

COMPARATIVE TAXONOMY OF THE BIVALVE FAMILIES ISOGNOMONIDAE, INOCERAMIDAE, AND RETROCERAMIDAE

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ABSTRACT. Fossil Isognomonidae (Pteriacea) can be difficult to distinguish externally from the biostratigraphically important Mesozoic family Inoceramidae (Ambonychiacea?). Internal details of ligament area morphology provide valuable taxonomic data at the family and species levels, as documented for many New Zealand species. Definitive distinction between these two families is furnished by the shell structure underlying the ligament area: in Isognomonidae the ligament attaches to the inner (presumed nacreous) shell layer, whereas in Inoceramidae it attaches to the outer prismatic shell layer. *Retroceramus*, formerly included in Inoceramidae, has the ligament attached to the inner shell layer, and should be placed in the Pteriacean family Retroceramidae. These findings are consistent with a polyphyletic origin for the multivincular ligament in Isognomonidae and Inoceramidae.

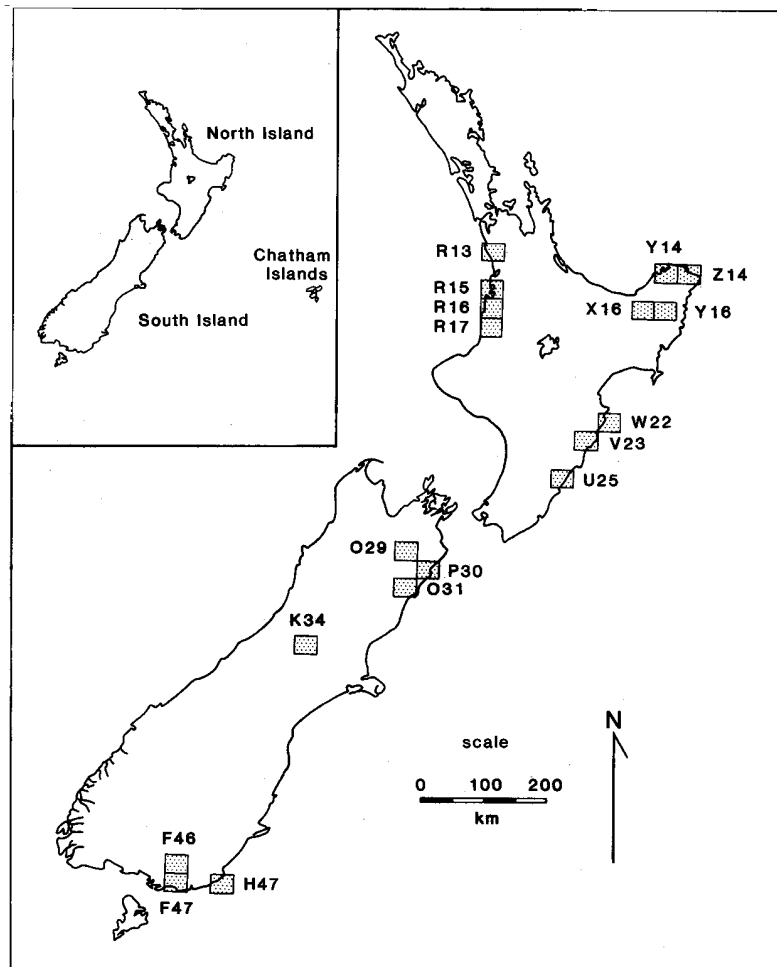
Two new species of *Isognomon* are described from New Zealand, *I. wellmani* (Palaeocene) and *I. rekohuensis* (Late Cretaceous). They probably lived on soft or shelly substrates with otherwise similar life habits to Recent forms.

RECOGNITION of two new species of fossil Isognomonidae (Bivalvia), and the need to distinguish these from biostratigraphically important Cretaceous taxa, prompted this paper. The new species are described from Late Cretaceous strata of the Chatham Islands and Palaeocene strata of Castle Hill Basin, Canterbury (map area K34, see text-fig. 1). Rocks of these ages are currently undergoing detailed study as part of the New Zealand Geological Survey's Cretaceous-Cenozoic Programme.

Bivalves, while not being biostratigraphically important in the New Zealand Palaeocene, are a major tool in global and local Cretaceous biostratigraphy. Those of family Inoceramidae formed the basis of Wellman's (1959) pioneering subdivision of the New Zealand Cretaceous, and their significance has since diminished little (for example, see Stevens and Speden 1978; Suggate *et al.* 1978). Both bivalves described herein closely resemble species of Inoceramidae, and have previously been assigned to that family.

Late Cretaceous rocks occur extensively throughout New Zealand, and are characterized by terrestrial coal measures and marine sandstone and siltstone sequences which are locally richly fossiliferous. Often complexly faulted and folded, they achieve a thickness of 1000–2000 m (Johnston 1980; Moore 1980). Comparatively unlithified and undeformed marine Cretaceous strata were first recognized on the Chatham Islands by Boreham (1959), subsequently described by Hay *et al.* (1970), and assigned to the Late Cretaceous by Speden (1976), Wilson (1976), Mildenhall (1977), and Strong (1979). They comprise conglomerate, sandstone, and fossiliferous tuff and limestone.

Palaeocene rocks, on the other hand, are not well exposed in New Zealand, being restricted mainly to thin sequences on the east coast of both islands. They generally consist of poorly fossiliferous commonly glauconitic mudstone, sandstone, and limestone, which in many places overlie Late Cretaceous strata. The Late Cretaceous-Palaeocene rocks of Castle Hill Basin, Canterbury, have a long history of description, beginning with Hector (1881) and McKay (1881), and were mapped most recently by Gage (1970). Lithologies at this locality include sandstone (carbonaceous at the base and glauconitic above) with minor mudstone, limestone, and rare shell-beds.



TEXT-FIG. 1. Map of New Zealand showing all fossil localities referred to in the text in terms of their NZMS 260 1 : 50 000 map sheet areas.

Material described is housed in the Geology Department, University of Auckland, Auckland; Geology Department, University of Otago, Dunedin; and the New Zealand Geological Survey, Lower Hutt. The following prefixes indicate specimen repositories and localities:

- L(AU) Specimen number, Geology Department, University of Auckland.
- AU Collection number, Geology Department, University of Auckland.
- OU Specimen number, Geology Department, University of Otago.
- TM Type Mollusca specimen number, NZ Geological Survey.
- WM World Mollusca specimen number, NZ Geological Survey.
- GS Collection number, NZ Geological Survey.
- L Palynology sample number, NZ Geological Survey.
- K34/f48 Fossil locality number of the New Zealand Fossil Record File, based on metric NZMS 260 1 : 50 000 map sheets. K34 refers to the map sheet number, and f48 refers to a unique fossil locality within that area. All New Zealand fossil localities mentioned in the text have their map sheets areas shown on text-fig. 1.

Synonymy lists employ the annotations outlined by Matthews (1973) to indicate degrees of confidence for references. Full bibliographic references for all bivalve taxa below superfamily level are given.

ISOGNOMONIDAE COMPARED TO INOCERAMIDAE AND *RETROCERAMUS*

Edentulous (in the adult stage), multivincular Pteriacea of variable form are included in Isognomonidae Woodring, 1925. Members of this family are sometimes difficult to distinguish from Inoceramidae Giebel, 1852, a problem addressed by a number of authors, notably Heinz (1932), Cox (1940), and Hayami (1960): see Table 1. As discussed below, failures to recognize some New Zealand fossil Isognomonidae, the uncertain taxonomic position of *Retroceramus* Koschelkina (1959), and evidence for greater phylogenetic distance between Isognomonidae and Inoceramidae than previously recognized, make it prudent to review differences between the two groups.

Prior to Cox (1955) most authors (Heinz (1932) being one notable exception) included nearly all inoceramids within the single genus *Inoceramus* Sowerby, 1814, which was grouped with the isognomonids and bakevelliids in Isognomonidae. Cox (1954, p. 47) wrote, 'The removal of *Inoceramus* and related genera from the Isognomonidae does not at present seem necessary . . .'. Indeed, he had earlier criticized Heinz (1932) for over-intensive subdivision of what was ' . . . formerly regarded as a single genus . . .', and stated, 'It is possible that two or three distinct genera and several subgenera may eventually prove to be distinguishable among the species hitherto included in *Inoceramus* . . .' (Cox, 1940, p. 125). Similarly, the genus *Isognomon* Solander in Lightfoot (1786), as used by Cox (1940, 1954) and Hayami (1957, 1960: see Table 1) included most species previously assigned to *Perna* Bruguière, 1789 (not *Perna* Retzius, 1788 (Mytilidae)) and now referable to several genera in Isognomonidae. (A number of other isognomonid genera had been described before 1960, but apart from *Crenatula* Lamarck, 1803, they were little used.)

Subsequent to Cox (1955) not only have *Inoceramus* and related bivalves been placed in their own family, Inoceramidae, but Kauffman and Runnegar (1975) tentatively suggested they should be removed to a different superfamily, Ambonychiacea. This was based on evidence for their evolution from the Permian *Atomodesma* Beyrich, 1864, as opposed to the widely accepted view that most Inoceramidae evolved from Isognomonidae (for example, Hayami 1957, 1960). Separation of the two families would not be remarkable given that many authors have postulated a polyphyletic origin for the multivincular ligament, the single most distinctive character of both taxa (Heinz 1932; Cox 1940; Hayami 1960; Browne and Newell 1966; Kauffman and Runnegar 1975; Dickins 1983).

External characters have generally been used to distinguish Isognomonidae from Inoceramidae (Table 1). Most importantly, Isognomonidae usually have terminal umbones which are little, if at all, incurved and commonly project beyond the rest of the anterior shell margin; they are rarely markedly prosocline; they may possess an anterior byssal gape; and they have a smooth, commarginally lamellose, or in a few taxa radially sculptured surface lacking commarginal plicae. Most Inoceramidae, on the other hand, generally possess a gibbous more or less incurved, subterminal umbo; they may be acline to strongly prosocline; most do not possess a byssal gape (recently some early forms with large byssal gapes have been referred to this family, for example *Permoceramus* Waterhouse, 1970); and almost all have commarginal or (in fewer taxa) radial plicae. These criteria hold true in most material examined, although in some cases differences may be subtle, for example compare *Isognomon rekohuensis* (sp. nov., described herein) and *Inoceramus opetius* Wellman, 1959. *Isognomon rekohuensis* has a weakly inflated, terminal, prosogyrate umbo projecting beyond the anterior end of the hinge line, whereas *Inoceramus opetius* has a more gibbous orthogyrate umbo close to, but not at, the anterior end of the hinge line (contrast Pl. 89, fig. 1e and Pl. 90, fig. 7). Both species are acline or nearly so, and *Isognomon rekohuensis* has only a narrow byssal gape, if any gape at all. The latter does bear the lamellose ornament characteristic of the family, but in addition it has weak commarginal plicae between the shell layers which resemble the weak and irregular external ornament of *Inoceramus opetius* (Pl. 89, fig. 1b).

TABLE 1. Descriptions of selected diagnostic and differential characters of Isognomonidae and Inoceramidae according to different authors.

	Inoceramidae	Isognomonidae
Gross shape	Equivalve except in aberrant species, variable outline with height in excess of length in most taxa (Cox 1940, p. 124). Subequivalve to strongly inequivalve (Cox 1969, p. 315).	Mesozoic species typically equivalent or mytiliform in outline except for Cretaceous aberrant forms (Hayami 1957, p. 99). Subequivalve to strongly inequivalve, rarely markedly oblique (Cox 1969, p. 322). Not at all or little incurved, at anterior end of hinge line (Cox 1940, p. 121). Terminal (Hayami 1957, p. 104).
Umbones	More or less incurved, situated towards anterior end of hinge line (Cox 1940, p. 125). More prominent than in Isognomonidae (Cox 1940, p. 125; Hayami 1960, p. 287). Small or rudimentary but present in many taxa (Cox 1940, pp. 124-125).	Completely absent except in very few species where rudimentary (Cox 1940, p. 125). Present or absent (Cox 1940, p. 121)
Anterior auricle	Present or absent (Cox 1940, p. 124; Cox 1969, p. 315). Absent in most taxa (Hayami 1957, p. 104).	
Posterior wing	Absent (e.g. Cox 1940, p. 124; Hayami 1957, p. 104; Cox 1969, p. 315).	
Byssal gape	Plane except where affected by radial ribs (Cox 1969, p. 315). Typically concentrically plicated or ridged non-lamellose shell (Cox 1940, p. 125). Concentrically lamellose or plicated (Cox 1969, p. 314).	With or without anterior byssal gape affecting both valves (Cox 1969, p. 321). Plane or undulating (Cox 1969, p. 321). Without concentric undulations (Cox 1940, p. 121). Smooth, concentrically lamellose, or irregularly undulating; radial ornament absent except in <i>Mulletia</i> (Cox 1969, p. 321).
Commissure	Narrow, or of moderate width, flat or concave, with numerous transverse ligamental pits which are wider than their interspaces. Most edentulous (Cox 1940, p. 124).	Wide, flat, with numerous narrow, transverse, more or less straight-sided ligament pits whose interspaces are wider than the pits in most taxa. Most edentulous, sometimes with one or more oblique tooth-like ridges underlying ligament area towards posterior end (Cox 1940, p. 121). Without hinge teeth in adult shell, ligament external, flat in most, pits reaching and indenting lower margin (Cox 1969, p. 321).
Surface ornament	Narrower than Isognomonidae (Cox 1940, p. 125; Hayami 1957, p. 104; Hayami 1960, p. 288). Pits more numerous than contemporaneous Isognomonidae (Hayami 1960, p. 288). Elongate ligamental groove may be ventral to, or be present without, transverse pits (Kauffman 1965, p. 86). Pits typically have curved sides and do not indent margins of area; edentulous except in <i>Parainoceramus</i> (Cox 1969, p. 315).	Smooth, concentrically lamellose, or irregularly undulating; radial ornament absent except in <i>Mulletia</i> (Cox 1969, p. 321). Area with rectangular pits and ridges of varying proportions, ridges affected by central cavity in some taxa (Pokhialaynen 1977, p. 57). Ligament attached to inner nacreous shell layer (Morris, pers. comm. 1986).
Ligament area		

Ligament area of Isognomonidae-type found in retroceramids and some inocerams. Otherwise pits oval or rounded rectangular with ridges verging dorsally and ventrally; and many complications to this, such as formation of small triangular pits on the interspaces, alternation of pits of different widths, and development of bi- and triserial pits (Pokhialaynen 1977, p. 57).

