LATE JURASSIC INOCERAMID BIVALVES FROM THE ANTARCTIC PENINSULA AND THEIR STRATIGRAPHIC USE

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ABSTRACT. The majority of inoceramid bivalves occurring in Late Jurassic temperate realm assemblages can probably be assigned to the genus *Retroceramus*. Although there are a few transitional forms, *Retroceramus* can generally be distinguished from the better-known genus *Inoceramus* by features of both the external and internal shell morphology. The replacement of *Retroceramus* by *Inoceramus* in the Early Cretaceous may reflect the adoption of an epibyssate mode of life, and probably represents one of a series of endo- to epibyssate life habit transitions that occurred during the evolutionary history of the Inoceramidae.

Four common Late Jurassic species of *Retroceramus* form the basis of an inoceramid zonation that can be used for local correlations within western Antarctica, and regional correlations throughout the Southern Hemisphere. Isolated exposures in the Antarctic Peninsula can be correlated with the Fossil Bluff Formation (Kimmeridgian-Albian) of eastern Alexander Island, and it should eventually be possible to correlate the latter unit with the extensive Jurassic Latady Formation (?Bajocian-Tithonian) of the Lassiter and Orville coasts. Used in conjunction with existing cephalopod biozones, this zonation scheme indicates that the lower levels of the Fossil Bluff Formation correlate with the Lower, Middle, and Upper Spiti Shales of the Himalayas and both the Ohauan and Puaroan stages of the New Zealand Jurassic. Tentative correlations can also be made with areas such as South America, New Caledonia, Indonesia, and Western Australia.

The occurrence of genera such as *Retroceramus*, *Anopaea*, and *Buchia* in western Antarctica does not necessarily indicate the existence of a late Jurassic anti-Boreal faunal realm. Available evidence suggests that the distribution of benthic faunas at this time was probably controlled by a series of distinctive sedimentary facies which extended around much of the southern margins of Gondwana, rather than by pronounced climatic zonation.

THE value of inoceramid bivalves in Cretaceous biostratigraphy has now been firmly established. They have been used extensively to erect local zonations in both the Northern and Southern Hemispheres, and there is a considerable volume of evidence to show that they may also be of prime importance in regional biostratigraphical correlations (e.g. Kauffman 1966, 1977*a*; Pergament 1978; Crame 1981*a*). Inoceramids appear to have been ecologically tolerant bivalves, able to live at various depths and on diverse substrates. They are one of the commonest elements in both temperate and tropical Cretaceous macro-benthic assemblages and are of particular importance in dating and correlating those sedimentary sequences that lack either ammonites or planktonic microfossils. Kauffman (1968, 1970, 1975, 1977*b*, 1978) has shown that, in addition to their wide facies tolerance, inoceramids had a potential mechanism for rapid, widespread dispersal (probably by means of a planktonic larval stage), and very fast evolutionary rates. In the Upper Cretaceous they may well offer a stratigraphical framework for regional correlations superior to that already provided by the ammonites (Kauffman 1975, p. 170).

Jurassic inoceramids, on the other hand, have been much less widely used in biostratigraphy, especially by European and North American geologists. This is no doubt partly a consequence of the existence of a ready alternative group of zone fossils in the ammonites, and partly a consequence of the comparative rarity of inoceramids in the European reference sections. However, viewed on a global scale, Jurassic inoceramids are a widespread group, dominating many macro-benthic assemblages in both the North and South Temperate faunal realms. They are known to be particularly abundant in the Siberia-Alaska region, Japan, and around the southern margins of

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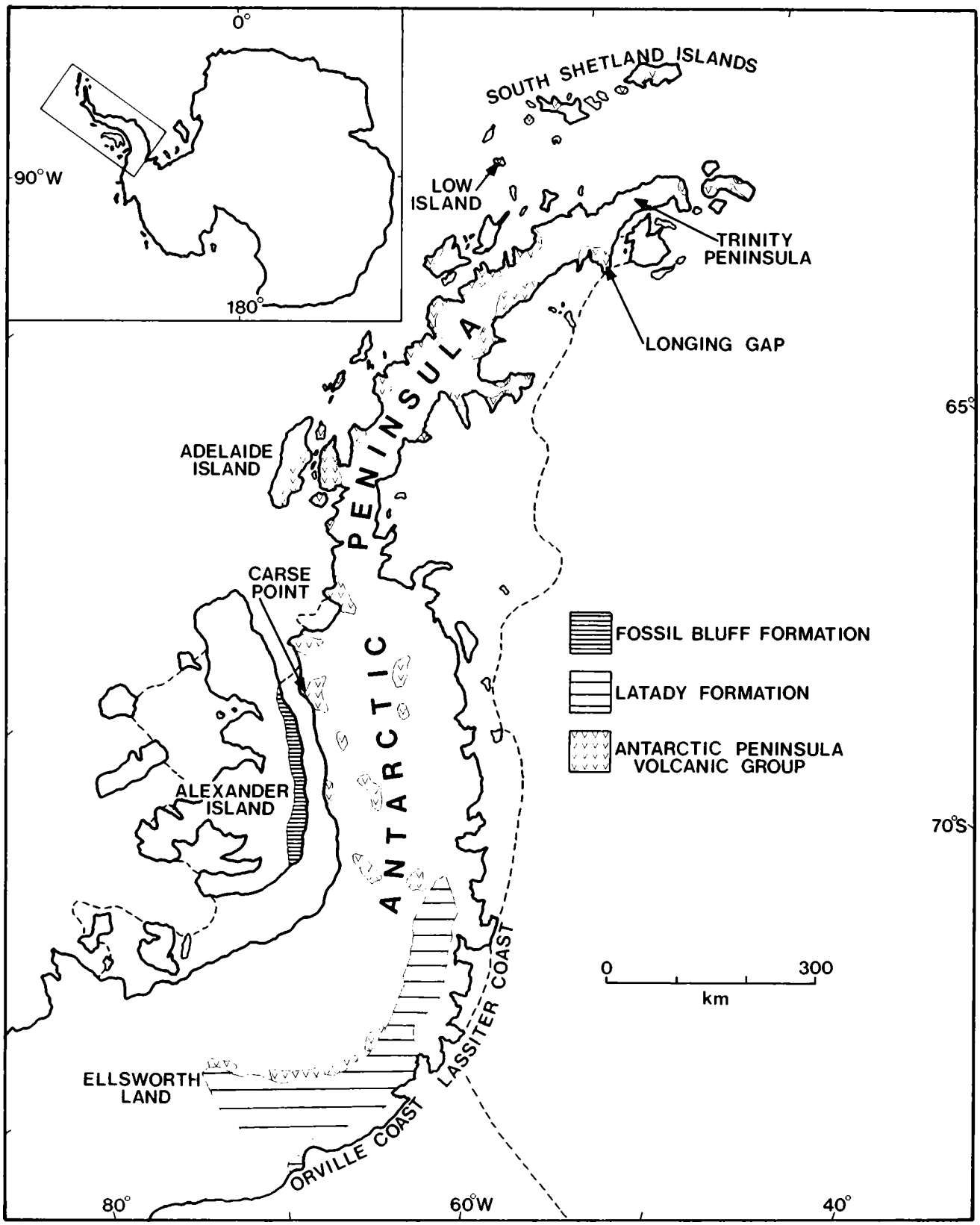


TEXT-FIG. 1. Sketch-geological and locality map of the Antarctic Peninsula. The map shows the principal outcrops of the three sedimentary formations from which Late Jurassic fossils have been obtained. The dashed lines indicate the approximate limits of ice shelves. (N.B. British geologists normally refer to the Lyon Nunataks-Behrendt Mountains region rather than Ellsworth Land.)

the ancient Gondwana supercontinent. Local zonations based on Jurassic inoceramids have been established for Siberia (e.g. Koshelkina 1957, 1959, 1960, 1963; Zakharov and Shurygin 1978), Japan (Hayami 1960, 1961), Himalayas (Spiti) (Stevens 1965), Indonesia (Stevens 1965; Westermann, Sato and Skwarko 1978), New Zealand (Fleming and Kear 1960; Speden 1970; Stevens and Speden 1978), and western Antarctica (Thomson and Willey 1972; Quilty 1977; Taylor, Thomson and Willey 1979). Both Hayami (1960, p. 227) and Koshelkina (1963, p. 136) have emphasized their potential in regional correlations, and Stevens (1965) has used them to help correlate Late Jurassic successions of the Himalayas (Spiti) with those of Indonesia and New Zealand.

It is the intention of this work to show the importance of Jurassic inoceramids in both local and regional biostratigraphy by concentrating on a group of Late Jurassic species from the Antarctic Peninsula (which for the purposes of this study is defined as the region in text-fig. 1 having its southern boundary at approximately latitude 72°S). These specimens were collected from a series of thick clastic and volcanogenic sedimentary rocks which accumulated in basins adjacent to an extensive island arc (e.g. Taylor *et al.* 1979; Thomson, in press). Similar sedimentary rocks of Middle to Late Jurassic age (the Latady Formation) are also known from the Lassiter and Orville coasts (Williams, Schmidt, Plummer and Brown 1972; Rowley 1978; Rowley and Williams, in press; Thomson, Laudon and Boyles 1978) and eastern Ellsworth Land (Laudon, Lackey, Quilty and Otway 1969; Laudon 1972) (text-fig. 1), and these too have yielded invertebrate assemblages rich in inoceramids. In time, it should be possible to establish a detailed succession of Middle to Late Jurassic inoceramid species for western Antarctica which will serve as a valuable reference section for the correlation of Southern Hemisphere Jurassic strata.

Southern Hemisphere Mesozoic rocks have in general received far less attention from biostratigraphers than their Northern Hemisphere counterparts, and there are still many gaps in our knowledge of both the nature and distribution of key index fossils. This is particularly so with the inoceramids, where considerable taxonomic and stratigraphical problems remain to be solved. Species concepts for Mesozoic bivalves are notoriously inconsistent, and those applied to Jurassic inoceramids are certainly no exception. Although most modern workers now base their species on the expected morphological variation within a fossil population (e.g. Hallam 1976, p. 246; Raup and Stanley 1978, p. 113), it is only too apparent that in the past a number of authors have applied a rigid species concept to the study of Southern Hemisphere inoceramids and identified new species on the basis of very limited material. Further problems are encountered when superspecific classifications are attempted. Heinz's (1932) famous paper on the classification of the Cretaceous Inoceramidae, containing no less than thirty-eight new genera, has now been dismissed by most workers as a classic example of 'over-splitting' (e.g. Sornay 1966, p. 26), and, perhaps in reaction to it, nearly all subsequent inoceramid classifications have been extremely conservative in their allocation of genera and subgenera. Indeed, the vast majority of described species have been assigned to a single genus, *Inoceramus*. By way of a contrast, Kauffman (1968) has argued strongly for a broader generic concept within the Inoceramidae, suggesting that features of the internal shell morphology, such as the hinge line, ligament pits, and muscle scars, could be used as additional taxonomic criteria. The very large number of apparently valid species and broad morphological variation shown by the group as a whole tend to support Kauffman's arguments, but, as will become apparent from the discussion below, there are considerable problems in assigning Jurassic species to meaningful generic groups.

Finally, it should be emphasized that the stratigraphical problems encountered in erecting detailed inoceramid biozones will be fully resolved only when many more specimens have been collected from accurately measured sections. As well as facilitating better correlations, precisely localized specimens will also greatly enhance the quality of current evolutionary and palaeobiogeographical studies.

A GENERIC CONCEPT FOR LATE JURASSIC INOCERAMIDS

It has not been generally appreciated that a variety of generic and subgeneric names are available for Jurassic inoceramids: Cox (1969) listed eight genera and six subgenera that are currently valid. That alternative names to *Inoceramus* are not more commonly used is probably a reflection of the considerable degree of confusion that exists today in Jurassic inoceramid taxonomy. It is hard to establish clear-cut working definitions for a number of genera and subgenera, and it is readily apparent that many of the available names have been inconsistently applied since their inception. Establishment of a viable generic concept must remain a major goal of Jurassic inoceramid palaeontology.

One of the first attempts to classify Jurassic inoceramids was that made by Rollier (1914), who thought that the majority of species could probably be referred to the subgenus *Inoceramus* (*Mytiloides*) Brongniart 1822. This was a rather bold and imaginative step to take, for hitherto *Mytiloides* had been regarded as an essentially Cretaceous subgenus, erected primarily to accommodate the distinctive Turonian species, *I. labiatus* (Schlotheim). At first sight, a number of Jurassic species do indeed seem to show the characteristics of this subgenus: the Liassic species, *I. falgeri* Ooster and some forms of *I. fuscus* Quenstedt (Aalenian–Bajocian), for example, have obliquely elongated outlines, fine concentric ornament, and short, oblique postero-dorsal wings. However, it is obvious that many Jurassic species do not possess either the typical outline or ornament pattern of this subgenus, and many of the more obliquely elongated types, such as *I. falgeri*, are still poorly known. At least some of the forms currently ascribed to *I. fuscus* may belong to *Retroceramus* (for a definition of this genus, see below), and it is apparent that until more precise information about the morphology of these Jurassic *Mytiloides*-like forms is available, it will not be possible to make anything other than tentative assignations to this subgenus. In particular, it will be argued below that detailed information on the structure of the hinge region and ligament pits is of crucial importance in generic diagnosis.

Cox (1969), Hayami (1975), and Quilty (1977) have all assigned the common Southern Hemisphere species, *I. galoi* Boehm, to the subgenus *Mytiloides*, but it will be suggested below that this species more likely belongs to the genus *Retroceramus* Koshelkina 1963. Hayami (1975, p. 51) also classified five other Japanese Jurassic species within *Mytiloides*: these are all small, rounded forms with faint to moderately developed concentric ornament (see Hayami 1960, pl. 15, figs. 11–16). *Inoceramus morii* Hayami (1960, pl. 15, figs. 11 and 12) appears to correspond well with the accepted *Mytiloides* morphology, but all the other species are of less certain affinity. Both *I. hashiurensis* Hayami and *I. hamadae* Hayami have erect outlines and appear to be prosogyrous, whilst *I.* (*Mytiloides*) sp. and *I.* aff. *fuscus* are known only from poorly preserved internal and external moulds, respectively. *Inoceramus* sp. aff. *I. galoi* (Hayami 1960, pl. 16, fig. 6) may well be a *Retroceramus*, belonging to the *R. morosus* Koshelkina group (Koshelkina 1969*b*, p. 76). Rollier (1914) established a second subgenus, *Mytiloceramus*, to contain certain Jurassic species which were obviously not obliquely elongated. The type of the subgenus, *I.* (*M.*) *polyplocus* Roemer, is medium-sized, has a distinctive rounded-rectangular outline, and is moderately inflated: there is no clearly delimited postero-dorsal wing. A noticeable additional feature of *I. polyplocus* is a byssal notch on the anterior margin, immediately beneath the umbo (e.g. Cox 1969, fig. C 47, 3). Hayami (1960, p. 299, pl. 15, fig. 7; 1975, p. 50) believed the Japanese species *I. karakuwensis* Hayami to be a *Mytiloceramus*, but Koshelkina (1969*b*, p. 60) reinterpreted it as a *Retroceramus*.

The first attempt at a comprehensive classification of Jurassic inoceramids was that made by Hayami (1960), who established four hypothetical stages in the development of the Inoceramidae. The first stage is marked by the development of the genus *Parainoceramus*, and is based on a morphologically cohesive group of small, simple forms restricted to the Upper Triassic–Middle Jurassic. The second, or differentiation, stage marks an explosive development of inoceramids at the Lower–Middle Jurassic boundary. Two groups (the *polyplocus* and *fuscus* groups) can be distinguished early in the stage, and later on three more appear (the *lucifer*, *retrorsus*, and *galoi* groups). The third, or *neocomiensis*, stage is marked by the appearance of strongly inequivalve

species in the Upper Jurassic–Lower Cretaceous. Inoceramids were held to be rare in this stage, but diversified again in the fourth stage, which covers the rest of the Cretaceous.

The *Parainoceramus* group can be maintained as a distinct genus (Cox 1969, p. N320; Duff 1978, p. 48) and, as already discussed, the *polyplocus* group can be contained within the subgenus (or possibly genus) *Mytiloceramus*. The *fuscus* group, on the other hand, is less easily classified. Hayami (1960) established this group for subrhomboidal to obliquely elongated species in which wings are undeveloped, the postero-dorsal area ill-defined, and the concentric ornament irregularly and weakly developed. He obviously envisaged it to be the main trunk of the Inoceramidae through the Middle and Upper Jurassic (Hayami 1960, fig. 1). Of the twenty or so species ascribed to it, some show strong *Retroceramus* affinities and others may belong within *Mytiloides* (Hayami 1975): among the residue are a number of poorly known European species. It would seem, then, that in all probability this is a hybrid group, containing the representatives of at least two, and probably three, genera. The three groups appearing later in the second stage (the *lucifer*, *retrorsus*, and *galoi* groups) have mytiliform to subrhomboidal outlines, strong concentric ornament, and usually possess a well-defined postero-dorsal wing: as such, they all show strong affinities to *Retroceramus* Koshelkina (see below). Whereas the *Parainoceramus* group is cosmopolitan, the *fuscus* group is essentially European in its distribution. The *lucifer* and *retrorsus* groups arose in the Northern Hemisphere Boreal realm, and the *galoi* group in the so-called anti-Boreal realm of the Southern Hemisphere. The *neocomiensis* group is poorly represented in the Jurassic, for only one strongly inequivalve species, *I. maedae* Hayami (?Callovian), has so far been described.

Until now, the validity of assigning the vast majority of Jurassic inoceramids to the genus *Inoceramus* has not been seriously questioned. Most Jurassic species had, after all, shell forms and ornament patterns similar to the well-known Cretaceous species, and it was logical to assume that they should be allocated to the same genus. Those subdivisions that were suggested (by Rollier (1914) and Hayami (1960)) related primarily to the establishment of subgenera within the genus *Inoceramus*. The first indications that many (perhaps all) Jurassic species might in fact belong to a genus other than *Inoceramus* were given by Koshelkina (1963), who based his remarks on a detailed examination of the prodigious Siberian Jurassic inoceramid faunas. Koshelkina (1963, p. 135) suggested that the following general differences could be established between Jurassic inoceramid species and their Cretaceous counterparts:

(i) All Jurassic species were equivalve, but many Cretaceous species clearly were not.
(ii) The ligament area of Jurassic species was of quite different structure, being characterized by large irregular ligament pits that often fall into two distinct size classes. In Cretaceous inoceramids the ligament pits are typically narrow, elongated, and of uniform size.
(iii) Many Jurassic species have non-terminal beaks.

Koshelkina (1957, p. 29) initially distinguished three groups of *Inoceramus* (the *retrorsus*, *formosulus*, and *vachrameevi* groups), which he used as the basis of the subgenera *Retroceramus*, *Fractoceramus*, and *Costoceramus*, respectively. However, these names were not validated until 1959, when type species were designated and the name *Striatoceramus* substituted for *Costoceramus* (Koshelkina 1959, p. 100). *Retroceramus*, the largest subgenus, is characterized by subrhomboidal to obliquely oval valve outlines and regular, concentric ornament, *Fractoceramus* has a mytiliform outline and irregular ornament, and *Striatoceramus* a triangular outline and distinctive combination of radial and concentric ribs. As it became apparent that the majority of species fell within *Retroceramus*, Koshelkina (1963) subsequently elevated this subgenus to generic status; *Retroceramus*, *Fractoceramus*, and *Striatoceramus* were retained as subgeneric divisions of the new genus. In the same paper, Koshelkina (1963) also proposed that four other genera of Jurassic inoceramids could be distinguished. *Arcticeramus*, based on *I. arcticus* Koshelkina, was established as a new genus to accommodate two markedly inequivalve Upper Jurassic species, and is equivalent in concept to Hayami's (1960) *neocomiensis* group. *Anopaea* Eichwald was retained as a distinct genus as it has such an unusual form (see Crame 1981*b*), and two new genera, *Pseudomytiloides* and *Lenella*, were created to accommodate certain small, mytiliform Lower Jurassic species. It is clear from both this 1963 paper and subsequent work (e.g. Koshelkina 1969*b*), that Koshelkina recognized only these four genera of Jurassic inoceramids. Nearly all the Jurassic species previously regarded as belonging to *Inoceramus* were now taken by him to belong within *Retroceramus*. A small number of species was assigned to the other three genera, and *Inoceramus* was essentially restricted to the Cretaceous. Thus the concept of *Retroceramus*, which was originally developed to facilitate description of a distinctive group of Siberian species, was greatly expanded to cover nearly all Jurassic inoceramids.

Koshelkina (1963, 1969*b*) had obviously carefully compared his material with other faunas, for he used specific names established by other authors and his synonymies contain a number of species from both Northern and Southern Hemisphere faunas, but it was surely an ambitious claim to make that virtually all Jurassic inoceramid species could now be accommodated within the genus *Retroceramus*. There are a number of Jurassic species which seem to depart from the accepted *Retroceramus* morphology, and others which are very poorly known. In particular, it should be emphasized that, unless the hinge region of a specimen is well preserved, it is often extremely difficult to confidently assign it to *Retroceramus*. Even some Siberian Jurassic inoceramids are difficult to classify in this respect (e.g. Zakharov 1966, p. 94).

FORM AND FUNCTION IN *RETROCERAMUS*

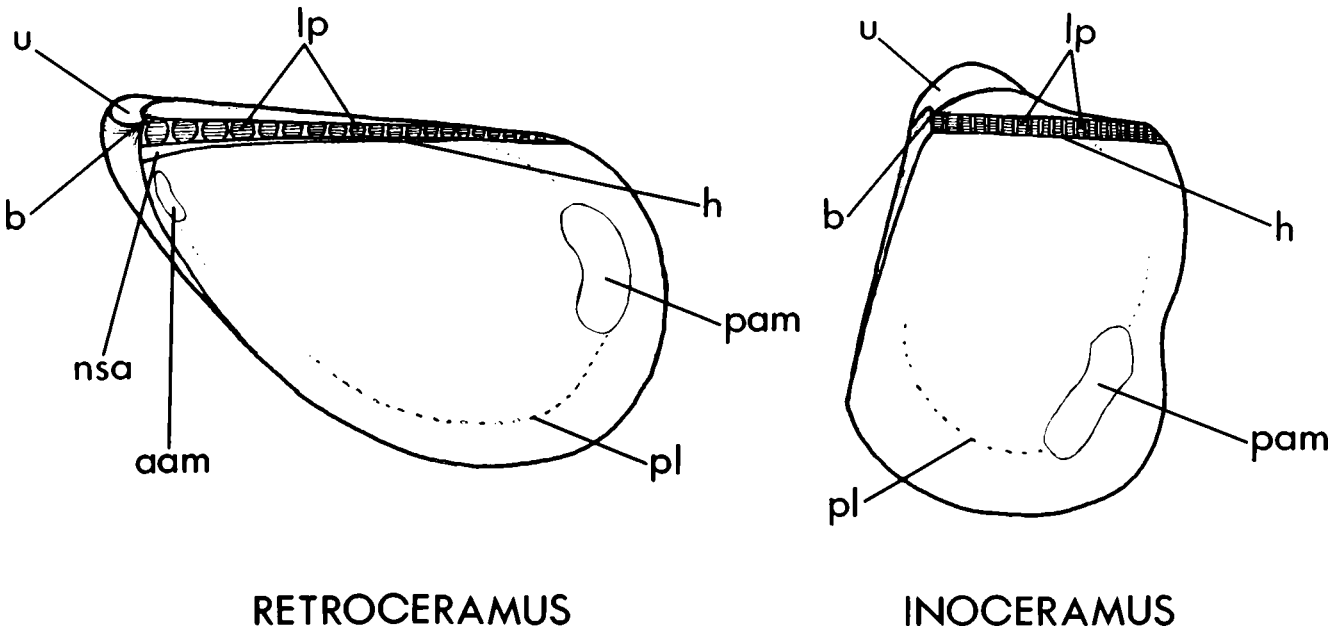
It is important to elucidate the differences between *Retroceramus* and *Inoceramus*, and establish whether these are such as to warrant the division into two separate genera. The salient features of the morphologies of *Retroceramus* and *Inoceramus* are summarized and compared in Table 1, which is largely based on descriptions and diagnoses given by Koshelkina (1963, 1969*a*, *b*) and Cox (1940, 1969).

