Journal of the Royal Society of New Zealand

ISSN: 0303-6758 (Print) 1175-8899 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzr20

Cenozoic and recent rhynchonellide brachiopods of New Zealand: Systematics and variation in the genus *Notosaria*

Daphne E. Lee & J.B. Wilson

To cite this article: Daphne E. Lee & J.B. Wilson (1979) Cenozoic and recent rhynchonellide brachiopods of New Zealand: Systematics and variation in the genus *Notosaria* , Journal of the Royal Society of New Zealand, 9:4, 437-463, DOI: 10.1080/03036758.1979.10421831

To link to this article: https://doi.org/10.1080/03036758.1979.10421831

© *Journal of the Royal Society of New Zealand, 1979, Vol. 9, No. 4, pp. 437-463, 16 figs*

Cenozoic and Recent Rhynchonellide Brachiopods of New Zealand: Systematics and Variation in the Genus *Notosaria*

DAPHNE E. LEE
Geology Department, University of Otago
and
J. B. WILSON
Botany Department, University of Otago

[*Received by the Editor, 12 September 1978; as revised, 19 February 1979*]

Abstract

Two species of the rhynchonellide brachiopod genus *Notosaria* are redescribed: *Notosaria antipoda* (Thomson), formerly placed in *Tegulorhynchia*, ranges from Early Oligocene to Early Miocene (Whaingaroan – Otaian) and *Notosaria nigricans* (Sowerby) from early Middle Miocene (Altonian) to Recent. A living new subspecies, *Notosaria nigricans reinga*, from near the Three Kings Islands north of New Zealand is described. Growth stages and morphological variation in living populations are described, and comparisons are made with fossil specimens of the same and other species.

INTRODUCTION

The distinctive black, ribbed brachiopod, *Notosaria nigricans*, first described as *Terebratula nigricans* by G. B. Sowerby in 1846, was transferred to the genus *Rhynchonella* by Davidson (1852). It has been subsequently redescribed by many systematists including Reeve, Dall, Woodward, Hutton, Suter, Thomson, Chapman and Crespin, and Hatai. Dall (1873) placed the species in *Hemithyris*, where it remained until Chapman and Crespin (1923) erected the genus *Tegulorhynchia* for ribbed rhynchonellide species of the southern hemisphere.

In 1959, Cooper proposed *Terebratula nigricans* as the type of a new genus, *Notosaria*, noting that it is distinguished from *Tegulorhynchia* in "ornamentation, beak characters and cardinalia". Three species and a subspecies (two from New Zealand) were included in *Notosaria*.

This study confirms Cooper's differentiation of the genus, proposes recognition of a new subspecies, reviews the definition of existing species and offers slight changes in the generic diagnosis.

The availability of live specimens of *Notosaria nigricans* has led to its being the subject of a number of detailed studies. Percival (1960), using material from the intertidal community in Lyttelton Harbour, gave "the most comprehensive account of development among articulate brachiopods" (Williams and Rowell 1966). Williams (1968) described the shell structure of these brachiopods, and Williams and Wright (1961) made frequent reference to *N. nigricans* in their study of the origin of the loop in articulate brachiopods. Rudwick (1962) examined filter-feeding mechanisms in the species, and MacKinnon (1977) described the formation of muscle scars in this and other species.

This study attempts to trace the fossil history of the genus in New Zealand Cenozoic rocks, to re-examine its systematic placing, to describe growth stages in the species, and to describe overall morphologic variation in the living and fossil species.

Some aspects of the ecology and palaeoecology of *N. nigricans* have already been described (Lee 1978).

Material Studied

The senior author has examined over 2 000 specimens of rhynchonellide brachiopods from the Auckland, Canterbury, and National Museums; the New Zealand Geological Survey; the New Zealand Oceanographic Institute; and the Geology Departments of the University of Canterbury and the University of Otago. Many fossil localities have been recollected (DL collections in the Geology Department, University of Otago), and several Recent collections have been made available on loan from the New Zealand Oceanographic Institute and the Portobello Marine Laboratory. Locality details for living and fossil *Notosaria nigricans* were presented in Lee (1978), and those for *Notosaria antipoda* are given here. Table 1 lists the New Zealand Tertiary series and stages from which species of *Notosaria* are known.

	Age/Stage (Symbol)		Series
PLEISTOCENE		(H)	Hawera
	Nukumaruan	(Wn)	Wanganui
	Castlecliffian	(Wc)	
PLIOCENE	Mangapanian	(Wm)	
	Waipipian	(Wwp)	
	Opoitian	(Wo)	
MIOCENE	Kapitean	(Tk)	Taranaki
	Tongaporutuan	(Tt)	
	Waiauan	(Sw)	Southland
	Lillburnian	(Sl)	
	Clifdenian	(Sc)	
	Altonian	(Pl)	Pareora
	Otaian	(Po)	
	Waitakian	(Lw)	Landon
OLIGOCENE	Duntroonian	(Ld)	
	Whaingaroan	(Lwh)	

Table 1.—New Zealand Series and Stages.

SYSTEMATIC DESCRIPTION

Phylum BRACHIOPODA

Class Articulata

Order RHYNCHONELLIDA Kuhn, 1949

Family Hemithyrididae Rzhonsnitskaya, 1956

Genus *Notosaria* Cooper, 1959

1959:	*Notosaria*	Cooper, *Smith.Misc.Coll.* 139(5):48-50
1965	*Notosaria*	Ager, in Moore (ed.) *Treatise Invert. Pal.* Pt.H. p:623
1968	*Notosaria*	Bowen, *Tuatara* 16(2):135-6
1971:	*Notosaria*	Dawson, *Jl.Roy.Soc.N.Z.* 1(2):161-2
1974:	*Notosaria*	Foster, *Ant.Res.Ser.* 21:49-50

Diagnosis of Adult Forms

Subpentagonal in outline with uniplicate fold in anterior commissure; ornamentation costellate to spinose; beak straight to suberect; foramen large, incomplete, hypothyridid; deltidial plates disjunct; crura radulifer in type; no inner or outer hinge plates; bilobed cardinal process; short median ridge; pallial marks numerous, primarily radial but anastomosing.

Species Included in the Genus

The following three species, and a subspecies, were assigned to *Notosaria* by Cooper (1959):

Rhynchonella nigricans Sowerby, Miocene to Recent, New Zealand.
R. nigricans pyxidata Davidson, Recent, Kerguelen Island.
R. nysti Davidson, Pliocene, Belgium.
Hemithyris sublaevis Thomson, Miocene, New Zealand.

Cooper had access to a pedicle and brachial valve of *Notosaria nysti* and confirmed the close similarities to the New Zealand species noted by Davidson (1874) in his original description. Foster (1974) has recently re-examined the few specimens known of the subspecies, *N. nigricans pyxidata,* and figured the hypotype and a brachial valve interior (1974 Pl 2 figs 15-18). According to Foster, this subspecies differs from *N. nigricans nigricans* in finer costellation and colour. Dr G. A. Cooper (pers. comm., 1978) is describing new material of *N. n. pyxidata* from Kerguelen Islands.

With regard to the New Zealand fossil species, it is probable that Cooper assigned *H. sublaevis* to *Notosaria* without having sufficient comparative material on hand. It was well-known to New Zealand palaeontologists (Thomson 1927 p. 153; Allan 1940 p. 280) that the species most closely related to *Notosaria nigricans* was *H. antipoda,* which it resembles in all characters except rib ornamentation. *H. sublaevis* similarly resembles *Tegulorhynchia squamosa* in all aspects except ornamentation. In the characters which Cooper used to separate *Notosaria* from *Tegulorhynchia,* viz., pallial markings, beak characters, and cardinalia (with the exception of ornamentation) *sublaevis* and *antipoda* are clearly generically distinct. *Hemithyris antipoda* Thomson is therefore transferred to *Notosaria* and *H. sublaevis* returned to *Tegulorhynchia.* It appears that differences in external ornamentation are primarily of use in specific discrimination. *Notosaria* and *Tegulorhynchia* both include spinose and non-spinose forms. A new subspecies known from the Recent only is described as *N. nigricans reinga* (see below).

Notosaria antipoda may be distinguished from *N. nigricans nigricans* in the possession of spinose, more strongly arched costellae and in the larger size of the foramen and the adult shell. *N. nigricans reinga* may be differentiated from *N. nigricans nigricans* in small maximum size, rounded foramen, and small anterior spinelets.

Notosaria nigricans nigricans (Sowerby) (Figs. 1, 2)

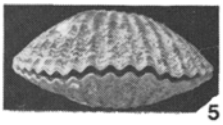
1846a: *Terebratula nigricans* Sowerby, *Proc. Zool. Soc. London* XIV p. 91
1846b: *Terebratula nigricans* Sowerby, *Thes. Conchyliorum* v1 (6-7), p. 342 plLXXI, Figs. 81-82).
1852: *Rhynchonella nigricans* (Sowerby), Davidson, *Ann. Mag. Nat. Hist.* (2)9(53) p. 375.
1854: *Rhynchonella nigricans* (Sowerby), Davidson, *Proc. Zool. Soc. London* XX (1852) p. 81-2 plXIV, Figs. 30-31.
1856: *Rhynchonella nigricans* (Sowerby), Woodward, *A Manual of the Mollusca,* p. 227, Figs. 138-139.
1861: *Rhynchonella nigricans* (Sowerby), Reeve, *Conch. Iconica* XIII p. 11, Fig. 1.
1873a: *Rhynchonella nigricans* (Sowerby), Hutton, *Cat. Mar. Moll. N.Z.* p. 87.
1873b: *Rhynchonella nigricans* (Sowerby), Hutton, *Cat. Tert. Moll. Echin. N.Z.* p. 137.
1873: *Hemithyris nigricans* (Sowerby), Dall, *Proc. Acad. Nat. Sci. Phil.* p. 196.
1880: *Rhynchonella nigricans* (Sowerby), Davidson, *Rept. Sci. Res. H.M.S. Challenger (1873-76) Zool.* 1: p. 24, 59-60, pl IV, Fig. 18.
1880: *Rhynchonella nigricans* (Sowerby), Hutton, *Man. N.Z. Moll.* p. 178.
1887: *Rhynchonella nigricans* (Sowerby), Davidson, *Trans. Linn. Soc. Lond.* (2) 4, Zool. p. 169, pl XXIV, Figs. 16-19.
1902: *Hemithyris nigricans* (Sowerby), Suter, *Trans. N.Z. Inst.* 34 p. 224.
1905: *Rhynchonella nigricans* (Sowerby), Hutton, *Trans. N.Z. Inst.* 37 p. 480.
1913: *Hemithyris nigricans* (Sowerby), Suter, *Manual N.Z. Moll.* p. 1076.
1915: *Hemithyris nigricans* (Sowerby), Thomson, *Geol. Mag.* Dec. 6. p. 388, 390, Fig. 2a.
1923: *Tegulorhynchia nigricans* (Sowerby), Chapman and Crespin, *Proc. Roy. Soc. Vict.* 35(2), p. 187, pl 1 Figs. 9–12. pl III Figs. 29–30.
1927: *Tegulorhynchia nigricans* (Sowerby), Thomson, *N.Z. Board Sci. Art. Man.* 7, p. 153.
1936: *Tegulorhynchia nigricans* (Sowerby), Hatai, *Bull. Biogeog. Soc. Japan* 6(20) p. 203.
1959: *Notosaria nigricans* (Sowerby), Cooper, *Smithsonian Misc. Coll.* 139(5) p. 48-50. P16B; 22C.
1960: *Tegulorhynchia nigricans* (Sowerby), Allan, *Rec. Cant. Mus.* 7(3), p. 267.

