Oyster shells as habitat: Encrusters and borings

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Stephen K Donovan and Werner de Gier (The Netherlands)

"*The talk* [between Nero Wolfe and Lon Cohen] *had covered the state of the Union, the state of the feminine mind, whether any cooked oyster can be fit to eat, structural linguistics, and the prices of books*" (Stout, 1975, p. 13).

Oysters have a close association with humanity, worthy of discussion as the above quotation demonstrates. They form the focus of several semi-popular books (for example, Stott, 2004; Kurlansky, 2007). The prevalence of oysters in shell middens on both sides of the Atlantic Ocean (Purdy, 1996; Milner *et al*., 2007; Hirst, 2019), and elsewhere (for example, Renfrew and Bahn, 2012, pp. 294-295), shows that they have been an important food source since prehistory. If the importance of oysters as food is today diminished in these areas, several factors must contribute, such as overfishing, pollution and reduced dependence of urban populations on fresh seafoods. This does not make an oyster any less interesting to the zoologist and palaeontologist (Yonge, 1960). Their robust valves make their preservation potential particularly high, so oyster-rich sedimentary deposits are locally common (Littlewood and Donovan, 1988; Donovan *et al*., 2014a; and Figs. 1 and 2 in this article). Even on stretches of modern coastline where oysters are rare, their valves are still tough enough to be found washed up on beaches after storms (Fig. 3). Even if bivalves that burrow into sandy substrates, such as razor shells, cockles and their kin, are numerically dominant as dead shells along many strandlines, they are nonetheless smaller, thinner-valved and commonly more delicate than the valve of an epifaunal oyster.