It might appear that the two genera could be distinguished on the basis of external appearance alone, because *Retroceramus* is typically narrow and obliquely elongated, and bears simple patterns of coarse concentric ornament, while *Inoceramus* is more erect and often has much finer or irregular

TABLE 1. A comparison of the typical morphological features of *Retroceramus* and *Inoceramus*

	Retroceramus	*Inoceramus*
Equality of valves	Equivalve.	Equivalve, subequivalve, and inequivalve.
Outline	Subrhomboidal to obliquely oval; typically narrow in the region of the beak and widening uniformly towards the ventral margin; oblique elongation often results in the anterior margin lying subparallel to the posterior margin; more rounded and oval outlines are known.	Ovate, rhomboidal, or trapeziform; typically higher than long; not or only slightly oblique.
Anterior margin	Prominent anterior margins frequently developed; such margins descend steeply, but not vertically, to the plane of commissure.	Anterior margin may or may not be strongly developed; usually descending vertically to the plane of commissure.
Ornament	Characterized by large, regularly spaced concentric ribs.	Concentric ribs variably developed: more or less regularly spaced.
Wings	A low postero-dorsal wing is characteristic.	A postero-dorsal wing may or may not be present.
Beaks and umbones	Beaks typically sub-terminal; umbones opisthogyrous but occasionally prosogyrous; umbones often strongly projecting above the hingeline.	Beaks may or may not be sub-terminal; umbones generally prosogyrous and may project strongly above the hingeline.
Hingeline	Typically long and straight; edentulous.	Of variable length; edentulous.
Ligament area	Broad; bearing large, irregularly spaced ligament pits with rounded-rectangular or oval outlines; a narrow, smooth area may be present between the row of pits and the hingeline.	Narrow; bearing a uniform series of narrow, trough-like ligament pits; pits separated by thin, upstanding interspaces.
Musculature	Apparently anisomyarian, with a large posterior adductor and small anterior adductor; pallial line represented by a discontinuous series of tiny pits and depressions.	Probably consistently anisomyarian, although the musculature of *Inoceramus* is still very poorly known.
Inferred mode of life	Predominantly endobyssate.	Predominantly epibyssate, but also endobyssate and free-living.

ornament (Table 1). These broad distinctions are indeed useful, but both shell form and ornament are notoriously variable characters. Koshelkina (1963, 1969*a*) has, in fact, suggested that *Retroceramus* can also have more rounded or oval outlines, as well as reduced or irregular patterns of concentric ornament. More reliable differences may be established by recourse to certain features of the hingeline and internal shell morphology. The ligament area in particular is significantly different in the two genera (text-fig. 2). In *Retroceramus*, it is broad and typically bears large, irregularly spaced ligament pits with rounded-rectangular or oval outlines. In some instances, these pits fall into two well-defined size categories, with broad and deep ones alternating with narrower and shallower ones (e.g. Koshelkina 1963, fig. 21; 1969*a*, figs. 3 and 4). An additional feature in some species is a narrow, smooth area between the row of ligament pits and the hingeline (text-fig. 2; Koshelkina 1963, fig. 21a). In contrast, the ligament area in *Inoceramus* is comparatively narrow and the pits are markedly uniform in size and shape: narrow and trough-like in appearance, they are separated by thin upstanding interspaces (e.g. Sornay 1966, fig. 2). In *Inoceramus* the ligament area is consistently set adjacent to the hingeline (text-fig. 2).



TEXT-FIG. 2. Hinge and ligament characteristics of *Retroceramus* and *Inoceramus*. The diagrams are sketch reconstructions of internal views of typical right valves. *Key*: aam, anterior adductor muscle scar; b, beak; h, hinge; lp, ligament pits; nsa, narrow, smooth area; pam, posterior adductor muscle scar; pl, pallial line; u, umbo.

To investigate the possible functional significance of these two types of ligament it is necessary to consider the form of the valves as a whole and their life positions. Inoceramids have, of course, been extinct since the Late Cretaceous, but it is still possible to judge how they may have lived by studying the life habits and attitudes of morphologically similar living species. By such a method the probable modes of life of a number of extinct Palaeozoic bivalve genera have been reconstructed (e.g. Bambach 1971; Stanley 1972; Watkins 1978). It can be deduced from the equivalve nature of *Retroceramus* that the life position was with the sagittal plane in an essentially vertical position (with respect to a horizontal substrate). The predominantly elongated-triangular form suggests a surface-living rather than a burrowing habit, and it can be concluded that *Retroceramus* had an epifaunal life-style similar to that of many Recent Mytilidae, Isognomonidae, Pteriidae, and Carditidae (comparative data from Stanley 1970, 1972). It would also seem safe to conclude (from

analogies with members of the above families) that a byssus was employed to maintain stability. The typical *Retroceramus* form, with the very anterior beaks, long opisthodetic ligament, and reduced anterior and enlarged posterior regions is, in fact, close to the classic heteromyarian form of the Mytilidae. Many common *Retroceramus* species resemble Recent mussels (see, e.g., Koshelkina 1963, 1969*a*, *b*) and it can be concluded that they had similar modes of life. Yonge (1953, 1962, 1976; also Yonge and Campbell 1968) has argued strongly that the heteromyarian condition arose as a functional response to crowded life conditions in epifaunal, byssally attached bivalves. He believes that after initial byssal attachment it was possible for bivalves to evolve by developing either their anterior or posterior regions. The former option would have offered no obvious adaptive advantages but the latter facilitated expansion of the region in which water currents were exchanged with the exterior: siphonal openings could be enlarged and significantly elevated above the crowded sea floor. The simultaneous formation of a narrow, pointed anterior also facilitated closer packing (especially by the formation of radiating clumps) and the valve was effectively streamlined to withstand strong water movements. Yonge and Campbell (1968, p. 38) emphasized that another important consequence of the evolution of the heteromyarian form was the hypertrophy of the byssal retractor muscles and their relative displacement to a position almost directly above the byssus. Stanley (1970, 1972) further stressed the importance of this structural modification, for a much stronger pull could now be exerted on the byssus and the shell very firmly clamped to the substrate. Indeed, in view of the demonstrated need of nearly all bivalves to maintain a stable position, this may be the prime reason for the evolution of a greatly expanded posterior region in so many types of epifaunal bivalve (Stanley 1970, 1972). Besides the Mytilacea, the heteromyarian form is well developed in the Dreissenacea, Carditacea, and Limacea (Yonge and Campbell 1968; Stanley 1972; Yonge 1976).

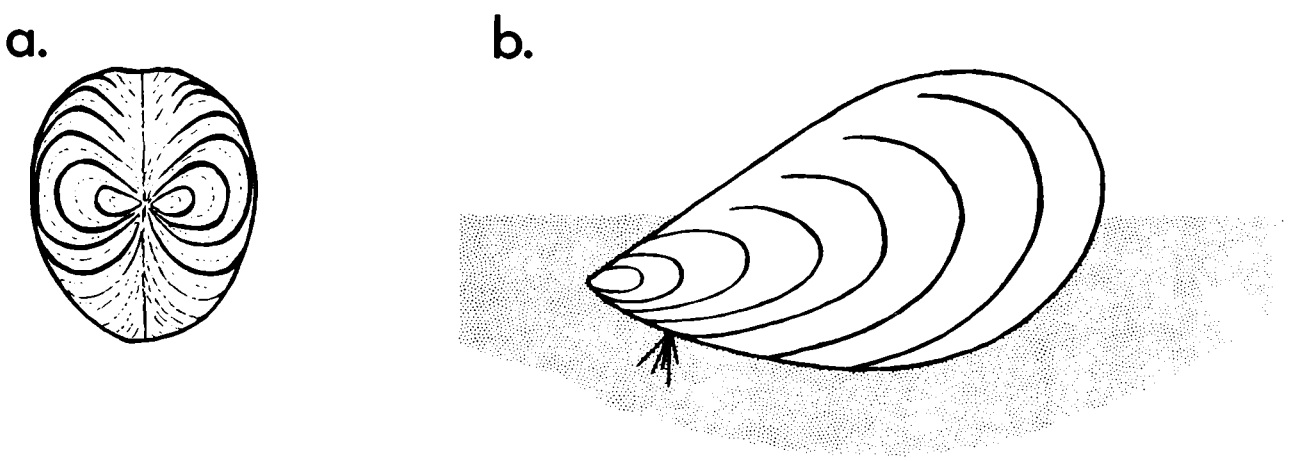
In recent years it has become increasingly apparent that many mytilid species, although byssally attached, actually live partially (or even wholly) buried within the sediment (e.g. Raup and Stanley 1978, p. 192). These forms have been termed endobyssate and can be morphologically distinguished from the true surface livers, or epibyssate species. By comparing Recent species of *Modiolus* (endobyssate) and *Mytilus* (epibyssate), Stanley (1970, 1972) has established a set of criteria by which such a distinction can be made. Endobyssate species typically have rounded-cylindrical outlines and pronounced anterior regions that are often drawn out into distinct lobes. The posterior byssal retractor muscles are situated above but well behind the byssus and the resultant force exerted by both these and the anterior retractors exerts a pull approximately parallel to the long axis of the shell: this effectively draws the shell down into the substratum. Epibyssate species, on the other hand, have more sharply triangular outlines and much reduced anterior regions. The posterior byssal retractors are inserted almost dorsal to the byssus and the resultant force exerted by these and the anterior retractors produces the strong clamping action described above. In cross-section, endobyssate species have rounded to wedge-shaped ventral margins and a maximum width at a point approximately midway between the dorsal and ventral margins. Epibyssate species have much flatter ventral surfaces and the maximum width lies close to the ventral margin (Stanley 1970, fig. 8; 1972, text-fig. 6).

Examination of some of the common *Retroceramus* species from Siberia suggests that they were very probably endobyssate. Equivalve, and with a rounded-elongate outline and evenly inflated cross-section, they would have achieved maximum stability by being at least partially buried within the substrate (text-fig. 3). Unfortunately, there is, as yet, very little evidence of the exact nature and position of the byssal opening in *Retroceramus*, but it would most likely have been a narrow slit situated in an antero-ventral position (by analogy with recent endobyssate species). *Retroceramus* probably lived with the antero-posterior shell axis inclined at an angle of anything up to 45° to the sediment surface, in a manner similar to that adopted by Recent species of *Modiolus* (text-fig. 3; Stanley 1970, fig. 7; 1972, text-fig. 3; Roberts 1975, p. 32). There are, however, some *Retroceramus* species which depart somewhat in outline and general appearance from the typical morphology (see Koshelkina 1969*a*, fig. 1). Some members of the subgenus *Fractoceramus*, such as *R.* (*F.*) *lucifer* (Eichwald) (e.g. Imlay 1955, pl. 8, fig. 7) have more angular, mytiloid outlines

and could well have been epibyssate, as indeed could less obviously elongated species such as *R.* (*R.*) *polaris* (Koshelkina) (e.g. Koshelkina 1962, pl. 9, fig. 5) or *R.* (*R.*) *eximius* (Eichwald) (e.g. Eichwald 1871, pl. 18, fig. 1). Certain types with wide, flat anterior margins could also be interpreted as epibyssate, but it is apparent in all the specimens examined to date that although these prominent anterior margins drop steeply to the plane of commissure, they are not actually perpendicular to it (see Table 1). Cross-sections of whole specimens show these anterior margins to form distinct V-shaped keels rather than flat platforms (e.g. see later, text-fig. 7*a* and Pl. 57, fig. 2), and in order to maintain maximum stability these must have been at least partially buried within the substrate.

It should be possible to verify the life-style of *Retroceramus* when more is known about its musculature. In comparison with epibyssate species, endobyssate mytilids have larger anterior adductor muscles (to cope with the correspondingly larger anterior region of the shell) but somewhat smaller byssal retractors which are inserted well behind (and above) the byssal stalk (Stanley 1970, 1972). *Retroceramus* appears to have been consistently anisomyarian, with a larger postero-dorsal adductor muscle and smaller (but nevertheless still plainly visible) anterior adductor (text-fig. 2) (Koshelkina 1963, fig. 20*b*; 1969*a*, fig. 5). The musculature is probably closer to that of *Modiolus* than *Mytilus*, but so far no clear traces of the pedal-byssal muscle system have been detected.

Southern Hemisphere *Retroceramus* display morphologies essentially similar to the prodigious Siberian forms and it can be concluded that the genus as a whole was predominantly endobyssate. Some species may well have been only partially endobyssate and a few entirely epibyssate (see also descriptions and discussion, below), but on the whole the principal life habit would seem to have been within, rather than on top of, the substrate. This contrasts markedly with the inferred life habits of *Inoceramus*, which were essentially epibyssate. This genus probably had its origins well within the Jurassic but did not become widespread until the Cretaceous. Inequivalve species are particularly common in the Early Cretaceous, and it is clear that these must have lived on top of the substrate with the sagittal plane either inclined or horizontal. Species with straight, shelf-like anteriors (where the anterior valve margins do drop perpendicularly to the plane of commissure) are also prominent, and later on in the Cretaceous there are a number of large, disc-like and heavy-shelled forms that rested on the sea floor without any obvious means of attachment (data from Woods 1912; Sornay 1966; Kauffman 1968). Some Cretaceous species, and in particular a number of elongated forms in the Late Cretaceous, were probably endobyssate (see, e.g., Stanley 1972, text-fig. 23), but these are thought to be types that secondarily reverted back to a semi-infaunal mode of life. In any event, available evidence indicates that a fundamental transition occurred in inoceramid life-styles at approximately the Jurassic–Cretaceous boundary. Here, predominantly



TEXT-FIG. 3. The presumed mode of life of *Retroceramus*. *a*, anterior view of a typical *Retroceramus* showing the well-rounded ventral margin. *b*, sketch reconstruction of the same specimen partially buried within soft sediment and anchored by an antero-ventral byssus.

equivalve, endobyssate species of *Retroceramus* were replaced by a mixture of equivalve, subequivalve, and inequivalve epibyssate species of *Inoceramus*. Internal changes must have accompanied these pronounced changes in external shell morphology, and it would appear that the most important of these was in the structure of the ligament area. Whereas *Retroceramus* is characterized by large, rounded, somewhat irregular ligament pits, *Inoceramus* typically has a more uniform series of narrow, elongated pits. Indeed, it may be that the evolution of the *Inoceramus* grade of ligament permitted full exploitation of epibyssate habits for the first time. Perhaps shallower water (even intertidal) environments could now be colonized and the potential ecological range of the family considerably expanded. Other internal changes (such as in the musculature) undoubtedly occurred at this time too, but these have yet to be elucidated.

SOUTHERN HEMISPHERE JURASSIC INOCERAMIDS

Taking all the above points into consideration, it can be concluded that there probably are good grounds for separating *Retroceramus* from *Inoceramus* at the generic level: their respective hinge and ligament areas are fundamentally different in structure. Of course, it must be emphasized that our knowledge of the internal morphology of all inoceramids is limited, and in particular there is still very little detailed information available for Jurassic species as a whole. Nevertheless, some corroborative evidence on the structure of the *Retroceramus* ligament area will be presented below from Southern Hemisphere species. Koshelkina's (1963) three subgenera (*Retroceramus*, *Fractoceramus*, and *Striatoceramus*) can still be retained as valid subdivisions of the genus *Retroceramus*.

However, whether all the Jurassic species previously regarded as belonging to *Inoceramus* can now be directly transferred to *Retroceramus* (*sensu* Koshelkina 1963, 1969*b*) is uncertain. It has already been argued that at least a small number of species probably belong to *Mytiloides* Brongniart and *Mytiloceramus* Rollier respectively, and these have traditionally been regarded as subgenera of *Inoceramus* (see Cox 1969, p. N317). Nevertheless, casual observations of a number of specimens suggest that both these subgenera were probably functionally endobyssate and species such as *I.* (*Mytiloceramus*) *polyplocus* (Aalenian–Bajocian) and *I.* (*Mytiloides*) *fuscus* (Aalenian–?Bajocian) may yet be shown to have greater affinities with *Retroceramus*. It should be re-emphasized, though, that the hinge region of these and nearly all other European Middle Jurassic inoceramids is poorly known. Some Late Jurassic European species, such as *I. nitescens* Arkell (Oxfordian), *I. inoceramoides* (Hudleston) (Oxfordian) (see Arkell 1933, pl. 28, figs. 1–3), and *I. expansus* Blake (Kimmeridgian) (see Blake 1875, pl. 12, fig. 7), at first sight seem to show greater allegiance to *Inoceramus* than *Retroceramus*, but again there is very little precise information available on their internal shell morphologies. The view taken here is that during the Middle and Upper Jurassic there were probably two distinct inoceramid stocks, represented by the genera *Retroceramus* and *Inoceramus*, respectively. The former was more abundant, especially in temperate realms, and it was not in fact until the Early Cretaceous that *Retroceramus* was superseded by *Inoceramus*. *Anopaea* Eichwald is another valid Late Jurassic genus (Crame 1981*b*), but *Arcticeramus* Koshelkina has a somewhat doubtful status. The hinge region of *Arcticeramus* has never been adequately described (Zakharov 1966, p. 94), and it may be that the species assigned to the genus (*A. arcticus* Koshelkina, *A. eichwaldi* Koshelkina, and *A. maedae* (Hayami)) are no more than early inequivalve representatives of the genus *Inoceramus*.

Two very distinctive groups of inoceramids, based on *I. haasti* Hochstetter 1863 and *I. galoi* Boehm 1907, respectively, have traditionally been recognized in Southern Hemisphere Late Jurassic faunas. *Inoceramus haasti* is medium to large in size, sub-erect to obliquely elongated, and shows a characteristic regular expansion of the valves in a ventral direction. However, its most distinctive feature is its concentric ornament, which consists of large, simple, regularly spaced ribs separated by wide and deep interspaces (text-fig. 4*b*). Originally described from New Zealand (Hochstetter 1863), *I. haasti* has subsequently been definitely identified from Indonesia (Wandel 1936) and Antarctica (Thomson and Willey 1972), and tentatively identified from Timor (Krumbeck 1923) and New Guinea (Skwarko 1967). *Inoceramus galoi*, an Indonesian species, is also medium to large in size and obliquely elongated, but it has a narrower form than *I. haasti* (text-fig. 4*a*). It, too, has

TEXT-FIG. 4. *Retroceramus* (*Retroceramus*) *galoi* (Boehm) and *R.* (*R.*) *haasti* (Hochstetter). *a* (left), internal mould of a left valve of *R. galoi* from a locality along the Whakapirau Road, south side of Kawhia Harbour, S.W. Auckland, New Zealand (M. R. A. Thomson collection, Cambridge). *b* (right), internal mould of a left valve of *R. haasti* (BMNH L.48032) from Kohai Point, Kawhia Harbour, New Zealand (specimen illustrated by Trechmann 1923, pl. 15, fig. 3). Both specimens × 1.

prominent concentric ribs but these are more rounded in cross-section and set closer together; as a rule, the width of the interspaces is approximately equal to that of the ribs (text-fig. 4*a*). This species has also been recognized in New Zealand (e.g. Trechmann 1923; Marwick 1953) and Antarctica (Quilty 1977), and tentative occurrences have been recorded from Japan (Hayami 1960), New Guinea (Glaessner 1945), New Caledonia (Avias 1953; Freneix, Grant-Mackie and Lozes 1974), and South America (Stehn 1924; Giehm 1960; Harrington 1961). Although believed to be Oxfordian in age in Indonesia by Wandel (1936), both these species have been consistently dated as Kimmeridgian in New Zealand (*I. galoi* being Heterian or Lower Kimmeridgian and *I. haasti* Ohauan or Middle Kimmeridgian) (e.g. Speden 1970; Stevens and Speden 1978). In any event, *galoi* seems to occur stratigraphically beneath *haasti* in both areas, and many workers have taken the two species to be end members of a morphological series. This belief was strengthened by the occurrence in New Zealand of transitional forms that showed an ornament pattern intermediate between that of *galoi* and *haasti*. These specimens were identified by J. B. Waterhouse (*in* Fleming and Kear 1960, p. 43) as *I.* cf. *subhaasti* Wandel, and the idea quickly became established that the latter species was a morphological intermediate between the two distinctive end members. The concept of a *galoi-subhaasti-haasti* evolutionary lineage has been widely promulgated (Fleming 1958; Fleming and Kear 1960; Stevens 1968; Speden 1970; Spörli and Grant-Mackie 1976; Glaessner 1945; Freneix *et al.* 1974).

Although members of the *galoi-subhaasti-haasti* group of species have always been regarded as belonging to the genus *Inoceramus*, there is considerable evidence to suggest that they should now be transferred to *Retroceramus*. In particular, *I. galoi* appears to show many of the typical *Retroceramus* features outlined above. In addition to its narrow, obliquely elongated form and strong concentric ornament, it clearly has a long, straight hinge and a smooth anterior margin that drops steeply to the plane of commissure (text-fig. 4*a*; Trechmann 1923, pl. 15, figs. 1 and 2;

Wandel 1936, fig. 2; Marwick 1953, pl. 12, fig. 2; Speden 1970, figs. 38 and 39; Quilty 1977, figs. 23 and 24). The hinge region of the type specimen is incomplete (Boehm 1907, pl. 10, fig. 1), but it would seem from an examination of some of the prolific New Zealand material (from south-west Auckland) that adult specimens typically have a low postero-dorsal wing (e.g. text-fig. 4*a*; see also Trechmann 1923, pl. 15, fig. 1). Most characteristic, however, is the presence of large ligament pits that can be grouped into two distinct size classes (Wandel 1936, p. 466; Boehm 1907, pl. 9, fig. 10). Indeed, in almost all respects, *I. galoi* is very close to *I. retrorsus* Keyserling, the type species of the genus *Retroceramus* (Boehm 1907, p. 69; Kruizinga 1926, p. 19; cf., e.g., Lahusen 1886, pl. 1, fig. 1, Koshelkina 1963, pl. 6, fig. 2a, and text-fig. 4*a*).

The description and illustrations of *I. haasti* given by Wandel (1936, figs. 4, 5*a* and *b*; pl. 19, figs. 1*a*–*c*; pl. 20, figs. 1 and 2) indicate that this species, too, has strong affinities with *Retroceramus*. Obliquely elongated and exhibiting prominent concentric ornament, it also has valves with a low postero-dorsal wing and a well-demarcated anterior margin. The ligament pits appear to be of more uniform size than those of *galoi*, but are separated by broad interspaces. The ligament region as a whole seems to be considerably thickened (Wandel 1936, p. 475). *Inoceramus haasti* has been directly compared with both *I. retrorsus* var. *tongusensis* Lahusen (1886, pl. 1, fig. 2; Kruizinga 1926, p. 19) and the North American species, *R. ferniensis* (Warren) (Wandel 1936, p. 467). *Inoceramus subhaasti* Wandel is a smaller, more variable species, but again shows good *Retroceramus* features. The obliquely elongated to subquadrate outline and prominent postero-dorsal wing are particularly reminiscent of some of the smaller Siberian *Retroceramus* species. Wandel (1936, p. 472) believed his *I. subhaasti* var. *denseplicata* to be very close to *I. retrorsus* Keyserling.