Ligament attached to outer prismatic shell layer (Koschelkina 1971, p. 44; Pokhialaynen 1972, p. 58; Morris, pers. comm. 1986).

Single variously shaped posterior adductor, pallial line complete or broken into discrete mantle muscle scars, pedal and byssal muscles sometimes evident in some taxa (Kauffman 1965, p. 86).

Comparatively thin except near hinge margin (Cox 1940, p. 124).

Thinner than contemporaneous Isognomonidae (Cox 1940, p. 125; Hayami 1960, p. 288).

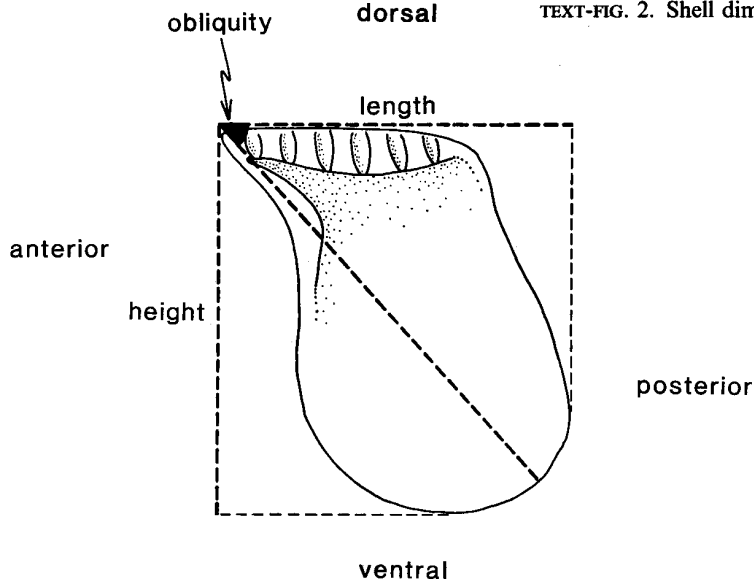
Musculature
Single large sub-central adductor scar (Cox 1940, p. 121; Hayami 1957, p. 104).

Pallial line typically discontinuous and broken into small pits (Cox 1969, p. 321).

Most very thick (Cox 1969, p. 321).

Musculature

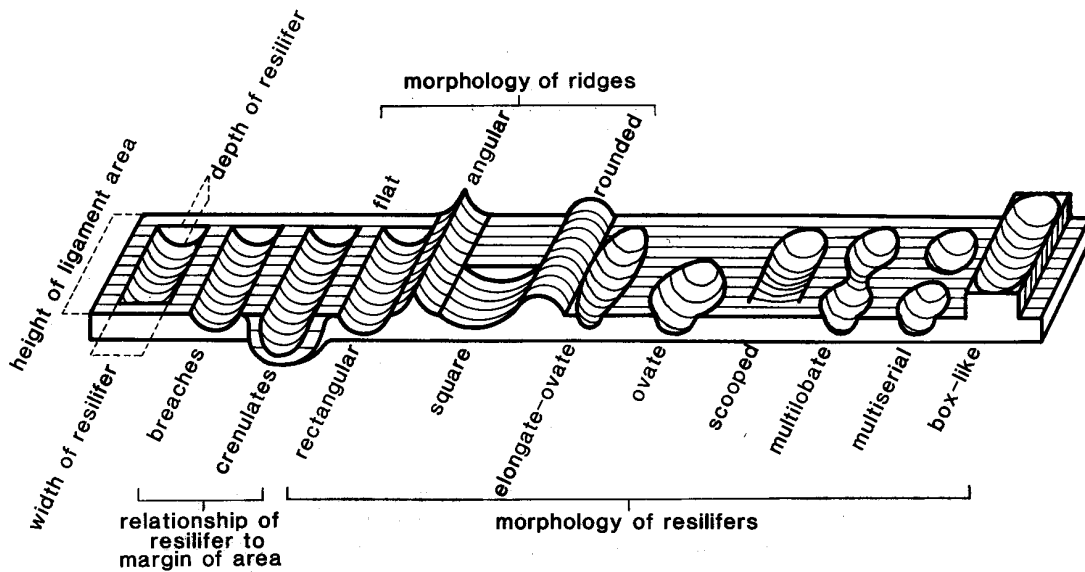
Shell structure



Details of internal morphology can provide useful diagnostic high- and low-level taxonomic data on fossil Isognomonidae and Inoceramidae (a fact stressed by many authors, for example Kauffman 1965, 1977; Tröger 1976; Zonova and Yefremova 1976; Yonge 1978; Zonova 1980a; Pokhialaynen 1985). Although such features are often difficult to observe and have in the past been poorly documented, an increasing amount of information on ligament area morphology is becoming available (Airaghi 1904; Kauffman 1965; Zonova and Yefremova 1976; Pokhialaynen 1969, 1977, 1985; Ivannikov 1979; Zonova 1980a, b, 1982). Use of such data must, however, be tempered with caution since details of the ligament area can be unstable at the species level (for example, Cox 1940, p. 122, this study *Isognomon* (*I.*) sp., Pl. 89, figs. 2-5) and family level (for example, Kauffman and Runnegar 1975, p. 36). In the present paper the ligament areas of several New Zealand Jurassic to Palaeocene Isognomonidae, Inoceramidae, and *Retroceramus* are described (Appendix, terminology explained in text-fig. 3) and illustrated for the first time. Table 1 summarizes differences between the ligament areas of Isognomonidae and Inoceramidae as perceived by some other workers. Of these characters the following appear to hold true in species described in the literature or examined first hand (excepting *Retroceramus*, discussed below).

Isognomonidae have a multivincular ligament in all cases, whereas Inoceramidae may carry in addition or exclusively an elongate longitudinal ligamental groove (Kauffman 1965; described in detail in Speden 1970b). Isognomonidae have monoserial resilifers on an area that is flat or only slightly concave (for example, Pl. 88, figs. 8 and 9; Pl. 89, figs. 1e, 2-7), whereas Inoceramidae have relatively numerous monoserial, multilobate, or multiserial pits (refer to text-fig. 3) on a weakly convex to strongly concave area (Pl. 90, figs. 4-14). In Isognomonidae the resilifers are nearly always approximately rectangular, breaching the ventral margin of the area, which may be crenulated (though this can vary between individuals of a population, compare Pl. 89, figs. 2 and 5). In Inoceramidae, on the other hand, resilifers may be rectangular to ovate and are commonly elongate-ovate (for example Pl. 90, figs. 9 and 13), they may or may not breach and do not markedly crenulate the ventral margin of the area, and they apparently never have the broad flat or concave interspaces common in Isognomonidae.

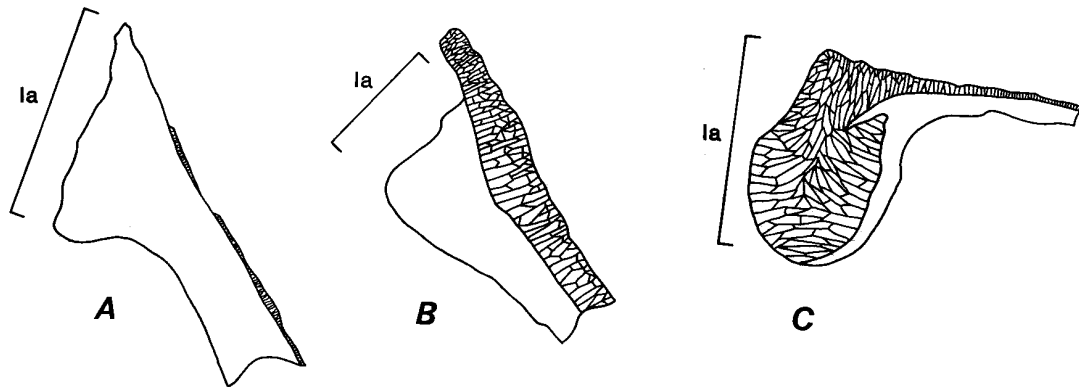
In all specimens examined by Dr N. J. Morris (British Museum, Natural History, written pers. comm. 1986) the ligament in Isognomonidae attaches to the inner, presumed nacreous, aragonitic



TEXT-FIG. 3. Schematic diagram of multivincular ligament area, explaining measurements and morphological terms used in this paper. For other terms and morphologies see Pokhialaynen (1977).

shell layer (see text-fig. 4A, terminology after Taylor *et al.* (1969), shell structures discussed briefly below), whereas in *Inoceramidae* it attaches to the outer, prismatic, calcitic layer (Koschelkina 1971; Pokhialaynen 1972; Morris, pers. comm. 1986; see text-fig. 4C). This distinction is maintained in eleven New Zealand Cretaceous *Inoceramus* species, five New Zealand Jurassic to Palaeocene *Isognomon* species (see Appendix), numerous younger New Zealand and world *Isognomonidae*, and the type species of the type genera of both families. The type species are *Inoceramus cuvieri* Sowerby, 1814 (two specimens seen, WM 14879 and 14880, these being casts of specimens B6683 and B20997, illustrated by Woods (1905, text-figs. 78 and 80 respectively) from the Sedgwick Museum, Cambridge, England, and kindly made available by Dr D. Price), and *Isognomon isognomon* (Linnaeus, 1758) (twelve specimens seen, WM 12064, from Stadbroke Island, Queensland, Australia). However, six New Zealand Jurassic *Retroceramus* species (formerly included in *Inoceramidae*) have the ligament attached to the inner shell layer (see text-fig. 4B and Appendix). Attachment of the ligament to different shell layers in *Inoceramus* and *Retroceramus* was noted previously by Koschelkina (1971, 1975, 1980) and Pokhialaynen (1972, p. 58), who referred to a 'padding' of prismatic 'ligamentat' beneath the ligament area of *Inoceramus s.l.*

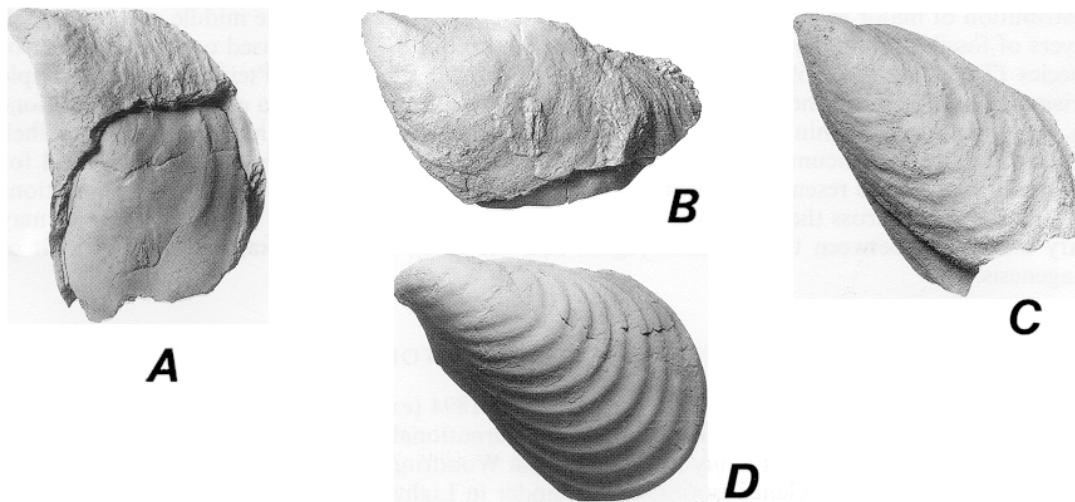
The phylogenetic and taxonomic significance of the relationship between the ligament and different shell layers is difficult to assess since few species descriptions include such detail and the state of this character through ontogeny is poorly known. Larval bivalves show remarkably little variation in ligament form, with differentiation occurring after settlement (Trueman 1969, p. 62). In Recent *Isognomon*, the dentate larva gives rise to a juvenile with a single amphidetic resilium. Subsequently the lamellar ligament extends posteriorly with (secondary) areas of fibrous ligament (forming resiliifers) appearing at intervals within it. Simultaneously the ligament area extends ventrally, with the more dorsal parts becoming separated and obsolete (structure and development of the ligament in *Isognomon* is discussed by Bernard 1898, Trueman 1954, Yonge 1968, and Siung 1980). It seems likely that the multivincular ligament of *Inoceramidae* formed in a similar manner since different growth stages of the same species show expansion of the ligament area in the posterior and ventral directions (for example, *Inoceramus cuvieri*, specimens WM 14879 and 14880).



