

UPPER CRETACEOUS INOCERAMIDS (BIVALVIA) FROM THE JAMES ROSS ISLAND GROUP AND THEIR STRATIGRAPHICAL SIGNIFICANCE

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ABSTRACT. The Upper Cretaceous sedimentary sequence of the James Ross Island group has traditionally been regarded as Campanian on the basis of an extensive ammonite fauna. However, inoceramid bivalves occur in the lower levels of the sequence and these suggest that the age range can be extended down to at least the Cenomanian. Members of the Upper Cenomanian *Inoceramus pictus* group are prominent in the Hidden Lake Beds and there are Turonian and Coniacian species from Cape Longing and Persson Island. The one *Inoceramus* so far collected from the Snow Hill Island Series has Turonian-Lower Senonian affinities.

Unfortunately, a detailed biostratigraphy cannot be erected yet as many of the specimens were collected loose. Senonian elements also occur in the Hidden Lake Beds and there is a strong probability that a number of specimens has been transported in glacial drift.

All the species described here either occur, or have very close relatives, in the Northern Hemisphere. This widespread distribution is taken as further evidence of the remarkable powers of dispersal of many inoceramids and underlines their considerable potential for long-distance stratigraphical correlations.

MUCH interest has been focused on the rich Mesozoic invertebrate faunas of the James Ross Island group (Fig. 1). In particular, the ammonites have been closely studied (Kilian and Reboul, 1909; Spath, 1953; Howarth, 1958, 1966) and used to place the late Mesozoic rocks of the Antarctic Peninsula within a world-wide stratigraphical context. Less well known, however, are a number of other invertebrate groups that were collected along with the ammonites but which have subsequently remained undescribed. This work describes one of these groups, the inoceramid bivalves, and shows how they can be used to extend considerably our knowledge of the Cretaceous biostratigraphy of James Ross Island. It has been argued elsewhere (e.g. Kauffman, 1968, 1970, 1975, 1977) that inoceramid bivalves have a potential equal to, and in some cases greater than, that of the ammonites for long-range stratigraphical correlation.

Present knowledge of the stratigraphy of James Ross Island is based principally on the work of Bibby (1966), who distinguished five lower stratigraphical units beneath the extensive Snow Hill Island Series* (Fig. 2; Bibby, 1966, fig. 1). The Lagrelus Point Conglomerates, and Lower and Upper Kotick Point Beds are essentially unfossiliferous, although Howarth (1966, p. 63) reported an indeterminate desmoceratid ammonite from the latter. Foraminifera were collected from within the Stoneley Point Conglomerates at Tumbledown Cliffs (Fig. 2) but, according to Macfadyen (1966), they are of little stratigraphical value. Macfadyen's (1966, p. 78) suggestion that the Foraminifera indicate a water depth of at least 300–400 m (and possibly much deeper) cannot be accepted here. The detailed lithological descriptions given by Bibby (1966) indicate that all five of the lower units were deposited in what was predominantly a near-shore facies.

Both ammonites and bivalves have been collected from the Hidden Lake Beds (Fig. 2). Five of the ammonites are identifiable and Howarth (1966, p. 63–64) has shown that one of them, *Submortonicerias chicoense* (Trask), indicates a Lower Campanian age. Whole specimens of bivalves are rare but there are a number of localities where external moulds of *Inoceramus* are common. Indeed, Bibby (1966, p. 22) claimed that a distinct *Inoceramus* bed could be traced from the northern shore of the bay north of Cape Obelisk to the Stoneley Point and Bibby Point areas (Fig. 2). A number of specimens from this bed are discussed in detail below.

The Hidden Lake Beds grade upwards into the Snow Hill Island Series, which crops out extensively on James Ross, Vega, Snow Hill and Seymour Islands (Fig. 1; Bibby, 1966, fig. 1). The rich ammonite fauna from the Snow Hill Island Series has been described by Spath (1953) and Howarth (1958, 1966), and a diverse bivalve fauna was provisionally identified by the late

* The term Snow Hill Island Series is used throughout this work in accordance with its usage by Bibby (1966). However, the term "series" as used here has no chrono-stratigraphical significance, and to conform to modern stratigraphical practice it should be re-defined as either "beds" or "formation".

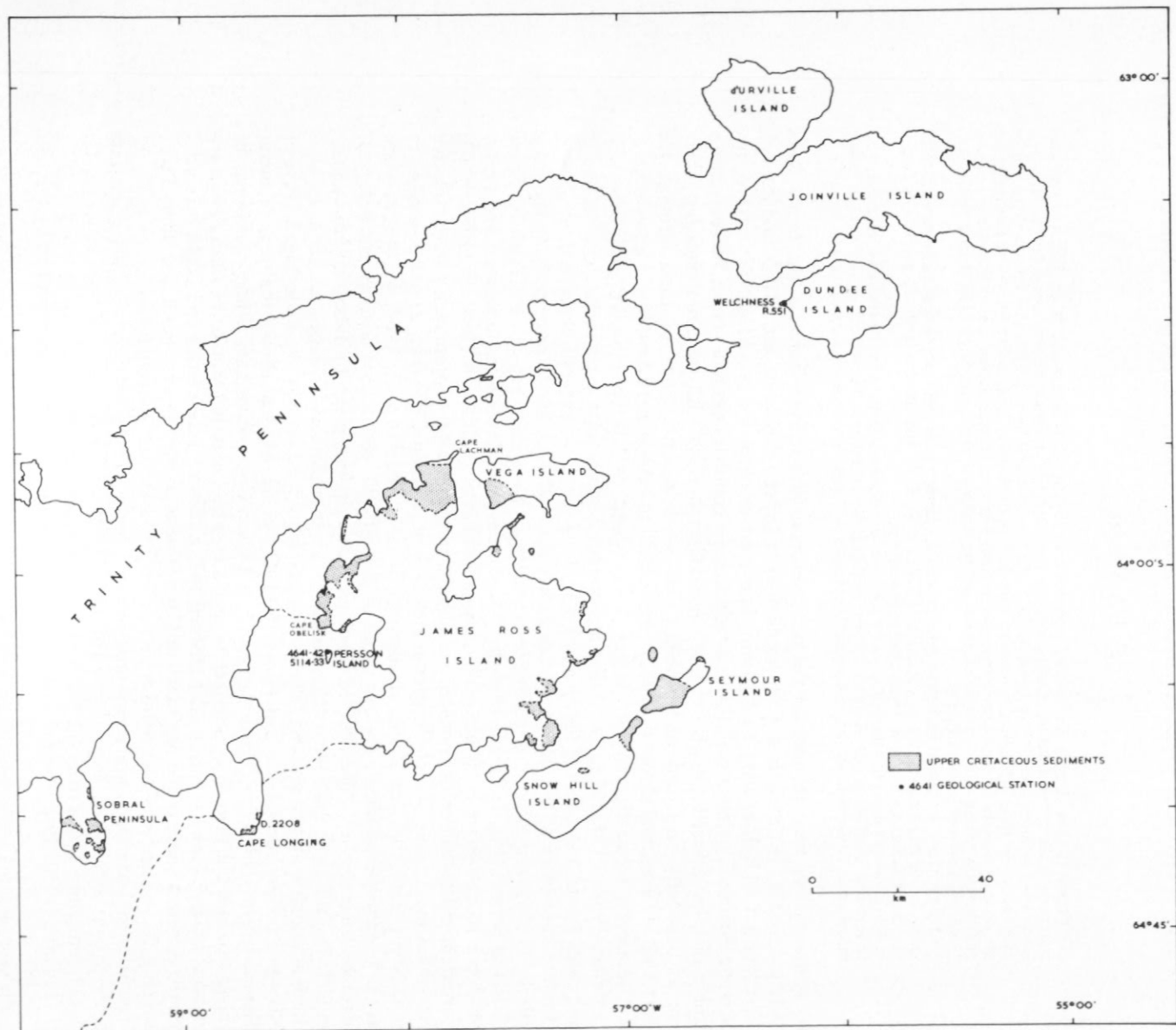


Fig. 1. Sketch map of Trinity Peninsula and the James Ross Island group showing the distribution of Upper Cretaceous sedimentary rocks and the positions of localities outside James Ross Island.

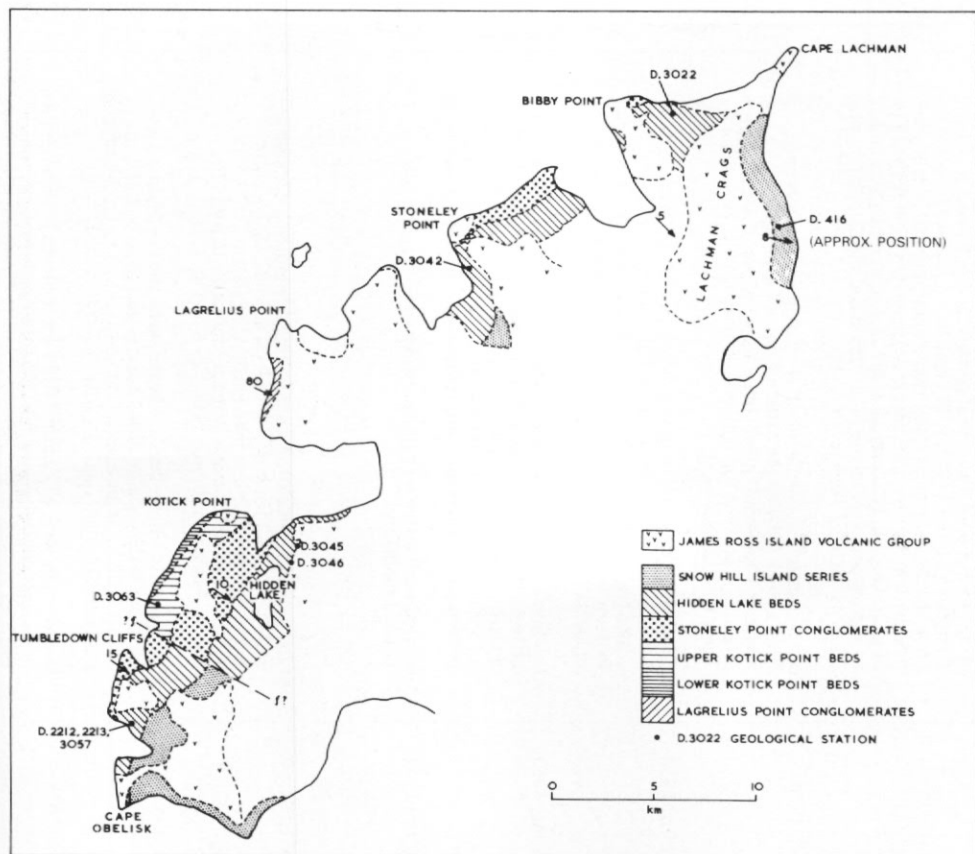


Fig. 2. Geological sketch map of north-western James Ross Island, showing the station positions (geological data after Bibby (1966, figs 1 and 6)).

Dr L. R. Cox (*in* Bibby, 1966, p. 23). In his revision of the ammonites, Howarth (1966, p. 68) concluded that the various faunas within the Snow Hill Island Series should be regarded as contemporaneous and ranging in age from upper Lower to Middle Campanian. On Seymour Island there is evidence that the sequence extends up into the Upper Campanian.

The inoceramid species described here indicate that the sedimentary sequence has a much more extensive age range than has previously been recognized. Considerable potential would seem to exist for erecting a detailed *Inoceramus* zonation and, for this reason, it is important to establish both precise localities and modes of occurrence. All the specimens were collected by geologists whose primary objectives were reconnaissance geological mapping. Unfortunately, it is certain that these workers collected both loose and *in-situ* specimens without differentiating between the two. In addition, there is virtually no information on the exact levels of occurrence of fossils within measured sections. However, such information as is available for each specimen is summarized in Table I.

