

Biogeographical and stratigraphical significance of the latest Turonian and Early Coniacian inoceramid/ammonite succession of the Manasoa section on the Onilahy River, south-west Madagascar

I. Walaszczyk*, R. Marcinowski, T. Praszkier, K. Dembicz, M. Bieńkowska

Institute of Geology, University of Warsaw, Al. Zwirki i Wigury 93, PL-02-089 Warszawa, Poland

Received 29 October 2003; accepted in revised form 2 May 2004

Abstract

Recent, bed-by-bed fossil collections from Manasoa on the Onilahy River, south-west Madagascar, reveal the stratigraphical succession of the inoceramid and ammonite faunas of the topmost Turonian through Lower and possibly lower Middle Coniacian of the area. Six successive interval inoceramid zones are recognised; from bottom upward these are zones of *Tethyoceramus modestoides*, *Tethyoceramus madagascariensis*, *Tethyoceramus basseae*, *Tethyoceramus ernsti*, *Inoceramus? nukeus*, and *Inoceramus* sp. aff. *pacificus*. The *T. modestoides* Zone lies within the Turonian. The base of the *T. madagascariensis* Zone marks the base of the Coniacian; all higher zones also lie within the Coniacian. The succession identified correlates well with other areas of the Southern Hemisphere and, to a lesser degree, with the Euramerican succession.

The inoceramid faunas of the topmost Turonian through lower Coniacian of Madagascar are very similar to those of Zululand and are closely related to other Southern Hemisphere faunas. The Madagascan faunas are, however, clearly distinct from Euramerican faunas. The rich ammonite assemblage of the Manasoa section is dominated by endemic species characteristic of the Malgascan province, with only few forms known from Japan, Alaska and Europe. All of the ammonites represent the *Barroisiceras onilahyense-Kossmaticeras (K.) theobaldianum* Zone, which is shown to correspond to possibly topmost Turonian and Lower Coniacian.

Taxonomic descriptions of the inoceramid species are provided, with range data and photographic documentation.
© 2004 Elsevier Ltd. All rights reserved.

Keywords: Inoceramids; Ammonites; Biostratigraphy; Biogeography; Correlation; Turonian; Coniacian; Madagascar; Southern Hemisphere

1. Introduction

The literature on the Late Cretaceous inoceramids of southern continents is unevenly distributed and undoubtedly inadequate. Most descriptions of faunas are not accompanied by precise section records, a fact that hinders stratigraphical and palaeontological interpretation. Better knowledge of this group, which is characterised by many cosmopolitan taxa and high rates of

evolution, would improve their use in biostratigraphy and in south–north stratigraphical correlations, as demonstrated recently even in the case of the endemic New Zealand fauna (Crampton, 1995, 1996).

The present paper details the inoceramid fauna of the topmost Turonian to basal Middle Coniacian succession at Manasoa on the Onilahy River, south-west Madagascar. Also documented are the ammonites, a group that is quite common in the lower part of the succession. The Manasoa section is one of the classic Madagascan localities (see Basse, 1947; Besairie, 1972, p. 367). It is also the type locality of several ammonite and inoceramid taxa, including *Barroisiceras onilahyense* Basse,

* Corresponding author.

E-mail address: i.walaszczyk@uw.edu.pl (I. Walaszczyk).

Tethyoceramus madagascariensis (Heinz) and *Tethyoceramus bassae* (Sornay, 1980). The co-occurrence of inoceramid and ammonite faunas, the accessibility of the section, and the abundance of fossils make the Manasoa on Onilahy section a perfect reference section for the topmost Turonian to basal Coniacian of the Southern Hemisphere. It clarifies a number of questions concerning the inoceramid biostratigraphy and biogeographic affinities of the Southern Hemisphere. The nature of the inoceramid fauna also allows a precise correlation, at least in a part of the succession, with the Euramerican biogeographical region.

The material considered herein was collected by the three junior authors (TP, KD and MB), during their 2001 expedition to Madagascar.

2. Lithological and faunal succession

The uppermost Turonian–lower Coniacian succession near Manasoa is exposed in the western bank of the Onilahy River (Fig. 1). It is composed of alternating beds of poorly cemented sandstone, dominating the succession, and relatively thin beds of distinctly harder calcareous sandstone (Figs. 2–4). Numerous horizons

of sandstone concretions occur in the lower half of the succession, and form more or less continuous beds. The whole succession is capped by basalts of Santonian–Campanian age (Besairie, 1930, 1972).

The lower two-thirds of the section (Fig. 2) is very fossiliferous up to bed 29. Inoceramids and ammonites dominate; other bivalves and gastropods are abundant locally. The fossils come mostly from the calcareous sandstone and concretionary horizons; a few come from the poorly cemented sandstone. They are preserved mostly with their shell intact, although collecting shelly specimens is very difficult because the shells are firmly attached to the matrix.

The succession starts with a unit 5 m thick (bed 0) of weakly cemented quartz sandstone with fine grains of mica, gypsum crystals, and numerous horizons with secondary cementation, up to 30 cm thick. No faunal remains were found in this unit, either in loose sands or in sandstones.

The oldest fossiliferous horizon is a 30–50-cm-thick bed (bed 1) of grey, strongly cemented calcareous sandstone capping bed 0 (Fig. 2), containing abundant ammonites, bivalves and gastropods. The fossils are scattered throughout the bed and do not show any preferred orientation. Both the lower and upper surfaces of the bed

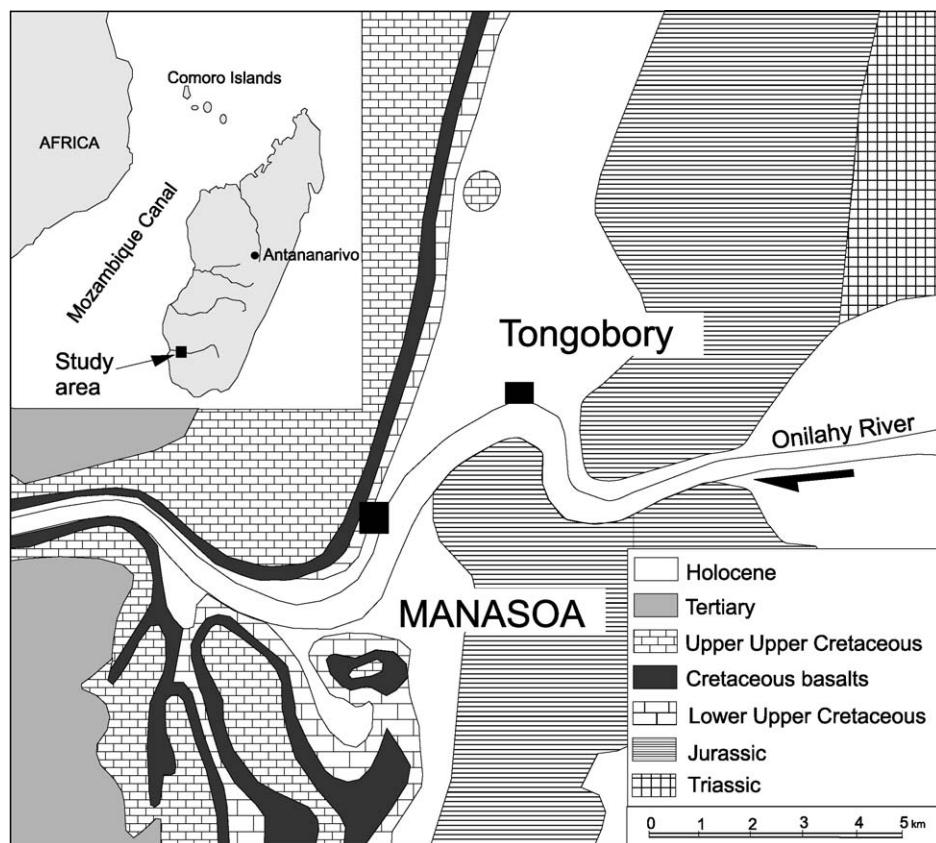


Fig. 1. Geological sketch-map of the area around Manasoa (simplified after Besairie, 1930). The Cenomanian–Santonian forms a narrow north–south outcrop below the basalts. Manasoa is a little more than 50 km east of St. Augustin on the west coast of Madagascar.

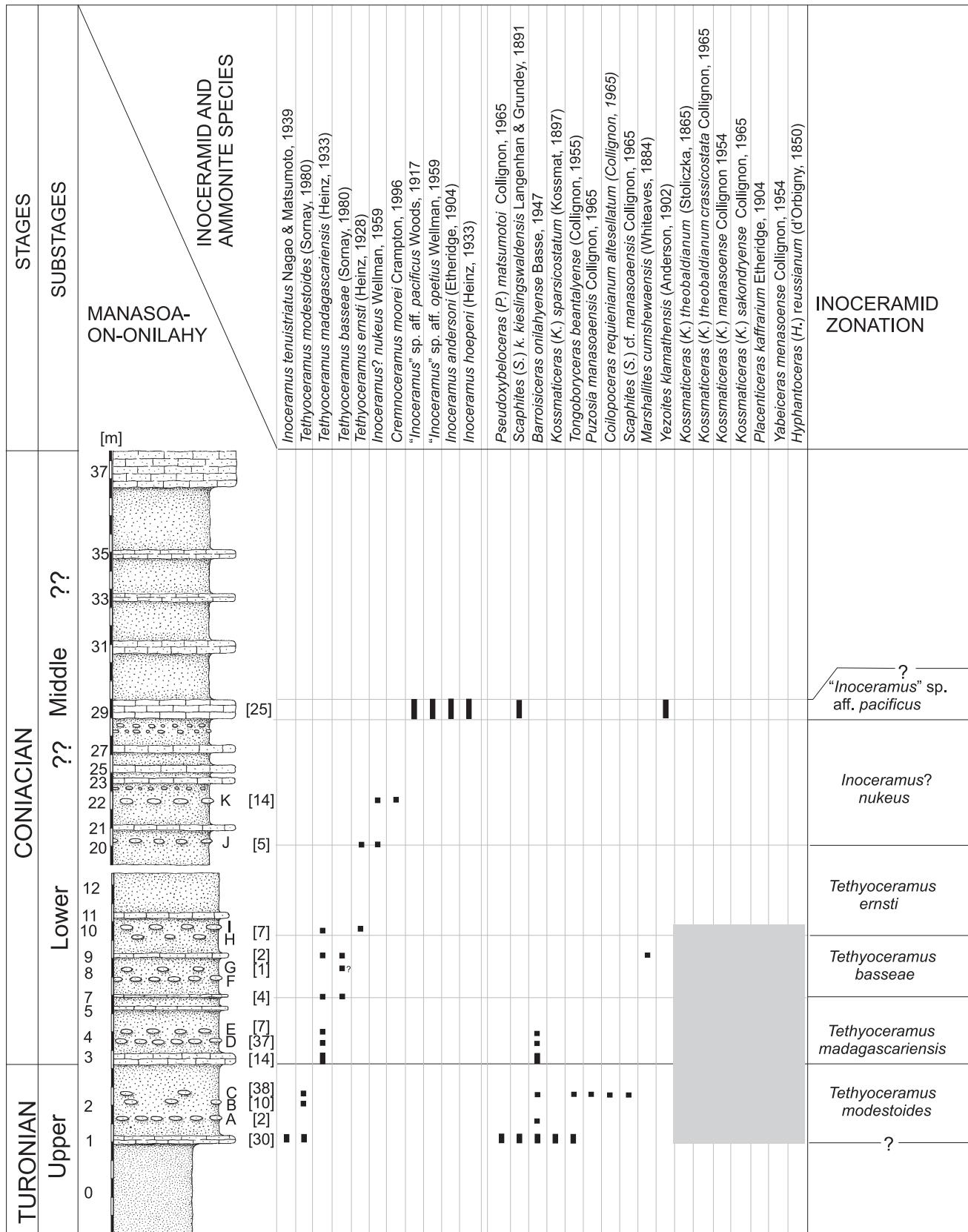




Fig. 3. View of the upper (A) and middle (B) parts of the succession in Manasoa.



Fig. 4. View of the lowermost part of the section (beds 1–3) (A), the base of bed 1 (B) and of bed 29 (C).

are very uneven, the lower one having a concretionary character (Fig. 4). The bed yielded a rich ammonite fauna of *Pseudoxybeloceras* (*Pseudoxybeloceras*) *matsumotoi* Collignon, 1965 (Fig. 7A); *Scaphites* (*Scaphites*) *kieslingswaldensis kieslingswaldensis* Langenhan and Grundey, 1891 (Fig. 10E) [= *Scaphites* (*Scaphites*) *meslei* de Grossouvre, 1894; *S. meslei* var. *masiopensis* Collignon, 1965; *S. arnaudiformis* Collignon, 1965]; *Barroisiceras* *onilahyense* Basse, 1947 (Fig. 7D), *Kossmaticeras* (*Kossmaticeras*) *sparsicostatum* (Kossmat, 1897) (Fig. 8) and *Tongoboryceras beantalyense* (Collignon, 1955). Although inoceramids are common, they are much poorer taxonomically. Besides single specimens of *Inoceramus tenuistriatus* Nagao and Matsumoto, 1939 (Fig. 11B) all other specimens collected are referred to *Tethyoceramus modestoides* (Sornay, 1980) (Fig. 12).

The overlying 4-m-thick unit (bed 2), is composed of poorly cemented, grey-green, fine-grained sandstone with scattered, irregularly and poorly preserved fossils. The lower half of the bed contains three distinct concretionary horizons (labelled, from bottom upward, A–C) yielding well-preserved ammonites and inoceramids. Horizon A, although not well seen in the field, represents a laterally continuous level of densely packed nodules. The fauna is relatively rare. The only ammonite found is *Barroisiceras onilahyense* Basse, 1947. Abundant and well-preserved inoceramids occur in horizon B. The concretions are much scarcer here. Rare nodules also occur in the next horizon (C), which is the most fossiliferous of the unit. Besides numerous inoceramids, representing the single species *Tethyoceramus modestoides* (Figs. 11, 12), the bed has yielded diverse ammonites: *Puzosia manasaensis* Collignon 1965 (Fig. 9E); *Tongoboryceras beantalyense* (Collignon, 1955) (Fig. 7C); *Barroisiceras onilahyense* Basse, 1947; *Coilopoceras requienianum altesellata* (Collignon 1965) (Fig. 10G); and *Scaphites* (*Scaphites*) cf. *manasaensis* Collignon, 1965 (Fig. 10D).

The overlying bed of strongly cemented, greyish green calcareous sandstone (bed 3), 50–70 cm thick, is lithologically very similar to bed 1. In contrast, however, it is not very fossiliferous, yielding, mainly in its uppermost part, inoceramid bivalves. Again, the inoceramids are poorly diversified with a single species, *Tethyoceramus madagascariensis* (Heinz, 1933) (Figs. 13A, 14A, B) represented. A single ammonite, *Barroisiceras onilahyense*, was found.

Above this, the next bed of poorly cemented sandstone (bed 4) contains two concretionary horizons, D and E. Horizon D, about 0.7 m above the base of the bed, contains numerous concretions spaced about 1 m apart. Some of these, ellipsoidal in shape and up to 50 cm across, are full of inoceramids and ammonites. Both groups, however, are monospecific, represented exclusively by *T. madagascariensis* (Fig. 13B, C, E–I) and *B. onilahyense* respectively.

Horizon E is located about 1.2 m above the base of the bed, and is composed of spherical concretions up to 30 cm in diameter, with rare inoceramids, represented by *T. madagascariensis* (Fig. 13D), and very rare ammonites, limited to a single species, *B. onilahyense*.

Higher up in the section, up to bed 29, well-preserved and abundant inoceramids are known from beds 10, 20 and 22. Very characteristic is the sample from bed 10, represented exclusively by huge, single-valved specimens, referred here to *Tethyoceramus ernsti* (Heinz, 1928) (Figs. 15–18). Bed 22, and possibly also bed 20, yield well-preserved material of *Inoceramus?* *nukeus* Wellman, 1959 (Fig. 19). Inoceramids have also been recorded from other beds, particularly between horizon E (bed 4) and bed 10, with well-preserved specimens of *T. madagascariensis* and *T. bassae* (Sornay, 1980) (Fig. 14C–G), but in these beds they are not abundant and do not form shell-beds. In the whole interval ammonites are extremely rare, with a single *Marshallites cumshewaensis* (Whiteaves, 1884) found in bed 9 (Fig. 10A).

A number of ammonite species from an interval below bed 10 down to bed 1 were found loose (Fig. 2). This material, composed usually of well-preserved specimens, contains mainly representatives of the genus *Kossmaticeras*, but also of the genera *Placenticeras*, *Yabeiceras* and a single find of *Hyphantoceras* (Figs. 2, 7B, E, 9A–D).

Ammonites and inoceramids are very common and diverse in bed 29. This shell-bed yielded *Yezoites klamathensis* (Anderson, 1902); *Scaphites* (*Scaphites*) *kieslingswaldensis kieslingswaldensis* Langenhan and Grundey, 1891 [= *Scaphites* (*Scaphites*) *meslei* de Grossouvre, 1894; *S. meslei* var. *masiopensis* Collignon, 1965; *S. arnaudiformis* Collignon, 1965], as well as *Inoceramus andersoni* (Etheridge, 1904) (Fig. 20B, F–H), *Inoceramus hoepeni* (Heinz, 1933) (Fig. 20D, K), “*Inoceramus*” sp. aff. *pacificus* Woods, 1917 (Fig. 20A, C, E, I, L), and “*I.*” sp. aff. *opetius* Wellman 1959 (Fig. 20J).

No fossils are known from the interval above bed 29.

3. Inoceramid succession

The inoceramid record is good enough in the lower half of the succession to allow inferences to be made about the phylogeny of *Tethyoceramus modestoides*, *T. madagascariensis* and *T. bassae*. These three undoubtedly form a succession of closely allied species, and are inferred to represent members of a single lineage (Fig. 5). *T. madagascariensis* is probably an anagenetic successor of *T. modestoides*. Higher up, *T. madagascariensis* gives way to *T. bassae*; the co-occurrence of *T. madagascariensis* and *T. bassae* indicates the cladogenetic event.

Tethyoceramus ernsti also belongs to this lineage. It may either represent an evolutionary successor of either *T. madagascariensis* or *T. bassae*, but details of the

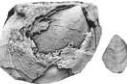
		EURAMERICA	MADAGASCAR	S. AFRICA	ANTARCTICA	NEW ZEALAND
SANT.			<i>Inoceramus neocaledonicus</i>		<i>Inoceramus neocaledonicus</i>	
CONIACIAN	Middle-Upper	<i>Volviceramus koeneni</i>	" <i>Inoceramus</i> " sp. aff. <i>pacificus</i>		" <i>Inoceramus</i> " sp. aff. <i>pacificus</i> [Zululand]	<i>Inoceramus pacificus</i>
		<i>Inoceramus gibbosus</i>	<i>Inoceramus?</i> <i>nukeus</i>		<i>Inoceramus nukeus</i>	
		<i>Cremonoceramus crassus - deformis</i>	<i>Tethyoceramus ernsti</i>			<i>Inoceramus opetius</i> <i>Inoceramus nukeus</i>
	Lower	<i>Cremonoceramus crassus inconstans</i>	<i>Tethyoceramus basseae</i>			
		<i>Cremonoceramus walt. hannoverensis</i> <i>Cremonoceramus deformis erectus</i>	First emigration <i>Tethyoceramus madagascariensis</i>			<i>Cremonoceramus bicorrugatus</i>
TURONIAN	Upper	<i>Cremonoceramus waltersdorffensis</i> <i>waltersdorffensis</i>	<i>Tethyoceramus modestoides</i>		<i>Tethyoceramus modestoides</i> [Alphard Group]	

Fig. 5. Correlation of the topmost Turonian–Coniacian of south-west Madagascar, as based on the Manasoa section with other areas of the Southern Hemisphere and Euramerican biogeographical region.

evolutionary transition are unclear at the moment. Its morphological consistency with other members of the *Tethyoceramus* lineage, however, suggests that this interpretation is highly probable.

