INOCERAMID LARVAL PLANKTOTROPHY: EVIDENCE FROM THE GAULT FORMATION (MIDDLE AND BASAL UPPER ALBIAN), FOLKESTONE, KENT

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ABSTRACT. It has long been postulated that inoceramid bivalves had a long-lived planktotrophic larval stage because of their cosmopolitan distribution in the Cretaceous. This is now proven by the discovery of large larval shells preserved on inoceramid adult umbones from the Gault Formation at Folkestone. The developmental structure of these larval shells indicates that they were planktotrophic, living in the water column for in excess of 50 days. However, neither the inoceramid larval shell shape nor the hinge structure throw any new light on the taxonomic affinities of this extinct bivalve family.

INOCERAMID bivalves are very important Cretaceous biostratigraphical indices because of their cosmopolitan distribution (Dhondt 1992). It has been postulated that this distribution was due to inoceramid larvae being long-lived in the plankton (Kauffman 1975). This paper convincingly verifies these theories, for the first time, via larval shells collected during faunal analyses of the Middle and basal Upper Albian Gault Formation at Folkestone, Kent (Text-fig. 1). These specimens were found attached to squashed and fragmented inoceramid bivalve umbones, thus indicating their completion of larval ontogeny and proving their familial affinities. These adult shells were either *Birostrina concentrica* (Parkinson, 1819), *B. sulcata* (Parkinson, 1819) or *Inoceramus anglicus* Woods, 1911, the commonest inoceramids in the Gault Formation.

The Middle and basal Upper Albian section at Folkestone, Kent (Text-fig. 1) comprises 11 metres of highly bioturbated blue–grey clays. The section was stratigraphically divided using the lithological descriptions and biostratigraphical breakdown of Owen (1971, 1975), and within this framework specimens were collected throughout the sequence. A study of these larval shells gives an insight into aspects of the ecology of the Inoceramidae, but little indication as to the family's problematical taxonomic affinities.

The specimens have been deposited in The Natural History Museum, London.

BIVALVE LARVAL DEVELOPMENT

The classification and identification of the different developmental forms of bivalve larvae have been reviewed comprehensively by Jablonski and Lutz (1983). The majority of bivalve larvae develops from fertilized eggs via a trochophore stage, into either veligers or the test cell larva of the nuculoids. Trochophores are non-feeding (i.e. gaining sustenance from their egg) invertebrate larval stages with biconical outline, ciliated equatorial band and apical tuft (Waller 1981; Palmer 1989). The veliger is the feeding larval stage with a developing shell, through-gut and a velum used for locomotion (Erdmann 1935; Palmer 1989).

Bivalve larval shell development generally occurs in two stages. The first shell growth is called prodissoconch I (prod.I) (Werner 1939), and this develops as part of the metamorphosis from trochophore to veliger (Cox 1969). As soon as the veliger starts feeding, prodissoconch II (prod.II) is developed (Werner 1939). Prod.I, which is laid down by the shell gland, is generally micropunctate but lacks growth lines, whilst prod.II is secreted at the mantle edge and has well-developed