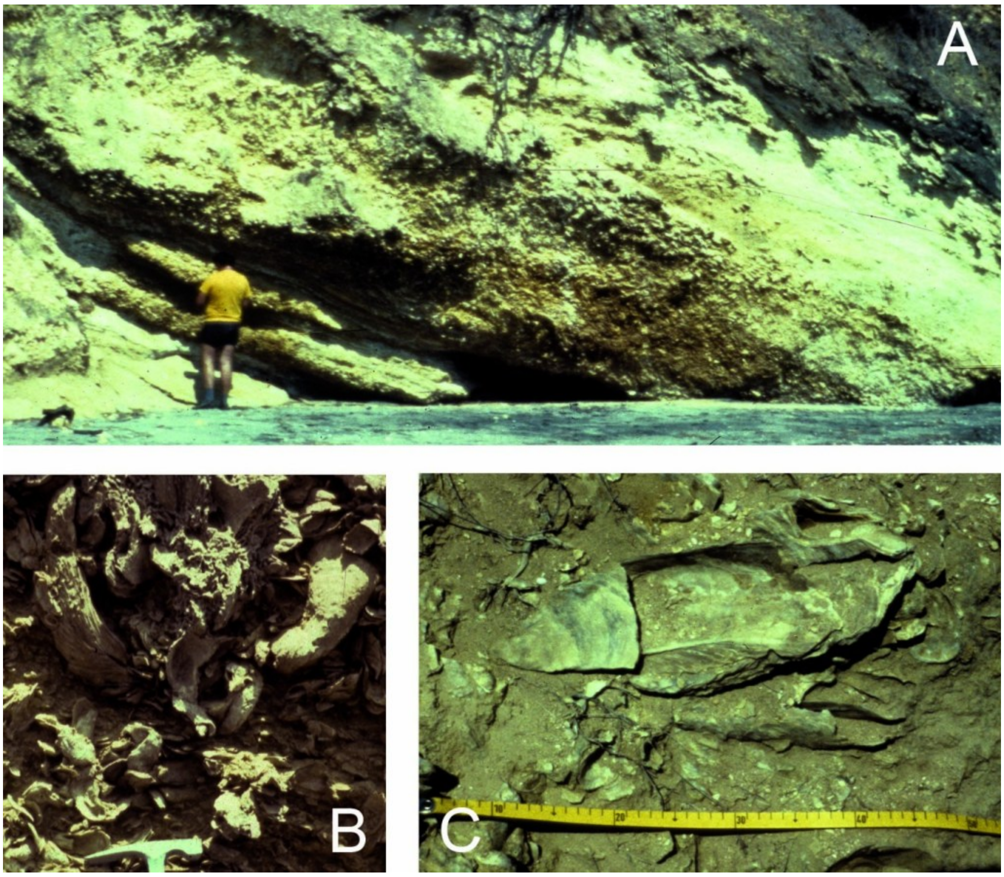

Fig. 1. Neogene oyster bed 3.3m in thickness, at Farquhar's Beach, near Round Hill, parish of Clarendon, south-central Jamaica (Littlewood and Donovan, 1988; after Donovan and Jackson, 2012, fig. 2).
(A) A younger SKD, 1987 vintage, standing in front of the oyster bed, which dips to the right. The bottom of the bed corresponds to the bottom of SKD's shorts.
(B) *Crassostrea virginica* (Gmelin) *in situ*, that is, preserved in life position. The curved adult shells are upright and encrusted by juvenile oysters. Hammer head (bottom) about 160mm long.
(C) A large, recumbent *C. virginica* that has lost most of one valve.
Scale in cm.

Because they are commonly large in size, oysters are obvious to collectors. Size matters – a large and robust valve will probably have a longer residence time on the seafloor than a small and more delicate shell. Further, oysters may be locally common in oyster banks (Fig. 1). The large valves of oysters will also present a greater surface area for invasive organisms, such as encrusters and borers. Thus, when assessing invertebrate diversity on a beach, anyone who just notes 'oyster' is likely to be missing evidence for other taxa.

