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First fossil evidence of a drill hole attributed to an octopod in a barnacle

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All modern cephalopods are versatile, opportunistic predators employing a variety of hunting techniques such as ambushing, luring, stalking, camouflaging and pursuing (Boyle & Rodhouse 2005). Extant octopods (Octopodidae) prey on a host of organisms including crustaceans, fish, molluscs, cephalopods, polychaetes, ophiuroids and foraminifers, and are able to structure subtidal communities (Nigmatullin & Ostapenko 1976; Moriyasu 1981; Nixon & Young 2003; Boyle & Rodhouse 2005). The methods of preying used by octopods are to capture with their arms and interbrachial web followed by pulling apart shells (McQuaid 1994), biting with the beak (Dodge & Scheel 1999; Voight 2000) or drilling (e.g. Nixon in press). Drilling frequently takes place in decapod crustacean prey (e.g. Boyle & Knobloch 1981), in mollusc shells (e.g. Nixon & Maconnachie 1988; Fig. 2, pls. I–VII), and also in modern barnacles, although rarely reported (Guerra & Nixon 1987; Nixon & Maconnachie 1988; Barnes 1999).

Drilling predation in the Cenozoic fossil record is a well-studied phenomenon. Most of the work has focussed on drill holes inferred to be produced by gastropods in shells of both bivalves and gastropods (e.g. Kowalewski *et al.* 1998; Kelley & Hansen 2003; Klompmaker 2009; Chattopadhyay & Dutta 2013), but these predatory drill holes are also known from other invertebrates such as echinoids (Kowalewski & Nebelsick 2003; Złotnik & Ceranka 2005), scaphopods (Yochelson *et al.* 1983; Klompmaker 2011), ostracods (Reyment *et al.* 1987; Reyment & Elewa 2003), polychaete annelids (Klompmaker 2012; Martinell *et al.* 2012), brachiopods (Baumiller *et al.* 2006) and barnacles (Gordillo 2013). Predation evidence of ancient octopods is, to date, inferred only from drill holes. The first report, known to us, of drill holes attributed to ancient octopods is that of Robba & Ostinelli (1975) showing Pliocene bivalves and gastropods from Italy exhibiting such holes. To describe these trace fossils more systematically, Bromley (1993) erected the ichnotaxon *Oichnus ovalis* for oval drill holes and he also documented similar drill holes attributed to octopods in scallops from the Pliocene of Greece, whereas Harper (2002) reported on similar-shaped drill holes in Plio–Pleistocene scallops from Florida. It should be noted that octopod drill holes do not have a uniform shape, as subcircular drill holes are also known (e.g. Arnold & Arnold 1969; Fig. 2C, H; Nixon & Maconnachie 1988; pl. 3A) and can be classified as *O. simplex* instead of *O. ovalis*. Renewed interest in this type of predation is evidenced by Todd & Harper (2011), who attributed subcircular drill holes in an Eocene bivalve to octopods, and Klompmaker *et al.* (2013) showed the presence of oval drill holes attributed to octopods in Plio- and Pleistocene decapod crustaceans.

The goal of this study is to report the first fossil evidence of a drill hole in a barnacle that can attributed to an octopod, thereby adding to the growing body of evidence of octopods drilling prey during the Cenozoic. The drill hole microhabitat was subsequently fouled by an encrusting foraminifer.

Materials and methods

To calculate the percentage of octopod drill holes in barnacles, the faunule of wall and opercular plates from the Florida Museum of Natural History (FLMNH) locality Pickett Bay 01 (FR001), Franklin County, Florida, USA, exposing semi-indurated siliciclastic sediments of the Lower Pliocene Intracoastal Formation was studied. Only entirely visible plates (i.e. without any covering of other organisms including barnacles and sediment particles) were counted to ensure that no such drill holes were missed. Additionally, the numbers of barnacles with all six wall plates entirely visible were counted. Other fossil barnacle collections housed at the FLMNH and in the Mizunami Fossil Museum (Japan) were surveyed, but did not yield convincing examples of drill holes attributable to octopods. A Canon Eos 5D (Mark II) camera was used to photograph the entire barnacle. This camera and an SEM, Zeiss Evo MA 10, were used for close-up images. Institutional abbreviation: UF – University of Florida, FLMNH (Invertebrate Paleontology), USA.