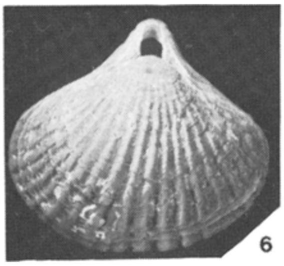

1

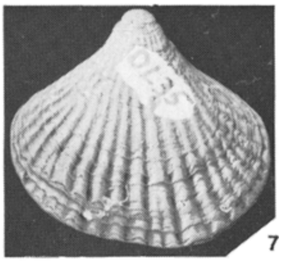

2

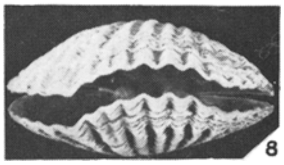

3

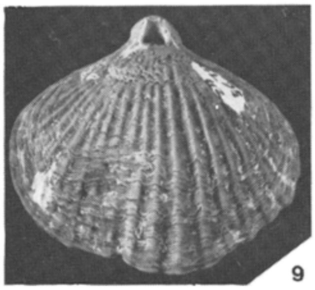

4


5

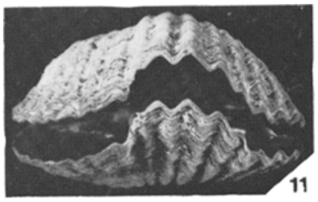

6

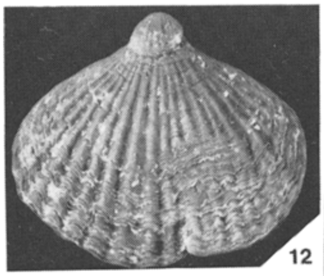

7

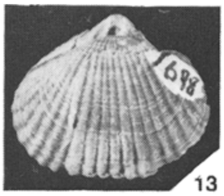

8


9

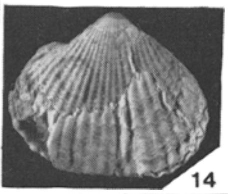

10


11


12

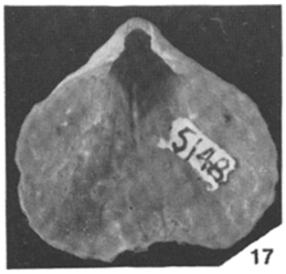


13

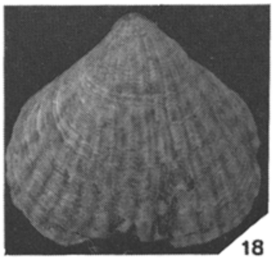

14

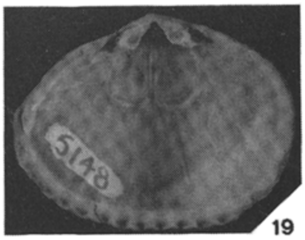

15


16



17


18



19

1965: *Notosaria nigricans* (Sowerby), Ager, *In* Moore, *Treatise Invertebrate Paleontology* Pt H, p H623-4, Fig. 508 2a-e.
1968: *Notosaria nigricans* (Sowerby), Bowen, *Tuatara* 16(2), p. 135-6, Fig. 2.
1971: *Notosaria nigricans* (Sowerby), Dawson, *Jl, Roy. Soc. N.Z.* 1(2), p. 161-2.
1974: *Notosaria nigricans nigricans* (Sowerby), Foster, *Ant. Res. Ser.* 21 p. 49-50.

Further references to *N. nigricans* are given by Dawson (1971 p. 161-2).

TYPE SPECIES (designated by Cooper 1959): *Terebratula nigricans* Sowerby, 1846.

TYPE LOCALITY AND TYPE SPECIMEN:

Sowerby (1846 p. 91) stated that "a single specimen of this very interesting species was found in the collection of the late G. Humphrey, without locality". The whereabouts of the type is unknown. The specimen probably came from Foveaux Strait, New Zealand. It has not been considered necessary to nominate a neotype since there is no doubt as to the status of this species (Int. Code Zool. Nomen. p. 81).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION:

Notosaria nigricans nigricans has a stratigraphic range in New Zealand from Middle Miocene (Altonian) to Recent. Specimens are known from each local stage (Table

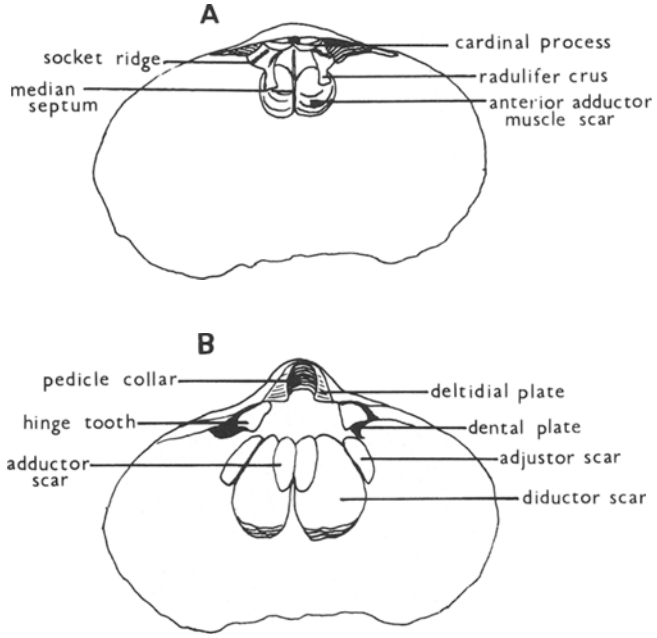


FIG. 2. Interior shell morphology of *Notosaria nigricans* (Sowerby). A brachial valve; B pedicle valve.

FIG. 1. (opposite) — External Morphology of *Notosaria nigricans* (Sowerby). 1. Dorsal view of immature specimen (L = 6.5 mm). 2-5. Respectively dorsal, ventral, lateral and anterior views of submature specimen (L = 12.5 mm). Note rectimarginate anterior commissure. (Figs. 1.1-5 from Ripa Island, Lyttelton Harbour. R. S. Allan Collection, University of Canterbury Geology Department, Recent.) 6-8. Dorsal, ventral and anterior views of mature specimen (L = 16 mm) showing increase in rib numbers, numerous growth lines and uniplicate fold. 9-12. Respectively dorsal lateral, anterior and ventral views of asymmetric adult specimen (L = 23 mm). Note numerous growth lines, deformed areas on shell probably caused by crowding, and marked uniplicate fold. (Figs. 6-12 from Tikoraki Point, Moeraki. DL 35. Recent.) 13-16. Dorsal and ventral views of 2 slightly crushed fossil specimens from Tainui Shellbed and Pinnacle Sand, Castlecliff. Castlecliffian X2. 17-19. Pedicle valve interior and exterior, and brachial valve interior of specimens from Target Gully, Oamaru. OU 5148. Altonian X2. All specimens coated with NH_4Cl.

1) subsequent to the Altonian with the exception of the Clifdenian (Middle Miocene) and Opoitian (Early Pliocene). Details of all fossil and Recent localities are given in Tables 2, 3 of Lee (1978), and the geographic distribution at selected stages is shown in Figure 2 (a-e).

DESCRIPTION (see also descriptions of growth stages):

External Characteristics (Fig. 1). Shell impunctate; outline subcircular in juveniles, subpentagonal in adult; width equal to length in juveniles, width greater in adults; valves subequal in juveniles; brachial valve deeper than pedicle in adults; anterior commissure rectimarginate in juveniles, uniplicate often asymmetric in adults; beak short and pointed in juveniles, moderately long and rounded in adults; nearly straight in juveniles to suberect in adults; foramen large, ovately triangular in juveniles to rounded in adults; hypothyridid; narrow triangular deltidial plates in juveniles, prominent in adults, disjunct; shell surface costellate, intersected by growth lines and varices; costellae increase in number by interpolation and bifurcation, 10-15 in juveniles, 15-25 in adults (measured around anterior commissure); black to dark brownish-grey colour, fossil shells dark grey to white.

Internal Characteristics (Figs. 2, 3). *Pedicle valve* with thick transversely striated pedicle collar elevated above valve floor; hinge teeth small in juvenile to large, corrugated in adult, supported by short, receding dental plates; muscle impressions large, wide, flabellate; pallial impressions consisiting of numerous radially directed anastomosing channels.

Brachial valve interior with deep corrugated sockets and thick overhanging socket ridges, crura of radulifer type, moderately long, flattened, attached to socket ridges; no inner or outer hinge plates; median septum short, low not reaching apex; cardinal process appears in juveniles as small shell overgrowth, in adult forms thick overhanging bilobed process with concentric growth ridges; pallial impressions as in pedicle valve.

Notosaria nigricans reinga n. subsp. (Fig. 4)

HOLOTYPE National Museum, Wellington. Registration No. NMBr 1361.

PARATYPES NMBr 1362; 1363; 1364 (entire specimen; pedicle valve; brachial valve respectively).

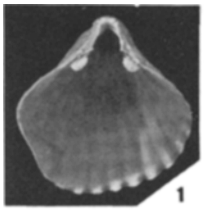
TYPE LOCALITY

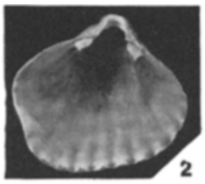
Off Three Kings Islands, in 805 m. AUZ 53. 34°00′S, 171°55′E. Coll. HMNZS "Tui", 17.9.1962.

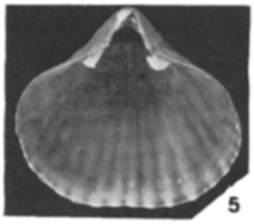
DESCRIPTION

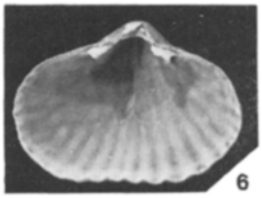
As for *Notosaria nigricans nigricans,* but shell small (maximum length of 150 specimens from 5 localities was 10.1 mm); foramen smaller and more rounded. Colour

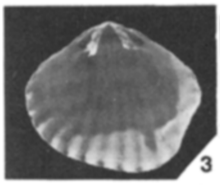
FIG. 3. (opposite) — Development of internal features of *Notosaria nigricans.* 1-2. Normal and tilted views of pedicle valve interior of asymmetric juvenile of length 12.4 mm showing small striated hinge teeth, hypothyridid foramen and weakly impressed muscle scars. 3-4. Similar views of brachial valve interior of same specimen showing early development of cardinalia and striated hinge sockets. OU 8484a. 5-8. Normal and tilted views of pedicle and brachial valves of larger specimen (length 13.9 mm) to show dental plates, curved radulifer crura, and more deeply impressed muscle scars. OU 8484b. 9-10. Pedicle and brachial valve interiors of juvenile (length 6 mm) showing part of the lophophore, crura and relatively large hypothyridid foramen. RSA1. Ripa Island, Lyttelton Harbour. University of Canterbury Geology Department. 11-13. Normal and tilted views of pedicle valve interior of mature adult shell (length 22.7 mm). Note well-developed pedicle collar, large hinge teeth supported by receding dental plates, deeply impressed muscle scars and pallial sinuses. 14-16. Three views of brachial valve interior of the previous specimen showing bilobed adult condition of the cardinal process short, curved radulifer crura socket ridges, deeply impressed muscle scars and pallial sinuses. OU 8484c. Specimens OU 8484a, b, c, are from Tikoraki Point, Moeraki. University of Otago Geology Department. All specimens coated with NH_4Cl.


