Acta Geologica Polonica, Vol. 48 (1998), No. 4, pp. 367-376

Ontogenetic variation and inoceramid morphology: a note on early Coniacian *Cremnoceramus bicorrugatus* (Cretaceous Bivalvia)

JAMES S. CRAMPTON

Institute of Geological and Nuclear Sciences, P.O. Box 30-368, Lower Hutt, New Zealand
E-mail: J.Crampton@gns.cri.nz.

ABSTRACT:

CRAMPTON, J.S. 1998. Ontogenetic variation and inoceramid morphology: a note on early Coniacian *Cremnoceramus bicorrugatus* (Cretaceous Bivalvia). *Acta Geologica Polonica*, **48** (4), 367-376. Warszawa.

Taxonomic studies of Cretaceous inoceramid bivalves are confounded by high levels of intraspecific morphological variation within the group. Such variation is illustrated here using *Cremnoceramus bicorrugatus* s. s. (MARWICK, 1926) from the lower Coniacian of New Zealand. This taxon displays a remarkable range of intraspecific variation that is the sum of three major components: 1) a basic set of ontogenetic transformations between the juvenile, immature and adult stages; 2) intra-populational variation in the relative timing or rate of developmental events; and 3) intra-populational variation in the rate of absolute growth. The first of these components was largely genetically determined, whereas the other two were probably influenced by extrinsic environmental factors. Taxonomic interpretation of *C. bicorrugatus* s. s. is not possible without some understanding of both the basic ontogenetic plan and developmental variations within that plan. Interpretation is facilitated by the profound and step-wise nature of the ontogenetic transformations. In many other inoceramids, however, ontogenetic transformations are more subtle but may be subject to equally significant intraspecific developmental variations. Therefore, inoceramid taxonomists should describe not only total population variation, but also should document ontogenetic development in any species. In this way it is possible to identify basic ontogenetic plans, constrain likely limits to intraspecific variation, and distinguish intraspecific from interspecific morphological variation.

INTRODUCTION

Despite a huge effort over the past century, the taxonomy of Cretaceous inoceramid bivalves remains comparatively poorly resolved at the species and genus level. This is because of widespread homoplasy within the group, the lack of easily classified character suites, high levels of intraspecific variability, and high rates of morphological evolution and speciation. The history of inoceramid systematics includes extremes of taxonomic "splitting" and "lumping" (*e.g.*, contrast HEINZ 1932 and WOODS 1911, 1912). This history has been covered in some detail elsewhere (SORNAY 1966, PERGAMENT 1978, POKHIALAINEN 1985a). Even today, taxonomic concepts and basic systematic practice vary considerably between workers (*e.g.*, discussion in CRAMPTON 1996a) and many taxa remain poorly diagnosed. Despite these problems, huge progress has been

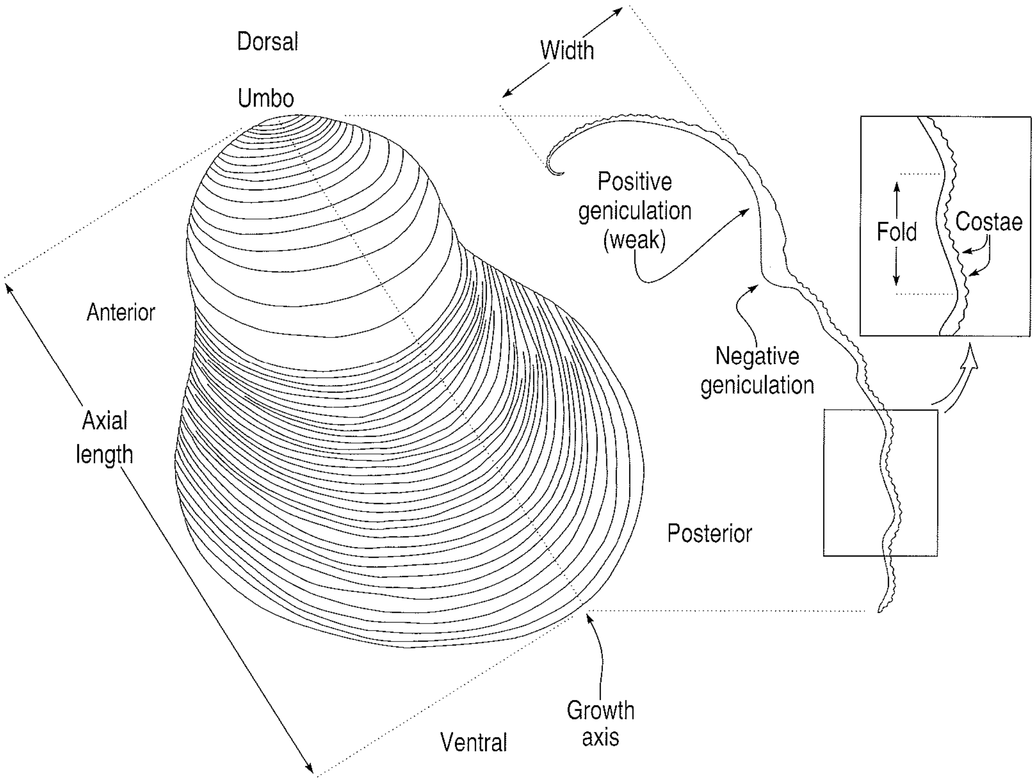


Fig. 1. *Cremnoceramus bicorrugatus bicorrugatus* (Marwick, 1926), left valve, showing morphological terms and biometric parameters mentioned in the text

achieved through the careful study of inoceramid lineages in key sections on all continents.

