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The family Nuculidae (Bivalvia: Protobranchia) in South Africa and Mozambique

by

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ABSTRACT

Nine species of the genera *Nucula* Lamarck, 1799, *Ennucula* Iredale, 1931, and *Brevinucula* Thiele, 1934, are here recorded from southern Africa and Mozambique. The sole Mozambican species is *Nucula (Lamellinucula) semen* Thiele, 1931, which occurs also in Durban Bay sediments dating from the mid-Holocene or perhaps late Quaternary.

New species: *Nucula (Nucula) planiculmen, N. (N.) subluxa, N. (Lamellinucula) rhytidopleura*; *Ennucula oliva.*

Revised status: *Nucula (Lamellinucula) sculpturata* Sowerby, 1904, for *N. pulchra auct. (N. pulchra* Hinds, 1843, is a *nomen dubium*).

New synonym: *Nucula fragilis* Boshoff, 1968 = *Nucula* [= *Ennucula*] *fragilis* Thiele, 1931.
Types figured: Lectotype (here designated) of *Nucula fragilis* Thiele, 1931, holotype of *N. aequalitas* Barnard, 1964.

Type localities corrected: *N. (L.) sculpturata, N. (L.) irregularis* Sowerby, 1904

Development: *Nucula planiculmen* and *N. subluxa* are incubatory.

INTRODUCTION

The Nuculidae is a relatively small family of protobranch bivalves, mainly characteristic of non-compacted and often reworked bioclastic sediments, at shallow littoral to abyssal depths. Five species were reported for southern Africa by Barnard (1964), and a 6th was added by Boshoff (1968), but practically nothing further has been written on the nuculid fauna of this region. The present study is based mainly on the Natal Museum collection of the group, comprising both littoral, and shelf and upper-slope material, the latter derived largely from the Natal Museum's dredging programme. Abyssal species are not considered.

ABBREVIATIONS

BMNH	–	The Natural History Museum, London
dd	–	shell empty when collected
d/l	–	ratio of *total* depth (valves joined) to length
h/l	–	ratio of shell height (umbo to ventral margin) to total shell length
LV	–	left valve
lve	–	living when collected
MNHP	–	Museum National d'Histoire Naturelle, Paris
NMSA	–	Natal Museum, Pietermaritzburg

NMDP	–	Natal Museum Dredging Programme
NMWC	–	National Museums and Galleries of Wales, Cardiff
OXUM	–	Oxford University Museum, Oxford
PF	–	*s.s. Pieter Faure*
RV	–	right valve
SAMC	–	South African Museum, Cape Town
V	–	valve(s)
ZMHB	–	Zoologisches Museum, Humboldt University, Berlin

'*Total depth*' is a measurement of two valves united (or in the case of incomplete shells, that of a single valve doubled); '*valve depth*' refers to that of a single valve. '*Greatest width*' is used for the point at which the valve bulges most.

Geographic subdivisions used in this paper are (west to east):

Namaqualand	Orange River to St Helena Bay
Atlantic Cape	St Helena Bay to Cape Point
False Bay	Cape Point to Cape Hangklip
Overberg	Cape Hangklip to Still Bay (Stilbaai)
Tsitsikamma Coast	Still Bay to Cape St Francis
E. Cape	Cape St Francis to Kei River
W. Transkei	Kei River to Umtata River
E. Transkei	Umtata River to Mtamvuna River
S. Natal	Mtamvuna River to Durban
N. Natal	Durban to Tugela River
S. Zululand	Tugela River to Leven Point
N. Zululand	Leven Point to Mozambique border

Agulhas Bank: This refers to the wide continental shelf between Cape Point and the Kei River, and is used mainly where the majority of records originate from deeper than approximately 50 m.