All the specimens described here either belong to, or are closely related to, common Northern Hemisphere species. It should be noted that the taxonomic status of many of these species is still uncertain and during the course of this work it has become apparent that a large number of forms could be profitably re-investigated. Taxonomic studies have undoubtedly been hampered by an inconsistent species concept for inoceramids and there are cases of both "lumping" and "splitting" in the literature. It is beyond the scope of this work to attempt a thorough taxonomic

TABLE I. THE OCCURRENCE OF INOCERAMID SPECIMENS IN THE JAMES ROSS ISLAND GROUP

Specimen number	Locality	Collector and date	Notes
4641, 4642, 5114-33	Northern end of the west side of Persson Island	A. Taylor (Operation Tabarin), 1945	Collected by Taylor <i>in situ</i> from sandstone beds 350 ft and 400 ft, respectively, above sea-level (W. R. Flett, field specimen register). At the former level, they are stated to occur in distinct shell beds. Conversely, Bibby (1966, p. 8; unpublished field notes) could find no <i>in situ</i> deposits on Persson Island and suggested instead that loose sediments may have been ice transported from the vicinity of Cape Obelisk. However, it would seem that Bibby was unable to make a complete survey of the island and Flett's opinion is here taken as the more reliable
D.416.1	Southern end of Lachman Crag, James Ross Island	W. N. Croft, 1946	Croft collected this and a number of other molluscan specimens from a small gully on the eastern flank of Lachman Crag. From a sketch in Croft's field notebook, it would appear that this gully is located towards the southern end of the crags (i.e. well within the Snow Hill Island Series)
D.2208.5 and 7	Cliffs at the southern end of Cape Longing	A. J. Standring, 1953	Sedimentary rocks, very similar in lithology to those of James Ross Island, crop out at Cape Longing but it is not clear (from Standring's field notebook) whether his specimens were collected loose or <i>in situ</i> . Even if they were loose, it is likely that they are of local origin
D.2212.4A, 5 and 6, D.2213.1	Northern side of the bay north of Cape Obelisk, James Ross Island	A. J. Standring, 1953	At station D.2212 the specimens were collected from loose material on top of a "whale-backed ridge". A small glacier exists in this area (Bibby, 1966, fig. 7) and it is almost certain that this ridge is a moraine. Specimens from station D.2213 were apparently collected from small outcrops (Standring, unpublished field notes)
D.3022.1	Approximately half-way between Bibby Point and the northern end of Lachman Crag, James Ross Island	J. S. Bibby, 1958-59	Collected <i>in situ</i> from an interbedded series of fine- and coarse-grained sandstones
D.3045.2, D.3046.3 and 4	Two small gullies, 1½ miles [2.4 km] north-east of Hidden Lake, James Ross Island	J. S. Bibby, 1958-59	At the former of these two localities Bibby measured a detailed section but he did not record the level at which fossils occur. Again, it is possible that both here and at station D.3046 loose specimens were collected. Extensive moraines occur in the Hidden Lake area (Bibby, 1966, figs 6 and 7)
D.3057.4, 5, 7 and 9	Northern side of the bay to the north of Cape Obelisk, James Ross Island	J. S. Bibby, 1958-59	Although an <i>in-situ</i> sequence of shales, grits and sandstones was recorded at this locality, the exposures appear to be small and isolated (Bibby, unpublished field notes). This locality is probably equivalent to Standring's stations D.2212 and 2213
R.551.1 and 2	Approximately 100 m south of the main accommodation building, Petrel Base (Argentina), Welchness, Dundee Island	J. A. Crame, 1978	The specimens were all collected from loose blocks in the prominent north-south terminal moraine. No solid outcrops were found in this area

revision of the species identified (with the exception of *I. madagascariensis* Heinz) and, for this reason, detailed synonymy lists are not given. However, references cited in each of the descriptions contain the most complete synonymies currently available. Generic and subgeneric divisions are based on those of Cox (1969) and the sculpture terminology follows Heinz's (1928b) scheme.

SYSTEMATIC DESCRIPTIONS

FAMILY INOCERAMIDAE GIEBEL 1852

Genus *Inoceramus* J. Sowerby 1814

Subgenus *Inoceramus* (*Inoceramus*) J. Sowerby 1814

Inoceramus sp. cf. *tenuis* Mantell 1822

Fig. 3a

Material

Two internal moulds of juvenile specimens from a locality near Hidden Lake (D.3045.2). The specimens are preserved in a pale grey fissile sandstone; both have been slightly crushed and distorted.

Description

Both specimens are obliquely rounded, strongly inequivalve and inequilateral. They have approximate lengths of 23 and 18 mm, respectively, but are incomplete. Although the umbonal regions of the right valves are moderately inflated, the margins are comparatively flat. On the larger of the two specimens, a shallow groove runs from the umbonal region to the postero-dorsal margin, delimiting a narrow wing (Fig. 3a). The anterior margin of the right valves appears to be straight, whereas the posterior and ventral margins are well rounded. The narrow pointed umbo of the larger specimen curves forward and slightly inwards. The left valves of both specimens are obliquely elongated and more evenly inflated than the right valves. Both have prominent, strongly projecting umbones (Fig. 3a). A long straight hinge line on the larger specimen forms an obtuse angle with the posterior margin.

Ornament on both right and left valves consists of a combination of two distinct elements. The first of these is a series of low concentric undulations that are closely spaced and regular in the umbonal region but more widely separated and irregular towards the ventral margin. Close to the latter they are between 1.0 and 1.5 mm in width. Superimposed on this primary ornament is a series of very fine secondary concentric ribs (Fig. 3a). Over the umbonal region these ribs occur regularly on the summits of the primary undulations but towards the ventral margin they become more irregularly spaced and occupy primary rib flanks as well as summits (Fig. 3a). Collectively, these ribs have the appearance of fine sharp *Anwachsrinnen*; they are generally symmetrical about the growth axis but on the larger of the right valves their course is somewhat irregular in the postero-dorsal region. On the small wing, the ribs become very fine and are swept forward towards the umbo.

Remarks

Apart from the obvious difference in size, these two specimens compare very closely with the type of *I. tenuis* Mantell (Woods, 1911, p. 271, figs 31 and 32, pl. 48, fig. 1a and b; Kauffman, 1972, pl. 81, fig. 1a and b). There are strong similarities too with the specimens of *I. tenuis* from Germany illustrated by Dietze (1959, pl. 1, figs 3 and 4) and from Russia illustrated by Dobrov and Pavlova (1959, pl. 1, fig. 2) and Pergament (1966, pl. 23, figs 3 and 4, pl. 24, figs 1-4). *Inoceramus tenuis* Mantell can be distinguished from *I. concentricus* Parkinson, another small, strongly inequivalve form, by the less prominent umbo on the left valve, comparatively longer hinge line and weaker concentric ornament. Superficially, *I. scalprum* Böhm appears to be a very similar to *I. tenuis* (e.g. cf. Woods' (1911) pl. 49, figs 2-4 of *I. etheridgei* n. sp., = *I. scalprum*

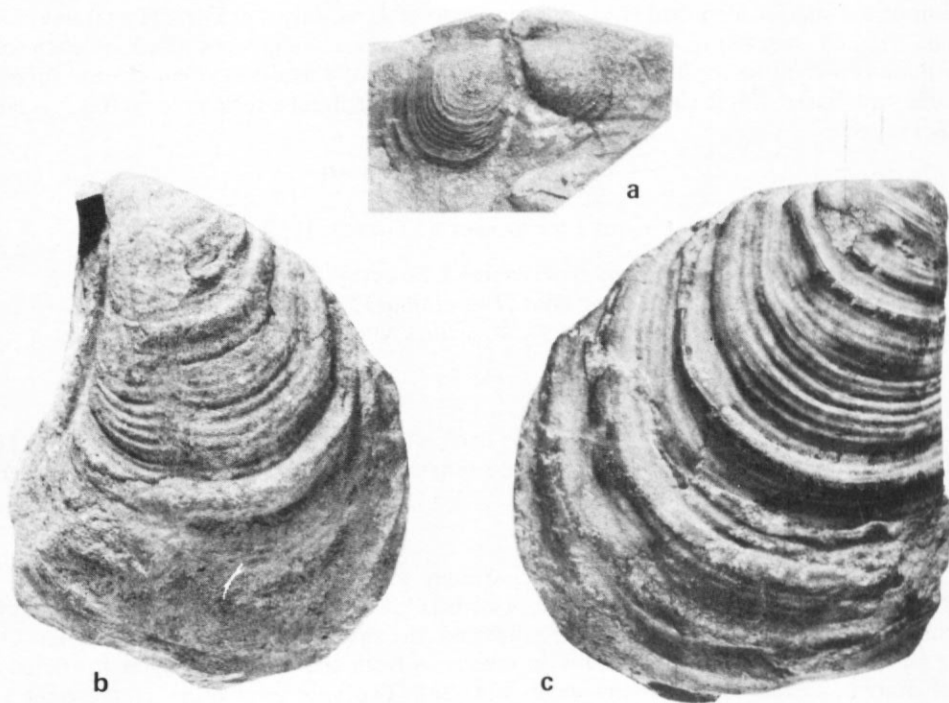


Fig. 3. a. *Inoceramus (Inoceramus)* sp. cf. *tenuis* Mantell; two internal moulds of juvenile specimens showing the right valves and strongly projecting umbones of the left valves; $\times 1$ (D.3045.2).
 b. *Inoceramus (Inoceramus) pictus pictus* Sowerby; internal mould of the left valve of an articulated specimen; $\times 1$ (D.2212.5).
 c. *Inoceramus (Inoceramus) pictus pictus* Sowerby; the same specimen, showing the right valve; $\times 1$ (D.2212.5).

Böhm 1915). It can be distinguished, however, by the less prominent umbo and less impressed postero-dorsal region of the left valve, and by the fact that it is more nearly equivalve. The Japanese species, *I. tenuistriatus* Nagao and Matsumoto (1939, pl. 24, fig. 8, pl. 26, figs 1–4) can be distinguished by virtually the same criteria. Heinz's (1928b, p. 61) suggestion that *I. pictus* Sowerby may be no more than a variety of *I. tenuis* Mantell cannot now be accepted (Dietze 1959, p. 860).

According to Woods (1912a, b), *I. tenuis* ranges from uppermost Albian to Middle Cenomanian. Heinz (1928c) regarded it as an Upper Cenomanian species in both northern Germany and South America, whereas Dietze (1959) established an European range of Lower to Upper Cenomanian.

Inoceramus pictus Sowerby 1829

Inoceramus pictus Sowerby is a widespread and highly variable species which has already been the subject of several detailed studies (e.g. Heinz, 1928d, e; Dietze, 1959; Pergament, 1966; Tröger, 1967). The range of variation about the type is in fact such as to permit the establishment of a series of subspecies. These are based primarily on differences in umbonal development, outline, degree of convexity and sculpture. *Inoceramus pictus pictus* Sowerby is characterized by its comparatively broad outline, moderate convexity and combination of regular *Anwachsringsen*

with irregular *Anwachsrünzeln* (Heinz, 1933, p. 245; Dietze, 1959, p. 861; Tröger, 1967, p. 36). *Inoceramus pictus bohemicus* Leonhard, a close relative, is less asymmetrical, feebly convex and possesses only *Anwachsringen* (cf. Leonhard, 1897, p. 26, pl. 5, fig. 1 a-c; Scupin, 1912-13, figs 31-33; Dietze, 1959, pl. 2, fig. 5; Tröger, 1967, pl. 3, figs 9-11). *Inoceramus pictus neocaledonicus* Jeannel is distinguished by the development of regular *Anwachsringen*, which merge ventrally into *Anwachstreifen*, and *I. pictus concentricoundulatus* Tröger has a conspicuous spatula-form outline. Both the latter species will be discussed in more detail below.

In Europe, the group of *I. pictus* occurs wholly within the Upper Cenomanian (Woods, 1911; Dietze, 1959; Tröger, 1967).

