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The Marine Fauna of New Zealand: The Molluscan Genera *Cymatona* and *Fusitriton* (Gastropoda, Family Cymatiidae)

by

A. G. Beu

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CONTENTS

FIGURES

Figs 4, 10, 11, and 12, printed on art paper, are out of sequence.

TABLES

The Marine Fauna of New Zealand: The Molluscan Genera *Cymatona* and *Fusitriton* (Gastropoda, Family Cymatiidae)

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ABSTRACT

Cymatona kampyla (Watson) is widespread in New Zealand and south-eastern Australia, and the following subspecies are recognised: *C. kampyla kampyla* (Watson), Recent, south-eastern Australia, and New Zealand and its subantarctic islands but not Macquarie Island; *C. kampyla tomlini* Powell, Recent, Macquarie Island; and *C. kampyla jobbernsi* (King), Pliocene and Pleistocene, central New Zealand. Radulae vary greatly, and Australian and New Zealand living populations show no consistent differences in shape or in radular features.

Fusitriton variation is plotted graphically, and Recent forms are classified as: distinct species—*F. galea* Kuroda and Habe, Japan; and *F. oregonensis* (Redfield), California to Japan; geographic subspecies—*F. cancellatus cancellatus* (Lamarck), South America; *F. cancellatus laudandus* Finlay, around New Zealand from the Three Kings Islands to Macquarie Island; *F. cancellatus murrayi* (E. A. Smith), South Africa; and *F. cancellatus retiolus* (Hedley), south-eastern Australia.*

The ecology of *Cymatona* and *Fusitriton* is discussed in terms of distribution (live and dead) with depth, latitude, and sediment type. Whereas *Cymatona* is endemic to Australia and New Zealand, *Fusitriton* has no fossil history there and did not reach the area until late Pleistocene or early Holocene. The abundance of relict dead shells of *Cymatona* is thought to have been caused by its ecological replacement by *Fusitriton* during that time.

INTRODUCTION

The Family Cymatiidae contains moderate-sized to very large, coarsely sculptured, varicate Mesogastropoda. Its members are recognisable by having two or fewer varices on each whorl of the shell, by the unusually well developed periostracum that almost always bears prominent bristles, by the horny operculum, by the large multispiral protoconch (usually lost in adults, except in *Cymatona*), by the lack of the deep excurrent notchat the top (posterior) end of the aperture that characterises the closely related Family Bursidae, and by the details of the taenioglossan radular teeth.

Most members of the family live on intertidal rocks and coral reefs or on the continental shelf. The only bathyal genera in New Zealand are *Cymatona* and *Fusitriton*, although *Ranella* has sometimes been dredged beyond the edge of the shelf. Elsewhere in the world *Ranella*, *Sassia (=Phanozesta)*, *Gyrineum (Biplex)*, *Fusitriton*, and *Distorsio (Rhysema)* are commonly found in bathyal depths. The shallow-water members of the family generally have unusually wide geographic ranges for benthic gastropods, as they have long pelagic larval lives, and some of the widely distributed species

***Note added in proof**

Cernohorsky *(Records of the Auckland Institute and Museum 14 (1977)*, p. 107*)* has pointed out that the correct name for the species here called *Fusitriton cancellatus* (Lamarck) is *Fusitriton magellanicus* (Röding).

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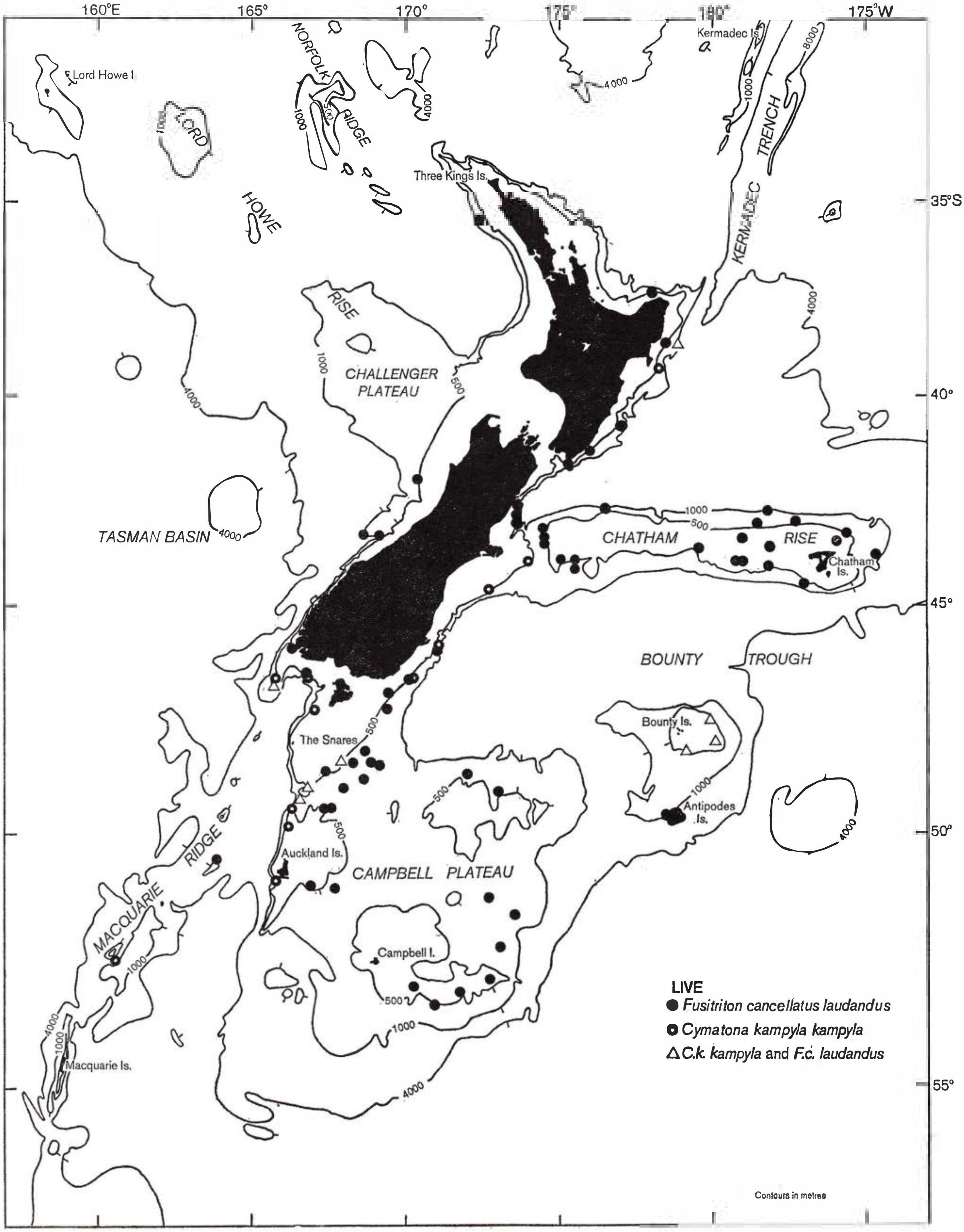


Figure 1 Distribution of NZOI benthic stations containing live *Cymatona kampyla kampyla* and *Fusitriton cancellatus laudandus*.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

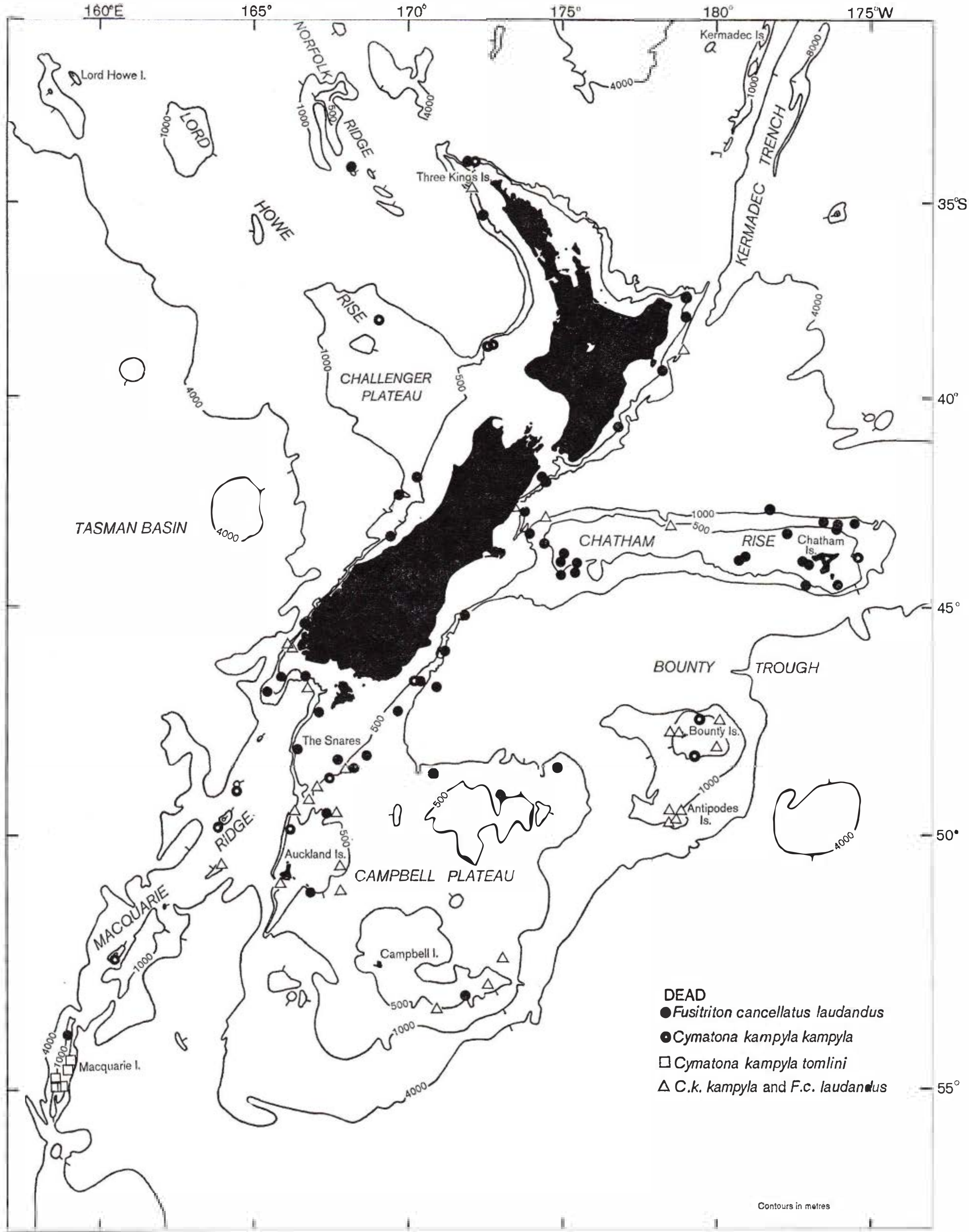


Figure 2 Distribution of NZOI benthic stations containing empty shells of *Cymatona kampyla kampyla*, *C. k. tomlini*, and *Fusitriton cancellatus laudandus*.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

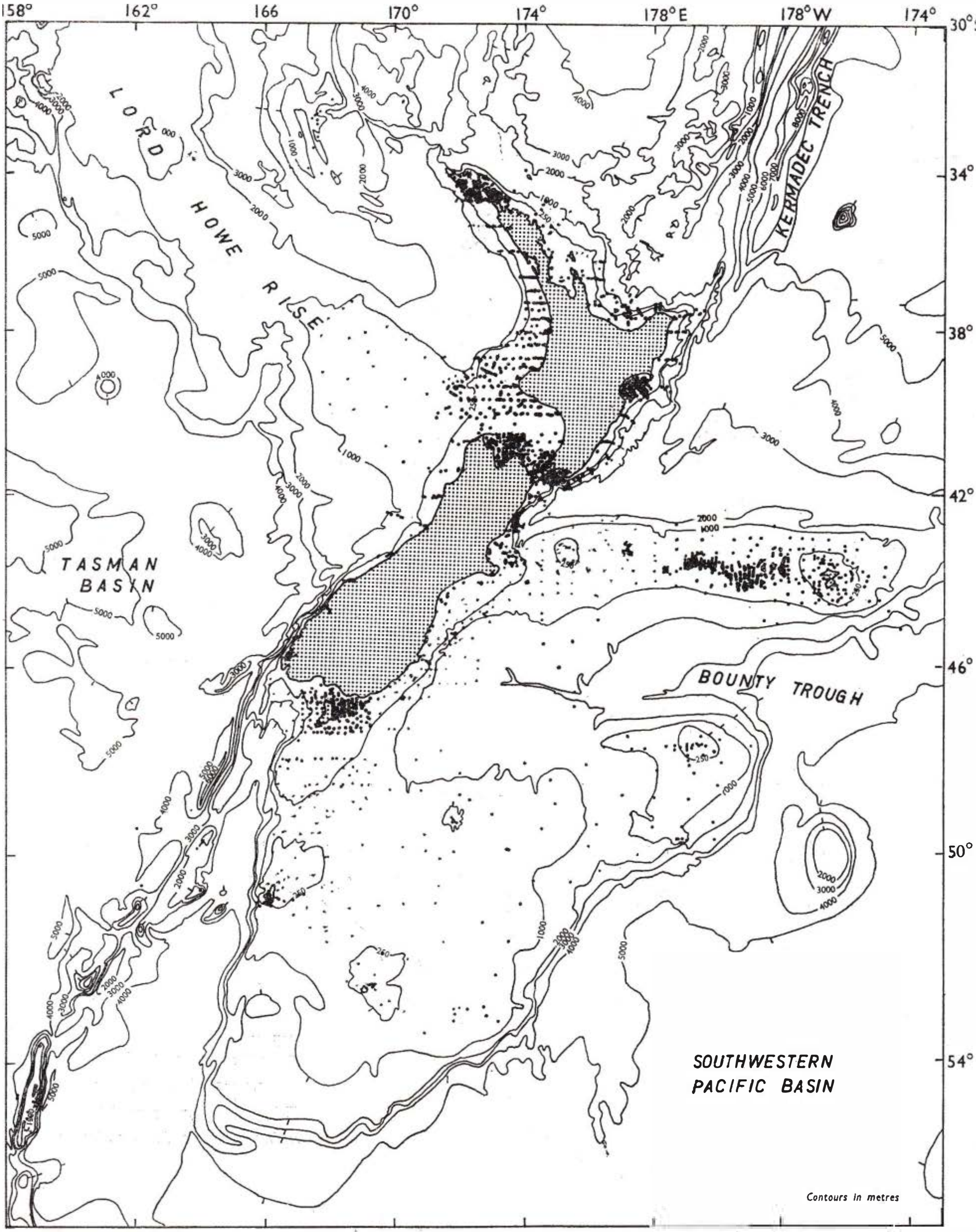


Figure 3 Distribution of NZOI benthic stations in the New Zealand region.

have undergone considerable geographic subspeciation. The present study shows that geographic subspeciation is also well developed in at least some of the bathyal members.

Fusitriton cancellatus laudandus Finlay was first recorded from New Zealand as a single beach shell, under the name *Priene retiolum* (Hedley), by Finlay (1924, p. 462). It is now commonly taken by commercial fish trawlers on the continental shelf off Cape Campbell and off South Canterbury and North Otago, on the eastern coast of South Island. Powell (1950, p. 73, 74) described the *Chlamys delicatula* – *Fusitriton* Community, living on hard sand on the outer part of the continental shelf off eastern Otago, and showed that it closely resembles the *Strongylocentrotus*–"*Argobuccinum*" (i.e., *Fusitriton oregonensis*) community of western Washington, U.S.A. Dell (1956, p. 85) noted that many of his shells of *Fusitriton* from off Otago contained the living animal, whereas most shells from off Cape Campbell were empty. He concluded that the subspecies is essentially bathyal, but has colonised the shelf in a few areas. The population on the shelf off South Canterbury and Otago is self-maintaining, but that off Cape Campbell evidently has been killed off and the few live specimens taken probably represent non-reproducing individuals originating from the bathyal zone. Dell (1956, p. 173) gave the depth range of *Fusitriton cancellatus laudandus* as from 37 to 603 m. Graham (1962) listed the depth zones from which he obtained *F. cancellatus laudandus* on the continental shelf off North Otago.

Cymatona kampyla had not been found in New Zealand before Dell (1956, p. 83) recorded its rare occurrence, but Tomlin (1948, p. 228) and Powell (1955, p. 97) had previously recorded a form of *Cymatona* from off Macquarie Island. Dell had only a few specimens of *Cymatona*, but Dawson (1965, p. 49, 50) later stated that it is common throughout the New Zealand Subantarctic, "particularly in shallower depths off the Bounty and Antipodes Is.". Beu (1967, p. 101) synonymised *Cymatium jobbernsi* King, from upper Pliocene siltstone at Palliser Bay, with *C. kampyla* (Watson). Dawson's mention of the abundance of *Cymatona* in southern New Zealand suggested that further investigation was warranted.

The many *Cymatona* and *Fusitriton* recently collected by the N.Z. Oceanographic Institute were made available to the writer and provided useful new information on the variation, ecology, distribution, and animal characters of both genera. *Fusitriton* in USNS *Eltanin* stations, on loan to Dr R. K. Dell during 1970–71, were examined at the National Museum, and provided additional material from New Zealand, from South America, and from seamounts geographically between the two.

In Appendix 1 are listed the N.Z. Oceanographic Institute stations containing Cymatiidae, and the latitude, longitude, depth, sampling gear, and sediment type of each station and the numbers of live and dead *Cymatona* and *Fusitriton* obtained there. The N.Z. Oceanographic Institute stations at which *Cymatona* and *Fusitriton* have been obtained are shown in Fig. 1 (for live specimens) and Fig. 2 (dead specimens). For comparison, the locations of all NZOI stations up to June 1969 are shown in Fig. 3.

TAXONOMY

Family CYMATIIDAE Iredale, 1913

Genus **Cymatona** Iredale, 1929

Cymatona Iredale, 1929: 177. Type species (by original designation): *Nassaria kampyla* Watson, 1885, Recent, New Zealand and south-eastern Australia.
Cymatoma Cotton, 1945: 255 (incorrect subsequent spelling).

The genus *Cymatona* is characterised by its relatively small size (40–60 mm high), elongate shape, weak sculpture of low, rounded, axial costae and spiral cords with small nodules at the sculptural intersections, relatively long siphonal canal bent slightly towards the dorsum and strongly to the left, low narrow varices every 240° around the shell, weakly developed periostracum, and disproportionately large, turbinate, white protoconch. *Fusitriton* differs from *Cymatona* in its markedly larger size (90–120 mm high), slightly smaller protoconch, relatively shorter and much straighter anterior canal, and less prominent, irregularly placed varices, tending to be spaced about every 200° around the shell.

Cymatona is closely related to *Sassia* Bellardi, which seems to have been the basic stock of all Cymatiidae other than the *Cymatium* group and is an abundant member of most of the Tertiary faunas of the world, surviving as about six widely distributed outer shelf and upper bathyal species. *Cymatona* differs from *Sassia* in the longer, more strongly bent siphonal canal, the much larger turbinate protoconch, and in the details of the radula. The two genera are similar in size, shape, sculpture, operculum, and in the relatively weakly developed periostracum.

A radula was extracted from a specimen of *Sassia remensa* (Iredale) (type species of *Phanozesta* Iredale, 1936, but closely resembling *Sassia apenninica* (Sassi), the fossil type species of *Sassia* Bellardi) from 135 m, off Botany Bay, New South Wales, presented by Mr T. A. Garrard. It differs from that of *Cymatona kampyla kampyla* in the central tooth having a much narrower base and a wider cutting portion bearing denticles almost as large as the main cusp; in the lateral teeth being markedly more highly arched, with a more sharply deflected, narrower cusp bearing one large inner denticle and five large outer ones; and in the inner marginal teeth having more massive, tall, quadrangular bases than those of *Cymatona*.

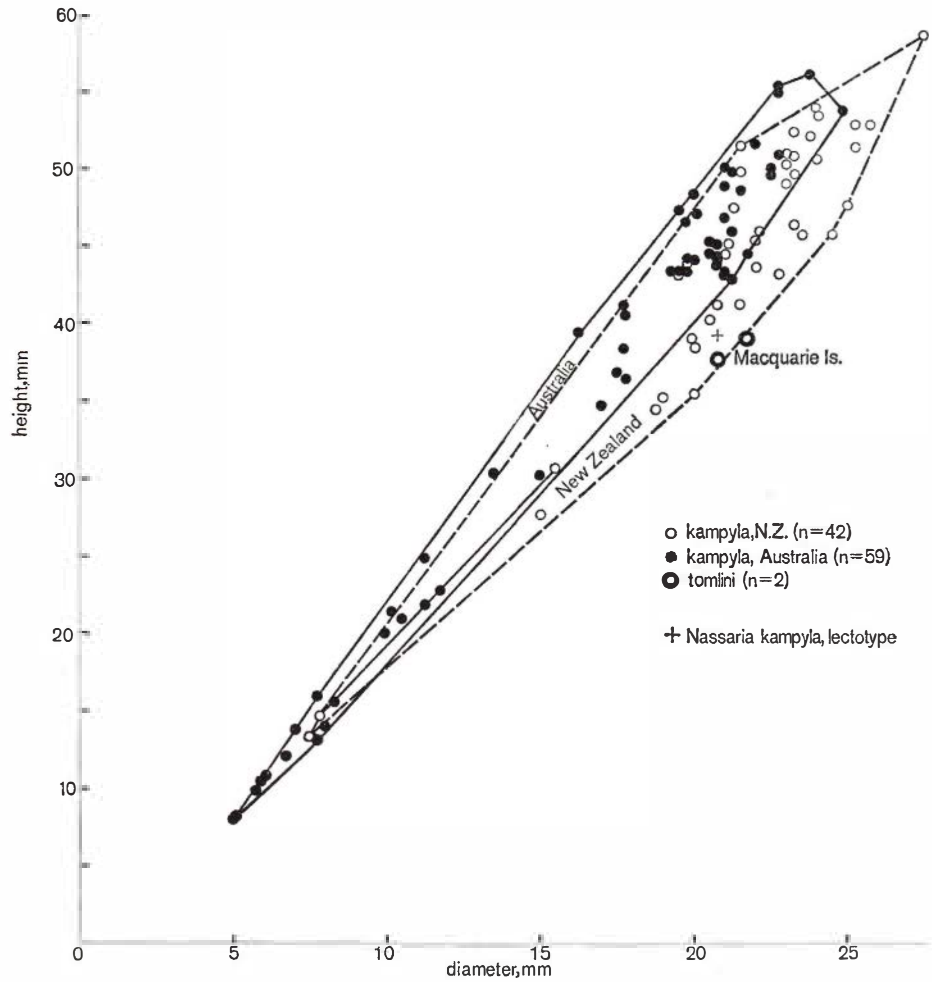
Cymatona is found only in south-eastern Australia, New Zealand, the New Zealand subantarctic islands, and Macquarie Island. A fossil ancestor of *C. kampyla* is to be described by the writer from bathyal Tongaporutuan (Upper Miocene) siltstone in Wairarapa District, New Zealand, and *C. kampyla jobbernsi* is found in bathyal Mangapanian and Nukumaruan (uppermost Pliocene and lower Pleistocene) rocks in South Wairarapa (Beu 1967, p. 101) and in Marlborough and Hawke's Bay.

Cymatona kampyla (Watson, 1885)

The type locality of *Nassaria kampyla* Watson is given as *Challenger* Stn 164b, in 750 m, off Sydney. The true origin of the Mollusca recorded from this station is uncertain. Iredale & McMichael (1962, p. 4, 5) gave a considered opinion that only six of the many molluscan species recorded are likely to be from Australia, most being from the Atlantic, and stated that *Cymatona kampyla* is the only one of these species that has been recollected in Australia. Fell (1958, p. 34) commented on similar confusion in material from nearby *Challenger* stations.

