures, with cell clusters connected by tunnels to central shafts, is more akin to *Cellicalichmus* (Genise, 2000). Still, in other ways, it is not quite comparable to known halictid nesting structures (Jorge Genise, personal communication, 2004).

Regardless of ichnotaxonomy, the size, shape, and geometric arrangement of the trace fossils described here are best explained as the products of halictid bee behavior. Their sizes are within the range of halictid bees (normally less than 20 mm) (Michener, 2000). Individual cells are flask-shaped, smooth-walled, closely spaced, and connect to tunnels, all characteristic of halictid bee cells (Genise, 2000; Michener, 2000; Hasiotis, 2003). Although cell caps are not evident in any of the specimens the geometry of the trace fossils, i.e., multiple cells clustered in association with a tunnel emanating from a main shaft, is similar to brooding structures made by bees (Genise, 2000; Michener, 2000; Hasiotis, 2003).

Little is known about the nesting and habitat range of *Agapostemon columbi*, the only

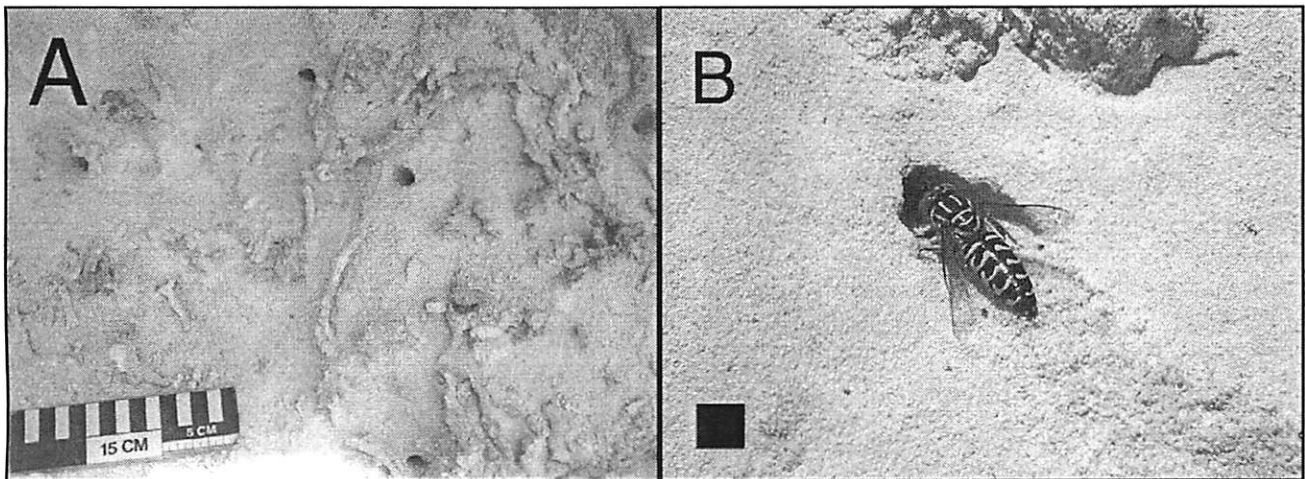


Figure 6. Hymenopteran burrows immediately above intertidal zones. A – Abundant burrows of sphecid wasp *Sphex jamaicensis* in sandy areas associated with root trace fossils, The Gulf (southeastern San Salvador). B – *Stictia signata* backing out of a freshly dug burrow in sandy area, Hanna Bay (northeastern San Salvador); box scale = 1 cm².

known halictid bee from San Salvador, although Elliott et al. (1986) observed this species entering abandoned nests of *Cerceris wallingensis*. This suggests the possibility of composite hymenopteran nests, but that is beyond the scope of this study. In June 2004, this author observed two wasp species (*Sphex jamaicensis* and *Stictia signata*) constructing, entering, and exiting burrows in sandy areas only 1-2 meters above the high-tide mark on San Salvador (Figure 6). These preliminary observations support the hypothesis that ecological zones occupied by ghost crabs and sphecid wasps overlap, even if temporarily, and suggest that, in the near future, halictid bees burrowing in the same areas may also be documented.

