

COMPOSITION AND DISTRIBUTION OF THE INOCERAMID BIVALVE GENUS *ANOPAEA*

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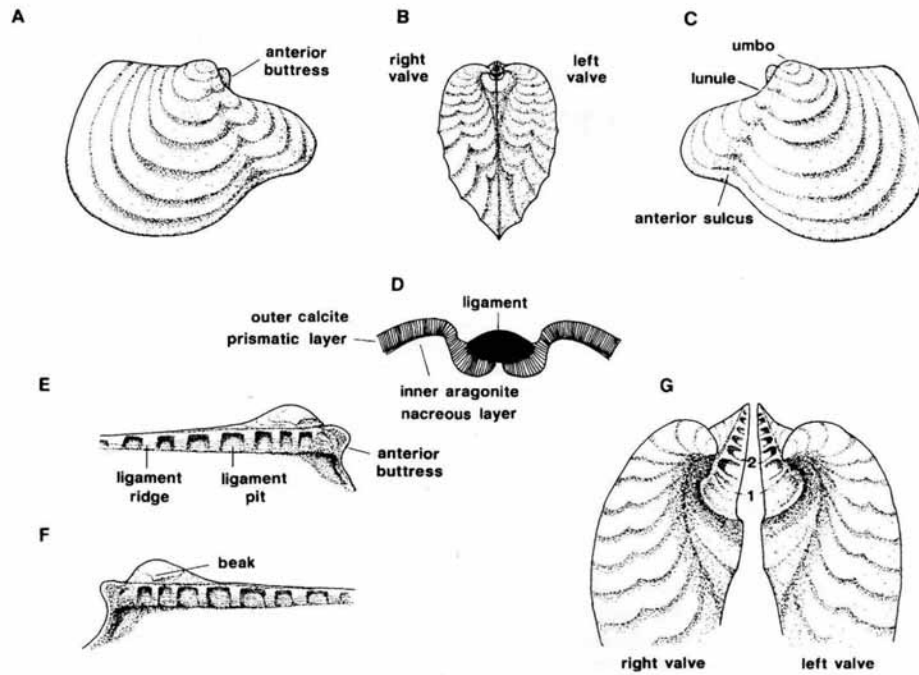
ABSTRACT. *Anopaea* is a distinctive Late Jurassic–Early Cretaceous inoceramid bivalve genus. Traditionally recognized by its elongate-pyriform outline and impressed antero-ventral sulcus, it is now apparent that it also has a distinctive hingeline. In each valve the thickened shell material of the hinge region terminates in a prominent fold, the anterior buttress; this often takes on the appearance of a small anterior 'ear'. Some fifteen taxa are now assigned to the genus and a further seven are probable members. The bulk of these forms fall within the Late Tithonian–Early Albian. *A. callistoensis* sp. nov., from the Late Tithonian–?Early Berriasian of the Antarctic Peninsula, and a probable new species from the Berriasian of the South Shetland Islands, are described. *Inoceramus constrictus*, from the Early Albian of Queensland Australia, can now be referred to the genus. It can be confirmed that, with only a very small number of exceptions, *Anopaea* was restricted to Late Jurassic–Early Cretaceous extra-Tethyan localities. In this sense it may be regarded as a genuine bipolar taxon, although amphitropical is perhaps a more accurate term.

PROBLEMS of generic discrimination remain at the forefront of taxonomic investigations into the widespread late Palaeozoic–Mesozoic bivalve family Inoceramidae Giebel, 1852. This is particularly so for the prolific Cretaceous representatives and there is currently an urgent need to clarify the definitions and status (i.e. taxonomic rank) of a wide variety of available names. One genus that would appear to be relatively stable is *Anopaea* Eichwald, 1861. Although still poorly known at the time of publication of the *Treatise* (Cox 1969), its status has subsequently been confirmed and its distribution extended to a variety of Late Jurassic–Early Cretaceous extra-Tethyan localities (e.g. Pokhialainen 1974; Crame 1981; Kelly 1984; Dhondt 1992). Its unusual form and essentially bipolar distribution have ensured that it is the focus of continued attention.

Nevertheless, despite the distinctive form of this genus (to be discussed in detail below), instances have been recorded of apparent transitions to the ubiquitous *Inoceramus*. These are perhaps most prevalent in the informal '*Inoceramus*' *anglicus* and '*I.* *neocomiensis* groups (e.g. Pokhialainen 1969a, p. 125; Saveliev 1962, pl. 2, fig. 1a; Crame 1985, p. 488). Of equal concern is the fact that some features of the *Anopaea* shell have never been explained satisfactorily. Foremost among these is the 'concave appendix, similar to the ear-like appendix of *Aucella* [= *Buchia*], situated in front of the beaks' (Eichwald 1865, p. 481). A similar 'anterior ear' was noted by Etheridge, Jr (1901, p. 25) on a specimen of *Inoceramus* [= *Anopaea*] *constrictus*. How could an apparently *bona fide* member of the Inoceramidae have a *Buchia*-like appearance? It is the intention of this study to redefine the diagnostic features of *Anopaea* using new material collected recently from the Antarctic Peninsula region and existing collections from Australia. With a firmer understanding of what constitutes membership of the genus, both its stratigraphical and geographical distribution can be reviewed. This in turn may help to constrain the nature and timing of bipolar events associated with the Jurassic–Cretaceous boundary (Crame 1993).

DISTINGUISHING FEATURES OF *ANOPAEA*

Anopaea is a small to medium sized bivalve (typically 50–80 mm in length) with a distinctive elongate-pyriform (i.e. pear-shaped) outline; the posterior is typically high and rounded, and the



TEXT-FIG. 1. Key morphological features of *Anopaea*. A, external view of a right valve; B, anterior view of a whole specimen; C, external view of a left valve; D, idealised cross-section through the hinge and ligament area (N.B. orientation of prisms in prismatic calcite layer is schematic only); E, left valve hinge area; F, right valve hinge area; G, exploded anterior view to show butresses at the anterior terminations of the ligament areas.

anterior narrow and pointed (Text-fig. 1). It is equivalve, or very nearly so, and moderately inflated. In front of the prominent beak in each valve there is a deep cordiform lunule and a variably developed anterior sulcus can be traced from the umbonal region to the antero-ventral margin. Here, the latter feature may form a deep embayment which effectively divides the shell into anterior and posterior 'lobes'. Possession of a multivincular ligament, thin prismatic shell layer and regular commarginal ornament provide a ready link to the Inoceramidae. Unfortunately, details of the musculature remain poorly known; general shell form strongly suggests an endobysate mode of life (Crame 1981, fig. 2).

