When the two species of *Nectocarcinus* were collected at the Auckland Islands in January, 1963, it was noted that at no time were they taken together in the same trawl haul. *N. bennetti* was taken between 10 and 15 fathoms at three localities in or just outside Port Ross, from bottoms of sand, dead shell and red algae, while *N. antarcticus* was taken between 14 and 15 fathoms at one locality in the same area from a bottom of abundant, finger-like sponges and some *Macrocystis* kelp. The following decapods were taken in association with these portunids: the cancrid crab *Cancer novaezelandiae* (Jacquinot), the hermit crab *Pagurus* sp. and the crangonid shrimp *Pontophilus pilosoides* Stephensen with *N. stephensoni;* the majid crab *Leptomithrax australis* (Jacquinot), the hymenosomatid crab *Halicarcinus planatus* (Fabricius) and the squat lobster *Galathea pusilla* Henderson with *N. antarcticus.* The hippolytid shrimp *Nauticaris marionis* Bate occurred with both species.

A surprising feature amongst material of *N. antarcticus* from Cook Strait northwards is the occasional occurrence of extremely small ovigerous females. Specimens examined can be listed with their respective carapace widths as follows: Colville Channel (26fms), 12.0mm, 14.4mm; Off East Cape (70fms), 29.4mm; between Foxton and Wanganui (50fms), 10.5mm (smallest ovig. ♀, see Griffin and Yaldwyn, 1965), and Tasman Bay (45–55fms), 13.6mm. At one stage it was suspected that these small ovigerous females might represent a different species. We can, however, find no consistent differences between them and typical *N. antarcticus.* All the specimens concerned are from depths greater than 25 fathoms but too little material is available to draw any conclusions regarding bathymetric or geographic variation at present. Northern examples certainly do not attain the size of Auckland Island specimens in either sex. At the Auckland Islands ovigerous females with carapace widths up to 65.7mm occur.

Distribution

New Zealand mainland from Cape Maria van Diemen to Stewart Island, Chatham Islands, Bounty Islands, Auckland Islands and possibly Campbell Island, 6–300fms. (Mr E. W. Dawson informs us that there is undoubted material of *N. antarcticus* from Campbell Id. in the N.Z. Oceanographic Institute collections.)

THE AUSTRALIAN SPECIES *N. integrifrons* AND *N. tuberculosus*

Large specimens of the two well-known Australian species of *Nectocarcinus* are easily distinguished from each other, the carapace differing markedly in convexity, tuberculation and hairiness; this has been clear from the time of Milne Edwards (1861: pls. 37 and 38) who provided excellent illustrations of the two species. However, small juveniles and even moderately sized adults have historically provided difficulties. The fact that the two species have been usually separated by the presence or absence of a central notch in the frontal margin, a feature which is variable —a notch is sometimes present in both species—and the shape of the first pleopods in the males, which is very similar in the two species (Stephenson and Campbell, 1960: 82–83, pl. 6, figs. A and B), made positive identification of small specimens extremely difficult and often virtually prevented a clear separation of a sample into two species, or alternatively, suggested the existence of two species in a sample when only one was present.

Examination of the large series of specimens of *Nectocarcinus* taken in Port Phillip Bay (Griffin and Yaldwyn, in press) eventually showed that but a single species, *N. integrifrons* (Latreille), was present, although the presence of a central notch in the frontal margin and the pattern of tuberculation of the carapace in some specimens at times suggested that *N. tuberculosus* A. Milne Edwards occurred sympatrically with *N. integrifrons.* Further examination of a number of features in the large series of specimens of both species reported on previously by Rathbun (1923) and by Stephenson and Campbell (1960) allowed a discrimination between

these species, the results of which are summarised in Tables II (juveniles) and III (adults). Table II is based on two males, carapace width ca 10 and 14mm, of *N. integrifrons* from the Port Phillip Survey material and a male, c.w. ca 13mm (Aust. Mus. P.5970) of *N. tuberculosus* from southern New South Wales; Table III is based on a male, c.w. ca 76.5mm (AM P.11422) of *N. integrifrons* from Port Phillip, Victoria, and a male, c.w. ca 85mm (AM E.6082), of *N. tuberculosus* from Bay of Fires, Tasmania. Small specimens of the two species are distinguished most obviously by the shape of the junction of the frontal and orbital margins and the ornamentation of the cheliped carpus. There are also differences in the shape of the penultimate segment of the abdomen in the males. The shape of this segment in large males is the same in both species—the proximal width is ca 1.3 times the distal width, the lateral borders are straight and the junction with the ultimate segment is a small notch. However, in moderately large to very large specimens there continue to be differences in the shape and ornamentation of the front and the ornamentation of the cheliped carpus. Specimens of *N. integrifrons* of intermediate size possess scattered hairs on the carapace and there are no greatly marked differences between intermediate specimens of the two species in arrangement of tubercles on the carapace.