A note of caution should perhaps be introduced here, for it is obvious that some confusion exists as to the precise identity of each of these three species. In the past there has been a tendency to allocate Southern Hemisphere Late Jurassic species to *galoi* if the concentric ribs are set close together, *haasti* if they are set far apart, and *subhaasti* if they are intermediate in density: other diagnostic criteria have often been largely ignored. Specimens from both Japan and the Philippines have been assigned to the *I. galoi* group by Hayami (1960, p. 307, pl. 16, fig. 6; 1968, p. 174, pl. 21, figs. 1–3), but these differ in several important respects from the well-known Indonesian and New Zealand material. Similar departures from the accepted *galoi* morphology are shown by at least some of the South American specimens currently assigned to the species (e.g. Stehn 1924, pl. 5, figs. 4 and 5). Further pronounced differences can be found between illustrated specimens of *I. haasti* from south-west Auckland, New Zealand. Zittel's (1864, pl. 8, figs. 5*a* and *b*) figures show the species to be erect, prosogyrous, and to have bilaterally symmetrical ornament: Trechmann's (1923, pl. 15, fig. 3; text-fig. 4*b*) specimen is clearly obliquely elongated, but Marwick's (1953, pl. 12, fig. 1) hypotype is again sub-erect and has symmetrical ornament. Clearly, the prime criterion for the identification of *haasti* in New Zealand has been the nature of the ornament, and little consideration has been given to the overall form of the valves. Similarly, a specimen assigned to *I.* cf. *subhaasti* from New Zealand (NZGS 9932, text-fig. 7*a*; here identified as *Retroceramus* (*Retroceramus*) sp. nov. 2—see below) has an intermediate rib density, but shows a number of marked differences in valve form from Wandel's (1936) type material. These specific distinctions have important taxonomic, biogeographic, and evolutionary implications, and will be discussed in more detail in the systematic section below.

Some of the poorly preserved medium to large, coarsely ribbed inoceramids from Indonesia, Himalayas (Spiti), and New Caledonia can also be tentatively referred to *Retroceramus*. Boehm's (1907) Indonesian species, *I. sularum* and *I. taliabuticus*, may perhaps belong within the *I. haasti* group (Kruizinga 1926; Wandel 1936) or, alternatively, be distinct species of *Retroceramus* in their own right (e.g. Koshelkina 1969*b*, p. 80 refers to *R. sularum* (Boehm)). It must be emphasized, however, that both these species are based on single, poorly preserved specimens. *Inoceramus sularum* may also be present in the Spiti Shales, but the specimen described by Holdhaus (1913, p. 421) is both worn and incomplete. *Inoceramus hookeri* Salter from the Spiti Shales has a rounded-rectangular outline, prominent concentric ornament, and a low, impressed postero-dorsal wing (Salter and Blanford 1865, pl. 23, fig. 1). Traces of broad ligament pits suggest greater affinities with *Retroceramus* than *Inoceramus*, but the species is known only from a single incomplete specimen. *Inoceramus hookeri* var. *crenatulinus* Salter (*in* Salter and Blanford 1865, pl. 23, fig. 2) belongs within *R. everesti* (Oppel) (see below).

Inoceramids from the Late Jurassic deposits of New Caledonia were interpreted by both Avias (1953) and Routhier (1953) within the concept of the *galoi-subhaasti-haasti* lineage, but owing to their poor state of preservation no positive identifications were possible. It will be pointed out below that some, at least, of their specimens may represent new and as yet undescribed species of *Retroceramus*: the specimens identified as *I.* cf. *subhaasti* by Avias (1953, pl. 23, fig. 3) and Routhier (1953, pl. 2, fig. 9) may be new species within the subgenus *Retroceramus* (*Retroceramus*), and Routhier's (1953, pl. 2, fig. 8) *Inoceramus* sp. could be a small *Fractoceramus*.

Two New Zealand Middle Jurassic species, *I. inconditus* Marwick and *I. brownei* Marwick, can also be reclassified within *Retroceramus*. The former of these two belongs within the subgenus *Fractoceramus*, and there are strong resemblances to Siberian species such as *R.* (*F.*) *lungerhauseni* Koshelkina (e.g. Koshelkina 1962, pl. 9, fig. 1; 1963, pl. 13, fig. 1) and *R.* (*F.*) *elegans* Koshelkina (e.g. Koshelkina 1962, pl. 9, fig. 4; 1963, pl. 12, fig. 2). Koshelkina (1969*b*, p. 75) identified the other species, *I. brownei*, as a *Retroceramus*, but did not assign it to a subgenus. A third New Zealand species, *I. marwicki* Speden, may possibly have *Retroceramus* affinities too. At first sight it would appear to be a typical *Inoceramus*, being small and erect, and possessing only faint concentric ornament. However, Speden (1970, p. 848) has suggested that *marwicki* may be a transitional species in an evolutionary lineage from *I. brownei* to *I. galoi*, both of which can now be assigned to *Retroceramus*: small, faintly ornamented species of this genus are known from Siberia (e.g. *R. elatus* Koshelkina (1969*b*, p. 53, pl. 8, figs. 1-5)).

To sum up, there is good evidence to show that the genus *Retroceramus* is well represented in the extensive Late Jurassic deposits of the Southern Hemisphere. *Anopaea* is also present (Crame 1981*b*), but there are apparently very few true members of the genus *Inoceramus*.

SYSTEMATIC DESCRIPTIONS

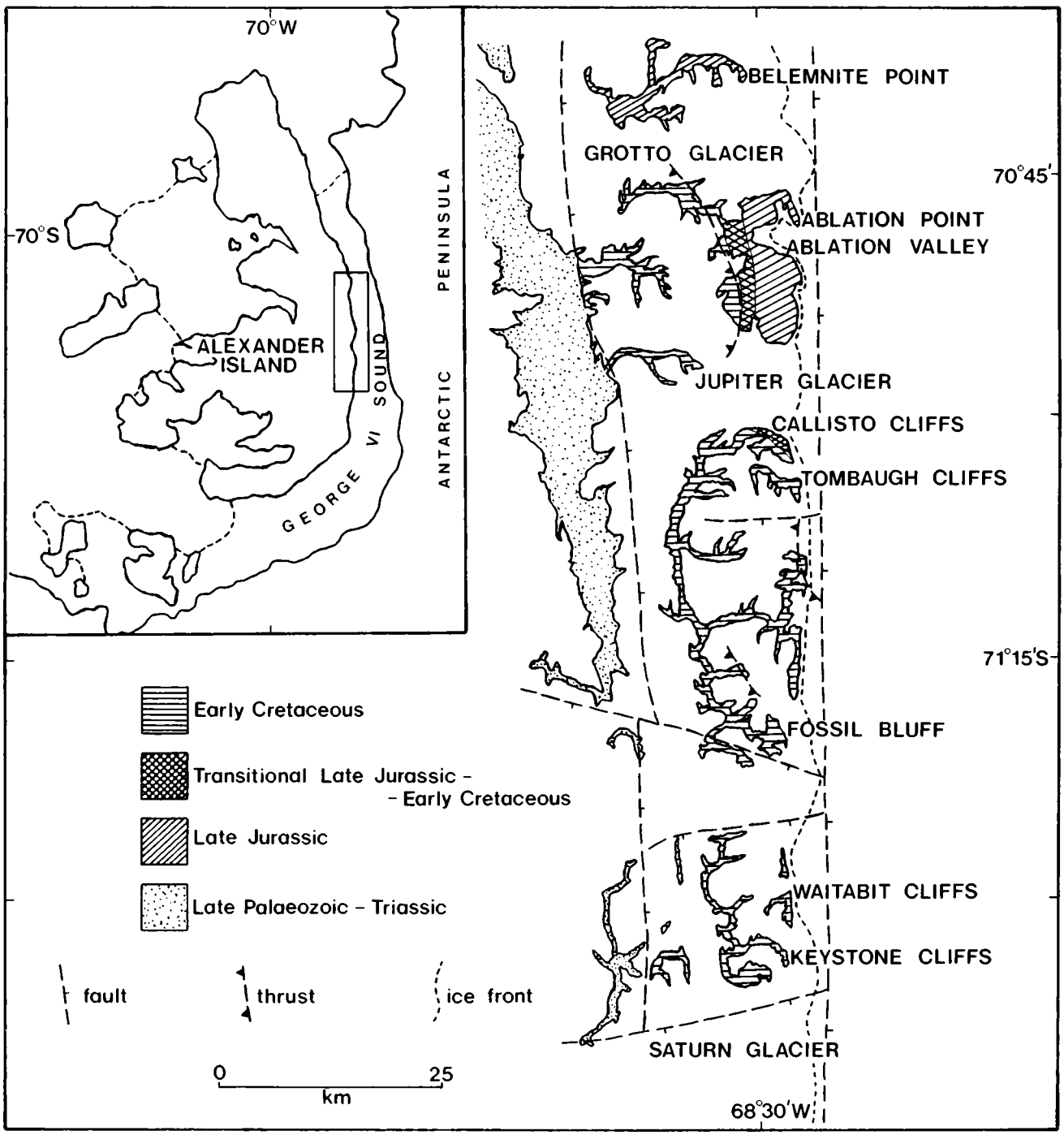
The poor state of preservation of so many Southern Hemisphere Late Jurassic inoceramids has consistently hampered detailed systematic studies. Collections from certain localities consist of no more than a small number of incomplete specimens, and many diagnoses have necessarily been based on very limited material. In only a few instances has it been possible to fully assess the range of morphological variation within and between closely related species. In an attempt to remedy this situation for the Antarctic Peninsula, a programme of intensive bed by bed collecting has been carried out in the Mesozoic Fossil Bluff Formation of eastern Alexander Island (text-figs. 1 and 5; see Taylor *et al.* 1979), and a similar programme has recently been initiated in the Latady Formation of the Lassiter and Orville coasts (Thomson *et al.* 1978).

At present, only one species from the Antarctic Peninsula, *Retroceramus everesti* (Oppel), is known from a comparatively large number of specimens (see below). Other well-known Southern Hemisphere species, such as *R. haasti* and *R. subhaasti*, are represented in the collections, but only in the form of broken or poorly preserved material. There are also several new species, but as these are all based on very limited material they have not been formally named. Instead, a system of open nomenclature has been adopted whereby material likely to represent a new species has been designated by a number (e.g. *Retroceramus* sp. nov. 1), and that resembling an existing species has been designated by the prefix 'cf.'. Wherever possible, the following measurements were taken:

shell length (L)—the length of the valve as measured along the direction of maximum growth (or growth axis) (*Wachstumsrichtung* of Seitz 1935).
shell width (W)—the maximum dimension perpendicular to the length.
length of hingeline (H).

The following angles, based on a scheme devised by Hayami (1960), were also measured:
α—the angle between the hingeline and the anterior margin (the apical angle).
β—the beak angle (or angle of umbonal inflation).
γ—the angle between the hingeline and postero-dorsal margin (the postero-dorsal angle).
δ—the angle between the hingeline and direction of maximum growth (the angle of obliquity).

The prefixes BMNH and NZGS denote specimens held in the British Museum (Natural History) and New Zealand Geological Survey collections, respectively: all the remaining specimens are held in the collections of the British Antarctic Survey, Cambridge. The following symbols have been used in the tables of measurements: LV—left valve, RV—right valve, *—approximate value.



TEXT-FIG. 5. Geological map of the central east coast of Alexander Island. The Fossil Bluff Formation comprises the Late Jurassic to Early Cretaceous strata.

Family INOCERAMIDAE Giebel, 1852
Genus RETROCERAMUS Koshelkina, 1963
Subgenus RETROCERAMUS (RETROCERAMUS) Koshelkina, 1963
Retroceramus (*Retroceramus*) *haasti* (Hochstetter, 1863)

Plate 57, figs. 1–4

1863 *Inoceramus haasti* Hochstetter, p. 190.
1864 *Inoceramus haasti* Hochstetter; Zittel, p. 33, pl. 8, figs. 5*a–c*.
1923 *Inoceramus haasti* Hochstetter; Trechmann, p. 275, pl. 15, fig. 3.
1923 *Inoceramus* sp. cf. *haasti* Hochstetter emend. Zittel; Krumbeck, p. 78, pl. 173, fig. 13.
1936 *Inoceramus haasti* Hochstetter emend. Zittel; Wandel, p. 573, text-figs. 4 and 5, pl. 19, fig. 1 and pl. 20, figs. 1 and 2.
1953 *Inoceramus haasti* Hochstetter; Marwick, p. 91, pl. 12, fig. 1.
(?)1967 *Inoceramus* sp. cf. *haasti* Hochstetter; Skwarko, p. 68, pl. 10, figs. 5 and 6.
1972 *Inoceramus haasti* Hochstetter; Thomson and Willey, p. 1, fig. 2.

Material. One broken internal mould (KG.701.74) from Ablation Valley, eastern Alexander Island (text-fig. 5), and an incomplete external mould (BMNH LL.10015) which probably comes from a moraine approximately 1·7 km north of Ablation Point.

Measurements. Comparative measurements are also given for the specimens illustrated by Trechmann (1923) (BMNH L.48032; text-fig. 4*b*) and Marwick (1953) (spec. no. TM.2374), and specimen BMNH LL.24175 (Pl. 57, figs. 1, 2).

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.701.74 (LV)	120*	72	0·60	—	62°*	—	—	45°*
L.48032 (LV)	100*	61	0·61	—	46°	40°*	—	32°*
TM.2374 (LV)	104	63	0·61	—	62°*	—	—	—
LL.24175 (LV)	92*	47*	0·51	—	42°*	40°	—	36°
LL.24175 (RV)	87*	56*	0·64	45*	59*	48	142*	50°

Remarks. Thomson and Willey (1972, p. 1) based their identification of *I. haasti* on a broken internal mould of a medium sized left valve (KG.701.74). The umbonal and hinge regions of this specimen are missing, but it can be judged to have been obliquely elongated and considerably expanded towards the ventral margin (Thomson and Willey 1972, fig. 2; Pl. 57, fig. 3). It bears the sharp, widely spaced concentric ribs that are so typical of this species and compares well with specimens of *I. haasti* illustrated by both Trechmann (1923, pl. 15, fig. 3; text-fig. 4*b*) and Wandel (1936, text-fig. 4 and pl. 20, fig. 1).

It should be emphasized again here that this is a species characterized primarily by its distinctive style of ornament: little attention has been paid so far to the form of the valves. Specimens from both New Zealand and Indonesia suggest that the valve outline varies from sub-erect to obliquely elongated (see p. 566 and Wandel 1936, text-figs. 4 and 5, pl. 20, figs. 1 and 2; pl. 21, figs. 1*a–c*), and it is likely that this is due to both original intraspecific variation and some degree of post-mortem distortion. A specimen from Kowhai Point, south-west Auckland, New Zealand (BMNH LL.24175, Pl. 57, figs. 1, 2) clearly shows how the latter can considerably affect the interpretation of valve morphology. This specimen, which is medium sized and moderately inflated, is noteworthy for the very prominent anterior margins on both valves. These are smooth and flat, and descend steeply (but not vertically) for a distance of approximately 3 cm to the plane of commissure. The right valve (Pl. 57, fig. 2) is apparently sub-erect and prosogyrous, although there are indications that the postero-dorsal area may originally have been more extensive. In contrast, the left valve (Pl. 57, fig. 1), although less complete, gives the appearance of having been narrower and more oblique. The valves of this specimen have been sheared and slightly crushed, and its exact form is hard to establish: the right valve seems to be erect and prosogyrous, and the left narrow and obliquely elongated (Pl. 57, figs. 1, 2). Inspection of Wandel's (1936) illustrations shows similar variation

from slightly prosogyrous (e.g. Wandel 1936, pl. 20, fig. 2) to opisthogyrous forms (e.g. Wandel 1936, text-fig. 4), but there is no consistent variation between the right and left valves.

Specimen BMNH LL.10015 from Alexander Island is a poorly preserved external mould of a large left valve bearing prominent concentric ribs of the *haasti* type (Pl. 57, fig. 4). The precise form of the valve is indeterminate, but it can be judged from the course of the ribs to have been obliquely elongated and ventrally expanded. A broken external mould of a small right valve from Low Island, South Shetland Islands (text-fig. 1), can also be tentatively referred to *R. haasti* (M. R. A. Thomson, pers. comm.).

Early evidence suggested that *R. haasti* was of Oxfordian age in Misol, East Celebes, and New Zealand (Wandel 1936, pp. 517–518). However, subsequent work on associated molluscan faunas placed the Ohauan stage, in which *R. haasti* occurs in New Zealand, in the Middle Kimmeridgian (Fleming 1958; Fleming and Kear 1960), and also suggested that the Misol occurrence may be as late as Lower Tithonian (Stevens 1965, p. 139). Thomson and Willey (1972, p. 17) lent some support to the earlier view of an Oxfordian age for *R. haasti*, as their specimen from Ablation Valley apparently comes from the same stratigraphical level as an Upper Oxfordian–Lower Kimmeridgian ammonite, *Perisphinctes* (*Orthosphinctes*) cf. *transatlanticus* (Steinmann) (Howarth 1958). This level, which occurs at the base of the Ablation Valley section (see later, text-fig. 9), is a sequence of slumped clastic sediments (known as the 'disturbed zone') whose precise age has yet to be established (Elliot 1974, p. 92) (see discussion section, below). Belemnites collected from the zone suggest an Upper Oxfordian–Middle Kimmeridgian age (Willey 1973), but it is apparent that all the fossils were collected from associated scree deposits rather than *in situ*. The occurrence of the top of the disturbed zone less than 100 m beneath a distinctive Tithonian ammonite fauna (text-fig. 9) (see p. 590) strongly suggests that at least part of the zone may range up into the Tithonian. Support for a Tithonian, or at least Kimmeridgian–Tithonian, age for *haasti* comes from more recent investigations in both Indonesia and New Zealand. Westermann *et al.* (1978) have identified *R. haasti* from near the top of a Kimmeridgian–Middle Tithonian sequence in the Sula Islands, Indonesia, and Stevens and Speden (1978) have indicated that one tenable interpretation of the New Zealand Jurassic ammonite faunas places the entire Ohauan stage in the Upper Tithonian (see discussion section, below). A Middle Kimmeridgian–Tithonian age range is accepted here as more likely for *R. haasti* than an Oxfordian–Kimmeridgian one.

There are strong similarities between *R. haasti* and certain Middle Jurassic Boreal species of *Retroceramus*. The more elongate forms of *haasti* (e.g. Wandel 1936, text-fig. 4), for example, are close to *R.* (*R.*) *elongatus* Koshelkina (e.g. Koshelkina 1963, pl. 15, fig. 4), and the squatter, more erect forms (e.g. Wandel 1936, pl. 19, fig. 1*a*) to types such as *R.* (*R.*) *marinus* Koshelkina (e.g. Koshelkina 1969*b*, pl. 21, fig. 1). Koshelkina (1969*b*, p. 76) has in fact suggested that Krumbeck's (1923) *I.* cf. *haasti* could be included within another Middle Jurassic species, *R.* (*R.*) *morosus* Koshelkina, but this identification is thought to be in error. As discussed above, Krumbeck's (1923, pl. 173, fig. 13) specimen of *I.* cf. *haasti* seems to be close to a number of other *haasti* specimens,

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EXPLANATION OF PLATE 57

Figs. 1–4. *Retroceramus* (*Retroceramus*) *haasti* (Hochstetter). 1, internal mould (with traces of shell material) of a whole specimen (BMNH LL.24175) viewed from the left side; from a locality near Kowhai Point, Kawhia Harbour, S.W. Auckland, New Zealand. 2, the same specimen viewed from the right side. 3, incomplete internal mould of a left valve (KG.701.74) from the south side of Ablation Valley, Alexander Island. 4, latex peel from an external mould of an incomplete left valve (BMNH LL.10015) from a moraine approximately 1·7 km north of Ablation Point, Alexander Island.

Figs. 5–6. *R.* (*R.*) *haasti* (Hochstetter) juv. (?). 5, internal mould of two incomplete single valves (KG.728.11) from a moraine approximately 1·7 km north of Ablation Point. 6, an internal mould of an incomplete single valve (KG.728.10) from the same locality. All specmens × 1.

CRAME, Inoceramid bivalves

and it would seem more appropriate to retain it within this species than to refer it to a less well-known Middle Jurassic Siberian species. That there is a strong similarity, especially in style of ornament, between species such as *haasti*, *elongatus*, and *morosus* is not disputed, but it is apparent that there are subtle differences between them in valve form and outline. This may indeed be no more than a striking example of homeomorphy between Middle and Late Jurassic species.

Retroceramus (*Retroceramus*) *haasti* (Hochstetter) juv. (?)

Plate 57, figs. 5, 6

1972 *Inoceramus* sp. δ; Thomson and Willey, p. 5, fig. 4*b*.

Material. Three incomplete internal moulds (KG.728.10 and 11) from a moraine approximately 1·7 km north of Ablation Point, eastern Alexander Island.

Description. The approximate dimensions of two of these specimens are 45 mm (length) by 30 mm (width), and of the third, 55 by 27 mm. They are all compressed and have incomplete margins. All three specimens are characterized by inflated umbonal regions that are clearly differentiated from the main body of the valve and bear traces of fine concentric ornament (Pl. 57, figs. 5, 6; Thomson and Willey 1972, fig. 4*b*). Over the rest of the valve prominent concentric ribs between 1·0 and 1·5 mm in width are developed: on the two valves on specimen KG.728.11 these ribs are evenly distributed (Pl. 57, fig. 5), but on specimen KG.728.10 they are somewhat irregular and discontinuous (Pl. 57, fig. 6). The course of the ribs suggests that all three specimens were approximately bilaterally symmetrical.

Remarks. The small size, finely ribbed umbonal stage, and regular concentric ornament suggest that these specimens may be juveniles of *R. haasti*. All three specimens compare well with probable juveniles of *I. haasti* from New Zealand (Spörli and Grant-Mackie 1976, text-figs. 10–12). A noticeable feature common to both the Antarctic and New Zealand specimens is the possession of a finely ornamented, upstanding umbonal region. Such an umbonal region seems to be a consistent feature of the juvenile stages of *R. haasti* (Wandel 1936, p. 466; Freneix *et al.* 1974, p. 462). Loose ammonites associated with specimens KG.728.10 and 11 have strong Tithonian affinities (Thomson and Willey 1972, p. 5; Thomson 1979, p. 32).

Retroceramus (*Retroceramus*) sp. cf. *subhaasti* (Wandel, 1936)

Plate 58, fig. 1

cf. 1936 *Inoceramus subhaasti* n. sp. var. *denseplicata* Wandel, p. 469, pl. 15, fig. 2, pl. 16, figs. 5*a* and *b*.
1975 *Inoceramus* cf. *subhaasti* Wandel 1936; Thomson, p. 34, fig. 3*b*.

Material. One internal mould of a single valve (KG.1258.9), preserved in fine-grained sandstone, and one whole specimen (KG.1258.66), preserved in mudstone, from Carse Point on the west coast of the Antarctic Peninsula (text-fig. 1).

Description. Specimen KG.1258.9 is a small, strongly inflated left valve with a narrow, rounded-rectangular outline (Pl. 58, fig. 1). Although the margins are incomplete and the specimen is slightly distorted, it can be judged to have been obliquely elongated. The maximum degree of inflation lies along the growth axis and there are steep descents to both the long, arcuate anterior margin and the remnants of the postero-dorsal wing (Pl. 58, fig. 1). The umbonal region is inflated and demarcated from the main body of the valve by a shallow, concentric sulcus. The umbo is twisted and in all probability projected strongly above the hingeline (Pl. 58, fig. 1). Low, rounded concentric ribs cover the valve. Between 1·0 and 1·5 mm in width, they appear to have been closely and regularly spaced over the valve surface: however, there is some evidence of crowding on the postero-dorsal wing close to the hinge margin (Pl. 58, fig. 1). The small whole specimen (KG.1258.66), although incomplete and partially distorted, has finely ribbed, strongly projecting umbones which are sharply differentiated from the more coarsely ribbed central areas of the valves (Thomson 1975, p. 34 and fig. 3*b*).