Synthesis of Components. The two distinctive components of these trace fossils, likely made by different tracemakers, in places are closely associated and directly connected to one another, thereby qualifying the structures as composite trace fossils. Based on an analysis of each component, the larger, vertical to oblique burrows were formed by ghost crabs (*O. quadrata*), whereas halictid bees similar to *Agapostemon columbi* formed the smaller shafts

and cell clusters. Trace fossils similar to each of the separate components are documented from the Rice Bay Formation (Curran, 1984; Frey et al., 1984; White and Curran, 1987; Curran and White, 1991), but this study is the first to recognize interconnections between the two.

Although the specimens of *Psilonichnus* are indistinguishable from others in the Rice Bay Formation, one important difference between halictid structures interpreted in the North Point and Hanna Bay Members is that the Hanna Bay cells and cell clusters are significantly larger than those in the North Point Member. One explanation for this size discrepancy is that the older North Point Member cell clusters may have been made by a different tracemaker species than those of the younger Hanna Bay Member, perhaps signifying differing colonization times of halictid species on San Salvador (H.A. Curran, personal communication, 2004). Testing of this hypothesis could provide insights into the natural history of hymenopteran reproduction and colonization rates in the Bahamas, particularly for times before human alteration of habitats.

Because these trace fossils were apparently unrecognized before this study, they

also may represent a more unconventional origin. For example, one way to disprove the composite trace fossil hypothesis proposed here is to demonstrate that they are actually compound trace fossils made by one species (*sensu* Rindsberg and Martin, 2003), such as *O. quadrata* or a similar species of decapod. In this scenario, the small sizes of the cells would be explainable as decapod brooding structures that are attached to the main burrow shafts. Verde and Martinez (2004) recently named a new ichnogenus, *Maiakarichnus*, in which this behavior offered an explanation for structures associated with thalassinidean tracemakers. Moreover, some characteristics of the cells and cell clusters, such as the upward orientations of cells, are not entirely compatible with standard traits associated with halictid bees (Jorge Genise, personal communication, 2004). Follow-up research should consider these and other alternative hypotheses for these enigmatic structures.

PALEOENVIRONMENTAL SIGNIFICANCE

Facies Delineation

Psilonichnus, the namesake of the *Psilonichnus* ichnofacies, is frequently regarded as indicating a semi-terrestrial facies in the foreshore on dune environments that are adjacent to fully marine environments (Frey et al., 1984). In the Bahamas, this facies is narrower than in more temperate areas, and its modern equivalents are more often restricted to the beach (uppermost foreshore to lower dunes). *Celliforma* and other trace fossils associated with hymenopteran brooding are fully terrestrial; as a result, their geographic range in ancient facies of the Bahamas is potentially broad. Accordingly, composite trace fossils consisting of components made penecontemporaneously by *O. quadrata* and halictid bees suggest much narrower facies than trace fossils made by each individual tracemaker.

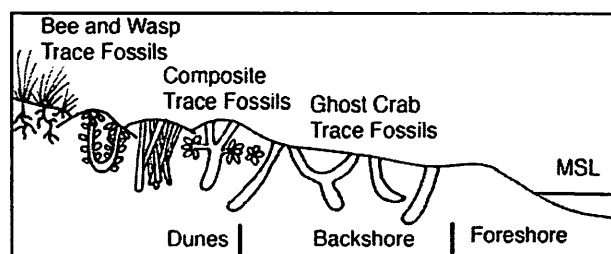


Figure 7. Idealized profile for foreshore-dune transition in trace fossil assemblages including hypothesized composite trace fossils of decapod-hymenopteran origin; MSL = mean sea level. Modified from Curran and White (1991).