EXPLANATION OF PLATE I

Figs 1–8. *Anopaea callistoensis* sp. nov., Late Tithonian–Early Berriasian?, Fossil Bluff Group, eastern Alexander Island. 1, KG.3404.268, paratype, internal mould of a right valve with traces of shell material, $\times 1.5$. 2, KG.3404.187b, paratype, internal mould of a left valve, $\times 1.5$. 3, KG.3404.435, paratype, internal mould of a juvenile right valve, $\times 1.5$. 4, KG.4209.14, paratype, internal mould of a right valve, $\times 1.5$. 5, KG.3404.190, paratype, internal mould of a left valve, $\times 1.5$. 6, KG.4209.87, paratype, internal mould of a right valve, $\times 1$. 7, KG.3404.183, holotype, internal mould of a right valve with traces of shell material, $\times 1$. 8, KG.3404.185, paratype, internal mould of a right valve, $\times 1$.

PLATE I



CROME and KELLY, *Anopaea*

To date, the only region of the *Anopaea* shell which has not been described adequately is the hingeline. Apart from the fact that it seems to be characterized by comparatively small rounded ligament pits, virtually nothing is known about it. However, some recently collected specimens from the Antarctic Peninsula region (described formally below as *Anopaea callistoensis* sp. nov. and *A. sp. nov?*) bear reasonably well preserved hingelines and form the basis, together with a revision of the Australian species *Anopaea constricta* (Etheridge, Jr), of a new reconstruction of this critical region of the shell. The sketches presented in Text-figure 1 are based upon a series of camera lucida drawings of specimens of the two new Antarctic species and the revised Australian form.

Perhaps the most striking feature to emerge from study of this new material is that some specimens do indeed show a small antero-dorsal *Buchia*-like ear (e.g. Text-figs 3A-B, D-E, 5A; Pl. 1, fig. 8). It is present in both left and right valves and takes the form of a rounded, buttress-like fold of shell material that is directed strongly inwards (i.e. towards the plane of commissure; Text-fig. 1). There is no evidence that the buttresses were true ears, in the sense that they are associated with byssal notches, or that they articulated with the other valve. Instead, it would appear that these features represent the anterior termination in each valve of a strip (or shelf) of thickened shell material running along the hingeline. Following the terminology of many Russian workers, such a structure should be referred to as the ligamentat (e.g. Pokhialainen 1969b, 1972). On internal moulds this shelf commonly has a shallow, concave cross-profile (Text-figs 1, 3). The net effect of two opposing shelves of thickened shell material would have been to increase the interumbonal distance (Text-fig. 1G). This in turn would have permitted, at least to some extent, the development of more inflated shells; as in endobysate arcids, it may well be that the development of more inflated forms was a strategy to promote greater stability (Savazzi 1987).

It is still unclear whether the material comprising the thickened hingeline is formed consistently from one particular shell layer. Examination of a series of specimens of *A. constricta* (see below) revealed this region to be composed of a thickened prismatic calcite layer (Text-fig. 1D-F; Pl. 2, fig. 6). It would appear that the ligament was mounted directly on this layer, as perhaps it is in most unequivocal members of the Inoceramidae (Crampton 1988). It is also apparent that, as in other true inoceramids, this prismatic calcite layer was in turn superimposed upon a thickened inner aragonitic layer (sheet nacre) which is particularly prominent in the umbonal region (Text-fig. 4A, C). Nevertheless, on one of the two small specimens assigned below to *Anopaea* sp. nov?, it is the inner aragonitic layer, rather than the outer calcitic one, which is considerably thickened in the hinge region (Text-fig. 4A). Although somewhat altered now, this appears to comprise sheet nacre up to 250 μm thick (Text-fig. 4A). Unfortunately, the ligament pits are missing on this specimen, but it cannot be discounted that they were mounted directly upon this aragonitic layer. Resolution of the composition of this important taxonomic feature must await the discovery of well preserved specimens.

Using an amended diagnosis for the genus *Anopaea* (see systematic section below), it has been possible to reassess critically those inoceramids which should be assigned to the taxon. The results of this survey are presented in Table 1, where two main categories are recognized: a group of species which can be assigned with some certainty to the genus, and a group of forms whose status is in some way questionable. Other taxa of less certain affinity are probably best attached with a degree of uncertainty to *Inoceramus*; in particular, the taxonomic position of '*I. deltoides* Crame (1985) and its allies cannot yet be resolved. The two new Antarctic species are described formally in the following systematic section, where the opportunity is also taken of redescribing the Australian Albian form, *A. constricta* (Etheridge, Jr). All the Antarctic material is stored in the collections of the British Antarctic Survey, Cambridge, UK.

TABLE 1. Taxonomic re-appraisal of the genus *Anopaea*. Abbreviations: BAS, British Antarctic Survey, Cambridge; CIRGEO, Centro de Investigaciones en Recursos Geológicos; DVTGU, Dal'nevostochnoye Territorial'noye Geologicheskoye Upravleniye; NHM, Natural History Museum, London; NZGS, New Zealand Geological Survey; SVKNIL, Severo-Vostochnogo Kompleksnogo Nauchno-Issledovatel'skogo Instituta.

Taxon	Type material	Range and occurrence	References and notes
I. Valid taxa			
<i>Anopaea brachowi</i> (Rouillier, in Rouillier and Vossinsky, 1849)	The original of <i>I. lobatus</i> Auerbach and Frears (1846, pl. 7, fig. 1) is held in the Museum of A. P. and M. A. Pavlov, Moscow. It is designated herein lectotype of <i>I. lobatus</i> Auerbach and Frears, 1846 and of <i>I. brachowi</i> Rouillier (1849)	Late Volgian, central Russian Platform; Late Volgian and Ryazanian, eastern England	Kelly (1984)
<i>Anopaea sphenoides</i> Gerasimov (1955)	Holotype: Geological Survey of the Central Areas, Moscow, Gerasimov Collection, No. 1086 (Gerasimov 1955, pl. 20, fig. 2); 3 paratypes (Gerasimov 1955, pl. 20, figs 3-5)	Late Volgian, Russian Platform and eastern England	Kelly (1984)
<i>Anopaea strambergensis</i> (Boehm, 1883)	Holotype: Unnumbered specimen figured by Boehm (1883, pl. 67, figs 1 and 3) is designated herein as the lectotype	Tithonian, Stramberger Schichten, Carpathian Alps	Boehm's (1883, pl. 67, figs 1-3) three specimens almost certainly belong to <i>Anopaea</i> ; however, he noted (Boehm 1883, p. 594) that these specimens are atypical and may have come from elsewhere
<i>Anopaea callistoensis</i> sp. nov.	Holotype: BAS, Cambridge, KG.3404.183; paratypes - as listed in this paper	Late Tithonian-?Early Berriasian, Alexander Island, Antarctica	This paper
<i>Anopaea</i> sp. nov?	(BAS, Cambridge, P.2151.1-3)	Early Berriasian, South Shetland Islands, Antarctica	This paper
<i>Anopaea gerasimovi</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12M/1	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea pivanensis</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/1	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea savrasovi</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/3	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)

TABLE 1. (cont.)