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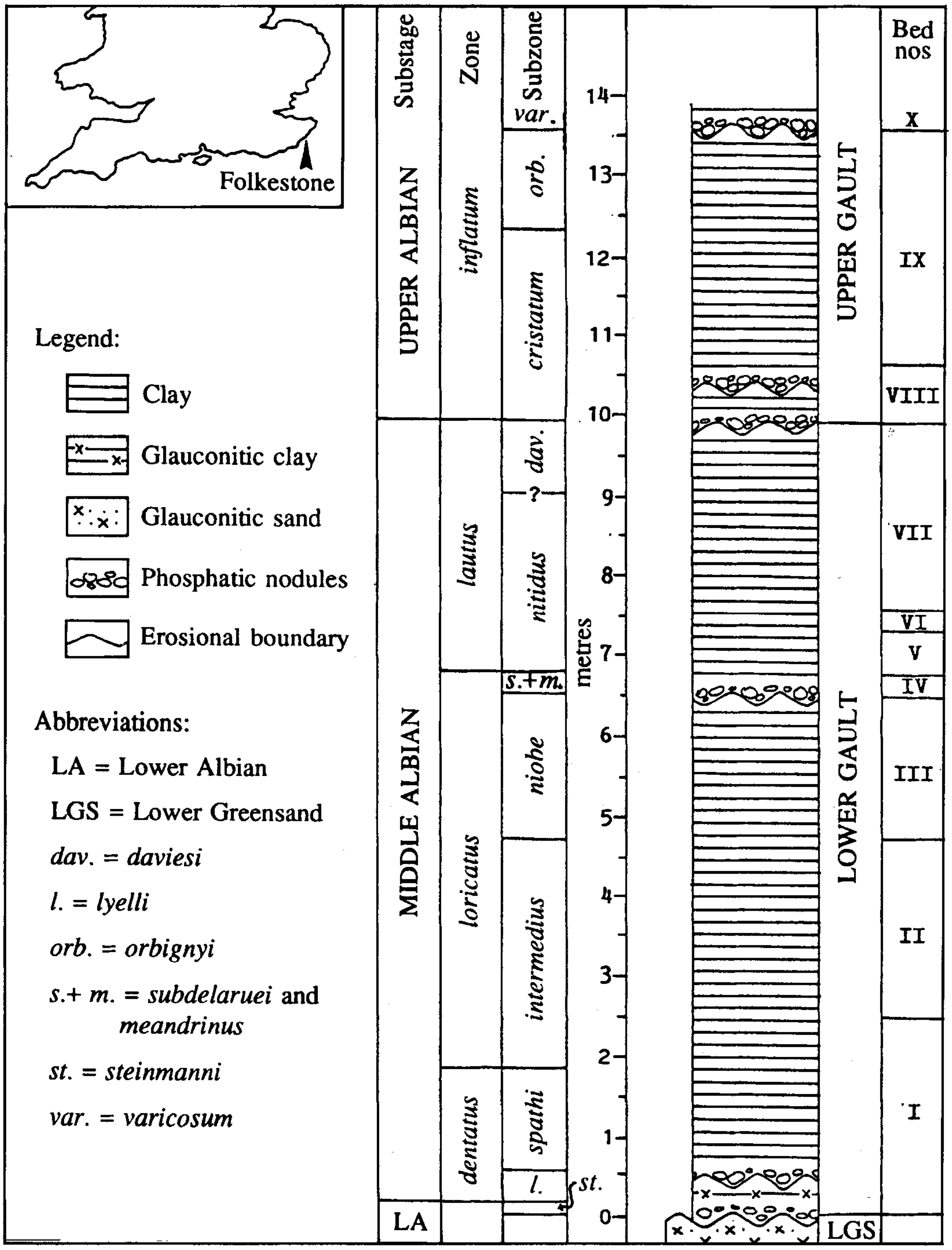


TEXT-FIG. 1. Location and stratigraphy of the Gault Formation study section at Folkestone, Kent.

growth lines (Ockelmann 1965). The larvae generally develop in the water column for a period of up to about six weeks, by which time they settle to the seafloor and begin forming the adult shell, or dissoconch (Thorson 1961).

Three main development forms have been observed in modern bivalve larvae, which are identifiable by the nature of their prod. I and prod. II; planktotrophic, lecithotrophic and direct. Planktotrophy describes larval development where the veliger feeds on plankton (Thorson 1946, 1950). In these larvae, prod. I is variably developed, whilst prod. II is well-developed (Ockelmann 1965). Lecithotrophic larval development occurs via the pelagic veliger feeding on the yolk of its egg (Thorson 1946, 1950). In most lecithotrophic larvae, prod. I is either the only larval shell or an insignificant precursor to prod. II (Ockelmann 1965). Lecithotrophic and planktotrophic larval shells can be similar in terms of prod. I and prod. II. They are differentiable, however, by the number of prod. II growth lines, due to planktotrophic forms generally spending longer within the plankton.