1


2


5


6

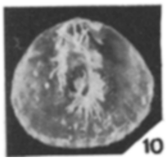

3

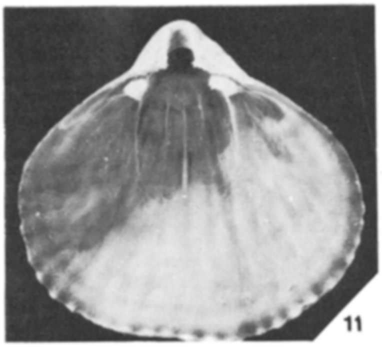

4

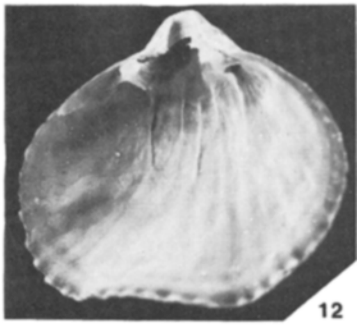

7

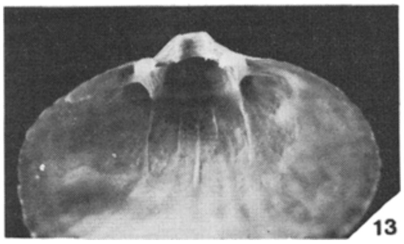

8

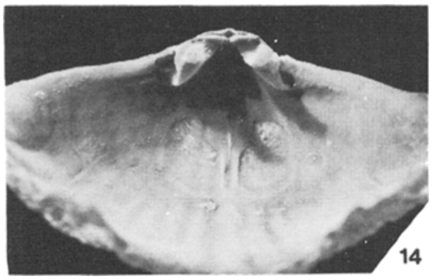

9

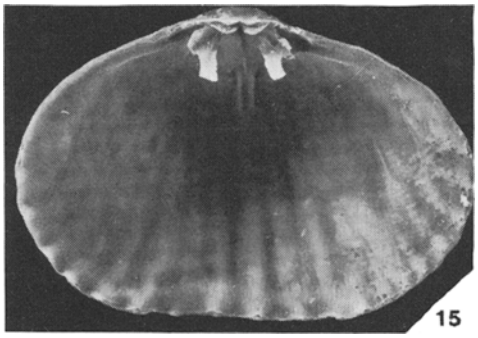

10

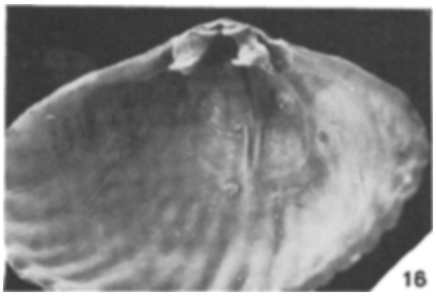

11


12


13


14


15


16

black to brownish white or cream, lighter in shells from deeper water. Well-preserved specimens possess small short spinelets around anterior commissure (Fig. 4.9).

REMARKS

A gap in distribution of several hundred kilometres separates this subspecies from *N. nigricans nigricans* (Lee, 1978). The northern subspecies appears to inhabit warmer water but lives at greater depths than its southern counterpart.

STRATIGRAPHIC DISTRIBUTION: Recent seas only.

LOCALITIES

Off Northeast Is, Three Kings, in 102 m. 34°08.5'S, 172°11'’E. NMBS392.
Off Three Kings Is, in 91 m. 34°11'S, 172°E. NMBS 394.
Off Three Kings Is, in 84 m. 34°10.8'S, 172°8.4'E. NZOI C760.
Off Kermadec Is. in 165-180 m. 30°33.8'S, 178°30.6'W. NZOI K857.

The subspecies present in other NZOI stations to the north of New Zealand is almost certainly *N. nigricans reinga.*

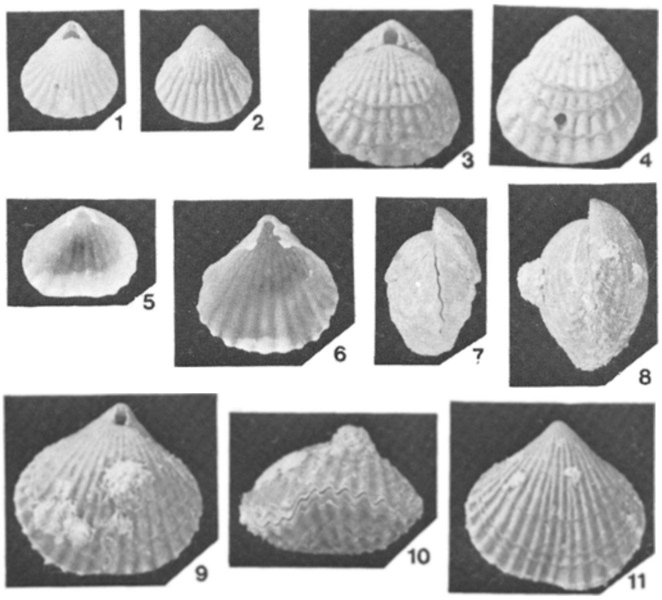


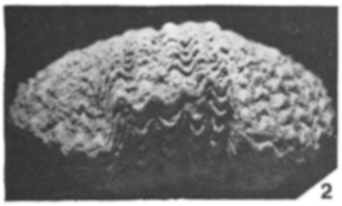
FIG. 4. — *Notosaria nigricans reinga* n. subsp. 4.1-2. Dorsal and ventral views of holotype, X2. NMBr 1361. 4.3-4.7. Dorsal, ventral and lateral views of paratype. Note bryozoan encrustations, shelf-like growth lines, and gastropod borehole, X2. NMBr 1362. 4.5-6. Interiors of brachial and pedicle valves of paratypes, X2. NMBr 1363, 1364. (Figs. 4.1-6. Holotype and paratypes from AUZ 53 off Three Kings Islands, 34°00'S, 171°55'E, in 805 m. National Museum, Wellington. Recent.) 4.8-11. Respectively lateral, dorsal, anterior and ventral views of bryozoan encrusted specimen. Note small spinelets around anterior margin X2. Off Kermadec Islands, 30°33.8'S, 178°30.6'W, in 165-180 m. N.Z. Oceanographic Institute K857. Recent. All specimens coated with NH_4Cl.

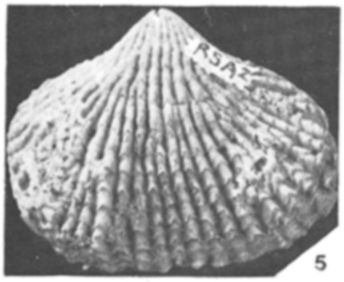
FIG. 5. (opposite) — *Notosaria antipoda* (Thomson). 5.1-2. Dorsal and anterior views of the holotype, X2. NMBr 1262, ? Greensand, Curiosity Shop, Rakaia River. Otaian Stage. 5.3-6. Respectively dorsal, ventral, lateral and anterior views of well-preserved adult specimen from "Fan Coral Bed". Note the characteristic imbricate rib structure, rather worn spine-bases, and increase in rib number by interpolation and bifurcation, X2. 5.7-11. Growth series showing range of variation and changes in exterior morphology during growth, X2. 5.12-13. Interior of pedicle and brachial valves. Pedicle valve carries encrustations of serpulid worms and bryozoans, X2. (Figs. 5.3-13. from "Fan Coral Bed", Upper Tuffs, Thomas Formation, Castle Hill Basin, R. S. Allan Collection, University of Canterbury Geology Department. Duntroonian-Waitakian Stage.) 5.14-16. Large, robust, abraded specimens of *N. antipoda* showing very large hypothyridid foramen. 5.14. N 34/f511, Mathesons Bay, X2. 5.15. N 38/f3, Motutapu Island, X2. 5.16. N 34/f12, Cape Rodney, X2. Figs 5.14-16. from basal Waitemata Group, Auckland region, University of Auckland Geology Department. Waitakian-Otaian Stage. All specimens coated with NH_4Cl.


1


3


4

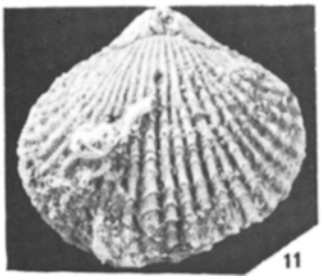

2

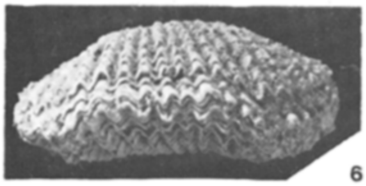


5

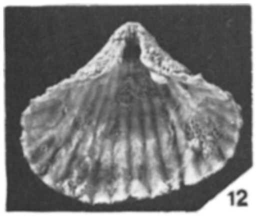

7

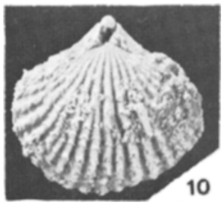

8

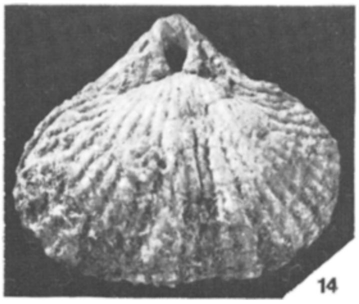

11

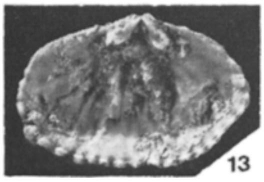

6

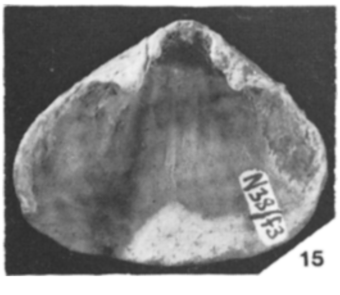

9


12

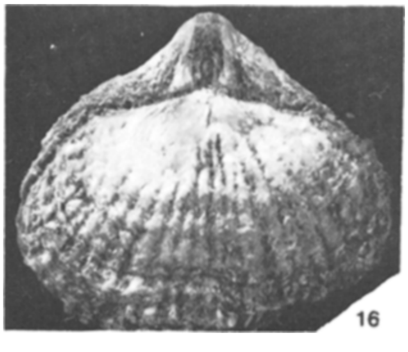

10


14


13



15


16

Notosaria antipoda (Thomson) (Fig. 5)

1864: *Rhynchonella nigricans* Suess, *Novara Exped., Geol. Theil Bdl,* Abth II, p. 60-61, Taf XIV.
1885: *Rhynchonella nigricans* (Sowerby), Hutton. *Q.J.G.S.* Nov. 1885 p. 553.
1905: *Rhynchonella nigricans* (Sowerby), Hutton. *Trans. N.Z. Inst.* 37 p. 481.
1918: *Hemithyris antipoda* Thomson *in* Park, *N.Z.G.S. Bull.* n.s. 20, p. 117.
1923: *Tegulorhynchia antipoda* (Thomson), Chapman and Crespin, *Proc. Roy. Soc. Vict.* 35(2), p. 184.
1937: *Tegulorhynchia antipoda* (Thomson), Allan, *Rec. Cant. Mus.* 4, p. 122, Pl 16, Fig. 3.
1959: *Tegulorhynchia antipoda* (Thomson), Cooper, *Smith, Misc. Coll.* 139(5), p. 51.
1960: *Tegulorhynchia antipoda* (Thomson), Allan, *Rec. Cant. Mus.* 7(3), p. 267.
1971: *Tegulorhynchia antipoda* (Thomson), Keyes, *Rec. Dom. Mus.* 7(9), p. 76.