TEXT-FIG. 4. Cross-sections through the ligament areas of representative Isognomonidae, Retroceramidae, and Inoceramidae, drawn from photomicrographs. Sections perpendicular to ligament area and approximately half-way between umbo and posterior end of area. All drawings oriented dorsal-up, shell interiors to the left, and planes of commissure vertical. Inner, presumed nacreous, shell layer shown blank, prism shapes indicated in outer prismatic shell layer. la = ligament area. A, *Isognomon* (*Isognomon*) sp. (see Appendix); TM 6790, H47/f6494; coast opposite Bloody Jacks Island, Tuhawaiki, Southland; $\times 3.3$. B, *Retroceramus* (*Retroceramus*) *haasti* (Hochstetter, 1863); TM 6792, R15/f8564; north side of Kowhai Point, from western tip for approximately 50–100 m east, Kawhia Harbour, south-west Auckland; $\times 10$. C, *Inoceramus opetius* Wellman, 1959; TM 6791, P30/f6895; middle branch of Wharf Stream, approximately 1.2 km upstream from junction with south-east branch, Marlborough; $\times 6$.

Since, in Isognomonidae, the first-formed dorsal part of the ligament lies very close to or on the boundary between the outer prismatic and inner nacreous shell (see, for example, Trueman 1954, fig. 2), the different states seen in Inoceramidae and Isognomonidae could only arise by differential thickening of the prismatic or nacreous shell layers respectively at the time of formation of the first resilium. Once established in the individual, this pattern apparently does not change, and it appears to be consistent over taxa that are geographically and temporally widely separated. Hence it is postulated that the relationship of the ligament to the inner and outer shell layers is a fundamental character fixed at the time of larval settlement, when other major adult growth configurations are established. Detailed ontogenetic studies and more exhaustive surveys of fossil Pterioidea are required to test this hypothesis.

Based on the present data, however, it seems that Jurassic *Retroceramus* species should be removed from Inoceramidae and accommodated in the family Retroceramidae Pergament in Koschelkina, 1971. A diagnosis of Retroceramidae is given below. Attachment of the ligament to the inner (rather than outer) shell layer separates Retroceramidae from Inoceramidae, and indicates close relationship between Retroceramidae and Isognomonidae. Most species of Retroceramidae are distinguished from Isognomonidae, externally, by their regular commarginal plicae, more prosocline shape, greater inflation, and more prominent subterminal umbones (compare text-fig. 5A and D). Internally, some taxa in the two families have very similar ligament area morphologies (compare Pl. 89, fig. 2 and Pl. 90, fig. 1). However, Retroceramidae have the ligament area inclined to the plane of commissure, and they commonly have relatively broad, somewhat irregular, square or ovate resiliifers, separated by broad, concave interspaces. In some taxa the interspaces resemble a second class of resiliifer (see Pl. 90, fig. 2). The morphology of the ligament area in *Retroceramus* is described and illustrated by Crame (1982) and Koschelkina (1963, 1969, 1971). Some taxa, apparently intermediate in form between Isognomonidae and Retroceramidae, can be difficult to assign to either family, and they support an inferred common ancestry of the two families in the Late Triassic or earliest Jurassic. For example, the Early Jurassic *Isognomon* (*Mytiloperna*?) sp. B



TEXT-FIG. 5. External morphology of typical and atypical Isognomonidae and Retroceramidae (see text for discussion). All specimens whitened with ammonium chloride sublimate. A, *Isognomon (Isognomon)* sp. (see Appendix); TM 6793, H47/f6494; left valve; coast opposite Bloody Jacks Island, Tuhawaiki, Southland; $\times 0.7$. B, *I. (Mytiloperna?)* sp. B (see Appendix); TM 4062, R15/f8006; left valve; 60–240 m north-east of stack at Ururoa Point, south-west Auckland; $\times 0.6$. C, *Retroceramus (Fractoceramus) inconditus* (Marwick, 1953); TM 2373, F47/f7492; Quarry Hills, Waikawa district, Southland; $\times 1$. D, *R. (R.) galoii* (Boehm, 1907); TM 6719, R15/f8553; point west of Heteri Promontory, across Waikutakuta Inlet, Kawhia Harbour, south-west Auckland; $\times 1$, negative reversed.

(see Appendix) has the smooth to lamellose surface and weakly developed umbo diagnostic of Isognomonidae, and the typically strongly prosocline shape of Retroceramidae (see text-fig. 5b). Indeed, members of the subgenus *R. (Fractoceramus)* Koschelkina, 1959, which are distinguished from most Retroceramidae by their weak and irregular ornament, differ little from *I. (Mytiloperna?)* sp. B (compare text-fig. 5b and c). Internally, the ligament area morphology of *I. (M.?)* sp. B resembles, in most respects, species in both families. However, the plane of the area is twisted, a character state not observed in other members of either family. Hence, while separation of the two families, Retroceramidae and Isognomonidae, is believed justified, it is acknowledged that some morphologically intermediate taxa may be difficult to assign to either family.

Furthermore, the different relationships of ligament and shell layers in Isognomonidae, Retroceramidae, and Inoceramidae are consistent with the postulated existence of two distinct Late Palaeozoic lineages of multivincular Pterioidea, included in superfamilies Pteriacea (containing Isognomonidae and Retroceramidae) and Ambonychiacea (containing Inoceramidae), as suggested by Kauffman and Runnegar (1975) and discussed above. The attachment of the ligament to the prismatic shell in *Atomodesma* sp. (Ambonychiacea, and an early member of Inoceramidae according to Kauffman and Runnegar, 1975) from the Early Permian of Queensland, Australia (B. Runnegar, University of New England, Australia, pers. comm. 1986) lends additional support to this phylogenetic scheme.

Other internal features, such as muscle scars and the presence and form of the umbonal septum (for example, on *Inoceramus rangatira*, Pl. 90, fig. 5), may prove useful in characterizing Isognomonidae, Retroceramidae, and Inoceramidae (see Table 1). As yet little is known about these characters in the latter two families, although Kauffman (1965) and Pokhialaynen (1985) briefly described patterns of musculature in inoceramids.

Details of shell microstructure are also likely to be of value in high- and low-level taxonomy of these groups. Again, little data is presently available, although at higher levels the taxonomic

distribution of major shell structures is known. While rarely preserved, the middle and inner shell layers of fossil Pterioida are assumed to have been nacreous aragonite, based on studies of recent species (Taylor *et al.* 1969). Waller (1978, p. 351) stated that all the Pterioida have a simple prismatic, calcitic outer shell layer and a nacreous aragonitic inner layer on each valve. Exceptions to, and variations within, this pattern were reviewed briefly by Pokhialaynen (1985). Shell microstructures are documented for the two new species of *Isognomon* described below, and for species of *Inoceramus* resembling them. More systematic studies are planned to discover variations in shell structure across the individual (for example, the form of prisms in the prismatic layer may vary immensely between the ligament region and the disc), between taxa, and as the result of diagenesis.

SYSTEMATIC PALAEOLOGY

Superfamily PTERIACEA Gray, 1847; *nom. transl.* Dall, 1894 (*ex* Pteriidae; = Aviculidae Goldfuss, 1820. Pteriidae retained under Article 40a of the International Zoological Code by Cox, 1969)

Family ISOGNOMONIDAE Woodring, 1925

Genus ISOGNOMON Solander in Lightfoot, 1786

Subgenus ISOGNOMON Solander in Lightfoot, 1786

Type species. *Ostrea isognomon* Linnaeus, 1764 (by tautonymy, = *O. isognomum* Linnaeus, 1758; see Rehder, 1967, p. 6).

Isognomon (Isognomon) wellmani sp. nov.

Plate 88; Plate 90, figs. 15–18

v. 1970 *Inoceramus matotorus* Wellman, 1959; Gage (p. 516).

Name. Named after Dr H. W. Wellman, formerly Professor of Geology at Victoria University, Wellington, in recognition of his contribution to the understanding of Cretaceous biostratigraphy in New Zealand.

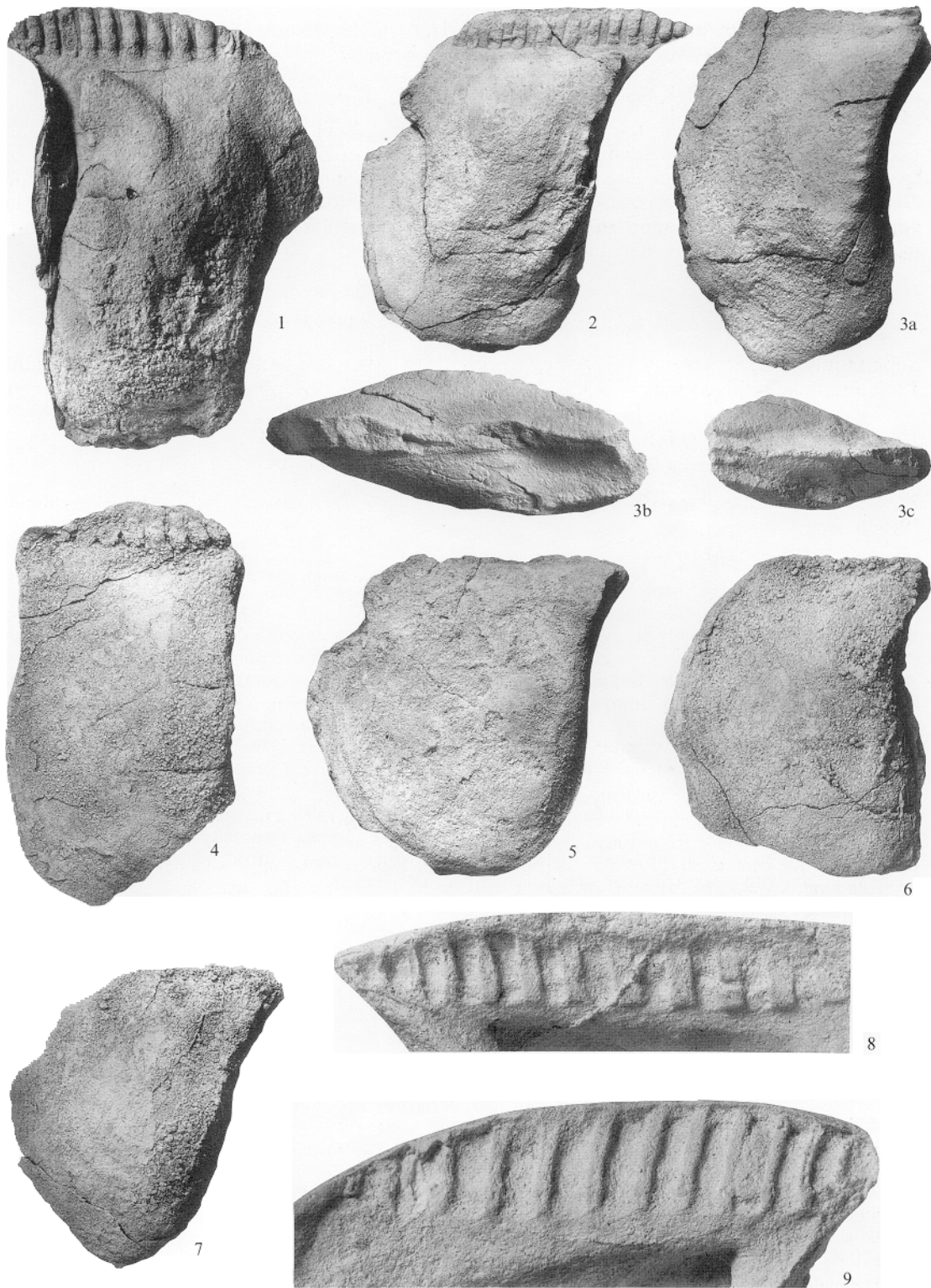
Material. Many specimens of both valves, several articulated, preserved as internal moulds and outer prismatic shell layers with internal faces exposed.

