Paläontologische Zeitschrift
2007, Vol. **81/3**, p. 267–282, 30-09-2007

The "*Inoceramus* limpet" *Gigantocapulus problematicus* (NAGAO & OTATUME, 1938) in New Zealand (Late Cretaceous Gastropoda or Monoplacophora, Gigantocapulidae n. fam.)

ALAN G. BEU, Lower Hutt

with 3 figures

BEU, A.G. 2007. The "*Inoceramus* limpet" *Gigantocapulus problematicus* (NAGAO & OTATUME, 1938) in New Zealand (Late Cretaceous Gastropoda or Monoplacophora, Gigantocapulidae n. fam.). – Paläontologische Zeitschrift **81** (3): 267–282, 3 figs., Stuttgart, 30. 9. 2007.

Abstract: Limpets up to at least 200 mm long occur widely in New Zealand early Haumurian (Campanian) rocks. Three specimens are in life position, attached to articulated specimens of *Isognomon*. The limpet has several unique characters – an apparently anterior marginal apex (all gastropod limpets have a central or posterior apex), an enormously thickened apical area, and a tongue-like projection, with a gape at each side, below the margin at the anterior – demonstrating that it belongs in *Gigantocapulus* HAYAMI & KANIE. The low shape, weak sculpture, and marginal apex indicate that it belongs in *G. problematicus* (NAGAO & OTATUME), previously reported only from Japan and Kamchatka. New Zealand material supports previous interpretations that the apex was anterior, and that *Gigantocapulus* was an epiparasite or, more probably, a filter feeder living sedentarily on bivalves. The shell is, uniquely, composed of calcite in multiple complex crossed-lamellar layers, very different from the aragonite shell with inner nacreous and outer prismatic layers of both early Palaeozoic and present-day tergomyans. Nevertheless, as the anterior(?) tongue-like projection, thickening and gapes closely resemble those of early Palaeozoic tergomyans, no other limpet-shaped molluscs are known with an anterior apex, and not all modern monoplacophorans are minute (*Neopilina* reaches at least 40 mm long), a position in Monoplacophora (= Tergomya) remains a possibility. However, *G. giganteus* (SCHMIDT) has a subcentral apex and is clearly cyclomyan rather than tergomyan. *Gigantocapulus* is probably a vanikoroidean gastropod, but could also be a tergomyan, a helcionelloidan, or a member of another, now extinct group of gastropods. Gigantocapulidae n. fam. is proposed.

Keywords: *Gigantocapulus* • Helcionelloida • Monoplacophora • Tergomya • Gastropoda • Late Cretaceous • Campanian • New Zealand

Kurzfassung: Napfschalen von bis zu 200 mm Länge sind in Neuseeland in Gesteinen des frühen Haumuriums (Campanium) weit verbreitet. Drei Exemplare befinden sich in Lebendstellung, angeheftet an artikulierten Exemplaren von *Isognomon*. Die Napfschalen haben mehrere einzigartige Merkmale – einen scheinbar anterioren randlichen Apex (alle Napfschnecken haben einen zentralen oder posterioren Apex), einen kräftig verdickten apikalen Bereich und einen zungenförmigen Vorsprung, mit seitlich klaffenden Öffnungen, unterhalb des Randes an der Vorderseite – die belegen, dass sie zu *Gigantocapulus* HAYAMI & KANIE gehören. Die flache Form, schwache Skulptur und der randliche Apex zeigen, dass die Schalen zu *G. problematicus* (NAGAO & OTATUME) gehören, welcher bisher nur von Japan und Kamtschatka bekannt war. Neuseeländisches Material bekräftigt bisherige Interpretationen, nach denen der Apex vorne liegt und dass *Gigantocapulus* ein Epiparasit oder, wahrscheinlicher, ein Filtrierer war, der sesshaft auf Muscheln lebte. Die Schale besteht, einzigartigerweise, aus mehreren kalzitischen komplexen Kreuzlamellen-Schichten und ist damit sehr verschieden von den aragonitischen Schalen mit innerer Perlmuttschicht und äußerer Prismenschicht, wie sie von frühpaläozoischen und rezenten Tergomya bekannt sind. Dennoch bleibt eine Position innerhalb der Monoplacophora (= Tergomya) möglich, da ein anteriorer(?) zungenartiger Vorsprung, Verdickung und seitliche Öffnungen den frühpaläozoischen Tergomya ähneln und nicht alle modernen Monoplacophoren winzig sind (*Neopilina* wird mindestens 40 mm lang). *Gigantocapulus giganteus* (SCHMIDT) hat jedoch einen subzentralen Apex und ist sicher cyclomyid und nicht tergomyid. *Gigantocapulus* ist möglicherweise eine vanikoroide Schnecke, könnte aber auch zu den Tergomya, den Helcionelloida oder einer ausgestorbenen Schneckengruppe gehören. Gigantocapulidae n. fam. wird aufgestellt.

Schlüsselwörter: *Gigantocapulus* • Helcionelloida • Monoplacophora • Tergomya • Gastropoda • Ober-Kreide • Campanium • Neuseeland

---

Address of the author: Alan G. Beu, GNS Science, PO Box 30368, Lower Hutt, New Zealand 5040; e-mail <a.beu@gns.cri.nz>

0031–0220/07/0081–267 $ 7.20

Introduction

Assessing the taxonomic position of limpet-shaped fossils has always presented problems, because the simple limpet shell shape has been adopted by a huge variety of gastropods, as well as most or all members of Class Monoplacophora (= Tergomya) (depending on whose definition of the class is followed). Characters allowing the distinction of shells of these diverse groups – muscle scars and apparent shell orientation, allowing assessment of whether the animal had undergone tortion, the defining character of Gastropoda – are subtle at best, and elusive for many fossils. Whether many of the early Palaeozoic limpets should be placed in Gastropoda or Monoplacophora remains uncertain as, indeed, does the taxonomic position of some of the relatively well known Palaeozoic "early gastropod" groups such as Helcionelloida and Bellerophontoidea. Some authors (particularly on Palaeozoic molluscs) prefer to adopt terms such as Tergomya rather than Monoplacophora, for definitely untorted endogastric molluscs similar to *Pilina* and *Neopilina*, to stress the distinction of the tergomyan condition (with the ring of muscle insertions dorsal to the shell apex; as distinct from all other cyclomyan molluscs, in which the shell muscle or ring of muscles encloses the apex) and the significance of Monoplacophora as a concept (HORNÝ 1965; WINGSTRAND 1985; PEEL 1991, PEEL & HORNÝ 1999). HARPER & ROLLINS (1982) discussed the distinction between Tergomya and Gastropoda carefully, following the inclusion of all untorted early limpet-like groups in Monoplacophora by RUNNEGAR & POJETA (1974), POJETA & RUNNEGAR (1976) and POJETA (1980). An excellent overview was provided by WAHLMAN (1992: 53–64), but the question of the distinction of gastropods from tergomyans remains uncertain (at least, among early Palaeozoic taxa) and is outside the scope of this paper. The present contribution just as inconclusively tries to arrive at a phylogenetic position for a large calcitic limpet that is moderately common in New Zealand Late Cretaceous rocks. The "*Inoceramus* limpet" (a vernacular name suggested by its consistent, intimate association with *Inoceramus* and/or *Isognomon* in both New Zealand and the North Pacific) has much in common with tergomyans, but characters suggesting this position are as confusing as the indicators of other possible positions.

Large limpets (simple, uncoiled, cap-shaped gastropods, or possibly tergomyans) are common at Haumuri Bluff, Marlborough, in the northern South Island of New Zealand (Fig. 1, locality 9). Specimens are 60–140 mm long, and incomplete shells represent specimens >200 mm long. They occur only in Tarapuhi Grit, within the original type section of the Haumurian New Zealand local stage (WARREN & SPEDEN 1978: 21). Piripauan and Haumurian stages of the Late Cretaceous have been revised substantially by CRAMPTON et al. (2000). Haumurian time occupies all of late Santonian to late Maastrichtian time (Late Cretaceous, 84.0–65.0 Ma) (CRAMPTON et al. 2000: fig. 12; CRAMPTON et al. in COOPER 2004: fig. 10.1); Tarapuhi Grit is Campanian. CRAMPTON et al. (2006: fig. 6; see also GSA data repository item 2006121, DR13) studied quantitative biostratigraphy of New Zealand Late Cretaceous rocks in greater detail to detect a eustatic signature, and constrained the age of Tarapuhi Grit to late early Campanian. Very similar limpets are widespread but less common in Haumurian rocks throughout central and northern New Zealand. The present paper describes morphological characters of the limpets, points out their taxonomic position in *Gigantocapulus* HAYAMI & KANIE, 1980, discusses their identification as *G. problematicus* (NAGAO & OTATUME, 1938) (previously recorded only from the North Pacific), and considers evidence for the orientation and higher classification of *Gigantocapulus*.

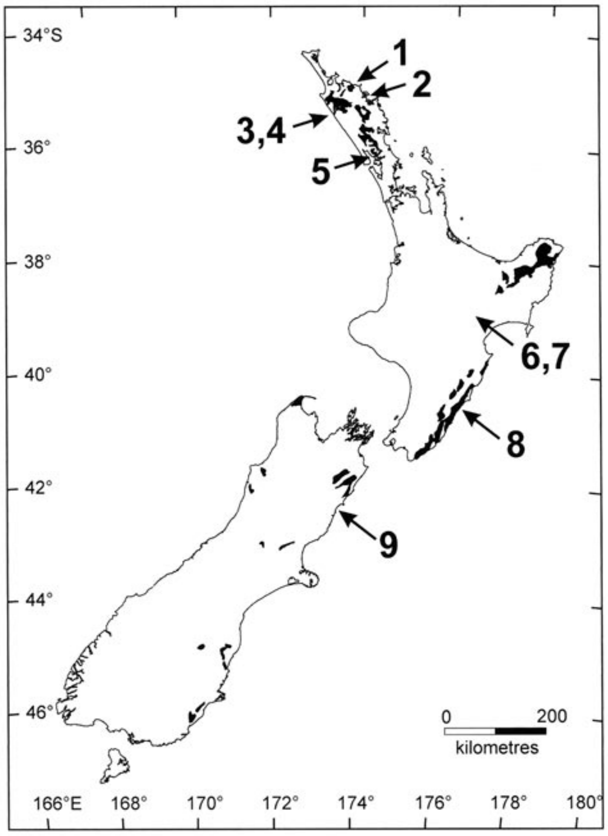


Fig. 1. Distribution of late Early and Late Cretaceous strata in New Zealand (from CRAMPTON 1996: fig. 2), showing localities for *Gigantocapulus problematicus* (numbered; see "Localities and material" in text). 1 = Whangaroa Harbour; 2 = Bay of Islands; 3, 4 = Hokianga Harbour; 5 = Kaipara Harbour; 6, 7 = Te Hoe River area, western Hawke's Bay; 8 = Mataikona River, E Wairarapa; 9 = Haumuri Bluff, Marlborough.