The larger of two syntypes of *Nassaria kampyla* Watson in the Mollusca Section, British Museum (Natural History) is shown in Fig. 4 a [p. 13]. Because of doubts about the locality of the specimen, and its implications if subspecies were to be recognised, the figured syntype (British Museum (Natural History) reg. no. 1887: 2: 9: 1246) is here designated the lectotype of *Nassaria kampyla* Watson, 1885. On the scatter diagram comparing height with diameter of populations of *Cymatona kampyla* (Fig. 5), the lectotype of *Nassaria kampyla* falls to the right of the field of Australian shells, in the field of New Zealand specimens, indicating that the shell almost certainly came from New Zealand rather than Australia. Some light is shed on the possible confusion of *Challenger* stations by examination of the list of stations near New Zealand (Hamilton 1896; Tizard *et al.* 1885, p. 463–7). Stn 164b, if it existed, was the last *Challenger* station near Australia, and Stns 165 to 165c and 166 to 166c were a series taken in deep water on the voyage from Sydney to Cape Farewell, New Zealand, at 900, 735, 464, 334, and 199 miles from Cape Farewell, followed by Stn 167, in 150 fm (270 m) 122 miles from Stephens Island, Cook Strait. As almost all Stn 164b molluscs are known not to be Australian species, it seems likely that the syntypes of *Nassaria kampyla* were included in the "164b" muddle by accident and really came from 165b or 166b, in deep water to the west of New Zealand. Certainly it seems that none of the species in Stn 164b can be regarded as authentically Australian, and it is considered here that typical *Nassaria kampyla* occurs in the New Zealand region.

Figure 5 Scatter diagram comparing height with diameter in populations of *Cymatona kampyla* (Watson).



Powell (1955, p. 98) commented that Australian specimens are all narrower than shown in Watson's figure (1886), and initially this seemed confirmed by the writer's examination of the few available Australian specimens (all immature) in New Zealand collections. Tomlin (1948, p. 228) stated that the specimens from off Macquarie Island, later designated the types of *Cymatona tomlini* Powell, agreed "down to the smallest detail with Watson's largest from *Challenger* Station 164B, said to have been off Sydney in 140 fathoms". Tomlin was obviously doubtful of the locality of Watson's specimens, and gave the impression that he suspected they might have come from Macquarie Island. During 1971 the writer was able to examine large suites of *Cymatona kampyla* in the Australian Museum, taken off New South Wales by Fisheries Research Vessel *Kapala*. These large populations of adult shells demonstrated that there is little, if any, consistent difference in shape between New Zealand and Australian specimens of *Cymatona kampyla*.

To evaluate possible morphological differences between Australian and New Zealand living populations of *Cymatona*, height and diameter of 42 New Zealand specimens and of 50 Australian specimens were measured and plotted on a scatter diagram (Fig. 5). This figure shows that more than 80% of Australian shells overlap New Zealand shells in shape, although they are similar in shape to only the narrower 60% of New Zealand shells. There is no consistent difference in shape between Australian and New Zealand populations of *Cymatona kampyla*, and separate Australian and New Zealand populations are not recognised. *Cymatona tomlini*, from Macquarie Island, is represented by the shortest and broadest shells known to the writer and its varices are markedly more expanded over the shoulder region than in other specimens seen, apart from a few specimens from southern New Zealand (e.g. NZOI Stn D82, Campbell Plateau); the Macquarie Island form is recognised as a geographic subspecies of *C. kampyla*. The New Zealand Plio-Pleistocene population is regarded as a further subspecies, so that taxa recognised in *Cymatona* are:

Cymatona kampyla kampyla (Watson, 1855), living, Australia and New Zealand.

kampyla jobbernsi (King, 1933), Pliocene and Pleistocene, New Zealand.

kampyla tomlini Powell, 1955, Macquarie Island.

As *Cymatona kampyla* has a planktotrophic veliger larva (Dell 1956, p. 84) it is assumed that genetic exchange occurs both between the two living subspecies, and across the Tasman Sea and prevents marked differentiation of Australian and New Zealand populations. The details of evolution of the subspecies are obscure, largely because of the lack of deep water facies in the Australian late Cenozoic succession, but it seems possible that all living forms evolved from the variable *C. kampyla jobbernsi*.

Cymatona kampyla kampyla (Watson, 1885).

Figs 4a–j, l–n; 6a, b, d–f; 7a–c; 12d–e

Nassaria kampyla Watson, 1885: 594; Watson, 1886: 405, pl. 14, fig. 12 (as *campyla* in plate caption).

Lampusia nodocostata Tate and May, 1900: 90; Tate and May, 1901: pl. 23, fig. 2.

Lotorium nodocostatum; Kesteven, 1902: 463, fig. 1; 479, fig. 4.

Fusitriton kampylum; Hedley, 1918: M66.

Cymatium (*Ranularia*) *tenuilirata* var. *nodocostata*; Bayer, 1933: 51.

Cymatona kampyla; Iredale, 1929: 177; Cotton, 1957: 3, fig. 20; Iredale and McMichael, 1962: 55.

Cymatoma [sic] *kampyla*; Cotton, 1945: 255; Dell, 1956: 83, pl. 13, figs 126, 132.

Cymatona kampyla kampyla is recognisable in the New Zealand fauna by its relatively small size (most shells are in the range 30 to 55 mm long); large, turbinate, white protoconch of $2\frac{3}{4}$ smooth, rounded whorls (bearing a prominently bristled periostracum on some very fresh specimens); tall spire; long siphonal canal bent markedly dorsally and to the left from the shell axis; low, narrow varices situated every 240° around the shell (i.e., every $\frac{2}{3}$ whorl); sculpture of about six to eight narrow, well-raised, widely spaced axial folds in each intervariceal space, crossed by two main spiral cords on spire whorls and about seven on the last whorl (forming small, narrowly rounded nodules at their junctions with the axial folds) and six to twelve fine, closely spaced, low, secondary, tertiary, and quaternary threads filling each spiral interspace; and rounded aperture with slightly flared, smooth inner lip and almost obsolete nodules inside the outer lip. The sculpture is identical to that of *C. kampyla tomlini*, but with narrower major elements and weaker nodules than in *C. kampyla jobbernsi*. One large New Zealand shell (NZOI Stn F124; Fig. 4d, e [p.13]) is unusually tall and narrow, and comparable with the narrowest Australian specimens seen.

A moderately large range of variation is seen in New Zealand populations. The spire whorls have two main spiral cords, but frequently there is a third one above the suture and often the intermediate spiral cords on the shoulder become stronger than usual, so that there may be as many as six major spiral cords. Specimens with many spiral cords tend to have rather rounded shoulders, and resemble *C. kampyla tomlini*. The two shells taken at NZOI Stn D82, between The Snares and the Auckland Islands, have strong spiral sculpture, axials coming well down over the base, the shoulder rather rounded, and varices expanded a little over the shoulder, so that they resemble *C. kampyla tomlini* more strongly than do any other New Zealand shells seen in this study. However, they were surrounded by many stations with typical *C. kampyla kampyla*, and their high spires and long siphonal canals show that they belong in the subspecies *kampyla*. Some populations from which very large numbers of specimens were obtained (notably NZOI Stns F94 and A744) contain only small shells, up to about 40 mm high, while most populations with fewer specimens (e.g., NZOI Stns F146, F124, F144) contain specimens up to 57 mm high. These size differences appear to be due to ecological competition within the population and thus to be phenotypic effects.

The colour pattern varies also. Small, dead shells collected from NZOI Stns D17 and D18, and a few others north of them on the Macquarie Ridge, and the few specimens taken on the Challenger Plateau (NZOI Stn D242) have bright, red-brown spiral cords and minute flecks of the same colour on the interstitial spiral threads. A few live shells collected from other stations show faint traces of this colour pattern, but almost all other live specimens are a uniform creamish white. As the substrates where all brightly coloured shells were taken consist largely of volcanic gravel and similar coarse material, whereas most other specimens were taken on somewhat finer substrates, this variation in colour may be a phenotypic variation associated with sediment type.

Most of the variation thus seems to be phenotypic, but the overall variation in shell form causing a few shells to resemble the neighbouring subspecies is assumed to be genetic.

RADULA: Radulae were removed and examined from three New Zealand specimens of *C. kampyla kampyla*: from a male and a female each about 40 mm high from NZOI Stn F94 (Fig. 6b, d) and from a female about 50 mm high from NZOI Stn F120 (Fig. 6a, e, f). Although basically similar, some features show a great degree of variation.

The central tooth is rather low and broad, with a broad bilobate basal plate, a relatively small main cusp, and four to six denticles on each side of the main cusp. The size of the cutting portion relative to the basal plate is highly variable, and in the female from Stn F94 (Fig. 6d) it is relatively much larger than in the other two radulae. The lateral tooth is large and solid, with a heavy, deep, elongate basal plate and a large hooked main cusp. The male from Stn F94 (Fig. 6b) has two or three small denticles on the inner edge of the main cusp, but these are not present in the other two specimens. Both specimens from Stn F94 have five to seven rather large denticles on the outer edge of the main cusp of the lateral tooth, and the number is the same in both laterals in a single row. In the considerably larger radula from Stn F120 (Fig. 6a, e, f) the number of these denticles varies in all possible ways. There are fewer denticles on the left lateral than on the right except near the oldest end of the ribbon, where there are no denticles at all on either lateral, even on teeth that are totally unworn (as shown by their cusps being extremely sharply pointed). Near the nascent end of the ribbon the right laterals have about three to five denticles while the left ones have none

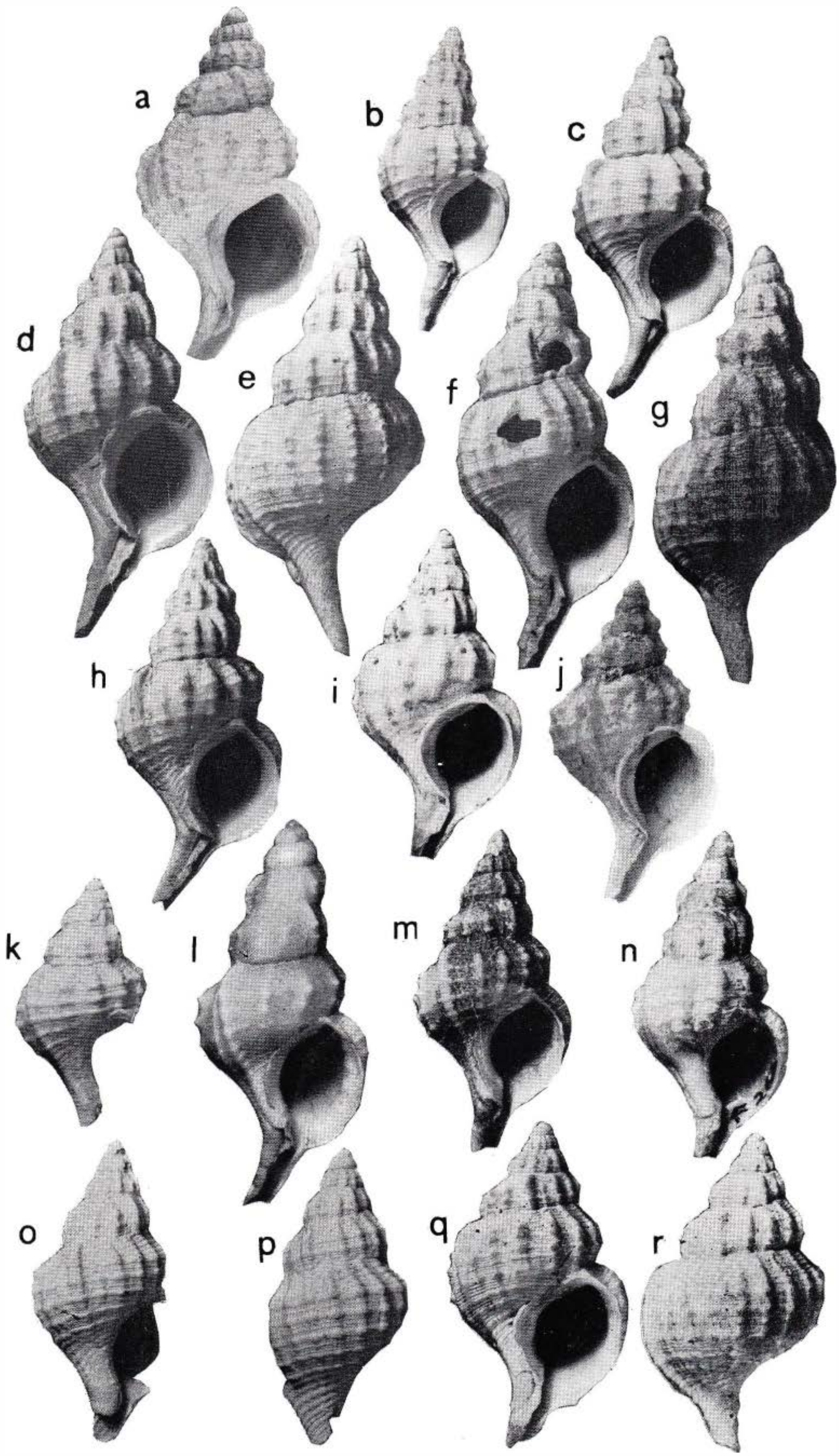


Figure 4 **a**, *Cymatona kampyla kampyla* (Watson), lectotype of *Nassaria kampyla* Watson, *Challenger* "sta. 164b" (off New Zealand?). British Museum (Natural History) no. 1887:2:9: 1246, 39.3 × 20 mm. **b**, **c**, *Cymatona kampyla kampyla*, adult specimens from New South Wales shelf (unlocalised), FRV *Kapala*, N.Z. Geological Survey, WM.10815, 48.9 × 21.7 mm and 54.3 × 24.9 mm respectively. **d**, **e**, *Cymatona kampyla kampyla* (Watson), NZOI Stn F124, Bounty Is, New Zealand, in 476 m; 57.6 × 26.4 mm. **f**, **g**, *Cymatona kampyla kampyla* (Watson), NZOI Stn F144, Campbell Plateau, New Zealand, in 596 m; unusually tall and narrow shell comparable with Australian ones, 51.4 × 21.6 mm. **h**, *Cymatona kampyla kampyla* (Watson), NZOI Stn F120, near the Bounty Is, New Zealand, in 494–512 m; 51.0 × 23.0 mm. **i**, **j**, *Cymatona kampyla kampyla*, specimens from a population containing a large number of small shells; NZOI Stn F94, Campbell Plateau, New Zealand, in 604 m, 40.3 × 20.5 mm and 34.5 × 18.8 mm respectively. **k**, *Cymatona kampyla jobbernsi* (King), N165/f948, Alpha Creek, White Rock Road, South Wairarapa, New Zealand, Mangapanian (late Pliocene); Victoria University Geology Dept, VM.776, 26.1 × 13.5 mm. **l**, *Cymatona kampyla kampyla* (Watson), 183 m, east of Cape Pillar, Tasmania; Suter colln, N.Z. Geol. Surv., WM.5383, 30.7 × 13.5 mm. **m**, *Cymatona kampyla kampyla* (Watson), 137 m, off Newcastle, New South Wales, Australia, MV *Challenge* per T. A. Garrard, National Museum of Victoria, F.23104, 38.5 × 17.8 mm. **n**, *Cymatona kampyla kampyla* (Watson), 82 m, off Botany Bay, New South Wales, Australia; Grigg colln, National Museum of Victoria, F26658, 36.4 × 17.8 mm. **o**, **p**, *Cymatona kampyla jobbernsi* (King), N165/f948, Alpha Creek, White Rock Road, South Wairarapa, New Zealand, Mangapanian (late Pliocene); Victoria University Geology Dept., VM.775, 31.2 × 15.0 mm. **q**, **r**, *Cymatona kampyla tomlini* Powell, NZOI Stn E228, south-east of Macquarie Is, in 148 m, 39.1 × 21.7 mm.

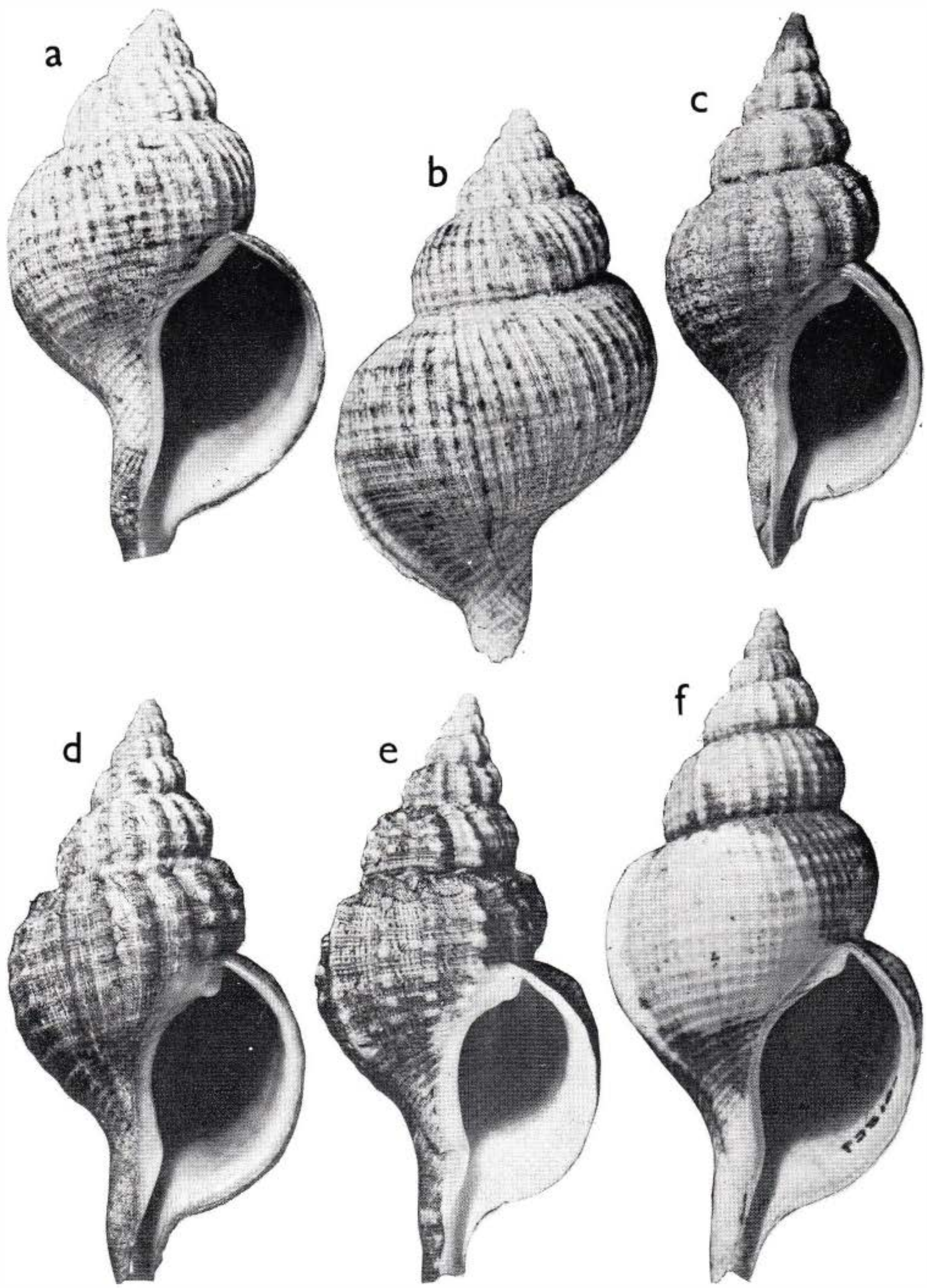


Figure 10 a, b, *Fusitriton cancellatus laudandus* Finlay, NZOI Stn E401, off eastern Otago, in 823–914 m; very short, finely sculptured specimen, 95.6 × 54.9 mm. **c, d,** *Fusitriton cancellatus laudandus* Finlay, NZOI Stn E424, off South Canterbury, 293 m; strongly sculptured specimens resembling *F. oregonensis*: **c,** 93.2 × 44.1 mm, **d,** 96.0 × 47.9 mm. **e,** *Fusitriton galea* Kuroda & Habe, trawled in 183–266 m, off Tosa Bay, Shikoku, Japan; N.Z. Geol. Surv., WM. 9301, 89.8 × 44.7 mm. **f,** *Fusitriton cancellatus retiolus* (Hedley), dredged in 137 m, east of Broken Bay, New South Wales, Australia, MV *Challenge*, per T. A. Garrard, National Museum of Victoria, F.23107, 118.6 × 55.3 mm.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*"; for "*Fusitriton cancellatus retiolus*" read "*Fusitriton magellanicus retiolus*".

Figure 6 **a**, *Cymatona kampyla kampyla* (Watson), laterals from near the oldest end of radula, NZOI Stn F120. **b**, Half-row of radula of *Cymatona kampyla kampyla* from NZOI Stn F94. **c**, Half-row of radula of *Fusitriton cancellatus laudandus* from NZOI Stn F80. **d**, *Cymatona kampyla kampyla*, central and right lateral teeth of female from NZOI Stn F94. **e**, Half-row, and **f**, lateral teeth, from nascent end of radula of *Cymatona kampyla kampyla* from NZOI Stn F120.

Note For "*Fusitriton cancellatus laudandus*" *read* "*Fusitriton magellanicus laudandus*".

to (rarely) three, and usually one or two. The number of these denticles tends to decrease towards the older end of the radula, although in a very irregular manner. The number of denticles on the central teeth also decreases slightly towards the older end of the ribbon.

The inner marginal tooth has a large square base and a long simple cusp. In the radula of the male from Stn F94 the base is relatively very large and the cusp strongly curved, while in the large radula from Stn F120 the base is relatively small and the cusp much more lightly curved. The outer marginal tooth has a relatively small, ill-defined base, and its main cusp shows a similar variation in degree of curvature to that of the inner marginal tooth.

A radula was extracted and mounted also from an Australian specimen of *Cymatona kampyla kampyla* from FRV *Kapala* Stn 71-13-01, south of Twofold Bay, southern New South Wales, 37°42′–39′S, 150°16′–17′E, 30 July 1971, in 393 m (Australian Museum, C. 84110). The central teeth are similar in shape to those in Figs 6b and 6d except that the dorsal outline of the main cusp is

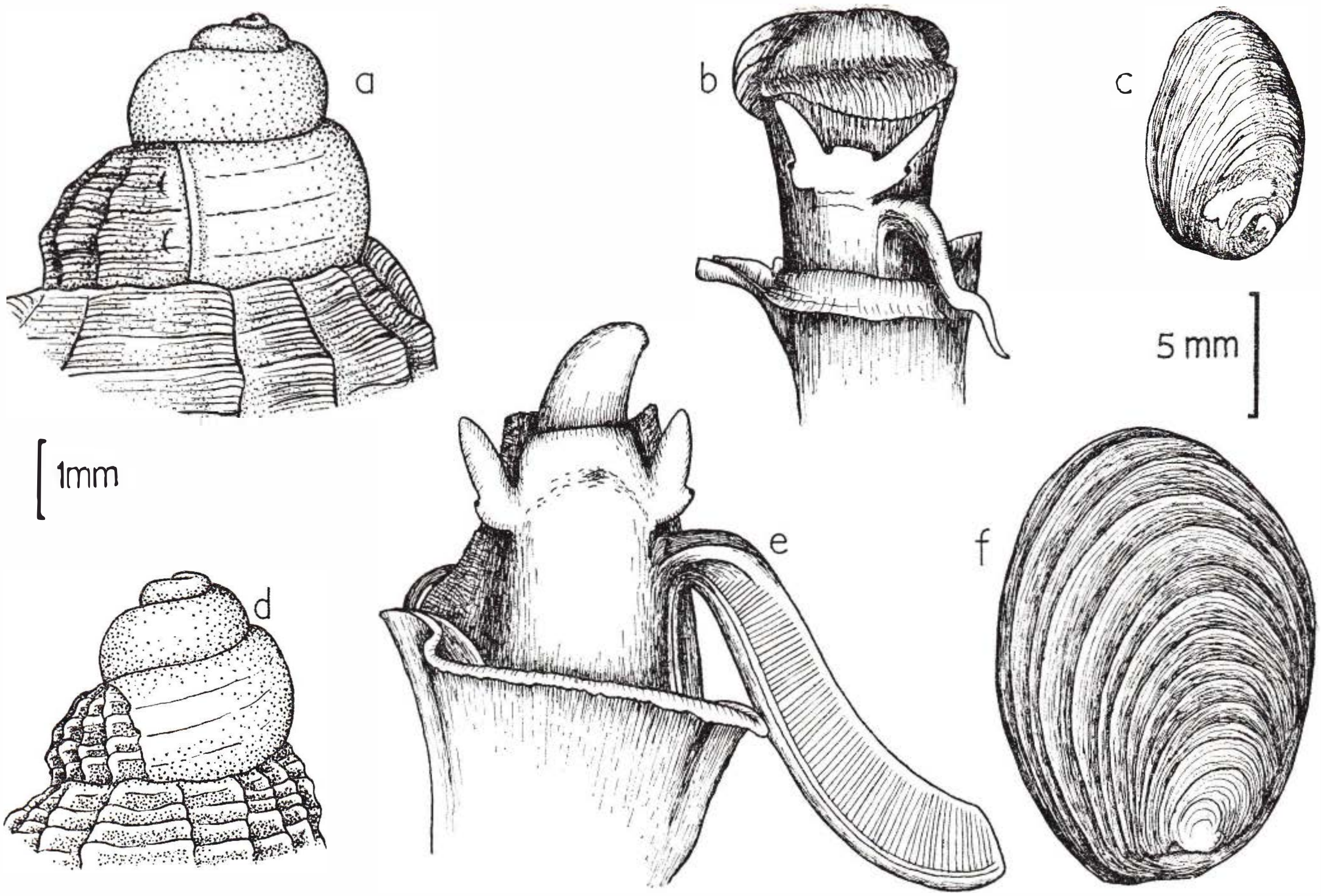


Figure 7 **a**, Protoconch of *Cymatona kampyla kampyla* (Watson); NZOI Stn F94, near The Snares, in 604 m. **b**, Anterior end of contracted male animal of *Cymatona kampyla kampyla* (Watson) removed from shell. Part of mantle reflected to show penis; NZOI Stn F120, near the Bounty Is, in 494–512 m. **c**, *Cymatona kampyla kampyla*, operculum; NZOI Stn F120, near the Bounty Is, in 494–512 m. **d**, Protoconch of *Fusitriton cancellatus laudandus* (Finlay); NZOI Stn F136, Campbell Plateau, in 547 m. **e**, Anterior end of expanded male animal of *Fusitriton cancellatus laudandus* (Finlay), removed from shell. Mantle naturally contracted; NZOI Stn D138, northern Campbell Plateau, in 668 m. **f**, *Fusitriton cancellatus laudandus* (Finlay), operculum; NZOI Stn F80, between The Snares and the Auckland Is, in 631 m. (Left-hand scale applies to protoconchs; right-hand scale applies to opercula.)