Type locality. K34/f48, K34 097770 (imperial grid reference NZMS1, S66/236960), GS 14183: in the lower part of the prominent 0.4 m thick oyster shell-bed at the top of Broken River Formation (after Gage 1970, modified by Andrews *et al.*, in press, described by Browne and Field 1985, and column from Field and Browne, written pers. comm. 1986), in the south bank of Broken River, approximately 700 m downstream from its confluence with Porter River, Castle Hill Basin, Canterbury (see text-fig. 1). Collected by J. S. Crampton and G. H. Browne, 1986.

EXPLANATION OF PLATE 88

Figs. 1–9. *Isognomon (Isognomon) wellmani* n. sp. All specimens from Broken River Formation, Broken River, Canterbury, NZ (Palaeocene). 1, TM 6689, K34/f48, holotype; internal mould left valve, $\times 0.7$. 2, TM 6690, K34/f48, paratype; internal mould right valve, $\times 0.7$. 3, TM 6691, K34/f48, paratype; *a*, steinkern viewed from right side, $\times 0.7$; *b*, anterior face of steinkern, dorsal to right, $\times 0.7$; *c*, dorsal view of steinkern, anterior to left, $\times 0.7$. 4, TM 6695, K34/f48, paratype; internal mould right valve, $\times 0.7$. 5, TM 6692, K34/f9096, paratype; steinkern viewed from right side, $\times 0.7$. 6, TM 6693, K34/f48, paratype; steinkern viewed from right side, $\times 0.7$. 7, TM 6694, K34/f48, paratype; steinkern viewed from right side, $\times 0.7$. 8, TM 6690, K34/f48, paratype; latex mould of ligament area of right valve, $\times 1.3$. 9, TM 6689, K34/f48, holotype; latex mould of ligament area, $\times 1.3$.

All specimens whitened with ammonium chloride sublimate.



CRAMPTON, *Isognomon (Isognomon) wellmani* n. sp.

Type specimens. Holotype: TM 6689, K34/f48, GS 14183 LV internal mould chosen for its reasonably complete outline and ligament area. Paratypes: TM 6690, K34/f48, GS 14183, RV internal mould; TM 6691, K34/f48, GS 14183, steinkern; TM 6692, K34/f9096, GS 67, steinkern; TM 6693, K34/f48, GS 14183, steinkern; TM 6694, K34/f48, GS 14183, steinkern; TM 6695, K34/f48, GS 14183, RV internal mould; TM 6697, K34/f48, GS 14183, thin sections showing subradial and tangential cross-sections through the prismatic shell layer on the discs of two valves; TM 6761, K34/f48, GS 14183, thin section showing longitudinal cross-section through the prismatic shell layer of anterior margin of articulated specimen.

Diagnosis. *Isognomon* of large size, subrectangular to mytiliform and acline to weakly prosocline; adult ligament area with approximately eleven deep rectangular resilifers which may be the same width as or considerably wider than their interjacent ridges.

Description. Dimensions (in millimetres, refer to text-fig. 2, outlines reconstructed where feasible):

Specimen	Length	Height	Width (both valves)	Obliquity
Internal moulds complete with ligament area				
TM 6689	~ 80	~ 107	—	~ 60°
TM 6690	> 77	~ 90	—	~ 45°
TM 6695	> 60	~ 100	—	~ 65°
Steinkerns, excluding ligament area				
TM 6691	> 63	~ 88	31	~ 65°
TM 6692	> 74	> 82	31	~ 50°
TM 6693	~ 64	~ 84	27	~ 60°
TM 6694	~ 75	~ 75	21	~ 45°

Shell large; variable in shape (Pl. 88, figs. 1, 2, 3a, 4-7), subrectangular to mytiliform, acline to weakly prosocline; prosogyrous with umbo at, or close to, anterior end of hinge line, which projects anteriorly beyond rest of shell; roughly equivalve, moderately inflated. Dorsal outline incomplete in all specimens, straight or gently convex. Anterior margin weakly to moderately concave dorsally, then becoming more or less straight before curving backward to ventral margin. Posteroventral outline slightly concave to convex. Posterior wing poorly defined, deep, outline not preserved on type material. No evidence for anterior auricle. Shell wedge-shaped in longitudinal section (Pl. 88, fig. 3c), maximum width close to anterior margin and approximately midway dorsoventrally (Pl. 88, fig. 3b). Anterior face roughly perpendicular to commissure; disc gently convex except posteriorly where it becomes slightly concave. Commissure flat, presence of byssal gape not determined.

External sculpture, as determined from thin sections through the outer prismatic shell layer (TM 6697 and 6761; Pl. 90, fig. 15), of irregular commarginal lamellae. These increase in density and prominence close to shell margins, especially on the anterior where individual lamellae may protrude by many millimetres. Shell layers interface with weak, irregular, commarginal plicae or lamellae.

Hinge edentulous, ligament multivincular (Pl. 88, figs. 8 and 9). Ligament area flat or slightly concave; parallel to or inclined a few degrees to commissural plane; scarcely undercut close to umbo. At least eleven rectangular, concave-floored resilifers on adult shell, which breach and may weakly crenulate the gently convex ventral margin of the area (refer to text-fig. 3). Inter-resilifer ridges more or less flat-topped, with sharp edges and steep sides. Relative and absolute widths of resilifers: ridges vary anteriorly to posteriorly from 2.7 mm:1 mm to 4 mm:1.5 mm on the holotype and from 2.5 mm:1.5 mm to 3 mm:3 mm on specimen TM 6690. Ligament area at least 12.5 mm high, no growth lines observed although they might be expected on better preserved material. Ligament attached to inner (nacreous) shell layer.

No adductor muscle scar visible on any of the type specimens. At least twelve discrete pallial muscle scars form a line close to and parallel to the anterior margin of the shell, from the umbo to the anteroventral part of the disc (Pl. 88, figs. 2 and 3a, b).

The shell is only partially preserved on the type specimens. The inner two layers, which probably consisted originally of nacreous aragonite (see earlier discussion) have been recrystallized and subsequently dissolved, leaving only a layer of granular calcite (removed in specimens TM 6689-6691) coating internal moulds and the internal faces of external shell layers. The external shell layer is preserved intact, and consists of polygonal regular simple prismatic to rod-type fibrous prismatic calcite (Pl. 90, figs. 15-18; terminology after Carter and Clark 1985). The shell achieves a maximum thickness close to the anterior margin, where the prismatic layer is at least 7 mm thick and the inner layers 10 mm or more thick. Total thickness towards the centre of the

disc, however, is probably only of the order of a few millimetres. Within the prismatic layer, prisms are reclined (dipping towards the shell boundaries), slightly sigmoid-shaped, generally smaller towards the outside surface, and commonly bearing transverse discontinuities (typically off-set, see Pl. 90, fig. 15) which rise to the outside surface of the shell at an acute angle, resulting in the lamellae already described. Where the shell is thick there may be many stacked lamellae. Where the shell is thin, in the centre of the disc, single prisms traverse the whole thickness of this layer, and achieve a maximum size of approximately 2 mm long \times 0.13 mm wide. Adjacent prisms show approximately coincident undulose, patchy, or relatively uniform extinction. Fractured prisms, examined under SEM (Pl. 90, fig. 17), display either a fine-grained granular substructure (granules $\sim 1 \mu$ across), or less commonly a smooth cleavage-like surface, while etching reveals the presence of longitudinal and transverse blocks approximately 10 μ across (Pl. 90, fig. 18). The latter probably result, in part, from closely spaced transverse tabulae 8–10 μ apart, visible under transmitted light (Pl. 90, fig. 16), and interpreted as accretion lines.

Distribution. Thus far *Isognomon wellmani* is known with certainty from only the type locality. Specimen TM 6692, collected by McKay in 1886, is from the 'Saurian Beds, Trelissic Basin', which most probably corresponds to the type locality, or very close by (G. H. Browne, pers. comm. 1986). It is very likely that further sampling, and re-examination of earlier collections, will reveal the presence of this bivalve in other Palaeocene and possibly Late Cretaceous faunas. Its distribution and biostratigraphic value, however, will be difficult to assess because of previous confusion with *Inoceramus matotorus* (discussed below).

Age. The Broken River Formation in the Castle Hill Basin has hitherto been considered entirely Haumurian (latest Campanian–Maastrichtian), based on the presence of *I. matotorus* Wellman and *Conchothyra parasitica* (Hutton) (Gage 1970; Browne and Field 1985). However, dinoflagellates in the matrix of the shell-bed at the type locality of *Isognomon wellmani* (K34/f48, sample L 12989) indicate a Teurian age (Danian–Landenian; G. J. Wilson, written pers. comm. 1986). This is consistent with Teurian ages for two pollen samples (K34/f9611 and 9612, samples L 4194 and 4195) from a short distance downstream and stratigraphically below the shell-bed; and a pollen sample (K34/f9565, sample L 1706) from just above Torlesse basement in Whitewater Creek, 5 km to the south-west (J. I. Raine, written pers. comm. 1986). Of the macrofossils from the type locality, '*Inoceramus matotorus*' has here been referred entirely to *Isognomon wellmani*, and re-examination of *C. parasitica* proved inconclusive: the specimens are poorly preserved but show traces of ornament that may be remnants of the prominent spiral cords characteristic of the Teurian *C. australis* (Marshall). The age of *I. wellmani* at its type locality is, therefore, considered Teurian (Danian–Landenian), based on fossil dinoflagellates and pollen.

Discussion. Prismatic shell in the Broken River Formation has, until now, been assumed to represent *Inoceramus matotorus* (Gage 1970). While little is known about the shape of *I. matotorus*, it may be distinguished from *Isognomon wellmani* by its huge adult size, juvenile ornament of irregular commarginal plicae (which do affect the internal mould), adult ornament of weak relatively regular frills (Wellman 1959, fig. 1), and nature of the ligament area (see earlier discussion, and description in Appendix). At present the two species cannot be distinguished simply from details of the prismatic shell structure, although *Inoceramus matotorus* appears to have more uniform and regular hexagonal rod-type fibrous prismatic shell than *Isognomon wellmani* (terminology after Carter and Clark 1985).

The presence of *Isognomon* at Broken River has been suggested previously by Sir Charles Fleming (in unpublished faunal lists), based on hinges observed *in situ* at the type locality of *I. wellmani*, and material collected in this region by McKay in 1880 (GS 6620 and 67 respectively); and by Professor J. D. Campbell (written pers. comm. 1986). However, no Cretaceous or Palaeocene *Isognomon* have hitherto been described from New Zealand, and furthermore, relatively few have been documented overseas.

Comparisons with other species are hindered by the poor preservation of both the material being described and much of that being compared. In addition, members of this genus can show extreme morphological variability. For example, Fischer-Piette (1976, pl. 1, 2) illustrated the huge range in form of Recent *I. isognomum* (Linnaeus, 1758) from a single population, and proposed a remarkable synonymy list (containing seventy-eight species names) for that bivalve. Furthermore, Durán-González *et al.* (1984) documented considerable genetic variation between geographically separated populations of Recent *I. alatus* (Gmelin, 1791). Even the small sample of individuals

being described here show a marked variation in morphology. Hence it is with caution that *I. wellmani* is described as a new species, and discovery of more and better preserved material may show that this form is indistinguishable from, and perhaps conspecific with, a number of other species mentioned below.

I. wellmani differs from *I. rekohuensis* (described herein) by its smaller size, its possession of a posterior wing, and its coarser ligament area structure. It resembles some Cretaceous and Palaeogene species from Australia, North America, Europe, USSR, and Japan in the outline of internal moulds, but is distinguished by its considerably larger dimensions.

I. wellmani is, however, very similar in size, shape, and ligament structure to *I. ricordeana* (Orbigny, 1845) (pp. 494–495, pl. 399, figs. 1–3; illustrated also in Woods 1905, figs. 16–18) from the Neocomian of Europe, and *I. sanchuensis* (Yabe and Nagao, 1926) (p. 57, pl. 12, figs. 1–4) from the Aptian–Albian of Japan. The former possesses a more projecting umbo, while the latter appears to be more strongly invaginated on the anterodorsal margin. In addition they are both considerably older than the present record of *I. wellmani*.

Of the few Palaeogene *Isognomon* described, *I. bazini* (Deshayes, 1860) (pl. 76, figs. 1–2; described in Deshayes 1861, p. 57) from the Thanetian of the Paris Basin most resembles *I. wellmani*. *I. bazini* is slightly smaller, has a straighter anterior margin with a less produced umbo, lacks a posterior wing, and has more numerous resilifers than *I. wellmani*.

Isognomon (Isognomon) rekohuensis sp. nov.

Plate 89, fig. 1a–e

vp. 1976 *Inoceramus opetius* Wellman, 1959; Speden (p. 385, fig. 1).

Name. Derived from the Maori name for the Chatham Islands: *Rekohu*.

Material. A single articulated bivalved specimen with all shell material preserved (though partly recrystallized).

Type locality. CH/f213, 772202 (imperial grid reference NZMS 240/298673), GS 11521: from the Kahuitara Tuff (Hay *et al.* 1970; Austin *et al.* 1973; Campbell *et al.*, 1988) in the northern half of the bay immediately south of Kahuitara Point, Pitt Island, Chatham Islands (see text-fig. 1). Collected by H. R. Katz and P. Hill, 1975.