Unknown is the phylogeny of *I.? nukeus* Wellman, the next form in the succession, which is accompanied by rare *?Cremonoceramus moorei* Crampton, 1966. *I.? nukeus* was described originally from New Zealand (Wellman, 1959) and subsequently, under the name *I. madagascariensis*, also reported from Antarctica and South America (Crame 1981, 1982, 1983; Crampton 1996). The widely accepted synonymy of *I.? nukeus* and *T. madagascariensis* first suggested by Crame (1981) is rejected here. Although both forms show close similarity in valve outline and LV (left valve) ornament, they differ, as demonstrated by the Madagascan material, in the general form (*T. madagascariensis* is distinctly inequivalve). Also, both species are clearly different stratigraphically. *T. madagascariensis* (Heinz) is a basal Coniacian species, whereas *I.? nukeus*,

according to the scheme inferred herein, should be ?mid–?late Early Coniacian. *C. moorei* is known hitherto only from New Zealand.

A very distinct faunal change marks the appearance of the next younger assemblage in the succession. Besides "*Inoceramus*" sp. aff. *pacificus*, which dominates the assemblage, it also contains *Inoceramus andersoni*, *I. hoepeni*, and "*Inoceramus*" sp. aff. *opetius*. Although the proper determination of these species is difficult at the moment and further study is required, it is a fauna displaying a close affinity to inoceramids of the Southern Hemisphere, and is clearly distinct from the Euramerican fauna.

4. Biogeographic affinity of the inoceramid fauna

The inoceramids of the latest Turonian and Coniacian of Madagascar are virtually identical to those from

EXTERNAL VIEW

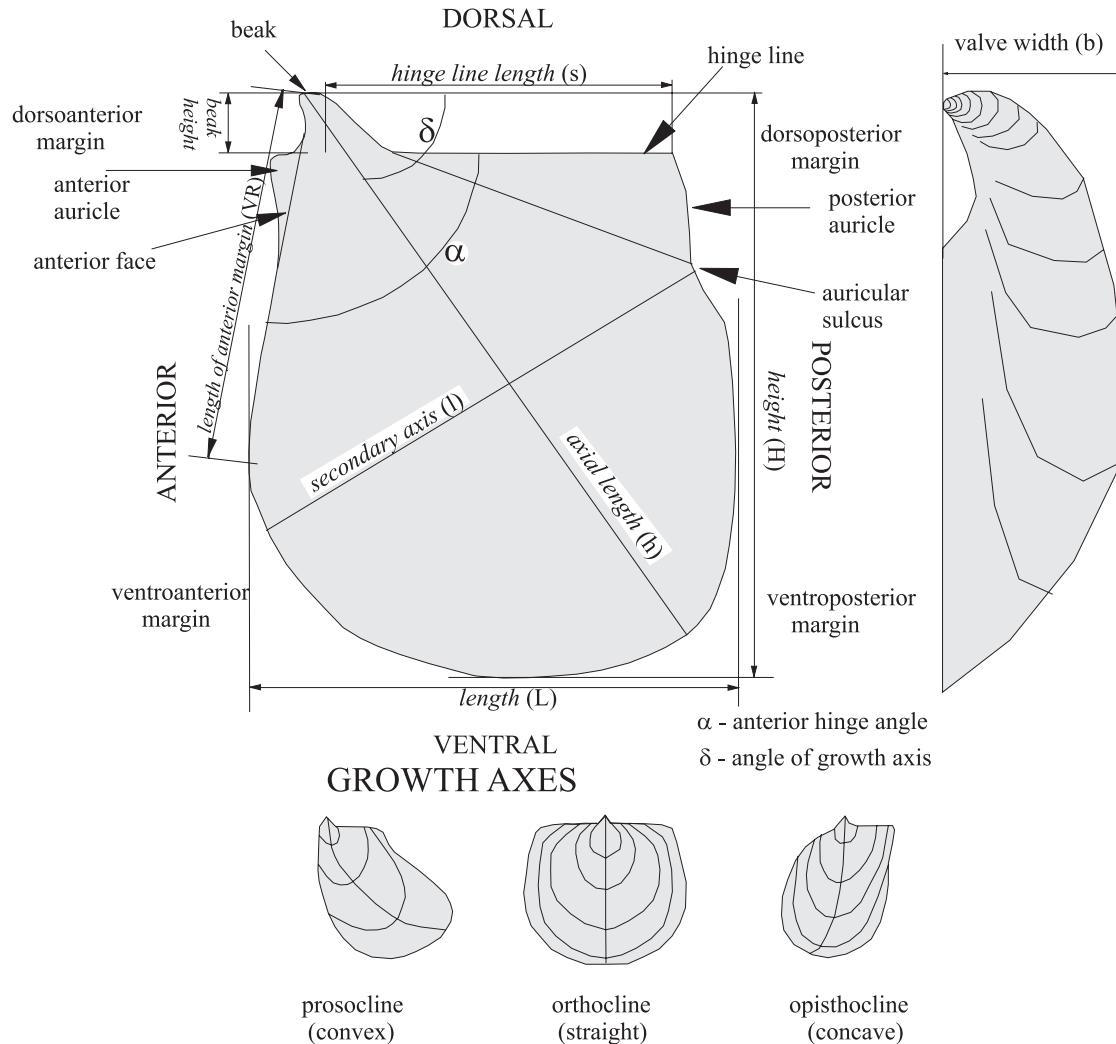


Fig. 6. External morphologic features, morphometric measurements and abbreviations used for inoceramid description.

Zululand. Biogeographically, inoceramids of both areas were hitherto interpreted largely in terms of European faunas (Heinz, 1929, 1933; Kauffman, 1978; Kauffman in Klinger et al., 1980). Doubts about the biogeographic identity of the Madagascan and Euramerican faunas were raised by Sornay (1980), who recognised a number of misidentifications of Madagascan forms.

Separation of the European and Madagascan faunas is supported herein by the studies of the Manasoa material. There is little doubt that the latest Turonian–Coniacian inoceramid fauna of Madagascar is different from that of Euramerica. Instead, as may be expected, it shows close affinity to faunas of the Indo-Pacific region (biogeographic units are used here after Kauffman 1973). It must be stressed, however, that at least in the lower part of the succession, characterised by the *Tethyoceramus* lineage, the path of evolutionary changes and morphotype succession parallels, to a considerable

extent, the changes observed within the Euramerican cremnoceramids, allowing a very precise correlation between these two faunas. The nature of this parallelism is not clear at the moment, but it may suggest that a genetic exchange between the two faunas operated from time to time. At least intermittent immigrations/emigrations also took place as, for example, the abrupt appearance of markedly advanced tethyoceramids in Europe (see Walaszczyk and Wood, 1999).

The former “European” interpretations of the Madagascan–Zululand latest Turonian–Coniacian inoceramid fauna resulted undoubtedly from the largely inadequate material typically comprising single specimens that had not been located precisely in the succession. The common iso- and heterochronous homeomorphy among inoceramids may be a cause of serious taxonomic problems in the case of poorly resolved faunal successions.

5. Biostratigraphy and biogeographic affinity of the ammonites

The ammonites from the Manasoa section comprise a taxonomically rich assemblage dominated by endemic species (see Fig. 2), characteristic of the Malagasy Province (Madagascar, Zululand and India). Only a few forms are known from outside this area. Two species have also been reported from Japan: *Yabeiceras manasoaense* Collignon, 1965, and *Coilopoceras requienianum altesellata* (Collignon, 1965) (see Matsumoto, 1971, and Kennedy and Wright, 1984 respectively). *Marshallites cumshewensis* (Whiteaves, 1884) is known from Alaska and *Yezoites klamathensis* (Anderson, 1902), described originally from California, has been reported from Japan (Tanabe, 1977). Of importance also is the presence of two European forms: *Hyphantoceras* (*Hyphantoceras*) *reussianum* (d'Orbigny, 1850) and *Scaphites* (*Scaphites*) *kieslinsgwaldensis* *kieslinsgwaldensis* Langenhan and Grundey, 1891.

As indicated above, heteromorph ammonites have the widest biogeographic distribution, a probable consequence of their tolerant planktonic life habit, and of broad environmental tolerance (see Marcinowski, 1974, 1980; Kennedy and Cobban, 1976). High endemism of other forms most probably reflects their epi-benthic mode of life in shallow-marine environments (ecomorphs of group A sensu Tanabe et al., 1978; Marcinowski, 1980).

Biostratigraphically, all ammonites collected in the Manasoa section lie within Collignon's (1965a,b) *Barroisiceras onilahyense-Kossmaticeras (K.) theobaldianum* Zone. Collignon (1965b) regarded this zone as representing the Middle Coniacian, and placed it above the Lower Coniacian *Peroniceras dravidicum-Peroniceras subtricarinatum* Zone. The ammonites of both zones were observed, however, in a reverse sequence by Kennedy and Klinger (1975; see also Kennedy, 1978) in the Early–Middle Coniacian succession of Zululand, suggesting an Early Coniacian age for the fauna of the *B. onilahyense-K. (K.) theobaldianum* Zone. This interpretation is confirmed herein. According to stratigraphical inferences based on the accompanying inoceramids, as well as the presence of *H. (H.) reussianum* and *C. requienianum altesellata*, forms known exclusively from the topmost Turonian and Lower Coniacian (see Collignon, 1965a; Tröger, 1968; Wright, 1979; Kennedy and Wright, 1984; Kaplan and Schmid, 1988; Kaplan and Kennedy, 1994, 1996; Summesberger and Kennedy, 1996), the *B. onilahyense-K. (K.) theobaldianum* Zone should be regarded as latest Turonian–Early Coniacian in age.

6. Inoceramid zonation

Five successive inoceramid zones are recognized in the Manasoa succession (Fig. 5). From the bottom

upwards these are zones of *Tethyoceras modestoides*, *T. madagascariensis*, *T. ernsti*, *Inoceramus? nukeus*, and “*Inoceramus*” sp. aff. *pacificus*. All are defined as interval zones and, as so far recognised, are characterised mostly by monospecific or low diversity assemblages. The correlations to Antarctica and New Zealand are based on the inoceramid successions as worked out by Crame (1981, 1982, 1983), Crampton (1995, 1996) and Crampton et al. (2001).

6.1. *Tethyoceras modestoides* Zone

The base of this zone is marked by the lowest occurrence of the index taxon and its top by the lowest occurrence of *Tethyoceras madagascariensis*. In the studied part of the Manasoa section, the base of the zone cannot be located; although *T. modestoides* appears in abundance in bed 1 we do not have any specimens from the basal bed 0, which may also belong to the zone.

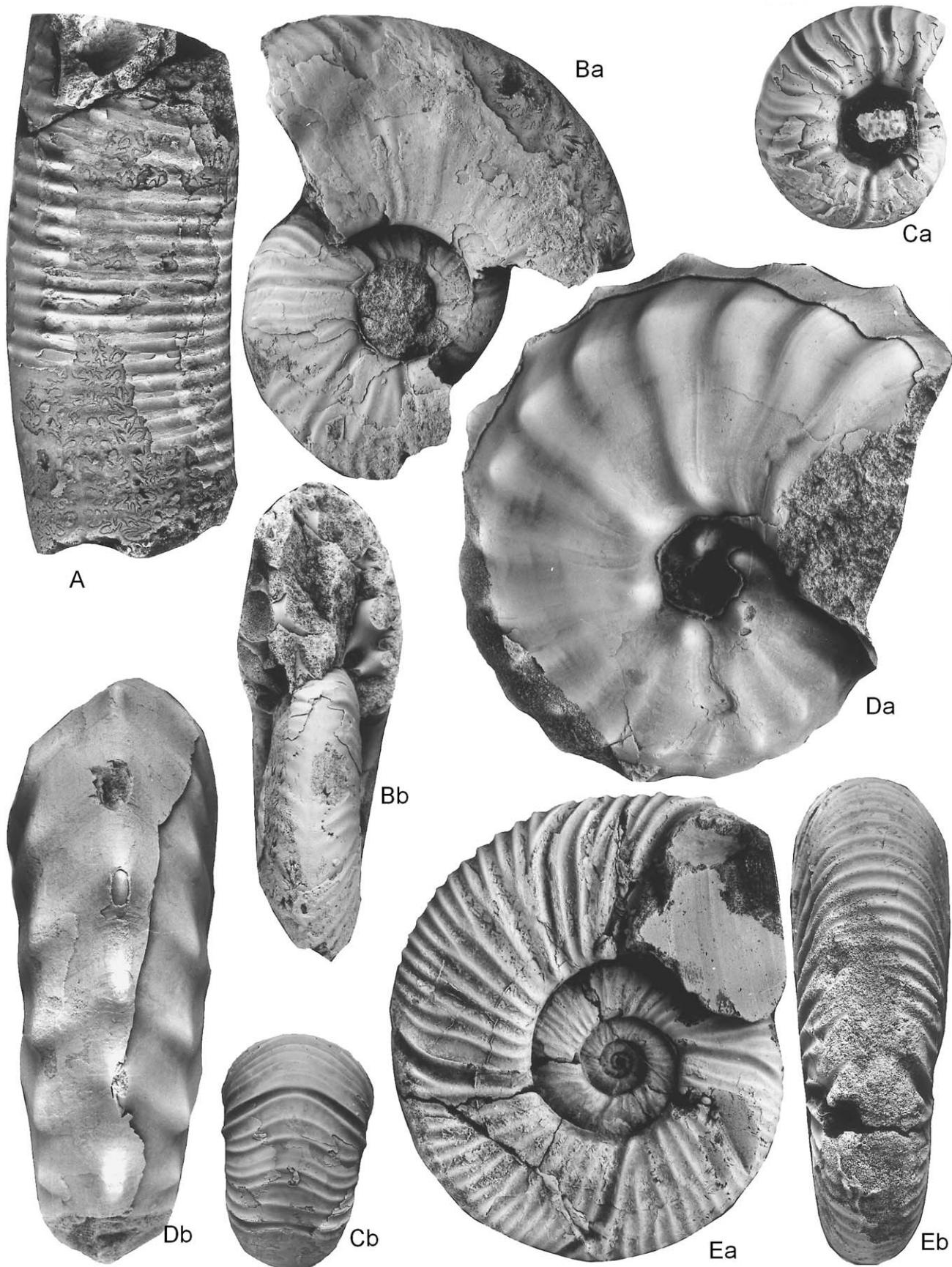
As far as inoceramids are concerned, the zone is almost monospecific, and other than the index species, only a few specimens of *Inoceramus tenuistriatus* have been recorded. In contrast, the zone yields a rich and taxonomically diverse ammonite fauna (Fig. 2).

6.2. *Tethyoceras madagascariensis* Zone

This zone begins at the lowest occurrence of the index taxon in bed 3 and ranges up to the lowest occurrence of *Tethyoceras basseae*. The most abundant and best preserved *T. madagascariensis* come from the concretionary horizons of bed 4. Above concretionary horizon E in bed 4, inoceramids become much less common, although specimens of *T. madagascariensis* were found up to bed 10. In comparison with the preceding zone, the ammonites become less common and markedly less diverse taxonomically. All of the specimens from the basal parts of beds 3 and 4 are *Barroisiceras onilahyense*; a single specimen from bed 9 is referred to *Marshallites cumshewensis*.

6.3. *Tethyoceras basseae* Zone

The base of this zone is defined by the lowest occurrence of the index taxon and the top by the lowest occurrence of *Tethyoceras ernsti*. The zone is very poorly documented, with only small numbers of stratigraphically relatively poorly located specimens. This hinders the precise placement of the zonal boundaries as well as proper understanding of the inoceramid sequence. The stratigraphically lowest specimen of *T. basseae* comes from a level around bed 7 and the highest from around bed 9.



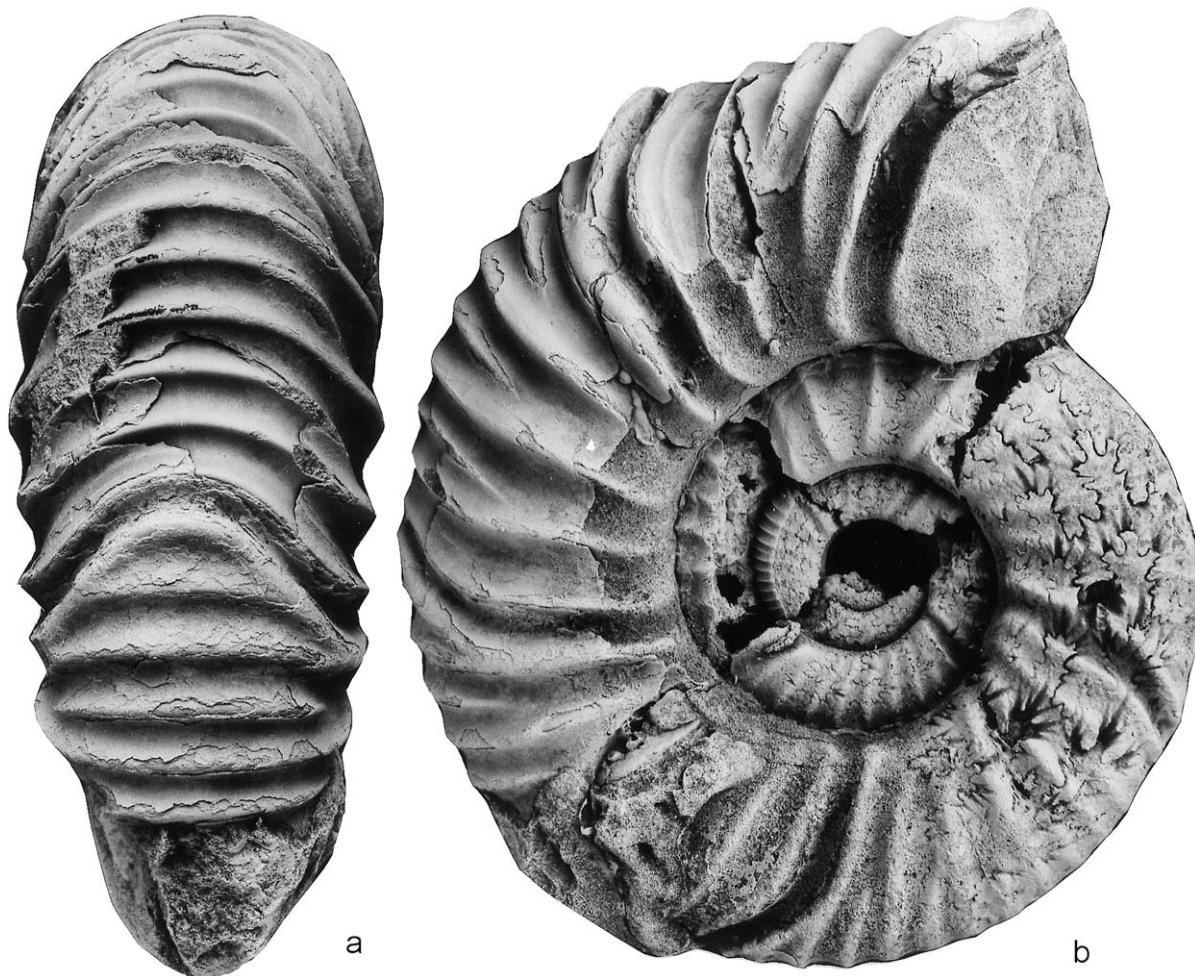


Fig. 8. *Kossmaticeras (Kossmaticeras) sparsicostatum* (Kossmat, 1897); ZI/31/066, bed 1: a, ventral view; b, lateral view. Both figures $\times 1$.