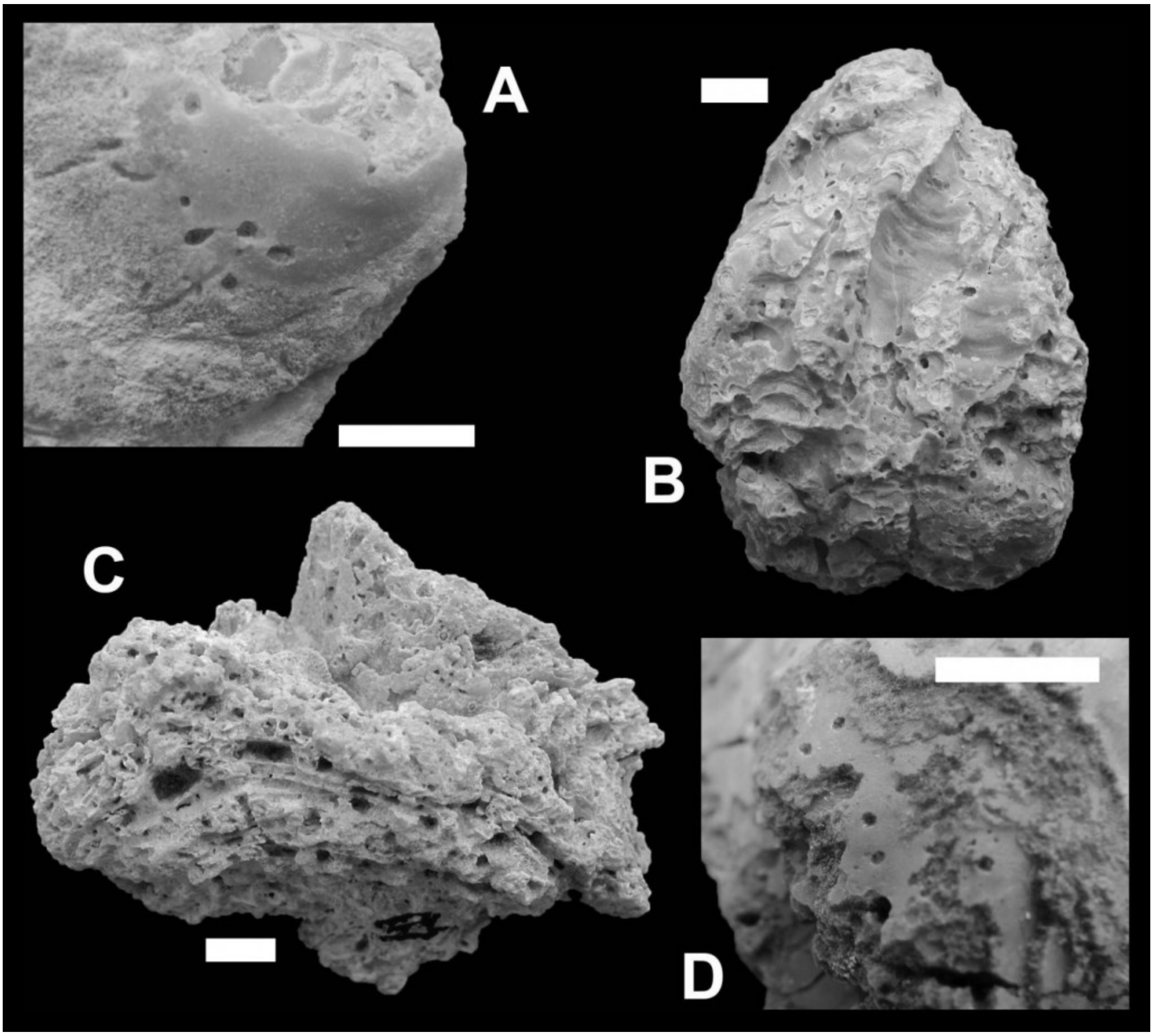

Fig. 2. Bored oyster, *Hyotissa antiguensis* (Brown) and cemented limestone, all derived from the Upper Oligocene Antigua Formation; all borings Recent (after Donovan *et al*., 2014a, fig. 6). Specimens in the collection of the Naturalis Biodiversity Center, Leiden (prefix RGM).
(A) RGM 791 217,*Rogerella*? isp. in centre, particularly the teardrop-shaped boring to the left.
(B) RGM 791 230, outer surface of valve showing bioeroded and corroded surface; bioroders*Entobia* isp. and *Gastrochaenolites* isp.
(C) RGM 791 232, three valves cemented together, all highly bioeroded by*Entobia* isp.
(D) RGM 791 231, apertures of*Entobia* isp. on external surface of shell.
Scale bars represent 10mm.

A valve washed up on a beach is likely to be the free valve. Examine your specimen. Is it fresh? The inner surface is more likely to be 'clean', suggesting only a brief, post-mortem residence on the seafloor. If there are borings or acorn barnacles (balanids) attached to the inner surface, then you know that the valve most probably had a period of residence on the seafloor for some little time after the death of the oyster.

Oysters and their disarticulated valves are used as a substrate by two functionally distinct groups of invertebrates: the borers and encrusters (cementers). We shall consider these two distinct groups separately, as an introduction to the oyster as a 'trap' for palaeoecological data. The following notes introduce several common ichnogenera and groups of invertebrates, but it is not exhaustive.