Central to an improved understanding of inoceramid taxonomy is the recognition and description of intraspecific variation. To this end, many workers have illustrated large populations or have developed a variety of biometric methodologies to describe this variation (*e.g.* Seitz 1935; Tanabe 1973; Noda 1975, 1988; Tröger & Röhlich 1980, 1982; Pokhialainen 1985b; Housa 1994; Crampton 1996b). In addition to variation between individuals, these studies have illustrated differences between growth stages of single individuals. Such ontogenetic variation can be very marked and may account for much of the total intraspecific morphological variation. In some cases, ontogenetic changes in form may be greater in magnitude than differences between species and may even bridge accepted generic boundaries (Crampton 1996b, fig. 7b, fig. 11, and discussion on p. 27-29). Despite these observations, relatively few studies have focussed on ontogenetic morphological changes (*but see* Tanabe 1973) or have considered the effects of variations in *rate* or *timing* of development and growth during ontogeny.

Ontogenetic variations in form are very conspicuous in the cosmopolitan(?) inoceramid genus *Cremnoceramus* Cox, 1969. This genus has been diagnosed primarily by the presence of a pronounced "geniculation", or more-or-less abrupt change in convexity and inflation, at some growth stage (*e.g.* Kauffman *in* Herm *et al.* 1979, Pokhialainen 1985a). Following Crampton (1996a, p. 74), a "positive" geniculation refers to an increase in convexity and a "negative" geniculation refers to a decrease in inflation (Text-fig. 1). Although the exact definition and content of this genus remain open to debate, there is little doubt that it represents a robust and monophyletic, genus-level taxon (see other papers in this volume).

Cremnoceramus is represented in the latest Turonian and early Coniacian of New Zealand by at least four species-level taxa (CRAMPTON 1996a), *Cremnoceramus bicorrugatus bicorrugatus* (MARWICK, 1926), *C. bicorrugatus matamuus* CRAMPTON, 1996a, *C. moorei* Crampton, 1996a, (Text-fig. 2) and *C.* sp. A aff. *C. bicorrugatus*. *Cremnoceramus bicorrugatus* s. s. is characterised by a truly remarkable range of ontogenetic variation, even in comparison to other species of *Cremnoceramus*. Furthermore, it is abundant on bedding planes and well preserved within a number of sections (CRAMPTON 1996a). Consequently, this species represents an ideal subject for a study of population variations in ontogenetic development. Such observations serve as a model for other inoceramid taxa in which ontogenetic variations are more subtle but equally important in taxonomic and phylogenetic inference.

Morphological terms and biometric parameters used throughout are shown in Text-fig. 1 and follow CRAMPTON (1996a). All figured specimens are lodged in the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand (specimen numbers prefixed "TM") or in the Geology Department, Victoria University of Wellington, New Zealand (specimen numbers prefixed "VM"). All fossil localities are registered in the New Zealand Fossil Record File (FRF), administered by the Geological Society of New Zealand.

MATERIAL AND METHODS

Cremnoceramus bicorrugatus s. s. is abundant in lower Coniacian strata throughout the eastern North Island and northeastern South Island of New Zealand (Text-fig. 3). In addition, it has been recorded from a small number of sites in the northernmost North Island. Key localities are listed in CRAMPTON (1996a). In particular, two sites have yielded very abundant and well preserved specimens. In the Mangaotane Stream section, in the central part of Raukumara Peninsula (Text-fig. 3), the range of *C. bicorrugatus* s. s. extends through approximately 120 m of the Karekare Formation (CRAMPTON 1996a, figs 12 and 14). The Karekare Formation is dominated by