Direct larval development also involves complete nourishment from the egg, but the larvae have no pelagic stage, developing directly to the dissoconch stage (Ockelmann 1965). This 'direct' development involves passing through the trochophore and veliger stages within the egg, which is usually protected within a brood or encapsulated system. Direct development larval shells have a large and often inflated prod. I that may exhibit irregular folds and wrinkles. Prod. II is not dissimilar to that observed in planktotrophic forms. The direct development larval bivalve shell is easily identifiable from a planktotrophic form by its ovate shape and long straight hinge-line (Ockelmann 1965).

Jablonski and Lutz (1983) suggested that there are some difficulties in using the term 'direct development' with respect to bivalve larval shell development, as it is normally only used in other organism larval systems to refer to development without a distinct intermediate veliger stage. Some workers only use the term 'direct development' with respect to bivalve larvae when this gradual differentiation into an adult occurs (Chia 1974). 'Direct development' as commonly used when describing bivalve larval growth is really a form of lecithotrophy (Sastry 1979), but without a planktonic phase.

DESCRIPTION OF THE GAULT CLAY LARVAL INOCERAMIDAE

A total of 42 inoceramid larval shells was studied; 39 from the Middle Albian and three from the Upper Albian. The well preserved Middle Albian specimens comprise 14 right valves, 11 left valves, a pair of valves and 13 of uncertain orientation. The poorly preserved Upper Albian specimens comprise two right valves and one left valve.