6.4. *Tethyoceramus ernsti* Zone

The lowest occurrences of the index taxon and *Inoceramus?* *nukeus* define, respectively, the base and top of this zone. The zone has, in fact, been documented from only two beds: 10, where the species is relatively common, and 20, where single specimens were found. The base of the zone is placed at the bottom of bed 10, where the lowest *T. ernsti* was found, and the top at the base of bed 20, from which the oldest specimens of *I.?* *nukeus* come. Most of the specimens of the latter have been recovered from bed 22.

6.5. *Inoceramus?* *nukeus* Zone

The base of this zone is marked by the lowest occurrence of *I.?* *nukeus* and its top by the lowest

occurrence of representatives of the “*Inoceramus*” sp. aff. *pacificus* group. The faunal documentation of the zone is rather poor. Unfortunately, all of the specimens are exclusively from bed 22. As in the case of the lower zones, the inoceramids of the *I.?* *nukeus* Zone form an almost monospecific assemblage of the index species. The only other species recorded is a single specimen of *Cremnoceramus moorei*.

6.6. “*Inoceramus*” sp. aff. *pacificus* Zone

This base of this zone marks a radical change in the inoceramid fauna. The *Tethyoceramus madagascariensis* lineage, ranging from the base of the succession up to the *T. ernsti* Zone and probably higher to the *I.?* *nukeus* Zone, becomes extinct, at least locally, and its place is taken by the assemblage composed of “*Inoceramus*” sp.

Fig. 7. A, *Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon, 1965; ZI/31/061, bed 1. B, *Kossmaticeras (Kossmaticeras) sakondryense* Collignon, 1954; ZI/31/062, from an unknown horizon: a, lateral view; b, ventral view. C, *Tongoboryoceras beantalyense* (Collignon, 1955); ZI/31/063, horizon C, bed 2: a, lateral view; b, ventral view. D, *Barroisiceras onilahyense* Basse, 1947; ZI/31/064, bed ?1: a, lateral view; b, ventral view. E, *Kossmaticeras (Kossmaticeras) theobaldianum crassicostata* Collignon, 1954; ZI/31/065, from an unknown horizon: a, lateral view; b, ventral view. All figures $\times 1$.

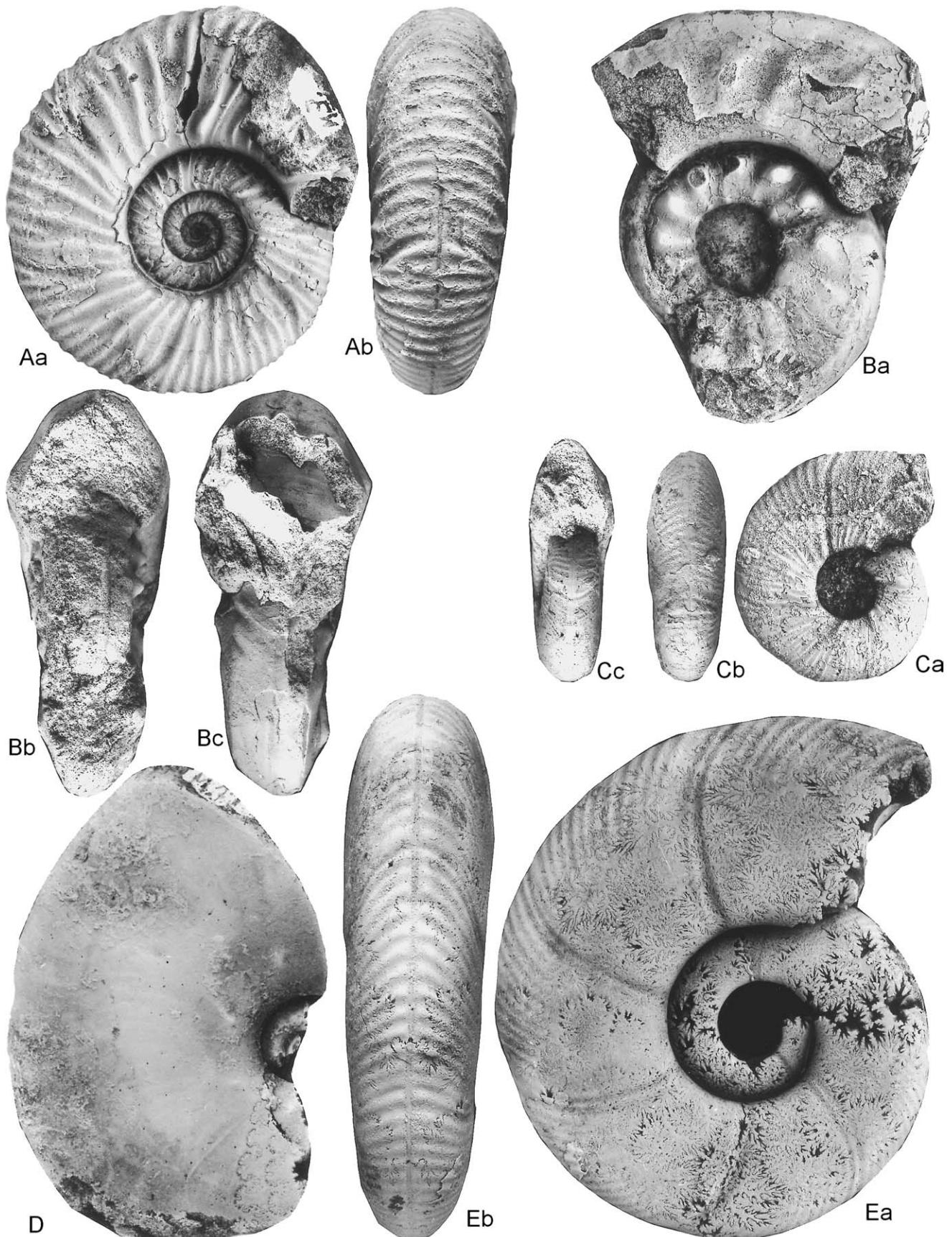


Fig. 9. A, *Kossmaticeras* (*Kossmaticeras*) *theobaldianum* *theobaldianum* (Stoliczka, 1865); ZI/31/067, from an unknown horizon: a, lateral view; b, ventral view. B, *Yabeiceras manasoense* Collignon, 1965; ZI/31/068, from an unknown horizon: a, lateral view; b, ventral view; c, frontal view. C, *Kossmaticeras* (*Kossmaticeras*) *manasoense* Collignon, 1954; ZI/31/069, from an unknown horizon: a, lateral view; b, ventral view; c, frontal view. D, *Placenticeras kaffrarium* Etheridge, 1904, ZI/31/070, most probably horizon C. E, *Puzosia manasoensis* Collignon, 1965; ZI/31/071, horizon C, bed 2: a, lateral view; b, ventral view. All figures $\times 1$.

aff. pacificus, *Inoceramus andersoni*, *I. cf. hoepeni*, and “*I.*” sp. aff. *opetus*. Unfortunately, this was recorded from only one bed (29); no faunal remains were found higher up the succession.

7. Correlation with Euramerica

Although we do not have many species-level taxa in common with the Euramerican biogeographic region, the overall similarity of the succession of inoceramid faunas of Madagascar and the Euramerican region (Walaszczyk and Wood, 1999; Walaszczyk and Cobban, 2000) allows, at least in a part of the record, a zone-by-zone correlation between these two areas (Fig. 5). The interpretation of this similarity is not clear, but the empirical data do not leave any doubt that we have a case of two records, geographically separate, that show the same pattern of morphological succession, interpreted herein as a case of parallel evolution.

The Madagascan inoceramid succession, *Tethyoceramus modestoides*—*T. madagascariensis*—*T. basseae*, and *T. ernsti* finds a parallel in the Euramerican succession represented by *Cremneceramus waltersdorffensis*—*C. erectus*—*C. deformis* (Fig. 5). The higher part of the record, represented by the *Inoceramus?* *nukeus* and “*Inoceramus*” sp. aff. *pacificus* faunas, differ from the Euramerican record, resembling more closely other Southern Hemisphere faunas.

Some of the turnover points within the Madagascan inoceramid faunas may quite easily be interpreted as speciation, whereas others may represent emigration/immigration events.

As demonstrated in Fig. 5, *T. modestoides* and *T. madagascariensis* are compared in evolutionary terms with *Cremneceramus waltersdorffensis* and *C. deformis erectus*. The appearance of the *Cremneceramus deformis* lineage, with its first representative, *C. deformis erectus*, is interpreted as a speciation event, from the *waltersdorffensis* ancestral lineage (Walaszczyk and Wood, 1999). One of the characteristic features of the *deformis* lineage is the appearance of the growth marks (Anwachsmarken of Heinz, 1928b), a very characteristic type of shell ornament. Instead, the succession of *T. modestoides*—*T. madagascariensis* seems to be anagenetic. The tethyoceramids differ from their Euramerican counterparts in their distinct inequivale form; at the same time, however, both *T. madagascariensis* and *C. deformis erectus* acquired growth marks. The latter, although known in some Cenomanian forms (*Inoceramus schoendorfi*), is characteristic of all the Early Coniacian cremnoceramids, and is such a rare ornament element that it may be used effectively in inoceramid correlation.

The successive faunas of both regions, i.e., *Cremneceramus deformis*—*C. crassus* in the Euramerican region

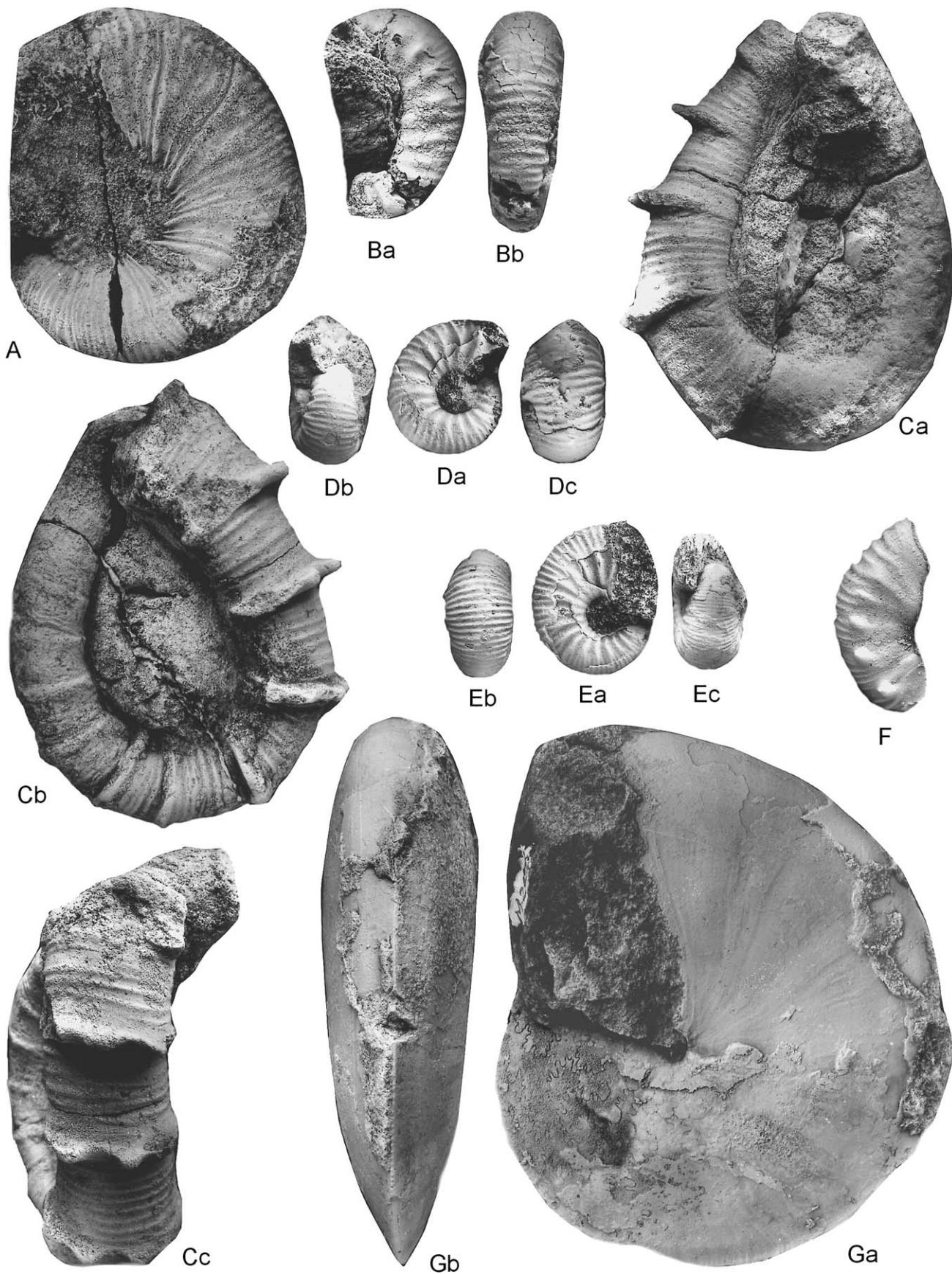
and *Tethyoceramus ernsti* in Madagascar, may be compared directly.

The comparison of the two younger faunas of *I.? nukeus* and “*I.*” sp. aff. *pacificus* is less confident. *Inoceramus?* *nukeus* (= *I. madagascariensis* of Crame, 1982, 1983, and Crampton, 1996) is widely distributed in the Southern Hemisphere, and besides Madagascar, is known from New Zealand, Antarctica and South America (Crame, 1983; Crampton, 1996). The *I.? nukeus* Zone is thus very useful for correlation in the Lower Coniacian of the Southern Hemisphere.

The succeeding “*I.*” sp. aff. *pacificus* assemblage represents a completely new fauna. It is much more diverse morphologically and taxonomically than all the other faunas below. It is represented by *I. andersoni*, *I. hoepeni*, “*I.*” sp. aff. *pacificus*, and “*I.*” sp. aff. *opetus*. Besides Madagascar, this assemblage is known from Zululand, as may be inferred from the published report by Kauffman (1978). It is represented by material from the Mfolozi River section (locality 13; see details in Kennedy and Klinger, 1975) (Kauffman, 1978, pl. 2, figs. 2, 3, 7, 10, 15) and possibly also specimens from the Mzinene River section (locality 71; see Kennedy and Klinger, 1975). The Zululand fauna is virtually identical; all of the species recognised in Manasoa are represented: *I. andersoni* (= Kauffman's *I. waltersdorffensis hannoverensis*, his pl. 2, figs 2, 10), “*I.*” sp. aff. *pacificus* (= Kauffman's *Mytiloides* (?) sp. aff. *M. lusatiae*, his pl. 2, fig. 3), *I. hoepeni* [= *Inoceramus* (*Inoceramus*) n. sp. aff. “*I. costellatus*” Woods of Fiege, 1930, pl. 5, fig. 10 and *I. uwajimensis* Yehara, 1924, pl. 3, fig. 2; pl. 4, fig. 2], and *I. sp. aff. opetus* (= Kauffman's *I. n. sp. aff. I. ernsti* Heinz—“*I.*” *koeneni* Müller and *I. selwyni*). Quite different taxonomically, and possibly also stratigraphically, are other forms of Kauffman reported by him to be Early Coniacian, namely specimens from False Bay (Kauffman, 1978, pl. 2, figs. 5, 6, 9, 12–14). They most probably represent a distinctly younger assemblage, presumably of latest Coniacian–Santonian age, and resemble the members of the *Inoceramus neocalledonius* group reported from Antarctica (Crame, 1983). Also belonging to the same group are *Inoceramus africanus* (Heinz) [non *Inoceramus africanus* sensu Kauffman in Herm et al., 1979 and Walaszczyk, 1992] described originally from the Upper Santonian of Madagascar (see Heinz, 1933; Sornay, 1964; discussion in Crame, 1983).

8. Systematic palaeontology

The morphological terms and measurements used herein follow Harries et al. (1996) and are shown in Fig. 6. The measurements of the selected specimens studied are given in Table 1. All the material examined is housed in the Museum of the Geological Faculty of the University of Warsaw, collection numbers ZI/31/006–ZI/31/078 and ZI/31/500–ZI/31/620.



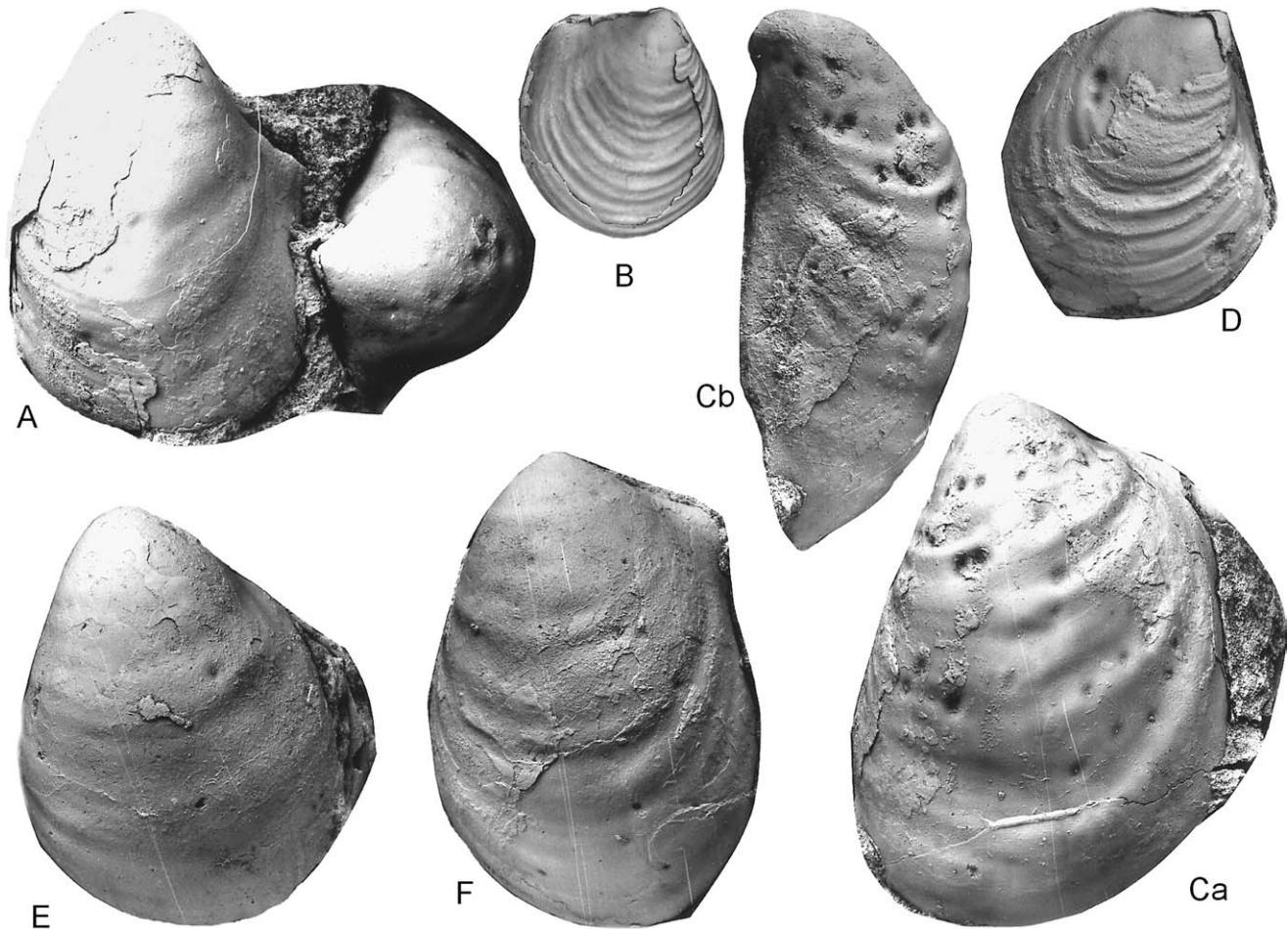


Fig. 11. A, C–F, *Tethyoceramus modestoides* (Sornay, 1980); bed 2, horizon C. A, ZI/31/006; $\times 1$. C, ZI/31/007; $\times 0.95$; a, lateral view; b, anterior view. D, ZI/31/008; $\times 1$. E, ZI/31/009; $\times 0.95$. F, ZI/31/010; $\times 0.85$. B, *Inoceramus tenuistriatus* Nagao and Matsumoto, 1939; bed 1; ZI/31/011; $\times 1$.