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus.*"

slightly embayed in the centre. The lateral teeth are similar in shape to those in Figs 6a, 6e, and 6f, with a rounded, strongly hooked main cusp. The number of denticles on the outer edges of the lateral teeth varies from side to side of one row and from row to row along the ribbon, ranging from three to six and most commonly with four or five on one tooth. As in the two New Zealand female specimens, there are no cusps on the inner edges of the lateral teeth. The range of variation of the denticles falls well within that of New Zealand specimens, and the only difference from New Zealand specimens is the slightly embayed dorsal outline of the central tooth, a feature that cannot be assessed without examination of much more material.

This variation in radular features is much greater than in the many other radulae of Cymatiidae examined by the writer, but considerable variation in such features as the shape of main cusps and numbers of denticles is characteristic of Cymatiidae, and shows that several radulae must be examined before taxonomic conclusions can be drawn from this feature.

ANIMAL: The anterior portion of the animal of a male specimen from NZOI Stn F120 is shown in Fig. 7b. It is a typical generalised cymatiid, with relatively large black eyes on small projections near the bases of the tentacles. The penis is relatively small, tapers regularly to a point, and often shows a marked bend at about half its length, presumably where it was folded in the mantle cavity.

The operculum of a different specimen from NZOI Stn F120 is shown in Fig. 7c. It is slightly eroded over the lower portion, but enough of the growth lines remain to show that the nucleus is situated just inside the lower right margin. The operculum is oval in shape, and slightly narrower at the top than at the bottom.

Inset 3*

DIMENSIONS: dimensions of all forms of *Cymatona* are given in Appendix 2.

GEOGRAPHIC RANGE: In Australia, from northern New South Wales to the Great Australian Bight, including Tasmania. The subspecies is quite common on the continental shelf, but living specimens also seem to be markedly more abundant in upper bathyal depths than they are around New Zealand. The subspecies is about equally as common as *Fusitriton* in recent deep samples from south-eastern Australia, whereas *Fusitriton* is markedly more common than *Cymatona* around New Zealand. In New Zealand *C. kampyla kampyla* has been taken in large numbers, mainly in the bathyal zone, at stations from Cook Strait and the Chatham Rise, south to the north side of Macquarie Gap and the southern edge of Campbell Plateau, and at two stations further north, one on Challenger Plateau and one in Hikurangi Trench. One dead shell was taken at each of four stations from North Taranaki to the Three Kings Islands, off western North Island, and the subspecies is probably distributed rarely all around North Island. South of Cook Strait it becomes more common southwards, occurring around all the subantarctic islands of New Zealand (apparently with the exception of Campbell Island), and dead shells are distinctly more common around the Bounty, Antipodes, and Auckland Islands than elsewhere. The significance of this is discussed in the section on ecology. The stations from which living and dead specimens of *Cymatona* and *Fusitriton* have been obtained around New Zealand (to June 1969) are shown in Figs 1 and 2. The subspecies is most abundant in the bathyal zone, and is rare in the neritic zone. By contrast, *C. kampyla kampyla* is as common on the shelf as in the bathyal zone in Australia, and *C. kampyla tomlini* is largely neritic.

LOCALITIES. AUSTRALIA: From 119 m, off Broken Bay, N.S.W. MV *Challenge*, N.Z. Geological Survey, WM. 9312, per T.A. Garrard; 82 m, off Botany Bay, N.S.W., National Museum of Victoria No. F26658; 119 m, off Newcastle, MV *Challenge* per T. A. Garrard, National Mus. Victoria F23104; 183 m, off Cape Pillar, Tasmania, Suter Collection, N.Z. Geological Survey (topotypes of *Lampusia nodocostata* Tate and May); and the following in the Australian Museum: C.2963, off Port Jackson Heads, N.S.W., "co-type" (syntype from *Challenger* material?); C.79199, off Newcastle, N.S.W., 32°46′–33°15′S, 152°16′–46′E, 153–300 fms, 5–12.5.1971, FRV *Kapala* Stn 71–08; C.71393, about 27 miles SE of Cape Everard, Victoria, 90–115 fms, FIS *Endeavour*, 9.5.1914; C.79193, E of Broken Bay, N.S.W., 33°34′S, 152°03′E, 21.4.1971, 300 fms, FRV *Kapala* Stn 71–07–02; C.79197, E of Broken Bay, N.S.W., 33°41′S, 151°55′E, 20.4.1971, 30 fms, FRV *Kapala* Stn 71–07–01; C.79179, E of Sydney, 33°40′–51′S, 152°45′–54′E, 13–17.4.1971, 250–275 fms, FRV *Kapala* Stn 71–06; C.80175, off Sydney, 548 m, 33°40′S, 151°50′E, FRV *Kapala*, June 1971; off Cronulla, N.S.W., four lots taken in 1963–65 by CSIRO Cronulla, in 40–100, 80, 100 and 200 m; 2 miles S of Tasman Head, South Bruny I, S.E. Tasmania, 43°33′45″S, 147°19′21″E, 73 m, 24.3.1970, FRV *Penghana*, C.31933, 40 miles S of Cape Wiles, S. Aust., 100 fms, FIS *Endeavour*; C.26006, Cape Jaffa, S. Aust., 300 fms; C.16256, off Port Kembla, N.S.W., 63–75 fms; C.71418, continental shelf off N.S.W.; C.56722, Oyster Bay, Tasmania; C.28974, off Cape Pillar, Tasmania, 100 fms (topotypes of *L. nodocostata*); C.71395, *Challenge* trawl 318, 156–160 fms, E of Newcastle, N.S.W., A. A. Racek, 2.7.1959; C.71394, dredged, 100 fms off Cape Pillar, Tasmania, June 1912 (topotypes of *L. nodocostata*); C.66471, 500 fms, off Twofold Bay, N.S.W.; C.64255, 75 fms, off Broken Bay, N.S.W., *Challenge*; C.24439, 300 fms, 27½ miles E of Sydney Heads, N.S.W.; C.71396, CSIRO Stn G3/201/60, 200 fms, off Sydney, N.S.W., 8.11.1960; C.66410, 80 fms, off Port Kembla, N.S.W.; C.71397, off Gabo I, N.S.W., 150–200 fms, Nov.–Dec. 1913; C.63375, 75 fms, off Newcastle, N.S.W., *Challenge*; E.5736, S of Cape Everard, Victoria, 200–260 fms, 22.10.1914, FIS *Endeavour*; C.26668, 35 miles E of Sydney, 800 fms; E.5745, Gabo I to Cape Everard Banks, Victoria, 100–200 fms, Oct. 1914, FIS *Endeavour*; C.66414, 75 fms, off Botany Bay, N.S.W.; C.63374, 90 fms, off Botany Bay, N.S.W., *Challenge*; C.73601, 30 miles S of Cape Everard, Victoria, 200 fms, 22.10.1914, FIS *Endeavour*; C.79056, E of Sydney, 75–150 m, HMAS *Gascoyne*, G2/55-57/62, CSIRO, 18.7.1962; C.80174, off Newcastle, N.S.W., 33°11′S, 152°23′E, 567–548 m, FRV *Kapala*, 29.4.1971; C.82471, off Sydney, 366–549 m, 34°40′–35°01′S, 151°07′–13′E, 25.5.1971, FRV *Kapala* Stn 71–11–06/07, 2½ miles NE of Beaching Bay, Maria Is, SE Tasmania, 42°27.5′S, 148°12′E, 82.5 m, 25.3.1970, FRV *Penghana*; C.82102, 50 miles SW to W of Cape Adieu, Gt Australian Bight, 79 m, G2/90/62, CSIRO, HMAS *Gascoyne*; C.82103, 25 miles E of Twofold Bay N.S.W., 159 m, 19.6.1962, CSIRO, HMAS *Gascoyne*; C.82106, 20 miles SE of Twofold Bay, N.S.W., 37°26′S, 150°15′E, 149 m, 19.6.1962, HMAS *Gascoyne* Stn G2/59/62; C.82107, 25 miles S of Tamboon Inlet, Gippsland, Vic.,49°8′50″S, 138°13′25″E, 95–100 fms, Stn 6, *Esso-Gipps*, May 1969; C.82111, 40–100 m, off Cronulla, N.S.W., CSIRO, Dec. 1963; C.82250, off mouth of Manning R., N.S.W., 45–50 fms, Knut Moller, trawler *Ben Bow*; C.82100, between Cape Howe and Lake Entrance, Vic., 75–300 m, CSIRO, 19–20.7.1962, HMAS *Gascoyne*, G2/58-62/62; C.79183, 25 miles E of Sydney, 150–200 fms, 6–7.4.1971, FRV *Kapala* Stn 71–05; C.79206, off Newcastle, N.S.W., 32°46′–51′S, 152°46′–42′E, 325 fms 7.5.1971, FRV *Kapala* Stn 71–09–01; C.82475, off Ulladulla, N.S.W., 35°25′–29′S, 150°50′–48′E, 549 m, 2.8.1971, FRV *Kapala* Stn 71–13–06; C.97204, off Newcastle, N.S.W., 33°11′S, 152°23′E, 310 fms, 29.4.1971, FRV *Kapala* Stn 71–08–05; C.16769, off Botany Heads, N.S.W., 50–52 fms, C.17973, off Wollongong, N.S.W., 100 fms; C.24439, 27½ miles E of Sydney, 250 fms; C.25895, 22 miles E of Narrabeen, N.S.W., 80 fms; C.35101, off Sydney; 410 fms; C.71348, off Gabo I, N.S.W., 30 fms; E of Sydney, 34°03′S, 151°37′E, 295 m, CSIRO, 18.7.1962, HMAS *Gascoyne* Stn G2/57/62; C.17132, off Wollongong, N.S.W., 100 fms, figured by Hedley, Proc. Linn. Soc. N.S.W., 27: 479, fig. 4; C.82933, 9½ miles NE Tasman I, SE Tasmania, 43°12′30″S, 148°13′45″E, 570.5 m, 24.3.1970, W. F. Ponder on FRV *Penghana*.

LOCALITIES. NEW ZEALAND: In addition to the N.Z. Oceanographic Institute localities in Appendix 1, *Cymatona* has been taken at only a few stations around New Zealand. Because all except one juvenile from off White Island (recorded by Dell, 1963, p. 216; detailed data confirmed by personal observation of National Museum material) are from areas where specimens have been obtained in N.Z. Oceanographic Institute samples, the localities have not been plotted on Figs 1, 2. The localities are: Chatham Islands 1954 Expedition Stn 52, 44°04′S, 178°04′W, Chatham Rise, in 475 m, National Museum M10426 (specimen figured by Dell, 1956, pl. 13 figs 126, 132); Portobello *Alert* Stn 54-13, Canyon E, ESE of Taiaroa Head, East Otago, in *c.* 550 m, National Museum (M9109); Victoria University of Wellington Zoology Dept. V.U.Z. Stn BOQ, Coll. 96, 41°31′S, 174°55′E, off Palliser Bay, in *c.* 695 m, National Museum M12979; National Museum B.S. 203, 37°30′S, 177°03′E, off White Island, Bay of Plenty, in *c.* 530 m, National Musuem M11278 (juveniles only); Portobello *Alert* Stn 54–22, Taiaroa Canyon (Canyon A) ENE of Taiaroa Head, East Otago, in *c.* 550 m, National Museum M9196; (juveniles only); Portobello *Alert* Stn 54–9, Papanui Canyon (Canyon E) ESE of Taiaroa Head, East Otago, National Museum M9427 (juveniles only); also several specimens from off Otago Peninsula, taken recently by MV *Munida*, held by Portobello Marine Biological Station.

Cymatona kampyla tomlini Powell, 1955.

Fig. 4q, r.

Nassaria kampyla; Tomlin, 1948: 228, pl. 2, fig. 5 (not of Watson, 1885).
Cymatona tomlini Powell, 1955: 97.

Powell (1955, p. 97) stated that the Macquarie Island form of *Cymatona* differed from the Australian *C. kampyla kampyla* by "being more heavily built, with a wider spire angle, more capacious whorls, a much shorter strongly recurved anterior canal, and longer axials, which extend over most of the base". Most N.Z. Oceanographic Institute specimens from Macquarie Island are worn and broken (one specimen from each of NZOI Stns C732a, D8, D9, E237a), but they demonstrate that Powell's distinguishing features are consistent and useful. The single well preserved dead shell from Stn E228 is figured in Fig. 4q, r [p.13]. An additional difference from other forms of *Cymatona kampyla* is that the varices are wider over the shoulder than they are lower down. Some specimens from Campbell Plateau (Stn D 82, mentioned under *C. kampyla kampyla*) resemble *tomlini* in some of these features, and *tomlini* is considered to be a geographic subspecies of *C. kampyla.*

DIMENSIONS: are given in detail in Appendix 2; the average height is 38 mm, diameter 20 mm.

GEOGRAPHIC RANGE: The subspecies is known only from the narrow continental shelf surrounding Macquarie Island, and is not present in any N.Z. Oceanographic Institute samples from deep water off the island. In view of the wide distribution of *C. kampyla kampyla* in Australia and New Zealand, and of its dispersal as planktonic larvae, it is remarkable that the subspecies has developed at Macquarie Island. Macquarie Gap in Macquarie Ridge immediately north of the island, with a maximum depth of slightly less than 4000 m and a width of about 55 km (Brodie & Dawson 1965) may present the partial barrier to dispersal necessary for the development of the subspecies, but it is relatively narrow and would not normally present a barrier to planktonic organisms. A westward current (that is, part of the circumpolar current) passing to the north of Macquarie Island would carry the larvae of *C. kampyla tomlini* clear of the island, and thus account for the distribution pattern.

Cymatona kampyla jobbernsi (King, 1933).

Fig. 4k, o, p.

Cymatium jobbernsi King, 1933: 341, pl. 35, fig. 1.
Cymatona kampyla; Beu, 1967: 101, pl. 1, fig. 7 (not *Nassaria kampyla* Watson, 1885).

Several fossil specimens are now available for comparison with the large collections of *C. kampyla kampyla* in the N.Z. Oceanographic Institute and the Australian Museum. All the fossil shells are more irregularly coiled and have broader and higher spiral cords than Recent shells, and are regarded as an ancestral subspecies of *C. kampyla.* The holotype of *C. jobbernsi* (in the N.Z. Geological Survey, TM. 3958) is a large incomplete shell with relatively greatly distorted whorls. Most fossils are somewhat decorticated, and the sculpture is shown best by two shells from Alpha Creek, a tributary of Mangaopari Stream near White Rock Road, 12 km south of Martinborough, southern Wairarapa (Mangapanian, upper Pliocene), Victoria University Geology Department Collection No. V1958, figured here [p.13].

DIMENSIONS: of specimens are given in Appendix 2; average height is 35 mm, diameter 18 mm.

LOCALITIES: Cliffs E of Lake Ferry, Palliser Bay, holotype (N.Z. Geological Survey, TM 3958); V1486, cliffs half mile E of Lake Ferry, Palliser Bay; V1489, large gully half way between Lake Ferry and Whangaimoana, Palliser Bay; V1490, second large gully W of Whangaimoana, Palliser Bay; V887, cliffs E of Whangaimoana, Palliser Bay; all Mangapanian (Beu 1967, p. 92). Also from GS. 4515 (=V1958), Alpha Creek, off White Rock Road, Martinborough, two specimens in N.Z. Geological Survey and three in Victoria University Geology Dept., Mangapanian; V2619, S55/229, "Hundalee conglomerate" (probably = Bourne Conglomerate), Conway River, Marlborough, Mangapanian (King 1933, p. 341); Motunau, North Canterbury, Nukumaruan, specimen in Canterbury Museum (M10273); GS1215, cliffs S of mouth of Wairoa River, northern Hawke's Bay (Nukumaruan).

TIME RANGE: Mangapanian and Nukumaruan (latest Pliocene and early Pleistocene).

Genus **Fusitriton** Cossman, 1903

Fusitriton Cossman, 1903: 109. Type species (by original designation): *Triton cancellatus* Lamarck, 1816 (= *Neptunea magellanica* Röding, 1798; *see* Cernohorsky 1977: 107), Recent South America.
Cryotritonium von Martens, 1903: 38. Type species (by subsequent designation, Powell, 1951): *Lampusia murrayi* E. A. Smith, 1891, Recent, South Africa.

Beu (1971) has shown that *Fusitriton* and *Cryotritonium* were "published simultaneously" within the meaning of the International Code of Zoological Nomenclature, and acting as first reviser, chose the name *Fusitriton* Cossman, 1903, for the genus named *Fusitriton* by Cossman and *Cryotritonium* by von Martens.

Von Martens (1903, p. 38) introduced *Cryotritonium* in the species heading "*Tritonium (Cryotritonium* n.*) Murrayi* E. Smith". At first sight it seems that the type species is determined by monotypy, but after his discussion of *murrayi*, Martens discussed the other species of *Fusitriton* (as now understood) as further species of *Cryotritonium*, without selecting a type. The first designation of a type species appears to have been by Powell (1951, p. 130), who stated: "Genus *Fusitriton* Cossman 1903/Type (o.d.): *Triton cancellatum* Lamarck = *Cryotritonium* Martens 1903, Type *Lampresia* [sic] *murrayi* Smith. . ."

The genus *Fusitriton* is characterised by its elongate fusiform shape, its weak and rather irregularly placed varices, its periostracum bearing many rather long, stiff, widely spaced bristles, and its sculpture of spiral and axial

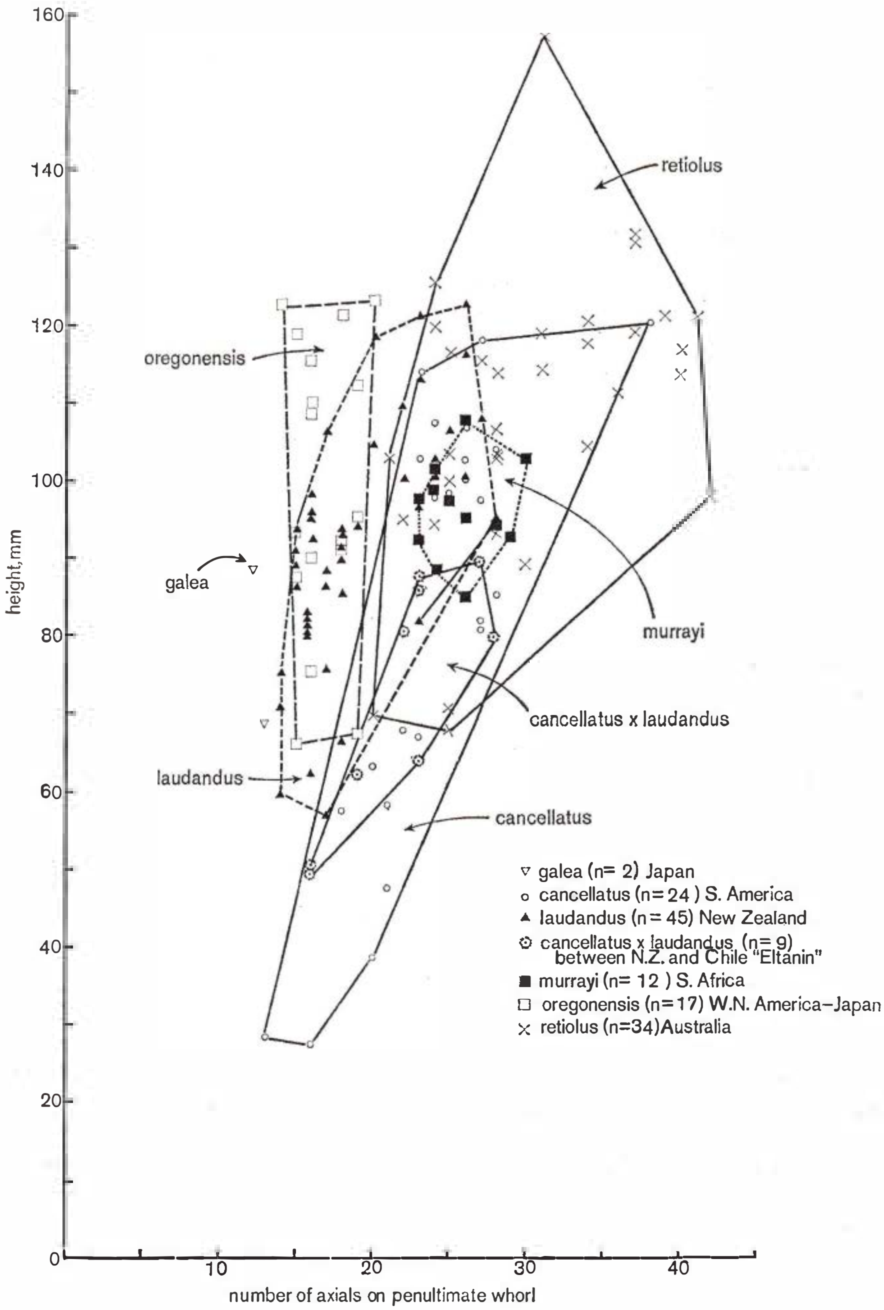


Figure 8 Scatter diagram comparing numbers of axial ribs with height in populations of *Fusitriton.*

Note For "*cancellatus*" read "*magellanicus*".

cords, approximately equal in height, with low nodules at their intersections.

The protoconch (Fig. 7d) had not been described until Smith (1970, pl. 44, fig. 1) figured a protoconch, enlarged about two times, of a New Zealand specimen; it is rather large, of three smooth rounded whorls, turbinate, white, and tilted at a very slight angle to the axis of the teleoconch. The operculum is regularly oval, with the nucleus situated a little in from the edge on the lower right margin (Fig. 7f).

Forms of *Fusitriton* are found around all the main land masses in the temperate regions of the Southern Hemisphere, but the species *F. galea* Kuroda & Habe (Fig. 11e) is restricted to eastern Shikoku and Honshu, south of Tokyo Bay, Japan (Smith 1970, text-fig. 10); one form extends from California to northern Japan. Fossils are known from the ?Pliocene and later in South America, Miocene and later in Japan and, in particular, in western North America, where the genus appears to have arisen from *Gyrineum* (= *Apollon*) or a similar genus during the Eocene or Oligocene (Smith 1970, p. 525). The earliest definite species is *F. dilleri* (Anderson and Martin, 1914), Oligocene to Middle Miocene, from Alaska, Washington, and California (Smith 1970, p. 503). All Recent forms are extremely similar, and show a considerable overlap of shell form and sculpture between the different "species". Some shells of *F. laudandus* Finlay examined resemble *F. galea* Kuroda and Habe from Japan and some resemble *F. cancellatus* (Lamarck) from South America. Thus the nomenclature of described taxa has long been problematical.

The most recent reviser, Smith (1970), ranked the described Recent species of *Fusitriton* as follows:

Fusitriton cancellatus cancellatus (Lamarck, 1816), South America;

F. cancellatus murrayi (Smith 1891), South Africa (= *algoensis* Tomlin, 1947);

F. galea Kuroda and Habe, 1961, Japan;

F. oregonensis (Redfield, 1846), California to northern Japan;

F. retiolus (Hedley, 1914), Australia and New Zealand (= *laudandus* Finlay, 1926, = *futuristi* Mestayer, 1927);

[*F. midwayensis* Habe and Okutani, 1968, Midway Island; here considered to belong in *Sassia* Bellardi.]