Taxon	Type material	Range and occurrence	References and notes
<i>Anopaea stempeli</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/2	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea</i> sp. indet.	(Single right valve, No. 1/11440)	Berriasian, Mangyshlak, Russian Fed.	Bogdanova (1988)
<i>Anopaea amurensis</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/4	Late Valanginian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea trapezoidalis</i> (Thomson and Willey, 1972)	Holotype: BAS, Cambridge, KG.18.31a; 4 paratypes, KG.18.31b-e	?Hauterivian-Barremian, Alexander Island, Antarctica	Crame and Howlett (1988)
<i>Anopaea</i> sp. nov. aff. <i>mandibula</i> (Mordvilko, 1949)	(BAS, Cambridge, KG.1682.37)	Albian, Alexander Island, Antarctica	Crame (1985)
<i>Anopaea</i> sp. nov.	(CIRGEO, Buenos Aires, PI 1467)	Early Albian, James Ross Island, Antarctica	Medina and Buatois (1992)
<i>Anopaea constricta</i> (Etheridge, Jr., 1892)	Holotype: Queensland Museum, Brisbane, F17/1241	Early Albian, Queensland, Australia	This paper
2. Taxa of less certain affinity			
<i>Anopaea? stoliczkai</i> (Holdhaus, 1913)	Holotype: unnumbered specimen figured by Holdhaus (1913, pl. 98, fig. 10a); as this now appears to be lost, a neotype may need to be designated from topotypes held in NHM, London (BPM 5051, 7198, ?7198, 7199 and LL 24167)	Tithonian, southern Tibe	Lack of a clearly defined antero-ventral sulcus and more rounded nature of some specimens cast some doubts upon affinity to <i>Anopaea</i> ; Crame (1981)
<i>Anopaea? verbeeki</i> Boehm (1904)	Holotype: unnumbered specimen figured by Boehm (1904, pl. 1, fig. 4a, b), by monotypy	Tithonian, Indonesia	Known from only one incomplete specimen (which may now be lost)
<i>Anopaea? windhouweri</i> Boehm (1904)	Holotype: unnumbered specimen figured by Boehm (1904, pl. 1, fig. 3), by monotypy	Tithonian, Indonesia	Known from only one incomplete specimen (which may now be lost)
<i>Anopaea?</i> sp. nov.	(Three specimens figured by Fleming [1958, figs 12, 14 and 15]; from boulders derived from NZGS locs. S62/523, 525 and 526)	Tithonian, New Zealand	<i>Inoceramus</i> n. sp. A, ?aff. <i>everesti</i> Oppel may be an <i>Anopaea</i> ; <i>Anopaea</i> n. sp. is incomplete; Fleming (1958)

TABLE 1. (cont.)

Taxon	Type material	Range and occurrence	References and notes
<i>Anopaea? mandibula</i> (Mordvilko, 1949)	Holotype: not yet traced	Early Albian, Mangyshlak, Russian Fed.	Although there are indications that this species is close to <i>Anopaea</i> (Saveliev 1962) there are also resemblances to <i>Inoceramus coptensis</i> Casey. The latter form may, in turn, be close to <i>Birostrina salomoni</i> (d'Orbigny) (J. S. Crampton, pers. comm. 1993)
<i>Anopaea?</i> <i>mandibuliformis</i> (Pokhialainen, 1969a)	Holotype: SVKNII, Magadan, No. 289	Late Berriasian–Early Valanginian, Myrgal region, Russian Fed.	By no means an obvious <i>Anopaea</i> ; Pokhialainen (1969a, pl. 3, fig. 3)
<i>Anopaea? attenuata</i> Eichwald (1965)	Holotype: unnumbered specimen figured by Eichwald (1865, pl. 21, fig. 4a), by monotypy	'Neocomian', Russian Platform	Possibly a juvenile; some juveniles of <i>A. callistoensis</i> sp. nov. have this narrow, elongated form

SYSTEMATIC PALAEOONTOLOGY

Order PTERIOIDA Newell, 1965
Family INOCERAMIDAE Giebel, 1852
Genus ANOPAEA Eichwald, 1861

Type species. *Inoceramus lobatus* Auerbach and Frears, 1846 *non* Münster in Goldfuss and Münster, 1835; subjective synonym of *I. brachowi* Rouillier, 1849.

Emended diagnosis. Small-medium sized, elongate-pyriform inoceramid with deep cordiform lunule; equivalve, or almost so; antero-ventral sulcus usually well developed; opisthodontic hinge based on thickened shell layer (or ligamentat); on internal moulds this thickened layer is represented in each valve by a concave gutter; ligamentat terminates in an anterior, ear-like buttress.

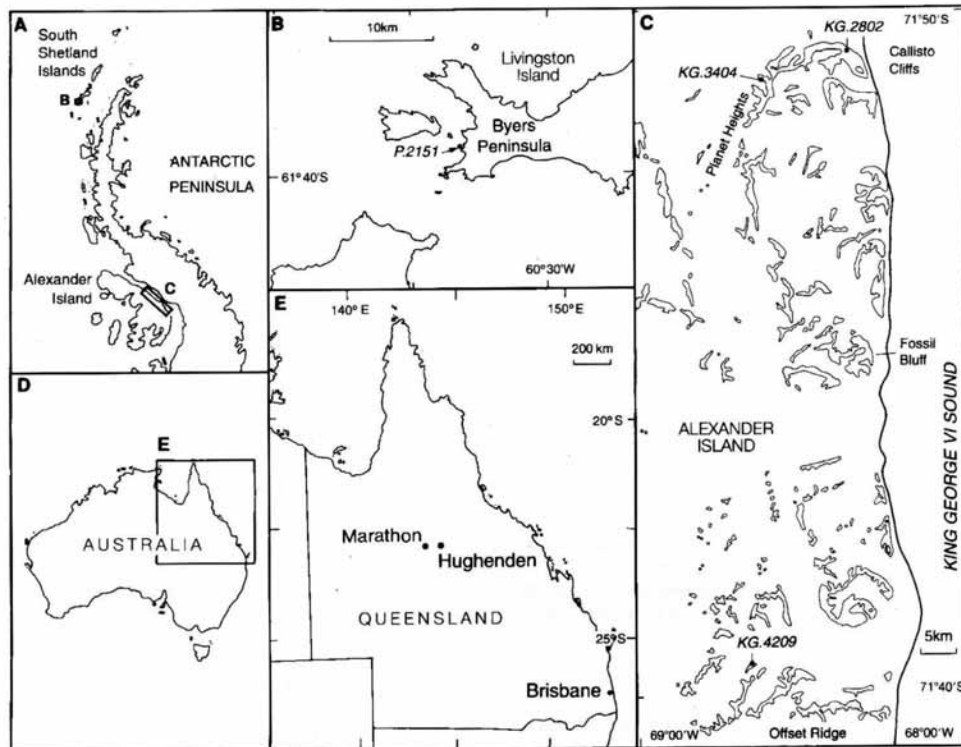
Included species and geographical range. See Table 1.