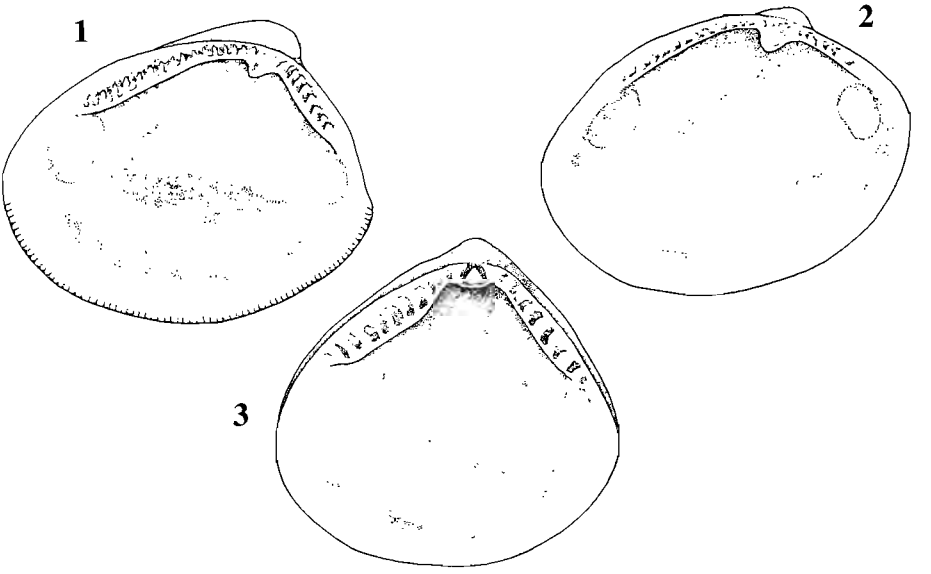
These geographic subdivisions should not be interpreted politically, e.g. the Eastern Cape subregion (with a largely endemic temperate fauna) is *not* equivalent to the modern Eastern Cape Province, which incorporates Transkei (a temperate/subtropical transitional region). Similarly 'Natal' is *not* equivalent to the modern province of KwaZulu-Natal, which includes the more tropical faunal region of Zululand.

TAXONOMY

Family Nuculidae Gray, 1824

There remains little agreement between the various classifications used by different writers on the Nuculidae, whose simple morphology appears to offer few useful characters. The most contentious character state is the presence or absence of crenulations along the inner ventral margin of the valves. This has been variously interpreted as significant at the subfamily (Maxwell 1988) or generic level (most authors), although more recently Gofas & Salas (1996) have pointed out that lack of marginal crenulations (the exposed ends of structural rods of aragonite) is a

symplesiomorphy. Further to the reasons given by the latter authors, crenulations are also absent in the obvious outgroup, the Nuculanoidea. It is in fact probable that rods and crenules have been independently lost in different nuculid lineages, as it appears that they may also be present or absent in different species of genus *Brevinucula* (*q.v.*). Nevertheless, solely for practical reasons I have continued to utilise *Ennucula* Iredale, 1931, as a means of grouping together non-triangular species with smooth margins.



Figs 1–3. South African nuculid genera: internal view of right valves. 1. *Nucula nucleus* (Linnaeus, 1758). 2. *Ennucula fragilis* (Thiele, 1931). 3. *Brevinucula aequalitas* (Barnard, 1964).

Key to genera of Nuculidae occurring in Southern Africa

1 Valves internally with distinct marginal crenulations (Fig. 1) ..... **Nucula**
– Valves with smooth margins 2
2 Triangular, chondrophore minute or absent (Fig. 3) ..... **Brevinucula**
– Ovate, chondrophore well-developed, oblique (Fig. 2) ..... **Ennucula**

Biogeographical notes

Analysis of the South African nuculids in terms of their faunal relationships is hindered by the lack of data on the Nuculidae of relevant regions. The Indo-West Pacific species are in particular need of revision. Furthermore, characters are few, and their polarity usually unclear or masked by homoplasy.