Inoceramus pictus pictus Sowerby 1829

Fig. 3b and c

Material

One complete internal mould (with traces of shell material) (D.2212.5) from station D.2212.

Description

Although both valves are well preserved, the left valve has been slightly crushed and parts of the postero-dorsal and ventral margins are missing. The specimen is slightly inequivalve and both valves are strongly inequilateral.

The obliquely elongated right valve (Fig. 3c) is longer than high, has a gently concave anterior margin (equal in length to just over half the total length of the valve) and convex ventral and posterior margins. The anterior edge drops steeply to the plane of commissure. There is a moderate degree of inflation but towards the postero-dorsal margin the valve flattens out slightly to form an indistinct wing. The prominent terminal umbo is curved forwards and inwards. Ornament consists of two strongly developed elements: narrow concentric ribs (or *Anwachsringen*) and larger irregular wrinkles (*Anwachsrünzeln*). Both the ribs and the interspaces between them are of the order of 1 mm in width. They are sub-symmetrical about the growth axis but become noticeably straighter on the postero-dorsal area. The strongly projecting wrinkles are sub-parallel to the concentric ribs but are irregularly spaced over the surface of the valve. They vary in width from 1 mm in the umbonal region to 5 mm towards the ventral margin.

The left valve is similar in most respects to the right valve but it is narrower, especially in the umbonal region (Fig. 3b) (cf. Dietze, 1959, p. 861). However, the umbo does not project above that of the right valve (Fig. 3b). Antero-ventrally, the left valve is slightly extended and the growth axis shows a more pronounced curve forwards in its latest stages.

Remarks

Specimen D.2212.5 compares well in general form and style of ornament with specimens of *I. pictus* from both Madagascar (Heinz, 1933, pl. 16, fig. 4; Sornay, 1965, pl. 13, figs 2, 3 and 5) and Europe (e.g. Dietze, 1959, pl. 2, figs 1 and 2; Tröger, 1967, pl. 3, fig. 1). The *Anwachsrünzeln* are more prominent than in any of the aforementioned specimens (Fig. 3b and c) but in this respect it is similar to a number of European Lower Chalk forms, including the holotype (Woods, 1911, fig. 36).

The specimen is inequivalve but not to the extent that previous authors have suggested for the *I. pictus* group (e.g. Dietze, 1959; Tröger, 1967). The left valve is slightly narrower (Fig. 3b and c) and in its antero-ventral extension shows some resemblance to *I. pictus bannewitzensis* Tröger (1967, p. 41, pl. 4, figs 1-3). The latter, however, generally has more striking "axe-form" valves and a growth axis that has a very pronounced bend towards the anterior margin in its later stages. It may well be that, as with *I. pictus neocaledonicus* (see below), a series of gradational forms links the type with this subspecies.

Inoceramus pictus pictus is restricted to the Upper Cenomanian (Dietze, 1959). In Europe it apparently occurs no higher than the *plenus* zone (= *gracile* zone of Rawson and others (1978)) (Tröger, 1967).

Inoceramus pictus neocaledonicus Jeannet 1922

Fig. 4a and b

Material

One internal mould from a locality on the northern shore of the bay to the north of Cape Obelisk (D.2212.4A); one more or less complete internal mould plus a number of fragments from the same general area (D.3057.4, 5, 7 and 9). Two internal moulds of single valves (R.551.1 and 2) from Dundee Island.

Description

The simple, regular rib patterns and distinctive outlines of this group of specimens link them unmistakably with the *I. pictus* Sowerby group. However, they belong to a distinct subspecies. The best-preserved specimen, D.2212.4A (Fig. 4a), is an elongated, rounded-rectangular left valve which is 1.3 times as long as high. Although clearly asymmetrical in the antero-dorsal region, the valve becomes more symmetrical ventrally. It is moderately convex, with the maximum degree of convexity being developed antero-dorsally. The concave anterior margin is equal in length to half the height of the valve and drops vertically to the plane of commissure. The postero-dorsal region is extended to form a low flat wing and the ventral margin is well rounded. The umbo is strongly coiled inwards and forwards, and projects above a straight hinge line which is about 30 mm in length. Simple, rounded concentric ribs are well developed in the juvenile stages. Up to a distance of approximately 25 mm along the growth axis they are of the order of 0.5–1.0 mm in width and are separated by narrow concave interspaces. Towards the ventral margin, however, the ribs become slightly broader, show a tendency towards the development of acute summits and are separated by interspaces up to 2 mm in width. In the ventral half of the valve the ribs are almost symmetrical about the growth axis.

The largest valve on specimen D.3057.7 (Fig. 4b) is approximately 1.4 times as long as high and, as far as can be judged, has a comparatively slender rounded-rectangular outline. The valve is moderately convex in the anterior and antero-dorsal regions but flattens out postero-dorsally and ventrally. The tip of the umbo is missing but, from the course of the ribs, it can be judged to have projected forwards. The anterior margin is straight to slightly concave and again drops

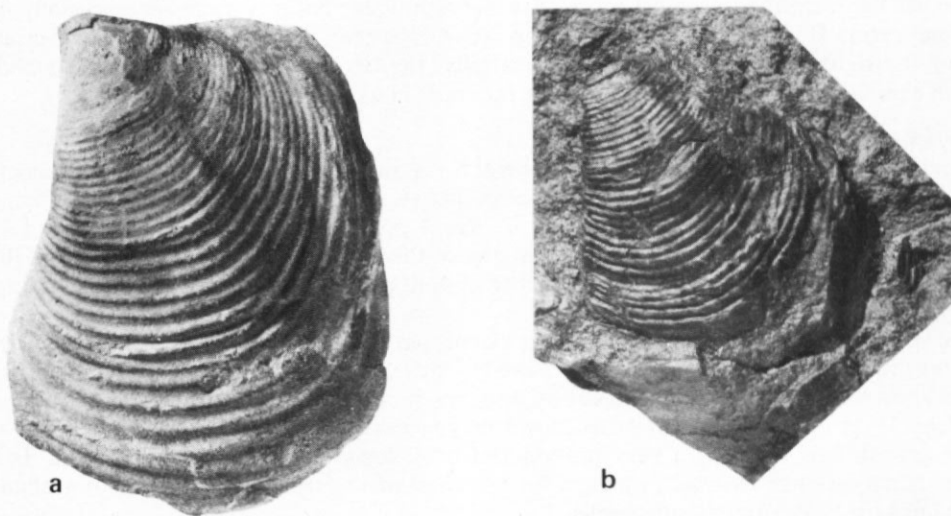


Fig. 4. a. *Inoceramus (Inoceramus) pictus neocaledonicus* Jeannet; incomplete internal mould of a left valve; $\times 1$ (D.2212.4A).
b. *Inoceramus (Inoceramus) pictus neocaledonicus* Jeannet; incomplete internal mould of a left valve; $\times 1$ (D.3057.7).

vertically to the plane of commissure. Fine concentric ribs, of the order of 1 mm in width and separated by narrow concave interspaces, cover the valve. Closely spaced initially, these ribs subsequently become elevated, in clusters of four or five, on the summits of low concentric undulations (Fig. 4b). Heinz (1928b) termed this style of ornament *Anwachsringreifen*. There is some indication that the *Anwachsringreifen* increase in size towards the ventral margin where there are also traces of irregular wrinkles (*Anwachsrünzeln*) (Fig. 4b).

Two species from Dundee Island (R.551.1 and 2) are here referred to *I. pictus neocaledonicus*. The larger of the two, specimen R.551.1, is similar in outline and general form to specimen D.2212.4A but it differs slightly in style of ornament. *Anwachsringen* are present but over the central and ventral areas of the valve they are separated by shallow concave interspaces up to 2.5 mm in width. However, this rather sparser pattern of ribbing is by no means atypical of members of the *I. pictus* group. Indeed, a specimen of *I. pictus* Sowerby (? = *I. pictus neocaledonicus*) illustrated by Dobrov and Pavlova (1959, pl. 1, fig. 5) shows a style of ornament similar to that of specimen R.551.1.

Remarks

The re-interpretation of *I. neocaledonicus* Jeannet as a subspecies of *I. pictus* Sowerby by Dietze (1959, p. 863) has subsequently been accepted by the majority of authors. Dietze based his comparison on the similarity in style of ornament (particularly the development of symmetrical *Anwachsringreifen*) between Jeannet's (1922, fig. 5) specimen and many European specimens of *I. pictus* Sowerby. This resemblance cannot be disputed but it remains to be proved that the two are similar in valve form and outline. Jeannet's (1922, fig. 5) specimen is incomplete and it has not been shown that it has either the sharply demarcated anterior margin or the broad, low postero-dorsal wing that are so characteristic of the *I. pictus* group. It may even be that the specimen is incorrectly orientated and that the valve illustrated by Jeannet is a right one rather than a left one. Seitz (1965, p. 90) cast doubt on the association of *I. neocaledonicus* with *I. pictus* and suggested, alternatively, a link with *Sphenoceramus lingua* (Goldfuss). At present, the balance of evidence favours Dietze's opinion to that of Seitz but the problem will only be fully resolved when either the type of *I. neocaledonicus* Jeannet is re-located or a replacement is designated. In the present work the position has been adopted, albeit rather tentatively, that *I. neocaledonicus* Jeannet is a valid subspecies of *I. pictus* Sowerby.

Specimen D.2212.4A compares closely in form and outline with Woods' (1911, pl. 49, figs 5 and 6) illustrations of *I. pictus* Sowerby (= *I. pictus neocaledonicus* in Dietze (1959, p. 863) and Tröger (1967, p. 50)). However, it differs somewhat in style of ornament in that it shows no tendency to develop either *Anwachsrünzeln* or *Anwachsringreifen*. In addition, there is a progressive increase in interspace width towards the ventral margin (Fig. 4a). Nevertheless, Woods' (1911, pl. 49, fig. 5) right valve has a postero-dorsal region very similar to that of specimen D.2212.4A and on both specimens the ribs become crowded and less distinct towards the wing margins. A third specimen, from Madagascar (Heinz, 1933, pl. 16, fig. 3), can be grouped with the previous two. It has the same rounded-rectangular outline and low postero-dorsal wing, and shows a regular development of fine concentric ornament (*Anwachsringen*). Neither *Anwachsrünzeln* nor *Anwachsringreifen* are present. Finally, the two specimens from Dundee Island and probably one from Russia (Dobrov and Pavlova, 1959, pl. 1, fig. 5) should also be included in this rather distinctive sub-group.

The ribbing style of specimen D.3057.7 is similar to that of *I. neocaledonicus* Jeannet (1922, fig. 5) but the specimen is altogether more convex and has a sharply demarcated anterior margin. It bears close similarities to a specimen of *I. pictus* from Madagascar (Heinz, 1933, pl. 16, fig. 4) (= *I. pictus neocaledonicus* in Dietze (1959, p. 863)). The latter specimen has clearly discernible *Anwachsringreifen* and *Anwachsrünzeln*. There is a general similarity too, between specimen D.3057.7 and Dietze's specimens F17 and F3 (Dietze, 1959, pl. 3, figs 1 and 2) from Germany. Specimens of *I. pictus neocaledonicus* from Russia (Pergament, 1966, pl. 27, figs 3 and 4, pl. 30,

figs 2–4) also clearly show the characteristic combination of *Anwachsringreifen* and *Anwachsrünzeln*.

Two sub-groups of *I. pictus neocaledonicus* may therefore be tentatively distinguished on the basis of rib pattern. The first of these is characterized by having only regular *Anwachsringen*, whilst the second has in addition either *Anwachsringreifen* or *Anwachsrünzeln* (or both) developed towards the ventral margin. The ornament style of the subspecies must thus be regarded as variable and certain forms (e.g. Heinz, 1933, pl. 16, fig. 3; Dietze, 1959, pl. 3, fig. 1; Pergament, 1966, pl. 25, figs 2 and 3) may well represent transitions to *I. pictus pictus* Sowerby. Generally speaking, however, the distinctive rounded-rectangular outline, lesser degree of asymmetry and characteristic combination of sculpture elements readily serve to distinguish *I. pictus neocaledonicus* from *I. pictus pictus*.