Some common borings in oyster shells

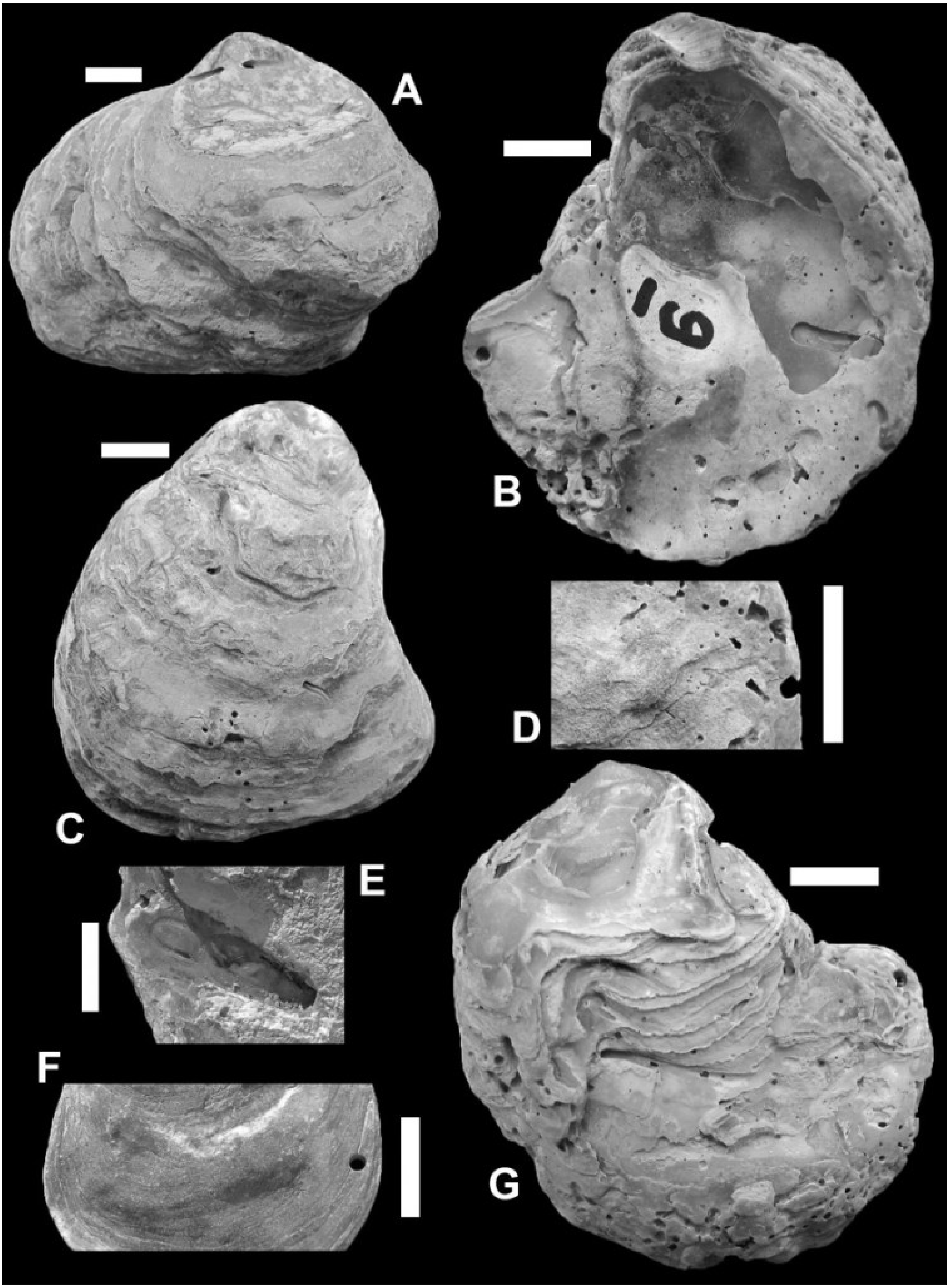

Fig. 3. Borings in the Recent oyster *Ostrea edulis* Linné, from various beaches on the Isle of Wight (after Donovan, 2014, pl. 2). All specimens in the collection of the Naturalis Biodiversity Center, Leiden, the

Netherlands (prefix RGM). All scale bars represent 10mm.
(A) RGM 791 577, external surface of valve with two borings of *Trypanites* isp. near umbo (at top).
(B, G) RGM 791 578, internal (B) and external (G) surfaces of valve with multiple borings. Identifiable borings include single, prominent *Oichnus simplex* Bromley (B, left; G, right); multiple small apertures of *Entobia* isp.; and *Caulostrepsis taeniola* Clarke (B, right of centre).
(C) RGM 791 579, external surface of valve with *Trypanites* isp. (just above centre); *Caulostrpesis taeniola* Clarke (just below centre); and apertures and/or chambers of *Entobia* isp. (in a line towards the middle of the commissure).
(D) RGM 791 580, external surface with *Entobia* isp. and *Oichnus simplex* Bromley.
(E) RGM 791 582, internal view, probable *Caulostrepsis* isp., but incompletely preserved.
(F) RGM 791 583, external surface with *Oichnus simplex* Bromley.

***Caulostrepsis* Clarke (Figs. 3B, C and E, and 6B and C):** *Caulostrepsis* is commonly produced by polychaete worms, such as the extant spionid *Polydora* spp. The boring is U-shaped, elongate and straight or sinuous, with the two parallel tubes separated by a central raised vane (obvious in Fig. 3C). The aperture of the boring has a figure-of-eight outline; the figured specimens are exposed in plan view, due to exfoliation of shell layers. It is commonly found parallel to the layered structure of the oyster valve.

Fig. 4. *Entobia cretacea* (Portlock), Natural History Museum, London, S.9015, clionoid sponge boring preserved in flint, chalk drift (= clay-with-flints?), Croydon, Surrey (after Donovan and Fearnhead, 2015, fig. 2). The thick bivalve shell, most likely an inoceramid, that was bored by the sponge has dissolved away, revealing the infilled and complex boring. Scale bar represents 10mm.

***Entobia* Bronn (Figs 2B-D, 3B-D and 4):** Commonly complicated (Fig. 4) sponge borings, with a series of globular chambers connected by canals and with external apertures, which appear as pores in shell surfaces (Figs. 2D, and 3B-D and G). Apertures are invariably multiple, either linear (Fig. 3C) or pepper pot-like in their distribution. It is commonly found parallel to the layered structure of the oyster valve.