The present ranges of five out of nine Recent South African species indicate these to be probably Indo-Pacific in origin. One of these, *Ennucula fragilis* (Thiele, 1931), has a known East African distribution. (Another East African element is *Nucula* (*Lamellinucula*) *sultana* Thiele, 1931, whose range previously extended as far south as Durban Bay, probably during the mid-Holocene hypsithermal (cf Ramsay 1995) or the last interglacial, but which is now extinct south of Mozambique.) Three other

species of *Lamellinucula* – *N. irregularis* Sowerby, 1904, *N. sculpturata* Sowerby, 1904, and *N. rhytidopleura* sp. n. – are characteristic of subtropical eastern South Africa and have probably evolved as peripheral isolates of tropical Western Indian Ocean taxa. However no obvious sister species have been traced, although it may be noted that the littoral Malagasy *N.* (*L.*) *tamatavica* Odhner, 1943, has similar sculpture to *N. sculpturata*, and *N. irregularis* and *N. rhytidophora* show some resemblance to the SE Asian *N.* (*L.*) *mitralis* Hinds, 1843, and *N.* (*L.*) *sumatrana* Thiele, 1925, respectively.

Only two species appear to be undoubted North Atlantic elements–the common Agulhas Bank species of *Nucula* appears indistinguishable from the European *N. nucleus* (Linnaeus, 1758), and *Brevinucula aequalitas* (Barnard, 1964) of the continental slope of eastern South Africa is doubtfully distinct from the largely abyssal *B. verrilli* (Dall, 1886) from the western and northern Atlantic Ocean, and West Africa. The absence of *N. nucleus* from the intervening eastern Atlantic and *B. verrilli* from the south-eastern Atlantic suggest long isolation. Although confirmation from the West African fossil record is obviously desirable, there is merit in Vermeij's (1992) suggestion, on the basis of various other molluscs with similar widely disjunct populations, that such trans-equatorial distributions were 'most likely during the Early Pliocene'.

The probably neotenous littoral species described here as *Nucula planiculmen* and *N. subluxa* have distributions perhaps indicative of those of Southern Ocean incursives. *N. planiculmen* is a cold temperate-water species, *N. subluxa* replaces it on the warmer eastern part of the Cape coast. Being incubatory at a size of only about 2 mm, these species could have been dispersed over fairly large distances in mats of floating vegetation.

Nucula Lamarck, 1799

Type species: (m.) *Arca nucleus* Linne, 1758.

Key to species of *Nucula* in southern Africa

1 Anterior (and sometimes posterior) dorsal margin with transverse plicae crossing the growth lines (subgenus *Lamellinucula*) 2 21
– Dorsal margins not crossed by transverse plicae (subgenus *Nucula* s. s) 5

2 Median face of valve smooth ..... **sultana** Thiele, 1931
– Median face of valve crossed by transverse ridges 3

3 Sculptured by concentric ridges; without a posteroventral angle 4
– Sculptured by oblique ridges; with a distinct posteroventral angle ..... **irregularis** Sowerby, 1904