Consequently, the idealized offshore-onshore profile of Bahamian ichnofacies proposed by Curran (1992, 1997) is potentially amended by the results of this study (Figure 7). In the Bahamas, the ranges of traces made by semi-terrestrial crabs (*O. quadrata*) and fully terrestrial hymenopterans (wasps and bees) will only overlap in the lower, shoreward-facing parts of dunes. Furthermore, hymenopteran brooding cells must remain above the water table for successful breeding to occur (Hasiotis, 2003). This means that, at the time of their construction, such traces must have been above both the high-tide mark and subsurface sands saturated by tides. Physical sedimentary structures (e.g., low-angle cross-bedding), the lack of macroscopic body fossils, paucity of root trace fossils, and proximity to other eolianites also support the conclusion that the facies examined in this study are from the lower parts of dunes. Observations by this author of modern wasps burrowing in sandy areas 1-2 m above the high tide mark confirm the possibility of insect burrowing in such areas.

Timing of Formation

The co-occurrence and interconnection of two distinctive trace fossils, made by arthropods with different ecological niches, implies a time gap between the formation of the components. Additionally with composite trace fossils the first tracemaker modifies the

substrate in a way that alters conditions for the secondary tracemakers occupying the space (Gingras et al., 2002; Gregory et al., 2004). For the trace fossils discussed here, the decapod structures are likely the oldest because side tunnels leading from burrow shafts presuppose the prior existence of the shafts. The shafts could thus be used as avenues for female hymenopterans in constructing subsurface brooding structures, without expending energy in digging their own shafts.

Relevant to any discussion of composite trace fossils in carbonate sediments is the timing of lithification with respect to each component, particularly because cementation of traces can be quite rapid in Bahamian carbonate sediments (Curran, 1992). Because the structures are burrows, both components must have been made before cementation occurred. In this case, the ghost crab burrows were made first, and either left open or buried (but not completely filled), and then exploited by halictid bees long enough to make multiple brooding structures. This sequence resumes as sites burrowed by the halictids were in well-drained sands above the water table at the time of burrowing. Hasiotis (2003) postulated that entrances, main burrow shafts and tunnels leading to the cells had the lowest preservation potential. In the San Salvador examples, all parts other than the burrow entrances are preserved. This implies that preservation was exceptional or the model proposed by Hasiotis (2003) is biased toward siliciclastic sediments, not taking into account potentially rapid cementation in carbonates.

In summary, the probable sequence for formation of these composite trace fossils is: 1) a sandy area at the beach-dune transition was occupied by burrowing ghost crabs above the high tide mark; 2) burrows remained open either during or after crab occupation, although top parts may have been shallowly buried by shifting sands; 3) female hymenopterans, probably halictid bees similar to *Agapostemon columbi*, entered these burrows and dug tunnels and brooding chambers (cells) laterally adjacent to the main crab-burrow shafts; 4) eggs were laid in chambers, which were also provisioned

with food for the larvae, and sealed; 5) brood developed into adults and may or may not have exited the chambers; and 6) structures were buried and cemented, although a sufficient number of trace fossils remained unfilled so that they were later noticeable as open structures. Additional factors include the timing of spring and neap tides, as well as insect breeding cycles; for example, a coincidence of neap tide and hymenopteran burrowing and brooding would have been more conducive for formation of composite structures.

CONCLUSIONS

This study has three main conclusions:

1. Composite trace fossils in a small outcrop of the North Point Member (Rice Bay Formation, Holocene), San Salvador Island, Bahamas, were formed in the lowermost (seaward) part of eolian dunes by decapods and hymenopterans.
2. The probable decapod tracemaker was the ghost crab *Ocypode quadrata* or a similar species, which made large-diameter, Y-shaped shafts that served as dwelling burrows and are identifiable as *Psilonichnus*. The probable hymenopteran tracemaker was a halictid bee, such as *Agapostemon columbi*, which made small-diameter tunnels and cell clusters adjacent to and connecting with the *Psilonichnus*; these are identifiable as either *Celliforma* or *Cellicalichnus*.
3. The composite trace fossils demonstrate different tracemakers, behaviors, and ecological needs, but together indicate a more narrow facies zonation than either component by itself. In this case, they indicate the uppermost foreshore or lowermost backshore in a beach profile.

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