The numerous fragments of *Inoceramus* on specimens D.3057.5, 7 and 9 most likely belong to *I. pictus neocaledonicus*.

In Europe and on the Pacific coast of the USSR, *I. pictus neocaledonicus* is consistently restricted to the Upper Cenomanian (Dietze, 1959; Pergament, 1966; Tröger, 1967).

Inoceramus sp. aff. *pictus neocaledonicus* Jeannet 1922

Fig. 5

Material

Two incomplete external moulds of single valves preserved in a fissile siltstone from Bibby Point (D.3022.1).

Description

The two valves have slender elongated outlines; pointed anteriorly, they appear to have well-rounded ventral margins. Their lengths are at least 60 and 38 mm, respectively. As the margins of the larger specimen are incompletely preserved, it is uncertain whether the small wing close to the umbo (Fig. 5) is anterior or posterior in position. If, as seems most likely, it is the remnant of a postero-dorsal wing, then the umbo would appear to be slightly curved in a posterior direction. Although the specimen has probably been crushed, the junction between the main body of the valve and the small wing remains clearly defined (Fig. 5). Such a distinct recession of the wing is rather unusual in specimens of the *I. pictus* group (see, however, Tröger, 1967, pl. 3 and 4). It would appear from the larger specimen that the hinge line was straight and that the umbo projected above it. In the smaller specimen there is no trace of a wing but the acute umbonal region and the ventral margin are well preserved (Fig. 5).



Fig. 5. *Inoceramus* (*Inoceramus*) sp. aff. *pictus neocaledonicus* Jeannet; latex cast from two external moulds of (?) left valves; $\times 1$, coated (D.3022.1).

Both valves are ornamented with fine, regular concentric ribs (*Anwachsringen*), which are symmetrical about the growth axis except in the umbonal region (Fig. 5). Initially, the ribs are less than 1 mm in width but they increase ventrally to just over 1 mm. They are well rounded in cross-section and are separated by deep narrow interspaces. On both specimens the narrow ribs are clearly raised up on broad concentric undulations to form *Anwachsringreifen* (Fig. 5). Between four and five ribs are grouped on each undulation and, as the ribs and the interspaces become broader towards the ventral margin, so do the *Anwachsringreifen*. The ribs are finer and grouped into bunches on both the anterior and posterior margins. On the small wing of the larger specimen the ribs are very fine, crowded and straight.

Remarks

Both valves are similar in appearance to the narrower forms of *I. pictus* from Madagascar (Sornay, 1965, pl. B, figs 3 and 5a). They also bear a striking resemblance to Jeannet's (1922, fig. 5) *I. neocaledonicus*. The correspondence in outline, degree of convexity and ornament is extremely close but it must be borne in mind that both Jeannet's specimen and the two described here are incomplete. In particular, the hinge lines and anterior and posterior margins of all three are imperfectly known. For the time being, it would seem best only tentatively to assign these two specimens to *I. pictus neocaledonicus*.

Inoceramus pictus aff. *concentricoundulatus* Tröger 1967

Fig. 6a

Material

One broken internal mould of a right valve from near Hidden Lake (D.3046.4). The specimen is preserved in a fine, grey sandstone matrix.

Description

Even though much of the ventral region is missing (Fig. 6a), it is readily apparent that this is a broad spatula-form valve. When complete, it must have had a length of at least 75 mm and a breadth of about 60 mm. It is gently convex with the maximum degree of convexity occurring in the antero-dorsal region. Towards the postero-dorsal and ventral margins the valve flattens out considerably. A straight postero-dorsal margin slopes downwards from the umbonal region to meet the ventral margin at an angle of 120° (Fig. 6a). All the indications are that the ventral margin was well rounded. The anterior margin is straight and drops vertically to the plane of commissure. The low indistinct umbo is twisted anteriorly. It overhangs the steep anterior margin but does not appear to have projected above the hinge line. Fine concentric ribs, generally just under 1 mm in width and rounded in cross-section, cover the valve. Both the ribs and the interspaces between them increase slightly in width towards the ventral margin. On the flattened postero-ventral margin the ribs become indistinct. There is some indication, especially in the region of the postero-dorsal margin, of grouping of the ribs into low *Anwachsringreifen* (Fig. 6a).

Remarks

The general form and ornament style link this specimen with the *I. pictus* Sowerby group. The rib pattern is similar to that of *I. pictus neocaledonicus* but in form and outline it is much closer to *I. pictus concentricoundulatus* Tröger (1967, p. 46, pl. 2, figs 1 and 2, pl. 3, figs 7 and 8) (see also Geinitz, 1872-75, pl. 46, fig. 10 = *I. pictus concentricoundulatus* in Tröger, 1967, p. 46). There is a particularly striking resemblance between specimen D.3046.4 and Tröger's (1967) pl. 2, fig. 1. The latter specimen has a broad, well-rounded ventral region and shows a very regular development of fine concentric ribs. Lack of a complete specimen, however, precludes positive identification with *I. pictus concentricoundulatus*.

Inoceramus pictus concentricoundulatus is an Upper Cenomanian species (Tröger, 1967).



Fig. 6. a. *Inoceramus (Inoceramus) pictus* aff. *concentricundulatus* Tröger; incomplete internal mould of a right valve; $\times 1$, coated (D.3046.4).
b. *Inoceramus (Inoceramus) pictus* Sowerby forma a; internal mould of a right valve; $\times 1$, coated (D.2213.1).

Inoceramus pictus Sowerby forma a

Fig. 6b

Material

One internal mould of a right valve from the bay to the north of Cape Obelisk (D.2213.1). The specimen is preserved in a coarse grey sandstone containing shell fragments and clasts of dark volcanic material.

Description

This is a small rounded-rectangular valve with a typical *pictus*-like outline. It would appear to have a gently curving postero-dorsal margin and well-rounded posterior and ventral margins (Fig. 6b). The anterior margin is straight and drops vertically to the plane of commissure. The valve is moderately convex with the apex of convexity occurring in the central and antero-dorsal regions. There is an even descent from the central region to the dorsal, posterior and ventral margins. The antero-ventral extremity is slightly extended and there is a pronounced bend in the growth axis in the later stages. Neither the postero-dorsal wing nor the umbonal area is well developed. A small pointed beak is visible, however (Fig. 6b), and this curves sharply forward to overhang the anterior margin. There are traces of a straight hinge line but its length cannot be determined.

Closely spaced, low, narrow concentric ribs (*Anwachsrinnen*) cover the valve. At their maximum development, close to the ventral margin, they are of the order of 0.75 mm in width and are separated by similar-sized interspaces. The ribs are symmetrical about the growth axis. There are no indications of either coarse sculpture elements (such as *Anwachsrundeln*) or the grouping of ribs into *Anwachsringreifen*.

Remarks

The general form, outline and sculpture link this specimen with the group of *I. pictus* Sowerby. However, it differs from *I. pictus pictus* in that it is slightly less asymmetrical, more evenly inflated and has no coarse sculpture elements. The closest comparison seems to be with small forms of *I. prefragilis* Stephenson (1952, e.g. pl. 12, fig. 12) from the Cenomanian of Texas.

From its inception, *I. prefragilis* has been regarded as a close relative of *I. pictus* Sowerby (Stephenson, 1952, p. 65) and it would appear that many specimens, especially those in the small- to medium-size range, are almost identical to the European *I. pictus*. Seitz (1959, p. 17) synonymized *I. prefragilis* Stephenson within *I. pictus* Sowerby but it is still possible that a case can be made out for the establishment of a variety, or even a subspecies, of *I. pictus* for small

forms close to Stephenson's (1952, p. 64) original description. For this reason, specimen D.2213.1 is separated off here as a distinct form of *I. pictus* Sowerby.

One of the specimens assigned to *I. pictus etheridgei* (Etheridge, Jun.) by Pergament (1966, pl. 35, fig. 1) is similar in valve form and outline to *I. pictus* forma *a* but it differs somewhat in ornament. Although fine ribs are developed, there is also a series of conspicuous growth pauses. The Japanese *I. tenuistriatus* Nagao and Matsumoto (1939, pl. 24, fig. 3, pl. 26, figs 1–4) is a small species with fine, regular concentric ornament, but it generally has a distinctive polygonal outline. Small forms of *I. flavus* Sornay and *I. heinzi* Sornay would also appear to be very close to the *prefragilis*-forma *a* group but it is doubtful if they possess such a regular ornament pattern (cf. Sornay, 1965, pl. A, figs 1 and 2, pl. B, fig. 4).

Finally, it should be mentioned that some forms of *I. pictus bohemicus* Leonhard are close to the *I. prefragilis* group (e.g. Tröger, 1967, pl. 3, figs 9–11). However, this subspecies is consistently flatter than *I. prefragilis* and has a less prominent umbo on the left valve.

Inoceramus prefragilis Stephenson is an Upper Cenomanian species (Stephenson, 1952; Kauffman, 1977).

Inoceramus apicalis Woods 1911

Fig. 7a

Material

One internal mould of a left valve from cliffs near the southern end of Cape Longing (D.2208.5). The specimen is preserved in a fine-grained grey sandstone.

Description

The valve has a length of 33 mm and a maximum width of 21 mm. It is elongated-rectangular in outline with rounded corners (Fig. 7a). It is moderately convex with the maximum degree of convexity being developed parallel to the growth axis. A narrow pointed umbo curves gently forwards and projects slightly above a long straight hinge line. The latter, together with the gently sinuous posterior margin, delineates a small triangular wing which is clearly recessed from the umbo (Fig. 7a). Although the anterior margin is incomplete, it would appear to have been gently convex. Faint concentric ribs cover the valve. These are narrow (less than 1 mm in width), closely set and regular in their distribution. On the wing there are indications that they become even finer and straight.

Remarks

Inoceramus apicalis Woods is one of a large group of Turonian species that closely resembles *Inoceramus lamarcki* Parkinson. Woods (1912b, p. 7) believed his *I. lamarcki* var. *apicalis* (= *I. apicalis* Woods of later authors) to be one of the earliest forms of the *I. lamarcki* group, in which the valves are only slightly unequal, concentric folds weakly developed and the posterior ear not sharply recessed. Specimen D.2208.5 compares well with Woods' (1912a) figured specimens (especially his pl. 53, fig. 5) and is also very similar to a specimen of *I. apicalis* Woods from Russia (Dobrov and Pavlova, 1959, pl. 2, fig. 4a and b).

There is a strong resemblance between *I. apicalis* Woods and certain small forms of *I. pictus* Sowerby (e.g. Geinitz, 1872–75, pl. 46, fig. 11 = *I. pictus pictus* Sowerby in Dietze, 1959, p. 861; Tröger, 1967, pl. 3, fig. 2a) but the former can be distinguished by its more regular outline, distinctive ear and finer ornament. *Inoceramus lamarcki lamarcki* Parkinson, although very variable, generally has much stronger concentric ornament and a broader umbonal region which is emphatically recessed from the wing. *Inoceramus inaequalis inaequalis* Schlüter is more strongly convex and has an umbo on the left valve which rises substantially above the hinge line (Tröger, 1967, p. 79).

Inoceramus apicalis ranges from Lower to Middle Turonian (Woods, 1912a; Tröger, 1967).

Inoceramus lamarcki lamarcki Parkinson 1819

Fig. 7b

Material

One internal mould of a left valve from cliffs near the southern end of Cape Longing (D.2208.7). The specimen is preserved in a fine-grained grey sandstone.