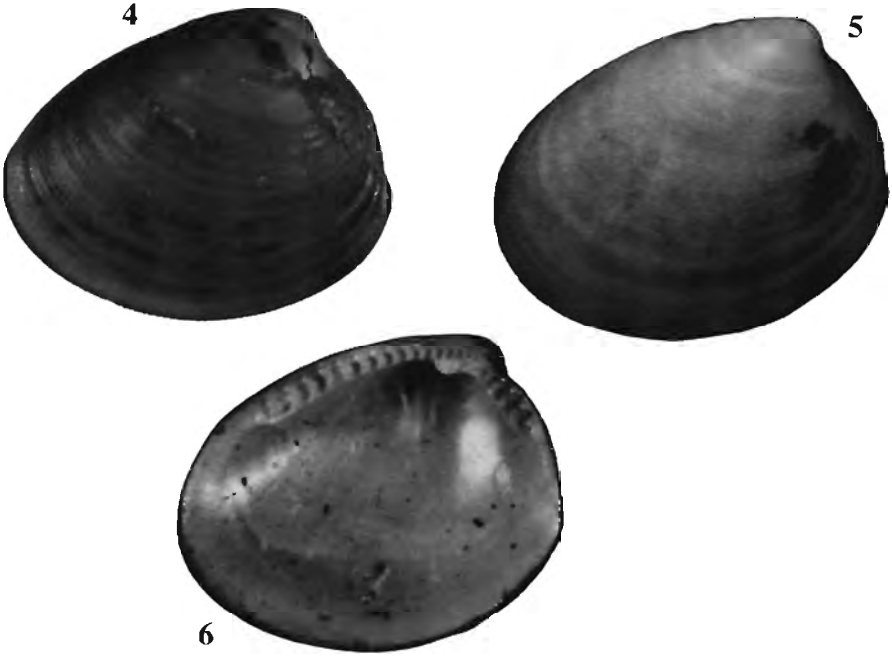
4 Concentric ridges strong, well-spaced, radial threads distinct; lunule indistinct ..... **sculpturata** Sowerby, 1904
– Concentric ridges fairly weak, crowded and irregular; radial threads faint, lunule distinct, convex ..... **rhytidopleura** sp. n.

5 Tiny (adult length not exceeding 2 mm); sculpture of regular concentric ridges, sometimes only in adult; 3–5 posterior hinge teeth; incubatory 6

- Adult length exceeding 10 mm; sculpture of growth-lines, an occasional one ridge-like, with fine but distinct radial riblets; 8–9 posterior hinge-teeth in 6–7 mm shell; non-incubatory.....**nucleus** (Linne, 1758)

6 Anterior and posterior series of teeth forming an arc; concentric ridges absent or developing only towards margins.....**planiculmen** sp. n.

- Anterior and posterior series of teeth inclined at a slight angle to each other; concentric ridges throughout.....**subluxa** sp. n.



Figs 4–6, *Nucula (Nucula) nucleus* (Linnaeus, 1758). 4. LV exterior, off Sandy Point, Transkei, 66 m, NMSA C4574, 10.7 x 8.6 mm. 5–6. *Nucula ?nucleus*: LV exterior and RV interior, SSE of Knysna, 103 m, NMSA V3168, 8.1 x 6.8 mm.

Subgenus *Nucula* s. s.

Diagnosis: Dorsal surface of shell without transverse ridges/corrugations.

Nucula (Nucula) nucleus (Linne, 1758)

Figs 4–6

Arca nucleus Linne, 1758: 695; Schenck 1935: 258, text-fig. 1 (neotype); Dance 1967: 8, pl. 5, fig. 2. Type locality: 'in Europa'.

Nucula nucleus; (South African references): Sowerby 1892: 66; Bartsch 1915: 181; Thiele in Thiele & Jaeckel 1931: 194 (36); Turton 1932: 214; Barnard 1964: 361; Kilburn & Rippey 1982: 153, pl. 35, fig. 1; (European references): Allen 1954: 457 *et sequ.* (comparative study); Tebble 1966: 25, pl. 1, fig. 1, textfig. 14c; Gofas & Salas 1996: 429, figs 1–7 (juvenile characters).

Nucula radiata (*non* Forbes & Hanley, 1853); Sowerby 1889: 157.

Nucula pulchra (*non* Hinds, 1843); Krauss 1852: 30.

Nucula sculpturata (*non* Sowerby, 1904); Bartsch 1915: 181; Turton 1932: 215.

Nucula convexa (*non* Sowerby, 1833); Turton 1932: 214.

?*Nucula tumidula* (*non* Malm, 1860); Thiele in Thiele & Jaeckel 1931: 195 (37).