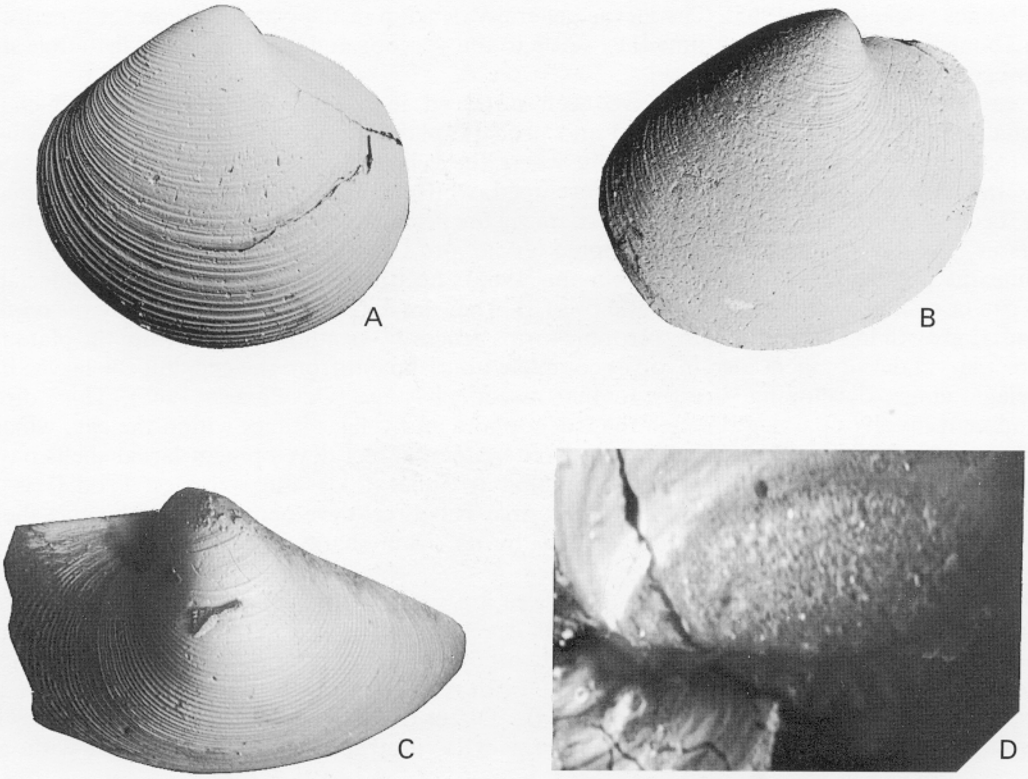
General description

The larval shells are apparently equivalve, opisthogyrous, longer than high, broader anteriorly than posteriorly, and with a prominent skewed umbo (Text-fig. 2A–C). The major part of the larval shell comprises prod. II, with prod. I being virtually imperceptible (less than 40 μm). Prod. I is micropunctate (Text-fig. 2D), and prod. II is marked by the presence of more than 50 growth lines that appear as well-defined ridges (Text-fig. 2A, C; Pl. 1).

Size and growth lines

Gault inoceramid larval size varies from the Middle to the Upper Albian. They have a mean height and length of 1·012 mm and 1·08 mm respectively in the Middle Albian; and 0·75 mm and 0·8 mm respectively in the Upper Albian. These size variations occur in larval shells that have similar numbers of growth lines, though are probably not found on the same inoceramid species. The Middle Albian specimens are either *Birostrina concentrica* or *Inoceramus anglicus* larvae, whilst the Upper Albian specimens are probably *B. sulcata*.

The 50 or so distinct growth lines on prod. II of Gault inoceramid larvae (Text-fig. 2A; Pl. 1) are not spaced uniformly across the shell. Instead, constrictions of growth can be observed with



TEXT-FIG. 2. Shape of inoceramid larval shells from Bed II of the Gault Formation, Folkestone; *intermedius* Subzone. A–B, LL41641, left valve. A, × 45; B, × 65. C, LL41639, dorsal view of the right valve, × 100. D, LL41641, prodissoconch II, × 725.

uniformly spaced growth lines packaged between. The number of growth lines sandwiched between constrictions is variable both between and within specimens. No obvious pattern can be discerned. Only the final growth increment has relatively constant numbers of well-spaced growth lines (6–9) in all specimens (Text-fig. 2A; Pl. 1).

The inoceramid larvae were therefore at least twice as big as most modern and ancient larvae, and had substantially more growth lines (LaBarbera 1974; Waller 1981; Tanabe and Zushi 1988; Palmer 1989; Malchus 1995).