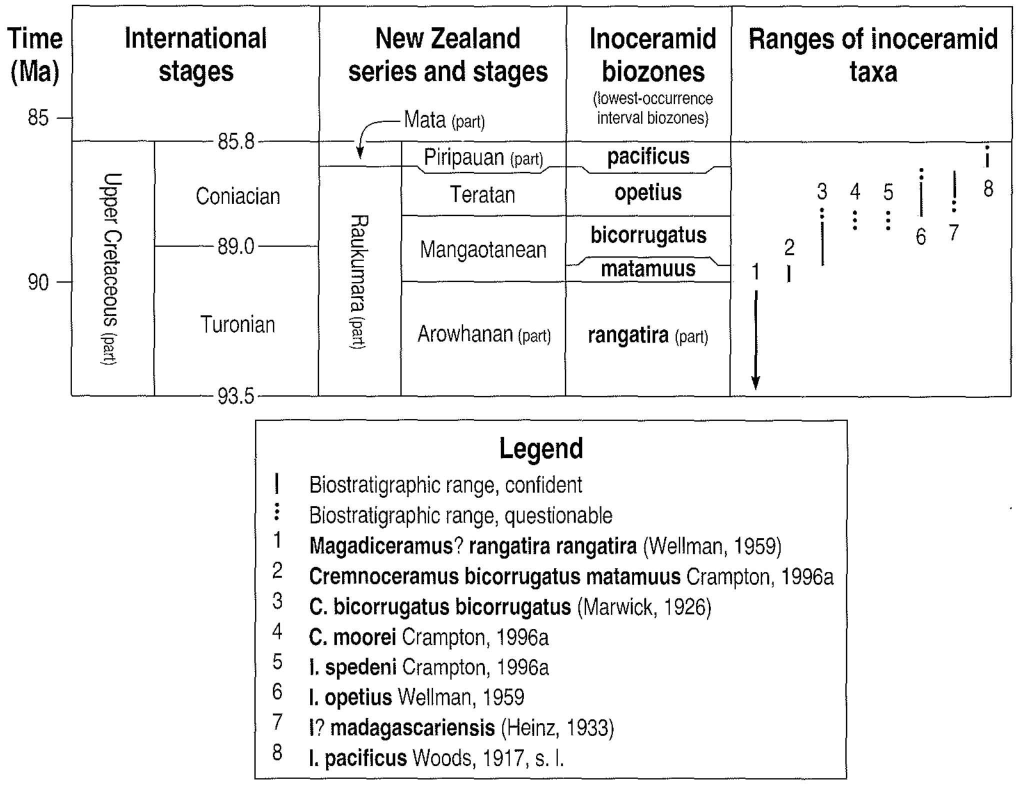


Fig. 2. Ranges of Turonian and Coniacian inoceramids in New Zealand and both local and international stages; International timescale *after* GRADSTEIN & *al.* (1995); correlations with the New Zealand timescale after CRAMPTON (1996a, with slight modification)

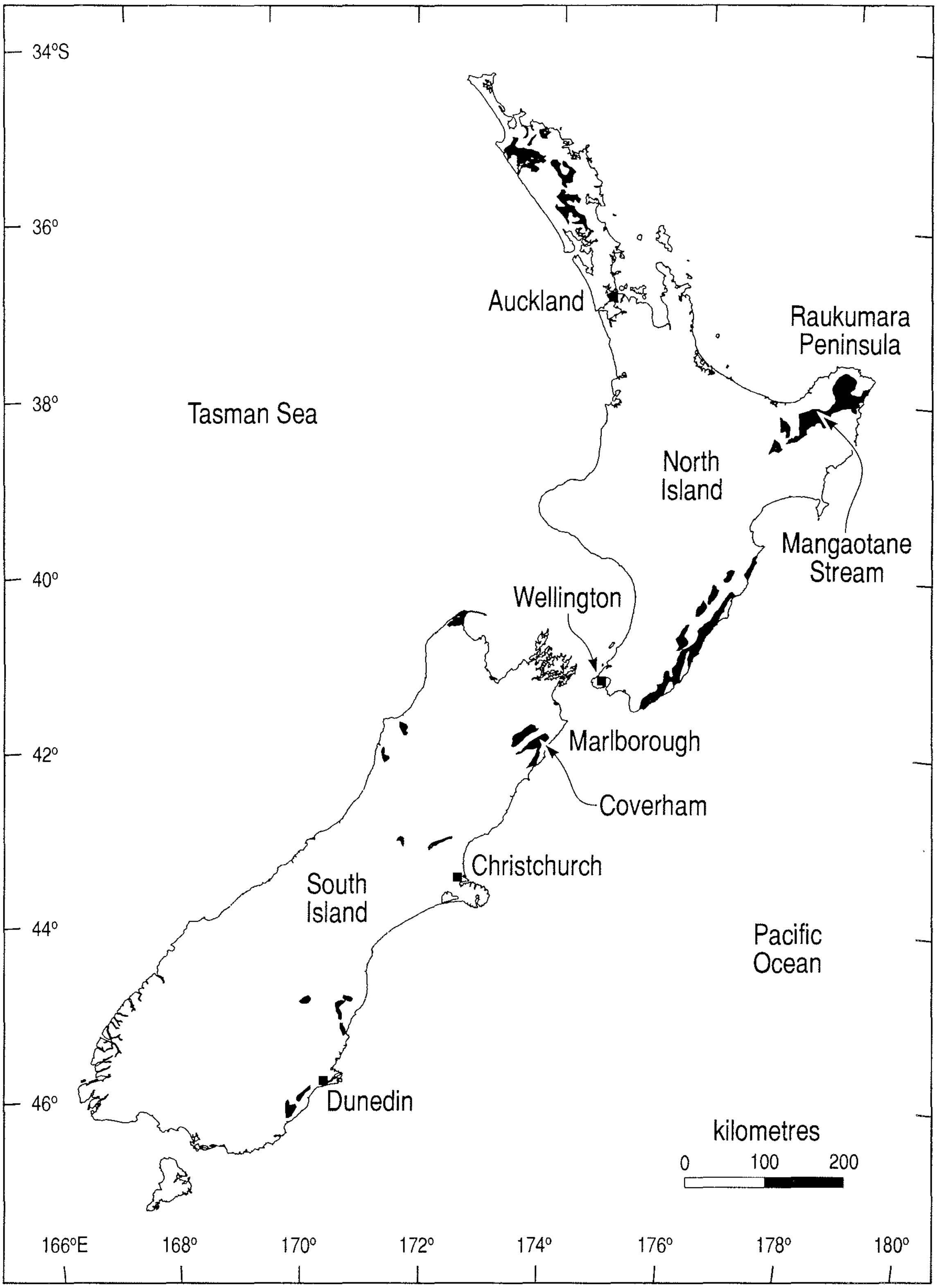


Fig. 3. Map of New Zealand showing distribution of uppermost Lower and Upper Cretaceous strata (black) and place names mentioned in the text; Coniacian strata are widely distributed throughout the shaded regions north of Auckland and between Raukumara Peninsula and Marlborough

mudstone and is inferred to have been deposited at outer shelf depths or greater. In the lower "Sawpit Gully" section, Coverham, Marlborough (Text-fig. 3), *C. bicorrugatus* s. s. forms dense shellbeds through at least 25 m of the Nidd Sandstone (*unpublished data*). The Nidd Sandstone is composed of muddy, poorly bedded sandstone and was probably deposited in a shallow marine environment (CRAMPTON & LAIRD 1997).

