Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*

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The geological history of octopus is virtually unknown, owing to lack of a preservable skeleton. Several octopod species today are known to drill holes in prey animals for the injection of venom. These borings are incipient trace fossils that have good fossilization potential, and are named *Oichnus ovalis* isp. nov. Their abundance in Pliocene assemblages suggests that they will be recognized elsewhere in Tertiary and perhaps older assemblages, providing greatly needed data on the earlier range and feeding habits of octopus.

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Tove Birkelund had a way with fossil cephalopods. She improved their taxonomy and used them efficiently in biostratigraphy. But she never studied their palaeoecology. The present paper deals with the palaeobiology of the octopus, a cephalopod that is thoroughly neglected by palaeontologists, because, having no skeleton, it is virtually unrepresented by body fossils.

Today, species of several genera of octopus occupy the summit of the trophic pyramid as top carnivore of marine benthic communities throughout the world's seas and oceans. Thus it follows that they must have had a long and similarly glorious past together with their close but well documented relatives the belemnoids. But we know only two species of bodily preserved fossil octopods. There are three well-preserved specimens of the early Late Cretaceous *Palaeoctopus newboldi* (Woodward 1896; Roger 1944, 1946) and a specimen from the Mississippian Mazon Creek fossil Lagerstätte, that represents a poorly preserved, "blob-like" coleoid, possibly an octopus (Solem & Richardson 1975).

This non-preservation paradox led Teichert (1967) to suggest an unlikely evolutionary radiation (Fig. 1) whereby all eight extant families of octopods were shown as having originated in the Quaternary! In general, however, the Octopoda show many primitive characters that indicate that the order evolved from early teuthid (squid) stock at the beginning of the Mesozoic (Donovan 1964; Jeletzky 1965, 1966). The Mazon Creek example may indicate an even earlier origin.

There is a possible route by which to circumvent this *impasse*. At least some species of octopods today bore tiny holes in skeleton-bearing prey in order to paralyze them. These small holes, incipient trace fossils, should also be eminently recognizable in geological material. After all, drill-holes produced by predatory gastropods are a popular subject for palaeosynecological research and support a truly enormous literature. The corresponding literature on fossil octopus drill-holes is virtually non-existent.

Octopods are larger, drill faster, and make more holes than most predatory gastropods. Therefore their trace fossils should be the better known, not *un*known. The present article hopefully will begin to relieve this imbalance.

Trace fossils frighten most geologists. Many palaeontologists insist that, when properly understood, each type should be ascribable to exact animal progenitors (Melville 1979). Many ichnologists insist, on the contrary, that they may never be so related to biological taxa (Bromley & Fürsich 1980; Bromley 1990).

The present study should therefore be unsatisfactory to both parties. For while, on the one hand, octopods today make a variety of drill-hole morphologies in different prey species, on the other hand, only one of these boring styles is truly characteristic of octopus predation. This is a

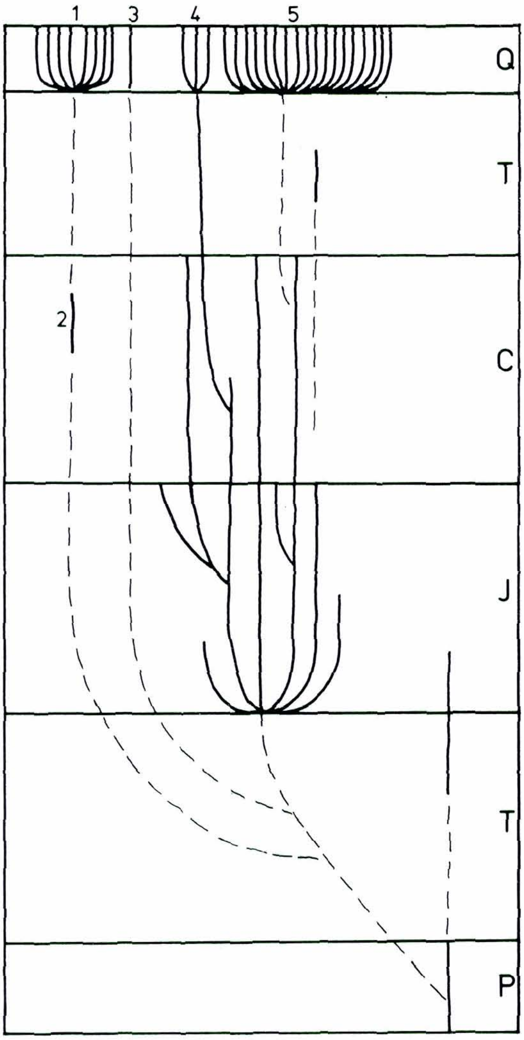

Fig. 1. An unlikely pattern of octopus and squid evolution from Permian to today, as envisaged by Teichert (1967). Octopoda – 1, the 8 extant families of octopods; 2, Palaeoctopodidae. Teuthida – 3, Vampyroteuthididae; 4, families of Myopsina; 5, families of Oegopsina. Modified after Teichert (1967, Fig. 20), where details of the fossil lineages may be sought.