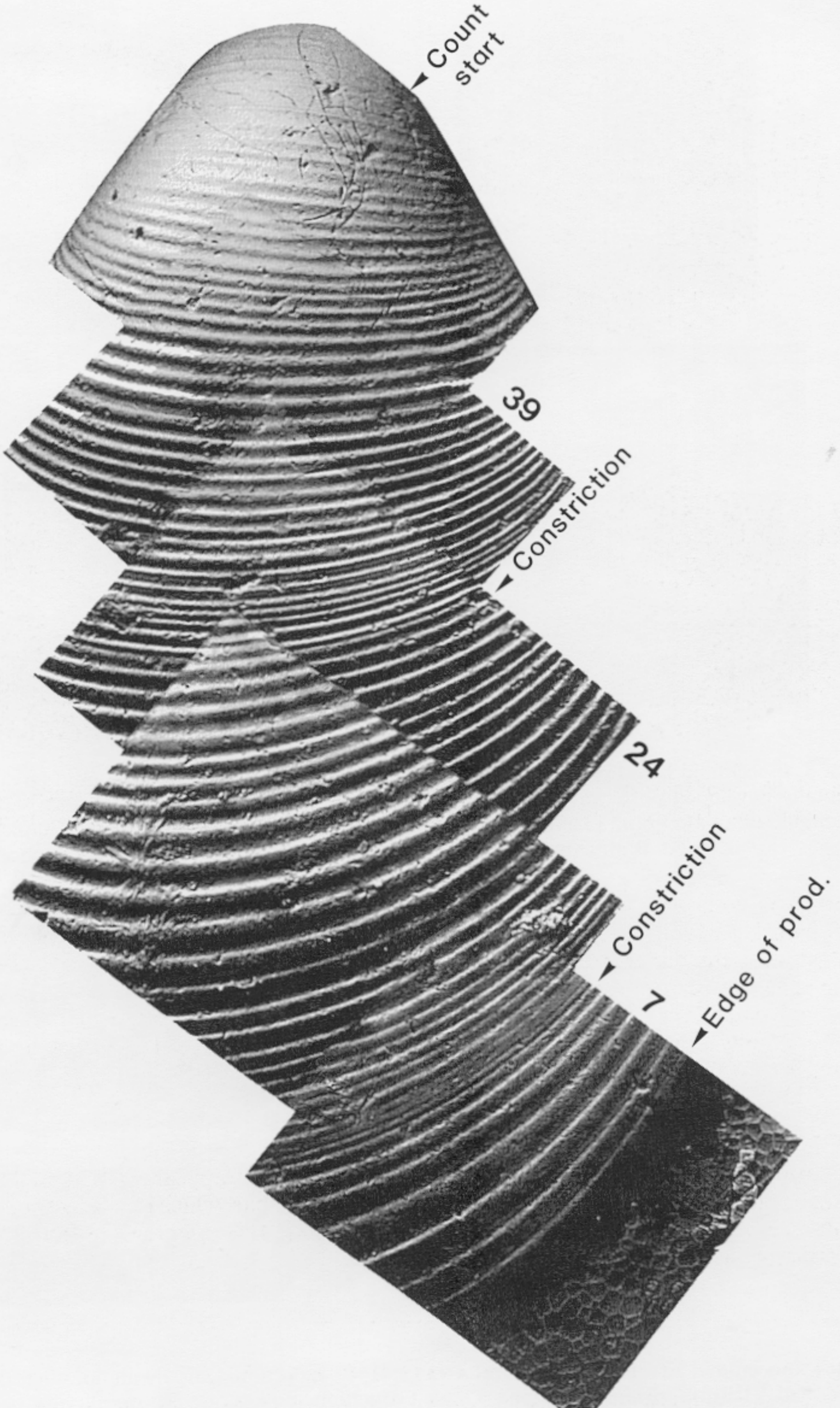
Muscle scars

In two specimens, muscle scars can be observed. Two scars appear to be attachment areas of posterior adductor muscles (Text-fig. 3A–B). A third muscle scar, which is subovate and smaller than the adductor, is situated towards the umbo (Text-fig. 3A). This is in the position postulated for a velar retractor muscle scar.