Age of *Gigantocapulus* localities

Evidence for the ages and correlation of New Zealand Cretaceous rocks is summarised by CRAMPTON et al. (in

COOPER 2004). Assembling the locality data and accompanying fossils (below) demonstrated that all records of *Gigantocapulus* in New Zealand are from early Haumurian rocks, and all belong in *G. problematicus*. At most localities *Gigantocapulus* is accompanied by the distinctive small oyster *Ostrea lapillicola* MARWICK, 1926 (10–20 mm long), regarded by WELLMAN (1959) as an index fossil of the Haumurian Stage, and at some localities *Gigantocapulus* is accompanied also by ammonites, belemnites, trigoniids, and diverse other taxa. Most *Gigantocapulus* specimens have also been collected with specimens identified as *Inoceramus*. The associated *Inoceramus* specimens traditionally have been identified as *I. matotorus* WELLMAN, 1959, and the few that are reasonably well preserved show the defining characters of *I. matotorus*: large size, wide shape, very weak inflation, and sculpture only of low, narrow, widely spaced comarginal ridges. CRAMPTON et al. (2000) and CRAMPTON et al. (in COOPER 2004) stressed that only very few, small Haumurian specimens can be identified confidently as *Inoceramus*, and then seem to belong in otherwise unknown species. Most of the large, flat, weakly sculptured specimens identified as *I. matotorus* do not have the hinge developed on the prismatic shell layer; this layer thins out below the hinge, indicating that the hinge is developed on the nacreous layer and this taxon most likely belongs in the Isognomonidae (J.S. CRAMPTON GNS, pers. comm.; CRAMPTON 1988, 1996: 53). However, at up to >600 mm long, they are far larger than most other taxa assigned there. It appears that an early Haumurian zone is recognisable at many localities in the North Island and in Marlborough, characterised by the occurrence of *Gigantocapulus problematicus*, *Ostrea lapillicola*, and the large, flat, prismatic shell traditionally identified as *Inoceramus matotorus*. CRAMPTON et al. (2000) and CRAMPTON et al. (in COOPER 2004) demonstrated a Campanian age for this zone. However, they emphasised that *Inoceramus* is not useful for biostratigraphy this high in the Cretaceous succession, and defined the base of the Haumurian Stage biostratigraphically by the lowest occurrence of the dinoflagellate *Nelsoniella aceras*. A new boundary stratotype for the Haumurian Stage was established in a section in Ben More Stream, Marlborough, by CRAMPTON et al. (2000).

Localities and material

Localities for the New Zealand material assigned to *Gigantocapulus problematicus* are shown on the accompanying map (Fig. 1), identified by the numbers listed below. The material is listed in order from north to south.

1. GNS Science collection number GS106, P04/f9494 (map sheet number in New Zealand Map Series 260, 1: 50 000, followed by individual locality number on that sheet in the New Zealand Fossil Record), N shore Whangaroa Harbour, E Northland, Haumurian New Zealand Stage; with ?*Inoceramus* sp., *Ostrea lapillicola*; 1 small *G. problematicus* (length (L) 38 mm).
2. GS728, P05/f9491, Waitangi River, opposite Waimate, Bay of Islands, E Northland, Haumurian; with ?*Inoceramus* sp., *O. lapillicola*; 1 small *G. problematicus* (L 38 mm), incomplete posterior end.
3. GS4905, O05/f9524, N side of the Narrows, Hokianga Harbour; Haumurian, with ?*Inoceramus* sp., *O. lapillicola*; 3 small, incomplete anterior ends of *G. problematicus*.
4. GS5356, O06/f7574, Ngamahanga Point, N side Hokianga Harbour, W Northland; Haumurian, with abundant *O. lapillicola*; 3 very small, incomplete *G. problematicus* (L 33, 37 mm).
5. GS734, Q08/f9011, Paparoa River, Kaipara Harbour, W Northland; Haumurian, with ?*Inoceramus* sp., *O. lapillicola*; 1 small *G. problematicus* internal mould (L 45 mm).
6. Mangahouanga Stream, Te Hoe River area, W Hawke's Bay; float boulders in stream, with terrestrial reptiles reported by J. WIFFEN and co-authors (see faunal list including reptiles, with references, in CRAMPTON & MOORE 1990: appendix): GS11359, V19/f6909, 1 almost complete internal mould of *G. problematicus* (L 68 mm), 1 complete internal and external mould (L 70 mm), exterior densely covered with *O. lapillicola* (Fig. 3F); and 1 large incomplete interior of a shell and its mould (L 138 mm, originally >160 mm); GS14267, V19/f181a, 3 small incomplete *G. problematicus* (largest L 59 mm).
7. GS8207, V19/f6649, Hook Stream, Te Hoe River, W Hawke's Bay, Haumurian; with ?*Inoceramus* sp., *O. lapillicola*; 1 very small (L >40 mm), poorly preserved *G. problematicus*, resembling those from Mangahouanga Stream.
8. GS8930, U25/F6613, Mataikona River ca. 11 km N of mouth, E Wairarapa district, Haumurian; with ?*Inoceramus* sp., *O. lapillicola*; 1 anterior tongue-like projection from *G. problematicus*.
9. Tarapuhi Grit, (Haumurian), Haumuri Bluff, Marlborough: GS13 (incorporating GS8, GS9), O32/f9506, mixed collection from Haumuri Bluff, Marlborough; with ?*Inoceramus* sp., *O. lapillicola*; 6 *G. problematicus*, all poor internal moulds (L 46, 51, 59, 70, 96, & 137 mm); GS6173, O32/f9506, with ?*Inoceramus* sp., *O. lapillicola*; 4 *G. problematicus*, ranging from complete shells to incomplete internal moulds (Figs. 3C, E) (L 67, >81, and >124 mm), the last originally ca. 180 mm, attached to ?*Inoceramus*; GS9835 & GS9836, O32/f9530, f9533, with ?*Inoceramus* sp., O. *lapillicola*; 1 *G. problematicus*, partial shell interior, 4 fragmentary anterior tongues, 1 complete shell (L 66 mm; Figs. 3A, D); GS10399, O32/f8849, with *O. lapillicola*; 1 fragmentary *G. problematicus*, apparently formerly attached to articulated ?*Inoceramus* with 1 cm-thick prismatic shell; GS14694, O32/f107, 1 large *G. problematicus* (incomplete, L 136 mm, originally >200 mm) attached to incomplete articulated ?*Isognomon* (Figs. 2A, D, 3H); GS15305, O32/f235, 3 *G. problematicus*; 1 anterior tongue fragment, 2 incomplete moulds (L 85, >105 mm).

Systematic palaeontology

Phylum Mollusca
?Class Gastropoda
?Superfamily Vanikoroidea GRAY, 1840

Family Gigantocapulidae n. fam.

Type genus: *Gigantocapulus* HAYAMI & KANIE, 1980.

Definition: A family of large to extremely large Mesozoic limpets with an elongate-oval shell, up to >400 mm long, apparently enveloping the entire animal. The shell is composed of calcite, apparently in multiple complex crossed-lamellar layers. The shell apex is apparently weakly to strongly anterior (although it could be interpreted as posterior), and is interpreted as located at the anterior(?) margin in the youngest species (*Gigantocapulus problematicus* (NAGAO & OTATUME, 1938), Campanian – early Maastrichtian), but subcentral to mid-anterior(?) in older species, i.e. cyclomyan. The external appearance of *G. problematicus* is very similar to that of the Cambrian monoplacophoran *Pilina unguis* (LINDSTRÖM, 1880) and the simplest Recent monoplacophorans such as *Vema occidua* MARSHALL (2006: 62, figs. 1C, G–I). The shell apex and anterior(?) slope are greatly thickened (14 mm thick in a total length of ca. 100 mm in *G. problematicus*); the shell is otherwise very thin for its size (ca. 1 mm thick). A tongue of shell protrudes at the anterior(?) margin, apparently protecting the head; the smooth edges of the retracted shell margin on each side of the tongue form gapes between the shell and the substrate where organs apparently were protruded, or water currents passed into the resting shell. The one possible muscle scar observed appears to be a continuous ring, although it is very vague at the anterior(?) end where the shell is greatly thickened. Specimens found in life position attached to one valve of an articulated pterioidean bivalve (Inoceramidae or *Isognomon*) apparently were either epiparasitic, feeding by intercepting the host's food or, more probably, were sedentary filter feeders.

Remarks: The unique characters of the large size, the calcitic composition, the hugely thickened shell apex, the tongue projecting at the mid-anterior shell margin, with a smooth, gaping, up-turned shell edge on each side of the tongue, and the possibly anterior position of both the apex and the tongue in *Gigantocapulus* demonstrate that a phylogenetic relationship between *Gigantocapulus* and *Capulus* MONTFORT, 1810 is unlikely. The new family Gigantocapulidae is therefore established here for the single genus *Gigantocapulus*, and tentatively referred to superfamily Vanikoroidea near the Hipponicidae. However, there is little evidence for its relationships; the taxonomic position is discussed further below. It is suggested below that at least *Brunonia grandis* MÜLLER, 1898 and *Deslongchampsia* MORRIS & LYCETT, 1851 are earlier Mesozoic members of the family.

DIENI (1990) reported the carinariid "*Brunonia*" *annulata* (YOKOYAMA, 1890) (referred to the Carinariidae by KASE 1988) from the Early Cretaceous of Sardinia, and proposed a subfamily Brunoniinae for it (retained in Carinariidae by BOUCHET et al. 2005: 251). However, this species is not the type species of *Brunonia* MÜLLER, 1898; the type species is *B. grandis* (COX & KNIGHT 1960: I237, figs. I51.1a, b) and in my opinion *B. grandis* is likely to be related to *Gigantocapulus*. Indeed, *Gigantocapulus* is possibly a synonym of *Brunonia*. If *B. grandis* is a gigantocapulid, the name Brunoniidae DIENI, 1990 would be an earlier name for Gigantocapulidae. The orientation and shell thickness of *B. grandis* require investigation for the taxonomy and nomenclature to be clarified, but HAYAMI & KANIE (1980: 692) stated that MÜLLER's original material of *B. grandis* is "said to have been lost".

Genus *Gigantocapulus* HAYAMI & KANIE, 1980

* 1980 *Gigantocapulus* HAYAMI & KANIE: 689.

Type species (by original designation): *Helcion giganteus* SCHMIDT, 1873, Campanian, North Pacific region.

Remarks: The association of giant limpets, up to >400 mm long, with large inoceramid bivalves in the North Pacific region has been known since the description by SCHMIDT (1873). KANIE (1975, 1977) reviewed and illustrated the five limpet species recorded from Late Cretaceous rocks of Japan and Sakhalin, and referred them to *Anisomyon* MEEK & HAYDEN, 1860. SOHL (1967: B36, fig. 10, pls. 8–11) showed that *Anisomyon* belongs in the pulmonate limpet family Siphonariidae, and has relatively small, tall, weakly sculptured or smooth shells with a lateral gap in the muscle scar, and most species have a radial ridge (termed the carination by SOHL) at the point of the muscle scar gap, forming the "siphon" to the lung. Most of the North Pacific limpets reviewed by KANIE (1975, 1977) clearly do not belong in *Anisomyon*, any more than the New Zealand records discussed here do. HAYAMI & KANIE (1980) assembled records of giant Cretaceous limpets from many localities in the North Pacific, and proposed the genus *Gigantocapulus* (records listed from northern and southern Sakhalin; Kamchatka; southern Alaska; British Colombia; Abeshinai, Hetonai, Urakawa and other localities in Hokkaido, northern Japan; and Matsuyama City in Shikoku, southern Japan). However, they included only *G. giganteus* expressly in *Gigantocapulus*, leaving the taxonomic position of other North Pacific Cretaceous limpets uncertain, although they suggested that *G. giganteus* possibly was derived from "*G.*" *cassidarius* (YOKOYAMA, 1890) (HAYAMI & KANIE 1980: 692).

Of the limpets included in *Anisomyon* by KANIE (1975, 1977), only *Gigantocapulus giganteus* and "*Anisomyon*" *problematicus* are referable to *Gigantocapulus*. HAYAMI & KANIE (1980: 690) pointed out the central to posterior apex and the presence of an internal septum (columella modified into a shelf) in "*Anisomyon*" *transformis* DUNDO in DUNDO & EFREMOVA, 1974, demonstrating that it belongs in superfamily Calyptraeoidea. KASE (1988) reinterpreted "*Anisomyon*" (or *Brunonia*) *annulata* (YOKOYAMA, 1890) as a carinariid heteropod (superfamily Pterotracheoidea), an apparently reasonable position based on its exceedingly thin shell of uniform thickness, its comarginal annulations, and its single prominent radial carina (which is anterior in present-day *Carinaria* species). The remaining species, *Anisomyon cassidarius*, has a much smaller, taller, narrower, more weakly sculptured and more nearly circular shell than the other species considered by KANIE (1975), and appears to be correctly referred to *Anisomyon*. The anterior position of the apex of *Gigantocapulus*, if correctly interpreted, is unknown among gastropods, as all limpets that are definitely referable to the Gastropoda (COX & KNIGHT 1960) have a central to posterior apex, so the position in Capuloidea suggested by HAYAMI & KANIE (1980) apparently is incorrect. This point is considered further below.