Age-range. Late Tithonian–Early Albian.

Anopaea callistoensis sp. nov.

Plate 1, figures 1–7; Text-figures 3A–B, D–E, 4B

- v. 1981 *Anopaea* sp. nov.(?) Crame, p. 213, pl. 2, figs e–j [Late Tithonian, Himalia Ridge Formation, Callisto Cliffs, Alexander Island, Antarctica].
v. 1988 *Anopaea* sp. nov.? Crame and Howlett, p. 15, fig. 6a [Late Tithonian, Himalia Ridge Formation, Planet Heights, Alexander Island, Antarctica].



TEXT-FIG. 2. Locality maps for the Antarctic Peninsula region and Queensland, Australia.

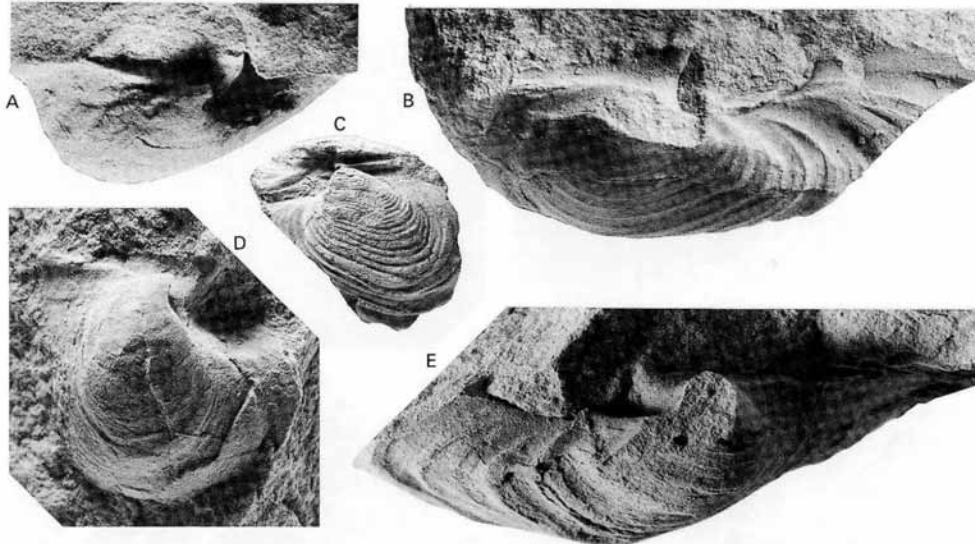
Type material. Holotype: KG.3404.183 (Pl. 1, fig. 7; internal mould RV). Paratypes: KG.2802, 30, 40, 43a, b, 53, 58, KG.3404.162, 167, 178, 183a, b, 184, 185, 186, 187a, 188, 189, 190, 191, 193, 194, 195a, b, 196, 197, 198, 268, 432, 433a, b, 434, 435, KG.4209.12, 13, 14, 19, 38, 39, 40, 42a, 43, 44, 45, 46, 47, 48, 59, 60a, b, 67, 85, 86, 87, 88, 89, 101, 104, 105, 122, 123, 124, 125, 126, 139, 142. All specimens from the Fossil Bluff Group of eastern Alexander Island (Text-fig. 2). At locality KG.2802 (western Callisto Cliffs, $71^{\circ} 01' S$; $68^{\circ} 03' W$), the specimens were obtained from the 91–99 m level in the measured section (Himalia Ridge Formation); at KG.3404 (northern Planet Heights, $71^{\circ} 02' 50'' S$; $68^{\circ} 36' 30'' W$) the specimens were obtained from approx. the 109–118 m level in the measured section (Himalia Ridge Formation); at KG.4209 (central Offset Ridge, $71^{\circ} 38' S$, $68^{\circ} 39' W$) the specimens were obtained from the 132–204 m level in the upper part of the Atoll Nunataks Formation to lower part of the Himalia Ridge Formation.

Occurrence. As for the type material. Associated macrofossils suggest that, at the two more northerly localities (KG.2802 and 3404; Text-fig. 2), the species has a Late Tithonian age (Butterworth *et al.* 1988; Crame and Howlett 1988); at the more southerly locality (KG.4209) it may range into the Early Berriasian. Precise placement of the Jurassic–Cretaceous boundary using macrofossils alone is not yet possible in Antarctica.

Derivation of name. After Callisto Cliffs, eastern Alexander Island.

Diagnosis. Weakly to moderately inflated *Anopaea* with subrectangular posterior and variably developed anterior sulcus; distinctive ornament of fine growth lines superimposed on low, commarginal folds.

Description. This species is equivalve (or very nearly so) and has the typical *Anopaea* outline, as described in the introductory section. Most specimens have the familiar elongate-rectangular form, with the length (L = anterior to posterior extremities) considerably in excess of the height (H = maximum dimension perpendicular to length). A sample of 25 specimens gave the following measurements (in mm): $\times L = 44.72$ ($SD = 21.04$, range = 16.0–92.0); $\times H = 34.0$ ($SD = 11.93$, range = 13.0–62.0); $\times H/L = 0.81$ ($SD = 0.21$, range = 0.52–1.47). A few juveniles have a much more erect profile (e.g. KG.3404.435; Pl. 1, fig. 3), but even in these there are still clear indications of the characteristic high, rounded posterior and narrower, pointed anterior.