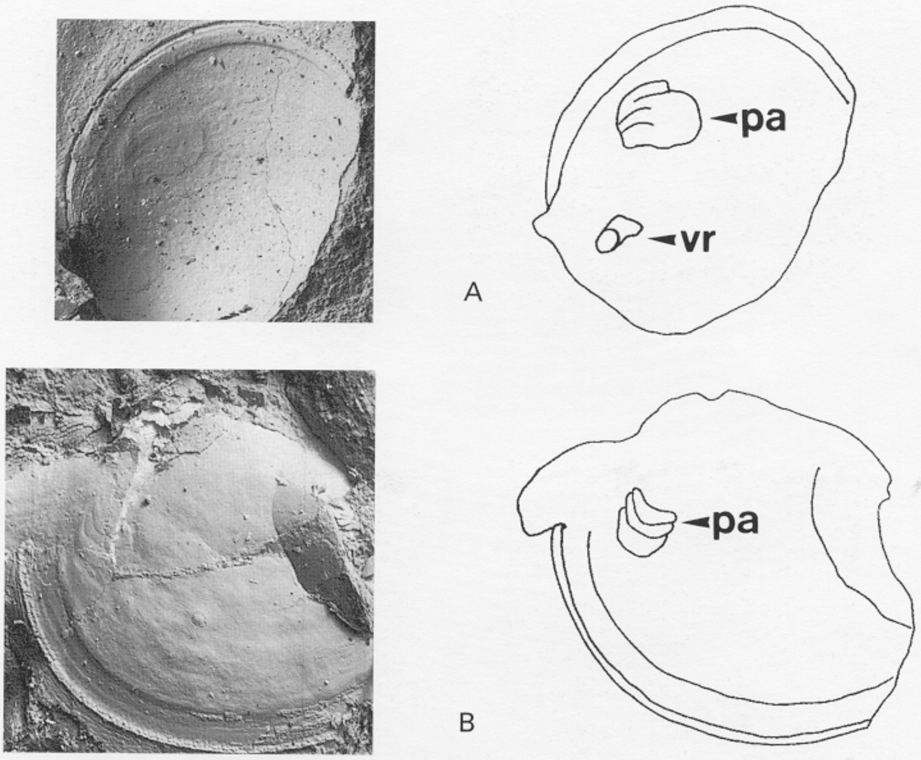
EXPLANATION OF PLATE 1

Composite of an inoceramid larval shell (LL41639) from the Gault Formation, Folkestone, showing growth line organization. Numbers indicate growth line counts between constrictions; × 27.