Though Stephenson and Campbell (1960: 83) repeat old records of *N. integrifrons* from New Zealand there is no recent record of this species known to us. As Chilton and Bennett (1929: 754) point out, three overseas workers reported it from New Zealand last century but it still "remains unknown to local naturalists". Bennett (1964: 14) firmly lists it as an Australian species incorrectly recorded from New Zealand.

THE REMAINING SPECIES *N. bullatus* AND *N. spinifrons*

In 1924 Balss described a new species of *Nectocarcinus*, *N. bullatus*, from the Juan Fernandez Islands off Chile in the south eastern Pacific. His description was

TABLE II.—Summary of differences between small specimens of *N. integrifrons* and *N. tuberculosus*.

Character	*integrifrons*	*tuberculosus*
Anterolateral teeth of carapace	sharp spines, 2nd in higher plane but parallel with posterior border of 1st.	2nd upwardly directed, not parallel with 1st.
Frontal margin of carapace	smoothly but weakly convex, uninterrupted or sometimes with a very shallow and minute central notch; junction with orbital margin smoothly rounded, a shallow concavity above antenna.	smoothly and obviously convex, with a strong, obvious V-shaped notch; junction with orbital margin forming a definite angle, a shallow notch above antenna.
Inner dorsal margin of cheliped carpus (wrist)	completely lacking spines or tubercles distal to spinous inner angle.	with a few long spines distal to spinous inner angle.
Lateral junction of penultimate and ultimate segments of male abdomen	very shallowly notched.	distinctly and deeply notched, lateral margin of penultimate segment distally and ultimate segment proximally strongly convex.
Shape of penultimate segment of male abdomen	lateral margins straight, distal margin ⅔ width of proximal margin.	distal margin and proximal margin subequal in width.

TABLE III.—Summary of differences between large specimens of *N. integrifons* and *N. tuberculosus*.

Character	*integrifrons*	*tuberculosus*
Anterolateral teeth of carapace	first 3 almost obtuse, very broad, with low tubercles on dorsal surfaces and lateral borders; 4th a short, sharp spine with numerous tubercles dorsally and laterally.	all 4 short, stout spines surrounded at their bases by small blunt tubercles.
Frontal margin of carapace	smoothly but weakly convex, with a shallow central emargination, bodered dorsally by a single row of numerous rounded tubercles with fewer tubercles behind them, a ventral row of tubercles not visible dorsally; junction with orbital margin rounded; a very shallow concavity above antenna.	almost straight, with a distinct narrow V-shaped notch centrally, bordered by a double row of prominent blunt tubercles both visible in dorsal view; junction with orbital margin almost a right angle; a deep semicircular notch above antenna.
Epibranchial region	with ill-defined groups of small, low blunt tubercles,	
	groups of tubercles merging with those on dorsal surface of anterolateral teeth, not continuing down posterolateral border.	groups of tubercles merging with groups surrounding anterolateral teeth and continuing partway down posterolateral border.
Protogastric and postfrontal regions	protogastric structures distinct, more steeply inclined anteriorly; postfrontal structures ill-defined, broad.	protogastric structures ill-defined, uniformly convex, tubercles more prominent anteriorly; postfrontal structures distinct, closer to midline than protogastrics.
Carapace surface	weakly tuberculate, tubercles more or less arranged in ill-defined short transverse rows; naked.	virtually smooth; densely tomentose, particularly anteriorly.
Inner dorsal margin of cheliped carpus (wrist)	about 10 low, blunt tubercles in line from tip of spine at inner angle to dorsal articulation with chela.	a few (about 4) short, stout spines on distal border of spine at inner angle.
Outer surface of cheliped palm	tubercles in transverse rows,	
	none more prominent or more darkly coloured than any other.	some more prominent and darker in colour than others, hand appears to be covered by scattered dark tubercles.

based on several males and an ovigerous female from Masatierra Island collected by K. Bäckström of the Swedish 1916–17 expedition. As the illustration of this species given by Balss (1924: fig. 2) was not labelled as to sex, and as the carapace width was given as only 6mm, it was thought advisable to re-examine the type material. Dr B. Hubendick (Naturhistoriska Museet, Goteborg, Sweden) kindly sent us two type specimens (registered as Crust. 5162) on loan and the following notes are based on an examination of this material.