The writer undertook measurement and graphical analysis of all available specimens of *Fusitriton* from outside the New Zealand region, and of 45 New Zealand specimens (including the most extreme), to try to evaluate the great variation and apparent similarity of world-wide taxa. Figures 8, 9 are scatter diagrams comparing height with diameter and number of axials on penultimate whorl with height. The first was chosen as an indicator of shape (relative height), and the second as an indicator of relative coarseness of sculpture. Numbers of axials were measured on the penultimate rather than last whorl to minimise the effect of apparently gerontic reduction in size, and in some specimens of the number of axials that occurs over the last quarter-whorl of Southern Hemisphere forms.

The results show that the "gerontic" reduction may be merely a normal progressive reduction in size and increase in numbers of axial ribs down the shell, so that in large adults some axials become so weak as to be almost unrecognisable; it is paralleled in the Northern Hemisphere *F. oregonensis* by great increase in amplitude and wave-length of the axial folds on the last half whorl, without any increase in their number or decrease in their spacing.

In the following discussion of the scatter diagrams, no attempt is made to recognise biologically valid taxa; a named form from each region is identified by its trivial name, as follows: *F. cancellatus*, S. America; *F. galea*, Japan; *F. laudandus*, New Zealand; *F. murrayi*, S. Africa, *F. oregonensis*, California to Japan; and *F. retiolus*, Australia. Dimensions, localities and numbers of specimens (n) for each taxon are shown in Appendix 3.

From the diagrams is deduced:

1 Scatter diagrams comparing both height and diameter with numbers of axial ribs were prepared initially, but were so nearly identical that only the former is presented (Fig. 8). The similarity evidently reflects the fact that shells of *Fusitriton* maintain their proportions very constantly throughout growth.

2 *F. oregonensis* (n = 17) has a broader range of shape than any Southern Hemisphere form, and overlaps all Southern Hemisphere taxa. However, *F. oregonensis* has fewer axial ribs than all southern taxa and, most notably, in the diagram comparing height with numbers of axials (Fig. 8) *F. oregonensis* (and *F. galea*, apparently) plot as a vertical band up the graph, demonstrating that the number of axials does not increase with increasing absolute shell size. Individual axial ribs merely increase their amplitude and wave-length to occupy the increasing space, whereas in all Southern Hemisphere taxa, extra ribs of constant size and uniform spacing are added between the original ones to occupy the increasing space.

3 *F. retiolus* (n = 34) exhibits a very great variation in the number of axial ribs, but almost always does not overlap with *F. laudandus* (n = 44) in axial numbers; large specimens are slightly taller and narrower than *F. laudandus* and reach a larger size than any other form.

4 Although the range of variation of *F. laudandus* encompasses forms broader than any others seen, it lies entirely outside the area of *F. cancellatus* in the diagram comparing height with diameter (Fig. 9) (i.e., is relatively narrower) except for the eight squattest specimens; also, in the diagram comparing height with axial number (Fig. 8), *F. laudandus* overlaps only moderately (i.e., has coarser sculpture than) *F. cancellatus*.

5 Geographical intermediates between *F. laudandus* and *F. cancellatus*, from USNS *Eltanin* Stns 1346 (54°50′S, 129°48′W, 549 m, n=2) and 1691 (53°56′S, 140°19′W, 362–567 m, n=7), resemble *F. cancellatus* in their fine sculpture but resemble *F. laudandus* in their relatively narrow shape.

6 *F. murrayi* lies entirely within the area of *F. laudandus* in the diagram comparing height with diameter, and overlaps the area of *F. cancellatus* only slightly more than do all but the squattest four *F. laudandus*; in number of axials it falls in the area of *F. cancellatus*; thus *F. murrayi* resembles *F. laudandus* in shape and resembles *F. cancellatus* in NUMBER of axials (although SIZE of axials, not measured, is still finer than in most *F. cancellatus*); this contradicts the statement by Smith (1970, p. 455) that "Southern species can generally be divided into two groups, one with a higher spire (material from Australia and New Zealand) than the other (specimens from South America and South Africa)".

7 *F. galea* has still fewer axial ribs than all specimens of *F. oregonensis*.

CONCLUSIONS:

1 Because of their markedly different type of growth, Recent Northern Hemisphere members of *Fusitriton* (*F. oregonensis* (Redfield) and *F. galea* Kuroda and Habe) are considered to belong in different species from all Recent Southern Hemisphere taxa.

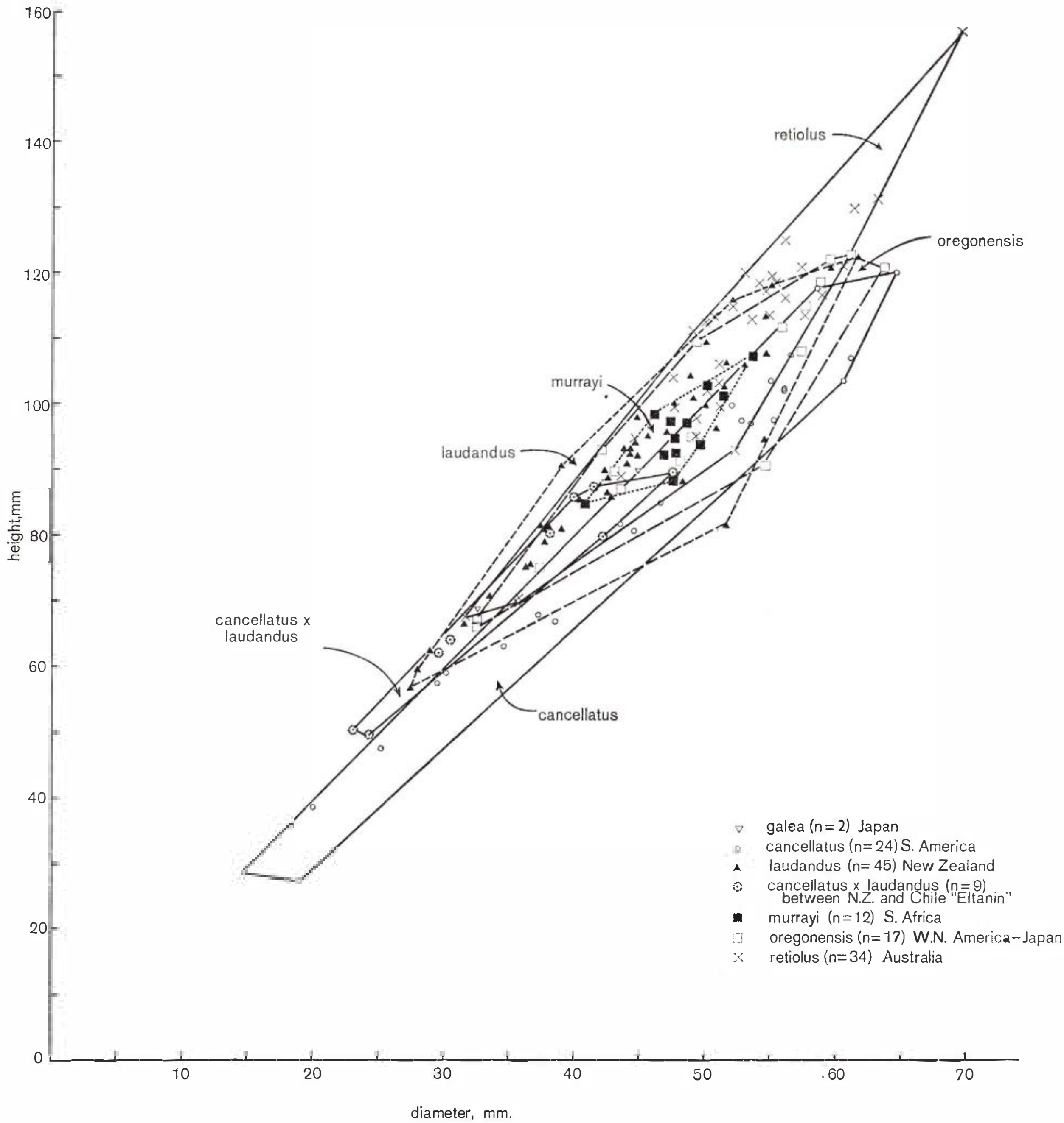


Figure 9 Scatter diagram comparing height with diameter in populations of *Fusitriton*. **Note** For "*cancellatus*" read "*magellanicus*".

2 All Recent Southern Hemisphere taxa in *Fusitriton* overlap slightly to markedly in all features, and are considered to be geographic subspecies of one wide-ranging species. The earliest name for the species is *F. cancellatus* (Lamarck). Judged by relationships suggested by Smith (1970, p. 500) the ancestor of this species in the Northern Hemisphere was probably the Californian Pliocene *F. scotiaensis* (Martin) rather than *F. oregonensis*. The geographically intermediate population between *F. laudandus* and *F. cancellatus* is also morphologically intermediate (resembling *F. laudandus* in shape but *F. cancellatus* in sculpture), suggesting frequent transport of larvae from Australia and New Zealand to South America in the west-wind drift, and thus frequent introduction of Australian and New Zealand genes to South American populations. This supports the suggestion that Southern Ocean populations are geographic subspecies of the one wide-ranging species.

3 *Fusitriton cancellatus laudandus* is a distinct subspecies from *F. cancellatus retiolus*.

In summary, the proposed classification of living forms of *Fusitriton* is:

Fusitriton cancellatus cancellatus (Lamarck, 1816), South America;

F. cancellatus murrayi (E. A. Smith, 1891), South Africa;

F. cancellatus retiolus (Hedley, 1914), Australia;

F. cancellatus laudandus Finlay, 1926, New Zealand;

F. galea Kuroda and Habe, 1961, Pacific coast of southern Japan;

F. oregonensis (Redfield, 1846), California to northern Japan.

Fusitriton midwayensis Habe and Okutani (1968, p. 48, pl. 3, fig. 6) is very small for the genus, and is probably not closely related; and is considered to belong in *Sassia* Bellardi. *Fusitriton antarcticus* Powell and *F. aurora* Hedley are conspecific, and belong in the recently-established buccinid genus *Antarctoneptunea* Dell (Dell 1972).

Fusitriton cancellatus (Lamarck, 1816)*

Triton cancellatus Lamarck, 1816: pl. 415, fig. 1; Liste, p. 4.

The circum-Southern Ocean species *Fusitriton cancellatus* differs from Northern Hemisphere species in having shorter, denser, and paler periostracal bristles, and in having more numerous and less prominent axial ribs because of its method of shell growth by increasing the number of axial ribs per whorl while keeping the size and spacing of the ribs constant, rather than by keeping their number constant and increasing their size and spacing. A geographic subspecies is recognised at each of the main land masses around the northern margin of the Southern Ocean (subspecies listed above) and two subspecies are discussed in more detail below.

Several authors have suggested that *Murex magellanicus* Gmelin, 1791 is an earlier name for *Fusitriton cancellatus* (Lamarck, 1816). Gmelin (1791: p. 3548) referred to the following figures:

"Knorr Vergn. 4. t.30. f.2.
Martin. Conch. 4. t.139. f.1297.
β Chemn. Conch. 10. t.164. f.1570."

The Knorr and Martini figures are of *Trophon gervesianus* (Pallas), while the Chemnitz figure is of *Fusitriton cancellatus*. The specimen figured by Martini (1780, p. 139, fig. 1297), is here designated the lectotype of *Murex magellanicus* Gmelin, 1791. Thus Gmelin's typical variety is a synonym of *Trophon gervesianus* (Pallas, 1796) and his variety β is an invalid senior synonym of *Fusitriton cancellatus*.

***Note added in proof**
Recently, Cernohorsky (1977, p. 107) has pointed out that *Neptunea magellanica* Röding, 1798 (Museum Boltenianum, p. 116) is an earlier name for the species called *Fusitriton cancellatus* (Lamarck) throughout this memoir. Wherever the name *Fusitriton cancellatus* appears, *Fusitriton magellanicus* (Röding) should be substituted. The name of the nominate subspecies is, of course, similarly affected.

Fusitriton cancellatus retiolus (Hedley, 1914).

Figs. 7d–f; 10f; 11c, h.

Argobuccinum retiolum Hedley, 1914: 73, p. 11, fig. 5; Gatliff and Gabriel, 1914: 99.
Fusitriton retiolus; Hedley, 1918: M66; Garrard, 1961: 14; Iredale and McMichael, 1962: 55; MacPherson and Gabriel, 1962: 155, fig. 185; J. T. Smith, 1970: 481, pl. 44, figs. 1–11 (in part); Wilson and Gillett, 1971: 78, pl. 53, fig. 2.

During the latter half of 1971, examination of large suites of *Fusitriton cancellatus retiolus* recently added to the collections of the Australian Museum brought out the following points. In Australian specimens the varices are high and solid in a much higher proportion of specimens (*c*. 70%) than in all other subspecies, and they tend to be quite regularly arranged at about 180° to 270° around the spire. Thus about 60% of specimens have a broad varix on the left side of the last whorl (with siphonal canal pointing down and the venter facing the observer), a feature hardly ever seen in any of the other Recent forms of *Fusitriton*. Also, as shown in Fig. 8, specimens of *F. cancellatus retiolus* are more finely sculptured than in *F. cancellatus laudandus*, about equal to *F. cancellatus cancellatus* although some are even finer, and are usually more coarsely sculptured than *F. cancellatus murrayi*. Specimens reach a markedly larger adult size than any other Recent forms, and are taller and narrower than any other subspecies. These differences, and especially the features of the varices, seem sufficient to maintain the Australian form as a distinct geographic subspecies.

RADULA: A radula was extracted and mounted from a specimen of *Fusitriton cancellatus retiolus* from FRV *Kapala* Stn 71-07-01, 33°41′S, 151°55′E, off Sydney, 20 April 1971, 300 fms (550 m) (Australian Museum, C.79172). It agrees exactly in almost all features with the radulae of specimens of *F. cancellatus laudandus* described below (p. 23; Fig. 6c). The only difference from radulae of New Zealand specimens is that the outer edge of the lateral teeth bears slightly more numerous denticles than in New Zealand specimens (six to nine, with eight on most teeth, whereas teeth with as many as seven denticles are uncommon in New Zealand specimens).

MATERIAL EXAMINED: MF 14812, National Museum, Wellington, off New South Wales, MV *Challenge*; F23107, National Museum of Victoria, in 137 m off Broken Bay, N.S.W., MV *Challenge*; F26654, National Museum of Victoria, dredged off N.S.W.; F26655, National Museum of Victoria, trawled in Bass Strait, Victoria (last three loaned by National Museum of Victoria); and the following material in the Australian Museum: C.79194, E of Broken Bay, N.S.W., 33°34′S, 152°03′E, 21.4.1971, 300 fms, FRV *Kapala*, Stn 71–07–02 (12 specimens); C.79201, off Newcastle, N.S.W., 32°46′–33°15′S, 152°16′–46′E, 153–300 fms, 5–12.5.1971, FRV *Kapala* Stn 71–08 (11 specimens); C.79184, E of Broken Bay, N.S.W., 33°41′S, 151°55′E, 20.4.1971, 300 fms, FRV *Kapala* Stn 71–07–01 (6 shells); C.79173, E of Sydney, N.S.W., 33°40′–51′S, 152°45′–54′E, 13–17.4.1971, 250–275 fms, FRV *Kapala* Stn 71–06 (4 shells); C.70729, 100–250 fms, S of Gabo I, N.S.W., FIS *Endeavour*, Paratype; C.71151, 120–125 fms, 25 miles E of Manly, N.S.W., in mud, 28.1.1960, *Challenge* (1 shell); C.71636, 130–150 fms, 20 miles off Wollongong, N.S.W., B. Goldman on *Marconis Star*, 30.7.1968 (1 shell); C.71148, deep water off Eden, N.S.W. (1 shell); C.81987, 45 fms, off Montague I, N.S.W. (4 shells); C.82486, SE of Broken Bay, N.S.W., 33°40′–35°00′S, 151°55′–58′E, 549 m. 14.7.1971, FRV *Kapala* Stn 71–12–02 (3 shells); C.82472, off Sydney, 366–549 m, 34°40′–35°01′S, 151°07′–13′E, 25.3.1971, FRV *Kapala* Stn 71–11–06/07 (4 shells); C.82035, 30 miles SSE of Sydney, 34°15′20″S, 151°25′21″E, 28.6.1971, 247 m, FRV *Kapala* Stn 71–10–02 (1 shell); C.81617, 60 fms, off Montague I, N.S.W., ex H. S. Mort Colln and Lee Woolacott Colln (1 shell); C.37002, 55–100 fms, Green Cape to Gabo I, N.S.W., FIS *Endeavour*, 3 paratypes; C.71149, off N.S.W. coast in 50–70 fms, pres. Capt. Knut Moller (1 shell); C.79207, off Newcastle, N.S.W., 32°46′–51′S, 152°46′–42′E, 324 m, 7.5.1971, FRV *Kapala* Stn 71–09–01 (6 shells); C.79174, E of Broken Bay, N.S.W., 33°34′S, 152°03′E, 21.4.1971, 300 fms, FRV *Kapala* Stn 70–07–02 (4 shells); C.79204, off Newcastle, N.S.W., 33°11′S, 152°23′E, 310 fms, 29.4.1971, FRV *Kapala* Stn 71–08–05 (4 shells); and additional material in spirit collection (total dry shells in Australian Museum: 65).

DIMENSIONS: Height typically 110 mm, diameter 50 mm (*see* Appendix 3).

DISTRIBUTION: northern New South Wales to the Great Australian Bight including Tasmania, taken in much smaller numbers than *Cymatona kampyla kampyla*.

Fusitriton cancellatus laudandus Finlay, 1926

Figs. 6c; 10a–d; 11a, b; 12a–f

Priene retiolum Finlay, 1924: 462 (not *Argobuccinum retiolus* Hedley, 1914).
Fusitriton laudandum Finlay, 1926: 399, pl. 20, fig. 65; Finlay, 1930: 250; Powell, 1933: 164; Iredale, 1937: 106; Powell, 1950: 74.
Fusitriton futuristi Mestayer, 1927: 189, fig. 6.
Fusitriton laudandus; Powell, 1955: 97; Dell, 1956: 85, fig. Radula A3; Powell, 1962: 94.
Fusitriton retiolus; J. T. Smith, 1970: 481, pl. 44, figs. 1–11 (in part).
Fusitriton laudanum [sic]; Glasby, 1972: 383, fig. 2.

The New Zealand subspecies *F. cancellatus laudandus* is the most coarsely sculptured subspecies of *Fusitriton cancellatus*. The only Recent form that is more coarsely sculptured is *F. oregonensis* (Redfield), which also has longer, thicker, and darker periostracal bristles. The periostracal bristles of the other Recent forms of *Fusitriton* are generally finer than those of *laudandus*, although there is considerable overlap in this feature between *F. cancellatus cancellatus* and *F. cancellatus retiolus*. The varices are weak and low and completely irregularly placed, giving the shells a very different appearance from the majority of Australian specimens. Australian shells differ also in their paler and shorter periostracal bristles and markedly finer axial sculpture than those of *F. c. laudandus*. *Fusitriton c. cancellatus* is shorter and broader than most New Zealand specimens, and usually markedly more finely sculptured. The South African *F. c. murrayi* is almost always markedly smaller and very markedly more finely sculptured than the other three subspecies, and occasionally (about 20% of shells seen) bears the broad, regularly placed varices that are otherwise characteristic of *F. c. retiolus*.

Specimens from a few stations, notably NZOI Stns E412 and E424, off the east coast of southern South Island, are more elongate than most others seen, and have unusually coarse spiral and axial cords and large nodules at the sculptural intersections, strongly resembling the Japanese *Fusitriton galea* Kuroda and Habe (*in* Habe 1961, append., p. 18). Shells from NZOI Stn E401, off eastern Otago, are more finely sculptured than usual and are short and broad, so that they strongly resemble (but are even broader than) the South American specimens of *F. c. cancellatus* (Lamarck) (Fig. 11f, g [p. 31]). The only other shell seen with these proportions is the single specimen from USNS *Eltanin* Stn 1974 (54°30′S, 158°59′E 112–124 m; east of New Zealand). Shells from all other stations are intermediate between those from NZOI Stns E412 and E401, and there can be no doubt that the extremes are merely part of the normal genetic variation within the subspecies. Most other large samples show variation approaching these extremes, and even the shells from NZOI Stn E401 are highly variable in form. The location, depth, and sediment type of the stations where the extreme variants were taken seem to have had no influence on their form, as in all cases there are "average" specimens in collections from nearby stations at similar depths and on similar sediments, and no variation has been seen in *F. c. laudandus* around New Zealand that could be attributed to the ecological conditions under which the animals lived (i.e., that is considered to be phenotypic).

The figured shells of *F. c. laudandus* (Figs. 10, 12 [pp. 14, 32]) have been selected to show the variation in form. The three specimens from NZOI Stn F122 show typical variation in form in a population with "average" sculpture. There are also two extreme specimens resembling *Fusitriton galea*, from NZOI Stn E412, and the most extreme, *cancellatus cancellatus*-like specimen from NZOI Stn E401.

The radulae of three specimens of *F. c. laudandus* were extracted and mounted, two from NZOI Stn F80 and one from the extremely tall *galea*-like specimen from NZOI Stn E412. A drawing of a radula from NZOI Stn F80 is given in Fig. 6c. The central tooth is rather low and broad, with a large, triangular main cusp having four to seven moderately large denticles on each side. The lateral tooth has a large triangular main cusp with a single small denticle on the inner edge and four to seven moderately large denticles on the outer edge. The basal plate of this tooth is comparatively small and is broad and elongate, with somewhat irregular margins. The inner marginal tooth has a moderately large square base and is rather strongly curved, with no denticles. The outer marginal tooth is remarkably long, extending further towards the central than do either the lateral or the inner marginal teeth, and is rather lightly curved with an ill-defined base.

Variation in the three radulae was minor. The denticles on both the central and the outer edge of the lateral teeth varied from four to seven, usually numbering five or six. As noted above, the lateral teeth of a radula of *F. cancellatus retiolus* (Hedley) had slightly more numerous denticles on the outer edge than on the New Zealand specimen. The small denticle on the inner side of the lateral tooth was always present, but varied in size. The number of denticles on the outer sides of the two laterals of one row was identical, as far as was checked. The most obvious and common variation was in the number of denticles on the two sides of the central tooth. These were more often different than the same, usually because of an extra minute denticle near the base of the main cusp on one side or the other. The figured central has seven denticles on one side and six on the other. An important feature is that the radula of the extremely elongate and coarsely sculptured specimen from NZOI Stn E412 did not differ in any significant way from those from NZOI Stn F80. Unfortunately, the animals from the short shells from NZOI Stn E401 could not be removed.

The gross external anatomy of a male specimen from NZOI Stn D138 is figured in Fig. 7e. The specimen is unusually well expanded, as the shell was broken in the trawl. The most notable feature is the large flattened blade-like penis with a broadly rounded end. The penes of all other Cymatiidae so far examined by the writer taper towards the end. Apart from this the animal is typical of Cymatiidae, with the tentacles (somewhat contracted in this specimen) bearing small black eyes near their bases. The animal is a uniform beige to cream colour.