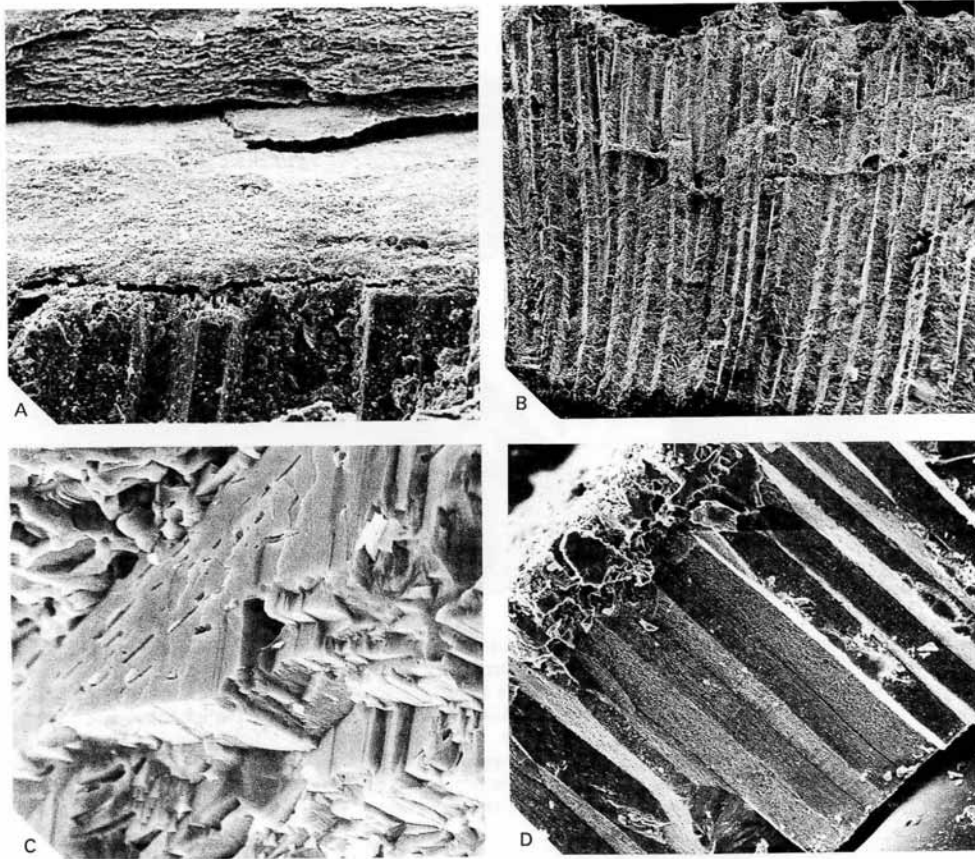
TEXT-FIG. 3. Hinge region and anterior buttress of *Anopaea*. A–B, D–E, *Anopaea callistoensis* sp. nov.; A, KG.3404.193, internal mould of a right valve exhibiting a prominent anterior buttress, $\times 3$; B, KG.3404.191, internal mould of a right valve, showing the concave shelf corresponding to the ligamentat and its abrupt anterior termination in a buttress, $\times 3$; D, KG.3404.434, internal mould of a right valve, showing a concave shelf and anterior buttress overhanging a deep lunule, $\times 3$; E, KG.3404.187b, internal mould of a left valve, showing a prominent anterior buttress, $\times 3$. C, *A. trapezoidalis* (Thomson and Willey), KG.18.31d, internal mould of a bivalved specimen, viewed from the left; the prominent shelf formed by the ligamentat can be seen along the hinge of the right valve, $\times 1$.

The valves are weakly to moderately inflated, with the maximum degree of convexity occurring in the umbonal and central regions; some specimens show a considerable degree of flattening towards the postero-dorsal and ventral margins. The umbones are prominent, prosogyrous and rise slightly above the hingeline. On the antero-dorsal side of the umbo there is a steep descent to the lunule, which is always well developed (Pl. 1, figs 1–8; Text-fig. 3). The antero-ventral sulcus is usually only weakly impressed. It can be traced on the holotype (KG.3404.183; Pl. 1, fig. 7) from the antero-ventral margin to almost the umbo, but on other specimens it is barely more than an indentation on the ventral margin (e.g. Pl. 1, fig. 1).

The best preserved hingelines are straight and a number clearly show the distinctive concave cross-profile (i.e. in dorso-ventral section; Text-fig. 3). The anterior termination of the hingeline in both valves is marked by a small, protruding buttress; on a number of specimens these features have a distinctive 'ear-like' appearance (Pl. 1, fig. 8; Text-fig. 3A–B, D–E). As stated previously, it is believed that the two buttresses simply rested against each other, for neither appears to have crossed the plane of commissure. Nevertheless, on two poorly preserved specimens, which may both have been distorted slightly (KG.3404.196, KG.4209.104), there are

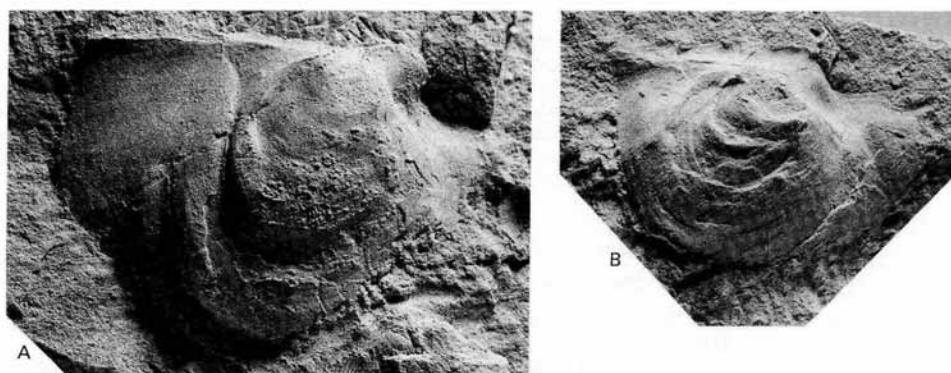
indications that the left buttress rested partly within the right. How widespread a phenomenon this may have been is not known at present.