Measurements. KG.1258.9 (LV): L 53 mm, W 24 mm, W/L 0·47, α 70°*, β 32°, δ 70°*. KG.1258.66 (LV): L 42 mm, W 22* mm, W/L 0·52, α 50°*, γ 144°*.

Remarks. Retroceramus subhaasti is a distinctive species, characterized by a sub-quadrate outline, strongly projecting, twisted umbones, and a long, straight hinge: the style of ornament may be somewhat variable (Wandel 1936), but the valve form is consistent and definitive. Specimen KG.1258.9 appears to possess all the typical *subhaasti* features, but as the hinge and postero-dorsal area are incompletely preserved it can only be tentatively referred to this species. Judging from the styles of ornament, both it and specimen KG.1258.66 are probably closest to Wandel's (1936) *I. subhaasti* var. *denseplicata* (e.g. Wandel 1936, pl. 15, fig. 2 and pl. 16, figs. 5*a* and *b*) (see also Thomson 1975, p. 34).

Retroceramus subhaasti may be distinguished from *R. haasti* by its more quadrate outline, prominent hinge and postero-dorsal wing, and strongly projecting umbo. The two species cannot, however, be satisfactorily separated on the grounds of ornament alone, for some varieties of *subhaasti* have concentric ribs almost as strongly developed and widely spaced as those of *haasti* (e.g. Wandel 1936, text-figs. 2 and 3). Attention should also be drawn to the fact that, like *R. haasti*, *R. subhaasti* shows strong similarities to a number of Middle Jurassic species of *Retroceramus*. In particular, there are striking resemblances to members of the *R. kystatymensis* group of species (Koshelkina 1963, p. 138). *Retroceramus vagti* Koshelkina (Callovian), a prominent member of this group, has a sub-quadrate outline, very long hinge, and strong concentric ornament, and approaches in form types such as *I. subhaasti* var. *intermedia* Wandel (cf. Koshelkina 1962, pl. 10, fig. 2 and Wandel 1936, pl. 18, fig. 3*a*). However, the correspondence is not exact, and this is again thought to be nothing more than a case of homeomorphy between Jurassic species of *Retroceramus*. Associated faunas rule out any possibility of systematic equivalence between *R. subhaasti* and members of the *R. kystatymensis* group.

In Indonesia, *R. subhaasti* is particularly common in the Lilinta Marls of Misol (Wandel 1936). These beds lie directly beneath the Lower Fatjet Shales containing *R. haasti* and can probably be dated as Middle Kimmeridgian (Stevens 1965, p. 139). *Retroceramus subhaasti* also occurs in the Sula Islands, but its stratigraphical position there is less certain. Most of the early specimens were collected loose from stream beds and there is no clear indication of stratigraphical separation between *R. subhaasti* and *R. galoi* (Wandel 1936, pp. 517–519). More recent collections suggest that *R. galoi* occurs both above and beneath *R. subhaasti*, and that both these species occur stratigraphically below *R. haasti* (Westermann *et al.* 1978, p. 98). *Retroceramus galoi* has an apparent range of Middle Oxfordian–Kimmeridgian and *R. subhaasti* of (?) Upper Oxfordian–Lower Kimmeridgian. However, systematic and stratigraphical studies are not yet complete in the Sula Islands (Westermann *et al.* 1978) and these ranges should only be regarded as tentative. Associated ammonites and belemnites date the sedimentary sequence from which specimens KG.1258.9 and 66 were obtained as Late Jurassic (Thomson 1975). Current interpretations of those genera and species present favour a Middle–Upper Tithonian age, but it is possible that this range may eventually be extended down into the Kimmeridgian (Thomson 1975, p. 41). At present, it would seem best to assign *R. subhaasti* only to an undifferentiated Middle Kimmeridgian–Tithonian age range.

Retroceramus everesti group

During recent field-work, a large number of inoceramid specimens with a distinctive ornament pattern of fine, closely spaced concentric ribs was collected from a thick Late Jurassic–Early Cretaceous section at Callisto Cliffs, eastern Alexander Island (text-fig. 5). Although predominantly incomplete or deformed, many of these specimens seemed to show close affinities with *I. everesti* Oppel (see Holdhaus 1913, pp. 415–417, pl. 98, figs. 12–14). Further investigations confirmed this similarity, and indicated that a number of other Late Jurassic–Early Cretaceous Southern Hemisphere inoceramids could also be linked to this distinctive species group. It would seem, in fact, that the *everesti* group is particularly common in Southern Hemisphere Jurassic–Cretaceous boundary beds. As such, it is potentially very useful for regional biostratigraphical correlations.

It will become apparent from the descriptions and discussions below that substantial morphological variation has been allowed within the *everesti* group: indeed, it is possible that several distinct subspecies may eventually be established within it. However, at present only one distinct morphological subgroup can be recognized. This is a group of small, finely ribbed specimens which occur at the base of the *everesti* zone at Callisto Cliffs: these specimens appear to be evolutionary precursors of *everesti*, *sensu stricto*, and are separated off here as a distinct variety, *R. everesti* var. *α*. As this variety occurs stratigraphically beneath *R. everesti* proper, it is described first below. Throughout the following descriptions emphasis will be placed on stratigraphical changes in morphology as seen in the Callisto Cliffs section.

Retroceramus (*Retroceramus*) *everesti* (Oppel) var. *α*

Plate 58, figs. 2-4

Material. Six incomplete single valves from the base of the Callisto Cliffs section, eastern Alexander Island. The collection consists of two external (KG.2802.32 and 319) and two internal (KG.2802.132 and 282) moulds of right valves, and one internal (KG.2802.230) and one external (KG.2802.286) mould of a left valve. All specimens are preserved in siltstone.

Description. The stratigraphically lowest specimen (KG.2802.32) is a small, obliquely elongated, external mould of a left valve: its length is approximately twice the maximum width. A latex peel shows the specimen to have been moderately convex, with the maximum degree of inflation occurring in the umbonal region and along the growth axis (Pl. 58, fig. 2). There are smooth descents from the latter to both the anterior margin and the long, straight hingeline. The posterior and ventral margins are incomplete, but are judged to have been well rounded (Pl. 58, fig. 2). The umbonal region is distinct, and the beak would appear to have been terminal. A long, low, postero-dorsal wing is distinct at its anterior end but posteriorly merges discretely into the main body of the valve (Pl. 58, fig. 2). The ornament pattern on specimen KG.2802.32 consists of a single set of low, rounded concentric ribs which are less than 1 mm in width and lie slightly asymmetrically about the growth axis (Pl. 58, fig. 2). In places these ribs are adjacent, but elsewhere they are separated by narrow, flat interspaces. The ribs tend to coalesce and become finer towards both the wing and the anterior margin: they are noticeably finer over the umbo (Pl. 58, fig. 2).

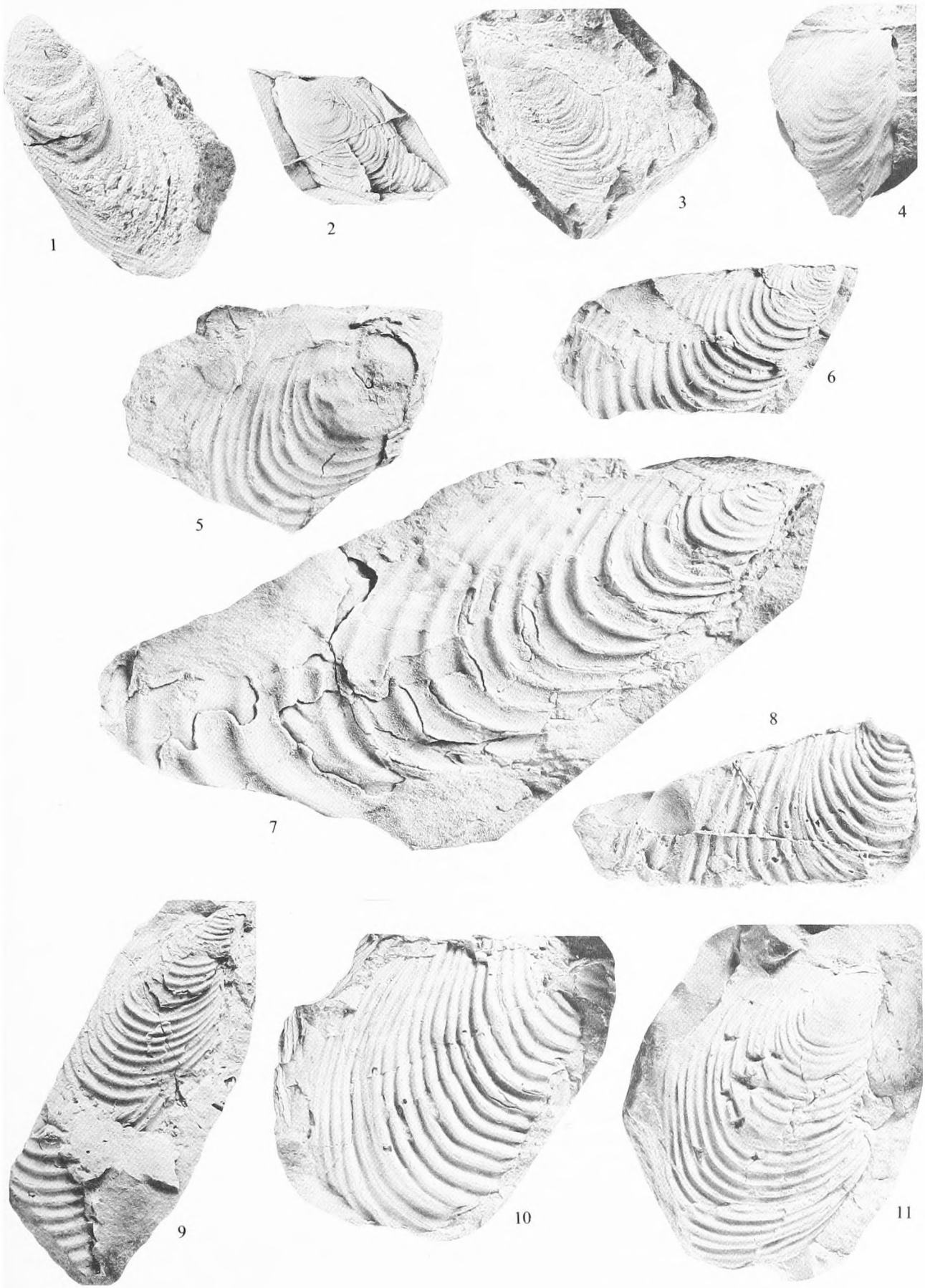
Specimens KG.2802.132 and 282 agree well with KG.2802.32. Specimen KG.2802.132 is particularly close, differing only in its larger size and slightly finer ornament (Pl. 58, fig. 3). Unfortunately, this specimen was collected from a small scree fan (one of only a few such specimens), and its exact level of origin is unknown. Specimen KG.2802.319, an incomplete external mould of a left valve, is slightly larger and more erect than the previous three specimens. Noticeably broader, it has distinct concentric ribs (1 mm wide and separated by similar-sized interspaces) developed towards the ventral margin. These seem to fuse into ill-defined groups towards the umbo, and become much finer on the flat postero-dorsal wing. This specimen may be a transitional form between the var. *α* and the main *everesti* group.

EXPLANATION OF PLATE 58

Fig. 1. *Retroceramus* (*Retroceramus*) sp. cf. *subhaasti* (Wandel). Internal mould of a left valve (KG.1258.9) from Carse Point on the west coast of the Antarctic Peninsula.

Figs. 2-4. *R.* (*R.*) *everesti* (Oppel) var. *α* from Callisto Cliffs, Alexander Island. 2, latex peel from an external mould of a left valve (KG.2802.32). 3, internal mould of a left valve (KG.2802.132). 4, incomplete internal mould of a right valve (KG.2802.230).

Figs. 5-11. *R.* (*R.*) *everesti* (Oppel). 5, incomplete internal mould of a right valve (with traces of shell material) (KG.2803.112). 6, latex peel from an external mould of a right valve (KG.2802.655a). 7, internal mould of a large right valve (partly covered by a thin shell layer) (KG.2802.384). 8, latex peel from an external mould of an incomplete right valve (KG.2803.655b). 9, internal mould of a more erect right valve (KG.2802.544). 10, latex peel from an external mould of an incomplete right valve (KG.2802.462). 11, plaster cast of a right valve (NZGS 5068) from Waikato South Head, Auckland, New Zealand (specimen illustrated by Marwick 1953, pl. 12, fig. 4). The specimen illustrated in fig. 5 is from Tombaugh Cliffs, Alexander Island, and those in figs. 6-10 are from Callisto Cliffs. All specimens × 1.



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The stratigraphically oldest right valve, KG.2802.230, has a very similar ornament style to that of KG.2802.32, 132, and 282. The low, narrow ribs are set close together and become finer and even more closely grouped towards the anterior and hinge margins (Pl. 58, fig. 4). However, this specimen seems to be more erect than oblique, and has a larger apical angle (see measurements, below) (Pl. 58, fig. 4). It is also more inflated than any of the left valves. The maximum degree of inflation again occurs in the umbonal region and along the growth axis, and there is a sharp drop from the latter to the anterior margin. Specimen KG.2802.286 (another right valve) is less well preserved, but also appears to be sub-erect in form and to be more inflated along the growth axis. The concentric ribs are very fine but are set slightly further apart than on any of the previous specimens. Some of the flat interspaces in the centre of the valve are up to 1·55 mm in width.

Measurements

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.2802.32 (LV)	35*	18	0·51	14	68°	35°	140°	47°
KG.2802.132 (LV)	43	25	0·58	16	67°	49°	141°	49°
KG.2802.282 (LV)	34	17	0·50	—	60°*	—	—	—
KG.2802.319 (LV)	45*	29*	0·64	19*	72°	—	119°	59°
KG.2802.230 (RV)	50*	30*	0·60	19*	79°	63°	140°*	55°
KG.2802.286 (RV)	40*	26	0·65	19*	59°	48°	136°	46°

Remarks. Retroceramus everesti var. α differs from *R. everesti* in its smaller size and finer concentric ornament. It occurs in the Callisto Cliffs section between approximately 92 and 545 m (see later, text-fig. 9).

Retroceramus (*Retroceramus*) *everesti* (Oppel, 1865)

Plate 58, figs. 5–11; Plate 59, figs. 1–11

(?)1833 *Inoceramus*?; Everest, p. 114, pl. 2, fig. 29.
(?)1865 *Inoceramus everesti* Oppel, p. 298.
1865 *Inoceramus hookeri* var. *crenatulinus* Salter; in Salter and Blanford, p. 95, pl. 23, fig. 2.
1913 *Inoceramus everesti* Oppel; Holdhaus, p. 415, pl. 98, figs. 12–14.
1913 *Inoceramus gracilis* Holdhaus, p. 417, pl. 98, fig. 15.
1936 *Inoceramus* cf. *steinmanni* Wilckens; Feruglio, p. 26, pl. 2, figs. 3–11.
1953 *Inoceramus* aff. *everesti* Oppel; Marwick, p. 92, pl. 12, fig. 4.
1960 *Inoceramus* sp. nov. *a* cf. *I. anglicus* Woods; Brunnschweiler, p. 26, pl. 2, figs. 3 and 6, and text-fig. 19.
1960 *Inoceramus* sp. nov. *b* cf. *I. anglicus* Woods; Brunnschweiler, p. 28, pl. 2, fig. 5 and text-fig. 20.
1960 *Inoceramus* sp. nov. *c* aff. *I. neocomiensis* d'Orbigny; Brunnschweiler, p. 29, pl. 2, fig. 4 and text-figs. 21 and 22.
1966 *Inoceramus*; Katz and Watters, p. 336, fig. 7.
1972 *Inoceramus pseudosteinmanni* Thomson and Willey, p. 5, figs. 5*a–h*, 6*a–c*, and 7*a*.

Material. Eight right valves, fifteen left valves, and numerous fragments from Callisto Cliffs (KG.2802), and two right and two left valves from Tombaugh Cliffs (KG.2803.2, 45, 46, and 112), eastern Alexander Island (text-fig. 5). All the specimens are incomplete internal and external moulds preserved in siltstone: no articulated specimens have yet been collected from Alexander Island.

Description. The best-preserved right valve, KG.2802.384, is an internal mould (covered in places by a thin prismatic shell layer) from the base of the *everesti* zone at Callisto Cliffs (see later, text-fig. 9). In some respects this specimen is slightly atypical of the species as a whole, for it is appreciably larger than any other specimen and has more widely spaced ornament. Although the margins are incomplete, specimen KG.2802.384 can clearly be seen to be narrow and obliquely elongated (Pl. 58, fig. 7). The hingeline appears to have been straight and of moderate length, the anterior margin gently arcuate, and the posterior margin well rounded. A feature of the valve is its very narrow apical angle and small, pointed umbo. The latter is only moderately convex and like the postero-dorsal wing, poorly differentiated from the main body of the valve (Pl. 58, fig. 7). The specimen as a whole is only weakly inflated. The ornament of specimen KG.2802.384 consists of

a single set of strong, regularly spaced concentric ribs (Pl. 58, fig. 7). In the umbonal and central regions of the valve these are 1·0–1·5 mm thick and are separated by flat interspaces 2–4 mm in width: ventrally, the ribs thicken to 2·5 mm and the interspaces increase to 5 mm. On the parts of the valve where shell material has been completely removed the ribs have a characteristically rounded cross-section (see also Thomson and Willey 1972, fig. 6). They continue without diminishing in strength across both the wing and umbo.

Specimen KG.2802.655a, from the top of the Callisto Cliffs section, agrees well in general form with KG.2802.384 (Pl. 58, figs. 6, 7), but is much smaller. However, it should be emphasized that, as with so many of these specimens, the margins are incomplete and the original dimensions can only be estimated (see measurements, below). Specimen KG.2802.655a shows the characteristic ornament pattern of simple, clearly defined ribs with symmetrically rounded cross-sections. The ribs are generally 1 mm in width at their summits and are separated by interspaces 1·0–1·5 mm in width: they are thus more closely spaced than on the previous specimen and are more typical of the *everesti* group as a whole.

The two specimens described so far both have umbones that are gently curved in an opisthogyral direction (Pl. 58, figs. 6, 7). This tends to accentuate their obliquity and suggests affinities with *Retroceramus* (see below). However, at least one right valve (KG.2802.544, an internal mould) is much less oblique and in fact has a slightly prosogyrous umbo (Pl. 58, fig. 9). This variation from oblique, opisthogyrous forms to sub-erect, slightly prosogyrous forms seems to be a characteristic feature of the *everesti* group. It occurs in left valves as well as rights (see below), and in a number of specimens from other areas. To some extent it might be explained by post-mortem distortion of what was certainly a thin-shelled species, but it must also reflect original variation in the alignment of the narrow, pointed umbo. There is no consistent stratigraphical separation between the two forms at Callisto Cliffs. Another distinctive feature of specimen KG.2802.544 is its finer ornament. The ribs are still clearly defined and evenly spaced, but their summits are even sharper (Pl. 58, fig. 9). They also show a tendency to fuse and become indistinct on the small postero-dorsal wing.

Specimen KG.2802.439 (an internal mould with traces of shell) is a small, oblique right valve in which the pattern of regular concentric ribbing is considerably disrupted. Clearly defined concentric ribs can be made out over the umbonal and ventral parts of the valve, but in the centre the ribs tend to thicken, fuse, and become uneven in their course. Irregular ribbing such as this is a feature of a number of specimens in the *everesti* group. Two incomplete right valves (KG.2802.462 and 655b) are broader forms with expanded postero-dorsal areas. In neither case are these areas considered to be true wings for they are not clearly separated from the main part of the valve and both still bear strong concentric ribs. On KG.2802.462 the ribs pass on to the area without changing course or diminishing in strength (Pl. 58, fig. 10), but on KG.2802.655b they curve sharply forwards and partially fuse (Pl. 58, fig. 8).

Left valves from near the base of the *everesti* zone at Callisto Cliffs all appear to be small to medium in size and obliquely elongated. Specimen KG.2802.472, a small, narrow internal mould, clearly has an opisthogyral umbonal region which projected slightly above a straight hinge (Pl. 59, fig. 3). The specimen is moderately inflated (with the maximum inflation lying just anterior to the growth axis) and the anterior margin is well demarcated. The ribs are simple, narrow (in the region of 0·5 mm wide at their summits), and regularly spaced. They curve sharply forwards and are set closer together on the postero-dorsal area, but remain individually distinct (Pl. 59, fig. 3). Specimen KG.2802.463, a partially distorted internal mould, is a broader and less inflated left valve (Pl. 59, fig. 9). The hinge and umbonal regions are missing, but the general form of the valve can be judged to have been obliquely elongated. The concentric ribs are particularly clearly and regularly spaced on this specimen. Approximately 0·75 mm in width at their summits, they have the characteristically symmetrically rounded cross-section, and over the central and ventral areas of the valve are separated by shallow interspaces between 2·5 and 3·0 mm in width (Pl. 59, fig. 9). There are traces of a fine prismatic shell layer (less than 0·5 mm thick) along the anterior edge of the valve. Less complete valves, such as KG.2802.417, 418, and 432, are medium sized, slightly to moderately inflated, and obliquely elongated. They all have simple, well-defined concentric ribs, and one of them, KG.2802.417, has an umbo which clearly projects above a short, straight hinge (Pl. 59, fig. 6).

Not all the left valves, however, are obliquely elongated and evenly ribbed. Specimen KG.2802.438, for example, is a broader, more erect form with a considerably expanded postero-dorsal area. Moderately inflated along the growth axis, there are even descents from the central area to the anterior and posterior margins. The ribbing in the central inflated area becomes considerably thickened and confused (in a similar manner to KG.2802.439), and diminishes in prominence towards both the anterior and posterior margins. Much of the extensive postero-dorsal area appears to have been almost smooth.

Perhaps even more striking is the variation shown by two specimens from near the top of the *everesti* zone at Callisto Cliffs. Like the right valve KG.2802.544, both KG.2802.538 and 540 are sub-erect in form and have prosogyrous umbones (Pl. 59, figs. 1, 4). Specimen KG.2802.540, an internal mould of a left valve,

is moderately inflated, with the maximum degree of inflation occurring along the growth axis. There are moderately steep descents to the long, straight anterior margin and small postero-dorsal wing. The tip of the umbo and beak are missing, but from the form of the valve they can be judged to have been narrow, pointed, and curved gently forwards (Pl. 59, fig. 4). The concentric ribs are particularly well defined and evenly spaced on this specimen. Symmetrical in cross-section and with narrow, acute summits, they are separated by shallow interspaces varying between 1 mm in width over the umbonal region and 2 mm towards the ventral margin. The ribs tend to die out towards both the anterior margin and the postero-dorsal wing (Pl. 59, fig. 4). Specimen KG.2802.538, an external mould of a left valve, is very similar in size, form, and style of ornament to KG.2802.540 (Pl. 59, fig. 1). The umbonal region and beak of this specimen are also missing, but they can similarly be judged to have been narrow, inflated, and curved gently forwards. Although reduced in strength, concentric ribs can still be distinguished on the postero-dorsal wing of this specimen (Pl. 59, fig. 1).