The two type specimens of *N. bullatus* Balss seen by us consist of an ovigerous female (carapace width 5.9mm, carapace length 5.3mm) and a non-ovigerous

female (carapace width 5.45mm, carapace length 5.0mm). No male specimen was sent to us. The specimen figured is a non-ovigerous female and the shape of the abdomen is accurately represented. Since Balss makes no specific mention of a holotype, these two specimens are to be considered syntypes. We here select the non-ovigerous female as the LECTOTYPE. Twelve other specimens from the type series are in the collections of the Naturhistoriska Museet.

Through the kindness of Dr John S. Garth and Miss Janet Haig (Allan Hancock Foundation, Los Angeles) we have been able to examine additional specimens of this species—2 ♂ ♂, c.w. 14.6, 24.6mm, 1 ♀, 20.2mm, off Juan Fernandez Id., 125–200 metres, *Anton Bruun*, 15/12/1965 (Sta. 65-IV-67).

All the material agrees with the generic characters given for *Nectocarcinus* by Stephenson and Campbell (1960: 82) except that the basal antennal article is completely free, *not* fused to the front (it is also narrow, as is usual for this subfamily). The antennules are not located in fossae, but lie in unrimmed shallow excavations. The fifth legs have the dactyls lanceolate but not ridged or grooved. Balss's figure shows the posterior margin of this dactyl sinuate. However, the feature is exaggerated—the posterior margin is in fact convex proximally but straight distally.

The shape of the front in the lectotype is not as shown in Balss's figure. The frontal lobes are much shorter and blunter, while the sinuses between the two medial lobes and the submedial lobes do not nearly reach back to the level of the internal orbital angle. In the *Anton Bruun* material, however, the shape of the front is as shown by Balss. The frontal and dorsal orbital margins are minutely tuberculate in all specimens. The fourth anterolateral teeth in the lectotype and in the ovigerous female (paralectotype) do not extend outwards beyond the third anterolaterals. There is a single spinule on the anterior margin of each anterolateral tooth, but that on the third tooth is very slightly larger than that on the fourth. Minute tubercles or spinules are also present ventrally on the anterior margin of the anterolaterals. In the three *Anton Bruun* specimens, however, the fourth anterolateral tooth projects laterally beyond the third and its posterior border is almost straight (see Pl. 3A). The second anterolateral tooth in these specimens bears only a single spinule on the anterior margin; the third tooth bears a single spinule in the two smaller specimens and two spinules in the largest specimen (the inner spinule is broken on the left tooth); the fourth tooth bears two spinules, the inner one ranging from smaller than the outer in the smallest specimen to subequal with the outer in the largest specimen.

The large rounded tubercles shown on the carapace in Balss's figure are in fact raised granulated structures, while the epibranchial ridge is a low and granulated band with the tubercles in the posterior part of the band tending to be the largest. The carapace is naked and there are granules along the outer edges of the anterolateral teeth. At least the right cheliped in Balss's figure is drawn from the ovigerous female as evidenced by the presence of two spinules larger than the others on the dorsal surface of the dactyl, a character not present in the lectotype. The two males from the *Anton Bruun* series have up to five larger spinules; in the female the dorsal edge of the dactyl possesses numerous small, close-set spinules. It appears that the left cheliped in the figure is also probably from the ovigerous female paralectotype.

The first pleopod of the larger *Anton Bruun* male is more or less straight but with the tip weakly curved abdominally; a band of spinules extends along the lateral surface for almost the whole length and curves on to the sternal surface distally. In general this is similar to the first pleopod of *N. antarcticus* as illustrated here.