Rigorous biometric analysis has not been possible in this study. Because of their large size, the difficulties of collecting from indurated formations and the remoteness of key localities, it has not been feasible to collect populations of adult *C. bicorrugatus* s. s. The present discussion is based instead upon laboratory examination of approximately 200 specimens from many localities, upon limited biometric data taken from CRAMPTON (1996a), and upon new field observations of within-bed populations.

MAJOR PATTERNS OF ONTOGENETIC DEVELOPMENT IN *CREMNOCERAMUS BICORRUGATUS* S. S.

Cremnoceramus bicorrugatus s. s. has been redescribed recently by CRAMPTON (1996a) who discussed the complex patterns of ontogenetic development in this taxon. Very marked ontogenetic changes affect the outline shape, sculpture, inflation, ligament area and shell microstructure. The present discussion is limited to major external features of the shell, namely the shape, sculpture and inflation.

Major patterns of ontogenetic change in external characters, the "ontogenetic plan", are illustrated in Text-figs 1 and 4. Three growth stages are recognised and these are termed juvenile, immature and adult.

1. The juvenile stage is inequivalve and comparativley weakly inflated in most specimens, although the left valve may be moderately inflated. It is strongly prosocline, the growth axis being directed towards the posterior. The juvenile has a sculpture of fine, regular, rounded commarginal folds or costae.

2. The transition between the juvenile and immature stages is gradational. The immature stage becomes more highly inflated than the juvenile, the right valve in particular increasing in width, resulting in an approximately equivalve shell. In some cases, the increase in inflation is relatively abrupt, resulting in a positive geniculation. The growth axis is directed ventrally, the valves becoming acline, subcircular and globose with development. The immature sculpture comprises broad, flattened costae separated by narrow furrows.

3. The transition between the immature and adult shell is abrupt and occurs at a very pronounced negative geniculation. The adult is more weakly inflated than the immature stage and is weakly to moderately prosocline. It has a sculpture of fine, regular, rounded commarginal costae superimposed upon large, commarginal folds.

This ontogenetic plan in *C. bicorrugatus* s. s. is affected, at all stages, by population variations in rates of development and growth. The effects of these variations are described below.

VARIATIONS IN THE RATES OF DEVELOPMENT AND GROWTH DURING ONTOGENY

It has not been possible to assign absolute ages to any particular growth stage. Commarginal costae on the surface of the shell may have formed in phase with regular, periodic environmental signals such as tidal, day/night, or seasonal cycles (*e.g.* JONES & QUITMYER 1996). If so, then simple counts of the costae could furnish some sclerochronological scale by which relative or absolute ages of individuals could be estimated. Such regular periodicities cannot be assumed, however. Even if costae formation was rhythmic, this periodicity might have varied from environment to environment, depending on water depth, temperature and seasonal or tidal influences. In addition, the periodicity of costae formation may have varied with age or growth stage of the individual. Attempts to correlate the numbers of commarginal costae with some environmental signal using geochemical and stable isotopic data have failed (*unpublished data*). Hence, in the absence of independent evidence for a regular periodicty of costae formation, no relative or absolute ages can been inferred for individuals.

For the purposes of this discussion, however, the major negative geniculation at the immature to adult transition is taken as a reference datum and, by convention, is *assumed to represent the*