It should be pointed out here that at least one oblique, opisthogyral left valve (KG.2802.545) (Pl. 59, fig. 2) has been collected from the same stratigraphical level as the prosogyrous specimens KG.2802.538, 540, and 544. Specimen KG.2802.545 (an internal mould with traces of shell material) is characterized by a long, arcuate anterior margin, a long, straight hinge, and an expanded postero-dorsal area (Pl. 59, fig. 2). As in KG.2802.472, the axis of maximum inflation lies anterior to the growth axis and there is a sharp descent to the anterior margin. The umbonal region is incompletely preserved, but can be judged to have been opisthogyrous (Pl. 59, fig. 2). The ornament on this specimen again consists of narrow, regularly arranged ribs which diminish in strength across the postero-dorsal wing.

Another striking trend shown by a number of left valves from the lower levels of the *everesti* zone at Callisto Cliffs is towards the development of coarse, irregular ribs. Specimens showing this trend are incomplete, medium sized internal and external moulds (KG.2802.407, 409–411). They all appear to have been obliquely elongated. On specimens KG.2802.407 and 410 the ribs take the form of broad folds between 2 and 3 mm in width and 2·0 and 2·5 mm in amplitude, and are asymmetric to sub-symmetric in cross-section. They are asymmetric about the growth axis, and are separated by irregular interspaces between 2 and 4 mm in width. Occasionally the ribs anastamose, both in the centre of the valve and towards the margins. Specimen KG.2802.412, a distorted external mould of a left valve, has fine, irregular ribbing over the umbonal region and coarse, irregular ribbing towards the ventral margin.

Numerous fragments found throughout the *everesti* zone at Callisto Cliffs show the characteristic types of *everesti* ornament. There are no clear traces of muscle scars or ligament pits on any of the specimens.

Measurements

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.2802.417 (LV)	76	35	0·46	17	60°*	48°	136°	55°
KG.2802.438 (LV)	81*	55*	0·68	30*	80°	48°	120°	59°
KG.2802.463 (LV)	74	42	0·57	—	51°	44°*	122°	65°*
KG.2802.472 (LV)	55	25	0·45	16*	52°	35°	129°	51°
KG.2802.538 (LV)	55	31	0·56	14*	83°	48°	116°*	60°
KG.2802.540 (LV)	64*	34	0·53	15	84°	43°	106°*	62°*
KG.2802.545 (LV)	49	26	0·53	20	59°*	33°*	123°*	50°
KG.2802.554 (LV)	65°	39	0·60	23*	78°*	52°	126°	64°
KG.2802.384 (RV)	120*	55*	0·46	45*	45°*	37°	155°	28°
KG.2802.439 (RV)	62*	28	0·45	—	41°	36°	—	36°
KG.2802.544 (RV)	50*	26*	0·52	18*	74°	49°	135°	58°
KG.2802.655a (RV)	55*	32*	0·58	18*	59°	39°*	143°	47°
KG.2803.112 (RV)	60*	36*	0·60	25*	63°	48°	122°	52°

Remarks. Specimens collected from the Callisto Cliffs section suggest that members of the *R. everesti* group are typically small to medium sized (for the genus), obliquely elongated (with a few notable exceptions), and weakly to moderately inflated. The group was evidently thin-shelled, for the valve margins seem to have been easily broken and there are only traces of the original shell material. Comparison of similar sized valves suggests that the species was equivalve.

The ornament pattern of narrow, well-defined concentric ribs is particularly diagnostic of the group. The ribs are typically evenly spaced and symmetrically rounded in cross-section, and in the majority of cases are of uniform strength across the whole valve surface. In particular, they are

clearly not weakened or excessively crowded over the umbonal region. There are, however, a number of distinct variants within the *everesti* group. The more erect, slightly prosogyrous forms would seem at first sight to be morphologically distinct, but they clearly have a typical *everesti* ornament pattern and cannot be separated on stratigraphical grounds from the more common oblique and opisthogyrous forms. Irregularly ribbed varieties occur at several levels, but never in such a way that they can confidently be separated into either distinct stratigraphical or morphological subgroups. The nature and degree of the variation shown by the Callisto Cliffs specimens suggest that a number of other Southern Hemisphere species can now be accommodated within the *R. everesti* group.

Inoceramus everesti Oppel, a Himalayan species, was first fully described and illustrated by Holdhaus (1913), who had access to a number of specimens from the Middle and Upper Spiti Shales. However, it is apparent that nearly all these specimens are small and incomplete, and the exact form of the original *I. everesti* still remains in some doubt. The largest illustrated specimen (Holdhaus 1913, pl. 98, fig. 12), an internal mould of a left valve, appears to be obliquely elongated, and judging from the form of the concentric ornament, probably had a slightly opisthogyrous umbo. The smaller specimens are much less obviously oblique (Holdhaus 1913, pl. 98, figs. 13 and 14*a–c*) and it would seem that the Himalayan material probably exhibits a range of variation similar to that seen in the Callisto Cliffs specimens. Such a trend is confirmed by examination of a series of undescribed specimens of *I. everesti* (from the Spiti Shales of Niti Pass) housed in the British Museum (Natural History). A small whole specimen (LL.1006) and several single valves (e.g. LL.1004, 1007, and 1011) clearly have erect outlines (e.g. Pl. 59, fig. 5), but specimen LL.1005 is a fragment of a more obliquely elongated left valve (Pl. 59, fig. 8), and LL.1009 may be a slightly obliquely elongated right valve (Pl. 59, fig. 7). Although the latter specimen apparently has a sub-erect outline, there are traces of a postero-dorsal wing and some indications that the valve may have extended for a considerable distance in a ventral direction. Indeed, this specimen is similar to the early stages of the oblique specimens KG.2802.384 and 655a from Callisto Cliffs (cf. Pl. 59, fig. 7 and Pl. 58, figs. 6, 7). *Inoceramus hookeri* Salter 1865 from the Spiti Shales of Niti Pass is probably a distinct species in its own right (within the genus *Retroceramus*) but *I. hookeri* var. *crenatulinus* Salter (*in* Salter and Blanford 1865, pl. 23, fig. 2) belongs within *I.* (= *R.*) *everesti*. It is interesting to note that the single specimen of this variety recorded to date shows a slight variation between the right and left valves, in a manner similar to that of the B.M.(N.H.) specimen (LL.24175) of *R. haasti* from Kowhai Point, south-west Auckland (Pl. 57, figs. 1, 2). Whereas the left valve is very slightly oblique (Pl. 59, fig. 11), the right valve is more erect and has a pointed, slightly prosogyrous umbo (Pl. 59, fig. 10). However, the specimen is incomplete and slightly crushed, and there is no evidence from the other specimens examined of a consistent morphological difference between the valves of *R. everesti* (as is also the case with *R. haasti*). It is also interesting to note that the valves of the specimen of *I. hookeri* var. *crenatulinus* have prominent anterior margins, with that of the left valve being particularly well rounded in cross-section. All the specimens from the Spiti Shales bear the distinctive *everesti* style of ornament.

Oppel (1865) based *I. everesti* on a series of incomplete steinkerns and impressions, one of which had previously been figured by Everest (1833, pl. 2, fig. 29). The latter specimen is likely to become the lectotype, but as the descriptions of it are so brief and the illustration so poor, its identity must be held in some doubt. Everest (1833, p. 114) gives no formal description, and Oppel (1865, p. 298) merely states that it is a broad, irregularly ribbed species. The illustration (Everest 1833, pl. 2, fig. 29) in fact seems to be upside down, so that the true outline is probably rounded-triangular, with a considerably expanded ventral region. There is even a possibility that this specimen could be an *Anopaea*, as *A. stoliczkai* (Holdhaus), a species with a rounded outline and fine, regular concentric ornament, is also known from the Spiti Shales (Crame 1981*b*). It can only be concluded that both the specimen and illustration are totally inadequate for diagnostic purposes and that Everest's (1833) and Oppel's (1865) identifications must be held in some doubt. The earliest reliable guide to the identification of *I. everesti* is that given by Holdhaus (1913), and it would seem prudent to formally regard his illustrated specimens (Holdhaus 1913, pl. 98, figs. 12–14) as plesiotypes of

I. everesti Oppel. *Inoceramus gracilis* Holdhaus (1913, p. 417, pl. 98, figs. 15*a–d*) can now be included within the range of variation established for the *R. everesti* group.

It became apparent at an early stage in this study that the inoceramids from Callisto Cliffs were very close to *I. pseudosteinmanni* Thomson and Willey (1972), a species common in the nearby Tombaugh Cliffs (text-fig. 5). They were obiously similar in size and degree of inflation, and both possess the distinctive *everesti* style of ornament. However, the exact form of *I. pseudosteinmanni* is not immediately obvious. All the specimens described by Thomson and Willey (1972, p. 7, figs. 5*a–h*, 6*a–c*, and 7*a*) are incomplete, with the larger specimens being particularly badly preserved.

The smallest specimens of *I. pseudosteinmanni* apparently have an erect outline (e.g. Thomson and Willey 1972, figs. 5*d* and *f*), but both the holotype (KG.401.520) (fig. 5*b*) and specimen KG.401.521 (fig. 5*h*) are slightly obliquely elongated. The two largest specimens (KG.401.514 and 524) (figs. 5*a* and *e*) have rounded-quadrate outlines, due principally to the development of extensive postero-dorsal areas. Additional material recently collected from Tombaugh Cliffs suggests that at least some of the larger specimens of *I. pseudosteinmanni* may have been obliquely elongated. Specimen KG.2803.112, for instance, an internal mould of a right valve which probably had an original length of at least 60 mm, has an oblique outline and sharply pointed umbo (Pl. 58, fig. 5). There was a comparatively long hingeline and an extensive postero-dorsal area which was only weakly differentiated from the main body of the valve. Specimen KG.2803.46, an external mould of a right valve, also appears to have been medium sized and slightly oblique, whereas KG.2803.45 has a quadrate outline and an extensive postero-dorsal area similar to those of KG.401.514 and 524 (see Thomson and Willey 1972, figs. 5*a*, *e*).

Although smaller and less complete, the specimens from Tombaugh Cliffs do show strong similarities to those from Callisto Cliffs and should now be included in the *R. everesti* group. The smaller specimens agree well with the smaller Spiti specimens (e.g. Holdhaus 1913, pl. 98, figs. 13 and 14; Pl. 59, figs. 5, 7), and forms such as KG.401.515a, 520, and 522 (Thomson and Willey 1972, figs. 5*b*, *c*, and *h*) agree with the less oblique specimens from Callisto Cliffs (e.g. KG.2802.538 and 544; Pl. 58, fig. 9; Pl. 59, fig. 1). There are, in addition, large fragments from Callisto Cliffs (e.g. KG.2802.554 and 555) which have remnants of extensive, flat, postero-dorsal areas very similar to those seen on KG.401.514 and 524 (Thomson and Willey 1972, figs. 5*a*, *e*) and on KG.2803.45.

The South American specimens included by Thomson and Willey (1972, p. 5) in the synonymy of *I. pseudosteinmanni* also fall within the concept of *R. everesti* (see Feruglio 1936, pl. 2, figs. 3–11; Katz and Watters 1966, p. 366, fig. 7). Again, all the specimens are poorly preserved, but they seem to correspond in general form, degree of inflation, and style of ornament with members of the *R. everesti* group. Both Leanza (1967, pp. 147–148) and Thomson and Willey (1972, p. 8) have suggested that two species groups can be distinguished within Feruglio's (1936) material, but

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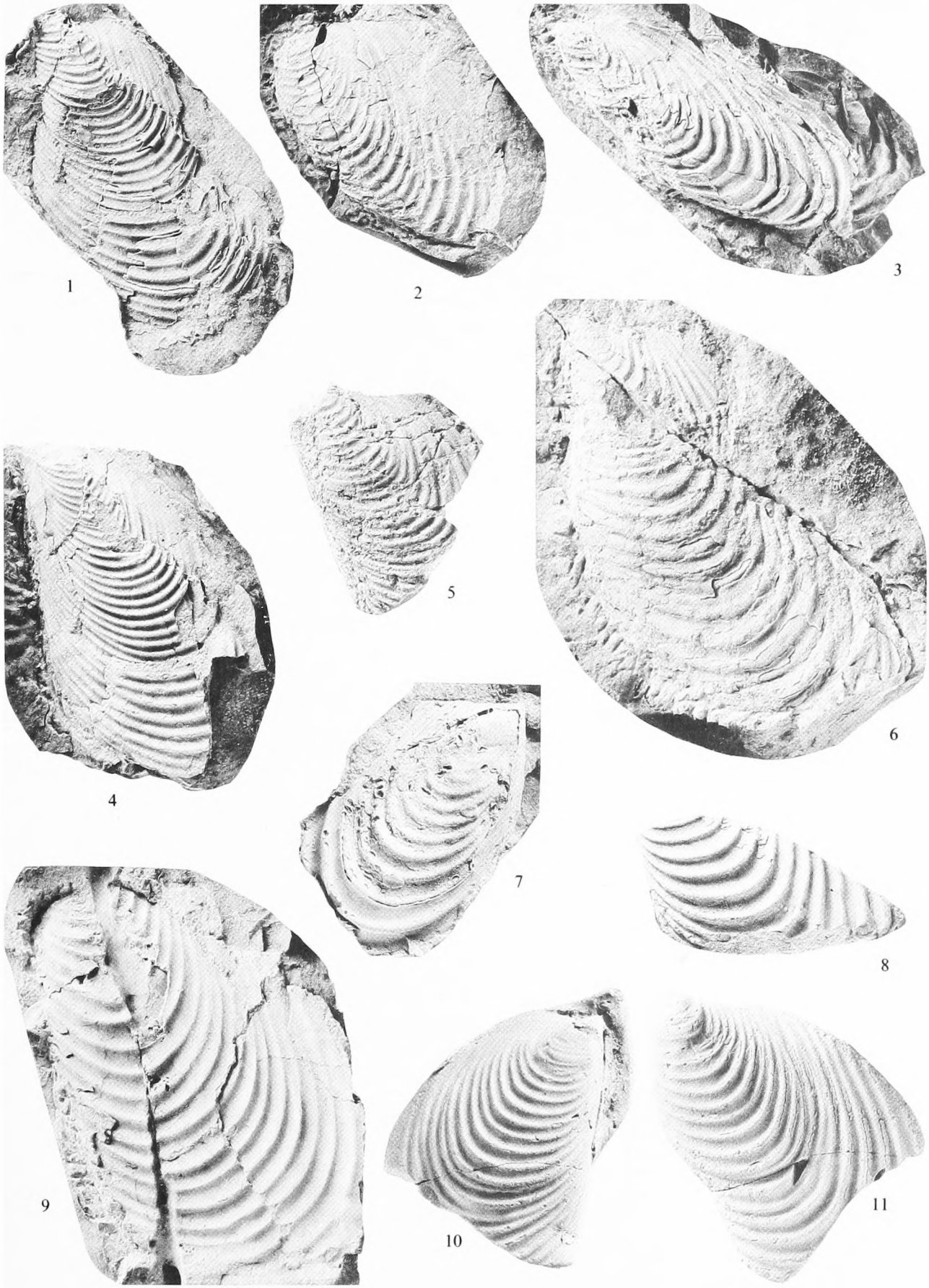
EXPLANATION OF PLATE 59

Figs. 1–11. *Retroceramus* (*Retroceramus*) *everesti* (Oppel). 1, latex peel from an external mould of an erect left valve (KG.2802.538). 2, internal mould of an oblique left valve (KG.2802.545). 3, internal mould of an oblique left valve (KG.2802.472). 4, internal mould of an erect left valve (KG.2802.540). 5, incomplete internal mould of a small left valve (BMNH LL.1006). 6, internal mould of a left valve (KG.2802.417). 7, latex peel from an external mould of a right valve (BMNH LL.1009). 8, incomplete internal mould of a small, oblique left valve (BMNH LL.1005). 9, internal mould of a left valve (KG.2802.463). 10, holotype of *Inoceramus hookeri* var. *crenatulinus* Salter (BMNH LL.1081) viewed from the right side. 11, the same specimen viewed from the left. The specimens illustrated in figs. 1–4, 6, and 9 are from Callisto Cliffs, Alexander Island, and those in figs. 5, 7, 8, 10, and 11 are from the Upper Jurassic Spiti Shales of the Himalayas. All specimens × 1.



CRAME, Inoceramid bivalves

in view of the poor state of preservation, and the wide degree of morphological variation shown by the group as a whole, it would seem better to regard all the specimens as belonging to *R. everesti*. The incomplete, partially distorted valves figured by Feruglio (1936, pl. 2, figs. 3–11) are particularly reminiscent of some of the specimens collected from Tombaugh Cliffs (see Thomson and Willey 1972, figs. 5*a–h*, and Pl. 58, fig. 5).

At least one potential member of the *R. everesti* group has been reported from New Zealand. Marwick (1953, p. 92, pl. 12, fig. 4) (Pl. 58, fig. 11) has illustrated a specimen from South Auckland which seems to be close to the Spiti Shales material, but because it is very weakly inflated he only tentatively identified it as *I.* aff. *everesti*. This specimen is particularly interesting because it is erect in form and has a slightly prosogyrous umbo (Pl. 58, fig. 11). It is similar in outline to specimen KG.2802.544 from Callisto Cliffs (Pl. 58, fig. 9), but is somewhat broader and has a more inflated umbonal region. The narrow, concentric ribs (generally less than 0·5 mm in width) are very similar to those of KG.2802.544. However, it should be pointed out that both the anterior and posterior margins of Marwick's specimen are incomplete, and the umbonal region is worn. No other *everesti*-type material has yet been described from New Zealand, although Marwick (1953, p. 92) mentions that the South Auckland collections include two undescribed juveniles and one fragment. Fleming's (1958, p. 384, fig. 12) specimen of *Inoceramus* n. sp. *A.* ? aff. *everesti* from North Canterbury may well be an *Anopaea* (Crame 1981*b*).

Inoceramus sp. nov. *a* from Dampier Land, Western Australia (Brunnschweiler 1960, pp. 26–27, pl. 2, figs. 3 and 6, and figs. 19*a–c*), seems to be close to *R. everesti*. Small to medium in size and subrhomboidal in outline, it has slightly opisthogyrous umbones and a distinct postero-dorsal wing. The ornament consists of fine, regular concentric ribs with rounded summits. The ribs are separated by interspaces of equivalent width over most of the valve surface, but there are indications of crowding towards the anterior margin and on the postero-dorsal wing. The specimens seem in fact to be more complete versions of those illustrated by Holdhaus (1913, pl. 98, figs. 12–14). The left valves (Brunnschweiler 1960, pl. 2, fig. 6, and fig. 19*c*) are particularly interesting in that they show how a seemingly sub-erect form can sometimes have a distinctly opisthogyrous umbo. Brunnschweiler's (1960, p. 28, fig. 20) *Inoceramus* sp. nov. *b* is similar to *I.* sp. nov. *a*, but is slightly more elongated and has irregular ribbing developed towards the posterior and ventral margins. The specimen is quite clearly oblique, and has a long, straight hinge and distinct postero-dorsal wing. The ribs are regular and well defined, and again there is a strong resemblance to members of the *R. everesti* group. In particular, Brunnschweiler's (1960) specimen illustrated in his figure 20*a* is similar in form to specimens such as KG.2802.472 and 655b from Callisto Cliffs (Pl. 58, fig. 8; Pl. 59, fig. 3).

The only obvious difference between Brunnschweiler's (1960) *I.* sp. nov. *a* and *b* and *R. everesti* is that the concentric ribs of the former two species are set slightly closer together. However, all the specimens illustrated by Brunnschweiler (1960) are incomplete, and it is possible that the interspace width increased slightly towards the ventral margin. It is also apparent that a third species, *I.* sp. nov. *c* (Brunnschweiler 1960, p. 29, pl. 2, fig. 4, and figs. 21 and 22), associated with the previous two, had much coarser and more widely spaced ribs. This species is known only from fragments, but it appears to have been a larger and less obviously oblique form. On the largest fragment (Brunnschweiler 1960, fig. 22*a*), the ribs are up to 2 mm in width at their summits and are separated by interspaces of up to 4 mm. The ribs occasionally anastamose in a manner reminiscent of specimens KG.2802.407–411 from Callisto Cliffs. Just as the latter are thought to be coarser-ribbed varieties of *R. everesti*, so *I.* sp. nov. *c* may be a coarser-ribbed variety of *I.* sp. nov. *a* and *b*. Thus, all three of Brunnschweiler's (1960) new species fall within the current concept of the *R. everesti* group, but it should be pointed out that a number of the original specimens have been lost (see Brunnschweiler 1960, p. 4).

There is some evidence that *R. everesti* may occur in the Sula Islands, Indonesia. Kruizinga (1926) reports that numerous finely ribbed *Inoceramus* fragments are present in the Late Jurassic *Aucella* Marls, and judging from his descriptions (Kruizinga 1926, pp. 21–22), these could well belong to *R. everesti*. When further collections have been made in this area, it may be possible to relate the stratigraphical occurrence of *R.*

everesti to that of other Southern Hemisphere index species (such as *R. galoi*, *R. subhaasti*, and *R. haasti*) in measured sections (see Westermann *et al.* 1978). Thus, in time, the Sula Islands may well become another standard stratotype for Southern Hemisphere Late Jurassic inoceramids. Some of the poorly preserved Jurassic inoceramids from New Caledonia (e.g. Avias 1953, pl. 23, figs. 6–8) may also belong to the *R. everesti* group.

The evidence for reassigning *I. everesti* to the genus *Retroceramus*, although strong, is perhaps slightly less convincing than for either *I. galoi* or *I. haasti*. This is principally because the hinge region of this species is poorly known. The hinge appears to have been long and straight, but is rarely preserved in its entirety. The structure of the ligament area, a crucial feature in generic diagnosis, is also poorly understood. The left valve illustrated by Holdhaus (1913, pl. 98, fig. 12) shows traces of rounded-rectangular ligament pits measuring approximately 2 × 1 mm, and separated by interspaces of equivalent width. A hinge fragment on B.M.(N.H.) specimen LL.1009 shows pits of similar shape and dimensions, separated by clearly defined interspaces up to 1·5 mm in width. Thus, although the pits are somewhat smaller than those normally associated with *Retroceramus*, they are comparatively broad, rounded, and widely spaced. The ligament area as a whole is probably closer to that of *Retroceramus* than *Inoceramus*. In his classification of Jurassic inoceramids, Wandel (1936, p. 467) included *I. everesti* within the *I. haasti* group. All the other members of this group (*I. haasti*, *I. subhaasti*, *I. retrorsus*, and *I. ferniensis*) can now be referred to the genus *Retroceramus*, and it would seem logical to reclassify *I. everesti* here too.

Retroceramus everesti is consistently smaller, less oblique, and more finely ribbed than either *R. haasti* or *R. galoi*. However, the largest form of *R. everesti* from Callisto Cliffs, specimen KG.2802.384 (Pl. 58, fig. 7), does show some similarities to certain varieties of *R. subhaasti*. Wandel (1936, p. 472) himself remarked upon the similarity between *I. subhaasti* var. *denseplicata* (Wandel 1936, pl. 15, fig. 2 and pl. 10, fig. 5*a*) and *I. everesti*, but stated that the latter was characterized by thinner concentric ribs. *Retroceramus subhaasti* is also typically more inflated than *R. everesti*, and has a more strongly projecting umbo (see p. 573). The resemblance is perhaps strongest between KG.2802.384 (Pl. 58, fig. 7) and *R. subhaasti* var. *intermedia* (Wandel 1936, pl. 18, fig. 3*a*). However, this variety clearly has the strongly projecting umbo which is so typical of the *subhaasti* group, and thicker concentric ornament.