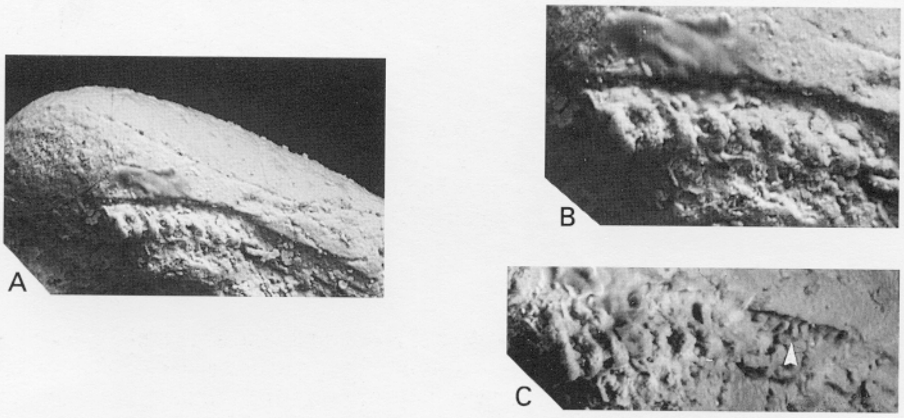
PLATE 1



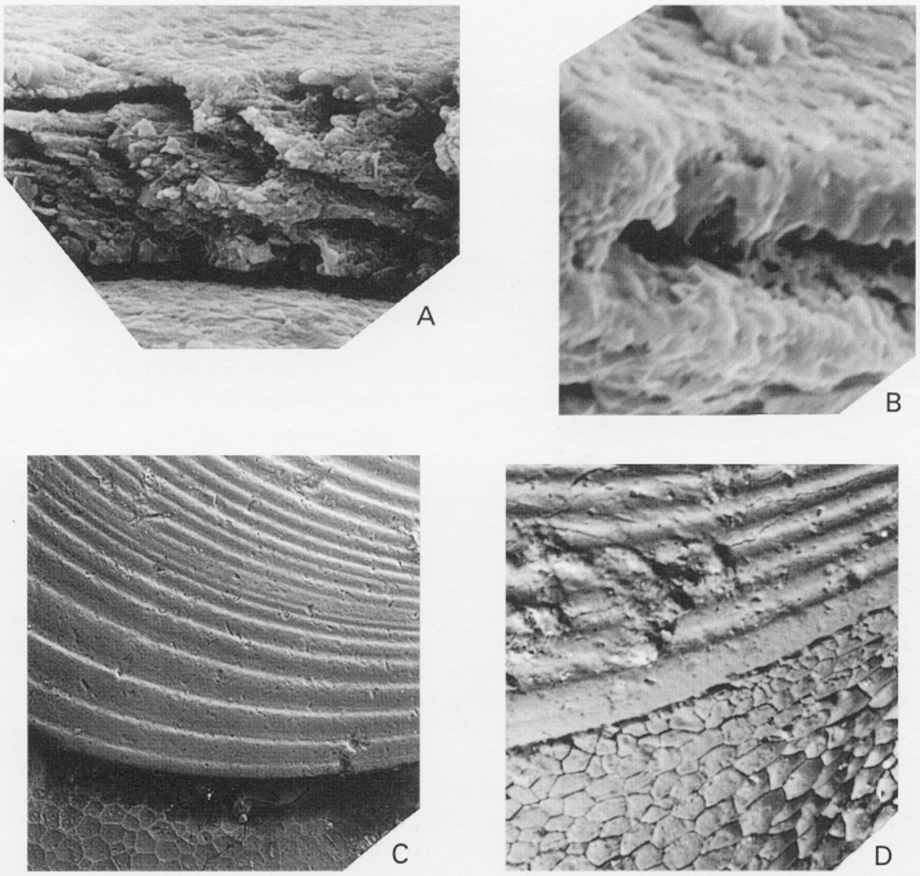
KNIGHT and MORRIS, inoceramid larval shell



TEXT-FIG. 3. Inoceramid larval musculature. A, LL41644, inner surface of an inoceramid larval shell showing incrementally developed posterior adductor (pa) and velar retractor (vr) muscle scars; × 28. B, LL41643, internal mould of an inoceramid larval shell showing incrementally developed posterior adductor (pa) muscle scar; × 50. Both from Bed V, *nitidus* Subzone, Gault Formation, Folkestone.



TEXT-FIG. 4. Inoceramid larval hinge structure. A–C, LL41640, inoceramid larval anterior hinge dentition of the left valve, Bed VIII(iii), *cristatum* Subzone, Gault Formation, Folkestone. A, overall view of the dentition, × 190. B, provincular teeth, × 350. C, denticles within the anterio-dorsal groove (marked by the arrow), × 350.



TEXT-FIG. 5. Inoceramid larval ultrastructure. A–B, LL41639. A, distally sloping inclined sheets of larval aragonite overlying nacreous dissoconch, × 4000. B, prodissoconch outer surface aragonitic prisms, × 8000. C–D, relationship between the prodissoconch and the outer prismatic calcite of the dissoconch. C, LL41639, × 225. D, LL41649, × 300. All from Bed I/II, *intermedius* Subzone; Gault Formation, Folkestone.

The posterior adductor scars appear to have formed by incremental growth. They exhibit distinct bandings parallel to their ventral margin (Text-fig. 3A–B), apparently related to constrictive growth periods. The maximum number of muscle growth bands found is three, which matches the number of different growth phases in prod. II of specimen LL41639 (Pl. 1).

Hinge definition

In our specimens, only the anterior hinge dentition is preserved, and then only in poor condition. The larval shells have numerous rectangular, 'taxodont'-like provincular teeth with rounded apices that are equal in size (Text-fig. 4A–B). They are evenly projecting and regularly arranged on a raised ridge parallel to the anterio-dorsal margin. They are separated from the dorsal margin by a narrow groove (Text-fig. 4B).

Distal to the provincular teeth and within the groove, close to the anterio-dorsal margin, there is a series of at least ten very much smaller denticles (Text-fig. 4C). The position of the ligament attachment cannot be ascertained from the specimens studied.