Nectocarcinus bullatus then, with its quadrilobate front, its epibranchial ridge, its moveable basal antennal article and its modified fifth leg is more closely related to the New Zealand and subantarctic *N. antarcticus/bennetti* group than to the

three Australian species. *N. bullatus* differs from the New Zealand group in that the carapace is mostly smooth with only a few discrete groups of granules, and the width of the carapace between the first anterolateral teeth is about ⅔ of the greatest carapace width (compared with ⅖ in *N. antarcticus* and *N. bennetti*).

Nectocarcinus spinifrons Stephenson is described and figured from three specimens dredged off Shark Bay, Western Australia, in 40fms (Stephenson, 1961: 92). The bilobed (though spinulate) front and the lack of epibranchial ridges link this species with the Australian *N. integrifrons/tuberculosus* group, but the fact that the basal antennal article is capable of a small amount of movement and that the fifth leg shows a certain degree of modification for swimming, indicate that *N. spinifrons* has a somewhat intermediate position between this Australian group and the New Zealand–Juan Fernandez grouping. Stephenson and Rees (1968) extend the known range of this species to South Australia with a record of a large male off Greenly Island from 44fms, and this specimen is illustrated here on Pl. 3B.

Key to Species of the Genus *Nectocarcinus*

1	Front entire or bilobate, edge tuberculate or spinulate. Dorsal surface of carapace without distinct transverse ridges		2
–	Front quadrilobate, edge smooth or minutely tuberculate. Dorsal surface of carapace with a medially interrupted tuberculate (epibranchial) ridge extending obliquely transversely from 4th anterolateral tooth		4
2 (1)	Front entire or shallowly divided medially, convex in dorsal view. Merus of cheliped lacking prominent spines except for one distally on dorsal border; palm of chela with a small distal spine on inner surface dorsally		3
–	Front divided medially by a deep V-shaped notch, weakly concave in dorsal view. Merus of cheliped with four to five spines on lower posterior border including one distally; palm of chela with a very large distal spine on inner surface dorsally		*N. spinifrons* Stephenson
3 (2)	Front entire or with very shallow medial notch, edge (in larger specimens) with single row of numerous small rounded tubercles. Carapace naked in larger specimens. Cheliped with inner upper margin of wrist, distal to spinous inner angle, with no spines or tubercles in smaller specimens and several (up to 10) low, blunt tubercles in larger specimens; outer surface of palm in larger specimens with transverse rows of uniformly coloured tubercles		*N. integrifrons* (Latreille)
–	Front with V-shaped medial notch, edge (in larger specimens) with double row of prominent blunt tubercles. Carapace tomentose. Cheliped with inner upper margin of wrist, distal to spinous inner angle, with a few long spines in smaller specimens and a few stout spinules in larger specimens with transverse rows of tubercles, mostly light in colour but with an irregular scattering of dark tubercles present		*N. tuberculosus* A. Milne Edwards
4 (1)	Carapace dorsally with numerous granules scattered over surface. Width of carapace between 1st anterolateral teeth (external orbital angles) about ⅖ greatest carapace width		5

–	Carapace dorsally with a few granular tubercles and some discrete groups of granules; width of carapace between 1st anterolateral teeth about ⅔ greatest carapace width	*N. bullatus* Balss
5 (4)	Surface of carapace naked and iridescent, sternum pale. Male abdomen with penultimate segment markedly convex laterally, greatest width (of penultimate segment) about twice length	*N. bennetti* Takeda and Miyake
–	Surface of carapace and legs tomentose, sternum dark. Male abdomen with penultimate segment weakly concave laterally, greatest width (of penultimate segment) barely exceeding length	*N. antarcticus* (Jacquinot)

HISTORICAL ZOOGEOGRAPHY OF THE NEW ZEALAND AND SUBANTARCTIC SPECIES

The Auckland Islands and Campbell Island are close to the southern limit for Brachyura. Only one species, *Halicarcinus planatus*, is known from further south at Macquarie and Kerguelen Islands (Yaldwyn, 1965). Seven species are known from the Aucklands, and six from Campbell, whereas some 21 species are known from Stewart Island and Foveaux Strait (Dell, 1968).