Retroceramus everesti also compares well with several Northern Hemisphere species. Small, regularly ribbed forms from Callisto Cliffs (such as KG.2802.472 and 545; Pl. 59, figs. 2, 3) show similarities to species such as *R. rhomboideus* (Voronetz) (Aalenian) from Siberia (Voronetz 1937, pl. 5, figs. 9 and 10, and pl. 10, figs. 2–4), and less regularly ribbed forms (such as KG.2802.438 and 439) to species such as *R. obliquiformis* (McLearn) (Callovian) from Alberta (e.g. McLearn 1924, p. 41, pl. 3, fig. 9). Two Japanese species, *R. utanoensis* (Kobayashi) and *R. ogurai* (Kobayashi) (both Bathonian), are close to *R. everesti*, but are too badly preserved for a detailed comparison to be made (Kobayashi 1926, pl. 11, figs. 1–3).

Available evidence suggests that *R. everesti* is present in both the Middle and Upper Spiti Shales, and thus has a stratigraphical range in the Himalayas of Lower Tithonian–Neocomian (Stevens 1965, p. 149; Helmstaedt 1969). The New Zealand specimen of *I.* aff. *everesti* is of Late Tithonian age (Stevens and Speden 1978, p. 264) and *I. pseudosteinmanni* from Tombaugh Cliffs is Early Berriasian (Thomson and Willey 1972, Table 2). Although there are obvious lithofacies and faunal differences, it would appear that the Callisto Cliffs section can be correlated with the central part of the Ablation Valley section (see later, text-fig. 9). The base of the Callisto Cliffs section is believed to be Late Tithonian in age, and the top Early Berriasian. The top of the Callisto Cliffs section correlates with the base of the Tombaugh Cliffs section (see later, text-fig. 9), and the range of *R. everesti* in Alexander Island can be established as Late Tithonian–Early Berriasian. Of the species synonymized within *I. pseudosteinmanni*, *Inoceramus* (Katz and Watters 1966, p. 336) comes from the Yahgan Formation of Patagonia, which spans the Jurassic–Cretaceous boundary, and *I.* cf. *steinmanni* Wilckens has a probable origin in sedimentary rocks of Upper Tithonian–Berriasian age (Feruglio 1936; Leanza 1967). The three new inoceramid species described by Brunnschweiler (1960) from Dampier Land, Western Australia, were also obtained from a thick sequence of transitional Jurassic–Cretaceous deposits. The Leveque Sandstone, in which the three species were found, is judged to be Early Neocomian, but it is possible that it may be partly Late Tithonian in age too (see discussion section, below).

It may be concluded that *R. everesti* is a small- to medium-sized species characteristic of Southern Hemisphere Late Tithonian–Early Berriasian strata. The valves are typically obliquely elongated, weakly to moderately inflated, and bear fine, regular concentric ribs. There are, however, a number of distinct variations on this basic theme: some forms clearly have more erect outlines, and others developed irregular or coarse ornament. The features shown by *R. everesti* are in fact such as to suggest that this species occupies an intermediate position between *Retroceramus* and *Inoceramus*.

In particular, the following features suggest an evolutionary trend away from the typical *Retroceramus* morphology towards that of *Inoceramus*:

(i) The specimens are generally smaller and less obviously oblique than many species of *Retroceramus*.
(ii) The shell is thinner than in many *Retroceramus* species, and the hinge and ligament areas are apparently reduced in thickness.
(iii) The ligament pits are probably transitional in form between those typical of *Retroceramus* and those typical of *Inoceramus*.
(iv) The ornament is finer than in most species of *Retroceramus*.

An intermediate position between *Retroceramus* and *Inoceramus* is further suggested by the consistent stratigraphical occurrence of the species at the Jurassic–Cretaceous boundary. *Retroceramus* is essentially restricted to the Jurassic, and *R. everesti* must be a member of one of the latest stocks of this genus. Data on Early Cretaceous inoceramids are sparse, but it would appear that nearly all the species so far described can be referred to *Inoceramus*.

Retroceramus (*Retroceramus*) sp. nov. 1

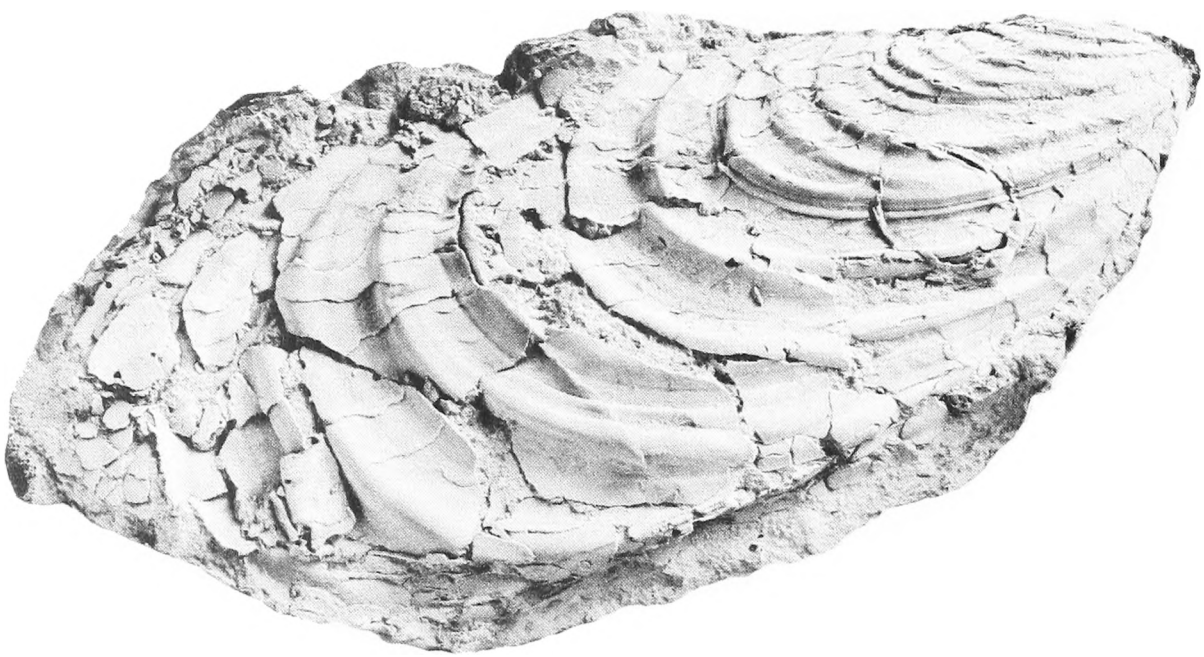
Text-fig. 6

(?)1953 *Inoceramus* sp. 'G' Sornay; *in* Routhier, p. 56, pl. 2, fig. 7.
1972 *Inoceramus* aff. *subhaasti* Wandel; Thomson and Willey, p. 3, fig. 3.

Material. One large but incomplete external mould (KG.701.76) from the same locality in Ablation Valley as the specimen of *R. haasti* (KG.701.74). The specimen is preserved in fine-grained, tuffaceous sandstone.

Measurements. KG.701.76 (RV): L 150* mm. W 62 mm, W/L 0·41, α 53°*, β 45°*, δ 34°*.

Remarks. This is a distinctive, narrow, obliquely elongated right valve that cannot be readily matched with any previously described species. In form and outline it resembles *R. galoi*, but the



TEXT-FIG. 6. *Retroceramus* (*Retroceramus*) sp. nov. 1. Latex peel from an external mould of a right valve (KG.701.76) from the south side of Ablation Valley, Alexander Island; × 1.

ribbing is altogether too coarse and widely spaced for it to be considered a member of that species (Thomson and Willey 1972, p. 3). There are obvious resemblances to the more oblique forms of *R. haasti* (e.g. Wandel 1936, text-fig. 4 and pl. 20, fig. 1), but the valve is consistently narrower than a typical *haasti*, showing no tendency towards marked postero-ventral expansion (text-fig. 6). The style of ornament differs from that of *R. haasti* in that there are fine secondary ribs intercalated between the prominent primaries. There is also some tendency for the primaries to fuse close to the ventral margin (especially in the umbonal region, see Thomson and Willey 1972, fig. 3 and text-fig. 6). The specimen resembles some of the poorly preserved Late Jurassic inoceramids from New Caledonia, and Thomson and Willey (1972, p. 3) compared it directly to *I.* sp. 'G' Sornay (*in* Routhier 1953, pl. 2, fig. 7). However, taking into account the poor state of preservation of this specimen and the fact that the hinge is missing, it can only be tentatively included in *R.* sp. nov. 1.

Routhier (1953, p. 56, pl. 2, fig. 9) illustrated a second obliquely elongated, coarsely ribbed inoceramid as *I.* sp. cf. *subhaasti*. This specimen, although of similar dimensions to KG.701.76, has thicker concentric ribs that have acute summits and distinctly triangular cross-sections. These ribs are set close together and continue almost undiminished in strength across the umbo. Such a style of ornament is in fact closer to that seen in certain Middle Jurassic Boreal species of *Retroceramus*, such as *R.* (*R.*) *porrectus* Eichwald (e.g. Koshelkina 1963, pl. 6, fig. 1) or *R.* (*R.*) *ferniensis* (Warren) (e.g. Warren 1932, pl. 2, fig. 1), than to any previously described Late Jurassic species. *Inoceramus* sp. A (Avias 1953, p. 169, pl. 23, figs. 1 and 2) from New Caledonia also appears to be medium sized, obliquely elongated and coarsely ribbed, but the specimens are too poorly preserved to enable any positive identifications to be made. *Inoceramus* sp. B (Avias 1953, pl. 23, fig. 3), apart from having a slightly more erect form, seems to be close to Routhier's (1953) *I.* cf. *subhaasti*.

From its association with *R. haasti* in Ablation Valley, *R.* sp. nov. 1 is judged to have an age range of Middle Kimmeridgian–Tithonian.

Retroceramus (*Retroceramus*) sp. nov. 2

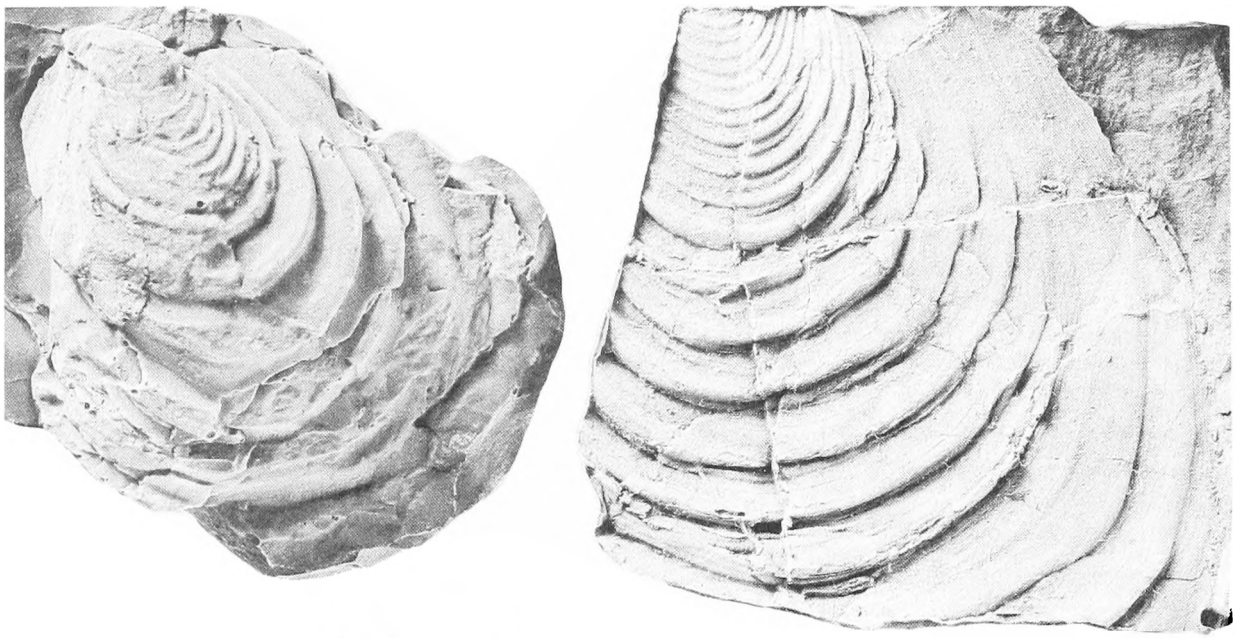
Text-fig. 7*a*, *b*

1972 *Inoceramus* sp.; Thomson, p. 97, fig. 3*c*.

Material. One incomplete external mould (T.535,10) from Adelaide Island (text-fig. 1). The specimen is preserved in a pale, grey-green tuff, and comes from a marine horizon at the base of a 3000 m volcanic sequence.

Description. This is a medium sized, rounded to sub-quadrate left valve. Although the anterior and ventral margins are missing, it can be judged to be broader and more erect than any of the previously described species (text-fig. 7*b*). It is only feebly inflated, but in all probability has been partially crushed. One of the most distinctive features of the specimen is its concentric ornament, for the ribs are markedly asymmetric in cross-section. Between 5 and 8 mm in width in the centre of the valve, they have long, gently descending dorsal (or umbonal) slopes, and short, nearly vertical, ventral slopes (text-fig. 7*b*). The ribs are clearly defined and regular in their course in the centre of the valve, but are much thinner (1·0–1·5 mm in width) over the umbo. They disappear completely in the postero-dorsal area where there is an ill-defined, almost smooth wing (text-fig. 7*b*).

Specimen T.535.10 compares well with an undescribed specimen in the New Zealand Geological Survey collections (NZGS 9932, text-fig. 7*a*) identified as *I.* aff. *subhaasti* Wandel. This specimen is an almost complete small- to medium-sized left valve. It too has a rounded-quadrate outline, but is considerably more inflated than the Adelaide Island specimen. A notable feature is that the anterior margin is broad and drops steeply to the plane of commissure (text-fig. 7*a*). The umbo is strongly prosogyrous and projects above a long, straight hingeline (text-fig. 7*a*). The ornament consists of prominent concentric ribs that again have the characteristic step-like profiles in cross-section. They are of similar dimensions to those of T.535.10, and also become noticeably finer over the umbo. The ribs die out on the indistinctly recessed postero-dorsal wing (text-fig. 7*a*).



TEXT-FIG. 7. *Retroceramus* (*Retroceramus*) sp. nov. 2. *a* (left), plaster cast of a left valve in the New Zealand Geological Survey collections (NZGS 9932) identified as *Inoceramus* aff. *subhaasti* Wandel; collected from Old Kihi Road, Hauturu, Kawhia. *b* (right), latex peel of an external mould of a left valve (T.535.10) from the south-western corner of the Mount Bouvier massif, Adelaide Island. Both specimens × 1.

Measurements. T.535.10 (LV): L 110* mm, W 73* mm, W/L 0·66, H 40* mm, α 80°*, β 55°*, γ 120°, δ 67°*. NZGS 9932 (LV): L 67 mm, W 54* mm, W/L 0·81, H 30* mm, α 81°, β 55°, γ 120°*, δ 66°.

Remarks. The two specimens described above appear to belong to a new species of *Retroceramus*. That a member of this genus could have a rounded-quadrate outline is not altogether unreasonable, for several Boreal species have similar growth forms. *Retroceramus* (*Retroceramus*) *eximius* Eichwald, for example, an Aalenian species, has a distinctly rounded-quadrate outline, as well as strongly projecting umbones (e.g. Eichwald 1871, pl. 18, figs. 1 and 2, and pl. 19, figs. 3 and 4), and *R.* (*R.*) *polaris* Koshelkina, a Bathonian species, has a rounded outline, coarse ribs over the main part of the valve, and finer ribs over the umbo (e.g. Koshelkina 1962, pl. 9, fig. 5). It is also apparent that in cross-section the prominent anterior margin of *R.* sp. nov. 2 was wedge-shaped rather than a flat shelf (text-fig. 7*a*), and thus the species would almost certainly have been functionally endobyssate.

Specimen NZGS 9932 from New Zealand is probably one of the specimens identified by J. B. Waterhouse (*in* Fleming and Kear 1960, p. 43) as *I.* cf. *subhaasti*. These specimens (none have been formally described or illustrated) subsequently assumed considerable importance in New Zealand Jurassic biostratigraphy, for they seemed to occupy intermediate morphological and stratigraphical positions between the well-known species *galoi* and *haasti* (Stevens 1965, 1968; Speden 1970). However, in both form and style of ornament, specimen NZGS 9932 clearly differs from all members of the *R. subhaasti* group and should not now be associated with that species. There may well be transitional forms between *R. galoi* and *R. haasti* in New Zealand (see, e.g., Stevens 1968, p. 62), but it has yet to be demonstrated that any of them belong to *R. subhaasti*. The postulated *galoi-subhaasti-haasti* lineage in New Zealand is currently in need of detailed revision (Spörli and Grant-Mackie 1976, p. 28).

Associated fossils from Adelaide Island (locality T535) have Late Jurassic affinities, but are undiagnostic as to stage level (Thomson 1972, p. 100). Specimen NZGS 9932 is dated as Ohauan

in New Zealand, and this stage is generally taken to be equivalent to the Middle Kimmeridgian (e.g. Speden 1970, p. 828). However, as mentioned previously, there is some possibility that the Ohauan stage may be as late as Late Tithonian.

Retroceramus (*Retroceramus*) sp. nov. (?)

Text-fig. 8

Material. Two incomplete single valves (D.3825.6 and D.4329.14) from Longing Gap, Trinity Peninsula (text-fig. 1). The specimens are preserved in a grey, finely bedded siltstone.

Description. These are two flattened and partially distorted external moulds. The margins of both specimens are incomplete, but their general form and regular ornament suggest affinities to *Retroceramus*. The largest specimen (D.3825.1) has a rounded-oval outline and can be judged to have been obliquely elongated (text-fig. 8). The anterior margin appears to have been long and arcuate, and the ventral and posterior margins well rounded. The umbonal region is not clearly differentiated from the main body of the valve but there are remnants of a long, straight hinge and narrow postero-dorsal wing (text-fig. 8). The concentric ribs are closely and evenly spaced over the umbonal region. They have symmetrical profiles and rise to acute summits less than 0·5 mm in width. The ribs become lower, more rounded, and more widely spaced towards the ventral margin (text-fig. 8). The largest of these later ribs are up to 4 mm in width and are separated by interspaces 11 mm in width. In the region of the postero-dorsal wing the ribs sweep sharply forwards and become much finer. There are faint traces of very thin secondary ribs on some of the primaries.

The second specimen (D.4329.14) also appears to have been obliquely elongated. Judging from the course of the concentric ribs, the anterior margin was long and arcuate, the ventral margin well rounded and the

TEXT-FIG. 8. *Retroceramus* (*Retroceramus*) sp. nov. (?). Latex peel from an external mould of a right valve (D.3825.6) from Longing Gap, Trinity Peninsula; × 1.

posterior margin gently rounded. The concentric ribs are again narrow and sharply defined over the umbonal region, but broader and more widely spaced towards the ventral margin. They also become much finer and crowded on the indistinctly recessed postero-dorsal wing.

Measurements. D.3825.6 (RV): L 155* mm, W 95* mm, W/L 0·61, α 82°, δ 47°. D.4329.14 (LV): L 63* mm, W 37 mm, W/L 0·59, H 33* mm, α 58°, γ 132°, δ 52°.

Remarks. There are obvious resemblances between these two specimens and members of the *R. haasti* group (see, e.g., Wandel 1936, text-figs. 4 and 5, pl. 19, fig. 1 and pl. 20, figs. 1 and 2; Pl. 57, figs. 1–4). The obliquely elongated outline and prominent concentric ornament, together with the presence of a distinct postero-dorsal wing and finer-ribbed umbo, all suggest allegiance to this species. However, the valves of *R. haasti* are typically moderately to strongly inflated and have much stronger, projecting concentric ribs. It should also be re-emphasized that the margins of these specimens are incomplete, and their true form is unknown. There is, again, some resemblance to certain elongated, coarsely ribbed Middle Jurassic species (such as *R.* (*R.*) *elongatus* and *R.* (*R.*) *borealis*), but no definite links can be established with either of these forms.

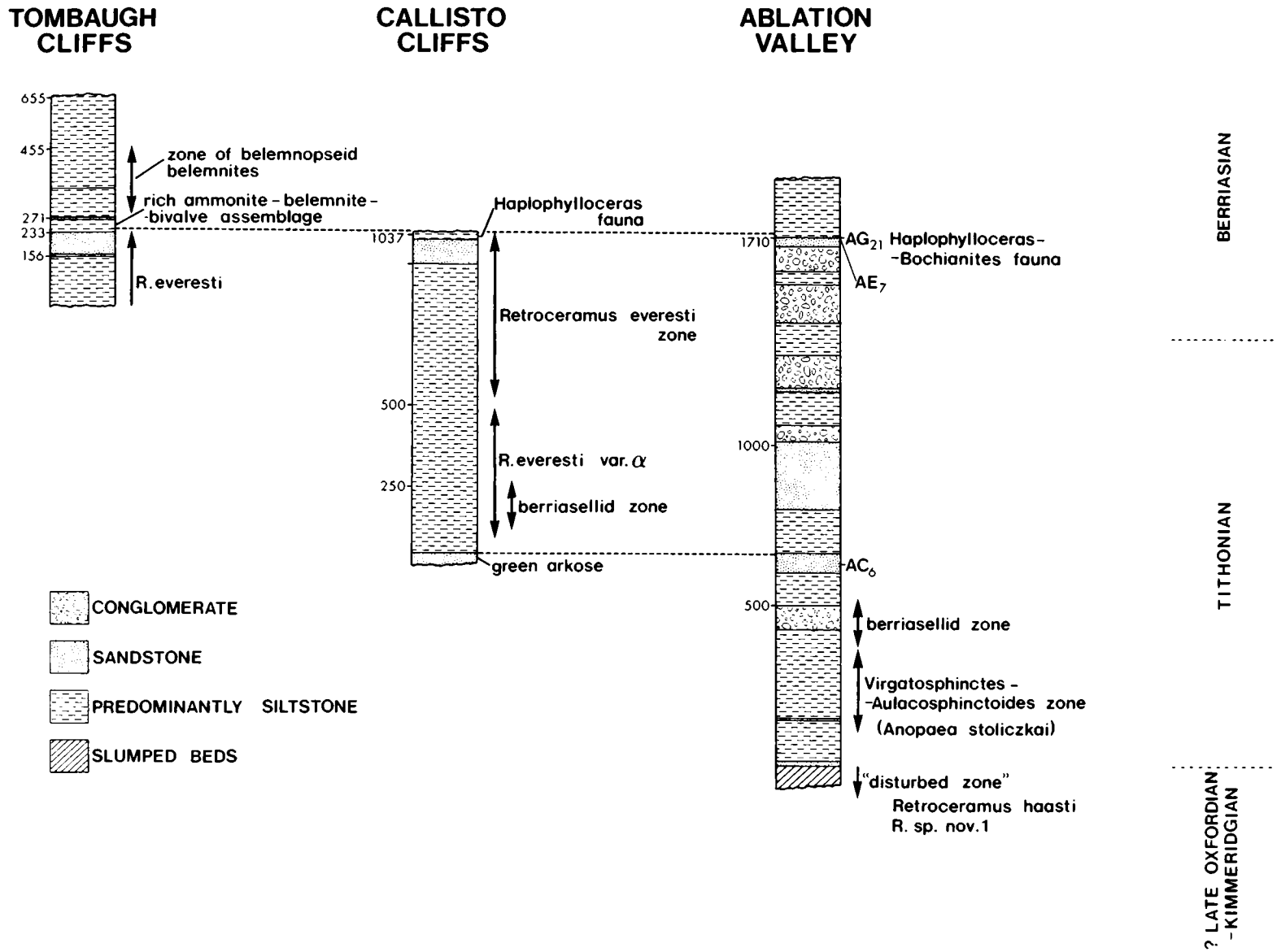
It can be tentatively concluded that these specimens belong to *Retroceramus* and have probable Late Jurassic affinities. Loose perisphinctid ammonites collected from the same general area have a probable Oxfordian or Kimmeridgian age (Aitkenhead 1975, p. 11; Bibby 1966, p. 8).