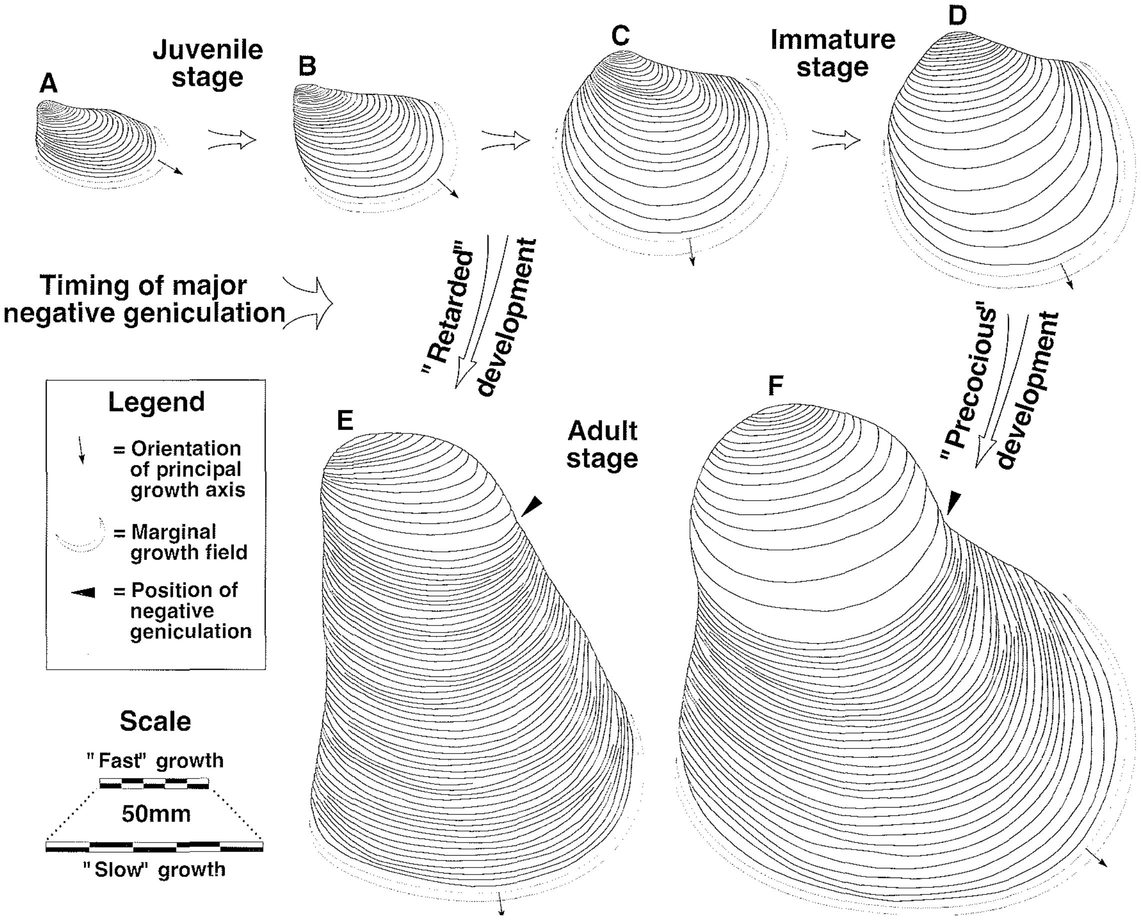


Fig. 4. Ontogenetic stages in the development of *C. bicorrugatus* s. s. showing the effects of varying rates of development and growth; the two scale bars shown apply to all growth stages and correspond to the extremes of "fast" and "slow" growth; see text for discussion

Fig. 5. Field photograph of extreme adult morph of *C. bicorrugatus* s. s., left valve, internal mould; the arrow marks the position of the major negative geniculation; this specimen displays "precocious" growth and has a large, globose immature stage; the adult shell is correspondingly long with a relatively expanded disc; specimen observed in the Nidd Sandstone in a tributary of Nidd Stream, Coverham, Marlborough (Text-fig. 3, grid reference P30/83271845); scale bar divisions in centimetres

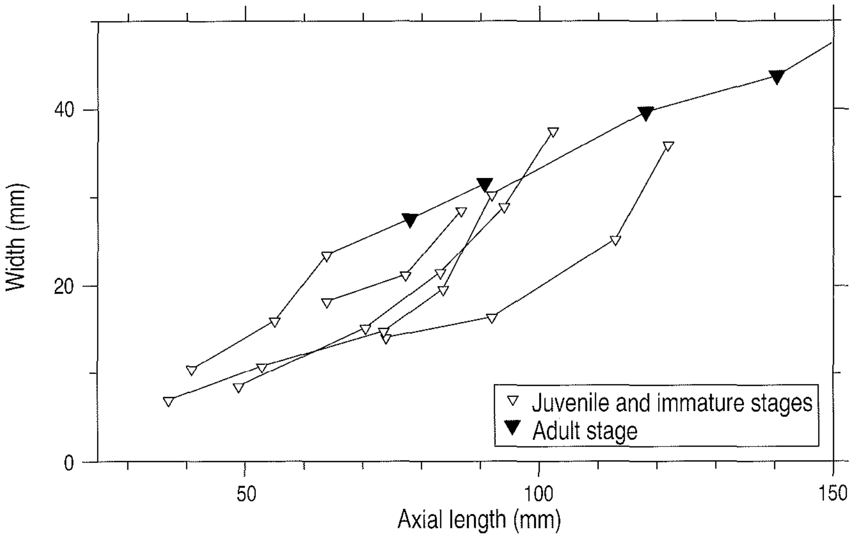


Fig. 6. Plot of width *versus* axial length for right valves of *C. bicorrugatus* s. s. (*after* CRAMPTON 1996a). Note that all individuals trace similar allometric curves but display varying offsets with respect to axial length, depending upon relative growth rates. In most individuals the allometric increase in width is relatively abrupt and forms a weak positive geniculation, although this is not readily apparent in most of the allometric curves because of the few data points

same absolute age in all individuals. Therefore, in comparisons between specimens, one might be termed "retarded" or "precocious" and "large" or "small" depending on the size and morphology of the shell at the negative geniculation. This assumption is certainly a gross over-simplification and, in reality, the geniculation probably formed at a range of ages in response to unknown environmental or intrinsic biological triggers. In the following discussion, terms relating to "rate" and "timing" of developmental events are enclosed by inverted commas to emphasise this underlying assumption. It should be noted that these terms relate only to population variation in individual patterns of development, not to evolutionary changes in developmental patterns.

Following this convention, much of the total morphological variation in adult *C. bicorrugatus* s. s. can be ascribed to changes in the relative rates of development and growth. These two factors are discussed and illustrated below.