Order: Pterioida Newell, 1965

Suborder: Pteriina Newell, 1965

Family: Inoceramidae Giebel, 1852

Genus *Tethyoceramus* Sornay, 1980

Type species. *Inoceramus (Tethyoceramus) basseae* Sornay (1980, pl. 1, figs. 1, 4, 6; pl. 2, figs. 1–3), by original designation.

Remarks: For emended diagnosis and discussion, see Walaszczyk and Wood (1999, pp. 419–421).

Tethyoceramus modestoides (Sornay, 1980)

Figs. 11A, C–F, 12A–J

1933 *Volviceramus* cf. *involutus* Sowerby; Heinz, p. 254, pl. 20, fig. 1.

1980 *Inoceramus (Tethyoceramus) madagascariensis modestoides* Sornay, p. 142, pl. 3, fig. 4; fig. 1.

1980 *Inoceramus (Inoceramus) ernsti* Heinz; Kauffman in Klinger et al., p. 310, fig. 10G–P.

1980 *Inoceramus (Inoceramus) frechi* Flegel; Kauffman in Klinger et al.; p. 314, fig. 10A–F.

Holotype. 402B from Eboro in Betsiboka, Madagascar, an original of Sornay (1980, fig. 1a, pl. 3, fig. 4).

Material. 64 specimens: ZI/31/006–ZI/31/010, ZI/31/012, ZI/31/014–ZI/31/021, ZI/31/500 and ZI/31/525–ZI/31/544 from horizon C of bed 2; ZI/31/013, ZI/31/557–ZI/31/572 from bed 1; ZI/31/555 and ZI/31/556 from horizon A of bed 2; ZI/31/015, and ZI/31/545–ZI/31/554 from horizon B of bed 2.

Fig. 10. A, *Marshallites cumshewensis* (Whiteaves, 1884); ZI/31/072, bed ?9; $\times 1$. B, *Yezoites klamathensis* (Anderson, 1902); 21/31/073, bed 29; $\times 1$. E, F, *Scaphites (Scaphites) kieslingswaldensis kieslingswaldensis* Langenhan and Grundy, 1891; E, ZI/31/075, bed 1; $\times 1.5$. F, ZI/31/074, bed 29; $\times 1.8$; a, lateral view; b, ventral view; c, frontal view. C, *Hyphantoceras (Hyphantoceras) reussianum* (d'Orbigny, 1850); ZI/31/076, from an unknown horizon; a, b, lateral views; c, ventral view; $\times 1$. D, *Scaphites (Scaphites) cf. manasaensis* Collignon, 1965; ZI/31/077, horizon C, bed 2; a, lateral view; b, ventral view; c, apertural view; $\times 1$. G, *Coilopoceras requienianum ?altesellatum* Collignon, 1965; ZI/31/078, horizon C, bed 2; a, lateral view; b, ventral view; $\times 1$.

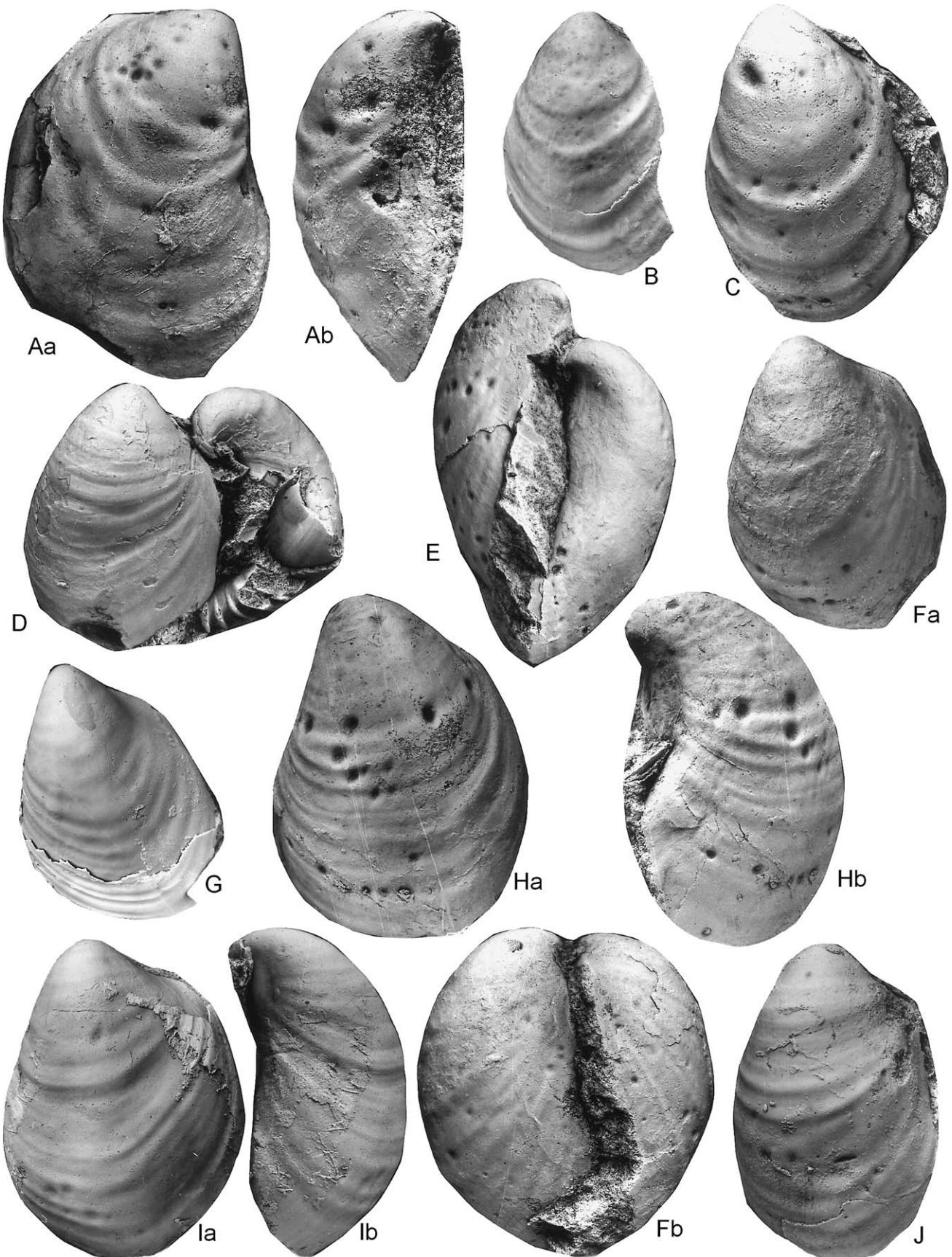


Fig. 12. A–J, *Tethyoceramus modestoides* (Sornay, 1980). A, ZI/31/012; $\times 0.95$. B, ZI/31/013; $\times 0.9$. C, ZI/31/014; $\times 0.9$. D, ZI/31/015; $\times 0.9$. E, ZI/31/016; $\times 1$. F, ZI/31/017; $\times 0.95$. G, ZI/31/018; $\times 0.9$. H, ZI/31/019; $\times 0.9$. I, ZI/31/020; $\times 0.95$. J, ZI/31/021; $\times 0.95$: a, lateral view; b, anterior view. A, C, E–J are from horizon C of bed 2; B is from bed 1; D is from horizon B of bed 2.

Description. Small to moderate size for the genus, inequilateral, inequivalue; left valve moderately to slightly more inflated than right (rarely strongly inflated), larger and with beak projecting to a greater degree above hingeline. The b/l ratio of left valve (LV) varies between 0.35 and 0.47, and of the right valve (RV) between 0.31 and 0.43. Beak pointed, curved anterodorsally. Posterior auricle small, subtriangular. Valve outline subtriangular to subovate; weakly inflated RV often subquadrate. Hingeline straight, moderately long. Anterior margin moderately long to long, straight or slightly concave, passing into narrowly rounded ventral margin. Posterior margin straight or slightly convex; in valves with well-developed posterior auricle, well-marked auricular sulcus. Anterior wall steep, moderately high, flattened.

Disc ornamentation consisting of weakly to moderately developed, irregularly spaced rugae; rugae more prominent in adult stage, becoming less so towards venter. Some specimens covered almost entirely with growth lines. Some shell fragments show indistinct growth lines, occasionally moderately raised.

Remarks. *Tethyoceramus modestoides* is very similar to *Inoceramus inaequivalvis* Schlüter, and representatives of this species were referred to Schlüter's taxon by Heinz (in collections; see remark in Sornay, 1980). The stratigraphical argument of Sornay to describe the Madagascan material as a separate species is not justified; both *T. modestoides* and *I. inaequivalvis* are Turonian. There are, however, morphological differences that allow separation of the two species. Schlüter's species is more inequivalue, it possesses a more prominent posterior auricle, and its umbonal part is more incurved dorsally. There are also Pacific inequivalue *Inoceramus* species, such as *Inoceramus pedalionoides* Nagao and Matsumoto, 1939, and *I. teshioensis* Nagao and Matsumoto, 1939, that may be related to the Madagascan species. Without knowing the biogeography of all of these species, this question cannot be solved here.

An inoceramid sample from the Alphard Group off South Africa, described by Klinger et al. (1980, fig. 10) is probably conspecific with *Tethyoceramus modestoides*. Based on differences in the ornament and the degree of inequivalveness, the sample was subdivided by Kauffman (in Klinger et al., 1980) into two species, and referred to *Inoceramus frechi* Flegel, 1905, and *I. ernsti* Heinz, 1928a,b. However, the South African material clearly differs from the original concepts of either of these two species. *Inoceramus frechi* is subrectangular in outline, has a well-differentiated posterior auricle and quite regular ornament composed of sharp-edged, raised rugae (see discussion and illustration in Walaszczyk and Tröger, 1996). *Tethyoceramus ernsti* Heinz, as recently discussed by Walaszczyk and Wood (1999), is a strongly rugate, massive species that is very inflated or

geniculated in the dorsal part. By contrast, all of the specimens illustrated by Klinger et al. (1980) appear to match the Madagascan *T. modestoides*, based on their axially elongated outline, irregular and relatively weak rugae, and small posterior auricle.

T. modestoides is very close to *T. madagascariensis* (Heinz). The latter differs from Sornay's species in its more regular and more prominent rugae and also in greater inequivalveness. Judging from the Manasoa record, *T. madagascariensis* is regarded herein as an evolutionary descendant of *T. modestoides*.

Occurrence. *T. modestoides* appears in bed 1 and ranges upwards through bed 2; also known from Zululand.

Tethyoceramus madagascariensis Heinz, 1933

Figs. 13, 14A, B, D, F

- 1930 *Inoceramus madagascariensis* Heinz; Besaire, p. 94.
- 1932 *Stolleiceramus madagascariensis* Heinz, Heinz, p. 59
- ?pars 1933 *Stenoceramus (Stenoceramus) madagascariensis* Heinz; Heinz, p. 252, pl. 20, fig. 2 [?non pl. 19, fig. 2].
- 1933 *Cymatoceramus (Cymatoceramus) cf. koeneni* (Müller); Heinz, p. 253, pl. 19, fig. 3.
- 1957 *Inoceramus langi* Choffat; Sornay (in Darteville et al.), p. 58, pl. 35, fig. 1.
- 1980 *Inoceramus (Tethyoceramus) madagascariensis* Heinz; Sornay, p. 11; pl. 1, figs. 2, 3, 5; pl. 2, fig. 4; pl. 3, figs. 1–3.
- non 1981 *Inoceramus (Inoceramus) madagascariensis* Heinz; Crame, p. 44, figs. 8, 9a, b.
- non 1983 *Inoceramus madagascariensis* Heinz; Crame, fig. 4g, h.
- 1992 *Inoceramus madagascariensis* Heinz; Walaszczyk, pl. 29, fig. 3; pl. 30, fig. 3.
- 1992 *Inoceramus ex gr. lamarcki* Parkinson; Walaszczyk, pl. 33, figs. 1, 2.
- non 1996 *Inoceramus? madagascariensis* (Heinz, 1933); Crampton, p. 70, fig. 35, pls. 16I–O, 17E.
- 1997 *Tethyoceramus madagascariensis* (Heinz); Walaszczyk, pls. 1–4.
- 1998 *Tethyoceramus madagascariensis* (Heinz); Walaszczyk and Wood, pl. 19, fig. 4.
- 1998 *Tethyoceramus* sp.; Walaszczyk and Wood, pl. 18, figs. 2, 4; pl. 19, fig. 4.

Lectotype. By subsequent designation of Sornay (1980, p. 11), the original of Heinz (1933, pl. 20, fig. 2) from the basal Coniacian of Manasoa, Madagascar.

Material. 50 specimens: 14 from bed 3: ZI/31/022, ZI/31/031, ZI/31/032, ZI/31/510, ZI/31/511, ZI/31/512, and

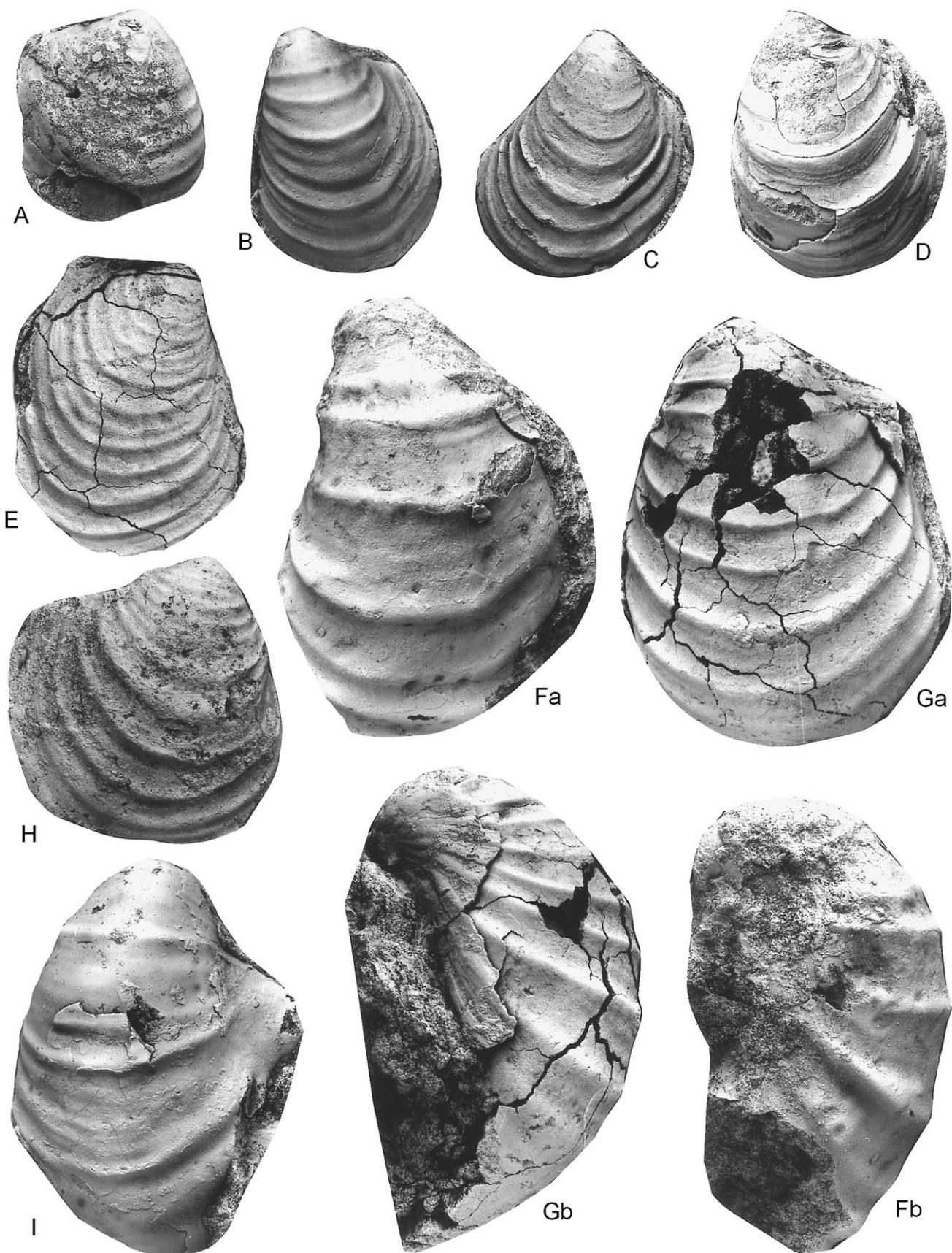


Fig. 13. A–I, *Tethyoceramus madagascariensis* (Heinz, 1933). A, bed 3; B–I, bed 4. A, ZI/31/022; $\times 1$. B, ZI/31/023; $\times 0.92$. C, ZI/31/024; $\times 0.90$. D, ZI/31/025; $\times 0.95$. E, ZI/31/026; $\times 0.96$. F, ZI/31/027; $\times 0.95$. G, ZI/31/028; $\times 1$. H, ZI/31/029; $\times 0.93$. I, ZI/31/030; $\times 0.92$: a, lateral view; b, anterior view.