Unfortunately, none of the material I have seen or that has been illustrated previously provides any indication of protoconch characters or orientation, or of definite internal muscle impressions, characters that are critical to establish the taxonomic position. KANIE (1975: fig. 2) illustrated muscle scars of Japanese specimens of *Anisomyon cassidarius* and "*A.*" *transformis*, but not of species referred here to *Gigantocapulus*. The interior of one New Zealand specimen (Fig. 3G) suggests that, if any muscle insertion is recorded, it was a complete but very shallowly impressed ring. If this is correct it probably rules out a position in Monoplacophora, although some early Palaeozoic taxa have the muscle scars very weakly impressed or in the form of a nearly complete ring (PEEL 1991; PEEL & HORNÝ 1999) and this character is little more significant than any other. It also seems equally possible that this comarginal impression reflects a fold in the shell wall rather than a muscle impression (e.g., as in the undoubted early Palaeozoic tergomyan *Pilina cheyennica* PEEL (1977: fig. 2)). WARÉN (1988), WARÉN & GOFAS (1996) and MARSHALL (2006), among others, have illustrated the minute cap-shaped apex (not certainly the larval shell; WARÉN 1988: 677) that characterises Recent Monoplacophora, unlike the coiled protoconch present in gastropods, so unusually well-preserved and, probably, very juvenile specimens will be required to determine the phylogenetic relationships from the apex of these fossils. B.A. MARSHALL (Museum of New Zealand Te papa Tongarewa, pers. comm.) pointed out that the small juvenile shell, up to about 10 mm in diameter, surrounding the apex in small complete specimens of *G. problematicus* (Figs. 3A, C) appears to have been circular, with a central apex, and the posterior (or possibly anterior) part of the shell grew allometrically during ontogeny. The spiral protoconch, resembling that of gastropods, illustrated for *Neopilina galatheae* by LEMCHE (1957: fig. 2) apparently is incorrect.

Another consideration of importance for the phylogenetic position of *Gigantocapulus* is shell structure and composition. An obvious connotation of the preservation in numerous late Cretaceous faunas with only oysters and the calcitic prismatic layer of pterioidean bivalves is that these limpets are composed of calcite. Microscopic examination of broken edges and the thick face of broken shell (Fig. 2E) indicated that the shell structure is complex crossed-lamellar calcite in all layers, with a uniform thin outer layer passing over the entire shell, and numerous parallel layers within the highly thickened anterior end. This is very different from the shell structure reported for all Recent monoplacophorans, which have a thin inner shell layer of nacreous aragonite, and a thicker outer layer of prismatic aragonite, in short, relatively thick prisms with their crystal axes normal to the shell surface (e.g. SCHMIDT 1959; MEENAKSHI et al. 1970; BOUCHET et al. 1983: pl. 1 fig. 5; WARÉN & BOUCHET 1990: figs. 4, 5; WARÉN & GOFAS 1996: figs. 13E, F). Some Cambrian monoplacophorans are reported to have had the same shell structure, based on SEM examination of moulds (RUNNEGAR 1985; KOUCHINSKY 2000), although KOUCHINSKY (2000: 138) reported a three-layered shell in both *Pilina unguis* and *Tryblidium reticulatum* LINDSTRÖM, 1880, with a thin outermost prismatic layer, a thick middle nacreous layer, and a thin innermost layer of fine lamellae without visible subunits. RUNNEGAR (1985) interpreted some shells of early Palaeozoic monoplacophorans and gastropods as calcitic rather than aragonitic, based on crystallography, although most seem to have been originally aragonitic. In contrast, limpet-shaped gastropods of the Patellogastropoda lack a nacreous inner shell layer, and their shells are composed of complex sequences of layers of aragonite and calcite arranged in prismatic, crossed-lamellar and fibrillar structures (MACCLINTOCK 1967), although the mineralogy of layers is not always clear in MACCLINTOCK's descriptions. In the present state of preservation of the *Gigantocapulus* shells the inner nacreous layer would not be expected to be preserved. It is not clear what recrystallisation of the prismatic outer layer would produce, but it seems likely that the prismatic structure would remain if the shells had been prismatic, as the prismatic calcite inner layer of their bivalve hosts is well preserved at almost all localities. As other aragonitic shells and the outer aragonitic layer of *Inoceramus* and *Isognomon* shells have been completely removed at most *Gigantocapulus* localities, and aragonitic shells have been replaced with coarse, sparry calcite at the few localities where they occur, it is very likely that *Gigantocapulus* was originally calcitic. Shell structure is as unusual as everything else about *Gigantocapulus*, but does not support a position in Monoplacophora.

The only other taxon I am aware of that is probably assignable to *Gigantocapulus* is *Helcion giganteus vancouverensis* WHITEAVES, 1903 from British Columbia (WHITEAVES 1903: 370, pl. 51 fig. 1), although the holotype is unusually equidimensional and has much of the exterior strongly abraded, so its position is uncertain. At about 100 mm in diameter it is also small for *G. giganteus*, suggesting that it is a distinct species. WHITEAVES (1903: 371) suggested that *Capulus corrugatus* WHITEAVES (1903: 364–365, pl. 45 figs. 2, 2a) might be based on juvenile specimens of the same taxon, and that certainly appears feasible – although WHITEAVES' (1903: pl. 45 fig. 2a) lateral view indicates that the apex lies at the posterior third, and is directed towards the anterior in *C. corrugatus*, an interesting orientation demonstrating that, if WHITEAVES was correct in associating these species, *Gigantocapulus* has an initially central apex that later becomes posterior – a cyclomyan gastropod condition (PEEL 1991: 20). Late Maastrichtian capulids(?) illustrated from the eastern USA by SOHL (1960: 92–95, pl. 10 figs. 1–4, 8–16) are all small and relatively simple, with posterior apices, and are probably correctly referred to either the Capulidae or the Hipponicidae despite some having prominent radial sculpture (*Capulus monroei* SOHL, 1960, *C. corrugatus* WADE, 1926, *C. cuthandensis* STEPHENSON, 1941, *Thylacus cretaceus* CONRAD, 1860).

DIENI (1990) reconsidered the synonymy and relationships of the probable carinariid he called *Brunonia annulata* (YOKOYAMA, 1890); his chresonomy lists 20 earlier references under the genera *Scurria, Acmaea, Capulus, Brunonia, Anisomyon* and *Palaelophacmaea*, from localities in Germany, Switzerland, Japan, and several areas of Russia; he recorded it newly from Sardinia. DIENI (1990) also reviewed the taxonomic history of limpets of this type, pointing out that the genus *Rhytidopilus* COSSMANN, 1895 was classified in Acroriidae, alongside the Siphonariidae, by COSSMANN (1895), COSSMANN (1901: 250) considered *Brunonia* MÜLLER, 1898 to be a synonym of *Rhytidopilus*, KANIE (1975, 1977) and HAYAMI & KANIE (1977) referred *B. annulata* to *Anisomyon* and/or "*Capulus*", KANIE (1983) and STANLEY & KANIE (1985) referred it to the chondrophorine hydrozoan genus *Palaelophacmaea*, related to *Porpita* and *Velella*, and KASE (1988) referred it to the Carinariidae. It seems likely to me that two groups require distinguishing. Those with a very thin shell of uniform thickness (including "*Brunonia*" *annulata* and *Rhytidopilus*) apparently belong in the Carinariidae, whereas those with a larger, thicker shell with an anterior(?) apex and a tongue-like anterior projection (Gigantocapulidae) probably belong in either Tergomya (that is, the class usually known as Monoplacophora) or more probably, an extinct group of gastropods. These fossils will need careful reassessment to determine which is which.

Gigantocapulus problematicus (NAGAO & OTATUME, 1938)

Figs. 2A–E, 3A–H

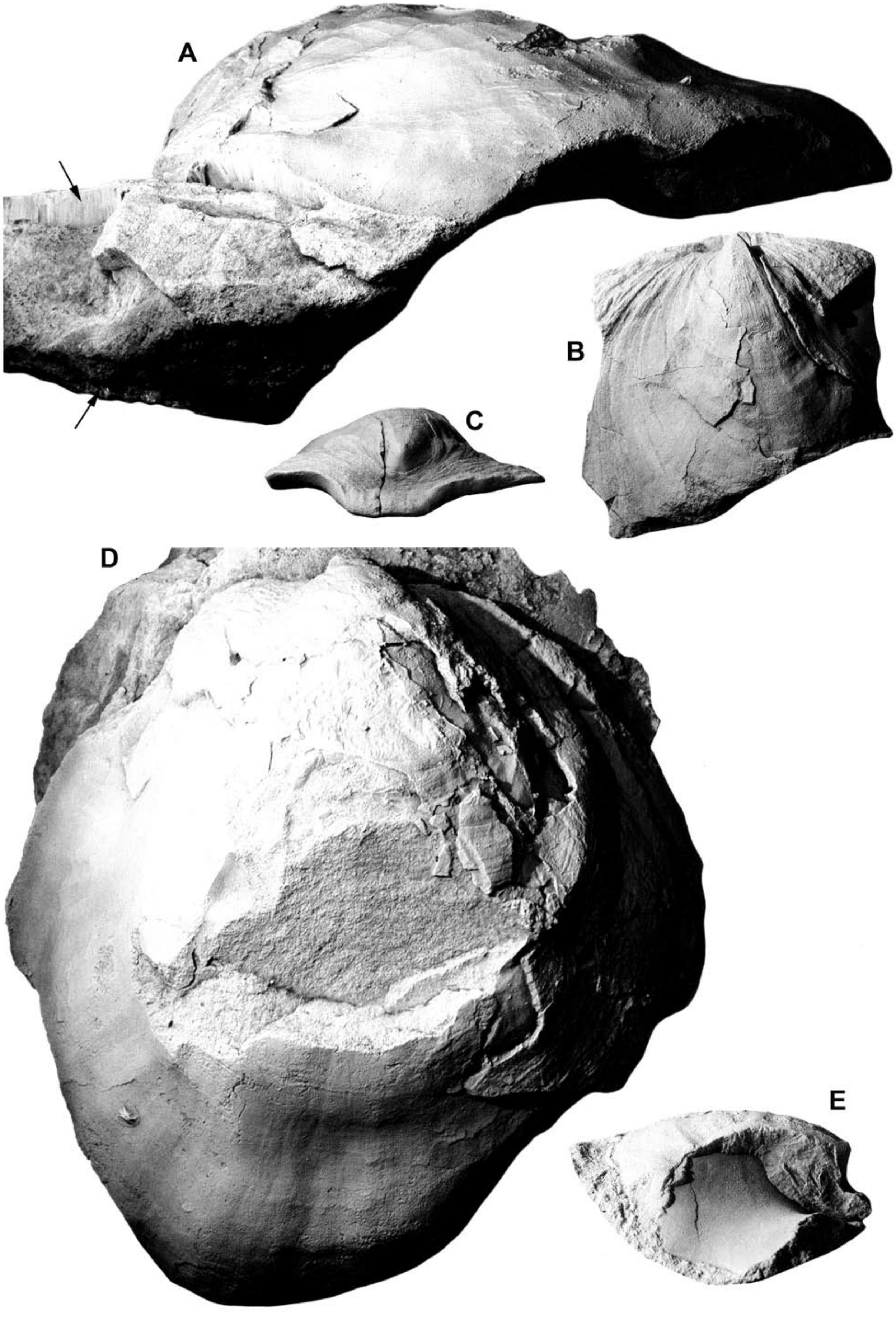
* 1938 *Helcion*? *problematicus* NAGAO & OTATUME: 51, pl. 4 figs. 1, 1a, 2.
1959 N. gen. ?aff. *Tryblidium* WELLMAN: 139.
1974 *Anisomyon korjakensis* DUNDO in DUNDO & EFREMOVA: 18, pl. 11 fig. 1, pl. 12 fig. 2.
1975 *Anisomyon problematicus* (NAGAO & OTATUME, 1938). – KANIE: 26, pl. 19, figs. 1, 2, pl. 20 fig. 1.
1977 *Anisomyon problematicus* (NAGAO & OTATUME, 1938). – KANIE: 58, pl. 2 fig. 6.
1977 "*Capulus*" *problematicus* (NAGAO & OTATUME, 1938). – HAYAMI & KANIE: 56.
1978 *Anisomyon*? sp. – WARREN & SPEDEN: 40, 50, tab. 5, fig. 24.4.
1990 *Gigantocapulus* n. sp.? CRAMPTON & MOORE: 341, 347, app. 1.