Larval shell ultrastructure

The ultrastructure of Gault inoceramid larval shells may be observed only in well-preserved specimens. In common with all known Recent bivalve larvae, the calcium carbonate component appears to be aragonite. It is characterized by inclined sheets that slope distally, and appears to be made up of smaller needle-like components (Text-fig. 5A–B). This is reminiscent of aragonitic crossed-lamellar ultrastructure of adult extant bivalves (Taylor *et al.* 1969; Carter 1990). The outer surface ultrastructure of the inoceramid larval shell is made up of aragonitic prisms (Text-fig. 5B). Similarly inclined and prismatic aragonitic ultrastructure is observed in prod. II of *Ostrea edulis* (Waller 1981, p. 60, fig. 147), although the inner aragonite prismatic layer of the oyster has not been found in inoceramid prod. II. The larval shell ultrastructure also appears to be highly porous, as if it was initially packed with organic material (Text-fig. 5A).

The majority of the inner surface of the inoceramid larval shell is underlain by the nacre of the dissoconch (Text-fig. 5A). The adult outer calcite prisms only occur below the periphery of prod. II (Text-fig. 5C–D). The same arrangement of prodissoconch and dissoconch is observed in the Ostreidae (Waller 1981).

DISCUSSION

Inoceramid larval palaeoecology

The Gault inoceramid larvae have features reminiscent of planktotrophic and lecithotrophic forms. The small size of prod. I (Text-fig. 2D) indicates that the original gametes were fertilized in the water (i.e. oviparous; Ockelmann 1965), and the numerous growth lines in prod. II (Text-fig. 2A; Pl. 1) indicate that they were planktotrophic. They probably spent in excess of 50 days in the plankton, given that one growth line in modern bivalve larvae is usually constructed in one day (Millar 1968). This now proven long-lived planktotrophic larval life-mode explains the cosmopolitan distribution of the Inoceramidae during the Cretaceous. In modern oceans, larvae remaining in the plankton for 50–60 days could be transported up to 150 and 500 km by a current of only 0·5 km/h (Schetema 1977). The Cretaceous marine realm included far more extensive shallow epicontinental seas than today because of the lack of polar ice caps. These were perfect areas for colonization and further distribution of the Inoceramidae.

Bivalve growth line organization, both larval and adult, has been linked to environmental (Baker 1964) and endogenous/genetic (Millar 1968) factors. The consistent number of growth lines observed on inoceramid larval specimens indicates a genetic control, whereas the random nature of the constrictions implies environmental factors. This suggests that inoceramid larval growth was mainly genetically controlled, but was sometimes modified by environmental factors (Millar 1968). The settling of the inoceramid larval shell was therefore also genetically controlled, with the final prod. II growth increment (Text-fig. 2A; Pl. 1) representing the first stage of pediveliger development (Bayne 1965). The continued larval shell growth suggests normal feeding, with the gradual starvation that is associated with pediveliger metamorphosis being recorded by non-growth.

The growth rate of bivalve larvae is affected by water temperature, with larger prodissoconchs of a given species occurring in cold water (Lutz and Jablonski 1978*b*). There is a decrease in inoceramid larval size between the Middle and basal Upper Albian, that could be attributed to increasing surface water temperature and climatic warming. However, the inoceramid larval shell size variability may be genetically controlled, as generic and specific classification of the specimens is problematical.

Inoceramid taxonomic affinities

The opisthocyrt veneriform shape of the inoceramid prodissoconch (Text-fig. 2A–B) resembles that of the Jurassic Gryphaeidae (Palmer 1989) and Recent Crassostrea (Chanley and Andrews 1971). The inoceramid larval hinge structure (Text-fig. 4A–C) resembles that of the Arcacea, Veneracea, Mactracea and Tellinacea (Rees 1950), as well as the Pinnidae (Booth 1979). However, though these morphological characters have been used previously to identify fossil bivalve larvae (Lutz and Jablonski 1978*a*), they are now recognized as being poor diagnostic characters for identification (Chanley and Andrews 1971; Lutz and Jablonski 1981). Therefore, the inoceramid larval characteristics described in this paper throw little light on the problem of the taxonomic affinities of the extinct Inoceramidae.

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