The species concerned are:

Jacquinotia edwardsi (Jacquinot), Auckland Ids., Campbell Id.
Leptomithrax australis (Jacquinot), Auckland Ids., Campbell Id.
Cancer novaezelandiae (Jacquinot), Auckland Ids.
Nectocarcinus antarcticus (Jacquinot), Auckland Ids., Campbell Id.
Nectocarcinus bennetti Takeda and Miyake, Auckland Ids., Campbell Id.
Chlorinoides filholi (Milne Edwards), Auckland Ids.
Leptomithrax richardsoni Dell, off Campbell Id.
Halicarcinus planatus (Fabricius), Auckland Ids., Campbell Id.

Apart from *Halicarcinus planatus* and the Chatham Rise *Nectocarcinus bennetti*, the six other species are all also known from the southern part of the mainland of New Zealand. The general interpretation of the distributional data might lead one to postulate that on the whole the brachyuran fauna of the Southern Islands consists of those species occurring on the mainland of New Zealand which have been able to extend their ranges to the south. This may well be true for all of them. *Jacquinotia* is a monotypic genus found living only in the southern part of the South Island in a much smaller size range than in the Southern Islands and usually only in deep water. Fossil records of *Jacquinotia* extend to the present latitude of Cook Strait.

The development of another species of *Nectocarcinus* in the Southern Islands, and its present occurrence with a second, more widely spread species in the same area seems somewhat anomalous.

The major climatic phenomenon which must have affected the distribution of animals in New Zealand in comparatively recent geological times is the last major Pleistocene glaciation. Fleming (1962a: 235) has discussed the distribution of the marine bivalve *Bassina* in New Zealand in relation to "the rigours of the later Pleistocene, when violent alternations of cold and warm climate completely eliminated many long-established lineages, particularly shallow water forms that could not survive by migration far to north or south".

There have been few discussions on the effect of the late Pleistocene glaciation on the marine fauna of New Zealand's Southern Islands but there can be little doubt that temperatures were lowered significantly. As a result there would be a drastic reduction in the number of species of many groups, either by forced migration to the north (if sea levels were lowered sufficiently by the widespread formation of terrestrial ice) or by extinction. On present indications this would have been

the fate of all the crabs except for *Halicarcinus planatus*. If some members of *Nectocarcinus* had been able to withstand colder conditions these may well have survived around the Auckland Islands while the rest died out, a situation in which theoretically two species could have evolved. On the mainland of New Zealand, *Nectocarcinus antarcticus* (which in spite of its specific name extends further to the north at present) could either have lived on in its present form, or have evolved into its present form from an ancestor common to both species. Around the Auckland Islands the surviving members of the genus could well have evolved to form the present *bennetti*. The general morphological differences between *bennetti* and *antarcticus* (though constant) are relatively slight except for the form of the first pleopods. This quite marked change in these important organs is just the kind of change which would prevent interbreeding of *antarcticus* and *bennetti* when their ranges overlapped with the onset of warmer conditions.

On this explanation it seems a relatively simple case of the development of two allopatric species while a barrier existed, involving changes of sufficient magnitude in a crucial organ to maintain genetic isolation when the ranges became sympatric later. If the last Pleistocene Glaciation was a major stimulus involved in this specific differentiation the time scale involved (approximately 20,000 years) is a very short one as far as marine biologists are concerned. At the same time, faced with a similar time scale and undoubtedly much more sever conditions on land, some New Zealand biologists have been prepared to accept the possibility of specific differentiation taking place within the same period for terrestrial organisms. In the case of *Nectocarcinus*, however, there is no necessity to invoke the last Pleistocene Glaciation as the causal agency. Cold periods earlier in the Pleistocene could equally well have been responsible.

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Note: While this paper was at page proof stage, the following study (published 30 October 1969) was sent to us.

TAKEDA, M.; MIYAKE, S., 1969. A small collection of crabs from New Zealand. *Ohmu, Occ. Pap. Zool. Lab. Fac. Agric. Kyushu Univ.* 2(8): 157–93, 7 figs., 3 pls.

Takeda and Miyake described and figured a new species of *Nectocarcinus, N. bennetti,* from 3 ♂♂ and 3 ♀♀ taken in 140m on the Chatham Rise, east of Banks Peninsula (44° 7.2'S, 175° 55.5'E). It became immediately clear that a *Nectocarcinus* from the New Zealand Subantarctic, about to be described as new by us, was identical with Takeda and Miyake's *N. bennetti.* The text of the present paper has been altered to suppress our manuscript name, but does not include Takeda and Miyake's new records of *N. antarcticus* and other details.

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