Type specimen. Holotype: TM 5453.

Diagnosis. *Isognomon* of large size, mytiliform and acline; ligament area smooth dorsally, and carrying approximately twenty-six resilifers ventrally, resilifers of variable size and becoming alternately wide-shallow and narrow-deep towards the posterior.

EXPLANATION OF PLATE 89

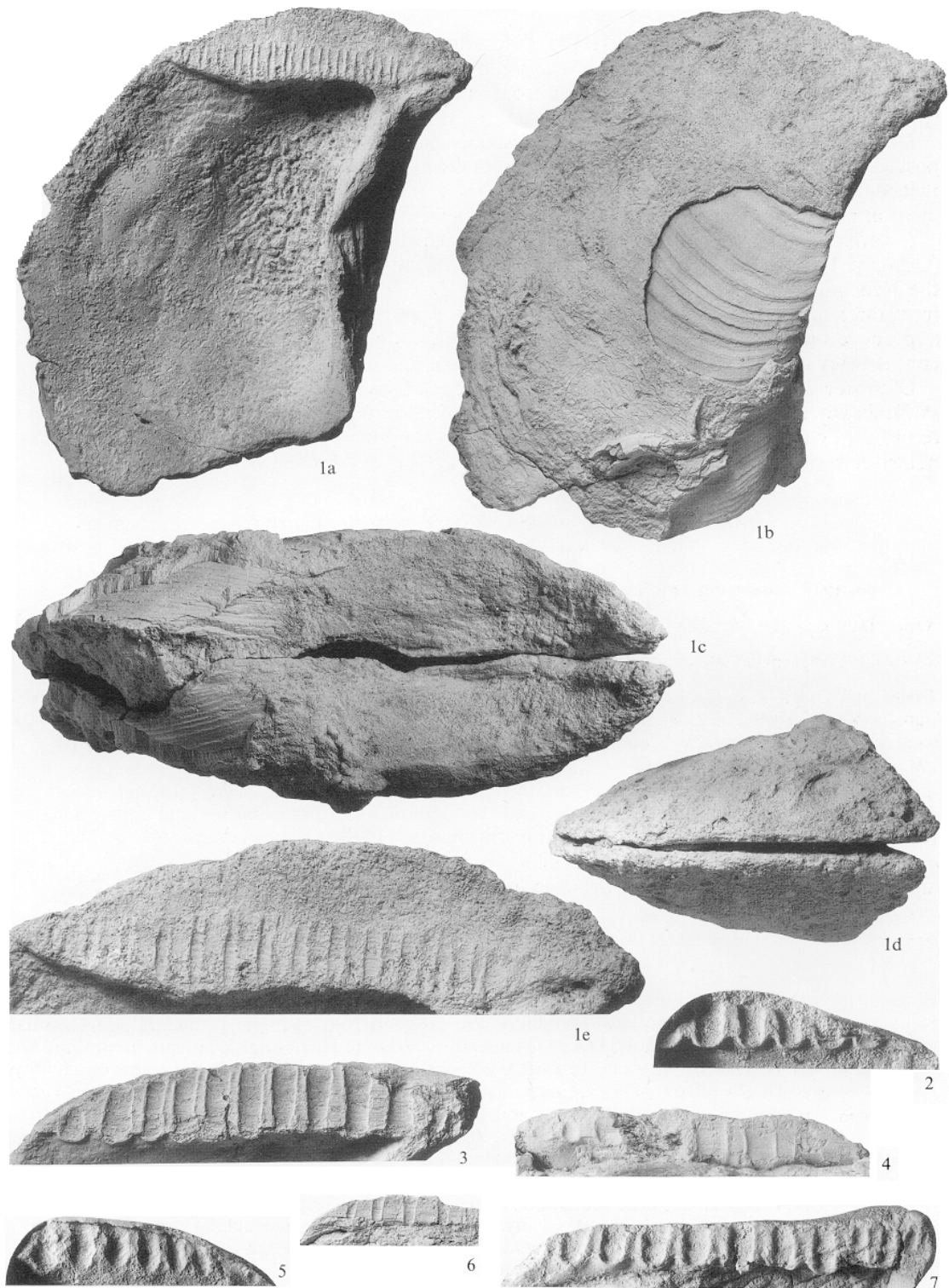
Fig. 1a–e. *Isognomon (Isognomon) rekohuensis* n. sp. TM 5453, CH/f213, holotype; Kahuitara Tuff, Kahuitara Point, Pitt Island, Chatham Islands (Late Cretaceous); a, external view of right valve, section of prismatic shell missing revealing irregular ribs on surface of inner shell layer, $\times 0.7$; b, internal view of left valve, $\times 0.7$; c, dorsal view of articulated specimen, anterior to right, $\times 0.7$; d, anterior face of articulated specimen, dorsal to right, $\times 0.7$; e, ligament area of left valve, $\times 1.3$.

Figs. 2–7. Segments of ligament areas of some New Zealand Jurassic *Isognomonidae*, dorsal-up in all figures. All figs. $\times 1.3$.

Figs. 2–5. *Isognomon (Isognomon)* sp. 2, OU 14399a, F46/f71; latex mould right valve, Mataura, Southland. 3, L(AU) 3614, H47/f001; left valve, Tuhawaiki, Southland. 4, TM 6701, H47/f6494; right valve, Tuhawaiki, Southland. 5, OU 14399b, F46/f71; latex mould right valve, Mataura, Southland.

Fig. 6. *I. (Mytiloperna)* sp. A. L(AU) 3413a, R16/f171; left valve, Kairimu Valley, south-west Auckland.

Fig. 7. *Isognomon (M.?)* sp. B. TM 4062, R15/f8006, paratype; left valve, Ururoa Point, south-west Auckland. All specimens whitened with ammonium chloride sublimate.



CRAMPTON, *Isognomon* (*Isognomon*), *Isognomon* (*Mytiloperna*)

Description. Dimensions (in millimetres, refer to text-fig. 2):

Specimen	Length	Height	Width (both valves)	Obliquity
TM 5453	113	142	59	55°

Shell large; mytiliform; acline; prosogyrous, umbo terminal and projecting beyond rest of anterior margin; equivalve; moderately inflated. Dorsal and posterior outlines form unbroken curve with more convex ventral margin. Anterior outline straight ventrally, concave dorsally. Anterior auricle and posterior wing absent. Wedge-shaped in longitudinal profile, maximum width at anterior margin and approximately one third of the way below the hinge line. Anterior face recurved from umbonal carina (although on the holotype this face may have been depressed during preservation). Disc gently convex to planar. Commissure planar, byssal gape narrow (although it is unclear whether this has resulted from the deformation suggested above). Small ear-like projections on anterior margins either side of the commissure (these are not auricles since they do not support and extend the hinge line).

External ornament of closely spaced, irregular, fine, commarginal lamellae. Interface between prismatic and nacreous shell layers carries weak asymmetrical plicae and is lamellose in places (Pl. 89, fig. 1*b*).

Hinge edentulous, ligament multivinular (Pl. 89, fig. 1*e*). Ligament area flat and inclined a few degrees to plane of commissure; somewhat undercut close to umbo. At least twenty-six rectangular, shallow, concave-floored resilifers which breach and weakly crenulate (judged from the shape of growth lines) the sigmoid-shaped ventral margin of the area (refer to text-fig. 3). Resilifers, separated by very narrow angular ridges, are differentiated posteriorly into alternate shallow wide (2.5 mm) and deeper narrow (1 mm) pits, this differentiation decreasing close to the umbo. They carry an ornament of fine transverse growth lines which vary between concave-up and convex-up on adjacent pits. The ligament area achieves a maximum height of approximately 18.5 mm, although the resilifers extend over only the ventral half of this, being truncated sharply, and leaving a smooth platform dorsally. Ligament attached to inner shell layer.

The posterior adductor muscle scar, shaped like an inverted comma, is situated midway between the dorsal and ventral margins (Pl. 89, fig. 1*a*). No pallial muscle scars are visible on the holotype.

The shell consists of an outer layer of polygonal rod-type fibrous prismatic calcite and an inner layer of coarse granular calcite, presumed to be recrystallized nacreous aragonite originally forming the middle and inner shell layers (discussed earlier). Over much of the disc the shell is somewhat less than 10 mm thick, comprising a thicker prismatic layer towards the margins, and thicker inner layers close to the umbo. Near the anterior margin the shell is approximately 20 mm thick. The structure of the prismatic shell layer is very similar to that described for *I. wellmani*: prisms achieve a maximum size of approximately 3.2 × 0.2 mm, they are reclined, sigmoid-shaped, larger towards the inside surface than towards the outer, and formed into discrete lamellae close to the outside surface. However, examination of *I. rekohuensis* prisms under SEM and transmitted light revealed little substructure, and the uniform coincident extinction and apparent fracture along cleavage planes may indicate diagenetic recrystallization.

Distribution. *I. rekohuensis* is known thus far from only the type locality. Fragments of prismatic shell from elsewhere in the Kahuitara Tuff (CH/f11 and CH/f11*a*) may represent this species (although an undescribed bakevelliid with thick prismatic shell also occurs in the Kahuitara Tuff). As with *I. wellmani*, the distribution of *I. rekohuensis* may be difficult to gauge due to confusion with species of *Inoceramus*.

Age. Macrofossils in the Kahuitara Tuff were originally assigned to the lower or middle Cretaceous by Boreham (1959). This unit was subsequently removed to the late Cretaceous based on Teratan-lowest Haumurian (Senonian) dinoflagellates (Wilson 1976), probable Mata Series (Campanian-Maastrichtian) palynomorphs (Mildenhall 1977), and poorly determinate Teratan to Haumurian foraminifera (Strong 1979). With the referral of *Inoceramus opetius* to *Isognomon rekohuensis*, the only age-diagnostic macrofossil from this formation is the Haumurian (latest Campanian-Maastrichtian) belemnite *Dimitobelus hectori* Stevens (1965) from the localities on the north-west of Pitt Island (CH/f587, Rocky Side, and CH/f466, Flower Pot Harbour).

A limestone filling cracks in the top of the Kahuitara Tuff at Flower Pot Harbour contains well-preserved late Haumurian foraminifera (Strong and Edwards 1979). Radiometric analyses from the Southern Volcanics and Whakepa Trachyte, which overlie and underlie the Kahuitara Tuff respectively, in the region of Kahuitara Point, gave dates of 77.3 ± 1 my and 79.0 ± 1 my (Grindley *et al.* 1977). These dates correspond to mid to late Piripauan (mid Campanian), according to the timescale of Stevens (1981).

Hence it seems likely that the Kahuitara Tuff is no older than Teratan (Coniacian), no younger than late Haumurian (late Maastrichtian), and is Piripauan (Campanian) at the type locality of *I. rekohuensis*.

Discussion. The holotype of *I. rekohuensis* was referred to *Inoceramus opetius* by Speden (1976). The external features of the two species are contrasted in the family discussion above. In addition, *I. opetius* has a variable ligament area with commonly multilobate or multiserial resilifers (see Pl. 90, figs. 6–8) which are constructed on the outer prismatic shell layer. The shell of *I. opetius* is much thinner than that of *Isognomon rekohuensis*, the prismatic layer being only about 1.5 mm thick on the disc of a large specimen, and having a polygonal simple prismatic structure.

I. rekohuensis is readily separated from most other Late Cretaceous and Palaeogene *Isognomon*, including *I. wellmani* (described herein) by its large size and delicate resilifers. However, *I. williardi* Stephenson (1923, pp. 125–126, pl. 23, figs. 1–3; pl. 24, figs. 1–2; pl. 25, fig. 3), from the Senonian of eastern United States, is remarkably similar to the present species, but its resilifers are not truncated dorsally and its ligament area is not undercut (although the latter is not a reliable character, see for example *Isognomon (I.)* sp.; Pl. 89, figs. 2 and 5).

The distinctive form of the ligament area seen in *I. rekohuensis* and *I. williardi*, as well as their shape, resemble members of the subgenus *I. (Hippochaeta)* Sangiovanni, 1844, notably *I. (H.) sandbergeri* (Deshayes in Sandberger 1863, p. 367, pl. 31, figs. 4–4a; and well illustrated in Ludwig 1864, pl. 13, fig. 1; pl. 14, figs. 1–3; pl. 15, figs. 1–1c) from the Middle Oligocene of France, and *I. (H.?) lamarcki* (Deshayes, 1830) (p. 284; illustrated in Deshayes 1837, pl. 40, figs. 7 and 8) from the Bartonian of France. However, in most species of *I. (Hippochaeta)* the area is very high, the differentiation of broad shallow resilifers and deep narrow grooves is much more marked, these grooves bifurcate dorsally in many species, and they appear to reach the dorsal margin of the area in all species. (These features are not well developed in *I. (H.?) lamarcki*, and hence its referral to this subgenus is queried.) Thus far, *I. (Hippochaeta)* is known only from Eocene to Pliocene rocks (Cox 1969).