form that has been recognized in shells of the same prey species of Pliocene and Pleistocene age and is named *Oichnus ovalis* herein. It should be noted, however, that while this trace fossil does not alone represent *the* drill-hole of octopods, it is nevertheless *a* drill-hole of octopods because no other taxon seems to be making such holes today.

Boring activity of octopods

After the first observation of octopus drilling predation (in oysters) was made by Fujita (1916), the habit was forgotten until rediscovered by Pilson & Taylor (1961). The species in both cases was *Octopus vulgaris*. Carter (1968), Arnold & Arnold (1969) and Wodinsky (1969) added further examples of drilling activity in this species. Rather naturally, these authors assumed that the radula was used as the boring tool, as in the drilling predatory snails. However, the elegant work of Marion Nixon has shown that the octopus bores mollusc shells not with its radula, which is too broad for the hole, but with the salivary papilla, which is supplied with horny thorns for the purpose (Nixon 1977, 1979a, 1979b, 1980; Nixon & Maconnachie 1988; Nixon et al. 1980). Crabs also are drilled in the same way (Guerra & Nixon 1987).

There is evidence that the physical penetration of the skeleton is assisted by chemical secretions also (Nixon & Boyle 1982; Nixon & Maconnachie 1988; Ambrose et al. 1988).

Eventually, other species also were found to drill prey: *Octopus cyanea* in nautilus (Arnold

Fig. 2. A common form of octopus boring as found in shells of pearly nautilus. In this example, the prey has apparently been rotated 90 degrees after initiation of boring, producing a cross-shaped bevel. The substrate is an adult *Nautilus pompillius* that was washed up as an empty shell on the Australian coast at Brisbane, Queensland. MGUH 22054. × 10.

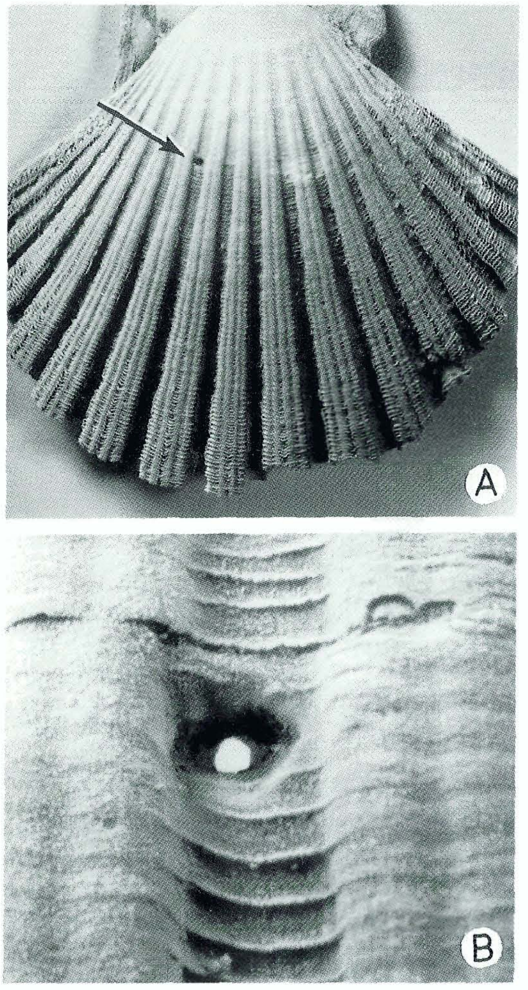

Fig. 3. A characteristic oval octopus penetration through the vaulted shell valve of *Pecten jacobaeus*, uppermost Pliocene, St. Paul's Bay, Lindos, Rhodes, Greece. MGUH 22055. A: location of the hole (arrow) is over the adductor muscle. × 2. B: close-up × 20.

1985) (Fig. 2); *O. dolfeini* in bivalves (Ambrose et al. 1988): and *Eledone cirrhosa* in crabs and barnacles (Boyle & Knobloch 1981; Nixon & Boyle 1982). Very few species as yet have been investigated, however, and the boring habit may prove to be widespread within octopods.