LOCALITIES: Apart from the large number of New Zealand Oceanographic Institute specimens listed in Appendix 1, New Zealand specimens have been examined from the following localities (all held by the National Museum unless otherwise noted): Victoria University of Wellington Zoology Dept. (V.U.Z.) Stn BOL, Coll. 49, 41°31.5′S, 174°48′E, Cook Strait, 128 m; V.U.Z. HUL, Coll. 53, 41°41′S, 175°17′E, off Cape Palliser, 457–640 m; V.U.Z. GUL, No. 54, 41°39.5′S, 175°17′E, off Cape Palliser, 91–366 m; V.U.Z. BOU, Coll. 96, 40°31′S, 174°55′E, off Cape Palliser, 695 m; V.U.Z. DOJ, Coll. 99, 41°34.5′S, 174°43.5′E, off Cape Palliser, 275 m; V.U.Z. FOJ, Coll. 101, 41°38′S, 174°53.5′E, off Cape Palliser, 1006 m; Chatham Islands 1954 Expedition (CIE) Stn 6, 43°40′S, 179°28′E, Chatham Rise, 401 m; CIE 7, 43°42′S, 179°55′E, Chatham Rise, 512 m; CIE 8, 42°47′S, 179°30′W, Chatham Rise, 183 m; CIE 29, 43°55.5′S, 177°08′W, Petre Bay, Chatham I, 172 m; CIE 40, 44°32′S, 176°05′W, SE of Pitt I, Chatham I, 283 m; CIE 41, 44°35.5′S, 176°04′W, SE of Pitt I, 603 m; CIE 58, 42°40′S, 177°59′E, Chatham Rise, 585 m; CIE 59, 43°40′S, 177°59′E, Chatham Rise, 530 m; CIE 60, 43°34′S, 175°30′E, Chatham Rise, 375 m; 73 m off Cape Campbell, many specimens; 91–110 m off Cape Campbell; 37–55 m off Kaikoura; National Museum B.S.214, 41°40′S, 174°30′E, NE of Cape Campbell, 110 m; B.S. 189, edge of Taiaroa Canyon, off East Otago, 220 m, MV *Alert*; B.S. 190, 45°45′S, 171°05′E, Papanui Canyon (Canyon B), off East Otago, 550 m; B.S. 191, 45°47′S, 171°07′E, (Canyon C), off East Otago, 457–547 m; trawled off Timaru, 46–100 m; trawled off Timaru, 110–130 m; 27–29 m, off Oamaru, J. Graham; 73–110 m, between Moeraki and Oamaru, J. Graham; Foveaux Strait oyster beds; 22–24 m, oyster bed north of Ruapuke I, Foveaux Strait (N.Z. Geol. Surv.); beach near Derry Castle Reef, Enderby I, Auckland Is, C. A. Fleming (N.Z. Geol. Surv.); fragment (probably fossil), Waikanae Beach, West Wellington, W. F. Ponder; *Eltanin* Stn 1974, 54°30′S, 158°59′E, in 112–124 m, E of New Zealand; also many specimens from East Otago, taken by MV *Munida* (Portobello Marine Biological Station). All these localities are within areas where specimens have been taken in N.Z. Oceanographic Institute samples, and are not plotted on Figs 1 and 2.

DIMENSIONS: Height ranges from 80–120 mm; diameter from 40–50 mm, rarely above 55 mm. Dimensions used for scatter diagrams (Figs 8, 9) are given in Appendix 3.

DISTRIBUTION: On the basis of N.Z. Oceanographic Institute material and published distribution data, *F. cancellatus retiolus* is distributed around New Zealand, from Norfolk Ridge and the Three Kings Islands to near Macquarie Island. The subspecies has been taken wherever sampling has been carried out in deep water all around New Zealand, particularly on the Campbell Plateau, and occurs less commonly in shallower water off Cape Campbell, between Banks Peninsula and Otago Peninsula, and around the New Zealand subantarctic islands. No specimens were obtained during the limited biological sampling carried out on the Challenger Plateau. Iredale (1937, p. 106) reported it trawled in 33 m off Westland, and it may be colonising the shelf there as it is off South Canterbury and North Otago. Details of the distribution are considered in the section dealing with ecology; *F. c. laudandus* is common in the upper bathyal zone.

Beach shells are known from only four localities: Powell (1950, p. 74) recorded a beach specimen from Ninety-Mile Beach, Northland; Dr W. F. Ponder collected a fragmentary specimen (probably fossil) from Waikanae Beach, Wellington; Dr H. J. Finlay collected a specimen at Taieri Beach, Dunedin, the basis of his original record of *Fusitriton* in New Zealand; and Dr C. A. Fleming collected a specimen from a beach near Derry Castle Reef, Enderby Island, Auckland Islands, in 1942 (Powell 1955, p. 97).

FOSSIL RECORD: No undoubted fossils of *Fusitriton cancellatus* subspecies are known from New Zealand, despite extensive collecting by N.Z. Geological Survey from bathyal late Pliocene and early Pleistocene siltstone in Wairoa District, Hawke's Bay, in the southern Wairarapa, in southern Marlborough, and at several localities in North Canterbury. The extinct subspecies *Cymatona kampyla jobbernsi*, closely related to forms now living with *Fusitriton cancellatus laudandus*, occurs at several of these fossil localities (listed above) and there are many rich fossil faunas in which *Fusitriton* would be expected to occur if it lived in New Zealand. It is concluded that *Fusitriton* reached New Zealand after early Pleistocene time.

The broken specimen of *Fusitriton cancellatus laudandus* collected by Dr W. F. Ponder on Waikanae Beach, West Wellington, is stained medium brown and has a similar appearance to presumed young (Holocene or late Pleistocene) fossils of species now extinct in the area, such as *Cominella (Eucomina) nassoides* subspecies, found on Wellington West Coast beaches at rare intervals. It seems likely that the specimen of *Fusitriton* is a fossil from a submarine outcrop of Holocene or late Pleistocene rock. No species collected from the young fossil fauna give any clue to its age, but the specimens have an obviously different preservation from the white or blue-grey shells commonly carried down the coast from the Castlecliff section, west of Wanganui, and are undoubtedly younger than Castlecliffian (Putikian Substage). Therefore *Fusitriton* probably reached New Zealand during Holocene or late Pleistocene time.

ECOLOGY

Cymatona kampyla kampyla and *Fusitriton cancellatus laudandus* in N.Z. Oceanographic Institute samples are listed in Appendix 1 together with data for each station. Over 11 years (from 1958–69) N.Z. Oceanographic Institute staff have established approximately 3500 benthic stations in the New Zealand region (of which approximately 3000 are on the continental shelf), and *C. k. kampyla* and *F. c. laudandus* were taken at 148 of them. Stations extend from the Three Kings Islands to Macquarie Island (Fig. 3).

This extensive sampling enabled an analysis of the autecology of *C. k. kampyla* and *F. c. laudandus* to be undertaken with respect to the three readily-determinable factors, latitude, depth, and sediment type. Minor aspects of their synecology (for example, how these subspecies are distributed in relation to each other on various sediments) were also studied. As only six specimens of *C. k. tomlini* were obtained no additional ecological consideration of them is possible.

The great number of samples lacking both *C. k. kampyla* and *F. c. laudandus* is largely explained by the location of the stations on the continental shelf, where both genera are uncommon or absent, except off eastern Otago where, as outlined above, *F. c. laudandus* is a common element in the shelf fauna. From a generalised viewpoint, live *F. c. laudandus* is very much more common than, and thus presumably dominant over, live *C. k. kampyla* in the New Zealand region.

Even below the edge of the continental shelf, there are many stations throughout the region (although very few on the Campbell Plateau) where no Cymatiidae were taken. However, from personal observation of Mollusca in N.Z. Oceanographic Institute samples the writer can state that *F. c. laudandus* is the most common and most widely distributed large gastropod in benthic samples from depths of about 150 to 1000 m between the Macquarie Gap and the Three Kings Islands.

Cymatiidae are active carnivores (*see*, for example, Chesher 1969; Laxton 1971; Smith 1970: 495); some are epifaunal but others (e.g., *Septa (Monoplex) parthenopea* (von Salis Marschlins) observed on sand flats in northern New Zealand) are partly-buried infaunal carnivores, usually found burrowing horizontally with the shell dorsum, siphonal canal, and proboscis protruding above the sediment. *Fusitriton c. laudandus* is presumably the main molluscan carnivore in New Zealand upper bathyal communities, and *C. k. kampyla* may also be an important carnivore. Both probably feed to a large extent on other gastropods and on bivalves and also on polychaetes, echinoderms, and tunicates which are known as food of intertidal *Charonia*, *Cabestana*, *Argobuccinum*, and *Mayena* species around New Zealand. *Fusitriton oregonensis* (Redfield) is reported by Smith (1970: 495) to feed on bivalves, arthropods, annelids, decapod crustaceans, and fish (although presumably it could not catch live fish under natural conditions). Being of much smaller size than *F. c. laudandus*, *C. k. kampyla* may feed on smaller animals. Other Mollusca presumed to be important carnivores in upper bathyal benthic communities are the species of the families Naticidae, Muricidae, Buccinidae, Volutidae, and Turridae.

BENTHIC SAMPLING PROGRAMME OF N.Z. OCEANOGRAPHIC INSTITUTE

Since the programme of regional sampling of the benthos was initiated by N.Z. Oceanographic Institute, cover of the continental shelf at intervals of 20′ of latitude has been completed (McKnight 1969: 12). More intensive sampling of shelf areas such as Hawke Bay, Cook Strait, and Foveaux Strait has supplemented this survey. Systematic sampling at somewhat greater intervals has been carried out over the continental slope, commonly to depths of 1500 m.

Sampling methods

One hundred and six of the 148 stations (72%) used here were made with a four-feet-wide ("medium") Agassiz trawl (TAM), and almost all others with various types of dredges, 22% being obtained with a conical mesh dredge (DCM) one foot wide at the mouth and three feet long. Sampling gear used at each station is listed in Appendix 1. The sampling was not intended to give quantitative results. All statistical diagrams and estimates in this study use frequencies of specimens (i.e., number per station) rather than total numbers, and a clear separation is maintained both between the frequency of dredged and trawled specimens and between the frequency of empty ("dead") shells and live animals taken.

Distribution anomalies

Stations at which *Cymatona kampyla* subspecies and *F. c. laudandus* were taken by N.Z. Oceanographic Institute in the New Zealand area are shown in Figs 1, 2. Two anomalies are apparent in the distribution pattern.

CHATHAM RISE Despite extensive sampling, almost no Cymatiidae were obtained on the central, flattest part of Chatham Rise, where Norris (1964) mapped a large area of glauconite concentration. Here the percentage of glauconite in the sediment exceeds 50%. NZOI Stn C605 with 36.2% glauconite in its sediment was the only station where Cymatiidae were obtained within the area circumscribed by the line of 10% glauconite concentration. From this station two live adult and one live juvenile *F. c. laudandus* were obtained. Mernoo Bank, the shallowest part of Chatham Rise, reaches 51 m, but for the remainder the crest of the rise lies at about 200 m. Depth is unlikely to be a limiting factor. In view of the large number of stations within the glauconite area where no Cymatiidae were obtained, and in the absence of other known ecological factors, it is concluded that Cymatiidae are intolerant of the coarse glauconite sand environment of Chatham Rise. A potassium/argon determination indicates a Tertiary age for the glauconite (Cullen 1967), and although some glauconite may still be forming at the present time, it is more likely that it is the glauconite itself, rather than the conditions of its formation, that the animals find unfavourable.

Glasby (1972) reported "quantities of sub-fossil" *Fusitriton cancellatus laudandus* from NZOI Stn D121, within the area bounded by the line of 50% glauconite concentration on Chatham Rise, in which the colonial zoantharians adhering to the shells are heavily coated with black glauconite up to 3 mm thick. Thus the factors that could contribute to scarcity of cymatiids on Chatham Rise include the reducing conditions necessary for the formation of glauconite; the relatively strong current action that keeps the crest of the rise free of terrigenous sediment; the coarse grainsize of the sediment; inability of their prey to live in the sediment for any of the above reasons; and increase of shell weight, and possibly interference with shell or periostracal secretion by the mantle margin, caused by deposition of glauconite on the shell.

CAMPBELL ISLAND No Cymatiidae were obtained closer than 70 km from Campbell Island although benthic stations have been occupied closer to the island. Summerhayes (1969, p. 23) showed a zone of bryozoan sand around the island, a zone of slightly glauconitic *Globigerina* ooze to the east of the island, and the whole surrounded by *Globigerina* ooze. The sand around the island consists entirely of bryozoan fragments, with none of the usual molluscan debris (C.P. Summerhayes pers. comm.), and this could indicate that some of the prey of Cymatiidae are absent near the island. N.Z. Oceanographic Institute samples from shallow water around the island lack *Argobuccinum* species as well, although the genus is present in collections from the Auckland Islands and The Snares. Powell (1955, p. 14) did not record any Cymatiidae from Campbell Island.

There is some evidence that the molluscan fauna of Campbell Island has a low species diversity. Powell (1955) listed only 70 species from there, and 169 from the Auckland Islands, but he pointed out that less dredging had been carried out around Campbell Island than around the Auckland Islands. This difference in sampling density still persists. Further sampling will be necessary to tell whether Cymatiidae are absent from Campbell Island as part of a low faunal diversity or whether Cymatiidae are the only family affected.

DISTRIBUTION

As well as geographic position and depth, a number of other ecological parameters are usually available for each N.Z. Oceanographic Institute benthic station. The regional distribution of temperature with depth around New Zealand as analysed by Ridgway (1969) covers the area of the present study. The charted distribution uses data from a series of temperature and salinity stations; temperature and salinity were not recorded at the benthic stations themselves. However, the chart shows that there is little change in temperature from north to south in the upper part of the bathyal zone. A further parameter, salinity, does not vary significantly in the depths under consideration (Ridgway 1969, figs 4, 6). A fifth complex of parameters is the bottom sediment type, on which data are available for 132 of the 148 stations analysed here. Thus we can examine the correlations of animal occurrence with depth, geographic position, and sediment type.

Distribution with depth

Fig. 13 and Table 1 show frequencies of live and dead *Cymatona kampyla kampyla* and *Fusitriton cancellatus laudandus* dredged and trawled with respect to depth. These histograms show:

1. Of dredged specimens, dead *Cymatona* greatly predominate over live ones, whereas of trawled ones dead specimens are only slightly more common than live ones.
2. The maximum frequency of dead dredged shells of *Cymatona* is at 300–400 m and of dead trawled shells is at 400–500 m, whereas those of both dredged and trawled live shells are at 600–700 m; similarly when combined dredged and trawled shells are considered, dead shells are most common at 300–400 m and live ones at 600–700 m.
3. The dredge collected a markedly higher proportion of dead : live *Cymatona* than did the trawl.
4. Over most of its depth range, live *F. c. laudandus* is slightly more abundant than are dead shells.
5. The high frequency of both live and dead trawled *F. c. laudandus* at 1400–1499 m is probably caused by large numbers of specimens trawled at two stations only. These were Stn F749, Chatham Rise, in 1427–1372 m, with 10 live and two dead examples and Stn E870, on the southern end of Norfolk Ridge, in 1488–1556 m, with 30 dead specimens that are perhaps fossil.

6 The number of *F. c. laudandus* dredged per station is so small as to make little difference to the graph of specimens trawled per station when they are combined (Fig. 13), whereas the frequency of dredged *Cymatona* slightly exceeds that of trawled specimens; i.e., dredging is a very inefficient way of collecting *Fusitriton* but is equally as efficient as trawling in collecting *Cymatona*.

7 Depth ranges: *(a) C. k. kampyla* was taken at few stations below 800 m; its range in these samples is 121–969 m (dead) and 124–913 m (live).

(b) A sample of 10 *F. c. laudandus* was trawled alive at 1427–1372 m, and its lower limit is probably below this depth; however, it is rare below 1000 m. In the present samples, its depth range is 62–1556 m. The shallowest known dredged specimen is from the Foveaux Strait oyster beds in 22 m, although four beach specimens are known. From the depth zones listed by Graham (1962, p. 57), it seems likely that specimens taken shallower than about 50 m in the New Zealand region are all transported dead shells.

CONCLUSIONS

a The frequency of live and dead specimens taken at a station depends on the sampling gear used.

b Live *C. k. kampyla* occur in markedly deeper water than the more common dead shells. Thus the depth distribution of dead shells of *C. k. kampyla* reflects an earlier distribution than the present one, and is probably of earlier Holocene or late Pleistocene age.

c There is no evidence of a relict distribution pattern for *Fusitriton cancellatus laudandus*.

d The frequency of specimens is generally lower for *F. c. laudandus* than for *C. k. kampyla*, although *F. c. laudandus* was taken at very markedly more stations than was *C. k. kampyla*.

Distribution with latitude

Fig. 14 and Table 2 show frequencies of live and dead *Cymatona kampyla kampyla* and *Fusitriton cancellatus laudandus* dredged and trawled compared with latitude, plotted in two-degree intervals. The histograms show:

1 *Cymatona kampyla* is most abundant, both dredged and trawled, in southern New Zealand (40°–54°S) although live shells have more restricted maxima (dredged: 48°–52°S; trawled: 46°–50°S) than do dead ones. No live shells were taken north of 38°S, and few north of 46°S.

2 A maximum of dead, trawled shells of *Cymatona* at 34°–36°S is caused by a very high number of specimens at only one station (E875, 34°39′S, W of Ninety-mile Beach, TAM, 40 dead *Cymatona*; the only other sample in this latitude range is E876, same location, 1 dead *Cymatona*).

3 The maximum of dead trawled *F. c. laudandus* at 34°–36°S is caused by the same anomalous station (E870) on the south end of the Norfolk Ridge as caused the maximum at 1400–1499 m on the depth histograms; the maximum in both live and dead trawled *F. c. laudandus* at 38°–40°S is caused by Stn E719, 38°46′S, off Gisborne, where 57 live and 42 dead shells were trawled in an area with otherwise low frequencies (E711, 39°18.8′S, 1 dead; E712, 39°20′S, 2 live; E717, 38°42′S, 3 live). Apart from these northern examples of sparse high frequencies the frequency of trawled *F. c. laudandus* per station rises gradually southwards to a maximum at 48°–50°S (i.e., ending at the southern end of Campbell Plateau) and then decreases again to Macquarie Island. Frequencies are nowhere high but small to moderate numbers occur at a large number of stations.

4 Again the bias towards trawling markedly greater frequencies of live and dead *F. c. laudandus* than are dredged is seen, and it is clear that dredges took specimens mainly in southern New Zealand (42°–54°S) where specimens are most abundant.

CONCLUSIONS

a The relict distribution of dead shells of *C. kampyla* is shown by the occurrence of almost all live shells in 46°–52°S, whereas dead shells were taken as far north as the Three Kings Islands, and a large sample was taken off Ninety-mile Beach (E875, 34°39′S, 40 dead *Cymatona*). This suggests a southward migration of *C. kampyla*, perhaps since the last glaciation.

b A similar anomalous northern distribution of dead shells is not shown by *F. c. laudandus*, except for NZOI Stn E870 in the southern edge of the Norfolk Ridge, where 30 dead shells were trawled on "firm sedimentary rock with barnacle plates" and may be fossils.

c Both subspecies are more common in the south than in the north, particularly on Campbell Plateau. Abundance drops off on Macquarie Ridge. For both subspecies occasional samples in the northern part of the range contained unusually high frequencies of specimens, suggesting that natural clustering may be a significant feature in their distribution.

Distribution with sediment type

Histograms (Fig. 15) show the frequencies of live and dead *Cymatona kampyla kampyla* and *Fusitriton cancellatus laudandus* taken on each type of bottom sediment (Table 3). Sediments of part of the studied area were mapped by Norris (1964) and Summerhayes (1969), but are greatly augmented by the present data. Shipboard descriptions and laboratory visual descriptions of sediments from stations listed in Appendix 1 were co-

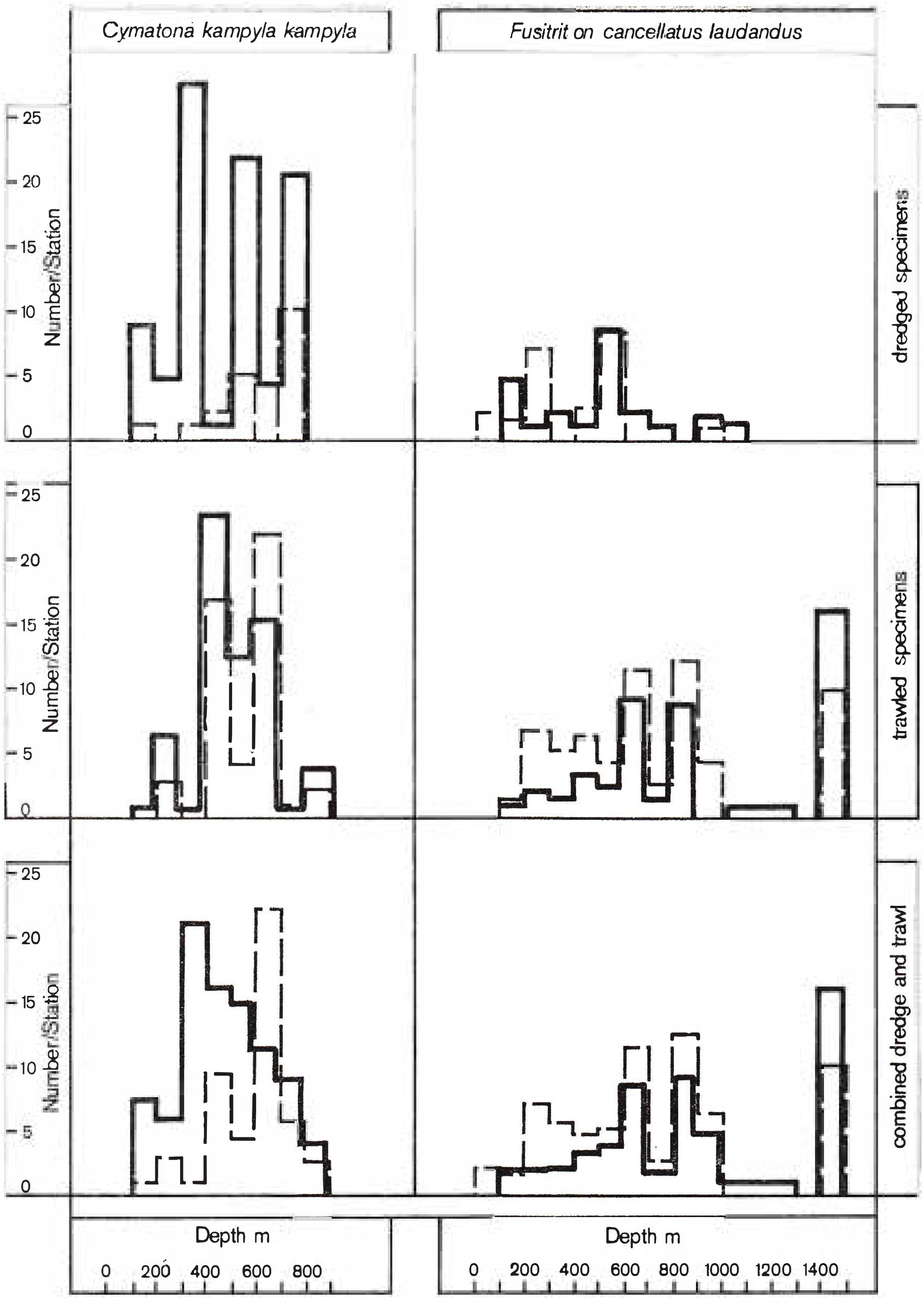


Figure 13 Frequencies of *Cymatona* and *Fusitriton* as a function of the depth at which live and dead specimens were dredged and trawled.

live – dashed line
dead – heavy continuous line

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

Table 1 Numbers of live and dead *Cymatona kampyla kampyla* and *Fusitriton magellanicus laudandus* in NZOI benthic samples, according to depth and methods of collection (data for Fig. 13).

Upper figures are number of specimens collected in each category, lower figures are the number of stations involved. The columns headed D and T represent stations at which specimens were obtained by dredging and trawling respectively. The columns headed C are the number of specimens and stations without regard to the method of collection.