Family RETROCERAMIDAE Pergament in Koschelkina, 1971

Type genus. *Retroceramus* Koschelkina, 1959. (The subgenus *Inoceramus (Retroceramus)* was first proposed informally by Koschelkina (1957), and was validated by Koschelkina (1959) with the designation of a type species (Crame 1982). The subgenus was elevated to generic level by Koschelkina (1962).)

Diagnosis. Various shaped edentulous multivincular Pteriacea bearing commarginal plicae that are large and regularly spaced in nearly all taxa, and in which the ligament is fixed to the nacreous shell layer.

Discussion. Other characters typical, though not necessarily diagnostic, of this family include marked obliquity of the valves (see text-fig. 5d); subterminal, moderately to strongly gibbous umbones; moderate to high angles between the planes of the ligament area and commissure; a flat to weakly concave ligament area; relatively broad rectangular to sub-ovate resilifers which in all (?) taxa breach and in most taxa crenulate the ventral margin of the area (refer to text-fig. 3; Pl. 90, figs. 1–3); and resilifer interspaces which are typically broad and concave. In some taxa these interspaces are sufficiently deep to appear as a second class of resilifer, resulting in alternating broad-deep and narrow-shallow pits separated by narrow angular ridges.

The family-group name *Retroceramidae* was first published by Koschelkina (1971), who attributed authorship to Pergament (1969, unpublished). Koschelkina's description of the type genus, *Retroceramus*, follows:

Shell equilateral or practically equilateral, with uneven sides, elongated along the axis of growth from the beaks, which are near the anterior margin, but not terminal. Sculpture concentric, less often radial. Prismatic and nacreous layers well developed. Ligament platform located upon nacreous layer. In adult forms it consists of ligamental pits and ridges varying in outline. Posterior muscle—adductor large, anterior—strongly reduced. Mantle line discontinuous

Lower Jurassic(?) Mainly in Middle Jurassic of Boreal province. Less numerous in Upper Jurassic. Lower Cretaceous?

The name *Retroceramidae* has subsequently been used by Koschelkina (1980) and Pokhialaynen (1985). Characters, facies relationships, and inferred life habits of *Retroceramus*, thus far the only genus referred to *Retroceramidae*, are described by Koschelkina (1963, 1969, 1971) and Crame (1982).

NOTES ON LIFE HABITS OF *ISOGNOMON WELLMANI* AND *I. REKOHUENSIS*

Recent *Isognomon* are physiologically tolerant filter-feeding byssate bivalves found in tropical and subtropical littoral or inner shelf low- to high-energy marine and estuarine environments. They typically live epifaunally in crowded beds attached by massive byssi to hard surfaces, and oriented vertically (ventral up) or with their right valves against the substrate. Less commonly they are found on or within soft substrates. (For accounts of the ecology and biology of Recent species of *Isognomon* see Read 1964, Yonge 1968, Siung 1980, and Reid 1985.) Similar life habits for *I. wellmani* and *I. rekoensis* cannot be assumed since they are considerably larger, more inflated, and thicker shelled than Recent species. Fürsich (1976, 1980, 1981) and Fürsich and Werner (1986) inferred that a number of fossil species from the Jurassic of Europe lived close to shore, were semi-endobysate in generally fine-grained sediments, and were probably opportunistically euryhaline, forming clusters and banks in hypersaline to mesohaline environments (i.e. hypersaline lagoons to brackish bays).

While few data are available on fossil-lithofacies relationships of the new species, sediments and faunas at both type localities suggest deposition in moderate- to high-energy shallow marine

EXPLANATION OF PLATE 90

Figs. 1-14. Segments of ligament areas and/or umbones of some New Zealand Jurassic *Retroceramidae* and Cretaceous *Inoceramidae*. All figures dorsal up, $\times 1.3$. All specimens whitened with ammonium chloride sublimate.

Fig. 1. *Retroceramus (Retroceramus) galoi* (Boehm, 1907). TM 6719, R15/f8546; right valve, Kawhia Harbour, south-west Auckland.

Fig. 2. *R. (R.) haasti* (Hochstetter, 1863). TM 6720, R15/f8564; left valve, Kawhia Harbour, south-west Auckland.

Fig. 3. *R. (R.) cf. subhaasti* (Wandel, 1936). TM 5774, R15/f8012; latex mould right valve, Kawhia Harbour, south-west Auckland.

Figs. 4 and 5. *Inoceramus rangatira* Wellman, 1959. Y19/f7494, Hapuku River, Marlborough. 4, TM 6712 umbo (umbonal septum directed into page) of right valve. 5, TM 6711, umbo and umbonal septum of left valve.

Figs. 6-8. *I. opetius* Wellman, 1959. 6, TM 6708, W22/f8504, right valve, Waimarama, Hawke's Bay. 7, TM 6707, V23/f16; left valve, Mangakuri River, Hawke's Bay. 8, TM 6709, U25/f6462; valve unknown, Akiteo River, Wairarapa.

Fig. 9. *I. concentricus* Parkinson, 1819. OU 4056, P30/f6551; left valve, Cover Creek, Marlborough.

Fig. 10. *I. fyfei* Wellman, 1959. TM 2114, X16/f9539, holotype; latex mould right valve, Motu River, East Cape.

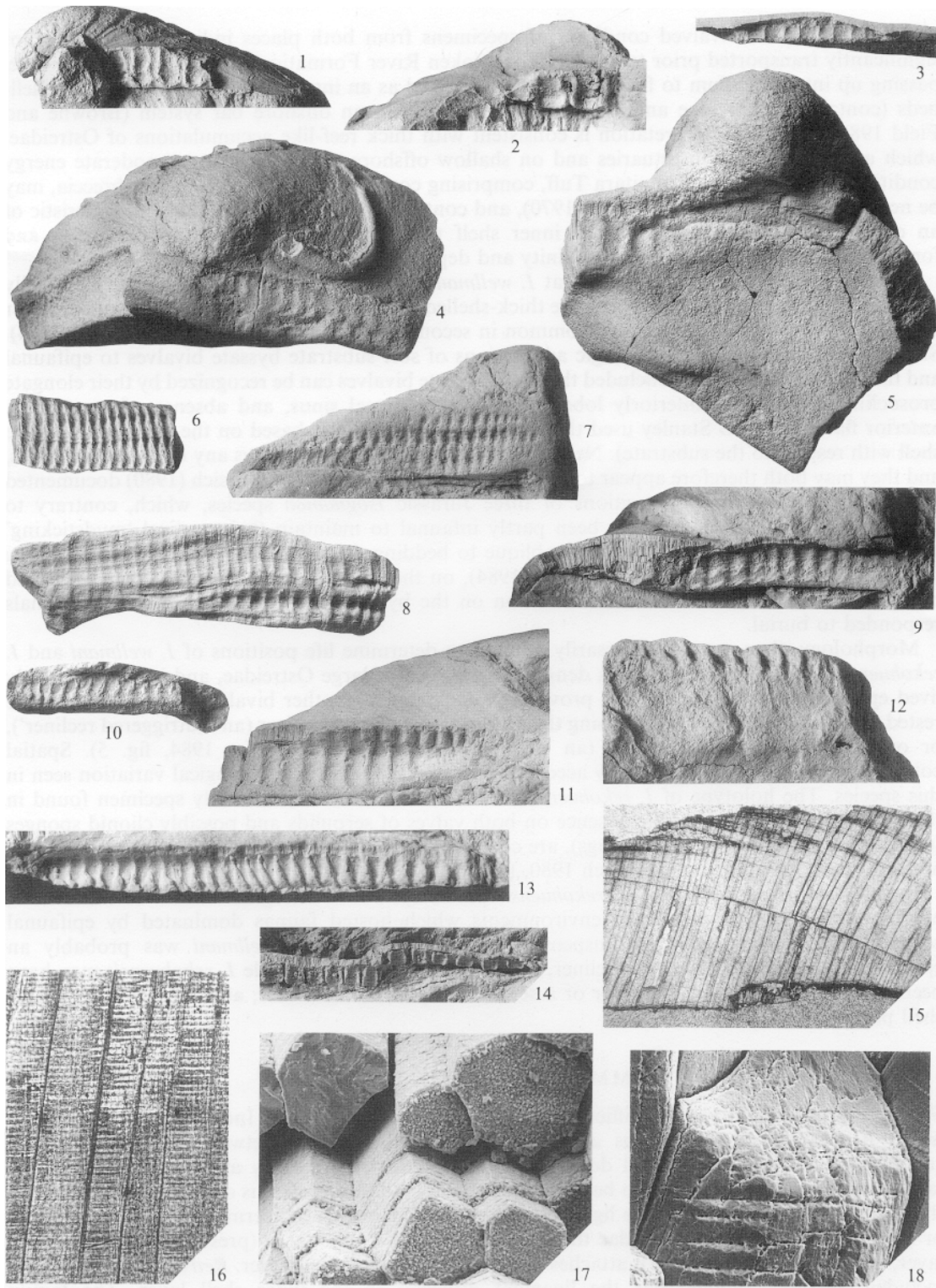
Fig. 11. *Inoceramus* sp. A. TM 6716, W22/f8504; left valve, Waimarama, Hawke's Bay.

Fig. 12. *I. bicorugatus* Marwick, 1926. TM 6704, Y14/f7850; right valve, Waikura River, East Cape.

Fig. 13. *I. australis* Woods, 1917. TM 6703; plaster cast right valve, Gisborne district.

Fig. 14. *Inoceramus* sp. B. TM 6717, Z14/f106; valve unknown, Taurangakautuku Stream, East Cape.

Figs. 15-18. Prismatic shell layer of *Isognomon (Isognomon) wellmani* n. sp. Broken River Formation, Broken River, Canterbury. 15 and 16, TM 6697, K34/f48; photomicrographs, plain polarized light, radial thin section from disc of shell, outside to top, margin to left. 15, entire thickness of prismatic layer, $\times 35$. 16, details of prisms showing transverse tabulae interpreted as accretion lines, $\times 216$. 17, SEM, oblique to long axis of prisms, showing granular substructure of most prisms, $\times 546$. 18, SEM, perpendicular to long axis of prisms, etched sample (90 seconds, 0.5% HCl), showing block-like substructure of prisms, $\times 762$.



CRAMPTON, *Retroceramus*, *Inoceramus*

environments. (The bivalved condition of specimens from both places indicates they were not significantly transported prior to burial.) The Broken River Formation is non-marine at the base, passing up into a medium to fine sandstone interpreted as an inner shelf deposit with thick shellbeds (containing Ostreidae and *Isognomon*), developed on an offshore bar system (Browne and Field 1985). Such an interpretation is consistent with thick reef-like accumulations of Ostreidae, which are found today in estuaries and on shallow offshore shelves subject to moderate energy conditions. Similarly, the Kahuitara Tuff, comprising coarse tuff, conglomerate, and breccia, may be non-marine at the base (Hay *et al.* 1970), and contains a diverse marine fauna characteristic of an epifaunal habit in a high energy inner shelf to subtidal environment (Speden 1976) and foraminifera typical of near normal salinity and depths of 5–50 m (Strong 1979).

Sedimentary relationships suggest that *I. wellmani* and *I. rekohuensis* lived on sandy or shelly substrates. Furthermore, both species are thick-shelled, particularly close to the dorsal and anterior valve margins: a stabilizing strategy common in secondary soft-bottom dwellers (Seilacher 1984). Stanley (1972) described morphologic adaptations of soft substrate byssate bivalves to epifaunal and infaunal life habits. He concluded that endobysate bivalves can be recognized by their elongate prosocline shape, dorsoanteriorly lobate shell, broad byssal sinus, and absence of appreciable anterior flattening (NB Stanley used the term 'ventral flattening', based on the orientation of the shell with respect to the substrate). Neither species described here displays any of these characters, and they may both therefore appear to have been epibysate. However, Fürsich (1980) documented the apparent preserved life positions of three Jurassic *Isognomon* species, which, contrary to theoretical predictions, must have been partly infaunal to maintain their vertical 'mudsticking' attitudes: umbo downwards, hinge line oblique to bedding, in a manner similar to Recent *Pinna* (terminology of Seilacher 1984). Seilacher (1984), on the other hand, interpreted these preserved positions as the result of 'unnatural' rotation on the byssus as the normally epifaunal animals responded to burial.

Morphology, then, cannot necessarily be used to determine life positions of *I. wellmani* and *I. rekohuensis*. The former occurs in a densely packed bed of large Ostreidae, and it most probably lived epifaunally, attaching to, and providing attachment for, other bivalves. It may either have rested on the right and left valves, using the posterior wing as a stabilizer (an 'outriggered recliner'), or on the flattened anterior face (an 'edgewise recliner', see Seilacher 1984, fig. 5). Spatial competition in such a situation may account for the intraspecific morphological variation seen in this species. The holotype of *I. rekohuensis*, on the other hand, was the only specimen found in the outcrop. Its shape, and the presence on both valves of serpulids and possibly clionid sponges (represented by abundant fine borings), are consistent with an edgewise reclining or semi-infaunal mudsticking life position (see Fürsich 1980, fig. 9).