***Gastrochaenolites* Leymerie (Figs. 2B and 5):** Club-shaped borings, commonly produced by bivalves boring into a substrate, such as a limestone or a robust shell (such as an oyster). A well-preserved *Gastrochaenolites* may preserve the valves of the borer, but beware – after the death of the boring bivalve, the hole may be invaded by other invertebrates, including nestling bivalves, but also encrusters such as bryozoans and worm tubes (Donovan, 2017a). It is commonly found perpendicular to the layered structure of the oyster valve.

Fig. 5. A modern boring moulded in latex. Club-shaped *Gastrochaenolites lapidicus* Kelly and Bromley, from the Recent of north Norfolk (modified after Donovan, in press, fig. 32.3), Naturalis Biodiversity Center, Leiden, specimen RGM 780 601. The 'cracks' show where the specimen was glued back together; this example was in a clast of chalk. Scale bar represents 10mm.

Fig. 7. A cluster of Recent oysters (background) bored by several live*Polydora* sp. annelid worms. These have produced a pattern of swirling borings, *Maeandropolydora* isp. The specimen was found during low tide at Jacobahaven – an artificial cove of the Oosterschelde marine inlet – in Zeeland, the Netherlands.

***Maeandropolydora* Voigt (Fig. 7):** Long and meandering borings produced by polychaete worms (Häntzschel, 1975, fig. 79.5). It is commonly found parallel to the layered structure of the oyster valve.

***Oichnus* Bromley (Figs 3B, D and F, and 6C-E):** Small, solitary, round holes in shells produced by a variety of organisms. Recent borings are most likely to be the spoor of predatory bivalves. *Oichnus* may be either penetrative (successful predation) or incomplete (failed predation), and commonly found perpendicular to the oyster valve.

***Rogerella* de Saint-Seine (Fig. 2A):** These are small, shallow, solitary borings made by acrothoracian barnacles. Their longitudinal section is sock-like and their aperture is teardrop-shaped (Häntzschel, 1975, figs 80.1, 80.2). It is commonly found perpendicular to the surface of the oyster valve.

Trypanites **Mägdefrau (Fig. 3A and C):** *Trypanites* are slender, cylindrical or subcylindrical, unbranched borings with a single entrance, and are commonly straight or curved. *Trypanites* ichnospecies may be perpendicular or parallel to the host shell.