Drilling mechanism

The purpose of octopus in drilling its prey is not, as in predaceous gastropods, to eat the animal through the hole, but merely to inject poison (e.g., Pilson & Taylor 1961). When it is relaxed, a bivalve may be opened, a snail extracted or a crab subdued. For this reason the holes are generally much smaller than gastropod predation holes, despite the generally larger size of the predator.

Drilling also proceeds relatively rapidly: an octopus may capture, kill and discard the cleaned valves of a large scallop all within 1½ hours (Nixon & Maconnachie 1988). Because drilling is so rapid, an octopus commonly drills two holes or more in the same prey, in order to speed the relaxation of the animal.

Predatory snails drill slowly, and commonly place the hole at a thin part of the skeleton where drilling is relatively easy (e.g., Ziegelmeier 1954). The octopus, on the other hand, normally chooses to inject venom into adductor muscles, commonly finding the spot with great precision and thereby displaying a remarkable knowledge of the anatomy of different species of prey. Arnold (1985), examining nautilus shells bored presumably by *O. cyanea,* found that holes proved fatal only where drilled over muscles.

O. bimaculatus and *O. vulgaris* produce accumulations of shells outside their shelters (Ambrose 1983) and from these middens the natural prey species may be examined. In Greek coastal waters, *O. vulgaris* particularly favours *Haliotis lamellosa* as a prey. This archaeogastropod is never drilled, however, as the shell already possesses exhalent openings for use by the octopus. Likewise, gaping bivalves, such as *Solecurtus strigilatus,* which is commonly eaten by *O. vulgaris,* never is bored.

Morphology of the boring

Several authors have remarked that octopus drillholes are variable in shape (e.g., Wodinsky 1969; Bromley 1970). However, the detailed work of Nixon et al. (1980) and Nixon & Maconnachie (1988) has shown that there is a certain correlation between hole shape and prey species. For example, *O. vulgaris* produces a highly characteristic, oval, tapering hole in shells of *Mytilus edulis, M. galloprovincialis* and *Pecten jacobeus* (Fig. 3), whereas a somewhat cylindrical hole is made in gastropods in general.

The characteristic oval boring is not made by

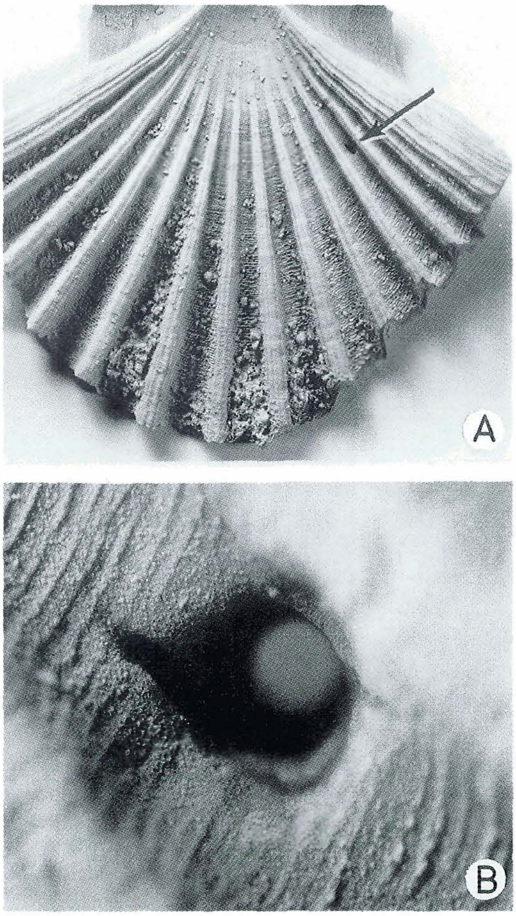

Fig. 4. A characteristic rounded oval boring in the flat valve of a *Pecten jacobaeus* from the Pliocene of Rhodes, Greece, 10 m below the top of the Kritika Formation at Kritika. MGUH 22056. A: the penetration (arrow) is located close to the adductor muscle (a near miss). Slightly enlarged. B: close-up, × 20. Note the gutter leading into the boring at left. The inner aperture is larger than in strictly oval borings.