In summary, *I. wellmani* and *I. rekohuensis* probably lived in marginal marine to inner shelf, moderate- to high-energy marine environments which hosted faunas dominated by epifaunal cemented and byssally attached suspension-feeding organisms. *I. wellmani* was probably an epibysate outrigger or edgewise recliner, attaching to other shells, while *I. rekohuensis* may have been an epibysate edgewise recliner or a semi-endobysate mudsticker, attaching to sediment or shell particles.

SUMMARY AND CONCLUSIONS

Fossil Isognomonidae can be difficult to distinguish externally from Inoceramidae, a problem which has resulted in erroneous age determinations. Differences between these families are summarized in Table 2. Internal details of ligament area morphology are characteristic at the family level. Definitive distinction between these two families, however, is apparently furnished by the shell structure underlying the ligament area (a character easily determined from whole shells or thin sections). In Isognomonidae the ligament attaches to the inner (presumed nacreous) shell layer, whereas in Inoceramidae it attaches to the outer prismatic shell layer. *Retroceramus*, formerly included in Inoceramidae, has the ligament attached to the inner shell layer. The family

TABLE 2. Summary of principal differences between Inoceramidae, Retroceramidae, and Isognomonidae.

	Inoceramidae	Retroceramidae	Isognomonidae
Shape	Acline to strongly prosocline	Typically moderately to strongly prosocline	Typically acline to weakly prosocline, strongly prosocline in few taxa
Umbones	Towards the anterior end of the hinge line or subterminal; more or less gibbous and incurved	Typically subterminal, more or less gibbous and incurved	Terminal, subterminal in a few taxa, not markedly gibbous or incurved
Byssal gape	Rare	Rare or narrow?	Present or absent
Surface	Ornament of commarginal or, in a few taxa, radial ribs	Ornament of commarginal ribs, strong, regular in nearly all taxa; radial in a few taxa	Surface smooth or characteristically lamellose; radial ornament present in very few taxa
Ligament area	Area multivincular or, in a few taxa, bearing elongate groove, concave or, in some taxa, flat; resiliifers relatively numerous, monoserial to multiserial, rectangular to ovate, do not markedly crenulate ventral margin of area; interspaces narrow	Area multivincular, typically flat to weakly concave, inclined to plane of commissure; resiliifers broad, monoserial, rectangular to ovate, may crenulate ventral margin of area; interspaces of most taxa relatively broad and concave, resembling a second class of resiliifer in some species	Area multivincular, flat or weakly concave, parallel or only weakly inclined to plane of commissure and relatively high in most taxa; resiliifers monoserial, typically rectangular, may crenulate ventral margin of area; interspaces narrow to broad, typically flat or concave
Shell structure beneath ligament area	Outer prismatic layer	Inner nacreous layer	Inner nacreous layer

Retroceramidae Pergament in Koschelkina, 1971, should therefore be used to accommodate those multivincular Pteriacea which bear typically strong, regular, commarginal plicae and which have the ligament attached to the inner shell layer. Thus far, only *Retroceramus* is referred to Retroceramidae.

The present data are consistent with a polyphyletic origin for the multivincular ligament in Inoceramidae and Isognomonidae; the evolution of Inoceramidae from *Atomodesma*; the removal of Inoceramidae from Pteriacea to Ambonychiacea; and a close relationship between Retroceramidae and Isognomonidae.

At the species level, details of ligament area morphology are valuable, if not essential, for discriminating between similar and, in many cases, morphologically highly variable species within families Isognomonidae, Retroceramidae, and Inoceramidae.

Many Mesozoic and early Tertiary *Isognomon*, like Recent species, occupied inner shelf to marginal marine environments. However, unlike Recent forms, it seems they were more typically epibyssate on or semi-endobysate in soft or shelly substrates. This difference in life habits accounts for the stabilizing structures common in fossil *Isognomon* (for example, *I. wellmani* and *I. rekohuensis*), such as a large anteriorly and dorsally thickened shell, elongate posterior wing, and broad flat anterior face.

APPENDIX. LIGAMENT AREA MORPHOLOGIES OF SOME NEW ZEALAND JURASSIC AND CRETACEOUS ISOGNOMONIDAE, RETROCERAMIDAE, AND INOCERAMIDAE

These descriptions are based on few specimens of each taxon and are intended as introductory notes (to facilitate the present discussion) pending more complete population-based taxonomic studies. Consequently, names by which some specimens are identified may require future revision. Brief descriptions of ligament area (refer to text-fig. 3 for an explanation of descriptive terms) and pertinent taxonomic comments are followed by repository catalogue and Fossil Record File numbers (abbreviations explained in the Introduction), relevant details of the whole specimens, locality information with grid references (where available), collector(s), and ages (ages are bracketed if based solely on the species under discussion). Map sheet areas of New Zealand fossil localities referred to are shown on text-fig. 1.

Superfamily PTERIACEA Gray, 1847; *nom. transl.* Dall, 1894 (*ex* Pteriidae; = Aviculidae Goldfuss, 1820 (see earlier))

Family ISOGNOMONIDAE Woodring, 1925

Genus ISOGNOMON Solander in Lightfoot, 1786

Subgenus ISOGNOMON Solander in Lightfoot, 1786

Type species. *Ostrea isognomon* Linnaeus, 1764 (see earlier).

Isognomon (Isognomon) sp.

Plate 89, figs. 2-5; text-figs. 4A and 5B

Ligament area morphology apparently very variable (compare Pl. 89, figs. 2-5, specimens from the same population). Area flat, at least six to seven broad concave rectangular resilifers (approximately 2-4 mm wide) separated by narrower flat to moderately concave ridges (approximately 1.7-2.5 mm wide), which on some specimens resemble a second class of resilifer (Pl. 89, fig. 4). Resilifers breach ventral margin of area on all specimens, and strongly crenulate it on some. Height of area approximately 2.7 mm close to umbo, and 6 mm or more posteriorly. Ligament attached to inner shell layer.

Material. L(AU) 3614, H47/f001, AU 11096. Plate 89, fig. 3. Shelly beak of LV. Jacks Bay, Tuhawaiki, Southland; N. Hudson, 1986. Temaikan (Bajocian-mid Callovian).

OU 14399a, F46/f071. Plate 89, fig. 2. Internal mould RV; length ~ 57 mm, height 72 mm. Stewart's Farm, near Maitua, Southland; M. C. Gudex?

OU 14399b, as for previous specimen. Plate 89, fig. 5. Internal mould RV; length > 56 mm, height 72 mm.

TM 6701, H47/f6494, GS 148. Plate 89, fig. 4. Partly shelly internal mould RV; length 54 mm, height 65 mm. Coast opposite Bloody Jacks Island, Tuhawaiki, Southland; A. McKay, 1873. Temaikan (Bajocian-mid Callovian).

TM 6702, H46/f6752, GS 7102. Not figured. Internal mould LV; length 43 mm, height 56 mm. Old coastal face, south-west side of Jacobs Hill, Catlins River, Southland; H46 567104; I. G. Speden, 1957. Temaikan.

TM 6790, H47/f6494, GS 148. Text-fig. 4A. Two thin sections perpendicular to ligament area, approximately half-way between umbo and posterior end of ligament area. Locality as for *TM 6701* (above).

TM 6793, as for previous specimen. Text-fig. 5A. Partly shelly LV; length 48 mm, height 63 mm.

Subgenus *MYTILOPERNA* Ihering, 1903

Type species. Perna americana Forbes in Darwin, 1846.

Isognomon (Mytiloperna) sp. A

Plate 89, fig. 6.

This species is referred to *Isognomon (Mytiloperna)* on the basis of its prosocline shape, subterminal beak, small size, lack of a distinct posterior wing, and small number of well-spaced resilifers (the first two criteria, atypical of most Isognomonidae, characterize this subgenus). However, it does also resemble some forms of Bakevilliidae King, 1850, notably *Cuneigervillia* Cox, 1954, and study of juvenile stages may reveal the presence of hinge teeth characteristic of the latter genus.

Ligament area flat, nearly parallel to plane of commissure. Few (probably no more than five or six) subrectangular resilifers, which narrow ventrally (from ~ 1.8 mm to ~ 1.2 mm), and breach but scarcely crenulate the ventral margin of the area. Interspaces wider than resilifers (~ 2 mm to ~ 2.5 mm), flat or weakly concave, most bounded by narrow upstanding rims. Area may become irregularly thickened and extended ventrally, its height on two similar-sized individuals being ~ 1.5 mm and > 4 mm. Ligament attached to inner shell layer.

Material. L(AU) 3413, R16/f171, AU 4604. Plate 89, fig. 6. Shelly RV and ligament area of LV; length (RV) > 30 mm, height ~ 25 mm. Paraohanga Stream, Kairimu Valley, Kawhia, south-west Auckland; R16 662189; D. A. Francis. Heterian (Early Kimmeridgian).

L(AU) 3412, as for above. Not figured. Internal and external moulds of RV; length 35 mm, height 23 mm.

Isognomon (Mytiloperna?) sp. B

Plate 89, fig. 7; text-fig. 5B

The specimen figured here, a paratype of *Inoceramus ururoaensis* Speden (1970a, pp. 836–842, figs. 12–20), is tentatively referred to *Isognomon (Mytiloperna)* based on its prosocline shape, weakly developed subterminal umbo, smooth to lamellose surface, and attachment of the ligament to the inner shell layer (see earlier discussion of family characters). It is distinguished from Retroceramidae by the weakly developed umbo and lack of commarginal plicae. This specimen, however, differs from typical *I. (Mytiloperna)* by being considerably more obliquely elongate, lacking a distinct posterodorsal angle, having a convex anterior margin, and having a strongly undercut ligament area. In addition the area (described below) of this specimen, while being similar to *I. (M.) ageroensis* Hayami, 1957 (pp. 101–103, pl. 6, figs. 4–8), has relatively abundant and uniform resilifers, which contrast with the well-spaced and somewhat irregular resilifers of most *I. (Mytiloperna)* and strongly resemble those of Retroceramidae described herein. Hence it is with caution that this fossil is referred to *I. (Mytiloperna)*, although it is removed from *Inoceramus* with some confidence. It is not yet clear whether *Isognomon (M.?) sp.* and the holotype of *Inoceramus ururoaensis* are conspecific.

Ligament area flat, slightly twisted so that it is subparallel to plane of commissure close to umbo, inclined posteriorly. Probably no more than ten broad (2–3 mm) rectangular resilifers on figured specimen, which breach and strongly crenulate ventral margin of area. Interspaces narrower (1.5–2 mm), weakly concave. Area 5.5–6.5 mm high. Ligament attached to inner shell layer.

Material. TM 4062, paratype, R15/f8006, ex Laws Collection. Incomplete LV; length > 75 mm, height > 41 mm. 60–240 m north-east of stack at Ururoa Point, south-west Auckland; R15 648431. Ururoan (Pliensbachian–Aalenian).

Family RETROCERAMIDAE Pergament in Koschelkina, 1971

Genus RETROCERAMUS Koschelkina, 1959

Subgenus RETROCERAMUS Koschelkina, 1959

Type species. Inoceramus retrorsus Keyserling, 1848.

Retroceramus (Retroceramus) aff. everesti (Oppel, 1865, p. 298)

Not figured here

Referred to *Retroceramus* by Crame (1982). Ligament area diminutive, poorly known. Ligament attached to inner shell layer.

Material. L(AU) 3597, R13/f6969, AU 4410. Internal mould, RV. Cliff in northern bank of Huriwai Stream just east of confluence with south-flowing tributary, Port Waikato, Auckland; R13 645184; A. B. Challinor, 1969. Puroan (Tithonian).

Retroceramus (Retroceramus) galoi (Boehm, 1907, p. 68, pl. 9, figs. 10–14; pl. 10, figs. 1 and 2)

Plate 90, fig. 1; text-fig. 5D

Referred to *Retroceramus* by Crame (1982). Ligament area steeply inclined ($\sim 45^\circ$) to plane of commissure, very weakly concave. Broad rectangular or elongate-ovate resiliifers (probably no more than nine or ten on figured specimen) ~ 2 mm wide separated by narrower concave interspaces (~ 1 mm wide, these concave interspaces constituting a second class of resiliifer, according to Koschelkina 1969). Resiliifers scarcely breach crenulated ventral margin of 4.7 mm high area. Ligament attached to inner shell layer.

Material. TM 6719, R15/f8553 (considered the same as R15/f8546), GS 5944. Partly shelly internal mould RV; length 43 mm, height 41 mm. Point west of Heteri Promontory, across Waikutakuta Inlet, Kawhia Harbour, south-west Auckland; R15 659401; K. J. McNaught, 1953. Heterian (Early Kimmeridgian).

Retroceramus (Retroceramus) haasti (Hochstetter, 1863, p. 190)

Plate 90, fig. 2; text-fig. 4B

Referred to *Retroceramus* by Crame (1982). Ligament area moderately inclined ($\sim 20^\circ$) to plane of commissure, very weakly concave. Broad (3–5 mm) square to ovate resiliifers breach crenulated ventral margin of area. Resiliifer interspaces broad (~ 1.7 mm) and markedly concave dorsally, narrow (< 1 mm) ventrally. Area 4 mm high. Ligament attached to inner shell layer.