The ornament on both internal and external moulds comprises a series of prominent commarginal folds with superimposed secondary growth lines (Pl. 1, figs 1-8). The primary folds generally have a wavelength of 2-4 mm, but on the ventral margins of the largest specimens they reach 6-7 mm across; they have acute to well



TEXT-FIG. 4. SEM photomicrographs of the shell structure of *Anopaea*. A, *Anopaea* sp. nov?, P.2151.3, detail from the postero-dorsal region of a right valve from the South Shetland Islands; contact between the inner nacreous (upper two-thirds of photograph) and outer prismatic calcite layer shown, $\times 280$. B, *A. callistoensis* sp. nov., KG.3404.188, outer prismatic calcite shell layer from the postero-dorsal region of a right valve, $\times 90$. C-D, *A. constricta* (Etheridge, Jr, 1901), F.21077. C, inner nacreous shell layer from the umbonal region of a right valve, $\times 2000$; D, F1317, outer prismatic calcite shell layer from the postero-dorsal region of a right valve, $\times 170$. B and D are perpendicular sections, A and C are slightly oblique.

rounded cross-profiles. The secondary growth lines are superimposed across the entire width of the valve but are at their clearest on the primary folds. Here they are regularly and evenly spaced, often on a sub-millimetre scale (Pl. 1, figs 6-7). Traces of a thin, simple prismatic shell layer are found on a number of specimens; in the postero-dorsal region of KG.3404.188 it reaches slightly in excess of 1 mm in thickness (Text-fig. 4B).



TEXT-FIG. 5. *Anopaea* sp. nov?, Berriasian, Byers Group, Livingston Island, South Shetland Islands. A, P.2151.1, internal mould of an incomplete right valve, showing a blunt, rounded anterior buttress overhanging a deep lunule; B, P.2151.2, internal mould of an incomplete right valve. Both $\times 3$.

Remarks. As remarked previously (Crame 1981, p. 213), there is considerable similarity between this taxon and the approximately coeval Russian species, *Anopaea brachowi* (Rouillier) and *A. sphenoidea* (Gerasimov) (Table 1). The resemblance is perhaps strongest with the latter, although *A. callistoensis* sp. nov. can be distinguished by its subrectangular posterior, and less regular commarginal folds. There may also be some overlap with *A. windhouweri* Boehm from the Tithonian of Indonesia (Crame 1981, p. 213). However, this species is based on a single specimen and efforts to trace it have so far proved unsuccessful. The range of Berriasian species described by Kapitza (1978) from the Far East of the Russian Federation (Table 1) is clearly distinct from this new form, as is *A. sp. nov?* from the South Shetland Islands, to be described below.

A specimen of *Anopaea* from Tithonian–Berriasian strata of the Nordenskjöld Formation, northeastern Antarctic Peninsula is not sufficiently well preserved to compare in detail with the Alexander Island material (Kelly and Doyle 1988).

Anopaea sp. nov?

Text-figures 4A, 5A–B

Material. Internal moulds of two small RV (P.2151.1, 2); external mould RV with shell material (P.2151.3, counterpart of P.2151.2). Locality P.2151 is on the northern face of Point Smellie, Byers Peninsula, Livingston Island, South Shetland Islands (62° 38' 55" S; 61° 09' 15" W) (Text-fig. 2). This locality is at approximately the 350 m level in a composite section through the President Beaches Formation of the Byers Group (Crame *et al.* 1993).

Occurrence. As for material. Associated macro- and microfossils indicate a Berriasian age for this locality; dinoflagellate cyst taxa in particular suggest that this can be refined to Early Berriasian (Crame *et al.* 1993).

Description and remarks. These two small right valves are almost certainly juveniles. The ventral regions of both of them are incomplete, but the dimensions can be estimated at 24 mm (L) by 18 mm (H) for P.2151.1, and 19 mm (L) by 13 mm (H) for P.2151.2. Despite their small size, both these forms are quite distinct from the smallest specimens of *A. callistoensis* sp. nov. and would appear to represent the basis of a new taxon. The hinge region of both specimens is well defined, showing the characteristic concave cross-profile (i.e. in a dorso-ventral section) and anterior termination in a distinct buttress (Text-fig. 5). Although there are no indications of an antero-ventral sulcus, it is clear that both specimens have a narrow, pointed anterior region. Traces of regular commarginal ornament characterize P.2151.1, but on P.2151.2 and P.2151.3 the pattern is much more irregular (Text-fig. 5).

Part of the reason for more irregular ornament on the smaller of the two specimens is that it bears traces of a thickened inner shell layer, which is particularly apparent on P.2151.3. This originally aragonitic layer is approximately 250 μm thick, and perhaps more than this in the hinge region where it is especially prominent (see above). It has a distinctive laminated-foliated texture (Text-fig. 4A) but was originally sheet nacre in composition. Although no unequivocal pits can be detected along the hinge of P.2151.3, it would seem possible that this was the layer on which the ligament was mounted. If this observation is correct, it would mean that in some taxa, or possibly the juveniles of some taxa, the ligament was not mounted on the outer prismatic shell layer (see above). The outer prismatic shell layer is far less prominent on specimens P.2152 and P.2151.3.

Anopaea constricta (Etheridge, Jr, 1901)

Plate 2, figs 1–6; Text-figures 4C–D

- v. 1872 *Inoceramus* allied to *I. problematicus* d'Orbigny: Etheridge, p. 344, pl. 22, fig. 4 [refigured here, Pl. 2, fig. 1; QM F1241; anterior missing therefore appears like *Inoceramus*].
- pv. 1878 *Inoceramus carsoni* M'Coy; Etheridge, Jr, p. 109 [Only the reference to *Inoceramus* allied to *I. problematicus* d'Orbigny; see Etheridge, Jr, 1872; i.e. QM F1241].
- vp. 1892 *Inoceramus carsoni* M'Coy; Etheridge, Jr (in Jack and Etheridge, Jr), p. 463 [Only QM F1241].
- v. 1901 *Inoceramus etheridgei* Etheridge; Etheridge, Jr, p. 22 [QM F1241].
- *v. 1901 *Inoceramus constrictus* sp. nov. Etheridge, Jr, p. 24, pl. 2, fig. 7 [GSQ F1317]; pl. 3, fig. 6 [GSQ F1316] [Rolling Downs Formation, Albian, Hughenden and Marathon Stations, Queensland].
- 1928 *Inoceramus constrictus* Etheridge, Jr; Heinz, p. 144 [Rolling Downs Formation, Hughenden and Marathon Stations, Queensland].
- pv. 1966 *Inoceramus sutherlandi* M'Coy; Ludbrook, p. 157 [Only the reference to *Inoceramus* allied to *I. problematicus* d'Orbigny; see Etheridge, Jr, 1872, i.e. QM F1241].
- pv. 1968 *Inoceramus constrictus* Etheridge, Jr; Day, p. 394, pl. 46, figs 1–8 [Ranmoor Member, Early Albian, Queensland].
- 1969 *Inoceramus constrictus* Etheridge, Jr; Day, p. 151 [Tambo fauna, Albian, Queensland].
- 1981 *Inoceramus constrictus* Etheridge, Jr; Crame, p. 216 [Early Albian, Queensland, Australia].
- v. 1990 *Inoceramus* cf. *sutherlandi* M'Coy; Rozefelds *et al.* p. 687 [QM F1241].