TYPE SPECIMENS

The holotype (Br1262) and two paratypes (Br1263) are in the brachiopod collection of the National Museum, Wellington. The holotype (Figs. 5.1, 5.2) has not previously been figured. One of two "paratypes" (collected by F. W. Hutton and identified by J. A. Thomson) in the Canterbury Museum was figured by R. S. Allan (1937).

Brachiopods labelled as *H. antipoda* by J. A. Thomson are to be found in the National Museum, Canterbury Museum, N.Z. Geological Survey, and the Geology Department, University of Otago. Many of these specimens, including those in the Canterbury Museum collection used by R. S. Allan (1937) to redescribe the species, are labelled as "paratypes". However, since Thomson used "paratype" to describe most of his comparative material, these brachiopods (with the exception of two paratypes associated with the holotype in the National Museum) are not paratypes as the International Code of Zoological Nomenclature would presently define them.

TYPE LOCALITY:

? Greensand, Curiosity Shop, Rakaia River, Otaian Stage.

DESCRIPTION

Shell similar to that of *Notosaria nigricans* (Sowerby) but often heavier and thicker, with a large hypothyridid foramen (Figs. 5.14, 5.15, 5.16). The main distinguishing features are the costellae. Those in *N. antipoda,* to quote Allan (1937), are "stout, strongly arched, imbricate near the anterior margin, and occasionally spinose", whereas those of *N. nigricans* are "slightly stouter, more gently rounded, non-imbricate, and without spines".

These projections, which are hardly "spines" in the true sense, are short, tent-like projections which are budded-off at the intersection of each costal ridge and growth line (see Figs. 5.3, 5.5, 5.6). They are similar to those described for *Tegulorhynchia doderleini.* Though in most fossil shells the "spines" are present only as broken stumps, they may be visible in protected anterior fold regions. The shell surface of *N. antipoda* is best described as *costellate,* since the ribs increase in number by both bifurcation and interpolation (Figs. 5.1, 5.3, 5.10, 5.11). The increasing irregularity of the ribs resulting from irregular spacing of growth-lines can be seen in a series of growth stages (Figs. 5.7-11).

It must be realised that other features noted by Allan (1937) such as degree of convexity of the dorsal valve, number of costae reaching the anterior margin, and degree of uniplication are all primarily a function of size and maturity and are of limited use in making taxonomic distinctions in rhynchonellide brachiopods.

Internal characteristics as for the genus. The internal features of a brachial and pedicle valve are shown in Figures 5.12 and 5.13.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

Notosaria antipoda is known from several localities of broadly similar age in three geographically distinct areas of the New Zealand mainland: Mid-Canterbury, Southland, and Auckland. The oldest are from the "Fan Coral Bed" or upper tuffs, Thomas Formation, Castle Hill Basin, which are Duntroonian — Waitakian in age. The type specimens from Curiosity Shop, Rakaia River, are probably from the Otaian greensand, and a few other large but poorly preserved specimens occur in Otaian limestones at Fossil Point, Ashburton, and Blands Bluff.

A small number of specimens have been collected from limestones and mudstones in the Central Southland and Eastern Fiordland areas which range in age from Duntroonian to Otaian (F. M. Hyden pers. comm., 1978; J. Sise 1975).

Notosaria antipoda is widely distributed in the basal conglomerates and volcanic sandstones of the Waitemata Group in the Hauraki Gulf area. Suess (1864) figured a specimen of *Rhynchonella nigricans* from Cape Rodney which is attributable to *N. antipoda.* Clarke (1905) listed Little Omaha, Rodney, Waikopua, Papakura, Motutapu, and Cheltenham as localities for this species, and we list several more sites (Table 2). Specimens labelled "22" in red paint are conspicuous in several museum collections. They form part of a large collection made by J. Park in 1885 (Park 1886) from a locality called Slippery Creek, Auckland which has not been re-collected.

The Waitemata Group is considered to be Waitakian to Otaian in age.

Palaeoecology of NOTOSARIA ANTIPODA

Specimens from the basal volcanic grits, conglomerates and sandstones of the Waitemata Group are generally large, robust, abraded, with single and occasionally double valves. They occur with other large robust brachiopods including *Terebratella neozelandica* (Ihering) and a mixed fauna including littoral-shallow water forms such as *Haliotis, Cellana, Lepsiella* (Grant-Mackie 1965), barnacles including *Hexelasma,* bryozoans and coelenterates.

Skinner (1969) listed *N. antipoda* from similar conglomerates in the Colville Formation at Cape Colville. Here it occurs with *Mesopeplum,* glycymerids, pectinids, and large terebratulids. The sediments of the Colville Formation are considered by Skinner to have been laid down in a shallow-water environment.

The robust nature of these brachiopod shells, and the large foramen (indicating a massive pedicle) suggests that they occupied a high-energy environment and were perhaps attached during life to volcanic boulders or cobbles in shallow or sub-littoral conditions. The worn nature of the shells and the absence of individuals less than 14 mm long (Fig. 6A) suggests that they may have been transported some distance after death. Buckeridge (1975) concluded that mixed faunas in the Motutapu Island, Waitemata beds were the result of mass submarine flows carrying a shallow-water fauna into deeper water.

In marked contrast, the specimens of *N. antipoda* from the "Fan Coral Bed" appear to have occupied a relatively quiet environment and to have undergone little transport. The faunal list for the "Fan Coral Bed" is extensive (Gage 1970). Some 70 species of molluscs and some half-dozen species of brachiopods, as well as a rich fauna of corals is known. Squires (1958) considered that "the great development of corals found in the Trelissick Basin" (*Flabellum pavoninum circulare* (the Fan Coral for which the bed is named), *F. rubrum sphenodeum,* and *Balanophyllia (B.) salpynx*) is probably indicative of shallow shoals of corals in clear and sediment-free water. It is possible that the corals formed part of the substrate to which the brachiopods were attached.

Although Gage (1970, p. 524) notes that the upper tuffs are current-bedded and that fossils seem to have been concentrated by a scour-and-fill process, a size-frequency histogram (Fig. 6B) for *N. antipoda* shows that an almost complete range of double-valved shells from 5-22 mm long is present and this suggests that the brachiopods are nearly *in situ.*

Table 2.—List of Localities for *Notosaria antipoda.*

Fossil Record File Number	Grid Reference	Formation & Locality	Collector & Date	Repository & Museum No. where applicable
Duntroonian-Waitakian				
C43/f001 (m)	876213	Basal conglomerate	J. R. Sise, A. F. Cooper 1975	OU Geol. Dept.
S66/74	218958	"Fan Coral Bed", Upper Tuffs, Thomas Fmn, Porter & Thomas R.	P. A. Maxwell 1968	NZGS 11, 122
S66/643	218958	Thomas Fmn, Porter & Thomas R.	D. Lee, W. Lee, J. D. Campbell 1975	OU 5151, DL8
S66/	218958	"Upper Tuffs', junction Thomas & Porter R. (Trelissick F.) or E.?	J. A. Thomson, Nov. 1914	N.M.
Ld F45/016	814448	Calcareous mudstone, Chatton Formation, Waimumu Lime Quarry	F. M. Hyden 1977	OU Geol. Dept.
Ld E44/f001	476838	Limestone Quarry, Stag Stream	F. M. Hyden 1975	OU Geol. Dept.
Otaian				
E45/f003 Ld-Po	499515	*Aetheia* bed Forest Hill Formation, Centre Bush	F. M. Hyden 1975	OU Geol. Dept.
S82/419	214535	Curiosity Shop, Rakaia R.		N.M. Br 1262, Br 1263. Holotype + 2 paratypes. N.M. ZB 195
S82	214535	Greensands, Curiosity Shop, Rakaia R.	C. H. Linzey 1939 & B. W. Collins 1936	C.U. Geol. Dept.
N38/	465325	Slippery Creek, Papakura, South Auckland	J. Park, 25-26 Feb. 1885	"22" in red paint.OU5160 NZGS N.M. B274
N38/		W. side Motutapu Is.	J. D. Campbell 1965	OU 9411
N34/f11	368096	Basal conglomerate, Brownrigg Pt, Kawau Is.	A. M. Hopgood 1955	A.U. Geol. Dept.
N34/f12		Basal conglomerate, Cape Rodney		A.U. Geol. Dept.
N34/f511	309272	Base of Waitemata Sandstone, Mathesons Bay.	J. A. Grant-Mackie & students 1968	A.U. Geol. Dept.
N34/f531	329291	Basal conglomerates, Cape Rodney	P. L. Crabbe 1970	A.U. Geol. Dept.
N34/f533	379094	Fossil Point, Kawau Is.	P. L. Crabbe 1970	A.U. Geol. Dept.
N34/f540	307269	Basal conglomerates, Waitemata Group, Mathesons Bay.	P. L. Crabbe 1970	A.U. Geol. Dept.
N35/f514	868068	Basal conglomerate, Waitemata Group, Cape Colville	D. Skinner 1961	A.U. Geol. Dept.
N35/f515	869068	Small bay east of Cape Colville	J. A. Grant-Mackie 1969	A.U. Geol. Dept.
N38/f3	411715	Basal conglomerate, Waitemata Group, Motutapu Is.	–	A.U. Geol. Dept.
N42/f1	503678	Waitemata Group, Church Bay, Waiheke Is.	J. A. Grant-Mackie 1958	A.U. Geol. Dept.
N42/f654	514497	Waitemata Group, Whitford Quarry	J. A. Grant-Mackie	A.U. Geol. Dept.
N29/2		Cape Rodney, North Auckland	Cox 1880	N.M. B661 GS450

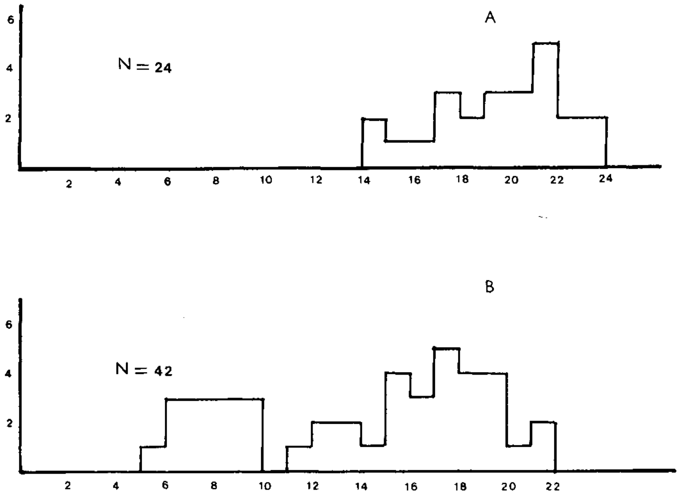


FIG. 6. Size-frequency histogram for two assemblages of *Notosaria antipoda*. A. Waitemata Group, Auckland. Waitakian-Otaian. B. "Fan Coral Bed", Castle Hill Basin. Duntroonian-Waitakian. Abscissa is length of pedicle valve in mm; ordinate is number of individuals.

Notosaria antipoda is also present in a shallow sub-tidal exposed rocky shore fauna from Mt Luxmore, Te Anau, where it occurs with *Cookia sulcata, Barbatia novaezelandiae, Maurea acutangulum,* and species of *Trochus, Haliotis, Limatula, Modelia* and *Terebratella.* This unusual fossil community is probably of Waitakian age.