Material. TM 6720, R15/f8564, GS 5955. Plate 90, fig. 2. Partly shelly internal mould LV; length 71 mm, height 84 mm. North side of Kowhai Point, from west of tip for ~ 50 –100 m east, Kawhia Harbour, south-west Auckland; R15 67434076; K. J. McNaught, 1953. Lower Ohauan (mid Kimmeridgian).

TM 6792, as for previous specimen. Text-fig. 4b. Thin section perpendicular to ligament area, approximately half-way between umbo and posterior end of ligament area.

Retroceramus (Retroceramus) marwicki (Speden, 1970a, pp. 842–850, figs. 22–34)

Not figured here

Here referred to *Retroceramus*. Ligament area diminutive. Resiliifers shallow, approximately square, 1.5 mm wide, breach and crenulate ventral margin of area. Interspaces narrower (~ 1 mm wide), flat or slightly concave. Area ~ 1.5 mm high. Ligament attached to inner shell layer.

Material. TM 4052, holotype, R17/f8636, GS 7886. Partly shelly internal and external moulds RV; length ~ 35 mm, height 43 mm. West side of Rauroa Stream, at the back of the flood plain, 480 m upstream of ford on Tuamatamairie Road, south-west Auckland; R17 65068961; I. G. Speden, G. R. Stevens, 1961. Upper Temaikan (late Bathonian–Callovian).

Retroceramus (Retroceramus) cf. subhaasti (Wandel, 1936, p. 469, pl. 15, fig. 2; pl. 16, fig. 5a, b)

Plate 90, fig. 3

Referred to *Retroceramus* by Crame (1982). Ligament area low and almost perpendicular to plane of commissure. Resilifers shallow, square, breach but only weakly crenulate ventral margin of area, and only slightly wider and deeper than concave interspaces (i.e. the 'interspaces' seem to form the second class of resilifer described by Koschelkina 1969). Width of resilifers ~ 2.4 mm, width of interspaces ~ 1.7 mm, height of area 2 mm. Ligament attached to inner shell layer.

Material. TM 5774, R15/f8012, GS 9937. Partly shelly internal mould LV; length > 68 mm, height ~ 65 mm. Old Kihī Road, Hauturu, Kawhia, south-west Auckland; R15 864420; G. R. Stevens, I. W. Keyes, 1968. Heterian (Early Kimmeridgian).

Subgenus FRACTOCERAMUS Koschelkina, 1959

Type species. *Inoceramus formosulus* Voronetz, 1937.

Retroceramus (Fractoceramus) inconditus (Marwick, 1953, p. 93, pl. 13, fig. 13)

Text-fig. 5c

Here referred to *Retroceramus*. This species is referred to subgenus *Fractoceramus* on the basis of its weak and irregular ornament which is atypical of the genus as a whole. A single specimen with poorly-preserved ligament area shows the ligament attached to the inner shell layer.

Material. L(AU) 3598, NC/f435, AU 7266. Not figured. Internal mould LV. South end of west coast of Uitoé Peninsula, New Caledonia; La Tontouta 0615775556; J. A. Grant-Mackie, 1975. Temaikan (Bajocian-Callovian).

TM 2373, holotype, F47/f7492, GS 2998. Text-fig. 5c. Internal mould LV; length ~ 45 mm, height 32 mm. Quarry Hills, Waikawa district, Southland; F47 060001; R. A. S. Browne, 1944. Temaikan (Bajocian-Callovian).

Superfamily AMBONYCHIACEA? Miller, 1877; *nom. transl.* Newell, 1965 (*ex* Ambonychiidae)

Family INOCERAMIDAE Giebel, 1852; *nom. transl.* Steinmann, 1903 (*ex* Inoceraminae)

Genus INOCERAMUS Sowerby, 1814

Subgenus indeterminate

Inoceramus australis Woods (1917, pp. 27-28, pl. 13, figs. 1-3)

Plate 90, fig. 13

Ligament area strongly concave with more than twenty-six (possibly twice this number) deep, sigmoid-shaped, elongate-ovate to ovate resilifers which are slightly oblique to the hinge line and become deeper and less elongate towards the posterior. Interjacent ridges upstanding, well defined, angular to rounded, higher and broader ventrally, ~ 2.5 mm between crests. Resilifers shallow steeply close to and breach but do not crenulate ventral margin of area. Area at least 7 mm high. Ligament attached to outer shell layer.

Material. TM 6703, GS 8385. Articulated specimen; length ~ 140 mm, height ~ 170 mm. Gisborne district, locality not known. (Piripauan (Campanian).)

Inoceramus bicorrugatus Marwick (1926, pp. 380-381, fig. 1)

Plate 90, fig. 12

Ligament area known, so far, from a single large poorly preserved specimen. Many ovate to square resilifers of moderate depth separated by narrow upstanding ridges, ~ 2.5 mm between crests. Depressed smooth platform ventral to resilifers. Total height of area > 14.5 mm, resilifers occupying dorsal ~ 4.5 mm. Ligament attached to outer shell layer.

Material. TM 6704, Y14/f7850, GS 11601. Articulated specimen; length ~ 280 mm, height > 370 mm. South-western tributary of Waikura River, East Cape; Y14 582736; R. T. Farmer, G. W. Grindley, 1975. (Mangaotanean (Turonian).)

Inoceramus concentricus Parkinson (1819, pp. 58–59, pl. 1, fig. 5)

Plate 90, fig. 9

Moderately concave ligament area with > 12 shallow elongate-ovate resilifers separated by low rounded ridges. 1.5 mm between ridge crests close to umbo, > 2.5 mm posteriorly. Resilifers barely breach and do not crenulate ventral margin of area. Height of area ~ 5.3 mm. Growth lines may be strongly formed to give stepped appearance. Area smooth beneath umbo. Ligament attached to outer shell layer.

Material. OU 4056, P30/f6551, GS 5815. Plate 90, fig. 9. Incomplete articulated specimen; length ~ 70 mm, height ~ 80 mm. Cover Stream 180 m upstream from junction with Wharf Stream, Marlborough; P30 826173; R. A. Cooper, 1953. Ngaterian (late Albian–early Cenomanian).

TM 6706, P30/f193, GS 14017. Not figured. Partly shelly LV; length > 88 mm, height > 120 mm. Wharekiri Stream, Marlborough; P30 748912; I. G. Speden, M. G. Laird, 1981. (Ngaterian (late Albian–early Cenomanian).)

Inoceramus fyfei Wellman (1959, p. 157, pl. 11, fig. 5)

Plate 90, fig. 10

On the holotype, the weakly concave and longitudinally undulose ligament area is steeply inclined to the plane of commissure and underlain by a smooth platform lying approximately parallel to the commissure. At least thirteen ovate, moderately deep resilifers separated by narrow upstanding ridges which are peaked at their ventral ends. Approximately 1.5 mm between ridges, area ~ 4 mm high. Ligament attached to outer shell layer.

Material. TM 2114, holotype, X16/f9539, GS 6277. Distorted internal mould RV; length ~ 55 mm. Mill Road, end branch road from No. 1 Quarry, Motu River, East Cape; X16 14171736; G. J. Lensen, 1956. (Ngaterian (late Albian–early Cenomanian).)

Inoceramus matotorus Wellman (1959, p. 155, pl. 10, fig. 1)

Not figured here

The holotype of this specimen displays a small part of the concave ligament area which carries shallow elongate-ovate to rectangular resilifers similar to those of *Inoceramus* sp. A illustrated in Plate 90, fig. 10. Approximately 2 mm between ridges, area 7 mm high. Ligament attached to outer shell layer.

Material. TM 2110, holotype, Y16/f7489, GS 1604. Distorted bivalved specimen; height ~ 220 mm. Lower part of Ihungia Stream, East Cape; M. Ongley, 1922. (Haumurian (Maastriichtian).)

Inoceramus opetius Wellman (1959, pp. 155–156, pl. 10, fig. 3)

Plate 90, figs. 6–8; text-fig. 4c

Weakly convex to weakly concave ligament area of variable form, parallel or inclined to plane of commissure. Resilifers monoserial, multilobate, or multiserial, probably no more than three rows of pits. Many columns of shallow resilifers, individual pits ovate or scooped where multiserial, otherwise formed into extended narrow troughs which are more or less lobate and separated by fine ridges which pinch and swell. Approximately 1 mm between ridge crests, area at least 8.5 mm high. Ligament attached to outer shell layer.

Material. TM 6707, V23/f16, GS 13069. Plate 90, fig. 7. Partly shelly LV; length ~ 80 mm, height ~ 107 mm. Castle Hill Station, Mangakuri River, southern Hawke's Bay; V23 419290; R. D. Black, 1981. Manganotanean–Teratan (Turonian–Santonian).

TM 6708, W22/f8504, GS 3225. Plate 90, fig. 6. Partly shelly incomplete RV. Approximately 3 km south of Waimarama, southern Hawke's Bay; J. D. H. Buchanan, 1983. (Teratan (Coniacian–Santonian).)

TM 6709, U25/f6462, GS 118. Plate 90, fig. 8. Isolated section of ligament area. Akitio River, eastern Wairarapa; J. Hector, J. D. Enys, A. McKay, 1873–1875. (Teratan (Coniacian–Santonian).)

TM 6791, P30/f6895, GS 9047. Text-fig. 4c. Thin section perpendicular to ligament area approximately half-way between umbo and posterior end of ligament area. Middle branch of Wharf Stream, approximately 1.2 km upstream from junction with south-east branch, Marlborough; P30 862170; W. D. M. Hall, 1962. (Teratan (Coniacian–Santonian).)

Inoceramus pacificus Woods (1917, p. 28, pl. 14, figs. 1-2)

Not figured here

A single specimen with a poorly preserved ligament area shows that the ligament attached to the outer shell layer.

Material. TM 6710, O29/f9863, GS 9355. Partly shelly internal mould RV. Ribble Stream, Awatere Valley, Marlborough; O29 612244; G. J. Lensen, 1964. Piripauan (Campanian).

Inoceramus rangatira Wellman (1959, p. 156, pl. 10, fig. 4)

Plate 90, figs. 4-5

This species differs from all those described thus far by possessing a thick umbonal septum. On the moderately inflated left valve the septum is slightly concave and parallel to, though depressed from, the plane of the ligament area, extending outwards > 27 mm. On the weakly inflated right valve, on the other hand, it is perpendicular to the area. Details of the resilifers are barely preserved on the specimens illustrated, and are, as yet, poorly known. Ligament attached to outer shell layer.

Material. TM 6711, O31/f9514, GS 6051. Plate 90, fig. 5. Umbo of LV. Long Creek, Hapuku River, Marlborough; O31 667782; H. E. Fyfe, 1935. Arowhanan (late Cenomanian).

TM 6712, as for above. Plate 90, fig. 4. Umbo of RV.

Inoceramus sp. A

Plate 90, fig. 11

Identified previously as *Inoceramus bicorrugatus* on the basis of its juvenile ornament and marked growth stop, this specimen has adult ornament and ligament area morphology very similar to *I. matotorus*. At present it cannot be referred to the latter with confidence.

Ligament area non-cylindrically concave, split into three longitudinal bands at ~ 40° to each other. Many relatively broad shallow elongate-ovate to rectangular resilifers which do not breach the ventral margin of the area, separated by low ridges which increase in height and width on the dorsalmost band of the area. Area pinches out close to umbo, and achieves a height of ~ 10 mm posteriorly, where the ridges are 2.5 mm apart. Ligament attached to outer shell layer.

Material. TM 6716, W22/f8504, GS 3225. Incomplete portion of LV. Location as for TM 6708 (*I. opetius*).

Inoceramus? sp. B

Plate 90, fig. 14

Known from isolated beaks with very distinctive ligament area, this taxon cannot at present be identified with any described species. Resilifers consist of ovate pits enclosed by raised box-like structures with sharp upstanding ridges on three or four sides. Areas between 'boxes' depressed and of varying widths. Resilifers carry transverse sculpture and decrease in size in one direction, from a width of 2.5 mm and a height of > 2.5 mm. Ligament attached to outer shell layer.

Material. TM 6717, Z14/f106, GS 13400. Distorted beaks and ligament areas. 400 m up south flowing tributary of Taurangakautuku Stream, East Cape; Z14 722725; I. G. Speden, 1979. Haumurian (Maastrichtian).

Inoceramus tawhanus Wellman (1959, pp. 156-157. Figured in Woods, 1917, pl. 4, fig. 1a, b)

Not figured here

From a single specimen with a poorly preserved section of the ligament area it would appear that the resilifers may alternate in size and strongly breach the ventral margin of the area. Ligament attached to outer shell layer.

Material. TM 6718, O29/f9630, GS 6534. Incomplete partly shelly LV. Near mouth of Limestone Creek, Awatere Valley, Marlborough; H. E. Fyfe, 1956. Ngaterian (late Albian-early Cenomanian).

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