Rate of development

The "rate" of development prior to the immature to adult geniculation, irrespective of absolute size, has a profound affect upon the adult morphology of *C. bicorrugatus* s. s. (Text-fig. 4, Pls 1 and 2). During juvenile and immature growth, the outline shape changes dramatically and continuously. This can be explained by changing growth fields within the mantle around the growing margin of the shell. During the juvenile stage, the growth field is confined to a relatively narrow arc and the greatest growth is in the posterior direction (Text-fig. 4A and 4B). During the immature stage the growth field is more uniformly distributed around a relatively wide arc and the axis of growth is in the ventral or postero-ventral direction (Text-fig. 4C and 4D). These growth fields carry through onto the adult shell. Hence, if development is "retarded" at the time of geniculation, the growth field is closer to the juvenile state and is confined to a relatively narrow arc. Therefore the adult shell is tall and short (in an antero-posterior sense, Text-fig. 4E). Conversely, if development is "precocious" at the time of geniculation, the growth field extends through a wide arc and the adult shell is relatively long, with an expanded disc (Text-fig. 4F). Examples of these variants are illustrated in Plates 1 and 2. Most specimens are morphologically intermediate between the specimens shown in Text-fig. 4 and Pl. 1 and 2; an extreme specimen is shown in Text-fig. 5. It must be stressed that this entire range of variation can be observed within intra-bed populations and, in particular, is readily apparent within shellbeds in the Sawpit Gully section, Marlborough.

Rate of growth

Changes in the "rate" of growth of *C. bicorrugatus* s. s. are more easily understood and also have a profound influence on adult morphology. Relatively "fast" growth results in "large" individuals irrespective of developmental stage; relatively "slow" growth results in "small" individuals. The variants described in the previous paragraph may occur as large or small individuals, with size varying by a factor of two or more as indicated in the scale bar for Text-fig. 4. This variation is illustrated in Text-fig. 6, showing the width of right valves *versus* axial length. All individuals trace similar allometric curves but display varying offsets with respect to axial length, depending upon relative growth rates. On this plot, the axial length at the negative geniculation varies between c. 65 mm and > 120 mm. In Pl. 2, Fig. 3, the geniculation occurs at an axial length of ca. 130 mm, whereas in Pl. 2 Fig. 1 this distance is just 66 mm. These two figured specimens are close to the extremes of size variation observed. Again, this entire range of variation is observed within intra-bed populations.

Other variations

Other variations are less easily identified without recourse to more rigorous biometric analyses. "Normal" intra-populational or ecophenotypic variations in morphology are sure to affect the course of ontogenetic development and to impact on the adult morphology of *C. bicorrugatus* s. s. In particular, such variations might explain a minor component of atypical and poorly understood morphotypes.

DISCUSSION AND CONCLUSIONS

Cremnoceramus bicorrugatus s. s. displays a truly remarkable range of intraspecific morphological variation. This variation is such that isolated growth stages or parts of different individuals could, with some justification, be mistakenly assigned to two or three inoceramid genera. The variation is the sum of three major components:

1. A basic set of ontogenetic transformations that define the "ontogenetic plan" and comprise three major developmental stages, namely the juvenile, immature and adult stages.

2. Intra-population variation in the "rate" of development or progress through the ontogenetic plan, variation that affects the form of the adult.

3. Intra-population variation in the "rate" of growth that determines the absolute size at any given ontogenetic stage.

The ontogenetic plan was clearly genetically determined. Variations in the rates of development and growth, on the other hand, may have been influenced to a great extent by extrinsic ecological and environmental factors. In the populations studied, these variations are apparently define a morphological continuum and, to date, there is no evidence to suggest that they have any taxonomic significance. Such variations may, of course, have furnished the raw materials for subsequent selection and evolution.

Systematic correlations between intraspecific variation in *C. bicorrugatus* s. s. and facies have not been explored here. Much of the variation recorded during this study, however, has been observed within strata that are inferred to have been deposited in both shallow marine environments (Nidd Sandstone, Coverham) and at outer shelf depths or greater (Karekare Formation, Mangaotane Stream). On present data there is little evidence for a strong correlation between facies and morphological variation. It is interesting to note that SEIBERTZ (1986) investigated facies effects upon the morphology of North American *Cremnoceramus*. He concluded that five previously recognised species represented no more than ecophenotypes of a single taxon. To date, his interpretations have not found wide acceptance amongst other inoceramid taxonomists.

The data described above have important implications for inoceramid taxonomy in general. In *C. bicorrugatus* s. s., the abundance of well preserved material and the very conspicuous, stepwise nature of ontogenetic changes have facilitated identification and understanding of the observed intraspecific variation. In particular, the effects of changes in the rates of development and growth are seen readily because the geniculation provides an ontogenetic datum for comparison between individuals. In other inoceramid taxa, ontogenetic changes typically are more subtle and involve transitions between character states that cannot be easily diagnosed. In such cases, however, intraspecific variations in rates of development and growth can still influence adult morphology greatly. In the absence of a clear understanding of both ontogenetic development and intraspecific variations in that development, the total adult intraspecific morphological variation may be open to misinterpretation.

In conclusion, I would argue that it is important to describe not only total population variations within inoceramid collections, but also to seek an understanding of the ontogenetic development of any species. In this way it is possible to identify basic ontogenetic plans, constrain likely limits to intraspecific variation, and distinguish intraspecific from interspecific morphological variation. In addition, attention to ontogenetic patterns provides the raw materials for evolutionary studies of heterochrony and heterotopy. In the case of *C. bicorrugatus* s. s., the distinctive ontogenetic plan may help identify likely evolutionary pathways between the genus *Cremnoceramus* and both ancestral and descendent inoceramid groups.

Acknowledgments

Institute of Geological and Nuclear Sciences contribution #1321. This research was supported in part by the Marsden Fund project entitled "Heterochrony, evolution and extinction in Mesozoic and Cenozoic Mollusca", administered by the Royal Society of New Zealand and funded by the Foundation for Research, Science and Technology. Earlier drafts were reviewed by Dr Alan BEU (IGNS, Lower Hutt, New Zealand) and Dr Peter HARRIES (University of South Florida, Tampa, Florida). Photographic plates were prepared by Wendy ST. GEORGE.