EPIFAUNAS

One Waitemata Group specimen carried a barnacle, and many of the brachiopods (and molluscs) from the Fan Coral Bed bore encrusting bryozoans and serpulid worms. A single pedicle valve (Fig. 5.12), unlike most of its fellows, is encrusted on the interior, showing that the epifaunal association must have developed after the death of the shell. No bored specimens were observed. Some degree of asymmetry is common, probably increasing with age, as is usual in *N. nigricans.*

GROWTH STAGES OF *Notosaria nigricans*

Although larval development in many living brachiopod species is well-known and detailed descriptions of adult morphology are common, post-larval morphologic changes have been neglected. Surlyk (1972) considered that it is of "great importance" in palaeoecological studies that juvenile specimens can be determined with "absolute certainty". The excellent figures in Surlyk's paper (Figs. 6-10) show that in many species the youthful shell bears little resemblance to the adult. Systematic descriptions of brachiopod species therefore should include, where possible, detailed accounts of growth stages. Percival (1960) gave a detailed account of larval development in *Notosaria nigricans,* and Cooper (1959) and Foster (1974) described adult shells, but as far as we are aware post-larval growth stages in this species have not previously been described.

We have labelled as morphologic "juveniles" shells with a length of less than 14-16 mm. At this stage in shell growth, length and width cease to be nearly equal, the shell increases in relative thickness, a marked fold deflection appears in the anterior commissure, and rib numbers increase. According to Rudwick (1970), many Recent brachiopods reach sexual maturity at a length of about 2/3 of adult size. Doherty (1976) mentions that *Terebratella inconspicua,* a terebratellid often found with *N. nigricans,* reaches reproductive maturity at a length of 14-16 mm. Normal adult size for both species is between 20-24 mm. If *N. nigricans* follows a similar course of development to *T. inconspicua,* then reproductive maturity will be attained at the same time as the "adult" shell form.

Ornamentation

The initial part of the shell, the protegulal node, is smooth (Fig. 7). At a length of about 0.5 mm 5 to 10 low costellae or ribs appear, and the number increases by interpolation to about 10-15 at 5 mm. Further interpolation and bifurcation of existing ribs continues till the adult contingent of 15-30 (average is 20-25) costellae is reached. The number of ribs in the "fold" region, which has been used as a taxonomic criterion in rhynchonellides by Chapman and Crespin (1923) and others varies considerably (from 4 to 10 in adult specimens).

Folding

Juveniles of all species of *Notosaria* examined are rectimarginate. The development of the uniplicate fold in the anterior commissure of *Notosaria nigricans* begins at a length of 6 to 10 mm and is generally distinct at a length of 14-16 mm, though there may be considerable variation in different populations. For example, in populations of *Notosaria nigricans reinga,* where maximum length observed is 11 mm, folding is present in shells at 4 mm in length. The development of the fold apparently occurs at the stage when the lophophore changes from a schizolophe to a spirolophe (Brookfield 1973). Rudwick (1970) states that "the median inhalent aperture of the schizolophe, flanked by exhalent openings, is gradually replaced by an exactly reverse arrangement, with a median exhalent aperture. Very commonly this aperture becomes marked by a median deflection". Figures 1.9, 1.10, 1.11 show the anterior commissures of a juvenile, a young and mature adult shell illustrating the development of the fold.

Growth Lines

These concentric lines, which in fact mark cessation of growth rather than periods of growth, have been the subject of intensive study over the past few years to ascertain if they correspond in a regular way to the age of the shell (Surlyk 1972; Doherty 1976). In this present study, though the number of conspicuous growth lines has been measured on 300 or so specimens, correlation with shell length is poor, partly because length itself is dependent on other environmental factors.

Cardinal Process

The description of the cardinal process of *Notosaria nigricans* as "transversely widely triangular, thickened and somewhat elevated" (Cooper 1959) cannot be applied to juvenile specimens and does not take into account the development of this feature. Figure 8 shows that at an early stage of growth (a, b, c) the cardinal process is represented by a small v-shaped pit or depression below the dorsal beak. Gradually the secondary shell of the cardinal process is secreted over the posterior portion of the cardinalial zone and across the depression between the crural bases (d, e, f). Eventually the enlarging cardinal process fuses (g, h, i) over the crural attachment region, and forms the large bilobed transversely crenulated outgrowth described by Cooper.

Growth patterns for other internal features such as hinge-teeth show that with a general increase in size the early form is retained. Formation of muscle scars in *Notosaria nigricans* is described by MacKinnon (1977).

FIG. 7. Magnified view of the early-formed protegulal node of a juvenile specimen of *Notosaria nigricans*. (SEM, x50).

Growth in Length, Width, and Thickness

Figure 9 illustrates the general pattern of length-width growth in *N. nigricans*. Initially the shell is nearly circular but becomes nearly pentagonal in adult forms with width generally greater than length.

Figures 10, 11 and 12 show the growth patterns in width-length, and thickness-length for four living populations of *N. nigricans,* and for fossil assemblages of *N. nigricans* and *N. antipoda.* McCammon and Buchsbaum (1967) suggested that length, width, and thickness, "reflect growth, both the growth pattern inherent in the species

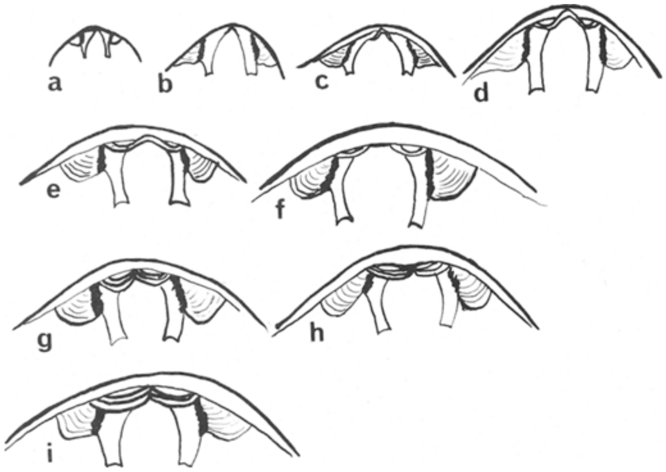


FIG. 8. Diagrammatic representation of development of cardinal process in *Notosaria nigricans*. Length of brachial valve as follows: (a) 2.4 mm; (b) 3.5 mm; (c) 4 mm; (d) 10.5 mm; (e) 11.9 mm; (f) 13.3 mm; (g) 15.5 mm; (h) 20 mm; (i) 22 mm.

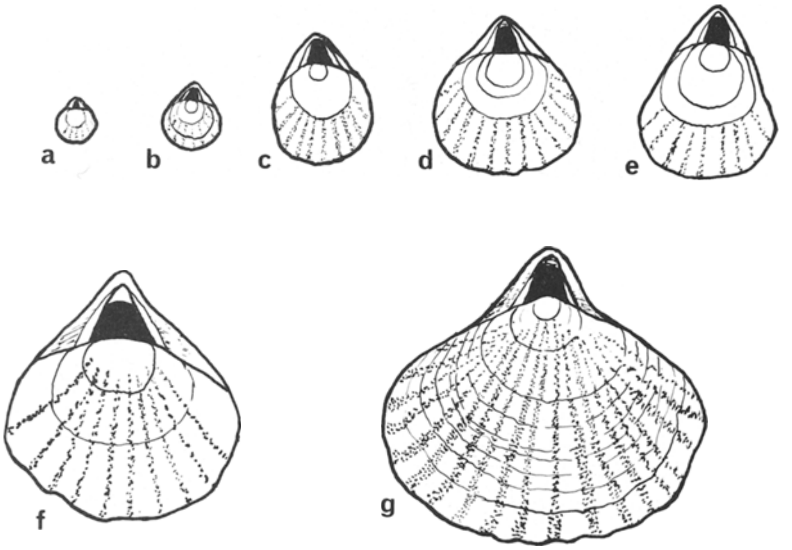


FIG. 9. Growth stages of *Notosaria nigricans* (Sowerby). Length of pedicle valve as follows: (a) 0.8 mm; (b) 1.35 mm; (c) 2.6 mm; (d) 3.2 mm; (e) 3.5 mm; (f) 5 mm; (g) 15 mm.

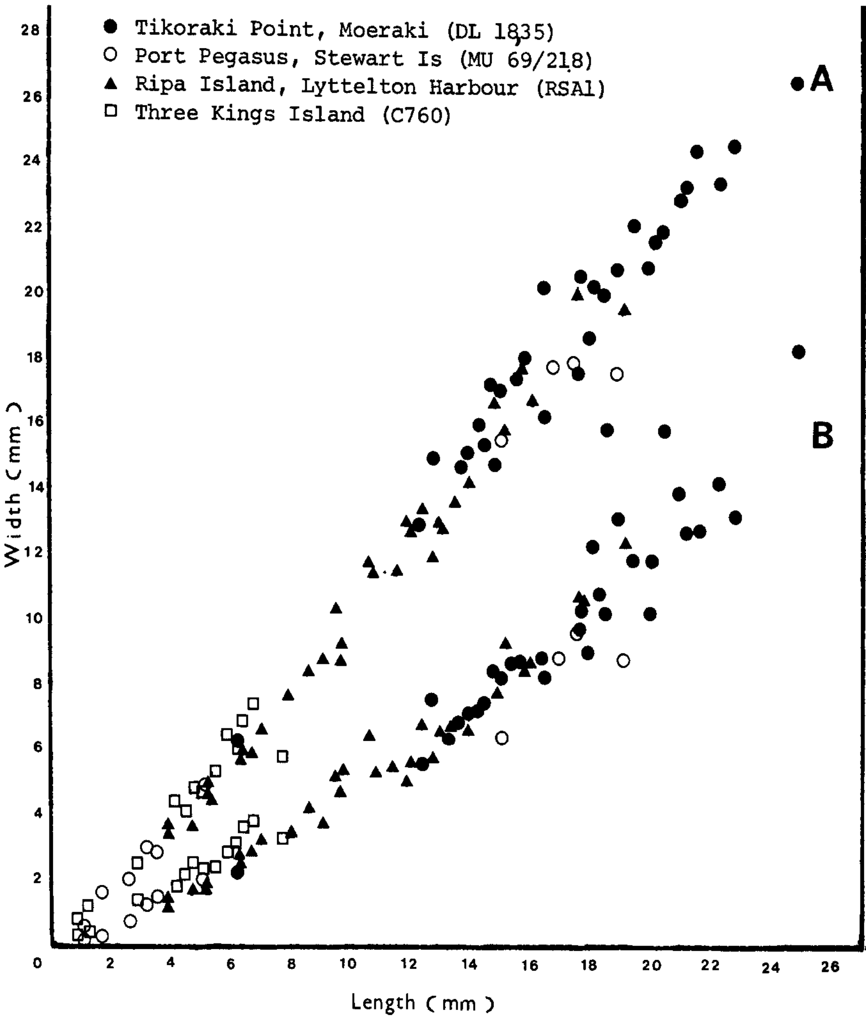


FIG. 10. Scatter diagram of width-length (A) and thickness-length (B) for samples from four populations of living *Notosaria nigricans*.