Description

This small inequilateral left valve has a rounded-rectangular outline (Fig. 7b). It is strongly convex with the apex of convexity running parallel to the growth axis. From the summit of the valve there is a vertical drop to the anterior margin and very steep descents in all other directions. Sections perpendicular to the growth axis reveal the convexity to be slightly asymmetric towards the ventral margin. The anterior margin, which is equal in length to three-quarters of the total shell length, is gently concave but the ventral margin is well rounded. The growth axis is characterized by a sharp bend in an anterior direction in its early stages.

A long (14 mm) straight hinge together with a slightly sinuous posterior margin delineates a triangular wing, which is sharply recessed from the umbonal region (Fig. 7b). The comparatively narrow pointed umbo rises above the hinge line and is twisted anteriorly. Faint impressions of small, square ligament pits occur along the hinge.

Ornament consists of low, regular concentric ribs that are well rounded and slightly asymmetric in cross-section. Towards the ventral margin in particular, the ribs tend to have slightly steeper dorsal than ventral flanks. Along the growth axis the ribs are 1.5–2.0 mm in width but they become narrower towards the anterior and posterior margins. Separated by gently concave interspaces of similar width, they are slightly asymmetric about the growth axis. On the wing there are faint traces of fine, sickle-shaped growth lines.

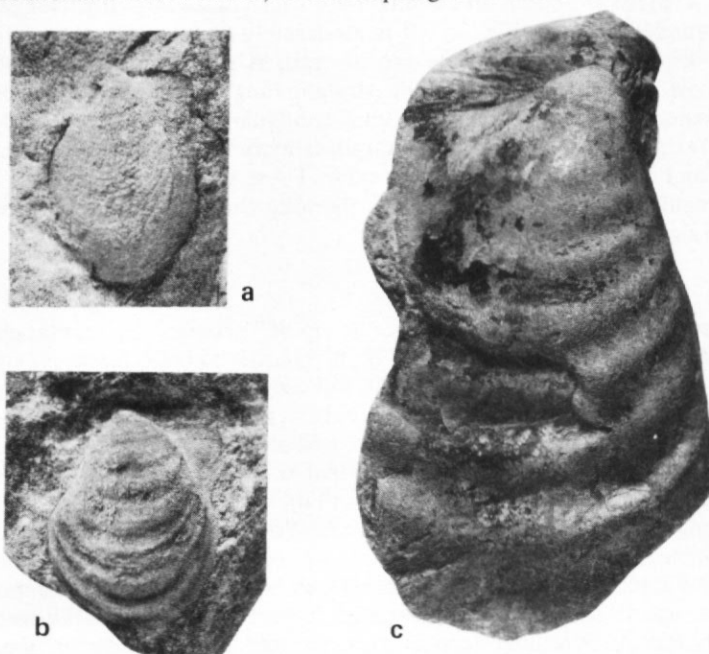


Fig. 7. a. *Inoceramus (Inoceramus) apicalis* Woods; internal mould of a left valve; $\times 1$, coated (D.2208.5).
 b. *Inoceramus (Inoceramus) lamarcki lamarcki* Parkinson; internal mould of a left valve; $\times 1$, coated (D.2208.7).
 c. *Inoceramus (Inoceramus) cuvieri* Sowerby; incomplete specimen, showing the right valve and umbonal region of the left valve. A thick shell layer partially covers the right valve; $\times 1$ (D.416.1).

Remarks

Specimen D.2208.7 closely resembles *I. brongniarti* Sowerby (Woods, 1912a, fig. 70, pl. 52, fig. 4a-c; Carter, 1972, pl. 1, figs 8 and 10). Available evidence suggests, however, that this species should now be included in the subspecies *I. lamarcki lamarcki* Parkinson (Tröger, 1967, p. 59). Woods (1912a, p. 317) separated the two on the basis of degree of development of the posterior wing but in all other respects they are similar. Moreover, many specimens assigned to *I. lamarcki* Parkinson have a posterior wing that is much less clearly recessed than that of the type. *I. lamarcki websteri* Mantell is another small inflated subspecies but it would appear to have a wing that is consistently less well differentiated from the umbonal region than either of the two previously mentioned forms (cf. Woods, 1912a, figs 71 and 72, 1912b, fig. 39). *Inoceramus inaequalis inaequalis* Schlüter has finer ornament and an even more inflated left valve (e.g. Wolansky, 1932, pl. 3, figs 29 and 29a; Tröger, 1967, pl. 7, fig. 6).

Woods' (1912a) broad form group of *I. lamarcki* extends from the Lower Turonian to the Lower Santonian; *I. lamarcki lamarcki*, however, is restricted to the lower Middle Turonian (Tröger, 1967).

Inoceramus cuvieri Sowerby 1814

Fig. 7c

Material

One incomplete right valve, to which is attached part of the hinge line and umbonal region of the corresponding left valve. The specimen was collected from a series of grey-green sandstones and conglomerates at Lachman Crags (D.416.1).

Description

The right valve has an estimated length of 80 mm and maximum width of 60 mm. It is strongly inequilateral, obliquely rounded and moderately inflated. The pointed terminal umbo is curved inwards and projects very slightly above the hinge line. From the convex umbonal region the valve flattens out postero-dorsally to form a prominent wing. This is bounded dorsally by the remnants of a long straight hinge (Fig. 7c). Narrow (less than 0.5 mm in width) ligament pits are spaced along the hinge at intervals of approximately 1.5 mm. The posterior margin would appear to have been slightly rounded and the ventral margin well rounded. The anterior margin, which is equal in length to approximately three-quarters of the total length of the valve, is straight and drops vertically to the plane of commissure. The angle between the anterior margin and the hinge line is 105°. Remnants of a thick, prismatic shell layer cover much of the valve. Generally it is 1.5 mm thick but in the umbonal region it is up to 2.5 mm thick. Fine, black platy laminae of the ligamental layer are also preserved in the hinge area.

Ornament consists of broad, low concentric plicae. In the central regions of the valve these have a wave-length of 7–8 mm and an amplitude of 1–1.5 mm. As they gradually increase in size towards the ventral margin, the concave interspaces between them (of equivalent width) become slightly deeper. The ornament apparently dies out on the wing.

The umbonal region of the left valve is similar to that of the right one.

Remarks

Inoceramus cuvieri Sowerby varies considerably in such features as the degree of prominence of the ribs, convexity of the valves, size of the posterior wing and the angle between the hinge line and anterior margin (see e.g. Woods, 1912a, p. 307–27, figs 78–84, pl. 53, fig 7). Woods (1912a, p. 320) envisaged *I. cuvieri* Sowerby as no more than a variety of *I. lamarcki* Parkinson, because many transitional forms exist between the two. Other workers, however, have taken *I. cuvieri* to be a distinct species (e.g. Adert, 1911; Dobrov and Pavlova, 1959; Jones and Gryc, 1960).

Specimen D.416.1 compares closely with Woods' more heavily ornamented examples of *I. lamarcki* var. *cuvieri* (e.g. Woods, 1912a, figs 78, 79 and 81). These forms are all

characterized by a sharply defined anterior margin, a prominent posterior ear and low wave-like plicae. Specimens illustrated by Dobrov and Pavlova (1959, pl. 2, fig. 3) and Jones and Gryc (1960, pl. 18, fig. 3) clearly belong in this form group too. The distinctive broad low plicae generally serve to distinguish the group from most members of the *I. pictus* Sowerby and *I. lamarcki* Parkinson groups. However, there are a few forms, such as *I. lamarcki stumcke* Heinz (e.g. Tröger, 1967, p. 67), which also have broad low plicae rather than true ribs, and it is often difficult to separate these from *I. cuvieri*. The Australian species, *I. australis* Woods (1917, p. 27, pl. 13, fig. 3), shows certain resemblances to *I. cuvieri* Sowerby (Heinz, 1928a, p. 122) but it is generally narrower in the umbonal region and has prominent upstanding ribs separated by deep concave interspaces. Such a ribbing style also characterizes the Japanese species *I. hobetsensis* Nagao and Matsumoto 1939 (e.g. Noda, 1975, pl. 32, figs 6–8, pl. 33, figs 1–7, pl. 34, figs 1–5) and *I. iburiensis* Nagao and Matsumoto (1939, pl. 31, figs 1 and 2, pl. 32, fig. 2) which otherwise closely resemble *I. cuvieri*.

Woods (1912a) gave the age range of *I. cuvieri* as Middle Turonian to Lower Santonian but in North America it is apparently restricted to the Middle Turonian (Kauffman, 1968, 1977).

Inoceramus madagascariensis Heinz 1933

Inoceramus sp. Woods, 1917, p. 28, pl. 14, figs 3a, b and 4.

Inoceramus glatziae Heinz, 1928d, p. 126.

Stenoceramus (*Stenoceramus*) *madagascariensis* Heinz, 1933, p. 252, pl. 19, fig. 2, pl. 20, fig. 2a and b.

Inoceramus nukeus Wellman, 1959, p. 155, pl. 10, fig. 2.

(?) *Inoceramus woodsi* Böhm; Dobrov and Pavlova, 1959, p. 135, pl. 4, fig. 1a and b.

Figs 8, 9a and b

Material

Approximately 30 single valves and four whole specimens (4641, 4642 and 5114–33) from the north-western corner of Persson Island (Fig. 1). Although there are a few traces of shell material, the specimens are predominantly preserved as internal moulds in fine- to medium-grained sandstone.

Description

At first sight, the variation shown by these specimens (Figs 8, 9a and b) is such as to suggest that more than one species may be present. More detailed examination, however, reveals a number of features common to all and it is believed that they can in fact be assigned to a single, but somewhat variable, species.

The specimens are all small to medium in size with an average length of approximately 50 mm. One incomplete specimen (5116) apparently had a length in excess of 70 mm. The species is equivalve but the valves are strongly inequilateral. The majority of them are elongated-rectangular in outline and moderately convex with the maximum degree of convexity being developed along the growth axis. Both slender (e.g. 5127; Fig. 8b) and more bulbous forms (e.g. 5118 and 5122; Fig. 8d–f) can be distinguished. On the best-preserved specimens (e.g. 5115a, 5118, 5120 and 5127) the umbo is seen to be comparatively narrow and pointed. It curves gently forwards and inwards, and rises slightly above the hinge line. The latter is straight and varies in length from approximately two-fifths to three-fifths of the total length of the valve. Posterodorsally, the valve becomes flattened to form a more or less distinct wing (e.g. 5118 and 5120; Fig. 8a and d). The latter, however, is never recessed from the umbonal region. The anterior margin of the elongated-rectangular forms is gently concave to concave and equal in length to just over half the total length of the valve. In most forms it is perpendicular, or almost so, to the plane of commissure (e.g. 5120 and 5127; Fig. 8a and b). The angle between the anterior margin and the hinge line is generally between 85° and 95°, although in a few specimens (e.g. 5114a;