Type material (not seen): *Helcion*? *problematicus*, holotype University of Hokkaido no. UH5992 (NAGAO & OTATUME 1938: 51, pl. 4 figs. 1, 1a); from lower sandy shale of Hakobuti Sandstone (early Maastrichtian) in the Hetonai area, Hokkaido, Japan; paratype UH5993, from the same member at Sososhizawa, Naka-hobetsu area, Hokkaido. *Anisomyon korjakensis*, type material presumably in Research Institute of Arctic Geology, St Petersburg; from the Lower Gangutskaya Subsuite in the northeastern Koryak Highlands and the lower and middle Impenvemskaya Subsuite in the central Koryak Highlands, Kamchatka. DUNDO & EFREMOVA (1974) did not identify type specimens.

Other records: KANIE (1975: 27) recorded a specimen of *Gigantocapulus problematicus* from the Minato Shale, Izumi Group, Awaji Island, southwestern Japan, and 3 specimens from the lower sandy siltstone (early Maastrichtian) of the Hetonai district, Hokkaido. DUNDO & EFREMOVA (1974) recorded material (as *Anisomyon korjakensis* DUNDO) from two localities in the Koryak Highlands, Kamchatka, eastern Russia; this name was synonymised with *G. problematicus* by KANIE (1975: 27). New Zealand material examined is listed above; it has long been labelled "?*Tryblidium*" (a name applying to early Palaeozoic Monoplacophora; KNIGHT & YOCHELSON 1960: I78, fig. 46.8) or "?*Anisomyon*" in GNS collections. WARREN & SPEDEN (1978: 40, 50, tab. 5, fig. 24.4) recorded and illustrated specimens from Tarapuhi Grit at Haumuri Bluff, as "*Anisomyon*?", and CRAMPTON & MOORE (1990) recorded material as "*Gigantocapulus* n. sp. ?" from Maungataniwha Sandstone (Piripauan – Haumurian) at Mangahouanga Stream, western Hawke's Bay, in a full faunal list from this formation.

Distribution: *Gigantocapulus problematicus* occurs in Late Cretaceous (Campanian – early Maastrichtian) rocks in Kamchatka and throughout Japan, as well as in Campanian rocks throughout central and northern New Zealand. This distribution implies a former near-continuous distribution between New Zealand and the North Pacific, or possibly dispersal as planktotrophic larvae.

Fig. 2. *Gigantocapulus problematicus* (NAGAO & OTATUME), Tarapuhi Grit, Haumuri Bluff, Marlborough, New Zealand, early Haumurian (Campanian) (locality 9), at natural size. **A, D**: GS14694, O32/f107, large specimen (length 137 mm, est. originally >200 mm) attached to articulated ?*Isognomon* specimen; left lateral view (**A**) showing parts of two prismatic valves of host (arrowed), and dorsal view (**D**) (see Fig. 3H for anterior view). **B, C, E**: GS6173, O32/f9506, incomplete specimen broken through shell apex, present width 57 mm; **B.** dorsal view with broken shell in place; **C.** anterior view showing upturned edges of shell on each side of anterior(?) tongue; **E.** right lateral view with right apical shell area removed, to show greatly thickened apex and anterior(?) slope.


A
B
C
D
E

NAGAO & OTATUME (1938: 41, pl. 1 figs. 12–14) recorded a moderately large "*Pedalion*" (= *Isognomon*) species from the type formation of *Gigantocapulus problematicus*, suggesting that it might live on *Isognomon* shells in the North Pacific as well as in New Zealand.

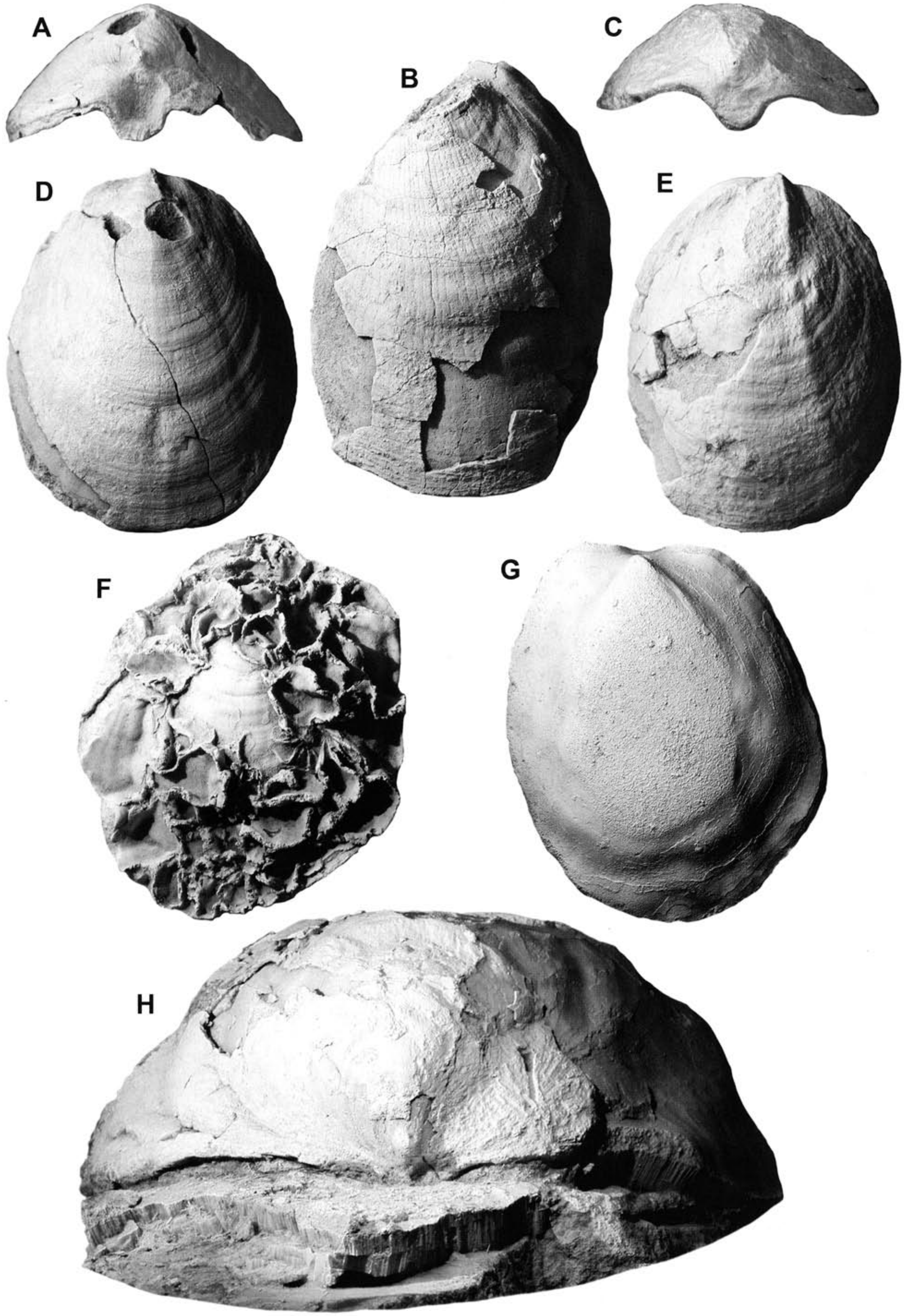
Remarks: Some of the New Zealand material referred here to *Gigantocapulus problematicus* is better preserved than the North Pacific material illustrated by KANIE (1975), and allows the recognition of characters in common with the type species, *Gigantocapulus giganteus* (SCHMIDT, 1873). In particular, the shell apex is marginal and a thickened, tongue-shaped projection immediately below the apex in all the better-preserved New Zealand specimens (Figs. 2C, 3A, C, H) is wider and has more clearly defined lateral edges than in *G. giganteus*, in which it is evenly semicircular in outline (HAYAMI & KANIE 1980: text-figs. 2a–c, 3). The distinctive tongue-like projection of *G. problematicus* resembles the operculum of *Neritopsis* (WENZ 1938: 412, figs. 1000, 1001; KAIM & SZTAJNER 2005) when the tongues are found as isolated, resistant shell fragments at some New Zealand Late Cretaceous localities. The only obvious possible function of the tongue-like projection seems to be to protect the animal while intercepting its *Inoceramus* or *Isognomon* host's food. This indicates that, as pointed out for *G. giganteus* by HAYAMI & KANIE (1980), the tongue and its associated shell apex apparently are anterior. *G. problematicus* therefore shares the most distinctive character of *Gigantocapulus* with *G. giganteus*, and clearly should be referred to *Gigantocapulus*.

A further highly distinctive character of *Gigantocapulus,* not reported previously, is the greatly thickened shell apex. The main, posterior (or possibly anterior?) area of the shell, behind the apex, is little more than 1 mm thick in most New Zealand specimens, but even relatively small specimens have a grossly thickened internal shell layer inside the apex, thinning towards the anterior projection where, however, it remains relatively thick. In a specimen estimated to have been 100 mm long, the shell at the apex is 14 mm thick, tapering off within 30 mm posterior to the exterior shell apex (but only 15 mm behind the apex on the internal mould) to be 1 mm thick, and tapering anteriorly to a tongue-like projection 5 mm thick (Fig. 2E). In the illustrated specimen (Figs. 2A, D, 3H) attached to an incomplete, articulated prismatic bivalve shell, the posterior (anterior?) main shell area is 1.5 mm thick in a shell estimated originally to have been at least 200 mm long, and it is <2 mm thick in the thickest specimen seen. The strongly thickened area splays out laterally from beneath the apex towards the anterior lateral extremities, producing a bilobed, concave depression in the anterior (posterior?) end of the internal mould (Fig. 3G), and complicates attempts to interpret possible muscle impressions. The shell interior at the margin on each side of the projecting tongue curves smoothly outwards, forming an obvious space for 20–40 mm on each side of the tongue where either bilaterally symmetrical organs were protruded under the shell edge by the living animal or water currents entered or left the mantle cavity, but this smooth, out-turned edge does not occur elsewhere around the shell margin. The only possible function I am aware of for the greatly thickened shell apex can have been to protect the otherwise thin *Gigantocapulus* shell from damage by abrasion as it protruded near the margin of the host shell. The protection seems likely to have been necessary because the limpet protruded its head and/or anterior feeding organ(s) over the edge of the host's shell, to draw in water or to feed inside the host on food gathered on its gills.