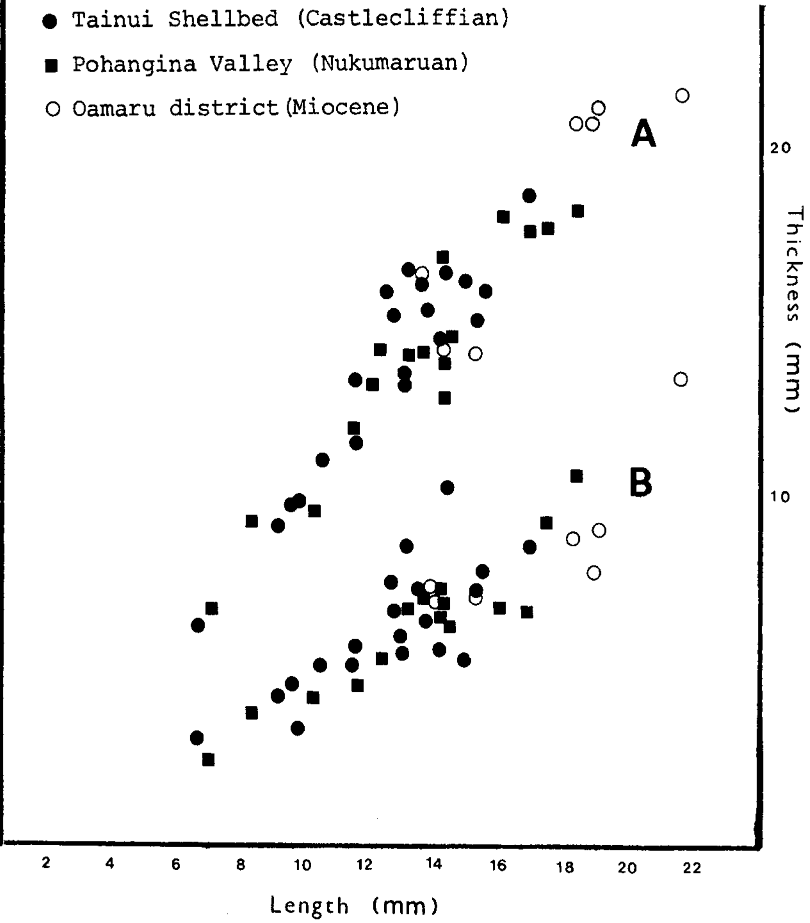


FIG. 11. Scatter diagram of width-length (A) and thickness-length (B) for three assemblages of fossil *Notosaria nigricans*.

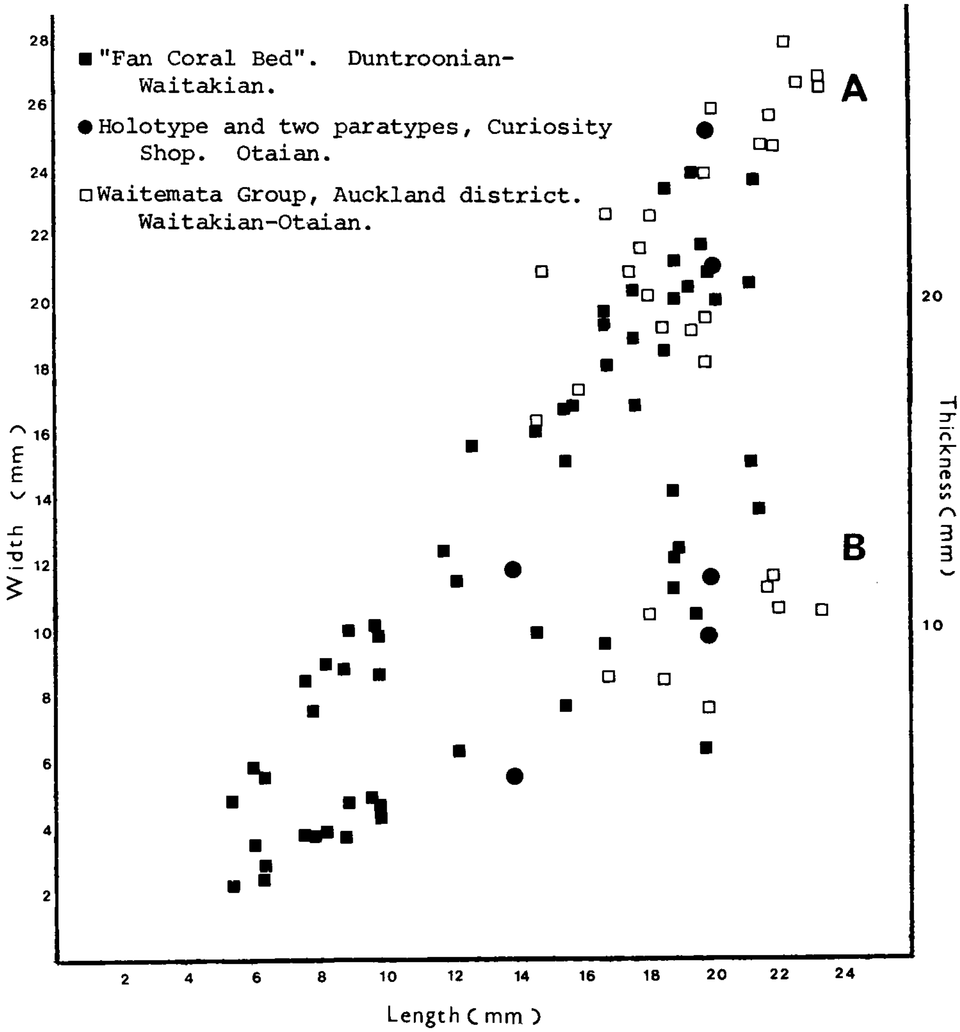


FIG. 12. Scatter diagram of width-length (A) and thickness-length (B) for three assemblages of *Notosaria antipoda*. (Note that thickness could not be measured for all specimens.)

and the maximum growth permitted by the environment". These authors presented a careful account of size and shape variation in three brachiopod species — *Magellania venosa, Terebratella dorsata,* and *Neorhynchia strebeli.* They noted that the first two species had an identical relative growth-ratio of width to length, and that size increase followed a slightly curvilinear growth trend, with length increasing more rapidly than width in old age.

The arithmetic plots of width-length for the species of *Notosaria* show some indication of a departure from a simple straight-line linear relation. Examining within-population variation, this is statistically significant only for fossil *N. nigricans* ($p < 0.05$). There is a similar indication of curvilinearity between the length and the thickness, but this is significant only for living *N. nigricans* ($p < 0.001$). In contrast to *M. venosa* and *T. dorsata,* specimens of both species of *Notosaria* increase in width more rapidly than length after the animal reaches a length 1/2 to 2/3 of its adult length. Length-frequency histograms for populations of *N. nigricans* were discussed by Lee (1978).

VARIATION IN THE GENUS *Notosaria*

In order to examine statistically the phenotypic variation characteristic of the genus, measurements were made on all available entire and uncrushed specimens of both living and fossil species of *Notosaria.* Measurements were restricted to characters of the shell exterior, since measurement of internal features necessitates destruction of the shell in Recent specimens and is impracticable in sediment-filled fossil specimens.

A total of 318 specimens was measured for length, width, thickness or inflation, brachial valve length, maximum number of costellae or ribs, counted around the anterior commissure, number of conspicuous growth lines, and degree of folding, using a subjective scale of one for a rectimarginate commissure (Fig. 1.5) to three for a pronounced fold (Fig. 1.11). The first three characters were measured normal to one another using watchmakers' calipers and were reproducible to ±0.2 mm. Details of the species, localities, ages and numbers of specimens measured are given in Table 3. They include two Recent populations, two Pleistocene, and two Miocene assemblages of *N. n. nigricans,* one Recent population of *N. nigricans reinga,* and one Oligocene and three Early Miocene assemblages of *N. antipoda.* The means and standard deviations of each of the seven characters for each assemblage are given in Table 3.

In comparing assemblages, it is necessary to keep in mind that the different populations may have different age structures or may be distinguishable by purely phenotypic differences. Either of these might be caused by the palaeo-environment, or — for fossil assemblages — by the fate of the shells since the death of the animals.

The nature of this variation in *Notosaria* was investigated by examining a living population, in which it is believed a range of ages would be found and in which variation would be phenotypic rather than genotypic. The Lyttelton population was used, mainly because it seemed to include a complete range of ages. Since there is currently no reliable way of aging individuals, age-related and environmentally-induced variation cannot be recognised as such and are initially examined together. The data for the 41 individuals of the population, for the seven characters, were subjected to a principal components analysis (Sneath and Sokal 1973).

The analysis (Table 4) successfully accounts for the variation within the population; a single component could account for 81% of the variation. This was especially true for length, width, thickness and brachial valve length, for which the first component accounted for between 96% and 98% of the variation. It seems likely that most of this variation is age-related, and the very high correlations implied between the measurements show that the shape of the brachiopods is constant as they grow. (For example, the correlation between length and width was 0.989.) This interpretation is supported by the scores of the individuals on the first component. These showed perfect discrimination between those specimens that had been considered as juveniles by visual inspection, those that had been considered adult, and those considered intermediate (Fig. 13).

The second component (Table 4) represents a contrast between those individuals with a large number of growth lines for their size, with considerable folding and with few ribs on the one hand, and those with opposite characteristics on the other. The cause of this type of variation is not certain. It might develop by some individuals growing more slowly than normal, and thus producing more growth lines for their size. This is supported by the observation that these individuals tended to be placed on the left of the first component, and were therefore small (Fig. 13). Since folding tends to increase with age it seems reasonable that they should also show more folding, though why fewer ribs should develop is unclear. The second component accounts for 10.2% of the variation, bringing the total to 91.3%.

Table 3.—Summary of Measurements on *Notosaria* Species (Measurements in millimetres)

	Length		Width			Thickness			Brachial valve length			Rib number			Growth lines			Folding		
Notosaria nigricans nigricans	Mean	S.D.	Mean	S.D.	A.M.	Mean	S.D.	A.M.	Mean	S.D.	A.M.	Mean	S.D.	A.M.	Mean	S.D.	A.M.	Mean	S.D.	A.M.
Lyttelton Harbour Recent (41)	10.9	4.0	11.2	4.8	15.12	5.6	2.7	7.74	9.0	3.3	11.80	17.8	2.5	19.47	6.6	2.8	8.80	1.3	1.1	2.03
Tikoraki Pt Moeraki Recent (119)	17.1	2.9	18.4	3.5	15.02	9.7	2.6	7.81	14.5	2.8	12.05	20.7	3.1	19.13	5.8	3.4	3.73	2.1	2.0	1.33
Wanganui Castlecliffian (26)	12.9	2.5	14.1	3.2	15.59	6.6	2.2	7.45	11.0	2.1	12.05	19.3	2.4	19.98	9.9	4.8	10.81	2.4	1.0	2.70
Hawkes Bay Nukumaruan (21)	13.5	2.9	14.0	3.1	14.72	6.4	1.8	6.81	11.2	2.4	11.75	19.7	2.7	18.99	8.4	2.4	8.81	1.9	0.9	2.04
Oamaru Altonian (6)	16.8	4.2	17.2	4.1	14.16	9.2	3.4	7.46	13.9	3.6	11.66	23.6	3.8	22.28	8.3	2.6	6.49	2.08	1.1	1.51
Waipara Altonian (5)	15.0	3.8	17.4	4.5	16.42	7.4	1.6	6.72	12.6	3.7	11.91	23.2	2.3	22.76	9.4	2.7	8.81	2.5	0.7	2.32
Notosaria nigricans reinga Three Kings Is. Recent (65)	5.5	0.7	5.6	0.9	15.75	2.8	0.6	8.50	4.6	0.6	11.94	15.5	1.6	20.07	4.5	1.4	10.60	1.0	0.7	2.93
Notosaria antipoda																				
Curiosity Shop Otaian (3)	17.9	3.5	19.5	6.9	15.11	9.0	3.1	6.50	15.0	3.7	11.78	25.3	5.9	23.34	12.3	2.5	9.68	2.3	1.2	1.51
Ashburton River Otaian (1)	13.2	—	17.6	—	18.68	8.3	—	8.91	10.8	—	11.59	18	—	18.49	6	—	6.65	3	—	3.20
Auckland Otaian (9)	20.6	2.1	23.1	2.5	15.53	10.6	3.1	6.39	16.8	1.9	11.37	20.8	3.9	17.47	15.3	4.5	10.79	2.3	0.7	0.93
Fan Coral Bed Duntroonian (22)	12.12	5.3	12.9	6.4	15.23	6.4	3.6	7.73	10.1	4.5	11.80	17.9	5.4	19.90	8.6	3.4	10.01	1.1	0.8	1.56

Number of specimens in parentheses. A.M. = adjusted mean

Component	1	2
% of variation accounted for	81.1	10.2
Correlation with:		
Length	+0.99	+0.05
Width	+0.98	+0.07
Thickness	+0.98	−0.05
Brachial valve length	+0.99	+0.07
Ribs	+0.71	+0.64
Growth lines	+0.74	−0.42
Folding	+0.87	−0.33

Table 4.—Variation Within the Living Lyttelton Population: Results of a Principal Components Analysis on the Individual Shells, Using the Seven Original Characters.