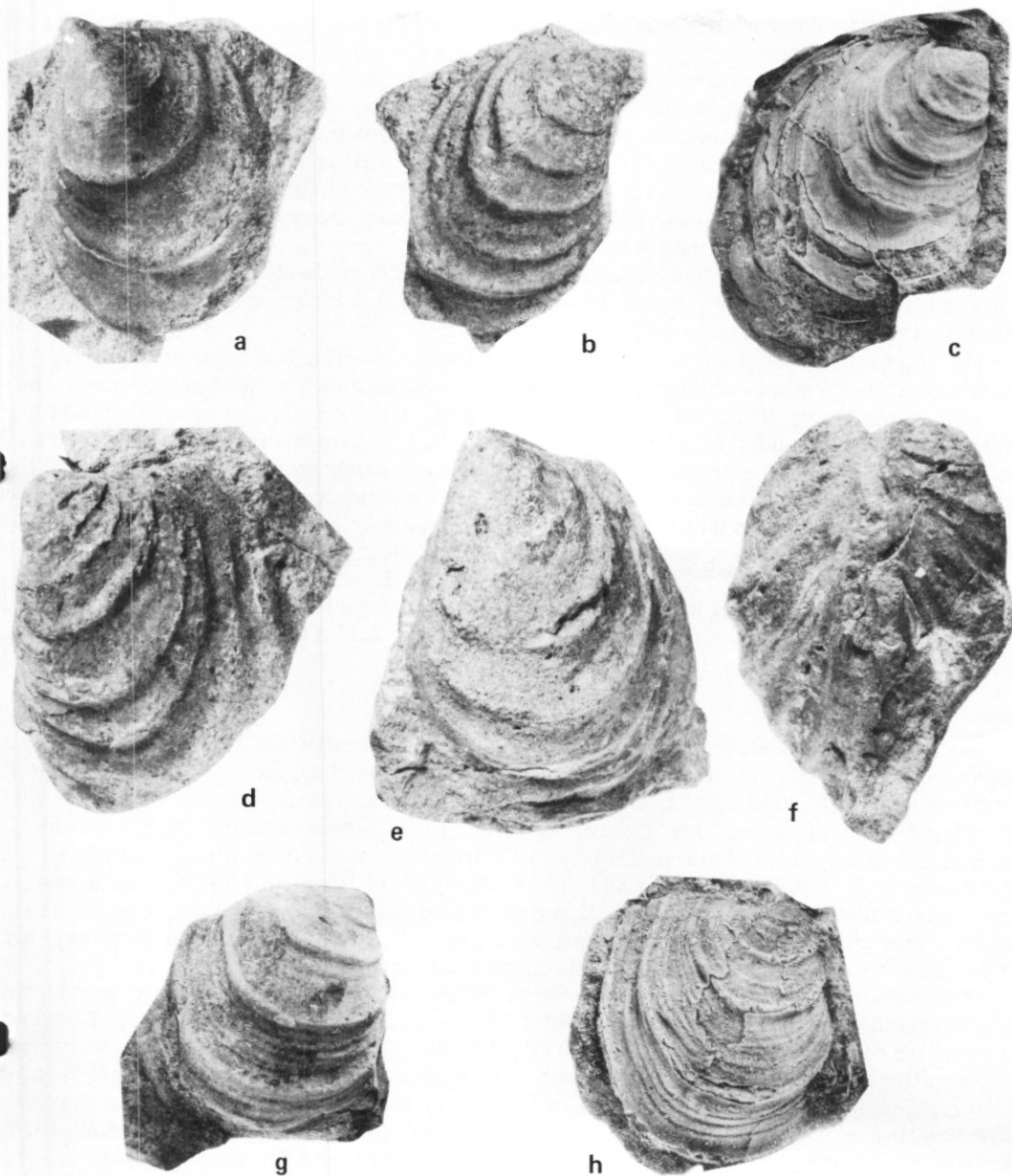


Fig. 8. *Inoceramus (Inoceramus) madagascariensis* Heinz.

- a. Internal mould of a left valve; × 1 (5120).
- b. Internal mould of a right valve; × 1 (5127).
- c. Latex cast from the external mould of a right valve, showing the two orders of concentric ornament; × 1 (5115a).
- d. Internal mould of a more bulbous left valve; × 1 (5118).
- e. Internal mould of a more bulbous specimen, viewed from the left side; × 1 (5122).
- f. Posterior view of the same specimen, showing the degree of inflation of both valves; × 1 (5122).
- g. Internal mould of a more rounded right valve, showing the two orders of concentric ornament; × 1 (5119c).
- h. Latex cast from the external mould of a more rounded right valve, showing the two orders of concentric ornament; × 1 (5114a).

Fig. 8h) there is a tendency towards a slight expansion of the antero-ventral area and the angle is closer to 100° . The ventral margin on all specimens is well rounded.

Three incomplete specimens (4641, 5119b and 5126; see e.g. Fig. 9a) have considerably expanded antero-ventral regions which give them much more rounded outlines. They all have angles between the anterior margin and the hinge line of approximately 100° and are noticeably flatter. A further specimen (5129; Fig. 9b) has an even more expanded antero-ventral area and a corresponding hinge-anterior margin angle of approximately 130° . In all these forms the growth axis (normally a shallow concave curve) is sharply displaced forwards; it seems likely that all four specimens have been partially crushed.

Specimen 5119c (Fig. 8g) has a rounded outline but is still moderately convex. It would seem to occupy an intermediate position between the rounded varieties and the more common elongated-rectangular forms.

The ornament consists of two orders of concentric ribs. The first-order ribs are sharply demarcated, 1–1.5 mm in width and well rounded in cross-section. On the larger specimens they become considerably thickened (to 2–3 mm in width) and may develop acute or flange-like summits (e.g. 5119b and 5129; Fig. 9a and b). Along the growth axis they are generally regularly spaced at intervals of 5–10 mm but on the wing they can become crowded (e.g. Fig. 8b). On the elongated-rectangular varieties, the ribs are noticeably asymmetric about the growth axis but on the more rounded varieties they become almost semi-circular (e.g. 5114a and 5119c; Fig. 8g and h). The second-order ribs are much better developed on some specimens than on others. Closely set, they are low, between 0.5 and 1.0 mm in width, and well rounded in cross-section (Fig. 8c, g and h). Between four and six secondary ribs are usually present between any two primaries. On specimen 5127, faint radial striae are visible on the anterior half of the valve, extending from the umbo to the ventral margin.

Remarks

The size, form, degree of convexity and style of ornament readily link these specimens with a distinctive group of Turonian–early Senonian species. Members of this group include *I. vancouverensis* Shumard and *I. ernsti* Heinz, together with some varieties of *I. lamarcki* Parkinson. The specimens are closest, however, to a further member of the group, *I. madagascariensis* Heinz (1933, p. 252). With the exception of the more rounded forms, all the specimens agree closely with Heinz's (1933, pl. 19, fig. 2, pl. 20, fig. 2a and b) illustrations. A conspicuous feature of Heinz's specimens is their regular first- and second-order concentric ribs. Other forms closely resemble *I. madagascariensis* in size, form and degree of convexity, but none of them shows this distinctive style of ornament so consistently.

Within the synonymy of *I. madagascariensis*, Heinz (1933, p. 252) included specimens from New Zealand which he had previously identified as *I. glatziae* Flegel (Heinz, 1928d, p. 126), and which were originally illustrated by Woods (1917, p. 28, pl. 14, figs 3 and 4) as *Inoceramus* sp. Apparently unaware of either of Heinz's publications, Wellman (1959, p. 155) assigned Woods' (1917, pl. 14, figs 3 and 4) specimens of *Inoceramus* sp., together with some additional material, to a new species, *I. nukeus* Wellman. The holotype of this species (NZGS 6427; Wellman, 1959, pl. 10, fig. 2) agrees well with Heinz's *I. madagascariensis* and the former should now be included within the synonymy of the latter.

There would seem to be some confusion, however, as to the exact interpretation of *I. nukeus* for a number of the specimens assigned to it by Wellman and subsequent workers at the New Zealand Geological Survey clearly do not agree with either Wellman's (1959) or Heinz's (1933) original descriptions. Examination of a series of New Zealand Geological Survey plaster casts in the British Museum (Nat. Hist.) has revealed at least four specimens that fall into this category. Specimen NZGS 6098, for example, although resembling *I. madagascariensis* in some respects, is much closer to the group of *I. vancouverensis* Shumard. A revision of all the specimens currently assigned to *I. nukeus* Wellman is required.

Of the specimens grouped by Tröger (1967, p. 89) into *I. vancouverensis* Shumard 1856, the following would appear to be close to *I. madagascariensis* Heinz:

- | | |
|---------------------------------|---|
| i. <i>I. cuvieri</i> Sowerby | in Geinitz, 1872–75, pl. 13, fig. 8. |
| ii. <i>I. striatus</i> Mantell | in Geinitz, 1872–75, pl. 13, fig. 10. |
| iii. <i>I. frechi</i> Andert | in Andert, 1911, pl. 1, fig. 8a and b. |
| iv. <i>I. costellatus</i> Woods | in Fiege, 1930, pl. 5, fig. 6. |
| v. <i>I. frechi</i> Andert | in Dobrov and Pavlova, 1959, pl. 9, fig. 4. |

Inoceramus vancouverensis seems to be consistently inequivalve with the umbo of the left valve being somewhat larger and more inflated than that of the right one. However, some specimens (e.g. *I. costellatus* Woods in Fiege, 1930, pl. 5, figs 6 and 7, = *I. vancouverensis* Shumard in Tröger, 1967) have subdued umbones and these are very similar in form to *I. madagascariensis*.

At least one of the specimens previously identified as *I. vancouverensis* can be tentatively referred to *I. madagascariensis*. Dobrov and Pavlova (1959, pl. 4, fig. 1a and b) illustrated a specimen of *I. woodsi* Böhm that is very close in almost all respects to *I. madagascariensis*. In particular, it has a virtually identical style of ornament to Fig. 8g, Heinz's (1933) pl. 20, fig. 2a and b, and Wellman's (1959) pl. 10, fig. 2. *Inoceramus woodsi* was erected by Böhm (1915, p. 598) to replace *I. costellatus* Woods 1912 which was pre-occupied by *I. costellatus* Conrad 1858. As all forms of *I. costellatus* Woods (= *I. woodsi* Böhm) now belong within the group of *I. vancouverensis* Shumard (Tröger, 1967, p. 89–95), the current interpretation of Dobrov and Pavlova's (1959, pl. 4, fig. 1a and b) specimen is that it also belongs in this group. Nevertheless, it seems to possess all the features of *I. madagascariensis* and should probably be transferred to that species.

The broader, more rounded forms of *I. madagascariensis* (e.g. Figs 8g, h and 9a) show certain resemblances to *I. ernsti* Heinz (cf. Tröger, 1967, pl. 14, figs 1–6; Dobrov and Pavlova, 1959, pl. 9, fig. 1, = *I. ernsti* Heinz in Tröger, 1967, p. 128) but the latter almost always has a much more convex profile than *I. madagascariensis* (e.g. Heinz, 1933, pl. 19, fig. 1a–c). It also has a broader more inflated umbo (e.g. Woods, 1911, fig. 85, = *I. ernsti* Heinz in Tröger, 1967, p. 128).

Although *Inoceramus madagascariensis* shows similarities to some members of the extensive *I. lamarcki* group (e.g. cf. *I. lamarcki* in Dobrov and Pavlova, 1959, pl. 3, fig. 1a and b), most forms within this group can be distinguished by the fact that the umbo is nearly always much broader and the wing more deeply recessed. *Inoceramus lamarcki* is also moderately to strongly inequivalve. *Inoceramus morator* Heinz (illustrated as *I. lamarcki* Parkinson in Woods (1911, fig. 67)) is fairly close to the broader forms of *I. madagascariensis*, whereas *I. lamarcki* var. *websteri* Mantell (Woods, 1911, figs 71 and 72) is similar to some of the smaller specimens. However, in both cases there are clear differences in form and detail of ornament. Similarities also exist to some specimens of *I. teshioensis* Nagao and Matsumoto, a variable Japanese species (Nagao and Matsumoto, 1939, pl. 24, figs 6, 7 and 9, pl. 26, figs 5–7; Noda, 1975, pl. 35, fig. 2).

It will be apparent from the foregoing discussion that the exact systematic status of *I. madagascariensis* is still in some doubt. Clearly, transitional forms exist between a number of closely related coeval species. Only when the variation within each of these species has been fully described will meaningful taxonomic revisions be possible.

Inoceramus madagascariensis ranges from Upper Turonian to Lower Coniacian (Heinz, 1933).