The smaller specimens attributed to *Gigantocapulus problematicus*, up to 70 mm long, have a narrower anterior(?) shell tongue than the larger specimens, and the tongue projects downwards rather than anteriorly. In several small, complete specimens it also forms a shallowly concave depression extending from the apex to the margin, similar to that illustrated for *Deslongchampsia appendiculata* (EUDES-DESLONGCHAMPS, 1842) (Jurassic, Europe) by COX & KNIGHT (1960: I233, figs. I145.2a–c). The anterior(?) tongue is definitely wider, thicker, more quadrate in outline, projecting forwards, and located much more closely below the apex in larger specimens. This suggests that two taxa are involved, but as the material comprises one size range, it is more probable that the limpet changed its habitat subtly after it reached a length of about 70 mm. As pointed out below, smaller specimens are also more weakly sculptured than larger ones, again suggesting the possibility of a habitat

---

Fig. 3. *Gigantocapulus problematicus* (NAGAO & OTATUME), New Zealand, early Haumurian (Campanian), at natural size. **A, D**: GS9835, O32/f9530, Tarapuhi Grit, Haumuri Bluff (locality 9), anterior(?) (**A**) and dorsal (**D**) views of small complete specimen with weak comarginal sculpture and a vertical, concave anterior(?) tongue; length 67 mm. **B**: GS6173, O32/f9506, Tarapuhi Grit, Haumuri Bluff, Marlborough (locality 9), dorsal view of incomplete specimen with sculpture of fine radial grooves; length 81 mm. **C, E**: TM5385, GS6173, O32/f9506, Tarapuhi Grit, Haumuri Bluff (locality 9), anterior(?) (**C**) and dorsal (**E**) views of another small complete specimen with weak comarginal sculpture, one prominent radial ridge, and a vertical, concave anterior(?) tongue; length 66 mm. **F, G**: GS14267, V19/f191a, Maungataniwha Sandstone, Mangahouanga Stream, Te Hoe River, western Hawke's Bay (locality 6); **F**. dorsal view of latex cast of mould of exterior showing weak comarginal sculpture, and many attached specimens of *Ostrea lapillicola* MARWICK; **G**. dorsal view of complete internal mould, possibly showing weakly impressed, apparently continuous muscle scar, and mould of thickened anterior(?) area and tongue; length 70 mm. **H**. Anterior(?) view of specimen in Figs. 2A, D, showing shell tongue pressed into host shell, with gapes on each side of tongue.


A
B
C
D
E
F
G
H

shift during ontogeny. Better understanding of these differences requires the collection of more specimens in life position.

The New Zealand material has several characters that distinguish it from *Gigantocapulus giganteus*. The shape is very low and wide, with height (H) about 13–20 % of length (L) (L estimated 200 mm, H 42 mm, = 21 %; L 105 mm, H 14 mm, = 13.3 %; L 70 mm, H 10 mm, = 14.3 %) and the highest point of the shell lies well behind (in front of?) the apex. In contrast, height ranges from about 40 % (in HAYAMI & KANIE 1980: pl. 87 fig. 2) to almost 100 % of length in *G. giganteus*, and the apex ranges from a little behind the anterior to almost central; it is also at the highest point in many tall specimens. The sculpture of New Zealand specimens is weak, with only very narrow, low, closely spaced radial grooves on some specimens (Fig. 3B), one to a few, weak, widely spaced radial ridges on others (Fig. 3E), and weak to moderately prominent comarginal folds on still others (Fig. 2D). Some of the best-preserved larger (incomplete) specimens have both moderately prominent comarginal folds and fine, closely spaced radial grooves and ridges, but comarginal folds are mostly limited to large specimens. In contrast, *G. giganteus* has very prominent radial and comarginal ridges and furrows. The reconstruction of a specimen of *G. giganteus* living on *Sphenoceramus schmidti* (MICHAEL, 1899) by HAYAMI & KANIE (1980: text-fig. 3) suggests that the prominence of sculpture in *Gigantocapulus* is a function of the substrate, that is, the sculpture is a xenomorphic copy of the host's sculpture. This is also indicated by ZONOVA's (1985) description of "coquinas" of *Inoceramus* and *G. giganteus* in the Krasnoyarsk River section, Sakhalin, in which the sculpture of the two taxa varies in close parallel as a result of unexplained "environmental changes". ZONOVA obviously did not realise that the limpets were living on the inoceramids, and copying their host's sculpture. If the prominence of sculpture in *Gigantocapulus* reflects that of the host, the New Zealand specimens seem to have lived on at least two different bivalves: most smaller specimens mainly on a finely sculptured bivalve, with sculpture of low comarginal ridges (apparently the species usually identified as *I. matotorus*) and most of the larger specimens on a more strongly comarginally folded bivalve. However, it is also conceivable that the one bivalve host developed comarginal folds as it grew, so that the xenomorphic sculpture of the *Gigantocapulus* specimens changed during ontogeny. It is clear, though, that no New Zealand *Gigantocapulus* specimens have very prominent, closely spaced comarginal folds resulting from living on prominently sculptured Piripauan (late Coniacian – Santonian) *Inoceramus* species such as *I. pacificus* WOODS, 1917 or *I. australis* WOODS, 1917 (CRAMPTON 1996: pls. 9–11); New Zealand specimens are all Haumurian (Campanian).

The final distinctive character is the strongly anterior (posterior?) position of the shell apex, hanging over the anterior(?) end of the shell in most specimens, or at the anterior(?) margin, hanging above the tongue-like projection, in the largest ones (Figs. 2A, D, 3H). In *Gigantocapulus giganteus* the shell apex ranges from slightly to well behind the anterior(?) margin, and is nearly central in some specimens. The distinctive characters of the New Zealand material are shared with the material of *G. problematicus* illustrated by NAGAO & OTATUME (1938: pl. 4 figs. 1, 1a; holotype) and KANIE (1975: pl. 19 figs. 1, 2, pl. 20 fig. 1; 1977: pl. 2 fig. 6). The unique anterior(?) end is clearly shown in these figures of North Pacific material; the internal mould of the greatly thickened anterior(?) shows clearly in KANIE's (1975: pl. 20 fig. 1) illustration. It therefore seems inescapable that the New Zealand material should be referred to *G. problematicus*, previously reported only from the North Pacific.

Mode of life

HAYAMI & KANIE (1980) reported specimens of *Gigantocapulus* in life position attached to articulated shells of Inoceramidae. They suggested a position in Capulidae for the limpets, based on this mode of life, and their assumption that, like capulids, *Gigantocapulus* fed by intercepting its host's food. CRAMPTON & MOORE (1990: 341) commented on collections containing *Gigantocapulus* in Maungataniwha Sandstone at Mangahouanga Stream, inland Hawke's Bay (Haumurian New Zealand Stage): "*Ostrea lapillicola* and *Gigantocapulus* sp. are always found with *Inoceramus* in collections typically containing abundant limids (*Pseudolimea* and *Limatula*) ... The gigantic epifaunal *Inoceramus matotorus* provided a host for the symbiotic *Gigantocapulus* (HAYAMI & KANIE, 1980), and both species provided substrates for *Ostrea* and probably also the limids (collections from V19/f6909 include a specimen of *Gigantocapulus* with *Ostrea* densely clustered on the shell exterior)" (Fig. 3F) (but note that J.S. CRAMPTON (GNS pers. comm. Sept. 2006; CRAMPTON 1996: 53) now interprets these large, flat, prismatic bivalves, lacking a hinge, as probable isognomonids rather than inoceramids). HAYAMI & KANIE (1980: text-fig. 3) also illustrated a reconstruction showing the tongue-like projection protruding slightly over the inoceramid host's shell margin. They inferred that the tongue-like projection provided protection for the limpet's head during feeding. The tongue-like projection and the shell apex therefore could only be anterior in their reconstruction. Apart from the anterior apex and the apparent special protection for the head, this appears similar to the mode of life of Recent *Capulus* species such as *C. ungaricus* (LINNAEUS, 1758) and *C. danieli* (CROSSE, 1858) (YONGE 1938; SHARMAN 1956; GARRARD 1961; HABE 1967), some of which feed by drilling a small hole through the host's shell (ORR 1962; specimens living on thin-shelled pectinoideans only), and others by protruding their proboscis over the shell edge and between the host's valves and gills. Any other taxonomic assignment would make it equally if not more likely that the limpet merely used the shell as a substrate, and was a sedentary filter feeder, e.g. as in the Hipponicidae (taxonomic position suggested by A. WARÉN, Swedish Natural History Museum, pers. comm.). A modification to HAYAMI & KANIE's (1980: text-fig. 3) reconstruction is necessary based on one New Zealand specimen. The large specimen of *G. problematicus* in GS14694 (O32/f107, Tarapuhi Grit, Haumuri Bluff) (Figs. 2A, D, 3H) is situated on one valve of a large, flat, articulated, prismatic shell, not obviously close to the shell margin; the protruding anterior(?) tongue is pressed against (and, presumably as a diagenetic effect, slightly into) the shell, leaving a gape ca. 5 mm high, particularly obvious for about 30 mm on each side of the tongue. This suggests (as described above) that the function of the tongue is either to allow the head and bilaterally symmetrical anterior organs to be protruded under the shell edge, or to allow inflowing water currents to enter or out-flowing currents to leave the mantle cavity, when the limpet was clamped down onto its host shell. It implies that the life position need not have been close to the host's shell margin. The apex of the specimen in GS14694 also is unique among specimens I have examined in being clearly asymmetrical, curled slightly to the right in anterior view (to the left in dorsal view), although this might be at least partly due to post-mortem distortion. The limpet lived on an essentially smooth bivalve, and has sculpture only of very low comarginal ridges, apart from an obscure radial ridge to the right of the apex in dorsal view (assuming the apex is anterior), extending over only about the first 40 mm of the shell's length.

I have previously (BEU 2004: 192–200) synonymised most of the Recent capulids discussed by HAYAMI & KANIE (1980: 695) with the single widespread Indo-West Pacific species *Capulus danieli*. I showed that (like *C. ungaricus* in the Atlantic) the same species lives on a variety of hosts, and feeds in slightly different ways governed partly by the host's shell, copying the sculpture xenomorphically of strongly sculptured hosts. In several localities in Cretaceous rocks of the North Pacific, inoceramids and *Gigantocapulus* are the only taxa found (DUNDO & EFREMOVA 1974; HAYAMI & KANIE 1977, 1980; ZONOVA 1985; SHIGETA et al. 1999), and HAYAMI & KANIE (1980) pointed out that the two species *Sphenoceramus schmidti* and *G. giganteus* have identical geographical and stratigraphical ranges. Along with the specimens found in life position attached to articulated inoceramids or isognomonids in both the North Pacific and New Zealand, this leaves little doubt that *Gigantocapulus* lived on the exterior of large, probably living bivalves. It possibly fed by intercepting the bivalve's food from its gills as capulids do. It is also possible that, like the semiparasitic pyramidelloidean limpet *Amathina*, it was "a sedentary gleaner of food particles travelling across the [host's] mantle edge" (PONDER 1987: 1, citing MORTON & MORTON 1983). It is more probable though, that it was a sedentary filter feeder.

Another possible mode of life deserving consideration (although not supported by any evidence) is at sulphide-rich springs ("black smokers") or, more likely, methane seeps, in which the giant inoceramids were at least partly supported by chemoautotrophic bacteria within their gills. In view of the "normal" quiet mudstone depositional environments where inoceramids occur, it seems more likely that their huge size (up to >1.5 m long in *Magadiceramus rangatira* (WELLMAN, 1959); CRAMPTON 1996: 86) could have been achieved as a result of zooxanthellae in their mantle tissues, as in the Recent bivalves *Tridacna* and *Corculum*, rather than of chemoautotrophic bacteria in the gills – although there is little evidence for this mode of life, and "giant" inoceramids were not limited to the photic zone. *Gigantocapulus problematicus* also is unlikely to have been chemoautotrophic, as (a) this species seems to have lived on a large isognomonid rather than an inoceramid, (b) *G. problematicus* and *Isognomon* occur together in shallow-water, coarse-grained lithologies, as well as slightly more offshore, finer ones, and (c) a variety of normal marine taxa such as nuculanids, pectinoideans, oysters, limids, trigoniids, venerids, *Panopea*, aporrhaids, *Rotularia*, ammonites, and belemnites occurs in the same assemblage as the isognomonids and limpets at a few localities (Haumuri Bluff, WARREN & SPEDEN 1978: fig. 26; Mangahouanga Stream, CRAMPTON & MOORE 1990).