O. vulgaris alone, however. Those made by *O. cyanea* in nautilus are identical (Fig. 2), as are those of *Eledone cirrhosa* in crabs. It is possible that the oval penetration occurs where the octopus is unable to rotate its prey while drilling, owing to its ungainly size or shape; in *Mytilus* spp. the hole tends to be placed in the umbo, right at the end of the shell. The cylindrical borings, on the other hand, tend to occur in smaller, handier substrates, which could be rotated during drilling by the octopus.

The oval holes commonly have a broad, scoop-shaped bevel externally, and an arcuate deeper portion, the work having stopped immediately a minute inner penetration was achieved. The cylindrical holes normally have a rounded external edge and a slightly more irregular form than the predation holes produced by muricid gastropods and with which they easily might be confused (Carriker & Yochelson 1968; Bromley 1981).

Commonly, also, a short groove or gutter may lead into the cylindrical hole of an octopus (Fig. 4), a feature that is not characteristic of muricid borings.

Ichnotaxonomy

The cylindrical penetrations of octopus resemble the ichnotaxon *Oichnus simplex* and are provisionally related to that trace fossil (Bromley 1981). The oval structures, however, are sufficiently characteristic as to deserve ichnotaxonomic separation on the basis of fossil material.

Ichnogenus *Oichnus* Bromley 1981.

Emended diagnosis: circular to subcircular holes of biogenic origin penetrating through skeletal substrates.

Discussion: the original diagnosis included pits having circular cross section that do not penetrate right through the substrate (Bromley 1981). These are particularly characteristic of echinoderm hosts and probably represent the work of parasites (e.g., Gale 1986), and have been separated as the ichnogenus *Tremnichnus* by Brett (1985). By so excluding these pits, the emended diagnosis of *Oichnus* is an improvement on the original.

Oichnus ovalis isp. nov.

Type material: Holotype: MGUH 22057, figure 5a. Paratype: MGUH 22058, figure 5b.

Locus typicus: the bay south of Cape Vagia and 1 km east of Kolymbia, Rhodes, Greece.

Stratum typicum: near the base of the yellow limestone unit that forms the foreshore of the bay: Upper Pliocene.

Diagnosis: oval *Oichnus* tapering subparabolically from a millimetre-sized external aperture to

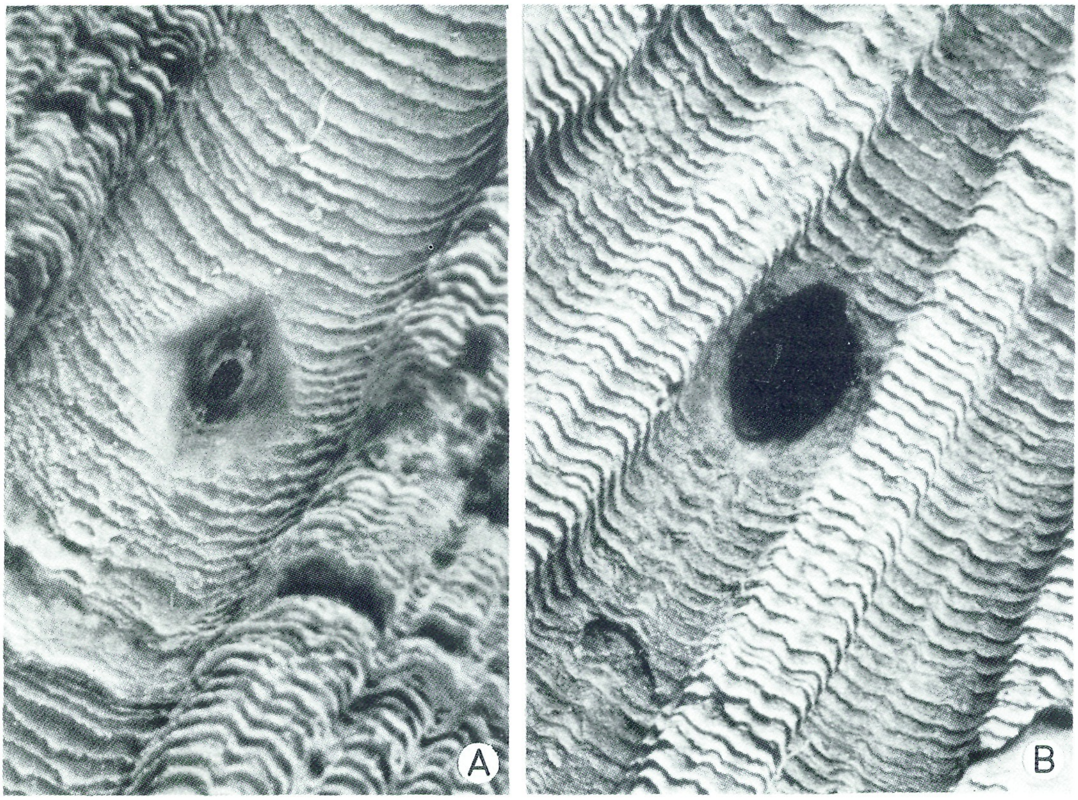

Fig. 5. A: *Oichnus ovalis*, holotype, in the flat valve of *Pecten jacobaeus*. × 15. B: *O. ovalis*, paratype, in the flat valve of another individual of *P. jacobaeus*. × 15. Same locality as holotype.