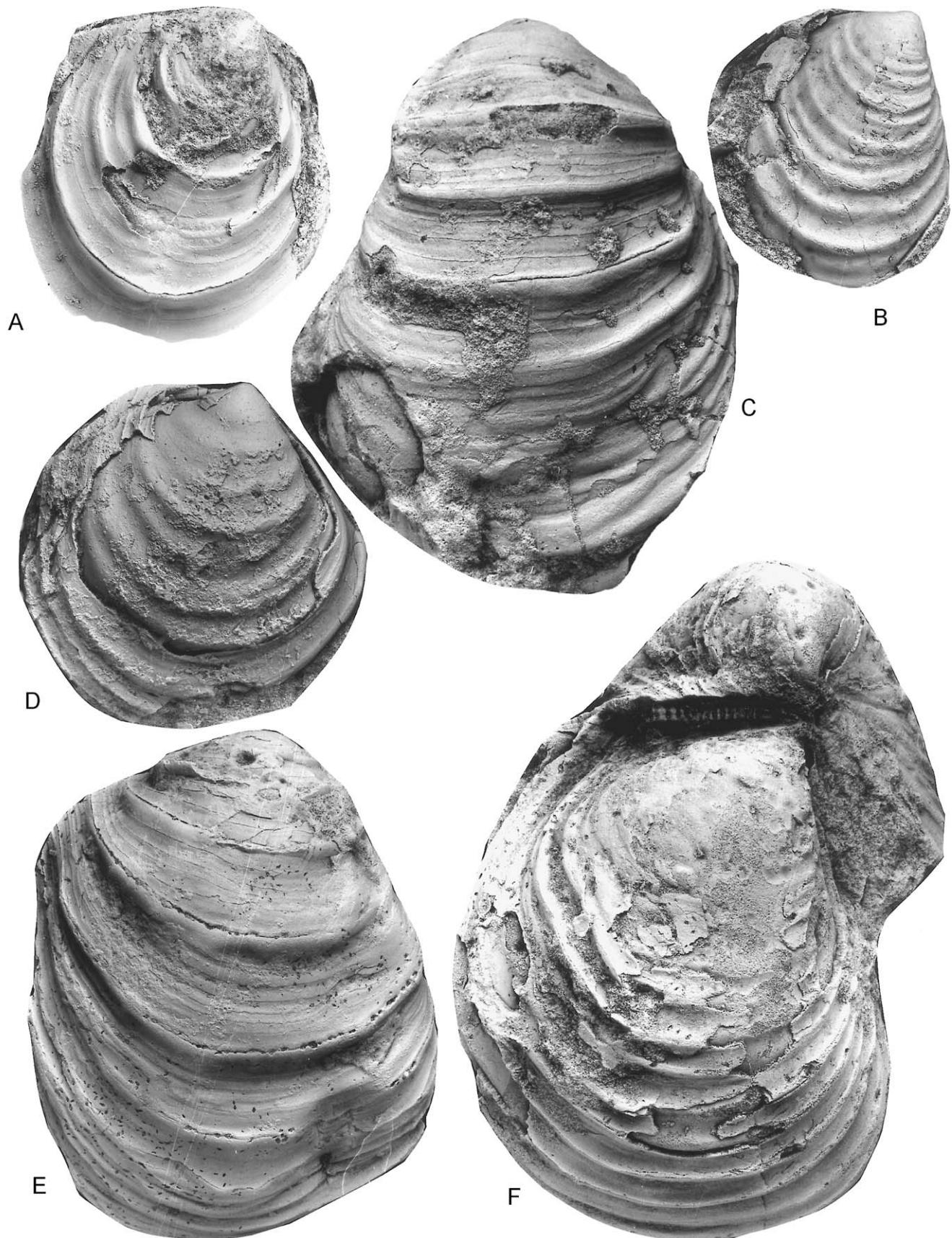


Fig. 14. A, B, D, F, *Tethyoceramus madagascariensis* (Heinz, 1933). A, ZI/31/031, bed 3; B, ZI/31/032, bed 3; D, ZI/31/033, bed 9; F, ZI/31/034, bed 10. A, B, F, $\times 1$; D, $\times 0.95$. C, E, *Tethyoceramus basseae* (Sornay, 1980). C, ZI/31/035, bed 7; $\times 1$. E, ZI/31/036, bed 7; $\times 0.95$.

ZI/31/586–ZI/31/593; 27 from horizon D of bed 4: ZI/31/023, ZI/31/024, ZI/31/026–ZI/31/030, ZI/31/501–ZI/31/507, and ZI/31/573–ZI/31/585; 6 from horizon E of bed 4: ZI/31/025, ZI/31/508, ZI/31/509, and ZI/31/594–ZI/31/596; ZI/31/592 from bed 7; ZI/31/034 from bed 10; ZI/31/033 from bed 9. All specimens preserve their original shape; most are internal moulds with small areas of shell preserved.

Description. The species is of small to moderate size for the genus, inequivale, inequilateral. The valves are suboval in outline with the LV distinctly more inflated than the RV; b/h ratio between 0.4 and 0.5. In the RV, this ratio is usually 0.2. In both valves the anterior margin is long, with VR/h ratio ranging between 0.6 and 0.7. The margin is straight, slightly concave below the umbo, or concave throughout. The anterior face is steep and high. The ventral margin is regularly rounded, passing into the rounded postero-ventral margin, and thence into straight or slightly convex posterior margin. The ventral and posterior margins are flattened. The hingeline is straight and relatively short. In the LV, the s/h ratio varies between 0.4 and 0.5; in the RV is slightly higher, between 0.5 and 0.6. The posterior auricle is very small, triangular in outline, elongated parallel to the hingeline. In the LV it is flat, and well separated from the strongly inflated disc. In the RV it is only weakly separated or the disc passes into the posterior auricle almost imperceptibly. Some specimens show geniculation.

The ornament of both valves is composed exclusively of the commarginal elements; these are regularly to subregularly spaced rugae, with occasional raised growth lines. The rugae are slightly asymmetrical with ventral slope steeper. Interrugae spaces are flat. The shelly parts on some specimens show clearly the presence of Anwachsmarken on the crests of rugae, the type of growth line so characteristic of cremnoceramids (see Heinz, 1928b).

Remarks. The range of morphological intraspecific variability is high. The variation concerns mainly the degree of inequivalveness, valve inflation and outline (particularly of the RV), and the ornament. The variation of valve inflation is particularly well marked in the case of LVs; RVs are less variable and usually weakly to moderately inflated.

T. madagascariensis is very similar to *I.? nukeus*, described from the Teratan Stage (Coniacian according to Crampton, 1995; see also Crampton et al., 2001) of New Zealand. Although the latter species was subsequently synonymised with Heinz' species (Crame, 1981; see also Crame, 1983; Crampton, 1996), the comparison of the New Zealand material (Woods, 1917, Wellman's 1959, and above all Crampton's 1996 specimens) with the topotype material of *T. madagascariensis* treated herein, shows that these species are

distinct morphologically. *I.? nukeus* is almost equivale and much less inflated than *T. madagascariensis*. Some other differences were already mentioned by Crampton (1996, p. 73), who pointed out that the specimens of *T. madagascariensis* as figured by Sornay (1980) are "comparatively large and possess relatively expanded discs and rounded ventral margins". He ascribed these differences, however, to intraspecific variability or preservational artefacts, but at the same time mentioned that the New Zealand material is identical to that from Antarctica. As is demonstrated by the fauna from Manasoa, forms identical to the New Zealand and Antarctic material also occur there, although distinctly higher stratigraphically. Consequently these should be referred to *I.? nukeus*. Thus, besides morphological differences, *T. madagascariensis* and *I. nukeus* also differ in their stratigraphical range; the former is an earliest Coniacian species whereas *I.? nukeus* occurs higher, in the highest Lower Coniacian, above an interval with *T. ernsti*.

Conspecific with *T. madagascariensis* is the specimen referred to *Inoceramus langi* Choffat by Sornay (in Darteville et al., 1957, pl. 35, fig. 1). Sornay's specimen differs markedly from Choffat's (1905, pl. 1, fig. 1) original; the latter is a *Cataceramus*-like species, subquadrate in outline and bulbous in shape, whereas Sornay's specimen is axially elongated with a narrow, strongly projecting umbo and a *Cremneceramus*-like ornament, typical of tethyoceramids.

Occurrence. *T. madagascariensis* marks the base of the Lower Coniacian and is limited to the lowermost part of the substage.

Tethyoceramus bassae (Sornay, 1980)

Fig. 14C, E

- | | |
|-------|---|
| 1930 | <i>Inoceramus ernsti</i> Heinz; Besairie, p. 94. |
| 1933 | <i>Tethyoceramus</i> (<i>Proteoceramus</i>) <i>ernsti</i> Heinz; Heinz, p. 251, pl. 19, fig. 1. |
| 1934 | <i>Tethyoceramus</i> aff. <i>emigrans</i> Heinz; Basse, p. 89. |
| 1980 | <i>Inoceramus</i> (<i>Tethyoceramus</i>) <i>basseae</i> Sornay, p. 137, pl. 1, figs. 1, 4, 6; pl. 2, figs. 1–3. |
| ?1999 | <i>Inoceramus</i> <i>basseae</i> Sornay; Ayyasami and Rao, pl. 1, figs. A, B. |

Holotype. By original designation, BA 1934-1, the original of Sornay (1980, pl. 1, fig. 1; pl. 2, figs. 2, 3), from the Coniacian of Manasoa on Onilahy, Madagascar.

Material. 4 specimens: ZI/31/035, ZI/31/036, and ZI/31/513 from bed 7; ZI/31/514 from bed 9.

Description. The species is of moderate size, strongly inflated, moderately to strongly inequivale. The LV is markedly more inflated than the RV, and both are

distinctly geniculated, with up to 90° positive geniculation angle. No change of obliquity is associated with the geniculation. The juvenile LV is moderately inflated, subquadrate in outline, prosocline, with a straight growth axis. The beak projects above the hingeline, and is incurved dorsally. The disc is triangular in outline; the posterior auricle is of moderate size, well differentiated. The anterior margin is relatively long, straight. The anterior face is steep, high. The ventral margin is regularly rounded. The adult stage is rectangular, distinctly higher than long.

The RV is moderately inflated, subquadrate in outline, prosocline. The growth axis is posteriorly convex. The beak is small, pointed, not projecting above the hingeline. The anterior margin is very long, straight. The hingeline is moderately long and straight.

Both valves are ornamented with distinct growth lines and regular, strong rugae. At the margins, rugae bear well-developed growth marks (Anwachsmarken of Heinz 1928b). The articulated specimen differs in its less regular rugation. An earliest juvenile part is ornamented exclusively with growth lines.

Discussion. *Tethyoceramus basseae* seems to be an evolutionary successor of *T. madagascariensis*; both species are characterised by a similar type of ornament (distinct rugae with Anwachsmarken), valve outline and inequivalveness. Whether we have here an anagenetic transition or speciation event is not possible to judge on our material; in the interval with *T. basseae* the *madagascariensis* morphotype is still present, but we do not have enough specimens to locate these specimens properly in the variability range of the whole population.

T. basseae is very close morphologically to *T. madagascariensis* and it is quite possible that forms referred herein to *T. basseae* are large, extreme variants of the latter species. Because of the small number of specimens available we decided to retain the original Sornay (1980) interpretation.

Tethyoceramids are morphologically a very plastic group, with several species-level taxa described so far, and constitute a common member of mid-Early Coniacian inoceramid assemblages in Europe. Among the well-known representatives are: *Inoceramus alpinus* Heinz, 1932, and *Tethyoceramus novalensis* Heinz, 1932 (both based on Airaghi's 1904 *I. cordiformis*), *I. humboldti* Eichwald (1865), *Inoceramus wandereri* (Andert 1911), and the recently described *I. pseudowandereri* Szasz (1985). In the same stratigraphical interval there are also a number of distinctive morphotypes, the taxonomic interpretation of which is unclear (see discussion in Walaszczyk and Wood, 1999). As pointed out by Walaszczyk and Wood (1999), tethyoceramids in the European Lower Coniacian have a "foreign" aspect, appear suddenly, and in quite a number of distinctive

morphotypes, giving an impression of an immigrant fauna. Their evolutionary appearance in Madagascar suggests the East African Province (according to Kauffman's 1973 biogeography) as their area of origin.

Occurrence. Known from the Lower Coniacian *Tethyoceramus basseae* Zone of Madagascar; most probably also occurring in Europe.

Tethyoceramus ernsti (Heinz, 1928a)

Figs. 15–18

- 1897 *Inoceramus bronniarti* Mantell; Inostranzeff, pl. 7, fig. 13.
 pars 1928a *Inoceramus ernsti* Heinz, p. 73.
 non 1933 *Inoceramus ernsti* Heinz; Heinz, p. 250, pl. 19, fig. 1 [= *Tethyoceramus basseae* (Sornay, 1980)]
 non 1980 *Inoceramus* (*Inoceramus*) *ernsti* Heinz; Kauffman in Klinger et al., p. 310, figs. 10G–P [= *Tethyoceramus modestoides* (Sornay, 1980)]
 pars 1992 *Cremnoceramus ernsti* (Heinz); Walaszczyk, p. 55, pl. 32, fig. 3 [non fig. 18 and pl. 32, figs. 1, 2 = *Inoceramus callosus* (Heinz, 1932)]
 non 1996 *Inoceramus* (*Cremnoceramus*) *ernsti* Heinz; Noda, p. 576, figs. 5, 6, 7.1–3.
 non 1998 *Inoceramus* (*Cremnoceramus*) *ernsti* Heinz; Noda and Matsumoto, p. 450, pl. 6, figs. 4–6; pl. 7, fig. 1; pl. 8, fig. 1.
 1998 *Tethyoceramus ernsti* Heinz; Walaszczyk and Wood, pl. 19, fig. 6.

Lectotype. By subsequent designation of Walaszczyk and Wood (1999, p. 428), the original of Inostranzeff (1897, pl. 7, fig. 13; reillustrated in Walaszczyk and Wood, 1999, pl. 19, fig. 6) from the Upper Cretaceous of the Caucasus; the original is housed in the collections of the State University in St. Petersburg, Russia.

Material. 7 specimens; ZI/31/37–ZI/31/40, ZI/31/515 and ZI/31/515, all from bed 10, and ZI/31/517 from bed 20.

Description. The species, attaining a large size for the genus, is equivalve or slightly inequivale, inequilateral. The valves are moderately inflated, with the maximum inflation dorsocentral, prosocline, rectangular in outline, higher than long. The beak is small, pointed, curved antero-dorsally, projecting only slightly above the hinge line. The hingeline is straight, moderately long. The anterior margin is long to very long, straight or weakly concave, particularly below the umbo. The anterior margin passes into rounded ventral margin, and thence into broadly convex posterior margin. The growth axis is straight or slightly convex posteriorly. The posterior

auricle is small, weakly separated from the disc, except on the earliest juvenile stage.

The valves are ornamented with commarginal rugae. The growth lines are rarely observed; the preserved shell fragments show clear Anwachsmarken. The interrugae spaces increase towards the venter, being up to 30 mm in adult stage. In the earliest juvenile stage the shell is almost smooth. On the posterior auricle the rugae are curved beakward.

Discussion. The problem of *Tethyoceramus ernsti* and its status with respect to *I. callosus* (Heinz, 1932) was discussed recently by Walaszczyk and Wood (1999). Woods' specimen (1912, text-fig. 85), which was commonly cited as a type of Heinz's species, is actually the holotype (by original designation) of *Inoceramus callosus*. The specimen of Innostranzeff (1897) from the Cretaceous of the Caucasus, mentioned in the original description of Heinz (1928a), was, therefore, designated as the lectotype of *T. ernsti*.

Both the former reports of *T. ernsti* from the region, i.e. of Heinz (1933) from Madagascar and of Kauffman

(in Klinger et al., 1980) from South Africa, were based on different concepts of this species. Heinz's specimen was referred subsequently to *Tethyoceramus basseae* by Sornay (1980), and Kauffman's form is *Tethyoceramus modestoides*.

T. ernsti is not uncommon in the *Cremonoceramus deformis*—*C. crassus* Zone of the Euramerican biogeographic region. A number of closely allied and possibly conspecific forms were illustrated by Szasz (1985) from the Lower Coniacian of Romania, and by Ivannikov (1979) and Kotubinsky (1974) from Ukraine.

Among the North Pacific forms referred to *Inoceramus ernsti* by Noda (1996) and subsequently Noda and Matsumoto (1998) there are two different species. The huge JG.H3023 (Noda, 1996, fig. 5; Noda and Matsumoto, 1998, pl. 7) is a representative of the *Inoceramus lamarcki* group, possibly related to the group of *Inoceramus hercules* Heinz—*Inoceramus annulatus* Goldfuss, known from the Upper Turonian—Lower Coniacian of Europe (Tröger, 1984). The other specimens (Noda, 1996, figs. 6.1, 2, 7.1–3; and Noda and Matsumoto, 1998, pl. 6, figs 4–6; pl. 8, fig. 1) are closer



Fig. 15. *Tethyoceramus ernsti* (Heinz, 1928a,b); ZI/31/037, bed 10; ×1.



Fig. 16. *Tethyoceramus ernsti* (Heinz, 1928a,b); ZI/31/038, bed 10; $\times 0.8$.

to *Tethyoceramus basseae* (Sornay, 1980), although their exact affinities are not clear. A specimen from Kamchatka (Pergament, 1971, pl. 33, fig. 2; pl. 34, fig. 3) is a single left valve that is rather poorly preserved. Pergament compared it with the Madagascan specimen of *I. ernsti* illustrated by Heinz (1933, pl. 19, fig. 1), which he designated the lectotype of the species.

Occurrence. By analogy to the succession within the Euramerican *Cremneceramus* zonation, the stratigraphical range of the species is interpreted as mid-Early Coniacian; besides Madagascar, *T. ernsti* is known from the Euramerican biogeographic region. The North Pacific reports are based on different concepts of *I. ernsti* and belong to other species.

Genus *Cremneceramus* Cox, 1969

Type species. *Inoceramus inconstans* Woods, 1912, by original designation.

Remarks. For description and discussion of the genus, see Walaszczyk (1992), Harries et al. (1996), Crampton (1996) and Walaszczyk and Wood (1999).

Occurrence. The genus is well known from the topmost Turonian and the Lower Coniacian of Europe

and North America. It also occurs in South America, Asia, and New Zealand, in presumably the same stratigraphical interval.

Cremneceramus moorei Crampton, 1996

Fig. 19D

compare:

1996 *Cremneceramus moorei* Crampton, p. 84, pl. 23, figs. A–L.

Holotype. By original designation, TM7885 (GS15131) from the Lower Coniacian of the Glenburn Formation, New Zealand (Crampton 1996, p. 84).

Material. A single specimen, ZI/31/048, from bed 22.