Phylogenetic relationships

The apparently anterior shell apex would be an otherwise unknown character if it can be proven in *Gigantocapulus*. All limpets definitely assignable to Gastropoda have a central to posterior apex: Capuloidea and related caenogastropod groups such as Calyptraeoidea and Vanikoroidea; Patellogastropoda, Vetigastropoda, Cocculiniformia, and Neritimorpha; the eulimid limpet *Thyca* (WARÉN 1980); and such widely divergent "higher" gastropod groups as the pyramidelloidean opithobranch limpet *Amathina* (PONDER 1987), all freshwater limpets such as *Ancylastrum* (Planorbidae; STANICIC 1998: figs. 17.33H, K), *Valencennius* (Lymnaeidae; ZILCH 1959: 97, fig. 310) and the many smaller taxa, all shelled opisthobranchs such as Umbraculida (BURN 1959, 1960; WARÉN & DI PACO 1996; WÄGELE et al. 2006), the limpet-shelled gastropterid *Sagaminopteron ornatum* TOKIOKA & BABA, 1964 (superfamily Philinoidea) (BURN 1973), and marine pulmonate limpets such as Siphonarioidea (STANICIC 1998: 1068–1069) and Trimusculoidea (STANICIC 1998: 1078–1079). Based partly on the similarity of the shell to that of *Umbraculum*, I considered the possibility that *Gigantocapulus* might be a secondarily untorted opisthobranch, but all such "higher" gastropod limpets have a posterior apex. It is most unlikely that they are related to *Gigantocapulus*. Even the vaguely limpet-shaped shell of the heteropod *Carinaria* has a posterior shell apex (NEWMAN 1998: 804–808) (although the shell is a small, very thin, relict structure covering only the visceral mass), with the simple, concave posterior slope shorter than the convex, prominently ridged anterior slope, and this needs to be considered when fossils such as "*Brunonia*" *annulata* are referred to the Carinariidae.

The only previously known limpet group with a strongly anterior apex is Class Monoplacophora (or Tergomya). A few exceptions tentatively were included in "Patellina" (now Patellogastropoda) by COX & KNIGHT (1960), but it is suggested below that these are either Gigantocapulidae or Carinariidae. The New Zealand specimens strongly resemble *Tryblidium unguis* LINDSTRÖM, 1880 (WENZ 1938: 91, fig. 58; although this is actually the type species of *Pilina* PERNER, 1925; KNIGHT 1941: 246, pl. 4 figs. 1a–d; KNIGHT & YOCHELSON 1969: I79, fig. 46.6), explaining the former use of the name "*Tryblidium*" for the New Zealand fossils. They also strongly resemble the simplest Recent monoplacophorans such as *Vema occidua* (MARSHALL 2006: 62, figs. 1C, G–I). However, New Zealand specimens have no hint of metamerically repeated muscle scars. Any muscle scars must necessarily have been very weakly impressed in a shell only 1 mm thick, but this is countered by the fact that even some minute Recent monoplacophorans such as *Micropilina tangaroa* MARSHALL, 1990 have weakly impressed, metamerically repeated muscle scars in a shell only 1.5 mm long (MARSHALL 1990: fig. 3) – although the other four small to minute taxa recently described from New Zealand by MARSHALL (2006) all lack muscle scars. A. WARÉN (pers. comm.) commented that only relatively few, old individuals of Recent monoplacophorans seem to have impressed muscle scars. There are also no other records of very large monoplacophorans after Middle Devonian time (KNIGHT & YOCHELSON 1960); the known Recent taxa are moderate-sized to minute, <1-40 mm long (*Neopilina galatheae* reaches 40 mm in length; A. WARÉN, pers. comm.).

The life habits of the medium-sized Recent monoplacophoran *Neopilina galatheae* LEMCHE, 1957 suggested by YONGE (1960: I9) were: "Possibly it collects organic debris from the bottom by means of frilled organs, which may be ciliated, situated at the margins of the mouth and which may be analogous, possibly even homologous, with the palp proboscides in the Nuculidae and Nuculanidae" (Bivalvia). YONGE (1960) noted that the gut of *N. galatheae* contained Radiolaria, and TENDAL (1985) reported xenophyophores (Protista, Sarcodina) in its gut. The ecology of the Recent monoplacophorans *N. galatheae* and *Vema ewingi* (CLARKE & MENZIES, 1959) was described further by MENZIES et al. (1959). Specimens of *V. ewingi* seemed to be associated with obvious trails on the sediment surface, and were assumed to creep on a thick layer of their own mucus, in depths of 5600–6300 m in the Peru Trench, on a substrate of soft greenish mud rich in diatoms, foraminiferans, sponge spicules, echinoid spines, and radiolarians. Their gut contents included diatoms, radiolarians, foraminiferans, sponge spicules, and many bacteria, so they are apparently unselective deposit feeders, ingesting the bottom sediment. CLARKE & MENZIES (1959) speculated that, despite their metamerically repeated foot muscles, small to minute Recent monoplacophorans can creep on the sediment. However, A. WARÉN (pers. comm.) stated that all subsequently collected Recent monoplacophorans have been found attached to rocks or other molluscan shells. The number of Recent species had risen to 15 by the time MARSHALL (1990) named *Micropilina tangaroa* from northern New Zealand, and the total has now risen to 33 (Recent world fauna summarised by MARSHALL 2006). Something comparable to the oral feeding palps described by YONGE (1960) was possibly present in *Gigantocapulus*, the spaces on each side of the anterior shell tongue either allowing anterior organs to protrude from beneath the shell or allowing water currents to enter the mantle cavity.

If *Gigantocapulus* is a monoplacophoran, several relatively large post-Devonian monoplacophorans must have gone unrecognised up until now. Other possible monoplacophorans that might help fill the gap in their time range include *Berlieria, Rhytidopilus* and *Brunonia* (COX & KNIGHT 1960: I237, fig. I51), which are said to have an anterior apex and certainly have an anterior radial structure – although as noted above, at least *Rhytidopilus* and "*Brunonia*" *annulata*, and possibly *Berlieria*, are likely carinariid gastropods. COX & KNIGHT (1960: I232) assumed that *Symmetrocapulus* DACQUÉ, 1933 has an anterior apex, but it could also be interpreted as posterior. *Brunonia grandis* MÜLLER, 1898 (Senonian, Germany) appears from the illustration by COX & KNIGHT (1960: I237, figs. I51.1a, b) to have a short anterior tongue-like projection similar to that of *G. giganteus*, and its apex is certainly anterior to the centre if the projection is anterior; it is closely similar to *Gigantocapulus* in appearance. As noted above, *Deslongchampsia appendiculata* (Jurassic, Bathonian – Oxfordian, Europe) (WENZ 1938: 225, fig. 426; COX & KNIGHT 1960: I233, figs. I45.2a–c) also has an anterior apex and an anterior shell tongue directed downwards, very similar to that of the smaller specimens of *G. problematicus*, and presumably functioning in a similar way. A position close to *Gigantocapulus* seems likely for at least *B. grandis* and *D. appendiculata*, and they might well belong in Gigantocapulidae.

If *Gigantocapulus* is a monoplacophoran, the extinction of large monoplacophorans apparently occurred concurrently with that of inoceramids and large isognomonids near the end of Cretaceous time. However, a position in Monoplacophora seems very unlikely. Possible interpretations of the phylogenetic position of *Gigantocapulus* are numerous, because of the numerous suggestions about the relationships and shell orientation of early limpet-shaped shells by many authors. The POJETA

& RUNNEGAR "school" has contended that all early Palaeozoic molluscs with an undivided shell should be referred to Monoplacophora. They then were able to derive all other classes from Monoplacophora (e.g. RUNNEGAR & POJETA 1974; RUNNEGAR & JELL 1976; POJETA & RUNNEGAR 1976; POJETA 1980). HARPER & ROLLINS (1982) and WAHLMAN (1992) cautioned a more considered approach, in which (e.g.) some of POJETA & RUNNEGAR's Monoplacophora, including only a part of the Bellerophontoidea, were referred to the Gastropoda. YOCHELSON (1978, 1979) and PEEL (1991) followed this approach further, based on concepts and terms proposed by HORNÝ (1965, and in other papers listed by PEEL 1991) and WINGSTRAND (1985). PEEL (1991) clearly defined the important distinction between (a) endogastric and exogastric shells, and (b) tergomyan and cyclomyan shells. Exogastric shells (essentially, the Tergomya) have an anterior apex directed anteriorly, that is, the sub-apical surface is anterior, water currents enter anteriorly or laterally, and the supra-apical surface and exhalent currents are posterior. Exogastric shells (all other limpet-shaped shells) have a posterior apex directed posteriorly, the supra-apical surface is anterior, water currents enter laterally, and the sub-apical surface and exhalent currents are posterior. Tergomyans are untorted limpets in which the apex lies outside the circle of muscle scars, whereas cyclomyan shells are also untorted limpets or more spirally coiled shells in which the muscle scar or ring of scars encloses the apex. Tergomyans include all undoubtedly untorted monoplacophorans such as *Tryblidium* and *Pilina*, with an anterior apex, that is, they are exogastric. (It should be noted, however, that it is not certain that living monoplacophorans are tergomyan; the muscle insertions of such taxa as *Neopilina galatheae* and *Micropilina tangaroa* are nearer to the shell margin than the apex is). Cyclomyans include a wide range of taxa, from early Palaeozoic limpets onwards. Some of the simplest-shelled taxa include *Helcionella*, *Anabarella* and planispirally coiled "monoplacophorans" such as *Latouchella*, in which the apex was interpreted by PEEL and others as posterior, that is, they are endogastric, with moderately to very complex posterior shell margin modifications to allow the outflow of the mantle water currents. PEEL (1991) proposed a new class Helcionelloida to contain the early Palaeozoic limpets he interpreted as endogastric cyclomyans, particularly *Helcionella*, *Anabarella*, *Eotebenna*, *Latouchella* and *Yochelcionella* (PEEL 1991: fig. 11). It certainly seems likely that POJETA & RUNNEGAR's (1974) interpretation of molluscan phylogeny is oversimplified, and urgent consideration should be given to adopting the class name Tergomya in place of the now widely accepted Monoplacophora.