REFERENCES

COX, L.R. 1969. Systematic descriptions; family Inoceramidae GIEBEL, 1852. *In:* MOORE, R.C., TEICHERT, C., MCCORMICK, L. & WILLIAMS, R.B. (*Eds*), Treatise on invertebrate paleontology; Part N; Mollusca 6; Bivalvia 1, N314-N321. *University of Kansas and the Geological Society of America*; Boulder Colorado.

CRAMPTON, J.S. 1996a. Inoceramid bivalves from the Late Cretaceous of New Zealand. *Inst. Geol. Nuc. Sci. Mon.*, **14**, 1-188. Lower Hutt.

— 1996b. Biometric analysis, systematics and evolution of Albian *Actinoceramus* (Cretaceous Bivalvia, Inoceramidae). *Inst. Geol. Nuc. Sci. Mon.*, **15**, 1-80. Lower Hutt.

CRAMPTON, J.S. & LAIRD, M.G. 1997. Burnt Creek Formation and Late Cretaceous basin development in Marlborough, New Zealand. *N.Z. Jl Geol. Geophys.*, **40**, 199-222.

GRADSTEIN, F.M., AGTERBERG, F.P., OGG, J.G., HARDENBOL, J., VAN VEEN, P., THIERRY, J. & HUANG, Z. 1995. A Triassic, Jurassic and Cretaceous time scale. *In*: BERGGREN, W.A., KENT, D.V., AUBRY, M.P. & HARDENBOL, J. (*Eds*), Geochronology, time scales and global stratigraphic correlation. *SEPM Spec. Publ.*, **54**, 95-126. SEPM; Tulsa.

HEINZ, R. 1932. Aus der neuen Systematik der Inoceramen. Beiträge zur Kenntnis der Inoceramen XIV. *Mitt. Miner.-Geol. Staat. Inst. Hamb.*, **13**, 1-26. Hamburg.

HERM, D., KAUFFMAN, E.G. & WIEDMANN, J. 1979. The age and depositional environment of the "Gosau"-Group (Coniacian-Santonian), Brandenberg/Tirol, Austria. *Mitt. Bayer Staatsslg. Paläont. Hist. Geol.*, **19**, 27-92. München.

HOUSA, V. 1994. Variability and classification of inoceramids. Exemple [sic] of *Inoceramus bohemicus* LEONHARD from the Cenomanian of Korycany (Czech Rupublic). *In*: Proceedings of the 3rd Pergola International Symposium, *Palaeopelagos Special Publication*, **1**, 181-202.

JONES, D.S. & QUITMAYER, I.R. 1996. Marking time with bivalve shells: oxygen isotopes and season of annual increment formation. *Palaios*, **11**, 340-346.

MARWICK, J. 1926. Cretaceous fossils from Waiapu Subdivision. *N.Z. Jl Sci. Technol.*, **8**, 379-382.

NODA, M. 1975. Succession of *Inoceramus* in the Upper Cretaceous of Southwest Japan. *Mem. Fac. Sci. Kyushu Univ., Ser. D Geol.*, **23**, 211-261. Kyushu.

— 1988. Notes on Cretaceous inoceramids from Sakhalin, held at Tohoku University, Sendai. *In:* J.A. GRANT-MACKIE, K. MASUDA, K. MORI & K. OGASAWARA (*Eds*), Professor Tamio KOTAKA commemorative volume on molluscan paleontology. SAITO HO-ON KAI special publication, 137-175. *The Saito Gratitude Foundation*, Sendai.

PERGAMENT, M.A. 1978. The history of study of inocerams as a key group of Late Cretaceous faunas (1814 – 1960). *In*: M.A.PERGAMENT (*Ed.*), Jurassic and Cretaceous inocerams and their stratigraphic importance. (Materials of the III and IV All-Union Colloquia), 30-68. *Academy of Sciences of the USSR, Geological Institute*; Moscow. [*In Russian*]

POKHIALAINEN, V.P. 1985a. The basis for a supra-species systematics of Cretaceous inoceramid bivalves, pp. 1-37. *Dal'nevostochnyi Nauchnyi Tsentr, Severo-Vostochnyi Kompleksnyi Nauchno-Issledovatel'skii Institut*; Magadan. [*In Russian*]

— 1985b. The structure of inoceram populations. *In*: POKHIALAINEN, V.P. (*Ed.*), Bivalve and cephalopod molluscs of the Mesozoic of the north-eastern USSR, 91-103. *Dal'nevostochnyi Nauchnyi Tsentr, Severo-Vostochnyi Kompleksnyi Nauchno-Issledovatel'skii Institut*, Magadan. [*In Russian*]

SEIBERTZ, E. 1986. Paleogeography of the San Felipe Formation (mid-Cretaceous, NE Mexico) and facial effects upon the inoceramids of the Turonian/Coniacian transition. *Zentbl. Geol. Paläont., teil 1*, **1985**, 1171-1181. Stutgart.

SEITZ, O. 1935. Die Variabilität des *Inoceramus labiatus* v. SCHLOTH. *Jb. Preuß. Geol. Landesanst., N.S.*, **55**, 429-474. Berlin.

SORNAY, J. 1966. Idées actuelles sur les inocérames d'aprés divers travaux récents. *Annls Paléont. (Invert.)*, **52**, 57-92. Paris.