Depth (m)	*Cymatona*									*Fusitriton*									No. of stations at particular depth		
	live			dead			total			live			dead			total					
	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C
0– 99 ..	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2			
	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	11	1	0	1
100– 199 ..	2	0	2	77	2	79	79	2	81	4	6	10	9	8	17	13	14	27			
	2	0	2	9	2	11	10	2	12	3	4	7	4	6	10	5	9	14	12	9	21
200– 299 ..	0	3	3	9	32	41	9	35	44	14	49	63	2	15	17	16	64	80			
	0	1	1	2	5	7	2	5	7	2	7	9	2	7	9	3	11	14	4	14	18
300– 399 ..	1	0	1	165	2	167	166	2	168	0	21	21	12	4	16	12	25	37			
	1	0	1	6	2	8	6	2	8	0	4	4	6	2	8	6	5	11	8	5	13
400– 499 ..	2	17	19	2	94	96	4	111	115	10	33	43	2	36	38	12	69	81			
	1	1	2	2	4	6	2	4	6	4	5	9	2	10	12	6	10	16	7	10	17
500– 599 ..	5	13	18	43	76	119	48	89	137	17	57	74	17	31	48	34	88	122			
	1	3	4	2	6	8	2	6	8	2	13	15	2	11	13	3	17	20	3	18	21
600– 699 ..	0	44	44	13	76	89	13	120	133	0	163	163	2	98	100	2	261	263			
	0	2	2	3	5	8	3	5	8	0	14	14	1	11	12	1	17	18	3	17	20
700– 799 ..	10	1	11	41	4	45	51	5	56	0	24	24	1	13	14	1	37	38			
	1	1	2	2	3	5	2	3	5	0	9	9	1	7	8	1	12	13	2	14	16
800– 899 ..	0	5	5	0	16	16	0	21	21	0	74	74	0	90	90	0	164	164			
	0	2	2	0	4	4	0	4	4	0	6	6	0	9	9	0	11	11	0	11	11
900– 999 ..										1	14	15	2	0	2	3	14	17			
										1	3	4	1	0	1	1	3	4	1	3	4
1000–1099 ..										0	0	0	1	1	2	1	1	2			
										0	0	0	1	1	2	1	1	2	1	1	2
1100–1199 ..										0	0	0	0	1	1	0	1	1			
										0	0	0	0	1	1	0	1	1	0	1	1
1200–1299 ..										0	0	0	0	1	1	0	1	1			
										0	0	0	0	1	1	0	1	1	0	1	1
1300–1399 ..										0	0	0	0	0	0	0	0	0			
										0	0	0	0	0	0	0	0	0	0	0	0
1400–1499 ..										0	10	10	0	32	32	0	42	42			
										0	1	1	0	2	2	0	2	2	0	2	2
1500–1599 ..																					
Totals ..	20	83	103	350	302	652	370	385	755	48	451	499	48	330	378	96	781	877			
	6	10	16	26	31	57	27	31	58	13	66	79	20	68	88	28	100	128	42	106	148

ordinated on a simplified basis and the major sediment feature assessed. For example, cobbles in *Globigerina* ooze were ignored, and the sediment classified as ooze; "sandy mud" was classified as mud and "muddy sand" as sand. Sediment types of the 132 stations for which data are available were classified into the following six categories:

terrigenous gravel, 20 stations;

terrigenous sand (may include some *Globigerina* ooze), 24 stations;

terrigenous mud (may include some *Globigerina* ooze), 36 stations;

bryozoan debris (A careful attempt was made to include only "pure" bryozoan debris stations, but may include some mixed bryozoan and molluscan debris), 11 stations;

molluscan debris (includes stations with mixed molluscan and bryozoan debris), 11 stations;

Globigerina ooze (includes foraminiferal sand), 30 stations.

The histograms (Fig. 15) show:

1 *Cymatona kampyla* was taken abundantly dead but rarely alive on terrigenous gravel, abundantly dead but less commonly alive on terrigenous sand, very rarely dead and not at all alive on terrigenous mud, abundantly dead but not at all alive on bryozoan debris, and slightly more commonly dead than alive on both molluscan debris and *Globigerina* ooze. Its order from greatest to least abundance is *Globigerina* ooze, terrigenous gravel, terrigenous sand, bryozoan debris, molluscan debris, terrigenous mud. Live samples on molluscan debris and *Globigerina* ooze are anomalous in that more shells were trawled than were dredged, all other samples being consistently the reverse.

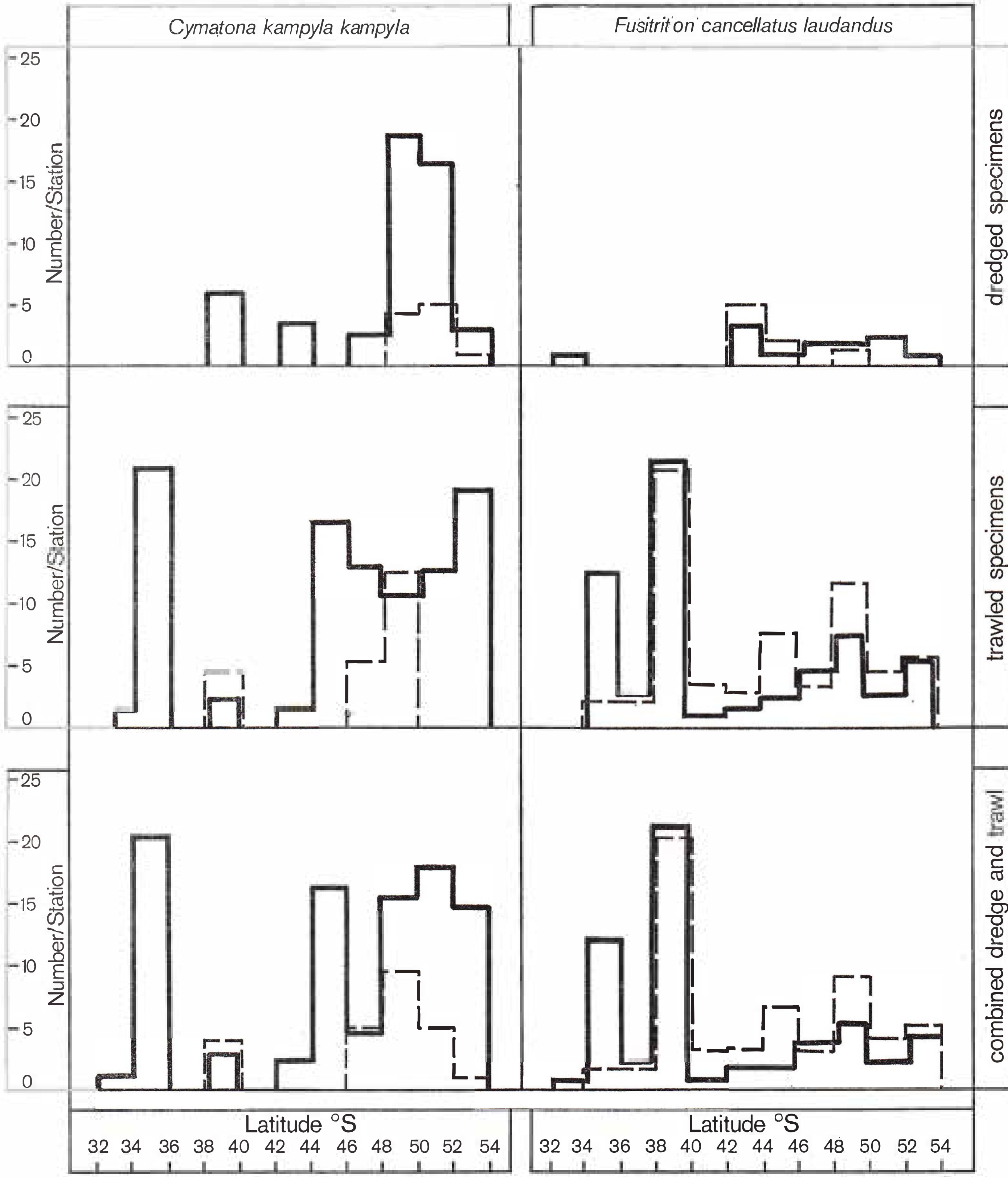


Figure 14 Frequencies of *Cymatona* and *Fusitriton* as a function of the latitude at which live and dead specimens were dredged and trawled.
live – dashed line
dead – heavy continuous line

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

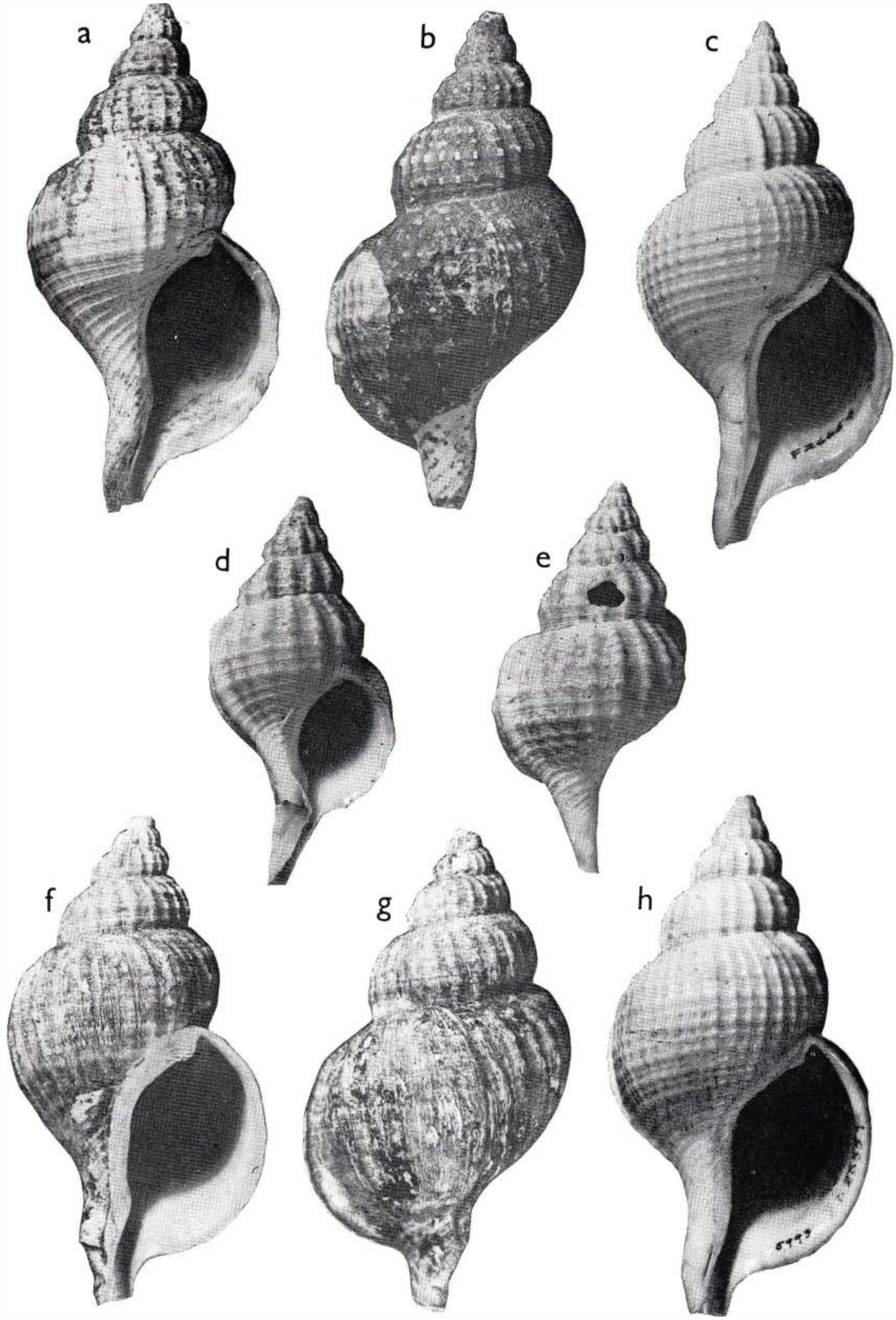


Figure 11 **a**, **b**, *Fusitriton cancellatus laudandus* Finlay, trawled in 90–110 m off Cape Campbell, Marlborough, New Zealand, trawler *Futurist*; holotype of *Fusitriton futuristi* Mestayer; National Museum, M.1399; 100.6 × 48.8 mm. **c**, *Fusitriton cancellatus retiolus* (Hedley), dredged off New South Wales, Australia; F. Hartley colln, National Museum of Victoria, F.26654; 131.4 × 63.2 mm. **d**, **e**, *Cymatona kampyla kampyla* (Watson), NZOI Stn F120, near the Bounty Is, New Zealand, in 494–512 m; 53.0 × 25.2 mm. **f**, **g**, *Fusitriton cancellatus cancellatus* (Lamarck), trawled off Montevideo, Uruguay; N.Z. Geol. Surv., WM.9302; 113.4 × 58.9 mm. **h**, *Fusitriton cancellatus retiolus* (Hedley), trawled in Bass Strait, Victoria, Australia; Gatliff colln, National Museum of Victoria, F.26655; 103.4 × 51.5 mm.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*"; for "*Fusitriton cancellatus retiolus*" read "*Fusitriton magellanicus retiolus*"; and for "*Fusitriton cancellatus cancellatus* (Lamarck)" read "*Fusitriton magellanicus magellanicus* (Röding)".

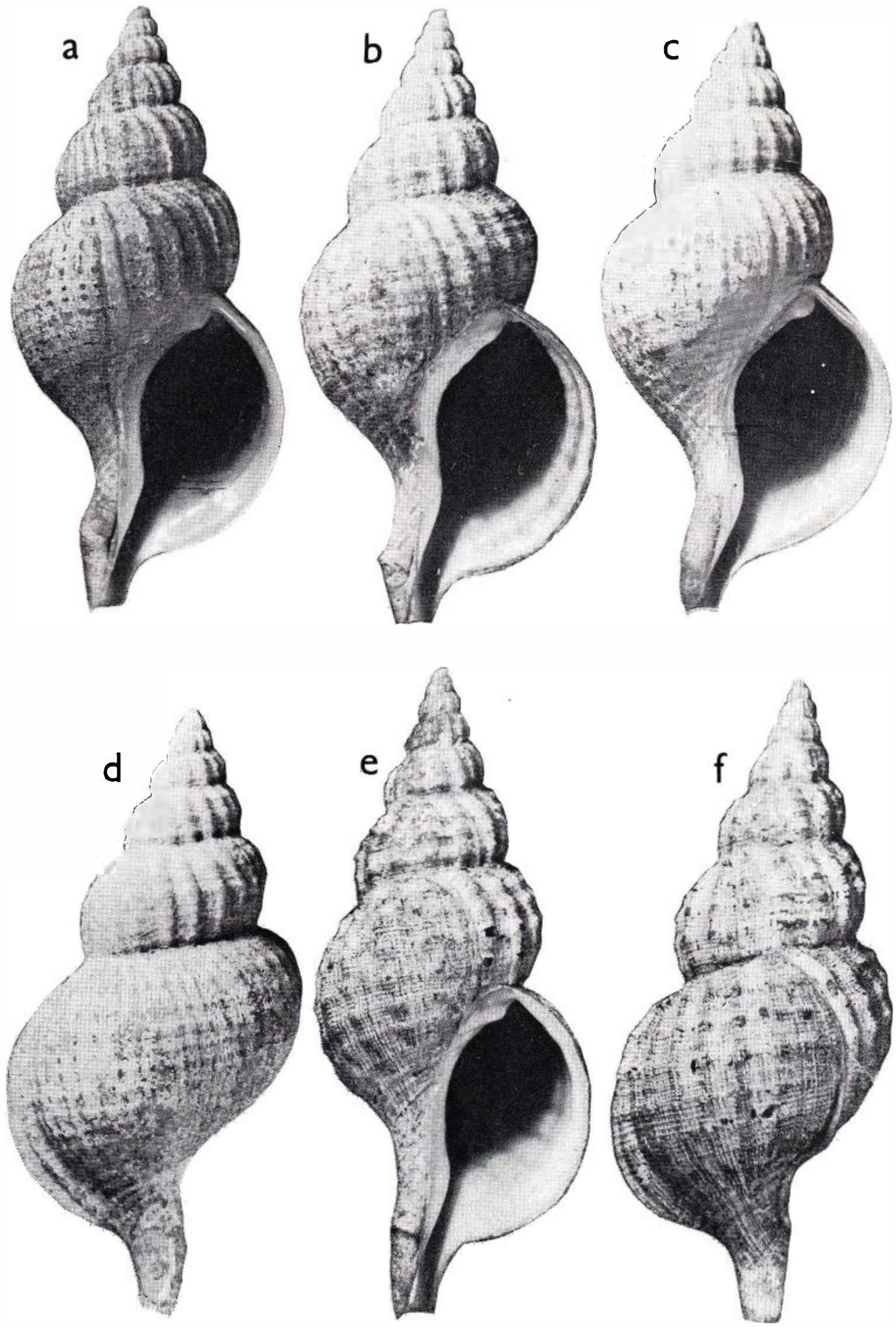


Figure 12 *Fusitriton cancellatus laudandus* Finlay. **a–d** Specimens from one population, NZOI Stn F122, near the Bounty Is, in 252 m; **a**, 116.4 × 50.0 mm; **b**, 118.6 × 53.2 mm; **c**, **d**, 121.4 × 58.3 mm. **e, f,** very tall, strongly sculptured specimen from NZOI Stn E412, off eastern Otago, in 249 m, 90.9 × 38.0 mm.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

Table 2 Numbers of live and dead *Cymatona kampyla kampyla* and *Fusitriton magellanicus laudandus* in NZOI benthic samples, according to latitude and methods of collection (data for Fig. 14).

Upper figures are number of specimens collected in each category, lower figures are the number of stations involved. The columns headed D and T represent stations at which specimens were obtained by dredging and trawling respectively. The columns headed C are the number of specimens and stations without regard to the method of collection.

Latitude (S)	*Cymatona*									*Fusitriton*									No. of stations at specified latitude range		
	live			dead			total			live			dead			total					
	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C
32°–33°59′	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	1			
	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	1	1	1	2
34°–35°59′	0	0	0	0	41	41	0	41	41	0	2	2	0	37	37	0	39	39			
	0	0	0	0	2	2	0	2	2	0	1	1	0	3	3	0	3	3	0	4	4
36°–37°59′	0	0	0	0	0	0	0	0	0	0	2	2	0	5	5	0	7	7			
	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	3	3	0	3	3
38°–39°59′	0	4	4	6	6	12	6	10	16	0	62	62	0	43	43	0	105	105			
	0	1	1	1	3	4	1	3	4	0	3	3	0	2	2	0	4	4	1	6	7
40°–41°59′	0	0	0	0	0	0	0	0	0	0	13	13	0	1	1	0	14	14			
	0	0	0	0	0	0	0	0	0	0	4	4	0	1	1	0	5	5	0	5	5
42°–43°59′	0	0	0	7	4	11	7	4	11	40	36	76	22	25	47	62	61	123			
	0	0	0	2	3	5	2	3	5	8	13	21	6	16	22	11	27	38	12	27	39
44°–45°59′	0	0	0	0	49	49	0	49	49	2	61	63	1	23	24	3	84	87			
	0	0	0	0	3	3	0	3	3	1	8	9	1	10	11	2	12	14	2	13	15
46°–47°59′	0	25	25	10	38	48	10	63	73	0	30	30	4	58	62	4	88	92			
	0	5	5	4	6	10	4	6	10	0	9	9	2	13	15	2	16	18	4	17	20
48°–49°59′	13	54	67	275	82	357	288	136	424	6	195	201	14	107	121	20	302	322			
	3	4	7	15	8	23	15	8	23	4	17	21	7	14	21	9	20	29	16	20	36
50°–51°59′	5	0	5	49	25	74	54	25	79	0	22	22	5	8	13	5	30	35			
	1	0	1	3	2	5	3	2	5	0	5	5	2	3	5	2	5	7	3	5	8
52°–53°59′	2	0	2	3	56	59	5	56	61	0	28	28	1	23	24	1	51	52			
	2	0	2	1	3	4	2	3	5	0	5	5	1	4	5	1	5	6	3	5	8
Total ..	20	83	103	350	302	652	370	385	755	48	451	499	48	330	378	96	78	877			
	6	10	16	26	31	57	27	31	58	13	66	79	20	68	88	28	100	128	42	106	148

2 *Fusitriton cancellatus laudandus* was taken in approximately similar abundance on all sediment types, and live and dead shells occur in broadly similar abundances on the one sediment. Its order from greatest to least abundance is terrigenous sand, molluscan debris, bryozoan debris, *Globigerina* ooze, and terrigenous mud approximately equal to terrigenous gravel. Both live and dead samples on molluscan debris are anomalous in that dredged specimens are markedly more abundant than trawled ones, the reverse of stations on other sediment types.

3 Frequencies of live *C. kampyla* are greatly exceeded by those of live *F. c. laudandus* on all sediments except *Globigerina* ooze, whereas frequencies of dead shells of *C. kampyla* exceed those of dead *F. c. laudandus* on all but terrigenous mud and molluscan debris, where they are comparable.

CONCLUSIONS

a Both *Cymatona kampyla* and *F. c. laudandus* avoid terrigenous mud, presumably because it is too adhesive for them to crawl in easily.

b A clear change in the sediment inhabited is shown by the differences between the frequencies of live and dead specimens of *C. kampyla* on terrigenous gravel, terrigenous sand, and in particular, bryozoan debris. This is presumably largely a reflection of the migration into deeper water shown in the comparison of frequencies with depth, as terrigenous gravel, terrigenous sand and bryozoan debris are the sediment types occuring in shallowest water, the first two around the main islands of New Zealand and the last around the subantarctic islands.

ECOLOGICAL CONCLUSIONS

1 The distribution of dead shells of *Cymatona k. kampyla* is a relict feature, reflecting a former late Pleistocene or Holocene distribution pattern. Specimens were formely more abundant in southern New Zealand, from 44°S to 54°S, in depths of 300 to 400 m, and on terrigenous gravel and sand, bryozoan and *Globigerina* ooze substrates, than *Fusitriton* is now. *Cymatona* has subsequently retreated southwards and into deeper water to be most abundant living at 600–700 m on Campbell Plateau on a *Globigerina* ooze substrate, almost entirely abandoning the terrigenous gravel and bryozoan substrates that occur in shallow water.

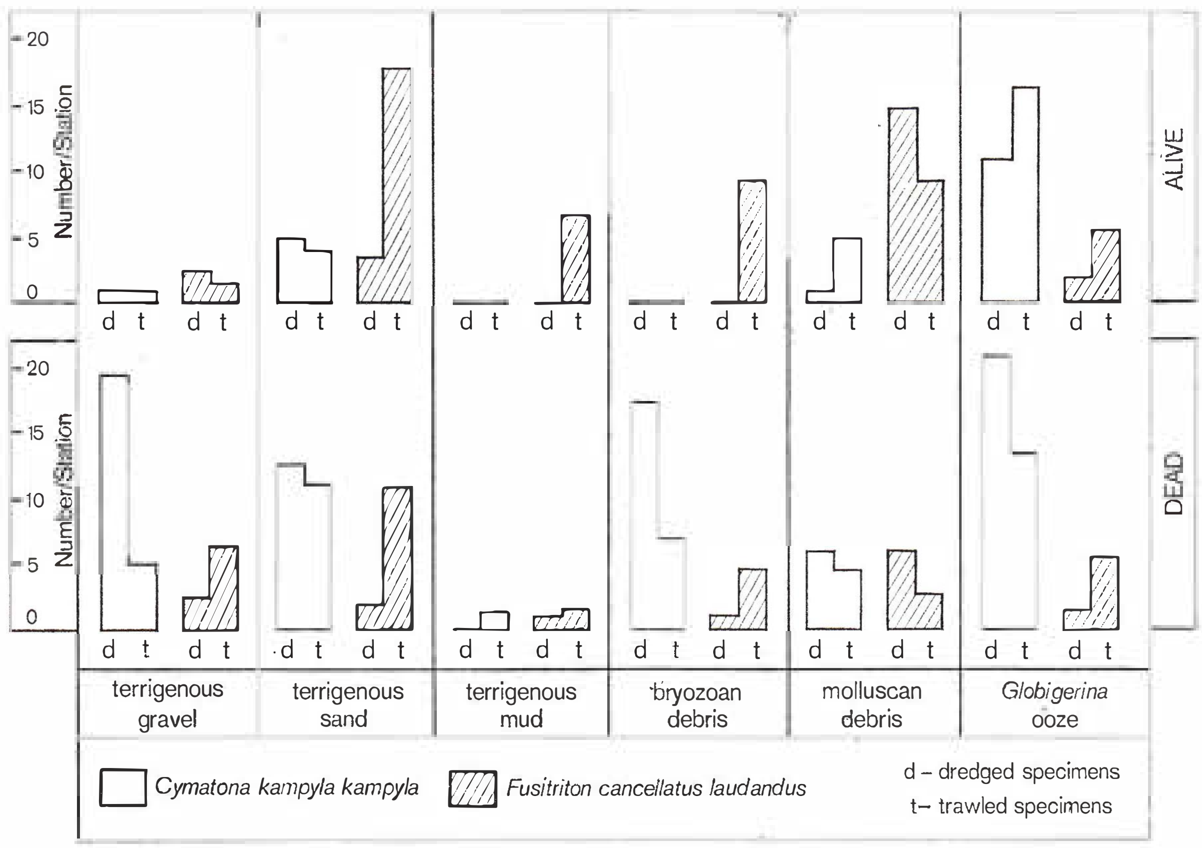


Figure 15 Frequencies of *Cymatona* and *Fusitriton* as a function of the sediment type at localities from which live and dead specimens were dredged and trawled.

Note For "*Fusitriton cancellatus laudandus*" read "*Fusitriton magellanicus laudandus*".

2 Except for sparse northern stations where high frequencies were obtained, *F. c. laudandus* is most common on Campbell Plateau in 600–900 m, although shells are common in 200–1000 m and extend below the lower depth limit of the survey. It is most abundant on terrigenous sand, although shells are common also on terrigenous gravel, bryozoan and molluscan debris, and *Globigerina* ooze.