Possible taxonomic positions for *Gigantocapulus* therefore are:

1. Tergomya: An originally untorted "monoplacophoran" with an anterior apex on an exogastric shell, and with anterior shell margin structures for inhalant water currents, and a greatly thickened anterior end and apex. The anterior area, including the apex, is heavily thickened in a cross-section of *Tryblidium reticulatum* shown by LINDSTRÖM (1884: pl. 1 fig. 31), and the anterior tongue-like projection and lateral gapes of both *T. reticulatum* and *Pilina unguis* shown by LINDSTRÖM (1884: pl. 1 figs. 27, 35) are extremely similar to those of *G. problematicus*, supporting this position. However, the complex crossed-lamellar calcite shell is completely foreign to Tergomya, and the absence of large tergomyans from the fossil record after Devonian time does not support this interpretation.
2. Helcionelloida: An originally untorted cyclomyan with a posterior apex on an endogastric shell, and with the marginal structures and apical thickening posterior. The similarities pointed out above to *Tryblidium* and *Pilina* could equally well apply here, but the shell structure argues equally strongly against this position. The internal mould of *Gigantocapulus problematicus* (Fig. 3G) gives the impression that it is cyclomyan and the near-central apex of *G. giganteus* clearly is cyclomyan, supporting this and the following two but not the first possible taxonomic position.
3. Gastropoda (a): A capuloidean or, more probably, vanikoroidean gastropod, living sedentarily on large bivalves, probably by filter feeding. The marginal structures and apex might then be either anterior or posterior. Once again, the shell structure and mineralogy seem to rule out such a position. All the apparent similarities to modern gastropods, based on the apparent mode of life, may well be entirely superficial.
4. Gastropoda (b): An otherwise unknown, apparently extinct gastropod group with a calcitic shell. Gastropods with a calcite outer shell layer I am aware of reported previously from Cretaceous to Recent faunas include only Muricidae (*Trophon*, *Pagodula*, and a few other genera) and Janthinoidea (particularly *Cirsotrema* and *Janthina*; possibly a few other genera, but not most taxa related to *Epitonium*) and it is faintly possible that *Gigantocapulus* is an exceedingly aberrant muricoidean or janthinoidean, but it seems more likely that it belongs in a previously unrecognised group. Again, the apex and marginal structures might be either anterior or posterior.

At present, there is not enough evidence to decide which of these positions is more likely, but (4) seems the most likely to me.

Conclusions

1. Large limpets attached to articulated inoceramid or isognomonid shells in New Zealand early Haumurian (Campanian) rocks belong in *Gigantocapulus problematicus*, formerly reported only from the North Pacific.

2. New Zealand specimens confirm the thickened tongue-like projection reported previously for North Pacific *G. giganteus*. The greatly thickened, marginal shell apex, apparently to protect an otherwise thin shell protruding near its host's shell edge, and spaces on each side of the tongue to allow either protrusion of organs or inhalant water currents support the interpretation of the apex and tongue as anterior, although they might also be posterior in an endogastric cyclomyan helcionelloidan or gastropod.
3. The epifaunal mode of life on bivalves suggests that *Gigantocapulus* was a sedentary filter feeder. If the shell apex of *Gigantocapulus* was anterior, it contrasts strongly with the posterior one of *Capulus* and *Hipponix*, and suggests that it belongs in an unrelated group; family Gigantocapulidae is proposed for it. However, the apex is just as likely to have been posterior.
4. Gigantocapulidae possibly belongs in Tergomya, but the lack of segmented muscle scars in *Gigantocapulus*, the absence of other large Mesozoic tergomyans, and the clearly cyclomyan condition of *G. giganteus* show that a position in Gastropoda is much more likely. A position in Vanikoroidea near the Hipponicidae is adopted tentatively, therefore, although a previously unrecognised, extinct gastropod group is just as likely.
5. *Brunonia* and *Deslongchampsia* are other possible members of Gigantocapulidae. If they are correctly assigned there, the correct family name would be Brunoniidae DIENI, 1990.

Acknowledgements

Dedicated to Klaus Bandel on his 65th birthday, in recognition of his contributions to understanding unusual Mesozoic gastropods. Funded by the New Zealand Government's Marsden Fund, administered by the Royal Society of New Zealand (grant GNS0404). I am grateful to Sven Nielsen (GFZ Potsdam) for inviting me to contribute to this volume, Itaru Hayami (University of Tokyo) for copies of his and Kanie's works, John Peel (Department of Earth Sciences, Uppsala University), Anders Warén (Swedish Natural History Museum, Stockholm) and Bruce Marshall (Museum of New Zealand Te Papa Tongarewa) for helpful suggestions that substantially improved the manuscript, and James Crampton (GNS, Lower Hutt) for contributing much material over several years, for advice on ages, localities, and the identity of New Zealand host bivalves, and for comments on the manuscript. Ian Raine (GNS) carried out a Fossil Record Database search for locality records. Kristin Garbett (GNS) found several obscure references, Heidi Schlumpf (GNS) took the photographs, and the map and plates were prepared by Philip Carthew (GNS).

References

BEU, A.G. 2004. Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 1. Revised generic positions and recognition of warm-water and cool-water migrants. – Journal of the Royal Society of New Zealand **34**: 111–265.

BOUCHET, P.; MCLEAN, J.H. & WARÉN, A. 1983. Monoplacophorans in the North Atlantic. – Oceanologica Acta **6**: 117–118.

BOUCHET, P.; ROCROI, J.P.; FRÝDA, J.; HAUSDORF, B.; PONDER, W.; VALDÉS, A. & WARÉN, A. 2005. Classification and nomenclator of gastropod families. – Malacologia **47**: 1–397 [distributor of this issue: Hackenheim (ConchBooks)].

BURN, R. 1959. Comments on the Australian umbraculacean Mollusca. – Journal of the Malacological Society of Australia **1** (3): 28–30.

BURN, R. 1960. On *Tylodina corticalis* (TATE), a rare opisthobranch from south-eastern Australia. – Journal of the Malacological Society of Australia **1** (4): 64–69.

BURN, R. 1973. Pearson Island expedition 1969 – 10. Opisthobranchs. – Transactions of the Royal Society of South Australia **97**: 201–205.

CLARKE, A.H. & MENZIES, R.J. 1959. *Neopilina (Vema) ewingi*, a second living species of the Paleozoic class Monoplacophora. – Science **129**: 1026–1027.

CONRAD, T.A. 1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. – Journal of the Academy of Natural Sciences of Philadelphia (2) **4**: 275–298 [not seen].

COOPER, R.A., ed., 2004. The New Zealand geological time scale. – Institute of Geological and Nuclear Sciences Monograph **22**: 1–284.

COSSMANN, M. 1895. Essais de paléoconchologie comparée, vol. 1. – 159 p., Paris (M. COSSMANN).

COSSMANN, M. 1901. Essais de paléoconchologie comparée, vol. 4. – 293 p., Paris (M. COSSMANN).

COX, L.R. & KNIGHT, J.B. 1960. Suborder Patellina. – In: MOORE, R.C., ed., Treatise on invertebrate paleontology. Part I, Mollusca 1: I231–I237, New York and Lawrence/Kansas (Geological Society of America and University of Kansas Press).

CRAMPTON, J.S. 1988. Comparative taxonomy of the bivalve families Isognomonidae, Inoceramidae, and Retroceramidae. – Palaeontology **31**: 965–996.

CRAMPTON, J.S. 1996. Inoceramid bivalves from the Late Cretaceous of New Zealand. – Institute of Geological and Nuclear Sciences Monograph **14**: 1–188.

CRAMPTON, J.S. & MOORE, P.R. 1990. Environment of deposition of the Maungataniwha Sandstone (Late Cretaceous), Te Hoe River area, western Hawke's Bay, New Zealand. – New Zealand Journal of Geology and Geophysics **33**: 333–348.

CRAMPTON, J.S.; MUMME, T.; RAINE, I.; RONCAGLIA, L.; SCHIØLER, P.; STRONG, P.; TURNER, G. & WILSON, G. 2000. Revision of the Piripauan and Haumurian local stages and correlation of the Santonian–Maastrichtian (Late Cretaceous) in New Zealand. – New Zealand Journal of Geology and Geophysics **43**: 309–333.

CRAMPTON, J.S.; SCHIØLER, P. & RONCAGLIA, L. 2006. Detection of Late Cretaceous eustatic signatures using quantitative biostratigraphy. – Geological Society of America Bulletin **118**: 975–990.

CROSSE, H. 1858. Diagnoses de coquilles nouvelles. – Revue et Magasin de Zoologie (2) **10**: 81.

DACQUÉ, E. 1933. – In: GÜRICH, G., Wirbellose des Jura. – Leitfossilien **7**: 1–272 [not seen].

DIENI, I. 1990. *Brunonia annulata* (YOKOYAMA, 1890) (Carinariidae, Mesogastropoda) nel Cretaceo inferiore della Sardegna. – Bollettino della Società Paleontologica Italiana **29**: 43–51.

DUNDO, O.P. & EFREMOVA, V.I. 1974. Field atlas of the Senonian index fossils of the northeastern part of the Koryak Highlands. – 28 p., Leningrad (Scientific Research Institute of Arctic Geology) [in Russian].

EUDES-DESLONGCHAMPS, J.A. 1842. Mémoire sur les patelles, ombrelles, calyptrées, fissurelles, émarginules et dentales fossiles des terrains secondaires du Calvados. – Mémoires de la Société Linnéenne de Normandie **7**: 111–130 [not seen].

GARRARD, T.A. 1961. Mollusca collected by MV "Challenge" off the east coast of Australia. – Journal of the Malacological Society of Australia **1** (7): 42–46.

Gray, J.E. 1840. Shells of molluscous animals. – In: Synopsis of the contents of the British Museum, ed. 42, second printing: 106–156, London (British Museum (Natural History)).

Habe, T. 1967. A new capulid snail, *Capulus spondylicola*, from Japan. – Venus **26**: 37–38.

Harper, J.A. & Rollins, H.B. 1985. Recognition of Monoplacophora and Gastropoda in the fossil record: a functional morphological look at the bellerophont controversy. – Proceedings of the Third North American Paleontological Convention, Montreal, August 1982 **1**: 227–232.

Hayami, I. & Kanie, T. 1977. A systematic survey of the Paleozoic and Mesozoic Gastropoda and Paleozoic Bivalvia from Japan. – The University Museum, University of Tokyo, Bulletin **13**: 1–154.

Hayami, I. & Kanie, T. 1980. Mode of life of a giant capulid gastropod from the Upper Cretaceous of Saghalien and Japan. – Palaeontology **23**: 689–698.

Horný, R. 1965. On the systematic position of *Cyrtolites* Conrad, 1838. – Sbornik Geologicky Ved Paleontologie **134**: 8–10.

Kaim, A. & Sztajner, P. 2005. The opercula of neritopsid gastropods and their phylogenetic importance. – Journal of Molluscan Studies **71**: 211–219.

Kanie, Y. 1975. Some Cretaceous patelliform gastropods from the northern Pacific region. – Science Reports of the Yokosuka City Museum **21**: 1–44.

Kanie, Y. 1977. Succession of the Cretaceous patelliform gastropods in the northern Pacific region. – In: Matsumoto, T., ed., Mid-Cretaceous events – Hokkaido symposium, 1976. – Palaeontological Society of Japan Special Papers **21**: 53–62.

Kanie, Y. 1983. Occurrences of some Cretaceous limpets in the Pacific and the U.S. western interior regions. – Science Reports of the Yokosuka City Museum **31**: 9–14.

Kase, T. 1988. Reinterpretation of *Brunonia annulata* (Yokoyama) as an Early Cretaceous carinariid mesogastropod (Mollusca). – Journal of Paleontology **62**: 766–771.

Knight, J.B. 1941. Paleozoic gastropod genotypes. – Geological Society of America Special Papers **32**: 1–510.

Knight, J.B. & Yochelson, E.L. 1960. Monoplacophora. – In: Moore, R.C., ed., Treatise on invertebrate paleontology. Part I, Mollusca 1: I77–I84, New York and Lawrence/Kansas (Geological Society of America and University of Kansas Press).

Kouchinsky, A. 2000. Shell microstructures in Early Cambrian molluscs. – Acta Palaeontologica Polonica **45**: 119–150.

Lemche, H. 1957. A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora. – Nature **179**: 413–416.

Lindström, G. 1880. Fragmenta Silurica. Opus studio N.P. Angelin inchoatum; curavit G. Lindström. – 60 p., Stockholm (Kongliga Svenska Vetenskaps-Akademiens) [not seen].

Lindström, G. 1884. On the Silurian Gastropoda and Pteropoda of Gotland. – Kongliga Svenska Vetenskaps-Akademiens Handlingar **19**: 1–250.