TANABE, K. 1973. Evolution and mode of life of *Inoceramus* (*Sphenoceramus*) *naumanni* YOKOYAMA emend., an Upper Cretaceous bivalve. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, **92**, 163-184. Tokyo.

TRÖGER, K.-A. & RÖHLICH, P. 1980. Zur Variabilität und Paläobiogeographie von *Inoceramus* (*Trochoceramus*) *janjonaensis* SORNAY aus dem Maastricht von Libyen. *Freiberger Forschungshefte*, **357** (C), 93-103. Freiberg.

— 1982. Zur Variabilität von *Inoceramus balticus haldemensis* GIERS aus dem Campan von Libyen. *Freiberger Forschungshefte*, **375** (C), 101-111. Freiberg.

WOODS, H. 1911. The Cretaceous Lamellibranchia of England. *Palaeontographical Society Monograph*, **2**, 261-284. London.

— 1912. The Cretaceous Lamellibranchia of England. *Palaeontographical Society Monograph*, **2**, 285-340. London.

PLATES 1 – 2

PLATE 1

Cremnoceramus bicorrugatus bicorrugatus (MARWICK, 1926) from the early Coniacian of New Zealand. Arrows mark the position of the major negative geniculation between the immature and adult growth stages. All specimens left valves, × 0.5 and whitened with ammonium chloride

1, 3, 5 – TM8023; views of juvenile, immature and adult growth stages respectively; internal mould, patches of recrystallised inner ostracum in region of umbo; collection GS14617, locality P30/f389: Nidd Sandstone, "Sawpit Gully" section, Coverham, Marlborough (*see* Text-fig. 3); the immature stage is of small to average size and displays "retarded" development (*cf.* Text-figs 4B and 4E); the adult is correspondingly short, most growth was directed ventrally, and the growth field was restricted to a comparatively narrow arc

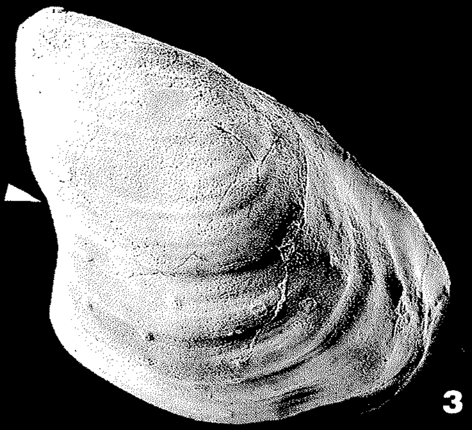
2 – TM8025. Juvenile specimen; internal mould and shell interface, recrystallised inner ostracum partially preserved; collection GS850, locality P30/f6102: Nidd Sandstone, Nidd Stream, Coverham, Marlborough (*see* Text-fig. 3)

4 – TM8043. View of immature growth stage (view orthogonal to plane of commissure at geniculation); internal mould and shell interface, recrystallised inner ostracum partially preserved; collection GS15205, locality P30/f389: Nidd Sandstone, "Sawpit Gully" section, Coverham, Marlborough (*see* Text--fig. 3); the immature stage is of average size and is more-or-less comparable to Fig. 4C

6 – TM8026. Immature specimen; outer ostracum preserved, somewhat abraded: collection GS11692, locality T26/f9533: Glenburn Formation, Motuwaireka Stream section, Ngahape area, Wairarapa, North Island (*see* CRAMPTON 1996a, Fig. 17); this specimen is relatively large and globose and displays "precocious" development (*cf.* Text-fig. 4D)

1

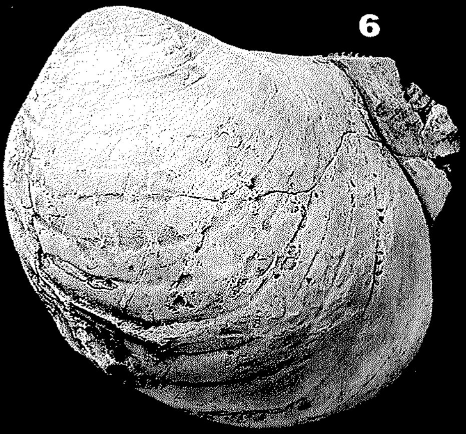
2



3

4

5



6

PLATE 2

Cremnoceramus bicorrugatus bicorrugatus (Marwick, 1926) from the early Coniacian of New Zealand. Arrows mark the position of the major negative geniculation between the immature and adult growth stages. All specimens × 0.5 and whitened with ammonium chloride

1 – TM8040; adult growth stage, right valve; internal mould with patches of outer ostracum preserved; collection GS11738, locality X16/f7726: Karekare Formation, Mangaotane Stream section, Raukumara Peninsula (*see* Text-fig. 3); the immature stage is small and globose and displays "precocious" development (*cf.* Text-fig. 4D)

2 – TM8032; adult growth stage, left valve; outer ostracum preserved, slightly deformed, anterior part of disc missing; collection GS14650, locality Y16/f782: Karekare Formation, Kokopumatara Stream, Mangaotane Stream catchment, Raukumara Peninsula (*see* Text-fig. 3); the immature stage is large and globose and displays "precocious" development; the adult is correspondingly long, with an expanded disc, and the adult growth field occupied a comparatively wide arc (*cf.* Text-fig. 4F)

3 – VM995; adult growth stage, left valve; internal mould, anterior part of adult disc missing; collection V1772, locality P30/f694: Nidd Sandstone, "Sawpit Gully" section, Coverham, Marlborough (see Text-fig. 3); comments as for Pl. 2, Fig. 2, above


1
2
3