STRATIGRAPHICAL DISCUSSION

Correlation of the Ablation Valley, Callisto Cliffs, and Tombaugh Cliffs sections, eastern Alexander Island

The Fossil Bluff Formation crops out in a narrow strip along the eastern margin of Alexander Island (text-figs. 1 and 5). It is bounded to the west by a major fault and to the east by George VI Sound. The topography of the area of outcrop consists of a series of isolated massifs separated by west–east trending glaciers draining into George VI Sound (text-fig. 5). There is a predominant south-westerly dip throughout the formation and in general the massifs become progressively younger from north to south. Late Jurassic strata are exposed at Belemnite Point and Ablation Point, and Aptian–Albian strata in the Waitabit Cliffs–Keystone Cliffs area (text-fig. 5) (Taylor *et al.* 1979). However, the stratigraphy is complicated by tectonic disturbances and pronounced lateral facies changes, and correlation between adjacent massifs is by no means straightforward. The formation is composed predominantly of clastic sediments (siltstones, fine to coarse sandstones, and conglomerates), and has an estimated total thickness of approximately 4000 m (Taylor *et al.* 1979; Thomson, in press).

Recent investigations (Elliott 1974) have shown that an extensive sedimentary sequence is exposed within the Ablation Valley massif (text-figs. 5 and 9). The beds in this region dip more westwards than south-westwards (although there are variations due to local folding and faulting) and Elliott (1974) has indicated that a total thickness of more than 2000 m of strata is exposed (ranging in age from ? Upper Oxfordian–Kimmeridgian to Berriasian). The oldest beds in the sequence, comprising the so-called 'disturbed zone', contain spectacular large-scale slump structures (see Bell 1975). The zone probably has a maximum thickness of about 350 m in the Ablation Point region but no accurate stratigraphical measurements have yet been made of it. Although no *in situ* fossils have been collected from it either, there are a number of loose specimens from associated screes. One incomplete perisphinctid ammonite has been identified as *Perisphinctes* (*Orthosphinctes*) cf. *transatlanticus* Steinmann (Howarth 1958), and there are four species of belemnite; *Belemnopsis* cf. *tanganensis* (Futterer), *B.* cf. *alfurica* (Boehm), *B.* cf. *gerardi* (Oppel), and *B.* cf. *keari* Stevens (Willey 1973). Collectively, these five species have been taken to indicate an Upper Oxfordian–Kimmeridgian age (e.g. Elliott 1974; Taylor *et al.* 1979; Thomson 1979). Two loose inoceramids, *R.* (*R.*) *haasti* and *R.* (*R.*) sp. nov. 1, have also been collected from the disturbed zone and the former of these suggests a probable Middle Kimmeridgian–Tithonian age. The most likely age for



TEXT-FIG. 9. Stratigraphical correlations between Ablation Valley, Callisto Cliffs and Tombaugh Cliffs, Alexander Island (see text-fig. 5). Collectively, these three sections comprise approximately the lower half of the Fossil Bluff Formation. The values to the left of each column indicate height in metres above the base of the section and those to the right of the Ablation Valley column are station numbers used by Elliott (1974). Stage boundaries are only approximate.

the disturbed zone would thus seem to be Kimmeridgian, but it is possible that it both ranges down into the Oxfordian and up into the Tithonian.

Between 125 and 400 m in the Ablation Valley section there is a sequence of fossiliferous shales characterized by a distinctive Tithonian ammonite fauna. Species of *Virgatosphinctes* and *Aulacosphinctoides* are particularly common (text-fig. 9), and many of these have strong Lower Tithonian affinities. However, certain Late Tithonian elements are also present in the fauna, and it is probably best to regard this zone as undifferentiated Tithonian in age (Thomson 1979, p. 31). Directly above, between approximately 400 and 500 m, there is another distinctive ammonite zone, characterized by berriasellids (text-fig. 9). Species of *Blandfordiceras* predominate, and the zone as a whole can best be dated as Late Tithonian (Thomson 1979, p. 31). Above this level the next distinctive faunal horizon does not occur until approximately the 1710 m level (text-fig. 9), where a *Bochianites–Haplophylloceras* ammonite assemblage and *Belemnopsis* belemnite assemblage represent the earliest Cretaceous (Berriasian) fauna (Thomson 1979, p. 31; Willey 1973, p. 55). The topmost levels of the section are entirely contained within the Berriasian (Elliott 1974).

Strata exposed in the Callisto Cliffs massif (text-figs. 5 and 9) can be correlated with the central portions of the Ablation Valley section. There is no indication of the *Virgatosphinctes–Aulacosphinctoides* assemblage in the Callisto Cliffs section but there is a distinctive berriasellid fauna between 117 and 264 m (text-fig. 9). Most of the specimens can probably be referred to *Blandfordiceras* and there would appear to be good agreement at the specific level with the Ablation Valley berriasellid zone (Thomson 1979). Unfortunately, there are no other distinctive ammonite horizons in the section. There is one specimen from the 317 m level which can possibly be referred to a Late Tithonian spiticeratid genus, but nearly all the other specimens found are undiagnostic phylloceratids. However, near the top of the section, at a level corresponding approximately to the distinctive *Bochianites–Haplophylloceras* horizon in Ablation Valley (text-fig. 9), there are a number of specimens that can be referred to *Haplophylloceras*: the topmost beds at Callisto Cliffs seem in fact to be equivalent to those at the 1710 m level in Ablation Valley (text-fig. 9). Here, in a sequence of bioturbated, silty shales, there is a very distinctive fauna which includes *Haplophylloceras* sp., *Belemnopsis alexandri* Willey, *Retroceramus everesti*, plant fragments and species of the bivalves *Grammatodon*, *Myophorella*, *Pinna*, and *Panopea*. This fauna is very similar to that found in beds AE_7 and AG_{21} at Ablation Valley (except that *R. everesti* is apparently absent here—Elliott 1974, p. 95), and the 1037 m level at Callisto Cliffs can be directly correlated with the 1710 m level in the Ablation Valley section (text-fig. 9).

The basal 40 m of the Callisto Cliffs section is composed of a distinctive green arkose that contains small conglomerate lenses, belemnite fragments, and large numbers of tiny indeterminate bivalve moulds. This arkose correlates well with a zone of very similar lithology in the lower levels of the Ablation Valley section (bed AC_6 of Elliott 1974, fig. 5). In fact, the thickness of strata between beds AC_6 and AG_{21} at Ablation Valley is almost exactly equivalent to that exposed in the Callisto Cliffs section (text-fig. 9). Nevertheless, it should be pointed out that although the respective sections compare well in thickness, they differ somewhat in lithology; none of the four prominent conglomerate beds present in the Ablation Valley section occurs at Callisto Cliffs (text-fig. 9 and Elliott 1974, fig. 5). In the latter area the strata are predominantly siltstones with intercalated sandstone bands. The conglomerates themselves vary considerably in thickness in the Ablation Valley massif and it is apparent that they pass laterally into sandstones and siltstones. Belemnites tentatively identified from Callisto Cliffs include *Belemnopsis gladiatoris* Willey, *B.* aff. *uhligi* Stevens, *Hibolithes antarctica* Willey, *H. belligerundi* Willey, and *H.* sp. nov. (?): the large, distinctive species, *B. alexandri*, occurs only in the topmost level (1037 m, text-fig. 9). *Retroceramus* (*Retroceramus*) *everesti* var. α is present between 92 and 545 m, and *R.* (*R.*) *everesti* between 623 m and the top of the section.

From all the foregoing palaeontological evidence, it can be concluded that the lower levels of the Callisto Cliffs section are Late Tithonian in age and the topmost levels Berriasian. The exact position of the Jurassic–Cretaceous boundary has yet to be determined, but it probably lies in the upper 200–300 m of the section, within the *R.* (*R.*) *everesti* zone (text-fig. 9).

Using both lithological and faunal criteria, it is possible to correlate the top of the Callisto Cliffs section with the lower levels of Tombaugh Cliffs (text-figs. 5 and 9). A prominent band of massive sandstones between 935 and 1014 m at the former correlates well with a similar zone between 160 and 233 m at the latter (text-fig. 9). Few fossils occur in either zone, but both exhibit similar lithologies. Massively bedded sandstones predominate, separated by thinner, finely laminated beds of sandstone and siltstone, and irregular seams of conglomerate. The massive sandstones contain conspicuous cannonball concretions and show traces of shallow cross-bedding. The 156 m of siltstones beneath these sandstones at Tombaugh Cliffs (text-fig. 9) have yielded several types of bivalve (including *R. everesti*), the ammonites *Substreblites*, *Phylloceras*, and *Sarasinella*, and the belemnites *H. antarctica* and *H.* sp. nov. (?) (Willey 1972, 1973; Thomson 1974). Above the massive sandstone zone there is a 38-m siltstone zone (text-fig. 9) containing a prolific invertebrate fauna. Ammonites present include *Phyllopachyceras* (?), *Neocosmoceras*, *Himalayites*, and an indeterminate berriasellid, and there are at least four species of the belemnite genus *Hibolithes*. *Retroceramus everesti* is common, and there are also representatives of the genera *Pinna*, *Myophorella*, *Panopea*, *Grammatodon*, and (?) *Lucina*. Although the correspondence in terms of species composition is not exact, it would appear that this sequence of fossiliferous beds can be correlated in general terms with similar prolific horizons at the 1037 m level at Callisto Cliffs and 1710 m level at Ablation Valley (text-fig. 9) (see also Taylor *et al.* 1979, p. 17). There is no evidence of the ammonites *Haplophylloceras* and *Bochianites*, or of belemnopseid belemnites in this zone (i.e. between 233 and 271 m, text-fig. 9), but the latter do occur only a short distance higher up in the sequence. *Belemnopsis alexandri*, *B. gladiatoris*, and *B.* aff. *uhligi* have all been recorded between 274 and 455 m (Willey 1972). *Retroceramus everesti* is absent above the 246 m level at Tombaugh Cliffs (text-fig. 9).

Correlation of these three sections enables a sequence of inoceramid species to be established for the lower levels of the Fossil Bluff Formation (text-fig. 9). With the addition of two further species, *R. subhaasti* and *R. galoi*, a comprehensive scheme of Late Jurassic inoceramid biozones can be erected (Table 2) that facilitates stratigraphical correlations on both local and regional scales. *Retroceramus subhaasti* is placed beneath *R. haasti* in accordance with its occurrences in Misol and the Sula Islands (Indonesia), and *R. galoi* beneath *R. haasti* in accordance with its occurrences in the Sula Islands and New Zealand. To date, no clear indication has been given as to whether *R. subhaasti* and *R. galoi* can be stratigraphically separated, and thus they are grouped together in Table 2. *Anopaea stoliczkai* (Holdhaus) occurs at Belemnite Point (text-fig. 5) in strata equivalent to the *Virgatosphinctes–Aulacosphinctoides* zone at Ablation Point (Crame 1981*b*). It thus occurs stratigraphically above *R. haasti* but beneath *R. everesti* (text-fig. 9 and Table 2).

TABLE 2. A sequence of Southern Hemisphere Late Jurassic inoceramid biozones and their stratigraphical ranges. The ranges for the upper three species are based on their occurrences in the lower Fossil Bluff Formation of Alexander Island and the lower two species on their occurrences in Antarctica, New Zealand, and Indonesia. N.B. In this table and text-fig. 10 the broadest possible stratigraphical ranges have been given to *Retroceramus galoi*, *R. subhaasti*, and *R. haasti*. It is likely that in the future these ranges will be considerably refined

Inoceramid biozones	Stratigraphical range
Retroceramus everesti (Oppel)	Late Tithonian–Early Berriasian
Anopaea stoliczkai (Holdhaus)	Tithonian
Retroceramus haasti (Hochstetter)	Kimmeridgian–Early Tithonian
Retroceramus subhaasti (Wandel) *Retroceramus galoi* (Boehm)	? Early Kimmeridgian–Tithonian

Stratigraphical correlation within the Antarctic Peninsula

The use of inoceramids in correlation is discussed for the following occurrences.

1. The specimens of *R.* sp. cf. *subhaasti* from Carse Point on the west coast of the Antarctic Peninsula (text-fig. 1) come from a thin (75 m) marine sequence exposed at the base of a thick (900 m) series of tuffs and lavas belonging to the Antarctic Peninsula Volcanic Group. Associated ammonites (principally species of *Kossmatia*) indicate a Middle to Upper Tithonian age for the sedimentary rocks, but belemnites and bivalves suggest a broader Kimmeridgian to Upper Tithonian age range (Thomson 1975). The presence of *R.* sp. cf. *subhaasti* suggests that the marine beds at Carse Point may correlate with a level below that of the disturbed zone at Ablation Valley (text-fig. 9 and Table 2), and this may well explain why *Kossmatia* has not so far been recorded from Alexander Island. It is interesting to note that in the Late Jurassic deposits of New Zealand a *Kossmatia* zone occurs stratigraphically some distance beneath a Tithonian *Aulacosphinctoides* zone (e.g. Stevens 1965, fig. 13; Stevens and Speden 1978, table 2), although it should be emphasized that the exact status of some of the New Zealand *Kossmatia* specimens is uncertain (Verma and Westermann 1973; Thomson 1975, p. 41).

2. Marine fossils have also been recorded from sedimentary volcanic rocks within the Antarctic Peninsula Volcanic Group of Adelaide Island (text-fig. 1). Although the stratigraphy of the latter has yet to be fully resolved, the fossils (from locality T.535 at the south-west corner of the Mt. Bouvier massif) probably occur at a level close to the base of a 3000 m sequence of lavas and volcaniclastic rocks (Dewar 1970; Thomson 1972). Most of the specimens within the assemblage are poorly preserved, but at least one ammonite and two bivalves have general Jurassic affinities (Thomson 1972). The two best preserved specimens are the bivalves *Retroceramus* sp. nov. 2 and *R.* sp. juv.: the latter is undiagnostic, but the former also occurs in New Zealand in the Middle Kimmeridgian Ohauan stage (p. 586). Thus, it is likely that the Mt. Bouvier assemblage can be correlated with either the *R. haasti* or *R. subhaasti* zones of the standardized succession (Table 2). The existence of perhaps as much as 3000 m of volcanic rocks above a Late Jurassic marine horizon suggests that the Antarctic Peninsula Volcanic Group on Adelaide Island ranges well into the Cretaceous (see also Taylor *et al.* 1979; Jefferson 1980).

3. Fossiliferous sedimentary rocks also occur in close association with the Antarctic Peninsula Volcanic Group along parts of the east coast of Trinity Peninsula (Aitkenhead 1975). At Longing Gap (text-fig. 1) a 107 m sequence of siltstones and shales has been recorded as the probable source area for a series of loose ammonites and bivalves (Standring 1953). The exact stratigraphical relationship of these sedimentary rocks to the volcanic rocks exposed further inland is uncertain, but the occurrence of several tuffaceous bands in the sequence suggests that their formation was at least in part coeval with the volcanism. The fossils from Longing Gap are all poorly preserved: they occur as moulds in a fissile siltstone and all have been crushed and partially distorted. The two best preserved bivalves can be tentatively assigned to a new *Retroceramus* species (*R.* sp. nov. ?) with possible Late Jurassic affinities (p. 587), and there are perisphinctid ammonites which can be compared to Oxfordian or Kimmeridgian species (Aitkenhead 1975; Bibby 1966). There is some possibility, therefore, of a correlation with the disturbed zone at Ablation Valley (text-fig. 9; Table 2), but this must be regarded as tentative.

4. A small collection of poorly preserved marine invertebrates from Low Island, South Shetland Islands (text-fig. 1), contains an inoceramid that can probably be referred to *R. haasti* (M. R. A. Thomson, pers. comm.). The fossils occur in a thick sequence of volcaniclastic sediments which accumulated in a basin adjacent to an active island arc (Smellie 1980). The stratigraphy of these sediments is complex and at present their total thickness is unknown. However, they are at least partly Late Jurassic in age (Smellie 1980), and when the precise level of the fossiliferous horizon containing the specimen of (?) *R. haasti* has been determined, it will be possible to correlate the sequence directly with the Alexander Island succession.

5. Although no precise correlations can yet be made between the Fossil Bluff Formation of Alexander Island and the Jurassic Latady Formation, which crops out extensively in the region immediately to the south of the peninsula (text-fig. 1), a tentative comparison between these two major sedimentary units can be attempted. The Latady Formation, which is predominantly composed of fossiliferous, shallow-water volcaniclastic sediments, can be traced from the Lyon Nunataks–Behrendt Mountains region (eastern Ellsworth Land) northwards through the Orville and Lassiter coasts. The most detailed palaeontological studies of it to date have been carried out in the former of these regions; Quilty (1970) has recorded Middle Bajocian, Lower Callovian, and Oxfordian ammonites, and Stevens (1967) and Quilty (1977) Kimmeridgian belemnites and bivalves. *Retroceramus galoi* is common in this region and the overwhelming affinities would appear to be with the Heterian stage of New Zealand (Quilty 1977). So far, only preliminary palaeontological investigations have been carried out on the Orville and Lassiter coasts, but in both these regions there are

good indications of extensive Late Jurassic faunas (Rowley 1978; Thomson *et al.* 1978; Rowley and Williams, in press). On the Orville Coast there are perisphinctid-dominated ammonite assemblages with Kimmeridgian–Early Tithonian affinities (Thomson 1980) and large, coarsely-ribbed inoceramids that can almost certainly be referred to both *R. haasti* and *R. subhaasti*. A Kimmeridgian–Tithonian (or Ohauan) age for the Orville Coast faunas is strongly supported by the widespread occurrence of the bivalve *Malayomaorica malayomaorica* (Krumbeck). An easterly 'younging' trend through the Latady Formation from the Middle Jurassic and Early Kimmeridgian (Heterian) faunas of the Lyon Nunataks–Behrendt Mountains region to the later Kimmeridgian and Tithonian (Ohauan) faunas of the Orville Coast is further emphasized by the occurrence of berriasellid ammonites at Cape Zumberge, the most easterly extremity of the Orville Coast (Thomson 1980). These ammonites may well correlate with the berriasellid zone exposed in the lower levels of the Fossil Bluff Formation of Alexander Island (text-fig. 9). At present, it would appear that the Latady Formation faunas essentially predate those of the Fossil Bluff Formation; perhaps there is no more than approximately 500 m of stratigraphical overlap between the two units (Table 2 and text-fig. 9).

Regional correlations

Spiti. Recent work on the ammonite faunas from the lower levels of the Fossil Bluff Formation has shown that there are very strong links with the Late Jurassic ammonites of the Spiti Shales of the Himalayas (Thomson 1979). The Middle Spiti Shales are characterized by a distinctive perisphinctid assemblage in which the genera *Virgatosphinctes* and *Aulacosphinctoides* predominate, and this compares well with the assemblage present in the Ablation Valley section between 125 and 400 m (text-fig. 9) (Arkell 1956; Thomson 1979). The Upper Spiti Shales contain genera such as *Spiticeras*, *Berriasella*, *Blandfordiceras*, *Himalayites*, *Kossmatia*, *Kilianella*, *Sarasinella*, and *Bochianites* (Arkell 1956, p. 407), and can be correlated with the Ablation Valley section above the 400 m level, with the whole of the Callisto Cliffs section, and with the Tombaugh Cliffs section below the 271 m level (text-fig. 9). This correlation is strengthened by the occurrence of *R. everesti* in the Upper Spiti Shales, Callisto Cliffs, and Tombaugh Cliffs.

The Lower Spiti Shales, containing *Belemnopsis uhligi* Stevens, *B. alfurica* (Boehm), and several ammonites with Oxfordian affinities, have a probable age range of Upper Oxfordian–Middle Kimmeridgian (Stevens 1965, p. 149). A large, coarsely ribbed inoceramid from the same beds has been identified as *Inoceramus* cf. *sularum* (Holdhaus 1913, p. 420), but it has already been suggested (p. 566) that this specimen may in fact belong within *R. haasti*. The occurrence of *B. alfurica*, ammonites with Oxfordian affinities, and an inoceramid which is perhaps close to *R. haasti*, all suggest a possible correlation of the Lower Spiti Shales with the disturbed zone in the Ablation Valley section (text-fig. 9).

Thus, the Lower, Middle, and Upper Spiti Shales can be directly correlated with the lower levels of the Fossil Bluff Formation in eastern Alexander Island (text-fig. 10). However, there is very little precise stratigraphical information available for the Spiti sequence and no detailed comparisons can be made between the two areas. The majority of the Spiti specimens are unlocalized, and there are, as yet, no accurately measured sedimentary successions available for correlation purposes (Arkell 1956; Helmstaedt 1969; Mouterde 1971).

New Zealand. The Late Jurassic deposits of New Zealand have been divided into three stages: the Heterian, Ohauan, and Puaroan (see, e.g., Marwick 1953; Stevens and Speden 1978). *Retroceramus galoi* serves as a useful indicator for the Heterian, in which there are also three ammonite zones (the *Epicephalites*, *Idoceras*, and *Kossmatia* zones, in ascending order); the boundary between the latter two zones has been taken to coincide with the Lower–Middle Kimmeridgian boundary (Arkell, *in* Fleming and Kear 1960). The *Kossmatia* zone continues into the overlying Ohauan stage, which is characterized by *R. haasti*. The distinctive specimen of *Inoceramus* sp. cf. *subhaasti* (= *R.* sp. nov. 2) occurs just above the Heterian–Ohauan boundary in the Lower Kowhai Point Siltstone (Fleming and Kear 1960).