Description and remarks. The specimen is represented by an incomplete, single left valve; the posterior auricle and beak are missing. It is a juvenile part, approximately 40 mm in axial length. It shows a relatively long, straight to slightly concave anterior margin, passing into a regularly rounded ventral margin. The posterior margin is not observed. The valve is axially elongated, apparently weakly oblique, although the hingeline is not preserved. Inflation is moderate, maximum in the dorsal part. The valve is ornamented with very regular, closely

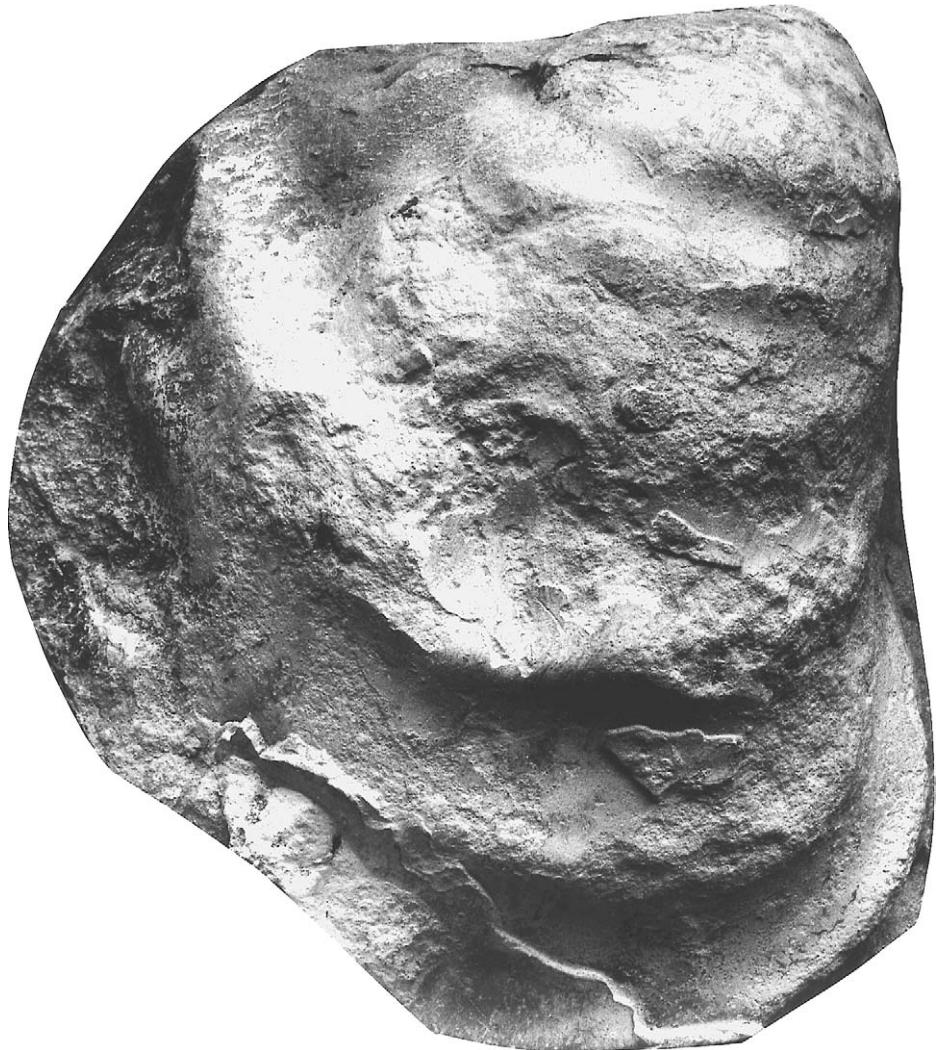


Fig. 17. *Tethyoceramus ernsti* (Heinz, 1928a,b); ZI/31/039, bed 10; $\times 0.75$.

spaced, sharp-edged rugae; the interrugae distances are maximally 3 mm, usually less. The edges bear well-developed Anwachsmarken. In the axial part, the ventral sides of the rugae are slightly crenulated.

The specimen possesses a general outline very close to, and type of ornament identical to that of *Cremnoceramus moorei* Crampton, 1996. It represents only the juvenile, immature part; the adult stage, when preserved, should extend beyond the juvenile and contact the latter along a negative geniculation.

Occurrence. The specimen comes from bed 22, where it co-occurs with *Inoceramus?* *nukeus*. Crampton (1995, 1996) reported *C. moorei* from the topmost part of the *Cremnoceramus bicornutus* Zone of New Zealand.

Genus *Inoceramus* J. Sowerby, 1914

Type species. *Inoceramus cuvieri* J. Sowerby, by subsequent designation of Cox (1969, p. N315).

Remarks. For description and discussion of the genus, see Harries et al. (1996).

Inoceramus? *nukeus* Wellman, 1959 Fig. 19A–C, E–H

- | | |
|-------|---|
| 1917 | <i>Inoceramus</i> sp.; Woods, p. 28, pl. 14, figs. 3, 4. |
| 1928c | <i>Inoceramus glatziae</i> Flegel; Heinz, p. 126. |
| 1959 | <i>Inoceramus nukeus</i> Wellman, p. 155, pl. 23, fig. 2. |
| 1974 | <i>Inoceramus</i> sp. cf. <i>Inoceramus stantoni</i> Sokolov; Chiplonkar and Tapasawi, p. 111 [not illustrated] |
| 1981 | <i>Inoceramus madagascariensis</i> Heinz, 1933; Crame, p. 44, text-figs. 8, 9a, b. |
| 1983 | <i>Inoceramus madagascariensis</i> Heinz; Crame, fig. 4g, h. |
| 1996 | <i>Inoceramus?</i> <i>madagascariensis</i> Heinz; Crampton, p. 70, pl. 16, figs. J–O; pl. 17, fig. E. |



Fig. 18. *Tethyoceramus ernsti* (Heinz, 1928a,b); ZI/31/040, bed 10; $\times 1$.

Holotype. By original designation, GS 3225, the original of Wellman (1959, pl. 23, fig. 2) from the Wairata River section, Teratan Stage, New Zealand.

Material. 17 specimens; ZI/31/042, ZI/31/046 and ZI/31/598–ZI/31/600 from bed 20; ZI/31/041, ZI/31/043–ZI/31/045, ZI/31/047 and ZI/31/601–ZI/31/607 from bed ?22; all specimens are internal moulds of single valves with usually small shell fragment attached.

Description. The species is small to moderately sized, with the maximum axial length measured being 82 mm. It is apparently slightly inequivale, inequilateral. The valves are poorly to moderately inflated, with maximum inflation in post-umbonal part. The umbo is small, pointed, projecting slightly above hingeline. The hinge-line is relatively long, straight. The anterior angle is relatively small, usually around 95° but ranging up to 115°. The anterior margin is relatively long, usually

around 60% of the axial length, slightly concave to concave, passing into long, widely rounded antero-ventral margin. The ventral margin is rounded or V-shaped in some specimens. The postero-ventral margin is long, broadly rounded. The posterior auricle is moderately large, moderately well or poorly separated from the disc.

The valve surface is ornamented with rugae and raised, very distinctive growth lines. The rugae, which are indistinct in the juveniles, become widely spaced very quickly, with flat-floored interrugae spaces. Two to three growth lines occur per rugae, usually markedly pronounced. The number of rugae in the interval varies between 20 and 50 mm axial length and is usually three, rarely up to five.

Discussion. The *madagascariensis* ornament type, weakly inflated and axially elongated valves, and its inequivale, subequivalve character, leave little doubt

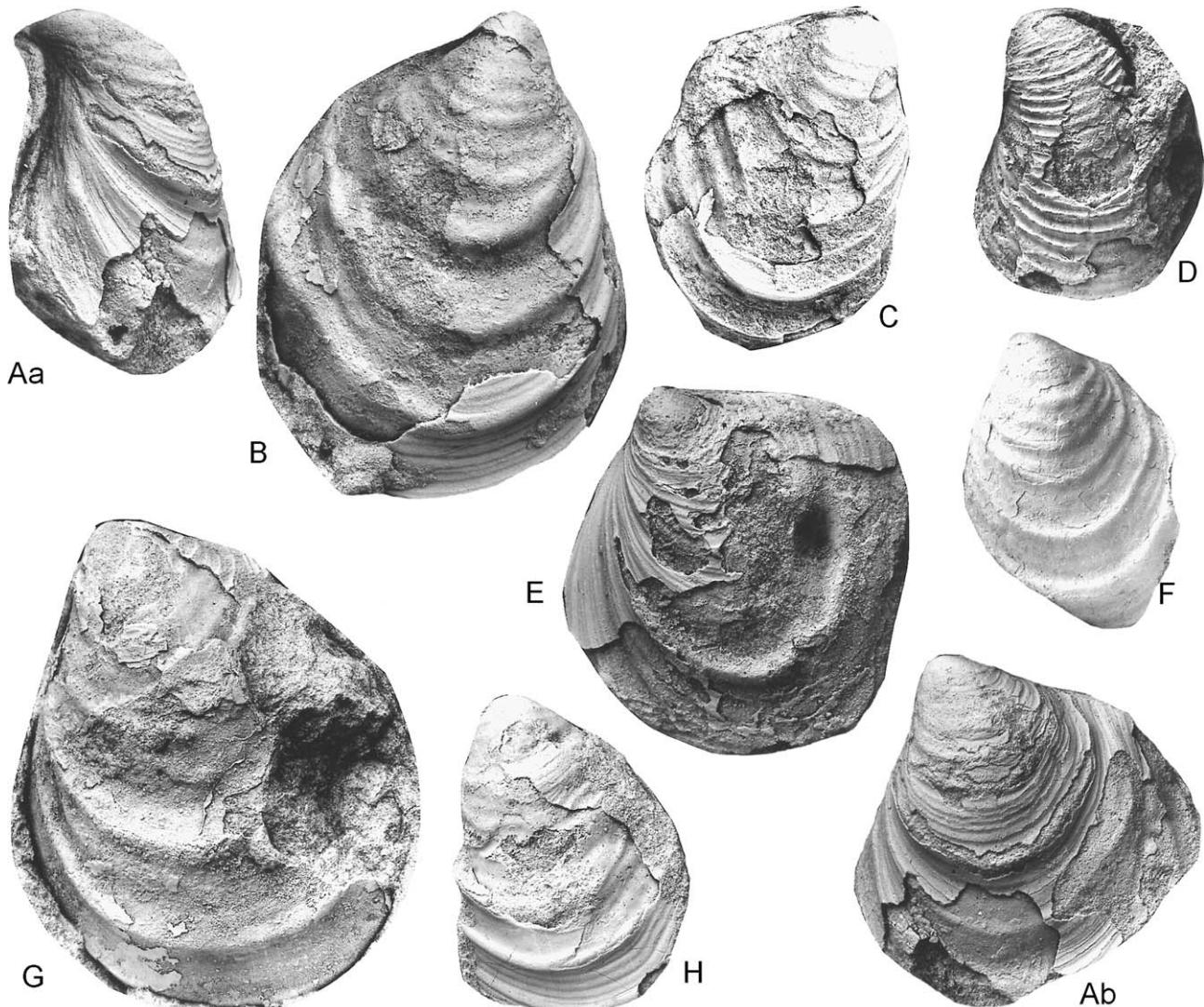


Fig. 19. A–C, E–H, *Inoceramus?* *nukeus* Wellman, 1959. A, C, E, F, H, bed 22; B, G, bed 20. A, ZI/31/041. B, ZI/31/042. C, ZI/31/043. E, ZI/31/044. F, ZI/31/045. G, ZI/31/046. H, ZI/31/047. D, *Cremnoceramus moorei* Crampton, 1996; ZI/31/048, bed 22. Apart from E, which is $\times 0.95$, all figures are $\times 1$: a, lateral view; b, anterior view.

that the sample studied herein should be referred to *I.?* *nukeus*. This species is very close morphologically to *T. madagascariensis*. The latter species, however, is distinctly inequivalve, and whereas its LVs, particularly those that are weakly to moderately inflated, are virtually identical to those of the New Zealand species, its RVs are quite different; they have a rounded to subrounded outline and usually quite distinct ornament. It must be added, however, that LVs of *T. madagascariensis* are usually markedly inflated, as is also the case with the type of the species. Consequently, *I.?* *nukeus* and *T. madagascariensis* are regarded here as separate species, and their synonymy, as proposed by Crame (1981; see also Crampton, 1996) is rejected. One other argument in favour of our interpretation is their stratigraphical range; *T. madagascariensis* is distinctly

older. All forms illustrated by Crame (1981, 1983) and Crampton (1996) are conspecific and represent *I.?* *nukeus*. To *I.?* *nukeus* we also refer *Inoceramus* cf. *stantoni* Sokolov, reported [although not illustrated] by Chiplonkar and Tapaswi (1974) from India [a plaster cast was made available through the courtesy of Prof. R.M. Badve, Poona].

Based on the Manasoa record, a distinct phylogeny is inferred for both species. Whereas *T. madagascariensis* is an evolutionary successor of *T. modestoides*, *I.?* *nukeus* seems to be a member of the *Inoceramus* lineage, rooted possibly in a Late Turonian form, such as *Inoceramus pedalionoides*. The suggested relationship as observed in the Manasoa section is very close to the situation known from Europe with the *Cremnoceramus* clade, spanning the topmost Turonian and lowest Coniacian, followed

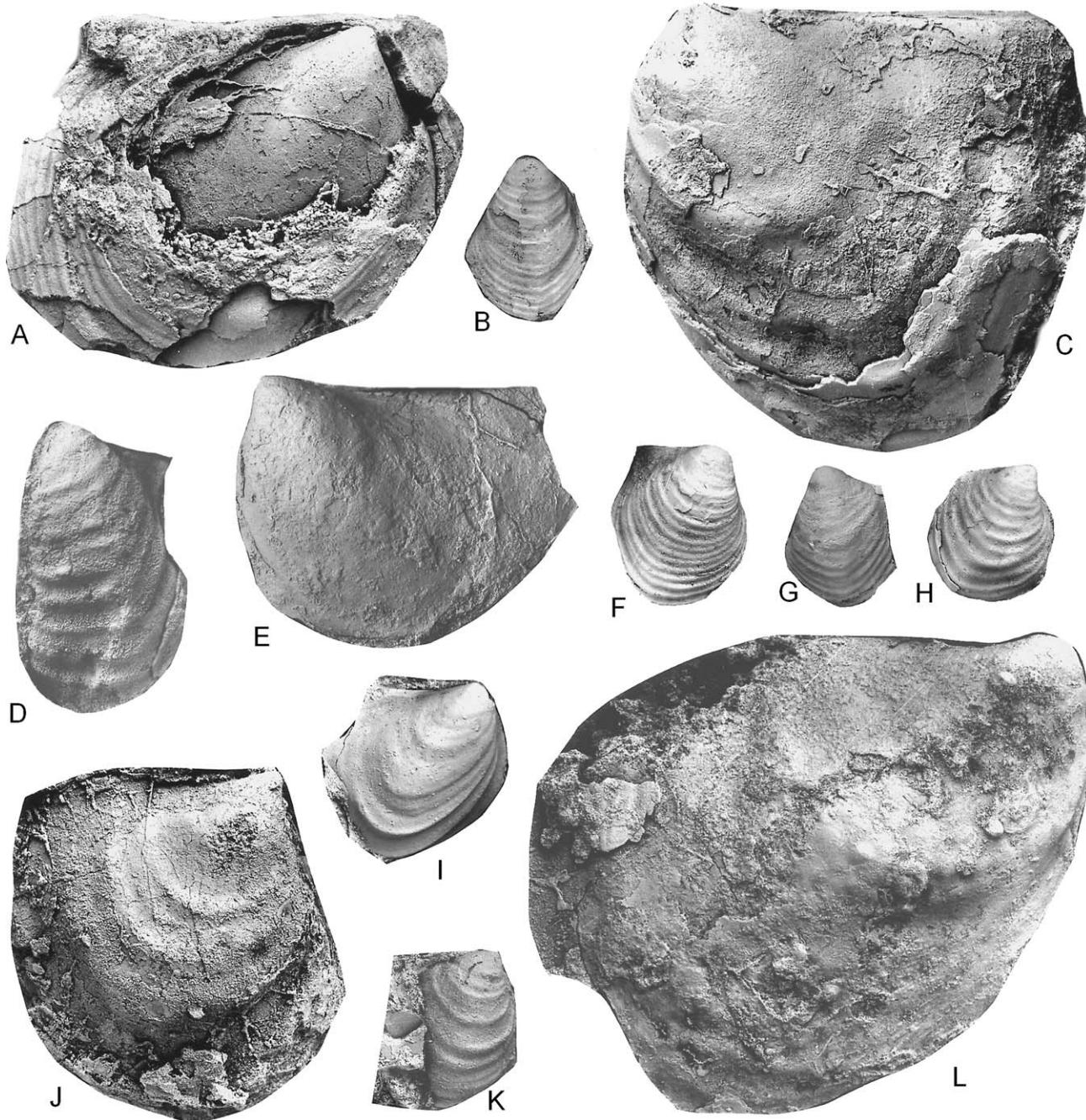


Fig. 20. A, C, E, I, L, “*Inoceramus*” sp. aff. *pacificus* Woods, 1917; bed 29. A, ZI/31/049; $\times 1$. C, ZI/31/050; $\times 1$. E, ZI/31/051; $\times 0.93$. I, ZI/31/052; $\times 1$. L, ZI/31/053; $\times 0.95$. B, F–H, *Inoceramus andersoni* (Etheridge, 1904); bed 29. B, ZI/31/054; $\times 1$. F, ZI/31/055; $\times 1$. G, ZI/31/056; $\times 1$. H, ZI/31/057; $\times 1$. J, “*Inoceramus*” sp. aff. *opetius* Wellman, 1959; bed 29; ZI/31/058; $\times 0.9$. D, K, *Inoceramus hoopeni* Heinz, 1933, bed 29. D, ZI/31/059; $\times 0.92$. K, ZI/31/060; $\times 1$.

by the *Inoceramus* clade, the earliest species of which is referred provisionally to *I. gibbosus* Schlüter (see Walaszczyk and Wood in Niebuhr et al., 1999).

I.? nukeus seems to be related to the *Inoceramus uwajimensis* group Nagao and Matsumoto, 1939 (the resemblance is particularly impressive in the case of numerous specimens illustrated by Pergament, 1971, referred by him to *Inoceramus stantoni* Sokolov).

Occurrence. In the Manasoa section *I.? nukeus* seems to be restricted to the upper part of the Lower Coniacian, although the Middle Coniacian record is too poorly known to give a reliable upper range. The species is widely distributed in the Southern Hemisphere, being known from Madagascar, New Zealand (Wellman, 1959; Crampton, 1996), Antarctica (Crame, 1981, 1983) and South America (see Crampton, 1996).