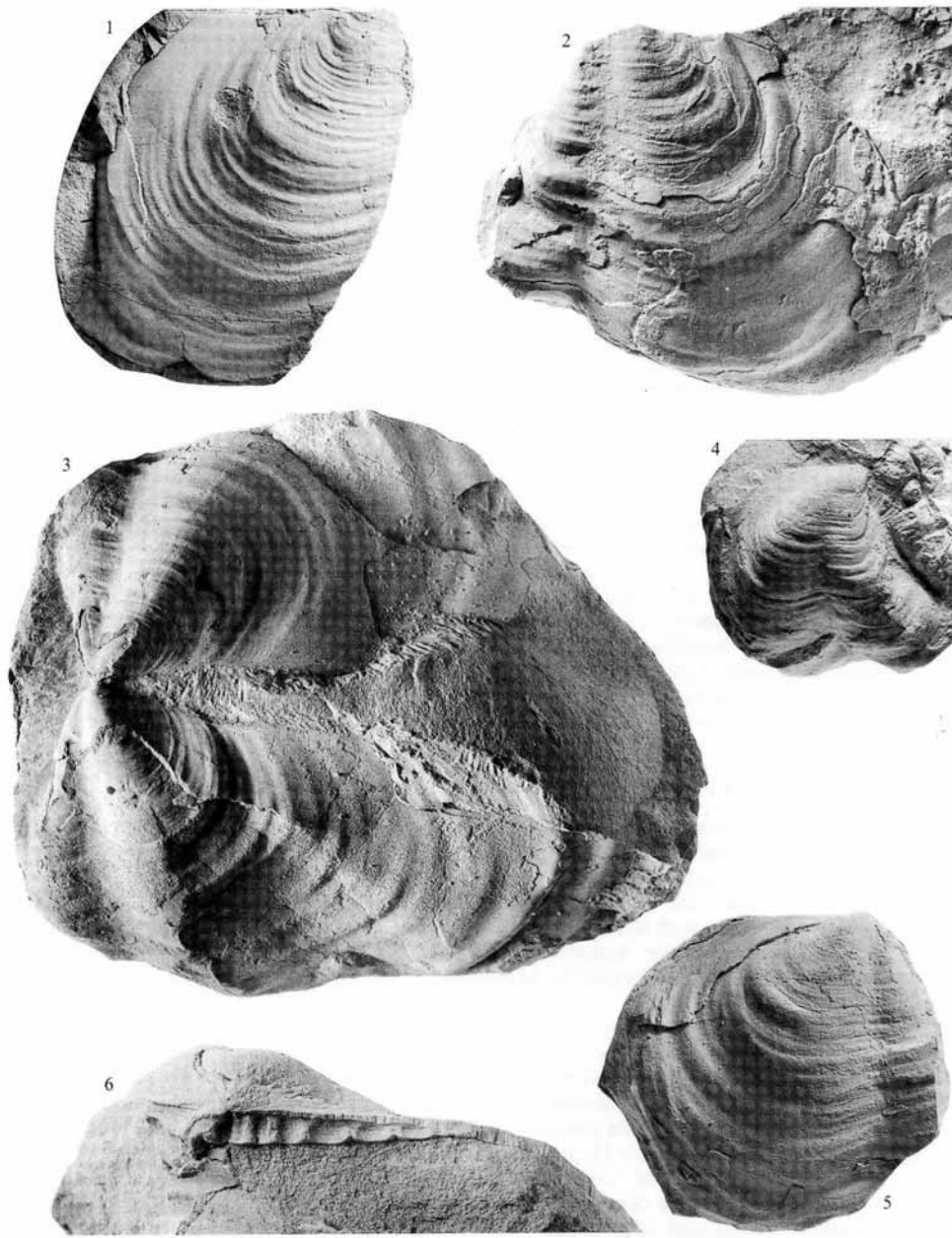
Type and other material. Etheridge, Jr (1901, pl. 2, fig. 7 and pl. 3, fig. 6) figured two syntypes, of which the latter is designated herein as lectotype (= GSQ F1316), and the former as paralectotype (= GSQ F1317). Both specimens are from the Early Albian Ranmoor Member of the Rolling Downs Formation, Queensland; the lectotype is from a locality behind the Hughenden Hotel, Hughenden, Flinders River (Text-fig. 2), and the paralectotype from Marathon Station, Queensland (Day 1968). Other material includes: QM F1241 – originally figured as *Inoceramus* allied to *I. problematicus* d'Orbigny (Etheridge, Jr 1872); QM F16384, F21071, F21072, F21077; as for paralectotype.

Occurrence. As for the type and other material. R. W. Day (pers. comm. 1991) believes that *A. constricta* is associated with *Beudanticeras flindersi* in a level immediately overlying the *Dimitobelus dayi* horizon of the Early Albian of Queensland, Australia.

Diagnosis. Moderately inflated *Anopaea* with well-rounded posterior margin and strongly impressed anterior sulcus.

EXPLANATION OF PLATE 2

Figs. 1–6. *Anopaea constricta* (Etheridge, Jr); Early Albian, Ranmoor Member, Rolling Downs Group, Queensland, Australia. 1, QM F1241, internal mould of a right valve, original of *Inoceramus* allied to *I. problematicus*, d'Orbigny, Etheridge, 1872, p. 344, pl. 22, fig. 4. 2, QM F21072, internal mould of a left valve, with traces of shell material. 3, QM F16384, internal mould of left and right valves in butterfly position. 4, QM F21071, internal mould of a right valve, with traces of shell material. 5–6, GSQ F1317, paralectotype; 5, internal mould of a right valve; 6, the same specimen viewed from the inside and showing detail of the hingeline. Figs 1–5 $\times 1$; Fig. 6 $\times 2$.



CRAME and KELLY, *Anopaea*

Description. The five best preserved specimens (GSQ F1317, QM F16384, F21071, F21072, F21077) show this species to range in length (L) from 50 to 110 mm and height (H) from 39 to 60 mm; mean H/L = 0.734. The same specimens show the typical *Anopaea* form, with perhaps the most striking feature being a deeply impressed antero-ventral sulcus (Pl. 2, figs 2–5); on all specimens this can be traced clearly into the earliest growth stages. As Etheridge, Jr (1901, p. 25) indicated, the maximum degree of inflation occurs immediately posterior to the sulcus, in the central regions of the valve. On the largest specimen (QM F16384), the postero-dorsal region is considerably flattened.