It must also be borne in mind that three of the characters, growth lines, ribs and folding, were discontinuous, being in general whole numbers. It would be impossible for these characters to be perfectly correlated with truly continuous characters, as the others were, so the figures of 81.1% and 91.3% of the variance explained are really very high.

At least it is possible to conclude that most of the age-related variation within a living population is linearily correlated, and that if there is much environmentally-induced variation it is closely correlated with that. Assuming that the same held for the original fossil populations, it should be possible to correct for age differences between the assemblages by using one of the characters as an age indicator. Length was marginally better correlated with the other variates and it was selected. In view of the high correlation between length and the first component (0.99), this is almost equivalent to using the scores on the first component.

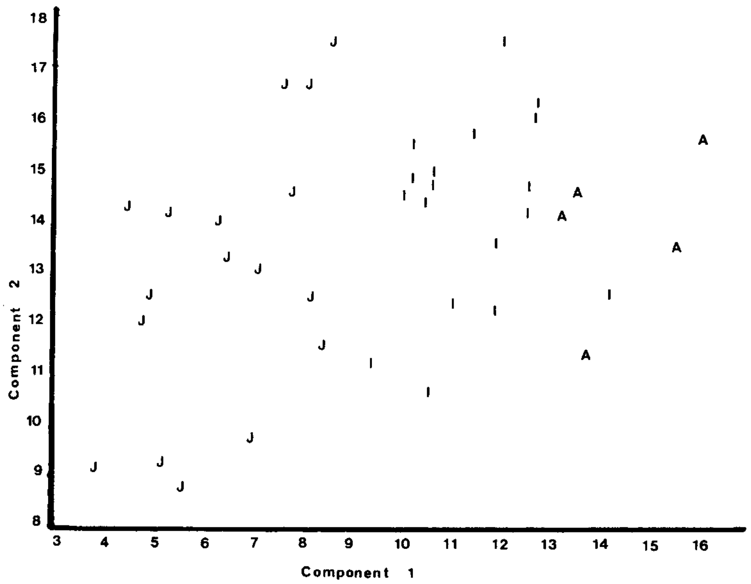


FIG. 13. Variation within the living Lyttelton population: the scores of the individual shells on the first two components of a principal components analysis on the seven original characters. J = juveniles; I = intermediates; A = adults.

The regressions on length of all other variates were therefore examined. The joint within-population regression ("common slope") was used, so that it would not include any between-assemblage differences. The separate regressions within each assemblage were examined, but they were not significantly different from each other. Curvilinear relations between length and the other variates were examined, but gave no improvement over the already close linear relations. These calculated regressions were then used to adjust the individual values to a standard length, length itself not being used. The means for these adjusted values are given in Table 3.

The assemblage means for the six characters, adjusted for age/size differences, were first used to classify the assemblages, fossil and living, using a cluster analysis (Sneath and Sokal 1973). (The data standardised to zero mean and unit variance, squared euclidean distance measure, average sorting strategy.) The resulting dendrogram is shown in Figure 14. It can be seen that there is imperfect correlation with the proposed taxonomic classification. The population of the new subspecies, *N. nigricans reinga* from the Three Kings Islands is revealed as most similar, in the quantitative characters measured, to a fossil assemblage of *N. nigricans nigricans,* and these two next most similar to a group that includes *N. antipoda* assemblages.

There is some separation between the two species, *N. nigricans* and *N. antipoda.* All the assemblages of *N. nigricans,* with the exception of the Moeraki population, form a single group, but this group also includes the fossil *N. antipoda* assemblage from the Fan Coral Bed. An *N. antipoda* assemblage (Curiosity Shop) forms another group with the two assemblages on the *N. antipoda/N. nigricans* boundary.

Beyond these two groups the classification "chains" (Lance and Williams 1967), three assemblages joining the rest, one after the other. Since the sorting strategy used

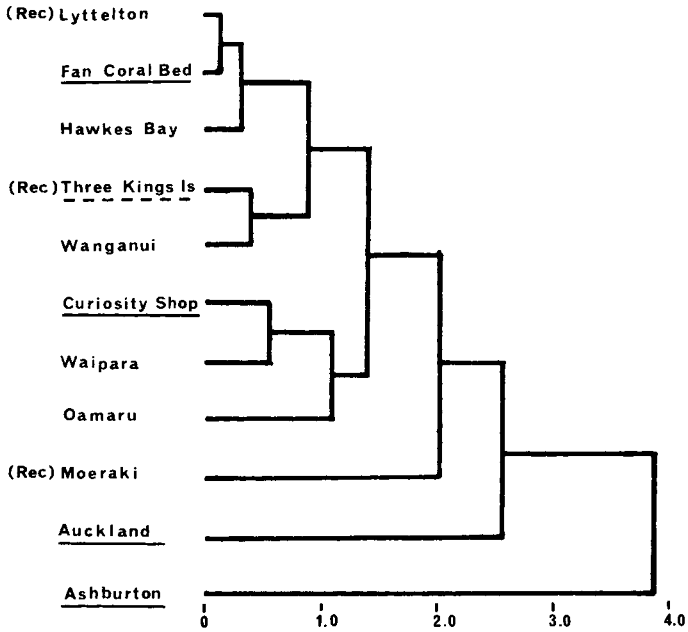


FIG. 14. — Similarities between the assemblages; the dendrogram from a cluster analysis classification of the assemblages using the means of the six adjusted characters. Key to species: *Notosaria nigricans nigricans;* dashed line = *Notosaria nigricans reinga;* solid underline = *Notosaria antipoda.* (Rec) = Recent.

(average) is "space-conserving" (Lance and Williams 1967) this must reflect the nature of the variation. That is, there are no clear groups, rather a central cluster with outliers differing in different ways. The Moeraki population is the most important of these outliers, apparently mainly because of its longer brachial valve. The other two outlier assemblages, Auckland and Ashburton, are small (nine and one individuals, respectively), and their isolated positions could be due to the atypical nature of the few representatives.

The dimensional (width, thickness, length of brachial valve) and the non-dimensional (ribs, growth lines, folding) characters were used separately in further cluster analyses in case either gave a classification that agreed better with the taxonomic one, but neither did.

A principal component analysis (P.C.A.) of the assemblages, again using the assemblage means, confirms this picture. (The P.C.A. started from the correlation matrix, and therefore effectively standardised the characters.) The first two components, which account for 62.5% of the variation (Table 5), show (Fig. 15) a central cluster of most of the *N. nigricans* assemblages, including the Fan Coral Beds assemblage of *N. antipoda.* The other assemblages of *N. antipoda* and the transitional boundary assemblages are indicated as being different from this cluster in different ways, with some similarity between the Curiosity Shop assemblage and the transitional pair. The Moeraki population of *N. nigricans* is not separated out on these two axes, but the third component (not shown) is mainly a contrast between this population and the others.

Component	1	2
% of variation accounted for	38.4	24.1
Correlation with:		
Width	+0.80	+0.30
Thickness	+0.87	–0.06
Brachial valve length	+0.20	–0.86
Ribs	–0.29	–0.71
Growth rings	–0.18	+0.26
Folding	+0.86	0.19

Table 5.—Similarities Between the Assemblages: The Results of a Principal Components Analysis on the Assemblage Means of the Six Adjusted Characters.

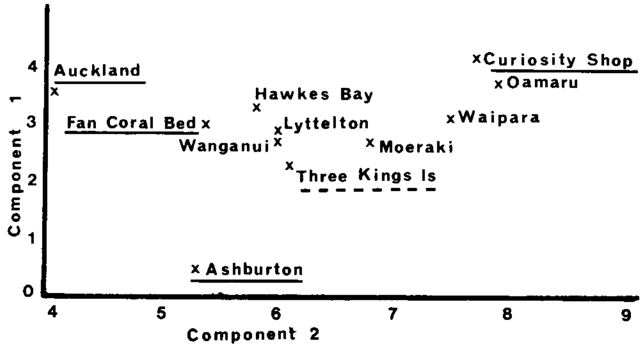


FIG. 15. Similarities between the assemblages: the scores of the assemblages on the first 2 components of a principal components analysis on the assemblage means of the 6 characters. Key as for Fig. 14.

Population means can be misleading, however. It is necessary to examine also the variation between individuals. A principal components analysis was therefore performed between the 318 individual shells, again using the six adjusted characters. As Table 6 shows, there were significant correlations remaining until four components had been extracted. These account for 83% of the observed variation. Figure 16 is a scatter diagram of the scores of the specimens on component 1, plotted against those on component 2. (These two components together account for 54% of the variation.)

The results generally confirm previous conclusions. The Moeraki population is indeed shown as generally different from the rest of the specimens, though there is considerable overlap with members of other assemblages, especially the fossil *N.*

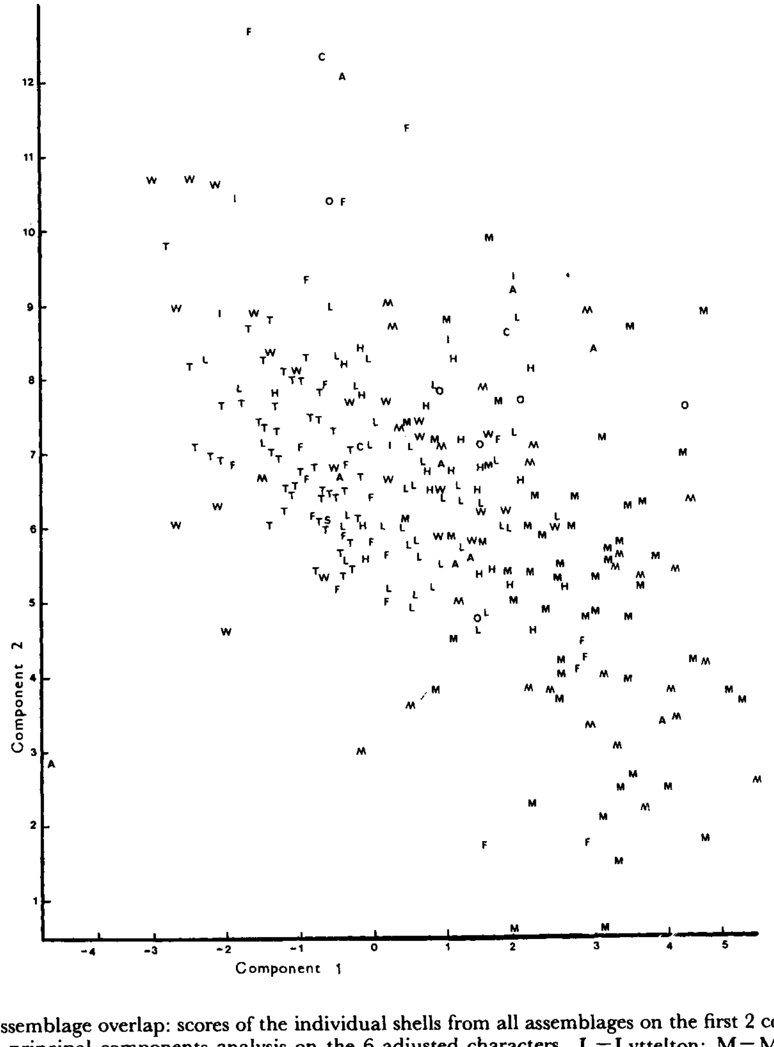


FIG. 16. Assemblage overlap: scores of the individual shells from all assemblages on the first 2 components of a principal components analysis on the 6 adjusted characters. L = Lyttelton; M = Moeraki; W = Wanganui; H = Hawkes Bay; O = Oamaru; I = Waipara; T = Three King Islands; C = Curiosity Shop; S = Ashburton; A = Auckland; F = Fan Coral Bed.