3 Both animals are infaunal carnivores that proceed with the shell dorsum and the proboscis protruding above the sediment, and appear to find terrigenous mud difficult to inhabit. *Fusitriton* probably protrudes above the sediment further than does the markedly smaller *Cymatona*, as shown by the greater abundance of *F. c. laudandus* in surface-skimming trawled samples than in samples taken with a dredge designed to dig into the sediment.

4 Both animals are absent around Campbell Island, perhaps partly as a result of a general low species diversity.

5 Both are intolerant of coarse greensand on Chatham Rise.

6 Both animals occur sparsely, but at some stations in high frequencies, around northern New Zealand, suggesting that they sometimes aggregate in clusters rather than spreading evenly over the seafloor. Mating or colonial occurrences of their (as yet unknown) prey are possible causes of clustering.

DISPERSAL TIMES AND ROUTES OF *FUSITRITON*, AND THEIR EFFECT ON *CYMATONA*

Dispersal and distribution

Cymatona kampyla jobbernsi (King) is a rare but characteristic fossil of bathyal Mangapanian (Upper Pliocene) siltstones in South Wairarapa and North Canterbury, but *Fusitriton cancellatus laudandus* is known fossil in New Zealand only by a possible Holocene or late Pleistocene specimen. As noted above *Fusitriton* did not arrive in New Zealand until Holocene or late Pleistocene time.

Table 3 Numbers of live and dead *Cymatona kampyla kampyla* and *Fusitriton magellanicus laudandus* in NZOI benthic samples, dredged and trawled from each of six sediment types (data for Fig. 15).

Upper figures are number of specimens collected in each category, lower figures are the number of stations involved. The columns headed D and T represent stations at which specimens were obtained by dredging and trawling respectively. The columns headed C are the number of specimens and stations without regard to the method of collection.

Sediment type	*Cymatona*									*Fusitriton*									No. of stations at particular sediment type		
	live			dead			total			live			dead			total					
	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C	D	T	C
gravel ..	2	3	5	117	20	137	119	23	142	19	5	24	13	38	51	32	43	75			
	2	3	5	6	4	10	7	4	11	7	3	10	5	6	11	10	6	16	14	6	20
sand	5	4	9	51	56	107	56	60	116	11	179	190	8	100	108	19	279	298			
	1	1	2	4	5	9	4	5	9	3	10	13	4	11	15	6	15	22	7	17	24
mud	0	0	0	0	5	5	0	5	5	0	61	61	1	30	31	1	91	92			
	0	0	0	0	4	4	0	4	4	0	19	19	1	20	21	1	33	35	1	35	36
bryozoan debris ..	0	0	0	104	27	131	104	27	131	0	19	19	3	9	12	3	28	31			
	0	0	0	6	4	10	6	4	10	0	2	2	3	2	5	3	3	6	7	4	11
molluscan debris..	1	10	11	18	9	27	19	19	38	15	37	52	18	8	26	33	45	78			
	1	2	3	3	2	5	3	2	5	1	4	5	3	3	6	3	6	9	4	7	11
Globigerina ooze ..	10	66	76	42	137	179	52	203	255	2	129	131	3	101	104	5	230	235			
	1	4	5	2	10	12	2	10	12	1	23	24	2	19	21	3	26	29	4	26	30
sediment not specified	2	0	2	18	48	66	20	48	68	1	21	22	2	44	46	3	65	68			
	1	0	1	5	2	7	5	2	7	1	5	6	2	7	9	2	11	13	5	11	16
Totals ..	20	83	103	350	302	652	370	385	755	48	451	499	48	330	378	96	781	877			
	6	10	16	26	31	57	27	31	58	13	66	79	20	68	88	28	100	128	42	106	148

Cymatona is known from the Upper Miocene (Tongaporutuan) onward in New Zealand, and the genus evidently evolved from *Sassia* or *Haurokoa* Fleming in Australia and New Zealand and has never lived elsewhere. The oldest undoubted *Fusitriton* is in the Oligocene to Middle Miocene of western North America (Smith 1970: 503). The genus has a long history in western North America and is also known from the Miocene and later in Japan and from the Pliocene (?) of western South America, but is not known fossil in South Africa or in Australia. This evidence of fossil history and time of arrival in New Zealand is interpreted in the following way, partly after Smith (1970, p.532 *et seq.*).

Fusitriton arose from *Gyrineum* Link or a similar genus during the Eocene or Oligocene in western North America, and spread to Japan by the Miocene and to South America by the Pliocene. During the Pleistocene, perhaps because of the lengthening of larval life resulting from the slowing of metabolism, itself caused by the cooling of the seas, it spread by means of the transport of planktonic larvae in the west-wind drift to South Africa and then to Australia and New Zealand. After the Pleistocene, temperatures rose and presumably the length of larval life decreased, thus decreasing gene interchange between distant populations, allowing subspeciation.

Ecological displacement of Cymatona kampyla kampyla

The distribution of dead *C. k. kampyla* shells is largely relict. Reasons for this appear to be available in the ecology and arrival time of *Fusitriton cancellatus laudandus*.

As outlined above, both are infaunal carnivores, living on similar substrates and feeding on similar invertebrates. This suggests that the two might be competitors for an ecological niche. The genus *Cymatona* is endemic to New Zealand and southeastern Australia, whereas *Fusitriton* arrived in the west-wind drift during the Holocene or late Pleistocene. It is suggested that, until the late Pleistocene, *Cymatona* subspecies occupied most niches now occupied by both *Cymatona* subspecies and *F. c. laudandus*. The influx of large numbers of the larger and presumably more successful carnivore *F. c. laudandus* must have caused competition for food. This may have caused a reduction in the numbers of *C. k. kampyla* and its restriction to a more limited distribution at greater depths on fewer sediment types than it occupied before *F. c. laudandus* arrived.

Other profound changes in almost all New Zealand subtidal benthic communities must have occurred when the carnivores *Argobuccinum* and *Fusitriton* arrived during the late Pleistocene, because of the consequent marked increase in predation and of competition for prey.

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APPENDIX 1

STATION LIST

N.Z. Oceanographic Institute Samples
containing *Cymatona kampyla* subspecies and *Fusitriton cancellatus laudandus* (to June 1969).

Note For "*Fusitriton cancellatus*" read "*Fusitriton magellanicus*".

Data for each sample are given in the following order:

N.Z. Oceanographic Institute station number; date; latitude, longitude, and approximate location of the station; depth; sampling gear; sediment type; and numbers of live and dead *Cymatona kampyla* subspecies and *Fusitriton cancellatus laudandus* taken at the station. Abbreviations for types of sampling gear are:

- TAM – medium (4 ft wide) Agassiz trawl,
- DCM – cone mesh dredge,
- DCMb – cone mesh dredge + sediment sampling bag,
- MD – Manihiki dredge,
- DD – Devonport dredge (modified naturalist's dredge),
- BD – bucket dredge,
- TM/DP – Menzies trawl + down-pipe corer,
- OT – commercial otter trawl.

A706 (4 Nov. 1962) 47°42.7′S, 178°43′E, Bounty Is, 311 m, DCM, dead shell (with bryozoa and gravel $\frac{1}{4}$–2 in), 7 dead *C. k. kampyla* and 3 dead *F. c. laudandus*.

A711 (5 Nov. 1962) 47°44.5′S, 178°26′E, Bounty Is, 476 m, DCM, sediment not sampled. 1 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

A717 (5 Nov. 1962) 47°55′S, 179°04′E, Bounty Is, 205 m, DCM, fine white sand with shell fragments. 1 dead *C. k. kampyla*.

A721 (6 Nov. 1962) 49°39.5′S, 178°53′E, Antipodes Is, 132 m, DCM, coarse bryozoan sand with glauconite. 13 dead *C. k. kampyla*.

A724 (7 Nov. 1962) 49°43′S, 178°30′E, Antipodes Is, 201 m, DCM, coarse bryozoan sand. 8 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

A727 (7 Nov. 1962) 49°38.7′S, 178°32′E, Antipodes Is, 130 m, DCM, sediment not known. 14 dead *C. k. kampyla* and 1 live and 1 dead *F. c. laudandus*.

A730 (7 Nov. 1962) 49°40.3′S, 178°53.5′E, Antipodes Is, 307 m, DCM, gravel (few volcanic pebbles). 24 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

A733 (8 Nov. 1962) 49°43.3′S, 178°45.3′E, Antipodes Is, 121 m, DCM, very coarse sand with shell and gravel $\frac{1}{4}$–1 in. 2 dead *C. k. kampyla* and 1 live *F. c. laudandus*.

A734 (8 Nov. 1962) 49°42′S, 178°44.3′E, Antipodes Is, 150 m, DCM, gravel $\frac{1}{8}$–2 in. with shell. 25 dead *C. k. kampyla* and 2 live and 5 dead *F. c. laudandus*.

A738 (9 Nov. 1962) 49°40.1′S, 178°47.3′E, Antipodes Is, 62 m, DCM, gravel up to 3 in. 2 live *F. c. laudandus*.

A740 (9 Nov. 1962) 49°41′S, 178°40.2′E, Antipodes Is, 315 m, DCM, gravel $\frac{1}{4}$–2 in. 58 dead *C. k. kampyla* and 4 dead *F. c. laudandus*.

A741 (9 Nov. 1962) 49°41.5′S, 178°51.5′E, Antipodes Is, 132 m, DCM, bryozoan sand. 15 dead *C. k. kampyla*.

A742 (9 Nov. 1962) 49°37.9′S, 178°52.4′E, Antipodes Is, 150 m, DCM, fine bryozoan sand. 3 dead *C. k. kampyla*.

A744 (9 Nov. 1962) 49°36.7′S, 178°48.1′E, Antipodes Is, 360 m, DCM, bryozoan sand. 61 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

A745 (9 Nov. 1962) 49°36.7′S, 178°50.5′E, Antipodes Is, 399 m, DCM, coarse shell sand, gravel $\frac{1}{4}$–$\frac{3}{4}$ in. 1 live and 9 dead *C. k. kampyla*.

A746 (15 Nov. 1962) 47°30′S, 179°30′E, Bounty Is, 159 m, DCM, "pebbles". 1 dead *C. k. kampyla*.

A908 (13 Sept. 1963) 43°27.3′S, 179°03′E, Chatham Rise, 459 m, MD, gravel $\frac{1}{2}$–4 in. (one concretion and sheared greywacke). 1 live *F. c. laudandus*.

A910 (13 Sept. 1963) 43°04′S, 178°39′W, Chatham Rise, 549 m, MD, medium-fine shell sand, gravel 1–9 in. (ferruginous concretion and volcanics). 2 dead *C. k. kampyla* and 15 live and 14 dead *F. c. laudandus*.

A911 (13 Sept. 1963) 42°45′S, 178°15′W, Chatham Rise, 909 m, MD, gravel $\frac{1}{2}$–2 in. 1 live and 2 dead *F. c. laudandus*.

A913 (14 Sept. 1963) 43°37′S, 178°11.5′W, Chatham Rise, 402 m, MD, gravel 1–6 in. 4 live *F. c. laudandus*.

A914 (15 Sept. 1963) 44°04′S, 178°11.5′W, Chatham Rise, 455 m, MD, gravel $\frac{1}{4}$–1 in. 2 live *F. c. laudandus*.

A916 (15 Sept. 1963) 43°58.5′S, 179°11′W, Chatham Rise, 274 m, MD, gravel $\frac{1}{4}$–3 in. (schist fragments). 7 live juvenile *F. c. laudandus*.

A917 (15 Sept. 1963) 43°56′S, 179°15′W, Chatham Rise, 203 m, MD, medium-coarse sand, gravel. 7 live and 1 dead *F. c. laudandus*.

C605 (26 April 1961) 43°40′S, 179°30′E, Chatham Rise, 441–461 m, DD, muddy fine sand. 3 live *F. c. laudandus*.

C618 (30 April 1961) 43°52′S, 175°20′W, east of Chatham Is, 623–688 m, DD, medium foraminiferal sand, gravel up to 3 in. 5 dead *C. k. kampyla*.

C619 (2 May 1961) 43°52′S, 174°48′W, east of Chatham Is, 502–777 m, DD, medium foraminiferal sand, with bryozoa. 2 live *F. c. laudandus*.

C732a (25 Nov. 1961) 54°29.5′S, 158°58.5′E, Macquarie I, 77 m, DD, medium sand, very small coarse shell sand, gravel. 1 dead *C. k. tomlini*.

C734 (25 Nov. 1961) 53°55′S, 158°55′E, north of Macquarie I, 360 m, DD, gravel 2 in. 1 dead and fragmentary *F. c. laudandus*.

D8 (20 April 1963) 54°52′S, 158°39′E, Macquarie I, 141 m, DCMb, fine shell sand, coarse shell, gravel up to 4 in. 2 dead *C. k. tomlini*.

D9 (20 April 1963) 54°52′S, 158°50′E, Macquarie I, 113 m, DCMb, "encrusted boulders". 1 dead *C. k. tomlini*.

D17 (23 April 1963) 52°31′S, 160°31′E, Vema Seamount, Macquarie Ridge, 124 m, DCMb, "6 in. blocks of angular crumbly mudstone". 1 live and 3 dead *C. k. kampyla*.

D18 (23 April 1963) same location as D17, 128 m, DCMb, gravel. 1 live *C. k. kampyla*.

D22 (26 April 1963) 50°38′S, 163°57′E, Macquarie Ridge, 682 m, DCMb, medium siliceous sand, with angular pebbles. 7 dead *C. k. kampyla* and 2 dead fragmentary *F. c. laudandus*

D39a (7 May 1963) 50°58′S, 165°45′E, Auckland Is, 549 m, DCMb, medium calcareous sand with pebbles 7 in. 5 live and 41 dead *C. k. kampyla*, 3 dead fragmentary *F. c. laudandus*.

D74 (12 May 1963) 50°55.6′S, 165°54.8′E, Auckland Is, 168 m, DCMb, sediment not known. 1 dead *C. k. kampyla.*

D82 (13 May 1963) 49°53′S, 166°12′E, between The Snares and the Auckland Is, 446 m, DCMb, sediment not known. 2 live and 1 dead *C. k. kampyla.*

D90 (17 May 1963) 43°50′S, 179°00′W, Chatham Rise, 399 m, DCMb, fine muddy foraminiferal sand. 2 dead *F. c. laudandus.*

D134 (12 Jan. 1964) 48°16′S, 168°43.5′E, Campbell Plateau, 677 m, TAM, foraminiferal sand with pebbles. 26 live and 13 dead *F. c. laudandus.*

D136 (12 Jan. 1964) 48°33.5′S, 169°10′E, Campbell Plateau, 713 m, TAM, fine foraminiferal mud. 1 live *F. c. laudandus.*

D138 (13 Jan. 1964) 48°32′S, 168°19.5′E, Campbell Plateau, 668 m, TAM, muddy medium sand, forams, pebbles ¾ in. 66 live and 34 dead *F. c. laudandus.*

D139 (13 Jan. 1964) 48°20.5′S, 167°46.5′E, Campbell Plateau, 150 m, TAM, coarse calcareous sand, shell, pebbles up to 1½ in. 1 dead *F. c. laudandus.*

D145 (14 Jan. 1964) 48°42′S, 167°27′E, Campbell Plateau, 362 m, TAM, fine-coarse bryozoan shell sand. 1 dead *C. k. kampyla* and 16 live *F. c. laudandus.*

D147 (14 Jan. 1964) 49°31′S, 167°25′E, Campbell Plateau, 574 m, TAM, fine sand, pebbles up to ½ in. 6 live and 1 dead *F. c. laudandus.*

D149 (14 Jan. 1964) 49°10.5′S, 166°51′E, Campbell Plateau, 454 m, TAM, very coarse bryozoan and shell sand, pebbles. 1 dead *C. k. kampyla* and 4 dead fragmentary *F. c. laudandus.*

D154 (16 Jan. 1964) 48°09′S, 166°23′E, The Snares, 159 m, TAM. 1 dead *F. c. laudandus.*

D159 (17 Jan. 1964) 49°01′S, 164°30′E, Macquarie Ridge, 741 m, DCMb, coarse bryozoan shell sand. 4 dead *C. k. kampyla*

D160 (18 Jan. 1964) 49°31.5′S, 166°15.5′E, between The Snares and the Auckland Is, 722 m, DCMb, foraminiferal sand, pebbles. 10 live and 37 dead *C. k. kampyla* and 1 dead *F. c. laudandus.*

D166 (19 Jan. 1964) 49°49′S, 163°51′E, Macquarie Ridge, 668 m, DCMb, sediment not known. 1 dead *C. k. kampyla.*

D175 (21 Jan. 1964) 50°36.5′S, 167°41′E, Campbell Plateau, 344 m, TAM, foraminiferal sand. 1 dead fragmentary *C. k. kampyla* and 3 live and 2 dead *F. c. laudandus.*

D176 (21 Jan. 1964) 51°06′S, 167°48.5′E, Campbell Plateau, 212 m, TAM, coarse to medium bryozoan and shell sand. 24 dead *C. k. kampyla* and 3 live and 5 dead *F. c. laudandus.*

D180 (22 Jan. 1964) 51°08.5′S, 166°51′E, Campbell Plateau, 465 m, TAM, sediment not known. 12 live and 1 dead *F. c. laudandus.*

D242 (2 Oct. 1964) 38°00′S, 169°03′E, Challenger Plateau, 337 m, DCMb, pebbles up to 2×2×¾ in. 6 dead *C. k. kampyla.*

E106 (11 Oct. 1964) 43°55′S, 177°10′W, Chatham Rise, 179 m, DCMb, grey green muddy sand. 2 dead *F. c. laudandus.*

E111 (12 Oct. 1964) 43°00′S, 176°30′W, Chatham Rise, 675 m, TAM, sandy mud. 1 dead juvenile *F. c. laudandus.*

E117 (13 Oct. 1964) 43°30′S, 176°00′W, Chatham Rise, 333 m, TAM, muddy sand with forams. 1 live *F. c. laudandus.*

E119 (14 Oct. 1964) 43°10′S, 176°00′W, Chatham Rise, 638 m, TAM, fine foram sand. 1 dead *F. c. laudandus.*

E120 (14 Oct. 1964) 43°02′S, 175°30′W, west of Chatham Is, 872 m, TAM, fine foram sand. 1 dead *F. c. laudandus.*

E121 (14 Oct. 1964) 43°19′S, 175°40′W, Chatham Rise, 693 m, TAM, muddy foram sand. 1 live *F. c. laudandus.*

E140 (17 Oct. 1964) 44°30.5′S, 176°00.7′W, S.W. of Pitt I, Chatham Is, 192 m, DCMb, shell with angular pebbles. 1 dead *F. c. laudandus.*

E146 (17 Oct. 1964) 44°30′S, 177°01′W, Chatham Is, 664 m, TM/DP, fine sand with forams. 7 live and 2 dead *F. c. laudandus.*

E159 (19 Oct. 1964) 44°01.5′S, 176°59′W, Chatham Is, 165 m, TM/DP, fine sand. 1 dead *F. c. laudandus.*

E165 (20 Oct. 1964) 43°02′S, 177°20′W, Chatham Rise, 591 m, TAM, sediment not known. 4 live *F. c. laudandus.*

E167 (20 Oct. 1964) 43°16′S, 177°45′W, Chatham Rise, 395 m, TAM, muddy fine sand. 2 dead *F. c. laudandus.*

E228 (24 Feb. 1965) 54°41′S, 158°55′E, Macquarie I, 148 m, DCMb/TAM, sediment not known. 1 dead *C. k. tomlini.*

E237a (27 Feb. 1965) 54°51′S, 158°38′E, Macquarie I, 155 m, DCMb, "small pebbles". 1 dead *C. k. tomlini.*

E315 (10 April 1965) 33°55′S, 171°55′E, Three Kings Is, 1002 m, DCMb, Bryozoa, shell, corals up to 1 in. 1 dead *F. c. laudandus.*

E400 (7 Oct. 1965) 46°00′S, 171°02′E, off eastern Otago, 622–678 m, TAM, muddy sand and forams. 10 dead *C. k. kampyla* and 1 live and 5 dead *F. c. laudandus.*

E401 (9 Oct. 1965) 46°00′S, 171°12′E, off eastern Otago, 914–823 m, TAM, foraminiferal sand. 6 live and 5 dead *F. c. laudandus.*

E404 (9 Oct. 1965) 47°20′S, 169°44′E, off eastern Southland, 761 m, TAM, foraminiferal sand. 3 live and 1 dead *F. c. laudandus.*

E407 (10 Oct. 1965) 46°40′S, 170°08′E, off eastern Southland, 278–305 m, TAM, medium shell sand. 5 live *F. c. laudandus.*

E408 (10 Oct. 1965) 46°40′S, 170°11′E, off eastern Southland, 518 m, TAM, medium shell sand. 5 live and 3 dead *C. k. kampyla.*

E409 (10 Oct. 1965) 46°41′S, 170°21′E, off eastern Southland, 743 m, TAM, fine shell sand. 1 dead *F. c. laudandus.*

E411 (10 Oct. 1965) 46°38.5′S, 170°59′E, off eastern Southland, 1275 m, TAM, medium foraminiferal sand. 1 dead *F. c. laudandus.*

E412 (11 Oct. 1965) 45°10′S, 171°41′E, off eastern Otago, 249 m, TAM, muddy sand with shell. 15 live and 2 dead *F. c. laudandus.*

E421 (15 Oct. 1965) 44°00′S, 175°00′E, Chatham Rise, 494 m, TAM, mud. 6 live and 1 dead *F. c. laudandus.*

E422 (15 Oct. 1965) 44°15′S, 175°00′E, Chatham Rise, 615 m, TAM, mud. 1 dead *F. c. laudandus.*

E424 (16 Oct. 1965) 44°40′S, 172°38′E, off South Canterbury, 293 m, TAM, medium-fine sand with shell. 19 live *F.c. laudandus.*

E429 (17 Oct. 1965) 44°00′S, 173°59′E, off Bank's Peninsula, 523 m, TAM, sandy mud. 1 live *F. c. laudandus.*

E433 (18 Oct. 1963) 43°43′S, 174°30′E, off North Canterbury, 571 m, TAM, muddy fine sand. 5 live *F. c. laudandus.*

E434 (18 Oct. 1963) 43°30′S, 174°30′E, off North Canterbury, 556 m, TAM, mud. 9 live and 1 dead *F. c. laudandus.*

E435 (18 Oct. 1963) 43°15′S, 174°29′E, off North Canterbury, 574 m, TAM, sandy mud with forams. 1 live *F. c. laudandus.*

E436 (18 Oct. 1963) 43°15′S, 174°00′E, off North Canterbury, 695 m, TAM, sandy mud with forams. 2 dead *F. c. laudandus.*

E711 (22 March 1967) 39°18.8′S, 178°13.8′E, off Hawke Bay, 490–428 m, TAM, mud. 1 dead *F. c. laudandus.*

E712 (22 March 1967) 39°20′S, 178°15.8′E, off Hawke Bay, 772–717 m, TAM, mud. 2 live *F. c. laudandus.*

E717 (23 March 1967) 38°42′S, 178°33.3′E, off Hawke Bay, 828–839 m, TAM, mud. 3 live *F. c. laudandus.*

E719 (23 March 1967) 38°46′S, 178°48′E, off Gisborne, 913–750 m, TAM, "fine brown sand". 4 live and 4 dead *C. k. kampyla.*
25 live adult and 32 live juvenile and 42 dead *F. c. laudandus.*

E724 (24 March 1967) 37°23.3′S, 178°00.5′E, off Cape Runaway, 695–631 m, TAM, mud. 2 live *F. c. laudandus.*

E738 (27 March 1967) 37°35′S, 179°03′E, off East Cape, 263–252 m, TAM, mud and fine sand. 1 dead *F. c. laudandus.*

E747 (29 March 1967) 40°43.2′S, 178°48.4′E, off eastern Wellington, 554–569 m, TAM, mud. 1 dead *F. c. laudandus.*

E748 (29 March 1967) 40°46′S, 176°55′E, off eastern Wellington, 739 m, TAM, mud. 2 live *F. c. laudandus.*

E749 (29 March 1967) 40°47′S, 176°57′E, off eastern Wellington, 913–997 m, TAM, fine sandy mud, pebbles up to 1½ in. 9 live *F. c. laudandus.*

E752 (30 March 1967) 41°40.7′S, 175°15.4′E, off Cape Palliser, 618–596 m, TAM, fine sandy mud. 1 live *F. c. laudandus.*

E755 (30 March 1967) 42°00.5′S, 174°25.4′E, off North Canterbury, 247–276 m, TAM, fine sandy mud. 2 dead *F. c. laudandus.*

E756 (30 March 1967) 42°01′S, 174°26.5′E, off eastern Marlborough, 885–969 m, TAM, fine sandy mud. 2 dead *C. k. kampyla* and 2 dead *F. c. laudandus.*

E757 (30 March 1967) 42°03.2′S, 174°27.2′E, off eastern Marlborough, 1081–1125 m, TAM, mud. 1 dead *F. c. laudandus.*

E759 (31 March 1967) 42°45′S, 173°40′E, off North Canterbury, 195–213 m, TAM, muddy fine sand. 2 live *F. c. laudandus.*

E760 (31 March 1967) 42°44.5′S, 173°43′E, off North Canterbury, 567–556 m, TAM, fine sandy mud. 1 dead *F. c. laudandus*.