Invertebrates that are common encrusters of oysters

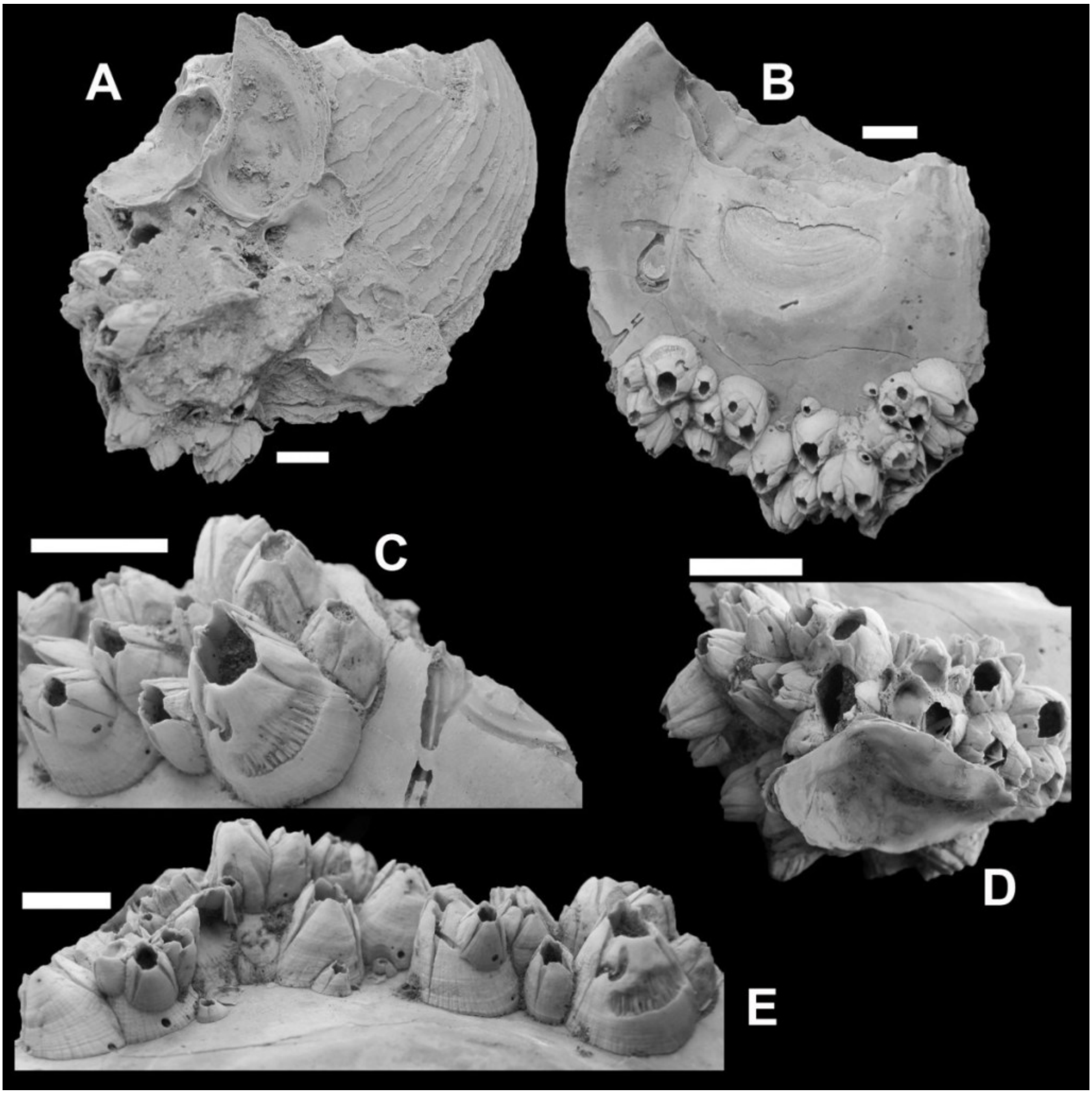

Fig. 6. Broken oyster valve, *Ostrea edulis* Linné (Naturalis Biodiversity Center, Leiden, specimen RGM 791 569), encrusted by oysters and the balanid (acorn barnacle) *Perforatus* sp. cf. *P. perforatus* (Bruguière), and bored by, possibly, muricid gastropods (after Donovan and Novak, 2015, fig. 1). Late Pliocene, south–east Spain.

(A, B) Outer (A) and inner surfaces (B) of broken valve showing encrustation by oysters and balanids externally, and balanids internally. The boring towards 10-11 o'clock from the left-hand balanids in (B) is *Caulostrepsis taeniola* Clarke.

(C) Detail of balanids and *C. taeniola* on inner surface; note small round holes, *Oichnus simplex* Bromley, near the bases of some balanids.

(D) Balanids at commissure on inner surface and encrusted, in turn, by an oyster.

(E) Balanids encrusting inner surface; note common *O. simplex* low on the shells.

Scale bars represent 10mm. Specimens not coated for photography.

Acorn barnacles (balanids) (Fig. 6): Acorn barnacles are gregarious and, if present, are commonly represented by many individuals. They are common on live oysters – next time you have them in a restaurant, examine the shell for balanids (Donovan, 2017b, fig. 1A, C). Post-mortem, the inner surface of the oyster will be available for infestation as soon as the soft tissues rot away (compare with Donovan *et al*., 2014b).

Bryozoans: The calcified colonies of encrusting bryozoans, mainly cheilostomes, are easily overlooked. They hug the surface of the shell and are most likely to be preserved in protected areas, in overhangs, depressions and between ribs on the external surface. If present with balanids, it is likely that a complex palaeoecological succession may be decipherable, with barnacles overgrowing bryozoan or bryozoan overgrowing barnacles or both.

Cementing bivalves (Figs 1B, 6A, D): The most likely cementing bivalves on any oyster shell will be a younger oyster, most likely of the same species. Oysters cement to a range of substrates, not least the shells of non-oyster bivalves (Donovan *et al*., 2020, figs 1, 3).

Tube-secreting 'worms': Calcareous worm tubes on oysters are likely to be spirorbids (more or less planar coiled) or serpulids, which are commonly larger, single or gregarious (various figures in Donovan, 2017a). They may adorn either surface of a dead oyster shell and may infest, in association with cheilostomes, large empty borings in a valve such as *Gastrochaenolites*.

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