Diagnosis (based on South African material): Shell oblong-trigonal, h/l 0.85–0.90, d/l 0.55–0.66, umbo rather angular and peaked, thick; posterior end truncate, slightly convex above, more or less angular below; lunule feebly delimited, escutcheon not defined; sculpture of growth-lines, some strengthened into irregular concentric ridges, with fine, weak to relatively strong radial threads (very fine on early part of dissoconch); hinge-plate not declivous in cross-section, chondrophore oblique, moderately projecting; tooth-line strongly dislocated, 11–14 posterior teeth, 20–25 anteriorly (at 9–13 mm length); periostracum dull olive-brown. Attains 13.4 mm length.

Distribution: Western Europe and Mediterranean; also continental shelf of South Africa from False Bay to eastern Transkei, in 40–350 m, in a range of substrates.

Type material: Schenck (1935) designated a left valve in the collection of the Linnean Society, London, as the neotype (although confusingly referring to all 6 valves as 'neotypes'). Dance (1967) objected on the grounds that this material was not in the original Linnean collection, but this would not affect potential *neotype* status. No specimens are listed by Wallin (1994) amongst the Linnean material in the Uppsala Zoological Museum.

Notes: I have compared South African material with authentic examples of *N. nucleus* from Britain, and, like others before me, can discern no differences. However, the two populations are widely isolated, the species being absent from West Africa (S. Gofas, *pers. comm.*), with the southernmost European records from southern Spain and the Mediterranean. It is highly likely that two species are involved, but further comparisons will need to be conducted at the molecular level.

Within southern Africa, *N. nucleus* is widespread and abundant on the Agulhas Bank and western Transkei Shelf, and samples examined are too numerous to be listed. However, the extremes of the range ascribed to it by Barnard (1964) have not been confirmed; thus the material from Luderitz (Namibia) and Saldanha (Atlantic Cape) could not be found in the SAMC collection (M. van der Merwe, *pers. comm.*). At the other extreme, his record from 'off Tugela River, 65–80 fath.' was either mislocalised or based on material of *N. rhytidopleura*, as extensive dredging within the Transkei has shown populations of *N. nucleus* to range only as far northward/eastward as Port Grosvenor (c. 29°58'E). However, it is possible that an occasional veliger might settle in southernmost Natal, as indicated by a single juvenile (dead but articulated) that was dredged just north of Port Edward in 140 m (NMSA D1391: NMDP); this shell lacks the sculpture of *N. rhytidopleura*, and appears to be referable to *nucleus*.

In Britain *N. nucleus* inhabits 'rather coarse bottoms of muddy gravel and coarse sand' (Tebble 1966), 'coarse muddy gravel' (Allen 1954). In South Africa, I have dredged it (living) on a wide range of substrate types, including firm grey mud, soft black mud, fine sandy mud, muddy sand, and coarse sand with calcareolite. Exploitation of such a broad spectrum of substrata by *N. nucleus* on the Agulhas Bank and Transkei Shelf might be explained by the apparent lack of competition with other Nuculidae, contrasting with the position in Britain where niche-partitioning of the substratum enables no less than five species to occur virtually sympatrically (Allen 1954). NMDP samples indicate the usual bathymetric range of *N. nucleus* in

South Africa to be 30–138 m, although worn beach shells (and one articulated shell from Kalk Bay in False Bay) indicate that it occasionally lives in shallower water. Curiously, off the Mgazi River in 180–350 m, is found a deep-water population (sympatric with *Ennucula fragilis* (Thiele, 1931)); one specimen from 300 m retains traces of mantle tissue, confirming it was living at that depth.

Beach-worn valves of *N. nucleus* were presumably responsible for early records of the European *Nucula radiata* Forbes & Hanley, 1849, *non* De Kay, 1843 [= *N. hanleyi* Winckworth, 1931], and of the offshore *N. sculpturata* Sowerby, 1904. Similarly, the valve now in the OXUM collection, recorded by Turton as the South Asian *Ennucula convexa* (Sowerby, 1833), is merely a worn and discoloured example of *N. nucleus*.