Component	1	2	3	4
% of variation accounted for	30.9	22.7	19.5	10.8
Correlation with:				
Width	+0.61	+0.17	-0.56	+0.38
Thickness	+0.53	-0.64	+0.02	+0.35
Brachial valve length	+0.26	-0.59	-0.53	-0.54
Rib number	+0.20	+0.70	-0.51	-0.12
Growth lines	+0.68	+0.28	+0.46	-0.26
Folding	+0.80	+0.08	+0.32	-0.09

Table 6.—Assemblage Overlap: The Results of a Principal Components Analysis on the Individual Shells from All Assemblages, Using the Six Adjusted Characters.

antipoda at Fan Coral Bed. The population of *N. nigricans reinga* from the Three Kings Islands is shown to be a uniform population and to some extent to be on the edge of the range of variation (one Wanganui outlier excepted). Its range of variation does, however, overlap with that of several other assemblages. It is interesting that it shows more overlap with some of the fossil assemblages (especially Wanganui) than with the living populations of *N. nigricans* from Lyttelton and Moeraki. Components 3 and 4 show exactly the same situation for the Moeraki and the Three Kings Islands populations. There is again no consistent separation of *N. antipoda* from *N. nigricans*. We conclude that, in the quantitative characters measured, *Notosaria* has shown no consistent evolutionary trend, and that there is therefore no correlation with stratigraphic position. Indeed the variation from the Miocene to the Recent is less than that found between present-day populations.

CONCLUSIONS

A revision of the rhynchonellide genus *Notosaria* has led to the inclusion of a new subspecies, *Notosaria nigricans reinga,* from Recent seas to the north of New Zealand, and the reciprocal transfer of *Tegulorhynchia antipoda* to *Notosaria,* and *Notosaria sublaevis* to *Tegulorhynchia.* The genus *Notosaria* now includes *Notosaria nigricans nigricans* (Sowerby), *Notosaria nigricans reinga* n. subsp., *Notosaria nigricans pyxidata* (Davidson), *Notosaria antipoda* (Thomson), and *Notosaria nysti* (Davidson).

Time ranges for the New Zealand species show a long continuous fossil record from the Oligocene to the Recent. *Notosaria antipoda* ranges from Whaingaroan to Otaian (Early Oligocene to Early Miocene) and *N. n. nigricans* from Altonian (Early Middle Miocene) to Recent. *Notosaria antipoda* is distinguished from *nigricans* chiefly on ornamentation and some poorly preserved specimens of Early Miocene age are therefore difficult to place.

At present most specific diagnoses and descriptions of brachiopod shells apply only to a "normal" adult shell. We argue that many juvenile brachiopods possess few if any of the diagnostic characters of the adult, and brachiopod descriptions must include ontogenetic changes. In *N. n. nigricans,* for example, the juvenile shell is subcircular in outline, rectimarginate, possesses few ribs, has a small v-shaped cardinal process; an adult shell is wider than long, possesses 20-25 costellae, is strongly folded and bears a large bilobed cardinal process. In this subspecies the change from morphologic juvenile to morphologic adult takes place at a length of 14-16 mm (about 2/3 of adult size) and appears to correspond to the onset of reproductivity maturity.

Morphologic variation within living populations and fossil assemblages of *Notosaria* species examined with respect to length, width, thickness, brachial valve length, rib number, growth lines, and degree of folding shows considerable variation in each of these characters. The variation in these characters corresponds only poorly to known stratigraphic and geographic distribution patterns. Although of limited direct taxonomic value in this case, analysis of variation in Recent populations must be taken into account in determining the limits of fossil brachiopod taxonomic groupings.

ACKNOWLEDGMENTS

Encouragement and critical advice from Associate Professor J. D. Campbell and Dr R. M. Carter helped greatly in the preparation of this paper. Mr E. W. Dawson kindly made available brachiopod collections from the N.Z. Oceanographic Institute. Dr F. M. Climo of the National Museum, Wellington, and Dr D. I. MacKinnon of the University of Canterbury lent material from collections in their care. Financial assistance from the N.Z. University Grants Committee is gratefully acknowledged.

REFERENCES

ALLAN, R. S. 1937. Type Brachiopoda in the Canterbury Museum. *Records of the Canterbury Museum* 4(3): 115-28.

—— 1940. Studies on the Recent and Tertiary Brachiopoda of Australia and New Zealand. Part II. *Records of the Canterbury Museum* 4(6): 277-297. 3 pls.

—— 1960. The Succession of Tertiary Brachiopod Faunas in New Zealand. *Records of the Canterbury Museum* 7(3): 233-268.

BOWEN, Z. D. and J. D. CAMPBELL 1973. Systematics and Evolution of the Brachiopod Genus *Rhizothyris* in the Oligocene-Miocene of New Zealand. *Journal of the Royal Society of N.Z.* 3: 141-160.

BROOKFIELD, M. E. 1973. The Life and Death of *Torquirhynchia inconstans* (Brachiopoda, Upper Jurassic) in England. *Palaeogeography, Palaeoclimatology and Palaeoecology* 13: 241-259.

BUCKERIDGE, J. 1975. The Significance of Cirripedes to the Palaeoecology of Motutapu Island. *Tane* 21: 121-129.

CHAPMAN, F. and I. CRESPIN 1923. The Austral Rhynchonellacea of the "Nigricans Series" with a special description of the new genus *Tegulorhynchia. Proceedings of the Royal Society of Victoria* 35(2): 170-193, pls XI-XIII.

CLARKE, E. 1905. The Fossils of the Waitemata and Papakura Series. *Transactions of the N.Z. Institute* 37: 413-21, pl XXXII.

COOPER, G. A. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. *Smithsonian Miscellaneous Collections* 139(5): 1-90, pls 1-22.

DALL, W. H. 1873. Catalogue of the Recent species of the class Brachiopoda. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1873: 177-204.

DAVIDSON, T. 1852. Sketch of a classification of Recent Brachiopoda based upon internal organisation. *Annals and Magazine of Natural History* (2)9(53): 361-77.

—— 1874. On the Tertiary Brachiopoda of Belgium. *Geological Magazine* Dec 2(1) No. 4: 150-159, pls 7-8.

DAWSON, E. W. 1971. A Reference List and Bibliography of the Recent Brachiopoda of New Zealand. *Journal of the Royal Society of N.Z.* 1: 159-174.

DOHERTY, P. 1976. Aspects of the feeding ecology of the sub-tidal brachiopod *Terebratella inconspicua* (Sowerby, 1846). M.Sc. thesis, Zoology Department, University of Auckland.

FOSTER, M. W. 1974. Recent Antarctic and Subantarctic Brachiopods. *Antarctic Research Series* 21. 189 pp.

GAGE, M. 1970. Late Cretaceous and Tertiary Rocks of Broken River, Canterbury. *N.Z. Journal of Geology and Geophysics* 13: 507-559.

GRANT-MACKIE, J. A. 1965. Ancient Life of the Auckland area. *11th New Zealand Science Congress:* 1-8.

KEYES, I. W. 1971. Type Specimens of New Zealand Cenozoic Invertebrates in the Dominion Museum. *Records of the Dominion Museum* 7(9): 65-84.

LANCE, G. N. and WILLIAMS, W. T. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. *Computer Journal* 9: 373-380.

LEE, D. E. 1978. Aspects of the Ecology and Paleoecology of *Notosaria nigricans* (Sowerby). *Journal of the Royal Society of N.Z.* 8(4): 395-417.

MCCAMMON, H. and R. BUCHSBAUM. 1967. Size and Shape Variation of Three Recent Brachiopods from the Strait of Magellan. *Antarctic Research Series* 2: 215-225.

MACKINNON, D. I. 1977. The formation of muscle scars in articulate brachiopods. *Philosophical Transactions of the Royal Society of London B. Biological Sciences* 280: 1-27.

PARK, J. 1886. Waitemata, Eden and Manukau Counties. *N.Z. Geological Survey Reports of Geological Explorations during 1885:* 147-164.

PERCIVAL, E. 1960. A contribution to the life-history of the brachiopod *Tegulorhynchia nigricans. Quarterly Journal Microscopic Science* 101(4): 439-57, Figs. 1-6.

RUDWICK, M. J. S. 1962. Filter-feeding mechanisms in some brachiopods from New Zealand. *Proceedings of the Linnean Society, London, Zoology.* 44: 592-615.

—— 1970. *Living and Fossil Brachiopods.* Hutchinsonian University Library: London.

SISE, J. 1975. The Mineralogy and Geochemistry of the Ultrabasic–basic Rocks of Mt Luxmore, Fiordland, New Zealand. M.Sc. thesis, Geology Department, University of Otago.

SKINNER, D. N. B. 1969. Colville Formation — A new formation possibly correlative with the Waitemata Group. *N.Z. Journal of Geology and Geophysics* 12: 349-60.

SNEATH, P. H. A. and SOKAL, R. R. 1973. *Numerical Taxonomy: The Principles and Practice of Numerical Classification.* W. H. Freeman and Co.: San Francisco.

SOWERBY, G. B. 1846. Descriptions of thirteen new species of Brachiopods. *Proceedings of the Zoological Society, London* (XIV) 1846: 91-5.

SQUIRES, D. F. 1958. The Cretaceous and Tertiary Corals of New Zealand. *N.Z. Geological Survey Palaeontological Bulletin* 29.

SUESS, E. 1864. Brachiopoden *in* Zittel, K. A. Fossilen Mollusken und Echinoderm aus Neu-Seeland. *Novara-Expedition. Geologischer Theil.* pp 56-61.

SURLYK, F. 1972. Morphological Adaptations and Population Structures of the Danish Chalk Brachiopods. *Biologiske Skrifter. K. Danske Videnskavernes Selskab* 19: 1-57.

THOMSON, J. A. 1918. *In* J. Park. The Geology of the Oamaru District, North Otago. *N.Z. Geological Survey Bulletin* 20: 117-119.

—— 1927. Brachiopod Morphology and Genera. *N.Z. Board Science and Art Manual 7.*

WILLIAMS, A. 1956. The Calcareous Shell of the Brachiopoda and its importance to their Classification. *Biological Reviews* 31: 243-287.

—— 1968. A history of skeletal secretion among articulate brachiopods. *Lethaia* 1: 268-287.

WILLIAMS, A. and A. J. ROWELL. 1966. Brachiopod Anatomy *in* Moore, R. C. (ed) *Treatise on Invertebrate Palaeontology Part H. Brachiopoda.* pH6-H57.

WILLIAMS, A. and A. D. WRIGHT. 1961. The origin of the loop in articulate brachiopods. *Palaeontology* 4(2): 149-76.

DAPHNE E. LEE
Geology Department
J. B. WILSON
Botany Department
University of Otago
Box 56
Dunedin
New Zealand.