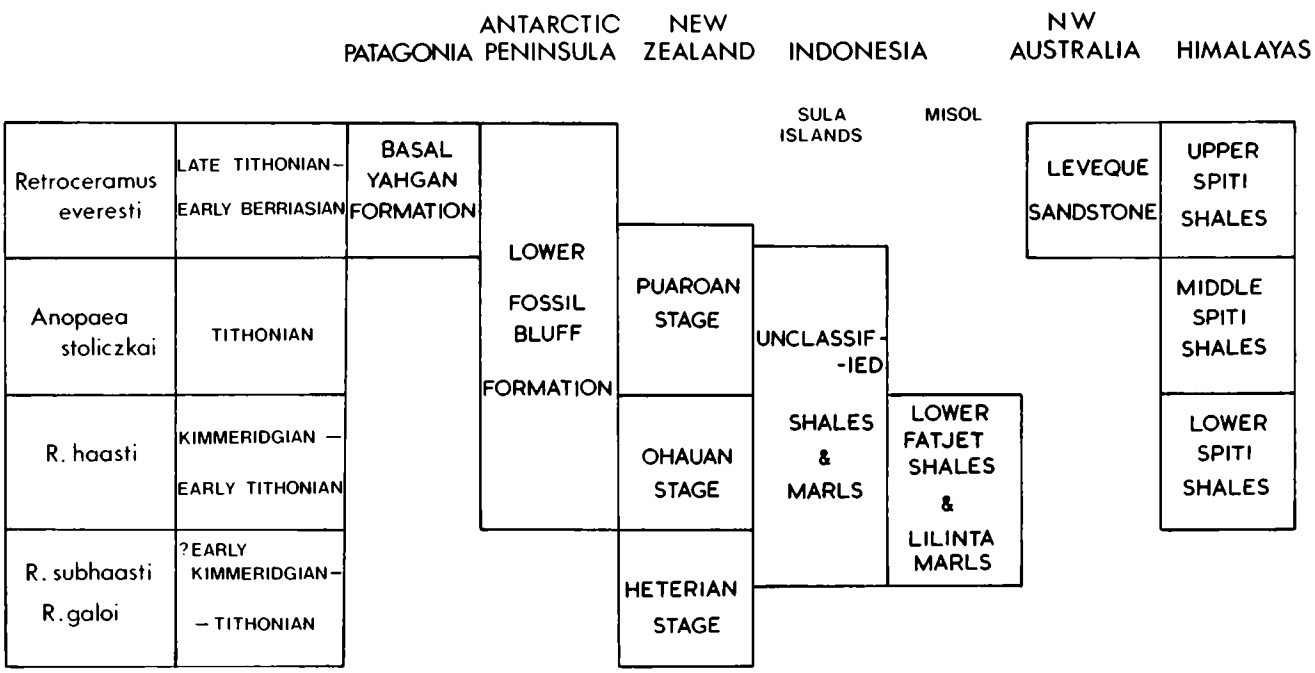
Two ammonite zones can be recognized in the Ohauan stage; a *Kossmatia* zone (continued from the top of the Heterian) and a later *Paraboliceras* zone (Arkell, *in* Fleming and Kear 1960). The latter passes up into an *Aulacosphinctoides* zone which marks the transition from Middle

Kimmeridgian to Lower Tithonian strata, and the beginning of the Puaroan stage (e.g. Stevens 1965, fig. 13; Speden 1970, table 1). This *Aulacosphinctoides* zone may be particularly useful for overseas correlations as it appears to have species in common with both Antarctica and Spiti. One specimen of *A.* aff. *sparsicosta* (Uhlig) from the 125–400 m zone at Ablation Valley (text-fig. 9) is close to the Puaroan species *A. brownei* (Marshall) (Thomson 1979, p. 22), and there may be several species of *Aulacosphinctoides* and *Uhligites* in common between the Puaroan stage and the Middle Spiti Shales (Stevens and Speden 1978, p. 268).

The Puaroan stage in New Zealand consists of a basal sequence of interbedded sandstones and conglomerates which passes up into a thick sequence of fossiliferous siltstones (the Puti Siltstones). The total thickness of the stage is approximately 1500 m (Stevens and Speden 1978, fig. 18). *Aulacosphinctoides brownei* ranges through most of the stage, but *R.* aff. *everesti* is restricted to the topmost levels (Stevens 1965, fig. 13). Other characteristic fossils include several species of *Buchia* and belemnites of the *B. uhligi* complex (Stevens and Speden 1978; Stevens 1965).

As no precise match can be made between the faunas of the Fossil Bluff Formation and those of the Heterian stage, it is likely that the latter (containing *R. galoi*) correlates with a level below that of the lowest exposed level in eastern Alexander Island (text-figs. 9 and 10). The overlying Ohauan stage contains *R. haasti* and thus correlates with at least part of the disturbed zone in the Ablation Valley section (text-figs. 9 and 10). In New Zealand, *R. haasti* occurs in the Lower Ohauan, between the *Kossmatia* and *Paraboliceras* zones (Stevens 1965, fig. 13).

The presence of a distinctive *Aulacosphinctoides* assemblage suggests that the Puaroan stage can be correlated with a fairly low level in the Fossil Bluff Formation (text-figs. 9 and 10). However, this *Aulacosphinctoides* zone is almost certainly much more extensive than the one exposed in Ablation Valley as it extends through several hundreds of metres of strata (Stevens 1965, fig. 13). *Retroceramus* aff. *everesti* occurs near the top of the Puaroan stage, which has traditionally been regarded as no younger than Middle Tithonian (e.g. Stevens 1965; Speden 1970). Thus, the Puaroan stage as a whole, which also contains belemnites of the *B. uhligi* complex and species of *Hibolithes* (Stevens 1965), correlates with approximately the middle levels of the Ablation Valley section and lower levels of the Callisto Cliffs section (text-figs. 9 and 10). The presence of *Aulacosphinctoides*,



TEXT-FIG. 10. Regional correlations in the Late Jurassic of the Southern Hemisphere. The stratigraphic units in each region have been correlated using the inoceramids listed at the left-hand side of the figure and associated ammonites and belemnites. Full details of the correlations are given in the text.

R. aff. *everesti* and belemnites of the *B. uhligi* complex suggests that it can also be correlated with the Middle Spiti Shales (Stevens 1965). In New Zealand, strata of Puaroan age are overlain by an essentially non-marine sequence (the Huriwani Formation) which probably spans the Jurassic-Cretaceous boundary (Stevens and Speden 1978).

It must be emphasized that the outline of New Zealand stratigraphy presented so far is essentially the conventional one based on the ammonite identifications of Arkell (*in* Fleming and Kear 1960) and the belemnite and buchiid bivalve determinations by Stevens (1965) and Fleming (1959), respectively. It has already been mentioned (p. 567) that an alternative view of the New Zealand Late Jurassic stratigraphy places the greater part of the entire sequence within the Late Tithonian. Enay (e.g. 1973) believes that there is no Early Tithonian in any part of the Indo-Pacific province, and that assemblages containing ammonites such as *Kossmatia*, *Paraboliceras*, and *Aulacosphinctoides* should all be regarded as Late Tithonian. Applying Enay's (1973) views to the New Zealand succession implies that the Heterian *Kossmatia* zone, and all succeeding zones, are Late Tithonian in age. As the Lower Heterian *Idoceras* and *Epicephalites* zones are presumably still assigned to the Lower Kimmeridgian, there must be a considerable non-sequence (spanning perhaps the whole of the interval between the Middle Kimmeridgian and the Middle Tithonian) within the Heterian stage. However, there is little evidence of a major break within the stratigraphical succession, and the existence of such a large diastem in the New Zealand Late Jurassic is questionable (Stevens and Speden 1978, p. 267). Obviously, the precise relationships of the New Zealand Late Jurassic stages to the international stratigraphical divisions have yet to be fully resolved (Stevens and Speden 1978, p. 267).

Indonesia. There is considerable potential for including the Late Jurassic inoceramid faunas of Indonesia within the zonation scheme outlined above. Preliminary investigations in the Sula Islands suggest that *R. galoi*, *R. subhaasti*, and *R. haasti* all occur within a 100–150 m sequence of silty shales that has an approximate age range of Kimmeridgian–Middle Tithonian (Westermann *et al.* 1978, p. 98). These beds, which also contain species of *Belemnopsis*, *Buchia*, and *Malayomaorica*, as well as occasional perisphinctid ammonites, can be tentatively correlated with the Lower Spiti Shales, the Ohauan stage of New Zealand, and the disturbed zone in the Ablation Valley section of Alexander Island (text-fig. 10). Overlying the silty shales is a sequence of marly claystones (100–500 m thick) containing *Haplophylloceras*, *Blandfordiceras*, *Virgatosphinctes*?, indeterminate haploceratids, phylloceratids, and lytoceratids, and the bivalves *Buchia* cf. *plicata* Zittel and *Anopaea*? *stoliczkai* (Westermann *et al.* 1978). The occurrence of the last-named species, together with an ammonite assemblage that includes both *Virgatosphinctes*? and *Blandfordiceras*, suggests a possible correlation with the level of the *Virgatosphinctes–Aulacosphinctoides* zone in the Ablation Valley section (text-fig. 9). This zone can be further correlated with the Middle Spiti Shales and the Lower Puaroan stage of New Zealand (text-fig. 10).

The occurrence in Misol of *R. subhaasti* in the Lilinta Marls and *R. haasti* in the Lower Fatjet Shales (Stevens 1965, table 13) suggests that these two rock units can be correlated with the Kimmeridgian–Middle Tithonian shales of the Sula Islands (text-fig. 10). However, the overlying Upper Fatjet Shales and Lower and Upper Fatjet Limestones apparently lack diagnostic fossils and cannot be readily correlated with beds in other regions.

New Guinea, New Caledonia, Timor, and Western Australia. Correlation by inoceramid biozones can also be extended to include the Late Jurassic deposits of regions such as New Guinea, New Caledonia, Timor, and Western Australia. Members of the *galoi–subhaasti–haasti* group of species probably occur in both New Guinea and New Caledonia (Glaessner 1945; Avias 1953; Routhier 1953; Stevens 1965; Skwarko 1967; see pp. 564, 566), and *R. haasti* is present in Timor (pp. 564, 566; Krumbeck 1923).

The presence of *Inoceramus* sp. nov. *a*, *b*, and *c* (= *R. everesti*) in the Leveque Sandstone of Dampier Land, Western Australia (Brunnschweiler 1960), may be particularly useful for correlating the Late Jurassic–Early Cretaceous deposits of the Canning Basin with those of other areas. The first prominent Late Jurassic deposit in the Canning Basin, the Alexander Formation, consists of

at least 70 m of siltstone with fine interbedded shale layers (Veevers and Wells 1961). It contains ammonites which have been tentatively identified as belonging to the genera *Virgatosphinctes* and *Kossmatia* (Ludbrook 1978, p. 224) and can probably be dated as Kimmeridgian–Early Tithonian (Veevers and Wells 1961). The oldest beds exposed in the Dampier Peninsula, the Langey Beds, have yielded specimens of *Belemnopsis* cf. *aucklandica* (Hochstetter), *B.* cf. *alfurica* (Boehm), *Kossmatia* cf. *tenuistriata* (Gray), and *Malayomaorica malayomaorica* (Krumbeck): they thus have a probable age range of Middle Kimmeridgian–Middle Tithonian (Brunnschweiler 1960), and may perhaps be taken to post-date the Alexander Formation (Ludbrook 1978, table 1). The Langey Beds pass up into the extensive Jowlaenga Formation (at least 230 m of sandstones and siltstones) which contains both Late Jurassic and Early Cretaceous faunal elements (Brunnschweiler 1960, p. 37). The succeeding Broome Sandstone is at least 300 m thick, but may be, in part, laterally equivalent to the Jowlaenga Formation (Veevers and Wells 1961). It is essentially a non-marine deposit and contains fossil plants with both Late Jurassic and Early Cretaceous affinities. The Leveque Sandstone, from which the specimens of *R. everesti* were collected (Brunnschweiler 1960), is believed to overlie the Broome Sandstone, but is known from only one isolated locality (where it is 10 m thick) (Brunnschweiler 1960; Veevers and Wells 1961). It has been assumed to be Neocomian, largely on the alleged affinities of its inoceramid fauna (Brunnschweiler 1960), but *R. everesti* is now known to transgress the Jurassic–Cretaceous boundary (p. 583), and it would appear that the Leveque Sandstone could equally well be Late Jurassic or Early Cretaceous (or both) in age (text-fig. 10).

South America. Although the former geological continuity of southern South America, the Scotia Arc, and the Antarctic Peninsula has now been established beyond doubt (see, e.g., Barker and Griffiths 1972, 1977), very few palaeontological correlations have been attempted between these now widely separated regions. This is partly due to the lack of detailed stratigraphical studies in certain key areas (especially in South America), and partly to the different tectonic settings of the major sedimentary basins. Whereas the Fossil Bluff Formation, in which comparatively shallow shelf sediments predominate, accumulated in a fore-arc or intra-arc basin, both the Cumberland Bay Formation of South Georgia and Yahgan Formation of southern Patagonia accumulated in an extensive back-arc basin (e.g. Suárez and Pettigrew 1976, fig. 7; Dott, Winn and Smith, in press, fig. 1). Deep-water turbidite facies predominate in both the latter formations and fossils are rare. However, Katz and Watters (1966) recorded several specimens of *Inoceramus* sp. (= *R. everesti*) from the Yahgan Formation of Navarino Island, and these may be of considerable importance for regional correlations (text-fig. 10).

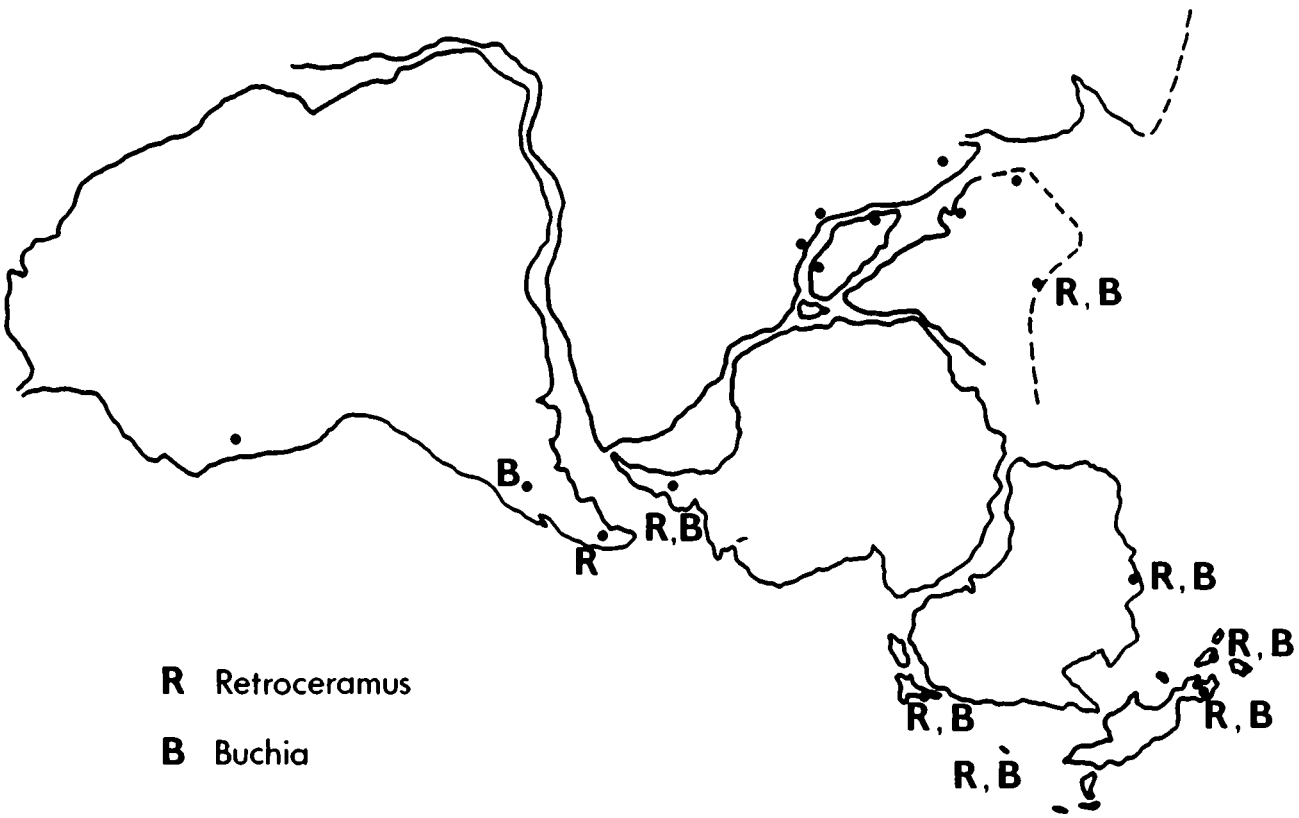
The Yahgan Formation is predominantly composed of volcaniclastic turbidites and shales, and has a total thickness in the region of 4–5 km. Its base is probably within the Late Jurassic, but it ranges up into well within the Neocomian (Winn 1978, p. 537). Although well exposed on Navarino Island, the Yahgan Formation cannot be accurately defined, and no type section has yet been established for it (Katz and Watters 1966). Judging from their occurrence between two prominent sills (Katz and Watters 1966, figs. 15 and 16), the specimens of *Inoceramus* sp. probably occur at least 1000 m above the base of an estimated 3000 m sequence, but no other distinctive faunal horizons have been recognized.

Strata of equivalent age to those of the Yahgan Formation can be traced further north in Patagonia along the Chile–Argentina border. Fossiliferous mudstones occur in both the Ultima Esperanza and Lago Argentina regions (Feruglio 1936, 1949; Dott *et al.*, in press), but again, very few specimens can be precisely localized. This is unfortunate, for the latter region has yielded a fossil assemblage that shows strong similarities to that found in parts of the Ablation Valley section of eastern Alexander Island. This assemblage, collected from the Cerro de los Fosiles (to the north of Estancia del Quemado), contains the ammonites *Aulacosphinctoides*, *Virgatosphinctes*, *Corongoceras*, *Berriasella*, *Blandfordiceras*, *Steueroceras*, and *Favrella*, as well as *Inoceramus* cf. *steinmanni* (= *R. everesti*) and *Belemnopsis patagoniensis* (Favre) (? = *B. gladiatoris* Willey 1973, p. 33) (Feruglio 1936, 1949, p. 169). It would appear that all the above-listed ammonites were collected

60–80 m above the base of a 1000 m section (Feruglio 1949, pp. 168–169). Approximately 200 m higher up in this section there is a *Holcoptychites* zone containing *Holcoptychites*, *Berriasella*, and *Acanthodiscus*, and 200 m above this a *Favrella* zone containing *Favrella*, *Phylloceras*, *Inoceramus anomaeformis* Feruglio, and *I.* aff. *posidonomyaeiformis* Maury (Feruglio 1936, 1949). The *Aulacosphinctoides–Virgatosphinctes–Berriasella* zone can be dated as Tithonian–Berriasian, and the *Holcoptychites* and *Favrella* zones as Berriasian, but it must be emphasized that the stratigraphy in this region can at best only be regarded as tentative. In a reappraisal of Feruglio's (1936) material, Leanza (1967) indicated that at the Cerro de los Fosiles locality, *I.* cf. *steinmanni* (= *R. everesti*) occurs at a level above that of the *Aulacosphinctoides–Virgatosphinctes–Berriasella* zone, but no indication is given as to the extent of this separation. It can only be concluded that the Cerro de los Fosiles locality correlates in general terms with the lower levels of the Fossil Bluff Formation in eastern Alexander Island. More precise stratigraphical data are required before a detailed correlation is attempted.

DISTRIBUTION

At first sight, the occurrence of the genus *Retroceramus* in Antarctica might be taken as evidence for the existence of a Late Jurassic Southern Hemisphere Austral (or anti-Boreal) faunal realm. It was obviously an important component of many benthic assemblages, and when taxonomic studies of the Lassiter and Orville Coast faunas have been completed there may well be an equivalent diversity of species in Antarctica to that known from the Siberia–Alaska region. However, it will be apparent from the foregoing stratigraphical discussion that *Retroceramus* is, in fact, distributed around much of what were the margins of the ancient Gondwana supercontinent (text-fig. 11). It can be traced from South America through Antarctica to New Zealand, Indonesia,



TEXT-FIG. 11. The occurrence of the genera *Retroceramus* and *Buchia* in the Southern Hemisphere. Black dots indicate localities where Late Jurassic bivalves have been collected: note the absence of both *Retroceramus* and *Buchia* from the Ethiopian province. The Late Jurassic reconstruction of Gondwana is based on that given by Smith and Briden (1977, Map 35).

North-west Australia, and the Himalayas, as indeed can other 'Boreal' genera such as *Buchia* and *Anopaea* (Fleming 1959; Stevens 1965; Quilty 1977; Taylor *et al.* 1979; Crame 1981*b*). These occurrences over a considerable latitudinal range (text-fig. 11) argue against any purely climatic control of distribution and suggest instead that there may well have been some form of control by the prevalent environments of deposition. The southern margins of Gondwana in the Late Jurassic were essentially formed by a series of narrow and deep tectonic basins comprising the so-called circum Gondwana geosynclines (see, e.g., Fleming 1979, fig. 2, and Audley-Charles 1978, fig. 3). Shelves along the inner edges of these basins would have sloped comparatively steeply into deep water and many appear to have been subjected to both high rates of sedimentation and periods of tectonic instability (see, e.g., Taylor *et al.* 1979, p. 38; Bell 1975). It would seem that the benthic faunas best able to cope with these sorts of conditions were low diversity-high abundance assemblages in which epifaunal bivalves (especially inoceramids and buchiids) predominated. Inoceramids and buchiids are conspicuously absent from the coeval Southern Hemisphere Ethiopian province (text-fig. 11), which was centred on a shallow epicontinental sea.

CONCLUSIONS

1. Most of the inoceramid bivalves occurring in Southern Hemisphere Late Jurassic temperate realm assemblages can be assigned to the genus *Retroceramus*. Typically obliquely elongated, equivalve, and bearing patterns of simple concentric ornament, *Retroceramus* can often be distinguished from *Inoceramus* on the basis of external morphology alone. However, a further diagnostic feature is available in the structure of the respective ligament areas. In *Retroceramus* the ligament pits are typically large, rounded-rectangular to oval in outline, and somewhat irregular in their distibution, whereas in *Inoceramus* they are narrow and elongated, and are typically arranged in a uniform series set adjacent to the hingeline.

A few Late Jurassic species cannot be easily assigned to either *Retroceramus* or *Inoceramus*, and some, such as *R. everesti* (Oppel), may be intermediate forms between the two genera. Similar problems in establishing clear-cut generic boundaries are encountered in other epifaunal bivalve groups (such as the Mytilidae—see Newell 1942).

2. *Retroceramus* was replaced by *Inoceramus* in the Early Cretaceous and it is thought that this change may be linked to the widespread assumption at this time of the epibyssate habit by inoceramids. Functional interpretations suggest that *Retroceramus* was an essentially endobyssate genus but that Early Cretaceous *Inoceramus* species were predominantly epibyssate. This fundamental change in life habit enabled new substrate types to be occupied and a variety of growth forms to be adopted, and thus paved the way for the progressive diversification of *Inoceramus* through the Cretaceous. This represents one of a series of major endo- to epibyssate life habit transitions which occurred during the evolutionary history of the Inoceramidae. Such transitons are probably best explained as a sequence of neotenous oscillations.

3. Four common species of *Retroceramus* (*R. galoi*, *R. subhaasti*, *R. haasti*, and *R. everesti*) can be recognized in Kimmeridgian to Tithonian strata in the Southern Hemisphere. Each of these species is characterized by a considerable degree of morphological variation and it is possible that future studies may permit the establishment of a number of subspecies. These four species occur in consistent stratigraphical succession around the southern margins of Gondwana and form the basis of an inoceramid biozonation scheme that can be used for both local and regional correlations. Small, isolated exposures within the Antarctic Peninsula can be correlated with the Fossil Bluff Formation of Alexander Island and in time it should be possible to correlate the latter unit in detail with the extensive Latady Formation of the Lassiter and Orville coasts, and eastern Ellsworth Land. Use of the same inoceramid biozones, together with those based on associated cephalopods, suggests that the lower levels of the Fossil Bluff Formation correlate with the Lower, Middle, and Upper Spiti Shales of the Himalayas and with the Ohauan and Puaroan stages of New Zealand. Correlations can also be extended to South America, New Caledonia, New Guinea, Indonesia, Timor, and Western Australia.

Late Jurassic inoceramid bivalves from western Antarctica offer considerable scope for further palaeobiological and biostratigraphical investigations. However, care must be exercised in the identification of species, for there are a number of apparent instances of homeomorphy between Middle and Late Jurassic forms. When taxonomic studies have been completed, western Antarctica should become one of the standard stratotypes for Late Jurassic inoceramid bivalves.

4. Although the Boreal bivalve genera *Retroceramus*, *Buchia*, and *Anopaea* are common in the Late Jurassic of western Antarctica, their presence does not necessarily indicate the existence of a Southern Hemisphere anti-Boreal faunal realm. Closer examination of the distribution of these three genera reveals that they can, in fact, be traced around much of what were the southern margins of Gondwana. Their distribution seems to have been controlled primarily by the prevalent sedimentary facies, rather than by the existence of any pronounced climatic zonation.

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