E772 (14–15 Oct. 1967) 42°00′S, 170°16′E, off Westland, 748 m, TAM, mud. 2 live and 3 dead *F. c. laudandus*.

E777 (16 Oct. 1967) 42°43′S, 169°45′E, off Westland, 731–712 m, TAM, mud. 2 dead *F. c. laudandus*.

E780 (16 Oct. 1967) 43°23.5′S, 169°27′E, off Westland, 252–206 m, TAM, mud. 1 dead *F. c. laudandus*.

E782 (16 Oct. 1967) 43°23′S, 169°03.5′E, off Westland, 823 m, TAM, mud. 1 live *F. c. laudandus*.

E783 (16–17 Oct. 1967) 43°23′S, 168°36.5′E, off Westland, 966 m, TAM, mud. 4 live *F. c. laudandus*.

E796 (20 Oct. 1967) 45°20′S, 166°45.5′E, off Fiordland, 251–226 m, TAM, muddy sand, pebbles ¼–1 in. 1 dead *C. k. kampyla*.

E797 (20 Oct. 1967) 45°20′S, 166°44.7′E, off Fiordland, 471–421 m, TAM, coarse sandy mud, pebbles. 1 dead *F. c. laudandus*.

E803 (21 Oct. 1967) 45°57′S, 166°09′E, off south-west Fiordland, 534–514 m, TAM, sediment not known. 47 dead *C. k. kampyla* and 8 dead *F. c. laudandus*.

E804 (21 Oct. 1967) 45°58.5′S, 166°18.5′E, off south-western Fiordland, 183 m, TAM, "encrusted boulders". 1 dead *C. k. kampyla* and 2 live and 2 dead *F. c. laudandus*.

E820 (23 Oct. 1967) 46°35′S, 165°58′E, north end of Macquarie Ridge, 220 m, TAM, "dead shell". 2 dead *F. c. laudandus*.

E821 (23 Oct. 1967) 46°43.5′S, 165°46.5′E, north end of Macquarie Ridge, 549 m, TAM, "encrusted boulders". 1 live and 8 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

E822 (23–24 Oct. 1967) 46°50.6′S, 165°36′E, north end of Macquarie Ridge, 682–781 , TAM, "encrusted boulders". 1 live and 2 dead *C. k. kampyla*, 1 live and 4 dead *F. c. laudandus*.

E823 (24 Oct. 1967) 46°55′S, 165°30.5′E, north end of Macquarie Ridge, 1046–1083 m, TAM, "1 pebble". 1 dead *F. c. laudandus*.

E826 (24 Oct. 1967) 46°37.5′S, 166°44.2′E, north end of Macquarie Ridge, 823 m, TAM, "2 pebbles with coral fragments". 1 live and 9 dead *C. k. kampyla* and 25 dead *F. c. laudandus*.

E827 (24 Oct. 1967) 46°35.5′S, 166°44.5′E, north end of Macquarie Ridge, 530–526 m, TAM, "2 small pebbles". 2 live and 5 dead *F. c. laudandus*.

E831 (25 Oct. 1967) 47°20.5′S, 167°03.8′E, south-west of Stewart I, 479–467 m, TAM, sediment not known. 1 dead *F. c. laudandus*.

E832 (25 Oct. 1967) 47°21′S, 167°05.7′E, south-west of Stewart I, 251–225 m, TAM, "dead shell". 1 live *F. c. laudandus*.

E840 (16 March 1968) 33°52′S, 172°16′E, Three Kings Is, 757–729 m, TAM, medium–coarse bryozoan shell sand. 1 dead *C. k. kampyla*.

E870 (20 March 1968) 34°05′S, 168°10′E, south end of Norfolk Ridge (? fossil), 1488–1556 m, TAM, "firm sedimentary rock with barnacle plates". 30 dead *F. c. laudandus* and many fragments.

E875 (21 March 1968) 34°39′S, 172°07′E, west of Ninety-Mile Beach, 489–492 m, TAM, medium sand with shell. 40 dead *C. k. kampyla* and 6 dead *F. c. laudandus*.

E876 (21 March 1968) 34°39′S, 172°14′E, west of Ninety-Mile Beach, 216–247 m, TAM, medium sand. 1 dead *C. k. kampyla*.

E879 (22 March 1968) 35°19′S, 172°25′E, west of Hokianga Heads, 768–786 m, TAM, fine sandy mud. 2 live and 1 dead *F. c. laudandus*.

E906 (28 March 1968) 38°39′S, 172°38′E, west of North Taranaki, 691–751 m, TAM, mud. 1 dead *C. k. kampyla*.

E908 (28 March 1968) 38°42′S, 172°45.5′E, west of North Taranaki, 256–336 m, TAM, mud. 1 dead *C. k. kampyla*.

F77 (12 Jan. 1965) 47°00′S, 169°30′E, off south-eastern Southland, 117 m, TAM, coarse shell sand. 1 live *F. c. laudandus*.

F79 (14 Jan. 1965) 49°04′S, 168°01′E, Campbell Plateau, 679 m, TAM, "light grey green sand". 1 live *F. c. laudandus*.

F80 (14 Jan. 1965) 49°00′S, 167°01′E, Campbell Plateau, 631 m, TAM, coarse to medium shell sand, "shell up to ½ in." 5 live and 6 dead *C. k. kampyla*, 30 live and 5 dead *F. c. laudandus*.

F90 (16 Jan. 1965) 49°30.5′S, 167°40′E, Campbell Plateau, 585 m, TAM, medium foraminiferal sand. 3 dead *C. k. kampyla* and 3 live and 3 dead *F. c. laudandus*.

F94 (17 Jan. 1965) 48°31′S, 168°01′E, Campbell Plateau, 604 m, TAM, medium foraminiferal sand, 39 live and 58 dead *C. k. kampyla*, 5 live and 24 dead *F. c. laudandus*.

F95 (17 Jan. 1965) 48°53′S, 168°39′E, Campbell Plateau, 646 m, TAM, sediment not known. 2 live *F. c. laudandus*.

F99 (18 Jan. 1965) 48°32′S, 168°54.5′E, Campbell Plateau, 706 m, TAM, fine foraminiferal sand. 8 live *F. c. laudandus*.

F104 (20 Jan. 1965) 48°40′S, 170°48.5′E, Campbell Plateau, 814–788 m, TAM, foraminiferal mud. 4 live and 6 dead *F. c. laudandus*.

F107 (20 Jan. 1965) 48°45′S, 172°00′E, Campbell Plateau, 658 m, TAM, foraminiferal mud. 1 dead *C. k. kampyla* and 15 live and 8 dead *F. c. laudandus*.

F109 (21 Jan. 1965) 49°11′S, 173°00′E, Campbell Plateau, 501 m, TAM, foraminiferal mud. 4 live and 2 dead *F. c. laudandus*.

F120 (25 Jan. 1965) 48°18′S, 179°16′E, Bounty Is, 494–512 m, TAM, foraminiferal mud. 7 live and 7 dead *C. k. kampyla* and 1 live *F. c. laudandus*.

F122 (26 Jan. 1965) 48°06′S, 179°57′W, Bounty Is, 252 m, TAM, medium foram sand, pebbles up to 1 in. 3 live and 5 dead *C. k. kampyla*, 4 live and 2 dead *F. c. laudandus*.

F124 (27 Jan. 1965) 47°34′S, 179°56′W, Bounty Is, 476 m, TAM, medium foram sand. 17 live and 6 dead *C. k. kampyla*, 10 live and 6 dead *F. c. laudandus*.

F136 (30 Jan. 1976) 51°20′S, 172°42′E, Campbell Plateau, 547 m, TAM, medium foram sand. 1 live *F. c. laudandus*.

F143 (1 Feb. 1965) 53°05.5′S, 170°13′E, Campbell Plateau, 380 m, TAM, medium foram sand. 1 live *F. c. laudandus*.

F144 (1 Feb. 1965) 53°29′S, 170°56′E, Campbell Plateau, 596 m, TAM, fine foram sand. 8 dead *C. k. kampyla* and 19 live and 5 dead *F. c. laudandus*.

F145 (1 Feb. 1965) 53°14′S, 171°48′E, Campbell Plateau, 435 m, TAM, fine foram sand. 1 live and 5 dead *F. c. laudandus*.

F146 (1 Feb. 1965) 53°00′S, 172°45′E, Campbell Plateau, 435 m, TAM, fine foram sand. 47 dead *C. k. kampyla* and 4 live and 10 dead *F. c. laudandus*.

F147 (1 Feb. 1965) 52°21′S, 173°09′E, Campbell Plateau, 611 m, TAM, fine foram sand. 1 dead *C. k. kampyla* and 3 live and 3 dead *F. c. laudandus*.

F148 (1 Feb. 1965) 51°43′S, 173°32′E, Campbell Plateau, 677 m, TAM, fine foram sand. 3 live *F. c. laudandus*.

F151 (3 Feb. 1965) 48°32′S, 174°50′E, Campbell Plateau, 814 m, TAM, fine foram sand. 3 live and 3 dead *F. c. laudandus*.

F749 (17 Aug. 1966) 44°01′S, 175°26′E, Chatham Rise, 1427–1372 m, TAM, mud. 10 live and 2 dead *F. c. laudandus*.

F750 (17 Aug. 1966) 44°15′S, 175°26′E, Chatham Rise, 594 m, TAM, mud. 1 live and 3 dead *F. c. laudandus*.

F755 (19 Aug. 1966) 43°00′S, 174°30′E, Chatham Rise, 854–748 m, TAM, sandy mud. 1 dead juvenile *C. k. kampyla* and 2 dead *F. c. laudandus*.

F760 (20 Aug. 1966) 42°45′S, 176°30′E, Chatham Rise, 705 m, TAM, mud. 3 live *F. c. laudandus*.

F766 (21 Aug. 1966) 41°25.6′S, 176°00.4′E, off south-eastern Wellington, 946–982 m, TAM, mud. 1 live juvenile *F. c. laudandus*.

F868 (2 Oct. 1968) 37°28.5′S, 179°03.5′E, off East Cape, 808–924 , TAM, muddy sand. 4 dead *F. c. laudandus*.

G29 (23 Feb. 1967) 43°48′S, 175°01′E, Chatham Rise, 439 m, BD, "grey green mud." 1 dead juvenile *F. c. laudandus*.

G153 (12 Nov. 1967) 42°45′S, 173°40′E, Chatham Rise, 137 m, OT, sediment not known. 1 dead *C. k. kampyla* and 1 dead *F. c. laudandus*.

G155 (12 Nov. 1967) 42°46′S, 173°39′E, off North Canterbury, 140–150 m, OT, sediment not known. 2 dead *F. c. laudandus*.

G157 (13 Nov. 1967) 43°09′S, 173°38′E, off North Canterbury, 143 m, OT, sediment not known. 1 live *F. c. laudandus*.

G162 (16 Nov. 1967) 42°55′S, 173°33′E, off North Canterbury, 100 m, OT, sediment not known. 2 live *F. c. laudandus*.

APPENDIX 2

DIMENSIONS OF *Cymatona*

	height mm	diameter mm
Cymatona kampyla kampyla **(Watson), New Zealand Recent:**		
NZOI Stn F124	57.6	27.4
	45.9	24.6
	49.8	21.6
	46.0	23.5
	49.5	23.2
NZOI Stn F120	51.0	23.0
	53.0	25.2
	46.4	23.3
	38.5	20.0
NZOI Stn D82	43.7	22.0
NZOI Stn F144	51.4	21.6
NZOI Stn F94	41.2	21.6
	40.3	20.5
	35.4	20.0
	34.5	18.8
	35.2	19.0
Mu 70–45, 495–520 m, Papanui Canyon, off Otago Peninsula, RV *Munida*	13.4	7.4
	14.7	7.8
	52.6	23.2
	53.0	25.7
	51.4	25.3
	52.3	23.8
	53.6	24.0
	45.2	21.1
	47.9	25.3
	54.0	23.9
	51.0	23.2
	47.5	21.2
	50.7	23.9
	49.1	23.0
	44.5	21.0
	45.6	21.9
	45.3	20.5
	50.3	23.0
	46.0	22.1
	44.0	19.7
	41.3	20.8
	43.2	22.8
	43.3	19.6
	39.0	19.9
	30.7	15.4
	27.8	15.0
(n=42)		
Cymatona kampyla kampyla **(Watson), E. Australia:**		
LECTOTYPE, *Challenger* "sta. 164b", (off New Zealand) British Museum (Natural History) no. 1877:2:9: 1246	39.5	20.6
F. 23104, National Museum of Victoria, 130 m, off Broken Bay, N.S.W., *Challenge*	38.5	17.8
	37.0	17.5
	34.9	17.0
F. 26658, National Museum of Victoria	41.3	17.8
	36.4	17.8
W.M.5385, N.Z.G.S., 180 m off Cape Pillar, Tasmania	30.5	13.5
	23.0	11.7
	15.7	8.5
C.73601, 30 miles S of Cape Everard, Victoria, 360 m, *Endeavour*, 22 Oct. 1964	51.8	21.9
	43.5	19.3
	39.4	16.2
	40.8	17.8
	22.0	11.2
	13.3	7.8
	14.1	8.0
	12.2	6.7
	10.6	5.9
	10.0	5.8
	8.2	5.0
C.79056, E of Sydney, N.S.W., 75–150 m, HMAS *Gascoyne*, CSIRO, 18 July 1962	30.2	14.9
	25.0	11.3
	20.9	10.4
	21.5	10.1
	20.0	9.9
	16.1	7.8
	13.9	7.1
	10.9	6.1
	8.3	5.1
C.82471, off Sydney, N.S.W., 366–549 m, FRV *Kapala*, 25 May 1971	55.5	22.7
	43.5	19.8
C.80174, off Newcastle, N.S.W., FRV *Kapala*, 29 April 1971, 567–548 m	44.3	20.7
C.79206, off Newcastle, N.S.W., 600 m, FRV *Kapala*, 7 May 1971	55.0	22.8
	56.2	23.8
	46.0	21.3
	44.2	19.8
C.79204, off Newcastle, N.S.W., 560 m, 29 April 1971, FRV *Kapala*	51.0	22.7
	49.0	21.0
	47.2	20.1
	43.0	21.3
	44.3	20.7
W.M.10815, N.S.W. shelf, FRV *Kapala*	54.3	24.9
	48.9	21.7
C.79199, off Newcastle, N.S.W., 280–550 m, 5–12 May 1971, FRV *Kapala*, Stn 71–08	50.3	21.0
	46.7	19.8
	43.6	21.0
	49.8	21.2
	46.8	21.0
	45.2	20.8
	45.3	20.5
	50.1	22.5
E.5745, Gabo I to Cape Everard Banks, *Endeavour*	48.5	20.1
E.5736, S of Cape Everard, 365–475 m, *Endeavour*	47.4	19.4
	44.7	20.4
C.24439, 550 m, 27½ miles E of Sydney	44.8	21.8
C.71395, *Challenge* trawl 318, 285–290 m, E. of Newcastle, N.S.W.	44.0	20.8
	43.6	21.1
C.26668, 1460 m, 35 miles E of Sydney	44.2	20.1
C.71396, CSIRO Stn G3/201/60, 365 m, off Sydney	43.4	19.4
C. 64256, 135 m, off Broken Bay, N.S.W.	49.7	23.4
(n=60)		
Cymatona kampyla tomlini **(Powell), Macquarie I:**		
NZOI Stn E228	30.1	31.7
NZOI Stn C732a	37.8	20.7
(n=2)		
Cymatona kampyla jobbernsi **(King), N.Z. Pliocene:**		
HOLOTYPE, Lake Ferry, Palliser Bay	35.7	21.0
VM.776, Alpha Ck., White Rock Rd	26.1	13.5
VM.775, Alpha Ck., White Rock Rd.	31.2	15.0
V.1486, cliffs E of Lake Ferry	42.9	22.5
(n=4)		

APPENDIX 3

DIMENSIONS OF *Fusitriton*

Note For "*Fusitriton cancellatus*" read "*Fusitriton magellanicus*".

Fusitriton cancellatus murrayi (von Martens), off Cape Town:

	Height mm	Diameter mm	No. Axials
MF.14522, National Museum	107.6	53.6	26
	101.6	51.3	24
MF.19288, National Museum	97.7	47.2	23
	88.4	47.4	24
	98.7	46.0	24
WM.10144, N.Z. Geological Survey	97.8	48.5	25
WM.8135, N.Z. Geological Survey	85.0	40.7	26
F.26889, National Museum, Victoria	95.2	47.6	26
	92.6	46.8	23
F.17146, National Museum, Victoria	92.8	47.7	29
	94.3	49.6	28
C.71152, Australian Museum	102.9	50.0	30
(n=12)			

Fusitriton cancellatus cancellatus (Lamarck), South America:

	Height mm	Diameter mm	No. Axials
MF.14522, National Museum San Antonio, Argentina	81.9	43.5	27
	85.3	46.4	28
MF.21345, off Ilha dos Lobos, Uruguay	120.7	64.5	38
	107.8	56.5	26
MF.21355, 37°22′S, 45°48′W, off Argentina	107.4	61.0	24
	104.0	55.0	28
	97.5	53.4	27
MF.17391, Punta Arenas, Chile	98.0	55.3	24
MF.21751, off San Antonio, Argentina	97.9	52.7	25
	102.8	56.0	23
MF.20977, 100 miles S of Ilha dos Lobos, Uruguay	100.2	52.0	26
	102.8	56.0	26
Eltanin 1283, 43°13′S, 97°43′W	118.2	58.5	27
Eltanin 369, 54°04′S, 63°35′W, 247–293 m, off Falkland Is.	68.0	37.2	22
	57.7	29.5	18
	58.2	30.2	21
Eltanin 740, 56°06′S, 66°19′W, 384–494 m, off Cape Horn	63.2	34.6	20
	81.0	44.5	27
Eltanin 1596, 54°39′S, 57°12′W, 124 m, between Cape Horn and S. Georgia	67.0	38.5	24
Eltanin 958, 52°56′S, 75°00′W, 90 m, Straits of Magellan	47.7	25.2	21
	38.8	20.0	20
	28.4	14.8	13
	27.2	18.9	16
WM.9302, off Montevideo	113.9	60.5	23
(n=24)			

Fusitriton cancellatus laudandus Finlay, New Zealand:

	Height mm	Diameter mm	No. Axials
Holotype, AM.TM.333, Auckland Museum; off Otago Heads, 80 m	100.2	50.0	26
Eltanin 1974, 54°30′S, 158°59′E, 112–124 m, E of New Zealand	82.0	51.2	23
NZOI Stn F122 (figured)	116.2	51.9	26
	118.6	55.1	20
	121.4	59.5	23
NZOI Stn E424 (figured)	93.4	44.2	15
	96.0	47.0	16
NZOI Stn E401 (figured)	94.9	54.5	28
NZOI Stn E412 (figured)	90.9	39.0	15
NZOI Stn A910 (not figured)	122.9	61.5	26
	113.8	54.5	23
	109.8	50.0	22
	95.8	45.6	16
	94.6	44.5	19
	86.5	42.7	17
	85.7	40.5	18
	66.7	31.5	18
	59.7	28.0	14
	57.0	27.5	17
NZOI Stn E433 (not figured)	107.9	54.4	27
	96.9	50.8	23
	100.5	47.4	22
	103.0	51.2	24
NZOI Stn E412 (not figured)	106.8	51.5	25
	93.7	44.3	18
	92.7	44.8	16
	90.2	42.3	18
	91.1	44.0	18
	86.8	42.6	15
	81.8	37.4	16
NZOI Stn E412	81.2	39.1	16
	81.0	37.7	16
	75.6	36.2	14
	79.2	73.8	16
	75.8	36.6	17
	71.0	33.5	14
	62.4	29.0	16
NZOI Stn E424 (not figured)	106.6	52.9	17
	104.8	48.8	20
	101.2	49.0	24
	98.2	44.8	16
	93.6	43.8	18
	88.5	48.2	17
	89.0	42.5	15
	81.7	38.0	16
(n=45)			

Fusitriton cancellatus retiolus (Hedley), E. Australia:

	Height mm	Diameter mm	No. Axials
MF.14812, off N.S.W., M V *Challenge*	102.9	50.0	21
Holotype, C.70730 (Aust. Mus.), 180–450 m, S of Gabo I, N.S.W., coll. FIS *Endeavour*	130.3	61.2	37
C.79194, E of Broken Bay, N.S.W., FRV *Kapala*, 550 m, 21 Apr. 1971	100.0	47.6	39
	114.0	57.7	40
	98.3	49.2	42
	70.8	35.8	25
	67.9	31.7	25
C.79184, as above, 20 Apr. 1971	114.3	53.6	31
	120.3	52.9	34
	114.0	54.8	28
	121.4	57.3	41
	89.2	43.5	30
C.71636, 20 miles off Wollongong, N.S.W. 235–275 m	117.0	58.7	40
C.71151, 220–230 m, 25 miles E of Manly, N.S.W.	113.1	50.1	28
Paratype, C.70729, 180–450 m, S of Gabo I, N.S.W.	104.4	47.6	34
C.79174, E of Broken Bay, N.S.W., FRV *Kapala*, 550 m, 21 Apr. 1971	132.0	63.1	37
	121.6	60.4	39
	106.8	51.0	28
	100.1	51.0	25

	Height mm	Diameter mm	No. Axials
C.82586, SE of Broken Bay, N.S.W., 549 m, *Kapala*	119.1	54.1	37
C.81987, 80 m, off Montague I, N.S.W.	157.5	69.6	31
	117.8	54.5	34
C.82474, off Sydney, N.S.W., 366–549 m, *Kapala*	93.7	52.3	28
	70.0	35.7	20
C.37002, 100–180 m, Green Cape to Gabo I, N.S.W.	111.4	48.9	36
	95.0	44.6	22
	95.5	49.3	24
C.71149, 90–130 m, off N.S.W.	115.6	52.1	27
C.71148, deep water off Eden, N.S.W.	113.5	55.6	25
F.26655, Bass Strait, *Endeavour*, 1915, National Museum of Victoria	103.5	51.0	28
F.27043, 90–130 m, off Gabo I, N.S.W., National Museum of Victoria	120.0	54.9	24
F.23107, 135 m, off Broken Bay, N.S.W. *Challenge*, National Museum of Victoria	119.0	55.3	31
F.26888, 180 m, off Gabo I, N.S.W., National Museum of Victoria	125.7	56.1	24
	116.6	56.0	25
(n=34)			

Fusitriton cancellatus subsp., between N.Z. and South America:

	Height mm	Diameter mm	No. Axials
Eltanin 1691, 53°56′S, 140°19′W, 362–567 m	64.1	30.5	23
	62.2	29.4	19
	50.2	23.3	16
	49.7	24.2	16
	87.4	41.5	23
	86.0	40.0	23
	80.8	37.1	22
Eltanin 1346, 54°50′S, 129°48′W, 549 m	89.7	47.4	27
	80.0	42.3	28
(n=9)			

Fusitriton oregonensis (Redfield), N. America-Japan:

	Height mm	Diameter mm	No. Axials
MF.5591, Kuiu I, Alaska, 65 m, National Museum	108.5	57.2	16
	123.2	61.0	20
	110.0	49.3	16
	112.1	55.8	19
	115.5	57.6	16
	93.3	42.0	15
	87.6	43.5	15
	75.2	37.2	16
MF.21753, Urukawa, Funka Bay, Hokkaido	91.8	48.0	18
	95.3	48.8	19
MF.8629, Kuiu I, Alaska, 90 m	118.8	58.7	15
	91.2	54.5	18
	90.0	42.9	16
	67.3	32.4	19
	66.2	32.5	15
MF.14521, Kuiu I, Alaska, 90 m	121.3	63.4	17
	122.6	59.4	14
(n=17)			

Fusitriton galea Kuroda and Habe, Japan:

	Height mm	Diameter mm	No. Axials
MF.21752, Ensyu-Nada, 90 m	68.6	32.4	13
WM.9301, off Tosa Bay, 183–266 m	89.8	44.9	12
(n=2)			

INDEX

Major page references are in **bold** type; page numbers of figures are in *italic*.

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