Table 1

Measurements and simple ratios of selected specimens

Specimen	Value	hmax	h	l	b	α	δ	VR	s	l/h	b/h	Illustration
<i>Inoceramus tenuistriatus</i> Nagao and Matsumoto, 1939												
ZI/31/011	LV	52.8	52.8	—	23.0	—	—	25.9	—	—	0.43	Fig. 11B
<i>Tethyoceramus modestoides</i> (Sornay, 1980)												
ZI/31/006	LV	60.0*	49.0	37.0	22.0	100	70	26.0	22.0	0.75	0.45	Fig. 11A
	RV	53.0	49.0	36.0	18.0*	104	70	28.	21.0	0.73	0.38	Fig. 11A
ZI/31/007	LV	76.0	64.0	51.0	25.5	97	68	39.0	26.5	0.80	0.40	Fig. 11C
ZI/31/009	LV	62.0	62.0	46.0*	29.0	95*	65*	30.0	—	0.74	0.47	Fig. 11E
ZI/31/010	LV	70.6	61.6	45.0	25.0	97	72	31.5	24.0	0.73	0.41	Fig. 11F
ZI/31/012	RV	70.0*	60.6	52.0	20.0	100	72	43.0	25.0	0.86	0.33	Fig. 12A
ZI/31/014	LV	65.0	48.0	38.0	19.6	95	72	29.0	19.5	0.79	0.40	Fig. 12C
ZI/31/015	LV	54.0	49.0	36.5	21.0	90*	70*	33.0	22.0	0.74	0.43	Fig. 12D
ZI/31/016	LV	59.0	55.0	43.0	18.5	—	—	—	—	0.78	0.37	Fig. 12E
	RV	57.0	55.0	42.0	17.0	—	—	—	—	0.76	0.31	Fig. 12E
ZI/31/017	LV	58.0	48.0	36.0	18.0	100	70	25.5	21.0	0.75	0.37	Fig. 12F
	RV	54.5	48.0	33	17.0	104	70	25.5	21.0	0.69	0.35	Fig. 12F
ZI/31/018	LV	55.0	52.0	37.0	20.0	94	63	31.0	20.0	0.72	0.38	Fig. 12G
ZI/31/019	LV	69.6	61.6	49.8	21.7	95	74*	37.0	—	0.80	0.35	Fig. 12H
ZI/31/020	LV	63.0	58.0	47.0	21.5	100	70	38.0	27.0	0.81	0.37	Fig. 12I
ZI/31/021	LV	61.7	56.9	41.3	21.8	92	70	36.0	21.0	0.73	0.38	Fig. 12J
ZI/31/500	RV	52.4	44.0	40.5	11.6	100*	68	28.0	25.0	0.92	0.43	Unillustrated
<i>Tethyoceramus madagascariensis</i> (Heinz, 1930)												
ZI/31/022	RV	41.0	35.0	34.5	10.5	105	75	26	20*	0.96	0.26	Fig. 13A
ZI/31/023	LV	50.0	44.0	35.6	20.0	90	66	30.0*	23.5*	0.81	0.45	Fig. 13B
ZI/31/024	LV	53.0	43.0	34.0	13.0	98	65	25.0	21.0	0.79	0.30	Fig. 13C
ZI/31/025	LV	53.0	50.8	43.0	20.6	105	70*	31.0*	23.0*	0.85	0.39	Fig. 13D
ZI/31/026	RV	57.0	48.0	40.0	11.0*	115	77	28.0	24.2	0.83	0.23	Fig. 13E
ZI/31/027	LV	86.0	58.0	44.0	24.4	90	62	40.0	32.0*	0.76	0.42	Fig. 13F
ZI/31/028	LV	89.0	71.0	58.4	26.7	108	68	43.0	42.0*	0.82	0.38	Fig. 13G
ZI/31/029	RV	57.0	52.0	47.2	13.6	113	78	31.0	26.0*	0.91	0.26	Fig. 13H
ZI/31/030	LV	78.0*	64.0*	49.0	28.0	100	68	41.0	35.0	0.76	0.43	Fig. 13I
ZI/31/031	RV	65.8	65.5	58.0	15.0	110	70	38*	32.0	0.88	0.23	Fig. 14A
ZI/31/032	RV	54.0	48.0	42.6	12.0	108	70	31.3	26.0*	0.89	0.22	Fig. 14B
ZI/31/033	RV	69	60	59	18	130	80	37.5	26	0.98	0.30	Fig. 14D
ZI/31/034	LV	120	83*	74	28.5	110	75	50	36*	0.89	0.34	Fig. 14F
ZI/31/501	LV	54.0*	40.8	31.0	18.5	96	68	23.0	17.8	0.76	0.45	Unillustrated
ZI/31/502	LV	49.0	46.5	38.0	15.4	94	68	27.0	26.4	0.82	0.33	Unillustrated
ZI/31/503	LV	71.0	53.6	44.7	20.3	90*	68*	34.0*	26.0*	0.83	0.38	Unillustrated
ZI/31/504	LV	88.6	63.0	49.0	26.3	105	68	38.0	31.5	0.77	0.42	Unillustrated
	RV	71.5	63.0*	20.7	—	—	—	—	—	0.33	—	Unillustrated
ZI/31/505	RV	67.6	62.8	53.6	17.0	110*	70*	40.0*	—	0.86	0.27	Unillustrated
ZI/31/506	RV	62.0	41.5	37.3	13.0	104	70	24.0	22.0	0.90	0.31	Unillustrated
ZI/31/507	RV	65.0	49.0	41.5	15.6	110	75	33.4	24.0	0.85	0.32	Unillustrated
ZI/31/508	LV	65.0	52.5	45.0	20.6	90	68	36.0*	29.6	0.86	0.39	Unillustrated
ZI/31/509	LV	71.7	51.0	41.7	18.0	106	70	32.0*	22.0*	0.82	0.35	Unillustrated
ZI/31/510	LV	73.5	59.5	49	25.8	100	70*	40	28.0*	0.83	0.44	Unillustrated
ZI/31/511	LV	82.5	70.0	55.8	25.5*	90	79*	47	31.5	0.80	0.36	Unillustrated
ZI/31/512	RV	52.0	42.0	38.7	10	110	75	25*	25	0.92	0.24	Unillustrated
<i>Tethyoceramus basseae</i> (Sornay, 1980)												
ZI/31/035	LV	105	80.5	67*	39	105	80	52	—	0.83	0.48	Fig. 14C
	juvenile	57	52	20	115	80	38	34	0.91	0.35	Fig. 14C	
ZI/31/036	RV	100	78.8	72	33	100	68	54	49	0.91	0.42	Fig. 14E
	juvenile	55	53	19	110	80	32	34	0.96	0.35	Fig. 14E	
<i>Tethyoceramus ernsti</i> (Heinz, 1928a,b)												
ZI/31/037	RV	128.0	113.0	102.0	37.0	—	—	—	—	0.90	0.33	Fig. 15
ZI/31/038	RV	147.0	116.0	98.0	32.0	110	78	70	44	0.84	0.28	Fig. 16
ZI/31/039	RV	190.0	190.0	145.0	63.0	—	—	—	—	0.76	0.33	Fig. 17
ZI/31/040	RV	170.0	114.0	90.0	30.0	92	65	74	63	0.79	0.26	Fig. 18
ZI/31/515	LV	137.0	89.0	79.5	24.5	105	68	49	45	0.89	0.28	Unillustrated
ZI/31/516	RV	102.0	—	—	—	—	—	—	—	—	—	Unillustrated
ZI/31/517	LV	81.5	75.3	62.0	14.6	100	54	49	38	0.82	0.19	Unillustrated

Table 1 (continued)

Specimen	Value	hmax	h	l	b	α	δ	VR	s	l/h	b/h	Illustration
<i>Inoceramus?</i> nukeus Wellman, 1959												
ZI/31/041	LV	51.0	43.0	37.0	10.6	97	58	23.0	26.0	0.86	0.25	Fig. 19A
ZI/31/042	RV	74.0	61.9	53	18.0	95	59	38	—	0.86	0.29	Fig. 19B
ZI/31/044	LV	60.5	50.6	39.8	10.4	100	65	—	26.0	0.79	0.21	Fig. 19E
ZI/31/045	LV	45.3	39.8	30.8	11.4	95	58	20.0	19.3	0.77	0.28	Fig. 19F
ZI/31/046	LV	76.0	65.0	53.0	17.0	103	61	30.4	29.0	0.82	0.26	Fig. 19G
ZI/31/047	LV	49.4	41.8	34.0	—	—	54	—	—	0.81	0.32	Fig. 19H
ZI/31/048	LV	43.0	—	—	—	—	—	—	—	—	—	Fig. 19D
ZI/31/518	RV	78.0	74.0	61.0	20.0	102	56	35	39.0	0.82	0.27	Unillustrated
ZI/31/519	LV	43.0	32.3	26.8	12.0	—	—	—	—	0.83	0.37	Unillustrated
“Inoceramus” sp. aff. <i>pacificus</i> Woods, 1917												
ZI/31/049	RV	70.0	64.0	55.5	12.5	120	45	18	34	0.86	0.19	Fig. 20A
ZI/31/050	LV	79.0	—	—	—	—	—	—	—	—	—	Fig. 20C
ZI/31/051	LV	56.0	52.0	43.0	19.0	110	40	12	39	0.83	0.36	Fig. 20E
ZI/31/052	RV	32.0	28.5	21.0	6.0	110	48	6.5	15.5	0.74	0.21	Fig. 20I
ZI/31/053	RV	101.7	61.0	50.0	10.4	118	48	13	38	0.82	0.17	Fig. 20L
<i>Inoceramus hoepeni</i> (Heinz, 1933)												
ZI/31/059	RV	48.7	33.8	26.2	17*	112	68	24*	17.8	0.78	0.50	Fig. 20D
ZI/31/060	RV	24.6	—	—	—	—	—	—	—	—	—	Fig. 20K
<i>Inoceramus andersoni</i> (Etheridge, 1904)												
ZI/31/054	LV	25.5	25.0	19.2	8.0	120	75*	15.5	—	0.77	0.32	Fig. 20B
ZI/31/055	RV	27.4	26.0	22.0	10.0	110	78	16.0	11.5	0.85	0.38	Fig. 20F
ZI/31/056	LV	23.0	19.0	16.0	8.7	122	82	14.0	10.5	0.84	0.48	Fig. 20G
ZI/31/057	RV	24.0	22.6	19.6	9.0	120*	80	15.0	11.0*	0.87	0.40	Fig. 20H
ZI/31/523	LV	26.5	26.5	22.0	—	110	74	—	15	0.83	—	Unillustrated
“Inoceramus” sp. aff. <i>opetus</i> Wellman, 1959												
ZI/31/058	RV	63.6	47	44	12	100	62	29.5	38	0.94	0.25	Fig. 20J
ZI/31/524	LV	74*	51.5	46	13*	106*	70	31	28	0.89	0.25	Unillustrated

See Fig. 6 for explanations of symbols. Linear measurements are in mm; *marks estimated measurement.

Inoceramus andersoni (Etheridge, 1904) Fig. 20B, F–H

- pars 1904 *Melina Andersoni* Etheridge, pp. 73, 74, pl. 2, fig. 8 [non pl. 2, figs. 7, 9, 10].
 1929 *Inoceramus andersoni* Etheridge; Heinz, p. 684, figs. 2, 3.
 non 1962 *Inoceramus cf. andersoni* (Etheridge, 1904); Bräutigam, p. 212, pl. 4, fig. 11.
 1978 *Inoceramus waltersdorfensis hannovrensis* Heinz; Kauffman, pl. 2, figs. 2, 10.
 non 1982 *Inoceramus andersoni* (Etheridge); Keller, p. 98, pl. 5, fig. 6.

Lectotype. By subsequent designation of Heinz (1929, p. 684), the original of Etheridge (1904, pl. 2, fig. 8), from the Coniacian of Umkwelane Hill, Zululand, South Africa.

Material. 15 specimens: ZI/31/054–ZI/31/057, ZI/31/523 and ZI/31/612–ZI/31/620; all single valves with parts of the shell preserved; all from bed 29.

Description. The species is inequilateral, ?equivalve and small (maximum axial length 32 mm). The valves are subquadrate in outline, moderately inflated, with

maximum inflation dorsocentral. The disc is subtriangular to regularly triangular in shape. The posterior auricle is well differentiated, triangular in outline. The beak is pointed, projecting slightly above the hinge line, curved antero-dorsally. The hingeline is straight, moderately long. The anterior margin is weakly concave, moderately long, passing into a broadly convex, rounded ventral margin and thence into a straight to weakly concave posterior margin. The anterior face is steep, with rounded margins. The growth axis is weakly convex posteriorly or nearly straight.

The valves are ornamented with very closely and regularly spaced commarginal rugae (?growth lines). The rugae spacing are variable through ontogeny; they may increase, remain constant, or decrease. The rugae are indistinct on the posterior auricle.

Discussion. The subquadrate outline, simple concentric ornament and small size make this species very similar to a number of forms spanning the Cenomanian–Coniacian of both the Euramerican biogeographic region and North Pacific biogeographic province. In Europe, the name was applied to the Late Turonian small form (Heinz, 1929; Bräutigam, 1962; Keller, 1982), presumably representing juveniles of *Inoceramus*

perplexus Whitfield. Among the Coniacian forms it resembles those referred commonly to *Inoceramus kleini* Müller (Assmus, 1963; Cech and Svabenicka, 1992) and/or *Inoceramus cf. frechi* Flegel or *Inoceramus cf. sturmi* Andert (see Heine, 1929). In the case of *I. perplexus*, *I. andersoni* differs in its ornament type, its more pronounced differentiation between the disc and the posterior auricle, and its higher anterior face. Final understanding of the relationships between *I. andersoni* and other Late Turonian and late Early–early Middle Coniacian small Euramerican forms, variably referred to as *I. costellatus*, *I. teshioensis*, *I. kleini*, *I. frechi*, and *I. stantoni*, requires further study.

Conspecific with *I. andersoni* is Kauffman's (1978, pl. 2, figs. 2, 10) *Inoceramus waltersdorffensis hannovrensis*, from the Coniacian II–III of Mfolozi Hill, Zululand, South Africa (locality 13 of Kennedy and Klinger, 1975). His larger specimen (Kauffman, 1978, pl. 2, fig. 10), represents a broader morphotype. Kauffman's specimens resemble forms from the *waltersdorffensis* group (compare Andert, 1934; Walaszczyk, 1992; Walaszczyk and Wood, 1999), but differ in their more inflated disc and concave anterior margin.

Inoceramus andersoni Etheridge is very similar to *Inoceramus hoopeni*, described by Heinz (1933) based on material from Madagascar. Both species have a similar outline, disc inflation, and posterior auricle, and differ mainly in the ornament. Instead of very closely and evenly spaced rugae, Heinz's species possesses the *perplexus*-type rugae: sharp edged, with gradual, ventralward increase of interspaces.

Occurrence. The type and Kauffman's (1978) Zululand material comes from the Coniacian II–III of Kennedy and Klinger (1975), suggested to be late Early or early Middle Coniacian. In the Manasoa section this species occurs exclusively in bed 29, which is interpreted as the lowermost Middle Coniacian.

Inoceramus hoopeni (Heinz, 1933)

Fig. 20D, K

- pars 1904 *Melina Andersoni* Etheridge, pp. 73, 74, pl. 2, figs. 7, 9, 10 [non pl. 2, fig. 8].
- 1933 *Striatoceramus hoopeni* Heinz, p. 246, pl. 18, figs. 2, 3.
- 1978 *Inoceramus* (*Inoceramus*) n. sp. aff. “*I. costellatus* Woods” of Fiege, 1930, pl. 5, fig. 10, and *I. uwajimensis* Yehara, 1924, pl. 3, fig. 2; fig. 4, fig. 2; Kauffman, pl. 2, figs. 1, 4, 8.
- non 1992 *Inoceramus hoopeni* Heinz; Walaszczyk, p. 38, pl. 21, figs. 1–7.
- 1999 *Inoceramus hoopeni* Heinz; Walaszczyk and Wood, pl. 19, figs. 2, 3.

Holotype. By original designation, the original of Heinz (1933, pl. 18, fig. 2; reillustrated in Walaszczyk and Wood 1999, pl. 19, fig. 2) from Antsalova-Bekopaka, Madagascar, housed in the Palaeontological Institute of the Museum of Natural History in Paris.

Material. 2 single valves; ZI/31/059 and ZI/31/060, both from bed 29.

Description. The species is small for the genus, inequilateral, ?equivalve. Valves are prosocline, weakly oblique, moderately inflated. The beak is small, pointed, curved slightly towards the anterior; not projecting above the hingeline. The valves are subrectangular in outline, with distinct, triangular disc, elongated parallel to growth axis, and subtriangular posterior auricle. The posterior auricle is well separated from the disc, extended postero-dorsally. Anterior margin is long, straight; may be slightly concave just below the umbo, then weakly convex. The ventral margin is rounded and passes into concave posterior margin; the concavity marks the auricular sulcus. The hingeline is straight and relatively long.

The valves are ornamented with regularly spaced, sharp-edged rugae, with interspaces increasing in width towards the venter. The rugae pass onto the posterior auricle. Growth lines were not observed, possibly because of poor preservation of the surfaces.

Discussion. Forms like *Inoceramus hoopeni* are inevitably the most difficult to interpret. It is because of their small size and very simple morphology, which are apparently repeated in separate inoceramid lineages. Very close morphologically to *I. hoopeni* are, e.g., *Inoceramus perplexus* from the lower Upper Turonian, as well as early forms of *Inoceramus kleini*, from the upper Lower and lower Middle Coniacian of the Euramerican biogeographic region. The specimens from Manasoa are identical morphologically to Heinz's type. Heinz (1933; and in Besairie, 1930) regarded his species as Late Turonian, based on direct correlation with the European record. On the other hand he mentioned the co-occurrence of *I. hoopeni* with *I. andersoni*, which would indicate late Early or even early Middle Coniacian as interpreted herein. The co-occurrence of both species is also indicated by the original, published material of Etheridge from Zululand, where the two species were found together (Etheridge, 1904, pls. 7–9). Consequently, the Manasoa specimens are referred to *I. hoopeni* although further material of this species may demonstrate that it should be synonymised with one or more of the Euramerican species.

Occurrence. As may be judged from the Manasoa sections the species is late Early or early Middle Coniacian; known from Madagascar and Zululand.

Forms left in open nomenclature

There are two forms that at the generic level are referred to here in open nomenclature and referred to “*Inoceramus*” sensu lato.

“*Inoceramus*” sp. aff. *pacificus* Woods, 1917

Fig. 20A, C, E, I, L

1978 *Mytiloides* (?) sp. aff. *M. lusatiae* (Andert); Kauffman, pl. 2, fig. 3.

Material. 8 specimens: ZI/31/049–ZI/31/053 and ZI/31/608–ZI/31/610; all single valves from bed 29.

Description. The species is of moderate to large size; strongly inequilateral, ?equivalve. The valves are strongly oblique, with δ between 52 and 54°, strongly prosocline. The beak is small, pointed, not projecting above the hingeline. The hingeline is relatively long and straight. The anterior margin is very short, consisting about 30–35% of the corresponding axial length, straight or slightly concave just below the umbo. It passes into very long, broadly rounded antero-ventral margin, and thence into rounded ventral margin. The posterior margin is short and straight. The growth axis is usually slightly convex anteriorly. The posterior auricle is of moderate size, triangular in shape, in the juvenile stage well separated from the disc, in adult the boundary is not seen. The ligament plate is massive, with simple rectangular to multilobate resilifers and flat ridges.

The shell ornament is observed in one adult and one juvenile specimen. It consists of raised growth lines; in the juvenile specimen the growth lines have the form of Anwachsringe (according to Heinz's 1928b classification). Indistinct, flat rugae are superimposed. The internal moulds are smooth or irregularly rugate. In the most adult part of the largest specimen, rugae are regular and widely spaced.

Discussion. In the high obliquity, strongly prosocline character and the type of ornament, the Madagascan specimens resemble the more oblique specimens of “*Inoceramus*” *pacificus* Woods, 1917 [cf. Crampton, 1996, pl. 13, figs. G, H; also Woods' (1917, pl. 12, fig. 17) specimen of *I. australis* referred subsequently to *I. pacificus* by Crampton, 1996]. In contrast to Woods' species, the Madagascan form clearly shows the presence of distinct rugae in the adult stage, and some of the specimens (e.g., Fig. 20L) show a moderate positive geniculation, not observed in *I. pacificus*. Comparison of the ornament is difficult as most of the specimens studied are represented by smooth internal moulds; only a single specimen bears partly preserved shell (Fig. 20A).

Undoubtedly conspecific with *I. sp. aff. pacificus* is *Mytiloides* (?) sp. aff. *M. lusatiae* (Andert) illustrated

by Kauffman (1978, pl. 2, fig. 3) from the Lower Coniacian of South Africa. *I. sp. aff. pacificus* also resembles some of the specimens referred by Noda (1992) to *Platyceramus troegeri* (= *Platyceramus tappuensis* Noda in Noda and Matsumoto 1998), particularly more oblique forms as, for example, the holotype (Noda, 1992, fig. 3).

Occurrence. The species is known so far from late Early/early Middle Coniacian strata of Madagascar and South Africa.

“*Inoceramus*” sp. aff. *opetius* Wellman, 1959

Fig. 20J

1978 *Inoceramus* n. sp. aff. *I. ernsti* Heinz, – “*I.*” *koeneni* Müller and *I. selwyni* McLarn; Kauffman, pl. 2, figs. 7, 11, 15.