a minute inner one. External aperture commonly rhomboid in outline.

Description: the outer aperture may be sharp and crisp in outline, or in some cases rounded and softly contoured. It is normally elongatedly oval in shape but commonly has a somewhat rhomboid form. The sides of the hole converge inward in a curved manner that in cross section resembles a parabola, leading to a very small inner opening that is usually oval. Walls smooth. Unfinished examples are abundant, where complete penetration has not been achieved.

Interpretation: produced today by octopod cephalopods in skeletons of prey animals, particularly molluscs, including gastropod shells reused by hermit crabs, as well as brachyuran crab carapaces. In contrast to the more cylindrical forms mentioned above, the oval variety here named may represent examples where the octopus has not turned the prey while drilling it.

Remarks: oval drill-holes have been documented in shells of oyster spat today, being the work of a predatory polycladid (turbellarian) flatworm (Woelke 1957). Little is known of this activity, but it appears that although the holes are oval, they are not bevelled, and are on a much smaller scale than those produced by octopus.

Repository: material with MGUH numbers is deposited in the Geological Museum of the University of Copenhagen, Denmark.

Palaeontological perspectives

Those groups of organisms that are of the highest ecological significance today, and yet have no fossil record, are a constant embarrassment for the palaeontologist. The presumed forests of hydroids, demosponges and sea-weeds that covered seafloors of the past remain inferred but undocumented. Yet some of these organisms may have left recognizable signs of their existence through their life activities.

Trematode flatworms (flukes) represent such a group of important yet unpreserved animals. Yet an example was recently published (Ruiz & Lindberg 1989) of recognizable trace fossils produced by trematodes in mollusc shells, and opening up a possibility of glimpsing the past history of at least some of these worms.

Considering its importance as top carnivore in recent marine communities, world wide, it is also embarrassing that the octopus is virtually unknown in the fossil record. As a "taphonomic loser", it is out of sight and therefore out of mind. Illogically, the octopus is never included in reconstructions of palaeocommunities.

The Pliocene molluscan faunas of Greece show borings identical to recent octopus drill-holes, similarly located on the shells of similar prey species. The trace fossils are not obvious; they require careful searching of shells having well-preserved surfaces. Robba & Ostinelli (1975) also described and illustrated octopus drill-holes from the Pliocene, in Italy. I am convinced that further search of earlier mollusc substrates will reveal older incidences of octopus predation. Engeser (1990) expressed similar optimism.

The borings of different species of octopods today are apparently indistinguishable. Do or did any other cephalopods have the ability to bore their prey? Were any ammonoids or belemnoids able to drill? Trace fossils may provide some answers to these questions.

Bond & Sanders (1989) found traces of injuries and damage in Mississippean ammonoids that correspond closely to those in recent nautilus shells; they reported no drill-holes although modern nautilus shells commonly bear several octopod borings. Were these workers looking for them?

Tsudy et al. (1989) suggested we look for evidence of bite traces on fossil lobster exoskeletons that would correspond to the recent predilection of nautilus for shed skins of these crustaceans. They were pessimistic, however, about distinguishing such damage from physical damage.

Neat, oval drill-holes, however, are unmistakable. I am optimistic that they will provide testimony for the earlier history of the octopus and its gastronomic preferences.

Dansk sammendrag

På grund af manglende skeletmateriale er oktopus'er ganske ukendte fossilt. Deres store rolle i recente marine samfund antyder, at de alligevel må have haft en lang geologisk historie. Flere arter oktopus borer i dag meget små huller i deres byttes skelet. Nogle af disse huller har en rhombisk eller oval form og er genkendelige som sporfossiler. De er fundet i Pliocæne skaller, og det forventes, at de vil blive fundet i ældre tertiære, og måske endda mesozoiske molluskskaller. De karakteristiske borehuller er blevet navngivet *Oichnus ovalis*.

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