Specimens QM F21071, F21072 and GSQ F1317 display well preserved hingelines. On specimen GSQ F1317, six ligament pits are preserved in a 15 mm strip of hinge immediately posterior to the beak (Pl. 2, fig. 6). Initially, the ligament pits are somewhat narrow and elongate but they broaden posteriorly until the fifth and sixth are comparatively large, oval features measuring 3×1.5 mm. The pits bear fine horizontal striations and are clearly mounted on the prismatic shell layer (Pl. 2, fig. 6). As this ligament surface is inclined at a steep angle to the plane of commissure, it would appear that the ligament must have been partially external (Text-fig. 1D).

On specimen GSQ F1317 (RV), the anterior end of the ligament region terminates in a prominent tongue-like buttress composed of prismatic calcite (Pl. 2, fig. 6). This feature has a length of approximately 4 mm and maximum width (in a dorso-ventral sense and close to its base) of nearly 2 mm; it curves gently towards the left valve but does not appear to have projected across the plane of commissure. The tongue-like appearance is enhanced by a concave upper surface (which is essentially dorsal in aspect) flanked by two sharply defined ridges. There are steep descents on all flanks of the buttress, and on the innermost border there is a small, but distinct, notch. It is unclear at present whether this may represent a point of contact with the left valve buttress.

Traces of a thin (< 1 mm) prismatic shell layer are preserved on the flanks of most specimens and there are also remnants of an altered inner nacreous layer (Text-fig. 4C–D). The ornament pattern on internal moulds is of broad commarginal folds (> 5 mm), with minor folds superimposed (Pl. 2, figs 1–5).

Remarks. Without doubt, this taxon is a *bona fide* member of the genus *Anopaea*. Its general form and style of ornament would seem to set it apart from most other species, although there is perhaps some overlap with *A? mandibula* (Mordvilko) and its allies. *Anopaea* sp. nov. aff. *mandibula* from the Antarctic Peninsula (Table 1) also exhibits a persistent antero-ventral sulcus (Crame 1985, text-fig. 9b), but in general both this form and *A. mandibula sensu stricto* (e.g. Saveliev 1962, pl. 5, figs 1–11) have finer and more closely spaced ornament.

DISTRIBUTION AND PHYLOGENETIC POSITION

Following the taxonomic reappraisal of *Anopaea*, it is possible to review its distribution in both time and space. The first occurrences in the stratigraphical record can now be confirmed as Tithonian (or Volgian in the Boreal realm), and in all probability this can be refined to the Late Tithonian (Table 1). At this time the genus was represented by the very distinctive *A. brachowi* and *A. sphenoides* in localities such as the Russian Platform and eastern England, and the not dissimilar *A. callistoensis* sp. nov. in the Antarctic Peninsula. There are also further probable Tithonian occurrences of *Anopaea* in the Carpathian Mountains, southern Tibet, Indonesia and New Zealand (see below).

New earliest Cretaceous (Berriasian) localities for the genus include the South Shetland Islands, Mangyshlak and the Far East of the Russian Federation (Lower Priamur) (Table 1). In the latter region the genus can also be extended into the succeeding Valanginian stage. Thereafter, however, the Early Cretaceous record of *Anopaea* is somewhat sketchy. *Anopaea trapezoidalis* from the Antarctic Peninsula occurs in strata that are judged to be younger than Valanginian but pre-Aptian in age; nevertheless, no diagnostic Hauterivian or Barremian fossils are yet known from the Fossil Bluff Group of Alexander Island (Crame and Howlett 1988). The next definite datum for the genus is the Albian, with a possible occurrence in Mangyshlak, and definite occurrences in Antarctica (both Alexander Island and James Ross Island) and Queensland, Australia; there is a strong probability that all these occurrences can be referred to the Early Albian.

As has been remarked on previously, it is rather striking how the bulk of these occurrences fall within the Late Jurassic–Early Cretaceous extra-Tethyan regions; *Anopaea* may be said to have had

an essentially bipolar distribution (Crame 1993, and references therein). However, it is necessary to qualify this statement, for a few records may in fact be from Tethyan localities. In particular, *A? strambergensis* occurs in the Stramberger Schichten in association with a Tethyan fauna, although Boehm (1883, p. 594) noted that the two specimens of this species were of somewhat atypical lithology; they may have originated from another bed, or possibly not from Stramberg at all. The Berriasian Mangyshlak record is also from a region of interdigitating Boreal and Tethyan facies, but it is clear that in this instance the specimen of *Anopaea* sp. indet. occurs in association with a *Buchia* bivalve assemblage (Bogdanova 1988). Lower latitude occurrences of the genus in the Southern Hemisphere include *A? stoliczkai*, if this is indeed a true member of the genus, and *A? verbeeki* and *A? windhouweri* from Indonesia. It can be concluded that, with a small number of exceptions, *Anopaea* had an essentially amphitropical distribution from at least the Late Tithonian to the Early Albian. In this sense it would indeed seem to qualify as a bipolar taxon. What perhaps should also be emphasized here is that new evidence is coming to light which suggests that this was not a deep water inoceramid. Although it was once suggested that *Anopaea* may have achieved widespread distribution via a deep water route (Crame 1981, p. 216), this now seems less likely. *Anopaea callistoensis* sp. nov., for example, is known to occur in association with a molluscan assemblage which suggests comparatively shallow-water, nearshore environments (Crame and Howlett 1988). Similar environments are also indicated for the coeval boreal species, *A. brachowi* and *A. sphenoides* (Kelly 1984).

The combination of features, such as the elongate-pyriform outline, antero-ventral sulcus, cordiform lunule and anterior buttress, serves to distinguish *Anopaea* at least at the generic level. It is becoming increasingly apparent that the latest Jurassic–earliest Cretaceous interval was a time of major turnover in global inoceramid faunas, with the replacement of *Retroceramus*-dominated ones by *Inoceramus sensu lato*-dominated ones (e.g. Pokhialanen 1974; Crame 1985). *Anopaea* flourished briefly in the transitional phase between these two great faunas but appears to have become increasingly rare through the latter part of the Early Cretaceous. Indeed, should *A? mandibula* prove not to be a member of the genus, it may be that, by the early Albian, *Anopaea* was restricted to southern high latitudes.

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