Inoceramus sp. aff. *madagascariensis* Heinz 1933

Fig. 9c

Material

One internal mould of a right valve from the northern shore of the bay to the north of Cape

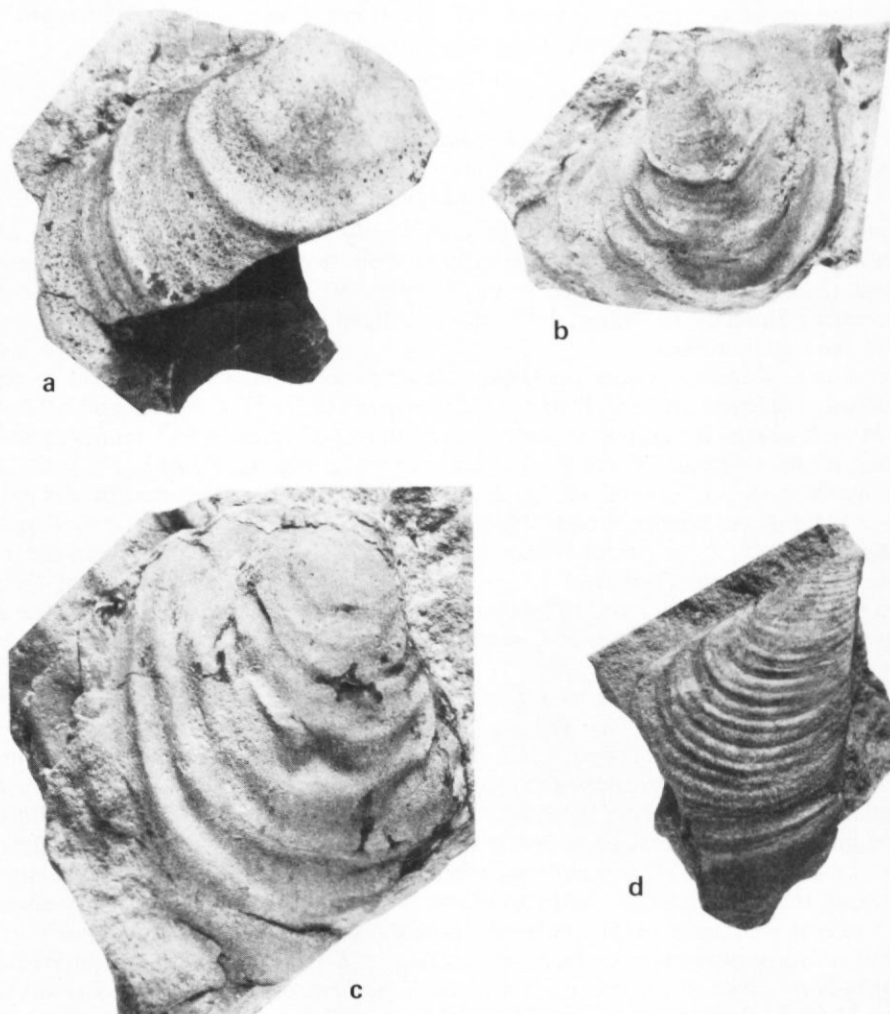


Fig. 9. a. *Inoceramus (Inoceramus) madagascariensis* Heinz; incomplete internal mould of a left valve with a considerably expanded antero-ventral region. The valve has a much more rounded outline and the concentric ribs show a tendency towards the development of acute summits; $\times 1$ (D.2212.6).
 b. *Inoceramus (Inoceramus) madagascariensis* Heinz; internal mould of a left valve with a greatly expanded antero-ventral region. The concentric ribs show a tendency towards the development of acute summits; $\times 1$ (D.2212.6).
 c. *Inoceramus (Inoceramus)* sp. aff. *madagascariensis* Heinz; internal mould of an almost complete right valve with parts of the test still adhering; $\times 1$ (D.2212.6).
 d. *Sphenoceramus* sp. cf. *lingua* (Goldfuss); incomplete internal mould of a right valve. Traces of a thin shell layer cover the valve; $\times 1$ (D.3046.3).

Obelisk (D.2212.6; Fig. 2). The specimen is preserved in a grey medium- to coarse-grained sandstone that contains small bedded fragments of *Inoceramus* shell material.

Description

The valve is of medium size, has a rounded-rectangular outline and is very inequilateral (Fig. 9c). It has a length of approximately 60 mm and a maximum width of 45 mm. It is moderately convex with the maximum degree of convexity being developed in the umbonal and central

regions. The valve margins are incomplete and partially crushed but it can be determined that both the posterior and dorsal margins were well rounded. Postero-dorsally, a large flat wing is indistinctly recessed from the main body of the valve. The anterior margin, which is equal in length to just over half the total length of the valve, has a sinuous outline. Initially, it is straight to very slightly concave and descends vertically to the plane of commissure. Thereafter, however, it becomes convex in outline and descends only moderately steeply. It would appear that the antero-ventral region was slightly extended. In sections perpendicular to the growth axis, the umbo can be seen to be moderately convex and symmetrically rounded. It terminates bluntly, is twisted slightly forwards and does not project above the hinge line. The latter, although incompletely preserved, seems to have been long and straight. It subtends an angle of 105° with the anterior margin. Isolated fragments of thin shell material adhere to parts of the valve surface.

Ornament seems to consist of a single set of prominent concentric ribs. Over much of the valve surface, however, the ribbing pattern is confused and indistinct (Fig. 9c). The ribs are most clearly seen in the postero-dorsal region where they are 1.5–2 mm in width, symmetrical to slightly asymmetrical in cross-section and have acute summits. They are separated by concave interspaces which vary in width from 2 to 4 mm. These simple ribs appear to have covered the rest of the valve but in both the umbonal and ventral regions they are indistinct and discontinuous. Although the valve may have been considerably abraded, it is possible that the confusion in rib pattern was due to damage during growth. A notable feature of the ornament is that postero-dorsally the ribs remain distinct and parallel to the valve margin (Fig. 9c).

Remarks

Although there are obvious differences in style of ornament, there is a general resemblance in size and form between this specimen and *I. madagascariensis* Heinz. The resemblance is strongest to those forms of the latter in which the second-order concentric ribs are only weakly developed (e.g. 5118 and 5122; Fig. 8d–f). In addition, a number of specimens of *I. madagascariensis* also show prominent postero-dorsal ribs, although it should be pointed out that these tend to be straight and to coalesce towards the hinge line (e.g. 5122 and 5127; Fig. 8b and e–f). Nevertheless, bearing in mind the possibility that this specimen has either been abraded or damaged during growth (or both), it is thought to be closer to *I. madagascariensis* than to any other species.

Specimen D.2212.6 shows similarities to some forms in the highly variable groups of *I. lamarcki* Parkinson (e.g. Woods, 1912a, fig. 68) and *I. vancouverensis* Shumard (e.g. Andert, 1911, pl. 1, fig. 8a and b = *I. vancouverensis vancouverensis* Shumard in Tröger, 1967) but in general it can be distinguished from the majority of forms within both these groups by the criteria already given on p. 47. In style of ornament, it also shows some similarity to *I. ernsti* Heinz (e.g. Woods, 1912a, fig. 85 = *I. ernsti* Heinz in Tröger, 1967) but its umbonal region would seem to be altogether too narrow for it to belong to that species (cf. Dobrov and Pavlova, 1959, pl. 9, fig. 1, = *I. ernsti* Heinz in Tröger, 1967). There is some agreement with *I. stillei* Heinz (1928a, pl. 2, fig. 2) but the latter is broader ventrally and has much more regular concentric ornament. There are also resemblances to the Japanese species *I. hobetsensis* Nagao and Matsumoto (1939, pl. 24, figs 6, 7 and 9, pl. 26, figs 5–7; Noda, 1975, pl. 35 fig. 2) and *I. teshioensis* Nagao and Matsumoto (see especially Noda, 1975, pl. 35, fig. 6).

Genus *Sphenoceramus* J. Böhm 1915
Sphenoceramus sp. cf. *lingua* (Goldfuss 1835)

Fig. 9d

Material

One internal mould of a right valve from the Hidden Lake area (D.3046.3). The specimen is preserved in a fine-grained grey-green sandstone.

Description

This small specimen has a distinctive narrow triangular outline. It is slightly but evenly inflated, oblique and very inequilateral. Much of the ventral region is missing but it can be judged that the length (of approximately 55 mm) was about twice the maximum width. There is a narrow terminal umbo which is not differentiated from the main body of the valve. The anterior margin is straight and equal in length to approximately two-thirds of the total length of the valve. It is bounded by a sharp carina and drops vertically to the plane of commissure. The slightly shorter posterior margin is also straight and subtends an angle of 55° with the anterior margin. The valve surface drops gently to the ventral margin which was apparently well rounded. Neither the hinge line nor the wing is preserved.

The ornament consists of a series of low closely spaced concentric ribs (Fig. 9d). These increase gradually in width from less than 1 mm in the umbonal region to approximately 2 mm towards the ventral margin. They tend to be slightly asymmetrical in cross-section (with steeper dorsal flanks) and some have more sharply defined crests than others. The ribbing becomes slightly confused towards the ventral margin but there is no indication of differentiation into two or more distinct size groups. The interspaces are narrow concave grooves.

Towards the posterior margin a number of ribs curve sharply forward and fuse to form a series of raised lips. These have acute summits and are noticeably discordant to the general trend of the ornament. It may well be that they mark the early stages of a distinct posterior carina but unfortunately not enough of the postero-ventral region is preserved for this to be verified.

Remarks

The narrow pointed umbo, sharply demarcated anterior region and regular pattern of ornament readily link this specimen to the genus *Sphenoceramus*. However, as the specimen is both incomplete and a juvenile, it cannot be easily assigned to a species. At first sight, it would seem to be very similar to both the type of *S. lingua* (Goldfuss) (1834–40, p. 113, pl. 110, fig. 5; Seitz, 1965, pl. 16, fig. 4) and juveniles of *S. cf. lingua* (Goldfuss) (Seitz, 1965, pl. 18, figs 3 and 5) but, as Seitz (1965, p. 88) has pointed out, the early stages of many species within the genus *Sphenoceramus* are remarkably similar. Nevertheless, there is some evidence to suggest that *S. lingua* is characterized by uniform weak ribs that remain undifferentiated throughout the adult stages (Seitz, 1965, p. 90–93, pl. 18, fig. 4, pl. 19, fig. 3). In comparison, most of the other species within the genus (e.g. *S. cancellatus* (Goldfuss), *S. patootensis* (de Loriol), *S. angustus* (Beyenburg), *S. patootensiformis* (Seitz) and *S. nasutus* (Wegener)) show strong differentiation of the ribs into at least two orders. These are most easily seen in the adult stages but on many specimens they can be detected in the earlier stages too. Specimen D.3046.3 has only one order of ribs and thus can be tentatively linked to *S. lingua*.

Sphenoceramus lingua ranges from Upper Santonian to Lower Campanian (Seitz, 1959, 1965).

DISCUSSION

Stratigraphical implications

The Upper Cretaceous succession in the James Ross Island group represents an essentially continuous 5 000 m sequence of clastic sedimentary rocks (Bibby, 1966). The collective thicknesses of the five lower horizons and the Snow Hill Island Series are estimated at 1 500 and 3 500 m, respectively. With such a thick succession and an abundance of stratigraphically useful fossils, it is somewhat surprising to find that no detailed biostratigraphic zonation has been attempted in this area. However, the lack of information on both localities and modes of occurrence has already been commented on, and to this should be added the fact that there is very little structural data available for the Snow Hill Island Series. Bedding planes are rare in the

uncemented sands and gravels, and there has almost certainly been extensive repetition of the sequence by folding (Bibby, 1966, p. 34). Spath (1953) could do no more than regard the various ammonite assemblages collected from within the Snow Hill Island Series as broadly contemporaneous, a view that has subsequently been upheld by Howarth (1958, 1966).

Collectively, the inoceramids described in this study indicate that the sequence ranges from Cenomanian (or possibly even uppermost Albian) to Lower Campanian (Table II). Whereas most of the ammonites come from the Snow Hill Island Series, nearly all of the inoceramids collected to date come from the area of outcrop of the Hidden Lake Beds. The stratigraphical level of the beds exposed on Persson Island and at Cape Longing is uncertain but it is believed that they occupy a position approximately equivalent to that of the Hidden Lake Beds (Figs 1 and 2). So far only one inoceramid has been collected from the Snow Hill Island Series (*I. cuvieri*).