Material. 2 specimens: ZI/31/058 and ZI/31/524; both from bed 29.

Description and discussion. The species is represented by two incomplete single valves, largely internal moulds with only small shell fragments attached. Judging from the two specimens it is a species of moderate size, prosocline, weakly oblique, weakly to moderately inflated; apparently equivalve, and inequilateral. The beak is small, pointed dorsally and curved slightly anteriorly. Besides the juvenile part the posterior auricle is poorly separated from the disc. The hingeline is of moderate length and straight. The anterior margin is apparently straight, weakly concave just below the umbo. The ventral and posterior margins are rounded. The valves are covered with irregular, low, concentric rugae, with superimposed growth lines; the character of the latter is observed on small shell fragments preserved in one of the specimens.

The valve outline and irregular concentric rugae make this species similar to *Inoceramus opetius* Wellman, 1959 [particularly the specimens illustrated by Crampton (1996, pl. 12)]. It also resembles some platyceramids, such as *Platyceramus tappuensis* (Noda, 1998) [= *Inoceramus* (*Platyceramus*) *troegeri* Noda, 1992] as well as some of the North Pacific specimens referred to *Platyceramus mantelli* (e.g., see Noda and Toshimitsu 1990, figs. 3, 4).

Occurrence. Topmost part of the Manasoa section; most probably late Early or early Middle Coniacian.

Acknowledgements

We thank Dr. James Crampton sincerely for a critical review and valuable comments on an earlier draft of the manuscript. Warm thanks are due to the late Jake M.

Hancock and Chris J. Wood, the journal referees, and to David J. Batten, the editor. The manuscript benefited greatly from their comments and improvements. Warm thanks also to Dr. Armand Rasoamaramanana, for field information and general advice during field work in Madagascar. Special thanks go to Jean Pierre Gorczewski, without whose help the Madagascan expedition would probably never have taken place.

References

- Airaghi, C., 1904. Inocerami del Veneto. *Bollettino Società Geologica Italiana* 23, 178–198.
- Anderson, F.M., 1902. Cretaceous deposits of the Pacific Coast. *Proceedings of the Californian Academy of Science* (3), Geology 2, 1–154.
- Andert, H., 1911. Die Inoceramen des Kreibitz-Zittauer Sandsteingebirges. *Festschrift des Humboldtvereins zur Feier seines 50 jährigen Bestehens*, pp. 33–64.
- Andert, H., 1934. Die Kreideablagerungen zwischen Elbe und Jeschken Teil III: Die Fauna der obersten Kreide in Sachsen, Böhmen und Schlesien. *Abhandlungen der Preussischen Geologischen Landesanstalt*, Neue Folge 159, 1–447.
- Assmus, G., 1963. Stratigraphie und Petrographie des Coniac im östlichen Teil der Halberstädter Mulde. Unpublished Diplomarbeit, Freiberg Technical University.
- Ayyasami, K., Rao, B.R.J., 1999. Dispersal of Cretaceous inoceramids in Gondwanaland. Ninth International Gondwana Symposium, pp. 341–355.
- Basse, E., 1947. Leu peuplements Malagaches de *Barroisiceras* (révision du genre *Barroisiceras* de Gross.). *Paléontologie de Madagascar* 26. *Annales de Paléontologie* 22, 97–190.
- Besairie, H., 1930. Recherches géologique à Madagascar. Thèses présentées à la faculté des Sciences de l'Université de Paris pour obtenir le titre d'Ingénieur-Docteur. Toulouse, 272 pp.
- Besairie, H. (in collaboration with Collignon, M.), 1972. Géologie de Madagascar I. Les terrains sédimentaires. *Annales Géologiques de Madagascar* 35, 463 pp.
- Bräutigam, F., 1962. Zur Stratigraphie und Paläontologie des Cenomans und Turons im nordwestlichen Harzvoland. Unpublished PhD thesis, University of Braunschweig, 261 pp.
- Cech, S., Svabenicka, L., 1992. Macrofossil and nannofossil of the type locality of the Brezno Formation (Turonian–Coniacian, Bohemia). *Věstník Českého Geologického Ústavu* 67, 311–326.
- Chiplonkar, G.W., Tapaswi, P.M., 1974. Bivalvia from the Upper Cretaceous of Trichinopoly District, South India—Part I: Inoceramidae. *Recent Researches in Geology* (Volume 3). A collection of papers in honour of Professor I.C. Pande, pp. 87–123.
- Choffat, P., 1905. Contribution à la connaissance des colonies Portugaises d'Afrique. II. Nouvelles données sur la zone littorale d'Angola. *Commission du Service Géologique du Portugal*, pp. 31–78.
- Collignon, M., 1955. Ammonites néocretacées du Menabe (Madagascar). II Les Pachydiscidae. *Annales Géologique du Service des Mines de Madagascar* 21, 1–98.
- Collignon, M., 1965a. Atlas des fossiles caractéristiques de Madagascar (Ammonites). Turonien. *Service Géologique*, Tananarive 12, 1–82.
- Collignon, M., 1965b. Atlas des fossiles caractéristiques de Madagascar (Ammonites). Coniacien. *Service Géologique*, Tananarive 13, 1–88.
- Cox, R.R., 1969. Family Inoceramidae Giebel, 1852. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology*, Part N. *Mollusca* 6, Bivalvia, vol. 1. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, pp. 314–321.
- Crame, J.A., 1981. Upper Cretaceous inoceramids (Bivalvia) from the James Ross Island Group and their stratigraphical significance. *Bulletin of the British Antarctic Survey* 53, 29–56.
- Crame, J.A., 1982. Late Mesozoic bivalve biostratigraphy of the Antarctic Peninsula region. *Journal of the Geological Society*, London 139, 771–778.
- Crame, J.A., 1983. Cretaceous inoceramid bivalves from Antarctica. In: Oliver, R.L., James, P.R., Jago, J.B. (Eds.), *Antarctic Earth Science. Proceedings of the Fourth International Symposium*, held at the University of Adelaide, South Australia, 16 to 20 August 1982, Canberra, pp. 298–302.
- Crampton, J.S., 1995. Revised inoceramid bivalve zonation and correlations for the Cenomanian to Santonian stages (Late Cretaceous) in New Zealand. In: *The Cretaceous System in East and South Asia, Research Summary 1995*. Newsletter Special Issue 2, IGCP 350, Kushu University, Fukuoka, pp. 49–59.
- Crampton, J.S., 1996. Inoceramid bivalves from the Late Cretaceous of New Zealand. Institute of Geological & Nuclear Sciences, Monograph 14 (New Zealand Geological Survey, Palaeontological Bulletin 70), 1–188.
- Crampton, J.S., Raine, I., Strong, P., Wilson, G., 2001. Integrated biostratigraphy of the Raukumara Series (Cenomanian–Coniacian) at Mangaotane Stream, Raukumara Peninsula, New Zealand. *New Zealand Journal of Geology and Geophysics* 44, 365–389.
- Dartevelle, E., Freneix, S., Sornay, J., 1957. Mollusques fossiles du Crétacé de la Côte occidentale d'Afrique du Cameroun à l'Angola. II. Lamellibranches. *Annales du Musée Royal du Congo Belge*, Turverun (Belgique), Série 8, Sciences Géologiques 20, 271 pp.
- Eichwald, E., 1865. *Lethaea Rossica ou Paléontologie de la Russie*, vol. 2, pp. 484–497.
- Etheridge, R., 1904. Cretaceous fossils of Natal, I. Umkwelane Hill deposit. *Second Report of the Geological Survey of Natal and Zululand*, pp. 67–90.
- Fiege, K., 1930. Über die Inoceramen des Oberuron mit besonderer Berücksichtigung der im Rheinland und Westfalen Vorkommenden Formen. *Palaeontographica* 73, 31–47.
- Flegel, K., 1905. Heuscheur und Adersbach-Weckelsdorf. Eine Studie über die obere Kreide im böhmisch-schlesischen Gebirge. *Jahresbericht der Schlesisches Gesellschaft der Vaterland Kultur* 3, 123–158.
- Harries, P.J., Kauffman, E.G., Crampton, J.S. (Eds.), 1996. Lower Turonian Euramerican Inoceramidae: a morphologic, taxonomic, and biostratigraphic overview. A report from the First Workshop on Early Turonian Inoceramids (Oct. 5–8, 1992) in Hamburg, Germany; organized by Heinz Hilbrecht and Peter Harries. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 77, 641–671.
- Heine, F., 1929. Die Inoceramen des mittelwestfälischen Emschers und unteren Untersemons. *Abhandlungen der Preussischen Geologischen Landesanstalt*, Neue Folge 120, 1–124.
- Heinz, R., 1928a. Das Inoceramen-Profil der Oberen Kreide Lüneburgs. Mit Anführungen der neuen Formen und deren Kennzeichnung. *Beiträge zur Kenntnis der oberkretazischen Inoceramen I*. *Jahresbericht des Niedersächsischen Geologischen Vereins zu Hannover*, 64–81.
- Heinz, R., 1928b. Über die bisher wenig beachtete Skulptur der Inoceramen-Schale und ihre stratigraphische Bedeutung. *Beiträge zur Kenntnis der oberkretazischen Inoceramen IV*. *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg* 10, 5–39.
- Heinz, R., 1928c. Über die Oberkreide-Inoceramen Neu Seelands und Neu Kaledoniens zu denen Europas und anderer Gebiete. *Beiträge zur Kenntnis der oberkretazischen Inoceramen VII*. *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut, Hamburg* 10, 110–130.

- Heinz, R., 1929. Ueber Kreide-Inoceramen der Südafrikanischen Union. Beiträge zur Kenntnis der oberkretazischen Inoceramen XI. Compte Rendu XV International Geological Congress, Pretoria, South Africa, vol. 2, pp. 681–687.
- Heinz, R., 1932. Aus der neuen Systematik der Inoceramen. Beiträge zur Kenntnis der oberkretazischen Inoceramen XIV. Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut, Hamburg 13, 1–26.
- Heinz, R., 1933. Inoceramen von Madagascar und ihre Bedeutung für die Kreide-Stratigraphie. Zeitschrift der Deutschen Geologischen Gesellschaft 85, 241–259.
- Herm, D., Kauffman, E.G., Wiedmann, J., 1979. The age and depositional environment of the “Gosau”- Group (Coniacian–Santonian), Brandenberg/Tirol, Austria. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 19, 27–92.
- Innostraneff, A., 1897. Au Travers de la Chaine Principale du Caucase. Recherches Géologiques à la Long de la Ligne Projété du Chemin de Fer de Vladikavkas–Tiflis au Travers du Col de l’Arkhotis. Edition de la Direction des Chemins de Fer de l’Etat, St. Petersbourg.
- Ivannikov, A.V., 1979. Inoceramids of the Upper Cretaceous in Southwestern Part of the East European Platform. Akademiya Nauk Ukrainskoy SSR, Institut Geologicheskikh Nauk, Kiev, 102 pp. (in Russian).
- Kaplan, U., Kennedy, W.J., 1994. Ammoniten des westfälischen Coniac. Geologie und Paläontologie in Westfalen 31, 1–155.
- Kaplan, U., Kennedy, W.J., 1996. Upper Turonian and Coniacian ammonite stratigraphy of Westfalia, NW-Germany. Acta Geologica Polonica 46, 305–352.
- Kaplan, U., Schmid, F., 1988. Die heteromorphen Ammoniten der Gattungen *Eubostrychoceras* und *Hyphantoceras* aus dem Turon NW-Deutschlands. Geologie und Paläontologie in Westfalen 12, 47–87.
- Kauffman, E.G., 1973. Cretaceous Bivalvia. In: Hallam, A. (Ed.), Atlas of Palaeobiogeography. Elsevier, Amsterdam, pp. 353–383.
- Kauffman, E.G., 1978. South African Middle Cretaceous Inoceramidae. Annales du Museum D’Histoire Naturelle de Nice 4 (17), 1–6.
- Keller, S., 1982. Die Oberkreide der Sack-Mulde bei Alfeld (Cenoman–Unter Coniac). Lithologie, Biostratigraphie und Inoceramen. Geologisches Jahrbuch A 64, 3–171.
- Kennedy, W.J., 1978. The middle Cretaceous of Zululand and Natal, eastern South Africa. Annales du Museum d’Histoire Naturelle de Nice 4 (18), 1–29.
- Kennedy, W.J., Cobban, C.W., 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. Special Papers in Palaeontology 17, 1–94.
- Kennedy, W.J., Klinger, H.C., 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. Bulletin of the British Museum (Natural History), Geology 25, 263–315.
- Kennedy, W.J., Wright, C.W., 1984. The Cretaceous ammonite *Ammonites requienianus* d’Orbigny, 1841. Palaeontology 27, 281–293.
- Klinger, H.C., Kauffman, E.G., Kennedy, W.J., 1980. Upper Cretaceous ammonites and inoceramids from the off-shore Alphard Group of South Africa. Annals of the South African Museum 82, 293–320.
- Kossmat, F., 1897. Untersuchungen über die Südindische Kreideformation. Beiträge zur Paläontologie der Österreich und Ungarn 11, 1–46.
- Kotsubinsky, S.P., 1974. Inocerams. In: Krymgoltz, G.J. (Ed.), Atlas of the Upper Cretaceous fauna of Donbass, pp. 76–86, (in Russian).
- Langenhan, A., Grundey, M., 1891. Das Kiesligswalder Gestein und seine Versteinerungen. Jahresbericht des Glatzer Gebirgs-Vereins 10, 1–12.
- Marcinowski, R., 1974. The transgressive (Upper Albian through Turonian) deposits of the Polish Jura Chain. Acta Geologica Polonica 24, 117–217.
- Marcinowski, R., 1980. Cenomanian ammonites from German Democratic Republic, Poland, and the Soviet Union. Acta Geologica Polonica 30, 215–325.
- Matsumoto, T., 1971. A monograph of the Collignoniceratidae from Hokkaido. Part. V. (Studies of the Cretaceous ammonites from Hokkaido and Saghalien—XXIII). Memoirs of the Faculty of Science, Kyushu University, Series D, Geology 21, 129–162.
- Niebuhr, B., Baldschuhn, R., Ernst, E., Walaszczyk, I., Weiss, W., Wood, C.J., 1999. The Upper Cretaceous succession (Cenomanian–Santonian) of the Staffhorst Shaft, Lower Saxony, northern Germany: integrated biostratigraphic, lithostratigraphic and down-hole geophysical log data. Acta Geologica Polonica 49, 175–213.
- Noda, M., 1992. *Inoceramus (Platyceramus) troegeri* sp. nov. (Bivalvia) from the Coniacian (Cretaceous) of Hokkaido and its systematic implications. Transactions and Proceedings of the Palaeontological Society of Japan, New Series 168, 1311–1328.
- Noda, M., 1996. Five inoceramids (Bivalvia) from the Upper Cretaceous of Hokkaido with some phylogenetic and taxonomic considerations. Transactions and Proceedings of the Palaeontological Society of Japan, New Series 184, 555–591.
- Noda, M., Matsumoto, T., 1998. Palaeontology and stratigraphy of the inoceramid species from the mid-Turonian through upper Middle Coniacian in Japan. Acta Geologica Polonica 48, 435–482.
- Noda, M., Toshimitsu, S., 1990. Notes on a Cretaceous bivalve *Inoceramus (Platyceramus) mantelli* de Mercey from Japan. Transactions and Proceedings of the Palaeontological Society of Japan, New Series 158, 485–512.
- Pergament, M.A., 1971. Biostratigraphy and inocerams of Turonian–Coniacian deposits of the Pacific regions of the USSR. Transactions of the Academy of Sciences USSR 212, 1–212.
- Sornay, J., 1964. Sur quelques nouvelles espèces d’Inocérames du Sénionien de Madagascar. Annales de Paléontologie (Invertébrés) 50, 167–179.
- Sornay, J., 1980. Révision du sous-genre d’Inocérame *Tethyceramus* Heinz 1932 (Bivalvia) et de ses représentants Coniaciens à Madagascar. Annales de Paléontologie (Invertébrés) 66, 135–150.
- Summesberger, H., Kennedy, W.J., 1996. Turonian ammonites from the Gosau Group (Upper Cretaceous; Northern Calcareous Alps; Austria) with a revision of *Barroisiceras haberfellneri* (Hauer, 1866). Beiträge zur Paläontologie 21, 105–177.
- Szasz, L., 1985. Contribution to the study of the *Inoceramus* fauna of Romania. I. Coniacian *Inoceramus* of Romania-Babadag Basin. Mémoires de l’Institut de Géologie et de Géophysique 32, 128–184.
- Tanabe, K., 1977. Mid-Cretaceous scaphitid ammonites from Hokkaido. Mid-Cretaceous Events—Hokkaido Symposium, 1976. Palaeontological Society of Japan, Special Papers 21, 11–21.
- Tanabe, K., Obata, I., Futakami, M., 1978. Analysis of ammonoid assemblages in the Upper Turonian of the Manji area, central Hokkaido. Bulletin of the National Science Museum, Series C (Geology & Paleontology) 4, 37–62.
- Tröger, K.-A., 1968. Bemerkungen zu *Hyphantoceras reussianum* (d’Orbigny). Freiberger Forschungsheft, Paläontologie C 234, 45–50.
- Tröger, K.-A., 1984. Über zwei aussergewöhnlich grosse Inoceramen-Arten aus dem Ober-Turon von Europa. Freiberger Forschungsheft C 395, 47–53.
- Walaszczyk, I., 1992. Turonian through Santonian deposits of the Central Polish Uplands; their facies development, inoceramid paleontology and stratigraphy. Acta Geologica Polonica 42, 1–122.

- Walaszczyk, I., 1997. Significance of the ligament area in species level taxonomy of inoceramid bivalves; how much variation is lodged in a single species? *Freiberger Forschungsheft C* 468, 289–303.
- Walaszczyk, I., Cobban, W.A., 2000. Inoceramid faunas and biostratigraphy of the Upper Turonian–Lower Coniacian of the Western Interior of the United States. *Special Papers in Palaeontology* 64, 1–118.
- Walaszczyk, I., Tröger, K.-A., 1996. The species *Inoceramus frechi* (Bivalvia, Cretaceous); its characteristics, formal status, and stratigraphic position. *Paläontologische Zeitschrift* 68, 393–404.
- Walaszczyk, I., Wood, C.J., 1999. Inoceramids and biostratigraphy at the Turonian/Coniacian boundary; based on the Salzgitter-Salder Quarry, Lower Saxony, Germany, and the Słupia Nadbrzeżna section, central Poland. *Acta Geologica Polonica* 48 (for 1998), 395–434.
- Wellman, H.W., 1959. Divisions of the New Zealand Cretaceous. *Transactions of the Royal Society of New Zealand* 87, 99–163.
- Woods, H., 1912. A monograph of the Cretaceous Lamellibranchia of England. Volume 2, Part 8. *Monographs of the Palaeontographical Society* (for 1911), 285–340, pls. 51–54.
- Woods, H., 1917. The Cretaceous faunas of the north-eastern part of the South Island of New Zealand. *New Zealand Geological Survey, Palaeontological Bulletin* 4, 1–41.
- Wright, C.W., 1979. The ammonites of the English Chalk Rock (Upper Turonian). *Bulletin of the British Museum (Natural History), Geology* 31, 282–332.
- Yehara, S., 1924. On the Izumi sandstone group in the Onogawa Basin Prov. Bungo and the same group in Uwajima, Prov. Iyo. *Japanese Journal of Geology and Geography* 3, 24–40.