Linnaeus, C. von 1758. Systema naturae per regna tria naturae ... editio decima, reformata. Tomus 1. – 823 p., Holmiae (L. Salvii) [facsimile reprint, London, British Museum (Natural History), 1956].

MacClintock, C. 1967. Shell structure of patelloid and bellerophontoid gastropods (Mollusca). – Peabody Museum of Natural History, Yale University Bulletin **22**: 1–140.

Marshall, B.A. 1990. *Micropilina tangaroa*, a new monoplacophoran (Mollusca) from northern New Zealand. – The Nautilus **104**: 105–107.

Marshall, B.A. 2006. Four new species of Monoplacophora (Mollusca) from the New Zealand region. – Molluscan Research **26**: 61–68.

Marwick, J. 1926. Cretaceous fossils from Waiapu Subdivision. – New Zealand Journal of Science and Technology **8**: 397–382.

Meek, F.B. & Hayden, F.V. 1860. Systematic catalogue with synonyma, of Jurassic, Cretaceous and Tertiary fossils collected in Nebraska, by the exploring expeditions under the command of Lieut. G. K. Warren, of U. S. Topographical Engineers. – Proceedings of the Academy of Natural Sciences of Philadelphia **12**: 417–432 [not seen].

Meenakshi, V.; Hare, P.; Watabe, N.; Wilbur, K. & Menzies, R. 1970. Ultrastructure, histochemistry, and amino acid composition of the shell of *Neopilina*. – Anton Bruun Reports **2**: 1–12.

Menzies, R.J.; Ewing, M.; Worzel, J.L. & Clarke, A.H. 1959. Ecology of the Recent Monoplacophora. – Oikos **10**: 168–182.

Michael, R. 1899. Über Kreidefossilien von der Insel Sakhalin. – Jahrbuch der Königlich Preussischen Geologischen Landesanstalt **18**: 153–164 [not seen].

Montfort, D. de 1810. Conchyliologie systématique, ou classification des méthodique des coquilles ... Tome second. Coquilles univalves, non cloisonnées. – 676 p., Paris (F. Schoell).

Morris, J. & Lycett, J. 1851. A monograph of the Mollusca from the Great Oolite. Part 1, Univalves. – 130 p., London (Palaeontographical Society Monograph).

Morton, B. & Morton, J.E. 1983. The sea shore ecology of Hong Kong. – Hong Kong (Hong Kong University Press) [not seen].

Müller, G. 1898. Die Molluskenfauna des Untersenon von Braunschweig und Ilsede. I. Lamellibranchiaten und Glossophoren. – Abhandlungen der Preussischen Geologischen Landesanstalt, Neue Folge **25**: 1–142 [not seen].

Nagao, T. & Otatume, K. 1938. Molluscan fossils of the Hakobuti Sandstone of Hokkaido. – Journal of the Faculty of Science, Hokkaido Imperial University, Series 4, Geology and Mineralogy **4**: 31–56.

Newman, L. 1998. Superfamily Carinarioidea. – In: Beesley, P.L.; Ross, G.J.B. & Wells, A., eds., Mollusca, the southern synthesis. Fauna of Australia volume **5**: 804–808, Melbourne (CSIRO Publishing).

Orr, V. 1962. The drilling habit of *Capulus danieli*. – The Veliger **5**: 63–67.

Peel, J. 1977. Relationships and internal structure of a new *Pilina* (Monoplacophora) from the late Ordovician of Oklahoma. – Journal of Paleontology **51**: 116–122.

Peel, J. 1991. Functional morphology, evolution and systematics of early Palaeozoic univalved molluscs. – Bulletin of the Geological Survey of Greenland **161**: 1–116.

Peel, J. & Horný, R. 1999. Muscle scars and systematic position of the lower Palaeozoic limpets *Archinacella* and *Barrandicella* gen. nov. (Mollusca). – Journal of the Czech Geological Society **44**: 97–115.

Perner, J. 1925. Die Gastropoden des baltischen Untersilurs. Von Ernst Koken; Fortgesetzt von Jar. Perner. – Mémoires de l'Académie Impériale des Sciences de St. Petersbourg, Classe Physico-Mathématiques (8) **37** (1): i–vii, 1–326 [not seen].

Pojeta, J. 1980. Molluscan phylogeny. – Tulane Studies in Geology and Paleontology **16**: 55–80.

Pojeta, J. & Runnegar, B. 1976. The paleontology of rostroconch mollusks and the early history of the Phylum Mollusca. – United States Geological Survey Professional Papers **968**: 1–88.

Ponder, W.F. 1987. The anatomy and relationships of the pyramidellacean limpet *Amathina tricarinata* (Mollusca: Gastropoda). – Asian Marine Biology **4**: 1–34.

Runnegar, B. 1985. Shell microstructures of Cambrian molluscs replicated by phosphate. – Alcheringa **9**: 245–257.

Runnegar, B. & Jell, P. 1976. Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. – Alcheringa **1**: 109–138.

Runnegar, B. & Pojeta, J. 1974. Molluscan phylogeny: the paleontological viewpoint. – Science **186**: 311–317.

Schmidt, M.F. 1873. Über die Petrefakten der Kreideformation von Insel Sachalin. – Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg (7) **19** (3): 1–37 [not seen].

Schmidt, W. 1959. Bemerkungen zur Schalenstruktur von *Neopilina galatheae*. – Galathea Reports **3**: 73–78.

Sharman, M. 1956. Note on *Capulus ungaricus*. – Journal of the Marine Biological Association of the United Kingdom **35**: 445–450.

Shigeta, Y.; Maeda, H.; Uemura, K. & Solov'yov, A.S. 1999. Stratigraphy of the Upper Cretaceous System in the Kril'on Peninsula, South Sakhalin, Russia. – Bulletin of the National Science Museum, Tokyo (C) **25**: 1–27.

Sohl, N.F. 1960. Archaeogastropoda, Mesogastropoda and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations. – United States Geological Survey Professional Papers **331-A**: 1–151.

Sohl, N.F. 1967. Upper Cretaceous gastropods from the Pierre Shale at Red Bird, Wyoming. – United States Geological Survey Professional Papers **393-B**: B1–B46.

Stanicic, J. 1998. Order Basommatophora; Superfamily Siphonarioidea; Superfamily Trimusculoidea. – In: Beesley, P.L.; Ross, G.J.B. & Wells, A., eds., Mollusca, the southern synthesis. Fauna of Australia volume **5**: 1067–1075, 1078–1079, Melbourne (CSIRO Publishing).

Stanley, G.D. & Kanie, Y. 1985. The first Mesozoic chondrophorine (medusoid hydrozoan) from the Lower Cretaceous of Japan. – Palaeontology **28**: 101–109.

Stephenson, L.W. 1941. The larger invertebrate fossils of the Navarro Group of Texas. – Texas University Bulletin **4101**: 1–641.

Tendal, O.S. 1985. Xenophyophores (Protozoa, Sarcodina) in the diet of *Neopilina galatheae* (Mollusca, Monoplacophora). – Galathea Report **16**: 95–98.

Tokioka, T. & Baba, K. 1964. Four new species and a new genus of the family Gastropteridae from Japan. – Publications of the Seto Marine Biological Laboratory **12**: 201–229 [not seen].

Wade, B. 1926. The fauna of the Ripley Formation on Coon Creek, Tennessee. – United States Geological Survey Professional Papers **137**: 1–272.

Wägele, H.; Vonnemann, V. & Rudman, W.B. 2006. *Umbraculum umbraculum* (Lightfoot, 1786) (Gastropoda, Opisthobranchia, Tylodinoidea) and the synonymy of *U. mediterraneum* (Lamarck, 1812). – In: Brodie, G.; Fahey, S. & Wells, F.E., eds., Contemporary studies into the systematics and evolution of opisthobranch molluscs. – Records of the Western Australian Museum, Supplement **69**: 69–82.

Wahlman, G.P. 1992. Middle and Upper Ordovician symmetrical univalved mollusks (Monoplacophora and Bellerophontina) of the Cincinnati arch region. – United States Geological Survey Professional Papers **1066-O**: 1–213.

Warén, A. 1980. Revision of the genera *Thyca, Stilifer, Scalenostoma, Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). – Zoologica Scripta **9**: 187–210.

Warén, A. 1988. *Neopilina goesi*, a new Caribbean monoplacophoran mollusc dredged in 1869. – Proceedings of the Biological Society of Washington **101**: 676–681.

Warén, A. & Bouchet, P. 1990. *Laevipilina rolani*, a new monoplacophoran from off southwestern Europe. – Journal of Molluscan Studies **56**: 449–453.

Warén, A. & di Paco, G. 1996. Redescription of *Anidolyta duebeni* (Lovén), a little known notaspidean gastropod. – Bollettino Malacologico **32**: 19–26.

Warén, A. & Gofas, S. 1996. A new species of Monoplacophora, redescription of the genera *Veleropilina* and *Rokopella*, and new information on three species of the class. – Zoologica Scripta **25**: 215–232.

Warren, G. & Speden, I. 1978. The Piripauan and Haumurian stratotypes (Mata Series, Upper Cretaceous) and correlative sequences in the Haumuri Bluff district, South Marlborough. – New Zealand Geological Survey Bulletin **92**: 1–60.

Wellman, H.W. 1959. Divisions of the New Zealand Cretaceous. – Transactions of the Royal Society of New Zealand **87**: 99–163.

Wenz, W. 1938–1944. Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. – In: Schindewolf, O.H., ed., Handbuch der Paläozoologie, Vol. 6: xii + 1639 p, Berlin (Gebrüder Borntraeger) [p. 1–480, 1938; 481–720, 1939; 721–960, 1940; 961–1200, 1941; 1201–1506, 1943; 1507–1639, i–xii, 1944; reprint 1960–1961, Berlin (Gebrüder Borntraeger)].

Whiteaves, J.F. 1903. Mesozoic fossils volume I. Part V (& last). – On some additional fossils from the Vancouver Cretaceous, with a revised list of the species therefrom. – 309–416, Ottawa (Geological Survey of Canada).

Wingstrand, K.G. 1985. On the anatomy and relationships of Recent Monoplacophora. – Galathea Reports **16**: 7–94.

Woods, H. 1917. The Cretaceous faunas of the north-eastern part of the South Island of New Zealand. – New Zealand Geological Survey Palaeontological Bulletin **4**: 1–41.

Yochelson, E.L. 1978. An alternative approach to the interpretation of the phylogeny of ancient mollusks. – Malacologia **17**: 165–191.

Yochelson, E.L. 1979. Early radiation of Mollusca and mollusc-like groups. – In: House, M.R., ed., The origin of the major invertebrate groups: 323–358, New York (Academic Press).

Yokoyama, M. 1890. Versteinerungen aus der Japanischen Kreide. – Palaeontographica **36**: 159–202 [not seen].

Yonge, C.M. 1938. Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. – Journal of the Marine Biological Association of the United Kingdom **22**: 453–468.

Yonge, C.M. 1960. General characters of Mollusca. – In: Moore, R.C., ed., Treatise on invertebrate paleontology. Part I, Mollusca 1: I3–I36, New York and Lawrence/Kansas (Geological Society of America and University of Kansas Press).

Zilch, A. 1959–1960. Gastropoda von Wilhelm Wenz. Teil 2. Euthyneura. – In: Schindewolf, O.H., ed., Handbuch der Paläozoologie, Vol. 6. Pt. 2: xii + 834 p, Berlin (Borntraeger) [p. 1–400, 1959; 401–834, i–xii, 1960].

Zonova, T.D. 1985. Peculiarities of the structure of the shell of radially ribbed inoceramids and limpet gastropods of the Campanian of the northern Pacific area. – Annual of the All-Union Paleontological Society **28**: 134–147 [in Russian].

Manuskripteingang / manuscript received 13. 11. 2006;
Manuskriptannahme / manuscript accepted 20. 1. 2007.