TABLE II. STRATIGRAPHICAL AGES SUGGESTED BY THE INOCERAMID SPECIES

<i>Inoceramid species</i>	<i>Locality</i>	<i>Age</i>
<i>S. sp. cf. lingua</i> (Goldfuss)	D.3046	Upper Santonian–Lower Campanian
<i>I. (I.) sp. aff. madagascariensis</i> Heinz	D.2212	(?) Upper Turonian–Lower Coniacian
<i>I. (I.) madagascariensis</i> Heinz	4641, 4642, 5114–33	Upper Turonian–Lower Coniacian
<i>I. (I.) cuvieri</i> Sowerby	D.416	Middle Turonian–Lower Santonian
<i>I. (I.) lamarcki lamarcki</i> Parkinson	D.2208	Lower Middle Turonian
<i>I. (I.) apicalis</i> Woods	D.2208	Lower–Middle Turonian
<i>I. (I.) pictus</i> Sowerby forma <i>a</i>	D. 2213	Upper Cenomanian
<i>I. (I.) pictus</i> aff. <i>concentricoundulatus</i> Tröger	D. 3046	Upper Cenomanian
<i>I. (I.) sp. aff. pictus neocaledonicus</i> Jeannet	D.3022	Upper Cenomanian
<i>I. (I.) pictus neocaledonicus</i> Jeannet	D.2212	Upper Cenomanian
	D.3057	
	R.551	
<i>I. (I.) pictus pictus</i> Sowerby	D.2212	Upper Cenomanian
<i>I. (I.) sp. cf. tenuis</i> Mantell	D.3045	Uppermost Albian–Upper Cenomanian

The commonest inoceramids in the Hidden Lake Beds are members of the *I. pictus* group. *Inoceramus pictus pictus*, *I. pictus neocaledonicus* and *I. pictus* forma *a* all occur at the locality on the northern shore of the bay to the north of Cape Obelisk (D.2212, D.2213 and D.3057), *I. pictus concentricoundulatus* occurs to the north-east of Hidden Lake (D.3046) and *I. sp. aff. pictus neocaledonicus* at Bibby Point (D.3022) (Fig. 2). A number of fragments are associated with the specimens from stations D.3057 and D.3022, and it is possible that some of these can also be referred to the *I. pictus* group. It is likely that the persistent *Inoceramus* bed that extends from the Cape Obelisk area to Stoneley Point and Bibby Point (Bibby, 1966, p. 22) is in fact a prolific level for this particular species group.

Three further inoceramids have also been collected from the Hidden Lake Beds. *Inoceramus sp. cf. tenuis* and *Sphenoceramus sp. cf. lingua* come from localities to the north-east of Hidden Lake (D.3045 and D.3046; Fig. 2) and *I. sp. aff. madagascariensis* from station D.2212. The age ranges of these three species are uppermost Albian–Upper Cenomanian, Upper

Santonian–Lower Campanian and (?) Upper Turonian–Lower Coniacian, respectively. Unfortunately, there is no record of the relative levels at which the various specimens were collected. The Hidden Lake Beds are approximately 307 m thick (Bibby, 1966) but no attempt has yet been made to subdivide them palaeontologically. It should also be pointed out that at least some of the specimens were collected loose (D.2212.4, 5 and 6; (?) D.3045.2, D.3046.3 and 4) (Table I) and these may well have been transported in glacial moraines. That specimens could have been transported considerable distances in this way is suggested by the occurrence of loose specimens of an Upper Jurassic perisphinctid ammonite (Spath, 1953, pl. 12, fig. 5) and a probable Lower Cretaceous bivalve (? *Aucellina andina* Feruglio; Bibby, 1966, p. 8) in the Cape Obelisk–Hidden Lake area. Spath (1953, p. 3) also recorded two loose ammonite fragments from the area to the south-west of Cape Lachman (Fig. 2).

Five ammonites have so far been collected from the Hidden Lake Beds (Howarth, 1966). *Desmophyllites* sp. (from station D.2212) and (?) *Gaudryceras* sp. (from station D.3042) are undiagnostic but the specimen of *Gaudryceras varagurense* Kossmat from station D.3046 suggests a Senonian age. This species is Lower Coniacian to Lower Santonian in Madagascar (Collignon, 1956) and closely related forms in Japan range from Santonian to Maastrichtian (Howarth, 1966, p. 58). *Tetragonites (Saghalinites)* cf. *cala* (Forbes) from station D.2212 has Upper Senonian affinities but the specimen has apparently been obliquely crushed (Howarth, 1958, p. 10). However, the specimen of *Submortonicerias chicoense* (Trask) (from station D.3057) is well preserved and has been used by Howarth (1966, p. 63–64) to assign a Lower Campanian age to the Hidden Lake Beds.

The occurrence of *Gaudryceras varagurense* at station D.3046 and *Tetragonites* cf. *cala* and *Submortonicerias chicoense* at stations D.2212 and D.3057 adds further confusion to the stratigraphy of these two localities. Bibby (1966, fig. 6) reported extensive moraines in both the Cape Obelisk and Hidden Lake areas, and it can only be assumed that some (or all) of the specimens were loose (see above). Cretaceous fossils have been collected from an extensive terminal moraine at Dundee Island (Crame, 1979; Ramos and others, in press) and overall there would seem to have been considerable scope for the extensive glacial transport of fossils in the James Ross Island area.

The specimens of *I. apicalis* (D.2208.5) and *I. lamarcki lamarcki* (D.2208.7) indicate a Lower–Middle Turonian age for station D.2208 at Cape Longing (Fig. 1). The only other fossil so far identified from this series of localities is a rather poorly preserved ammonite, *Tetragonites* cf. *epigonus* Kossmat (Howarth, 1958, p. 10). It is interesting to note that the type specimen of *T. epigonus* Kossmat, from the Trichinopoly Beds of southern India, is Turonian or Coniacian in age (Howarth, 1958, p. 10). From the occurrence of *I. madagascariensis*, a slightly younger age range of Upper Turonian–Lower Coniacian can be inferred for the succession on Persson Island.

The specimen of *I. cuvieri* (D.416.1) was collected *in situ* from a locality towards the southern end of Lachman Crags (Table I). The age range of this species (Middle Turonian–Lower Santonian) conflicts with that of the associated ammonites which are stated to be upper Lower and Middle Campanian (Howarth, 1966, p. 68). Again, it must be emphasized that there is no available information on the relative levels of the specimens and it would seem that some of the ammonites could have been loose (Spath, 1953, p. 58). It is possible that the Snow Hill Island Series ranges down into the Lower Senonian but further evidence is required to substantiate this point. A revision of the ammonites and dinoflagellates (see Hall, 1977, 1978) from the lower levels of the Snow Hill Island Series would be useful.

In summary, the following conclusions can be drawn:

- i. A suite of fossils from the Hidden Lake Beds has both Cenomanian and Senonian affinities. *Inoceramus* sp. cf. *tenuis* and members of the *I. pictus* group suggest the former, and *Sphenoceramus* cf. *lingua*, *Gaudryceras varagurense* and *Submortonicerias chicoense* the latter. There is a strong possibility that a number of these fossils were loose.

- ii. There is evidence of *in-situ* Turonian and Coniacian strata at Cape Longing and on Persson Island.
- iii. The extensive Snow Hill Island Series, traditionally regarded as Lower and Middle Campanian, may range down into at least the Lower Senonian.
- iv. Characteristic Upper Senonian inoceramid elements are noticeably lacking in the James Ross Island fauna. There is only one sphenoceramid and types such as cataceramids and the subgenera *Endocostea* Whitfield and *Haenleinia* Böhm are absent. One would expect, *a priori*, that this assemblage is essentially pre-Upper Senonian in age.

There is obviously considerable scope for detailed biostratigraphical studies in the James Ross Island area but further field work must be carried out in order to solve some of the outstanding problems outlined above. Only when fossils have been collected from a series of measured sections will it be possible for exact stage and zone boundaries to be established.

TABLE III. GEOGRAPHICAL DISTRIBUTION OF THE INOCERAMID SPECIES

	Europe	Japan	USSR (Pacific coast)	British Columbia	USA (western interior)	East Greenland	Southern India	Western India	Madagascar	South Africa	South America	Australasia	New Caledonia
<i>S. lingua</i>	x				x	x							
<i>I. (I.) madagascariensis</i>	?								x			x	
<i>I. (I.) cuvieri</i>	x	?			x			x					
<i>I. (I.) lamarecki lamarecki</i>	x					x		x					
<i>I. (I.) apicalis</i>	x												
<i>I. (I.) prefragilis</i>		?	?		x				?				
<i>I. (I.) pictus concentricoundulatus</i>	x												
<i>I. (I.) pictus neocaledonicus</i>	x		x						x			?	x
<i>I. (I.) pictus pictus</i>	x					x	?	x	x			?	
<i>I. (I.) tenuis</i>	x		x		x			x			x		
<i>I. (I.) concentricus</i>	x	x	x	x			?	x	x	x	?	x	

x Definite occurrence. ? Tentative occurrence.

Inoceramus concentricus, which occurs on Dundee Island (Fig. 1) (Crame, 1980), is included in the table. Its occurrence in Japan and on the Pacific coast of the USSR is in the form of Cenomanian sub-species.

Palaeobiogeography

One of the striking features of this assemblage is that all but two of the species are known to occur in Europe (Table III). Even the two exceptions, *I. prefragilis* (the probable equivalent of *I. pictus* forma *a*) and *I. madagascariensis*, have very close European relatives and their presence may be concealed only by the complexities of provincial taxonomies. It has perhaps not been generally appreciated in the past that so many inoceramid species have such widespread

distributions. However, Kauffman (1968, p. 204) has estimated that 50–70% of the species from the western interior of the USA have intercontinental or cosmopolitan distributions and an equivalent figure can be proposed for the Western European province. It is likely too that, when Southern Hemisphere faunas become better known, they will show similar high percentages of pandemic forms. Already it would appear that the *Inoceramus* faunas of both Madagascar (Sornay, 1964, 1965, 1968, 1969) and western India (Chiplonkar and Badve, 1976a, b) have strong European affinities.

The close correspondence with European inoceramids is no doubt due in part at least to the fact that the latter are much better known than those of almost any other province, but there still remains the intriguing probability that certain inoceramids were able to migrate directly between the European region and Antarctica. Part of the reason for this widespread distribution is that inoceramids were unusually tolerant forms able to adapt to, and thrive in, a variety of benthic habitats. However, their intercontinental distribution is almost certainly a reflection of the additional factor that their planktonic larvae had exceptional powers of dispersal. A considerable body of evidence has now been assembled to show that many Mesozoic bivalves achieved intercontinental and cosmopolitan distributions by virtue of their long-lived and environmentally adaptive larvae (Kauffman, 1968, 1975; Scheltema, 1977). Carried predominantly in surface currents, these larvae were transported for long distances across the shallow, warm epicontinental seas that predominated in the Cretaceous.

Strong links with European, western Indian and Madagascan faunas (Table III) may perhaps be taken to indicate the existence of a migration route through the eastern Mediterranean and proto-Indian Ocean. Extensive shallow seas, such as would facilitate rapid migration, certainly existed around the shores of the African continent, and throughout the greater part of the Cretaceous there must have been almost continuous shallow marine connections between Europe and the Antarctic Peninsula (data from maps in Kauffman (1973) and Smith and Briden (1977)). A possible objection to this theory is that it implies migration of bivalves from a temperate realm, across the tropical Tethyan Sea and back into a temperate realm. However, it has been argued elsewhere that the broad Cretaceous climatic zones would not have seriously hindered the widespread migration of tolerant bivalves (Kauffman, 1973; Scheltema, 1977), and Kauffman (1973, p. 372) has documented at least 12 other bivalve genera besides *Inoceramus* that were apparently able to cross from one temperate realm into the other.

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