Results

In total, two scuta and 365 wall plates of acorn barnacles were studied, including 78 wall plates from specimens with all six wall plates visible. One wall plate from the barnacle ?*Tamiasoma* sp. contained a drill hole attributed to an octopod, positioned in the radii of the carina (Fig. 1A,B). This is equivalent to ~0.3% of all wall plates examined. Assuming the presence of one drill hole per six wall plates to be sufficient to successfully prey upon the soft tissue of the barnacle, the predation percentage of this faunule is ~1.6%. The size of the drill hole is 1.08 by 0.64 mm for the outer and 0.40 by 0.24 mm for the inner diameter. The foraminifer encrusting one of the long sides of the wall of the drill hole (Fig. 1B,C) is identified as *Lobatula lobatula* (= *Cibicides lobatulus*), known from the Miocene and Pliocene of Florida (Cole 1931; Cushman & Ponton 1932) and has a maximum diameter of 0.29 mm.

Discussion

Encrusting foraminifer

We interpret *Lobatula lobatula* to have actively encrusted the drill hole wall of the barnacle instead of being washed into the drill hole and subsequently covered by sediment because: (1) the foraminifer fits snugly by following the outline of the wall; (2) exhibits a notch at the fourth chamber from the aperture to accommodate the fit; and (3) could not be rinsed from the wall as opposed to sediment surrounding the specimen after the drill hole in barnacle was discovered. To our knowledge, little has been published about the encrusting behaviour of this foraminifer from the pre-Holocene Cenozoic fossil record unlike for modern environments (e.g. Svavarsson & Ólafsdóttir 1999; Richardson-White & Walker 2011). Our research thus expands the knowledge of this behaviour and also reports on the additional evidence of encrustation of drill holes. Schmitt *et al.* (1983) indicated that the largest, oldest barnacle was often located over octopod drill holes on the kelp snail *Norissia norrisi*, suggesting the drill hole was a preferred place to settle.

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The microhabitat created by the drill hole in the barnacle likely served as a shelter against predators of *L. lobatula* and was an effective environment for preservation.

Drill holes attributed to octopods

The morphology of the drill hole suggest it was very likely produced by an octopod given its size, shape and form in being comparable to octopod drill holes in extant molluscs and crustaceans (e.g. Arnold & Arnold 1969; Boyle & Knobloch 1981; Nixon & Maconnachie 1988). The drill hole in a Recent acorn barnacle produced by *Octopus vulgaris* as reported in Nixon & Maconnachie (1988) is ovoid, contains a lip and is similar in size to those found in molluscs (their Table 1). Additionally, Guerra & Nixon (1987) indicated that the four drill holes in three specimens of the acorn barnacle *Semibalanus balanoides* had features similar to the octopod hole reported in Nixon & Maconnachie (1988), and Guerra & Nixon (1987) showed drill holes similar in shape to the drill hole in the barnacle in this study (compare their pl. 2 to Fig. 1B herein). Moreover, the dimensions of the outer (1.5–0.5 mm) and inner diameters (0.1–0.3 mm) in Guerra & Nixon (1987) overlap with the drill hole studied herein. Recently, a drill hole attributed to an octopod originating also from the Intracoastal Formation (but from a different locality) was noted in a merus of the crab *Platylambrus* sp. (Klompmaker *et al.* 2013). It exhibits a similar morphology (their fig. 3A–C).

Barnacles are not the main prey of octopods today. For example, Onthank (2008) reported that *Octopus* living in a tank did not eat barnacles and, as a result, no drilled plates were found. Nixon & Maconnachie (1988) even suggested that *Octopus* treated the barnacle *Semibalanus balanoides* attached to the gastropod *Gibbula magnus* (that also contained a hole) as a mollusc, speculating that drilling this barnacle may have been unintended. Guerra & Nixon (1987), who reported on three drilled specimens of *Semibalanus balanoides* with four holes attached to the undrilled gastropod shell *Patella vulgata*, did not refer to unintended drilling. The fact that three barnacles were drilled implies that drilling of these barnacles was intentional. We interpret the drill hole in the Pliocene barnacle reported herein to be intentional. This is supported by the fact that this barnacle is relatively large (18 mm width, 24 mm height) compared with most acorn barnacles from the studied faunule and thus would provide more food. Furthermore, the hole is located in a relatively thin portion of the barnacle shell (radii of the carina), suggesting that the predator may have been aware of a good location to get access to the soft tissue as soon as possible. Given the low percentage of octopod holes in plates of the Pickett Bay 01 locality, barnacles were probably not their main prey.

With new evidence emerging herein and in Klompmaker *et al.* (2013) octopods as a group already had a varied diet by the Pliocene consisting not only of molluscs (Robba & Ostinelli 1975; Bromley 1993), but also crustaceans including crabs and barnacles. It also suggests the presence of the boring organ, the salivary papilla within the buccal mass, in octopods at least since this time. Fossil stomach contents of octopods are unknown as they do not preserve well, but if found may not yield much evidence as cephalopods predominantly ingest the soft parts of their prey (Boyle & Rodhouse 2005). Discovering fossil evidence of predation by octopods on other prey known from the modern (e.g. fish, polychaetes, cephalopods, ophiuroids and foraminifers) may be difficult because of their low preservation potential, small size and/or common disarticulation. Perhaps the best fossils to target are Cenozoic nautiloids, provided that their shell is preserved. Saunders *et al.*

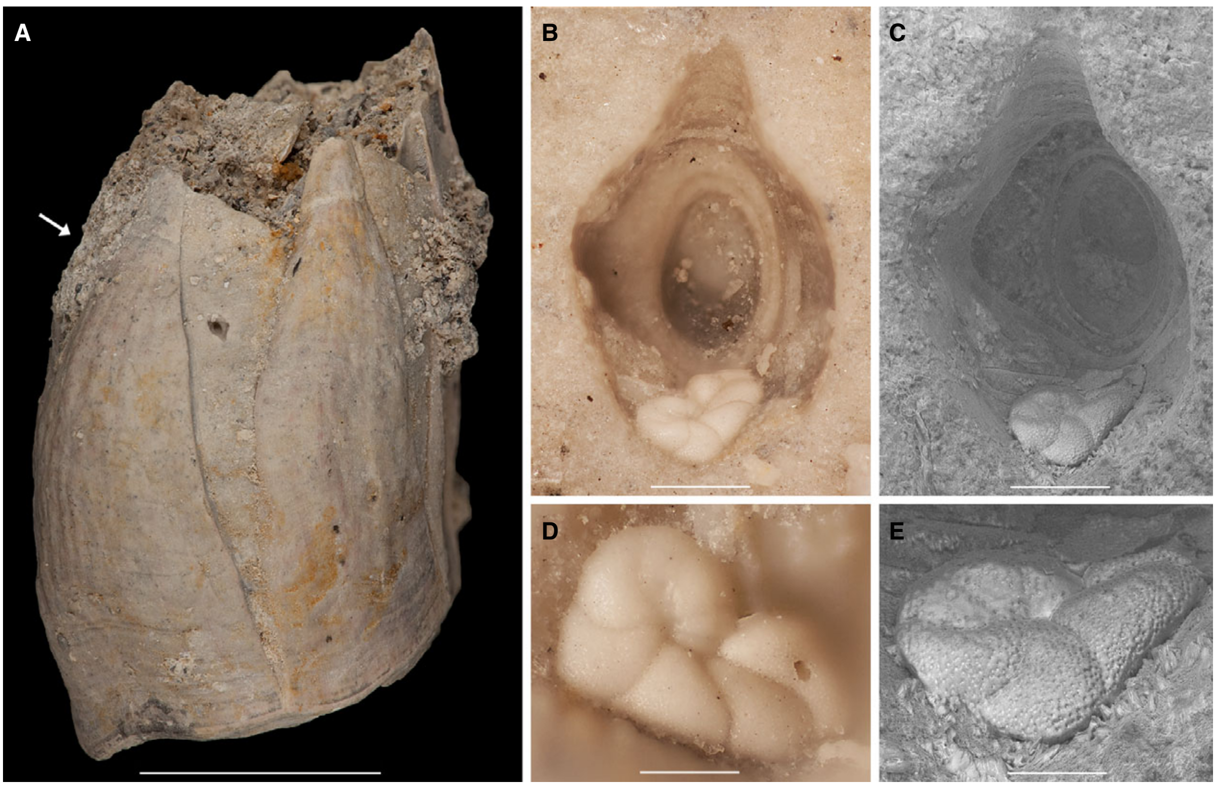

Fig. 1. The barnacle ?*Tamiasoma* sp. (UF 239559) from the Lower Pliocene Intracoastal Formation of Florida exhibiting an oval drill hole (UF 239560) attributed to an octopod (ichnotaxon *Oichnus ovalis*) and encrusted by the foraminifer *Lobatula lobatula* (UF 239561). (A) Barnacle with the drill hole located in the radii of the carina. The arrow points to the drill hole. (B, C) Close-ups of the oval drill hole with the foraminifer located on the left wall of the drill hole (light photography and SEM). (D, E) Close-ups of the foraminifer (light photography and SEM). Scale bars: A = 10.0 mm; B, C = 0.25 mm; D, E = 0.10 mm.

(1991) inferred a high drilling frequency as 57% of drift specimens of two Recent species of *Nautilus* were drilled by *Octopus*. Finding pre-Pliocene, additional Pliocene and Pleistocene fossil evidence of barnacles drilled by octopods is possible given that octopods had presumably evolved by the Late Cretaceous (e.g. Strugnell *et al.* 2006; Fuchs *et al.* 2009).

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