It is possible that a second species (Figs 5–6), closely allied to *N. nucleus*, occurs on the inner Agulhas Bank in 15–100 m, as indicated by a few enigmatic samples from various localities between False Bay and East London. Typical individuals of this differ from *N. nucleus* (with which they do not appear to be sympatric) in their lower and more recurved umbones (which produces a more oblong-ovate outline and strongly oblique chondrophore), slightly shallower valves (d/l 0.43–0.48, instead of 0.55–0.66), thinner shell, less sunken muscle scars, narrower hinge-plate and smoother surface, with faint radial striae and strengthened growth-lines posteriorly only. However, individuals with a similar outline but the shell-thickness and sculpture of *N. nucleus* also occur, suggestive of intergrading. This may merely be a case of incomplete speciation, but much more data are needed. A second unresolved question is whether a juvenile of this depressed morph/taxon was the basis for *Nucula distincta* Turton (1932: 214, pl. 55, no 1489, type locality Port Alfred.). The holotype of this in OXUM is badly damaged, and similar-sized (1.7 mm) juveniles are not available for comparison. Although *distincta* was synonymised with *N. nucleus* by Barnard (1964), it differs from comparable-sized juveniles of that in its low umbones, rounded posterior end, and thinner, translucent shell. It should be noted that the holotype of *N. distincta* resembles the two following dwarf species in size, but differs in its strongly rounded posterior end, less curved hinge-line and shallower valves.

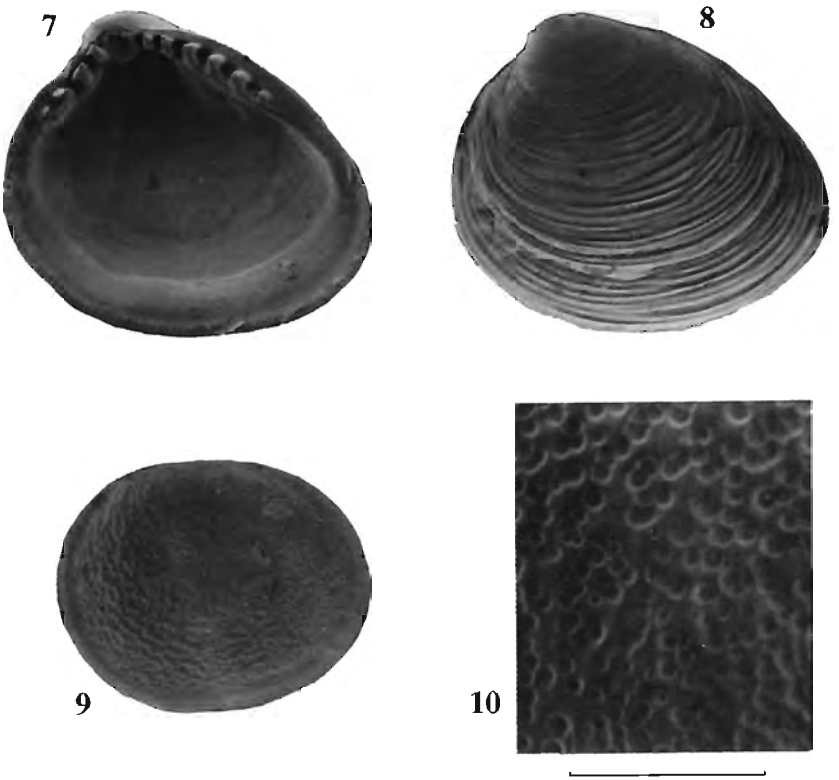
In view of observed variability, Thiele's records from the Agulhas Bank and slope of the deep-water European *Nucula tumidula* (Malm, 1860) may possibly have been based on material of *N. nucleus*. However, an unresolved sample from off Port St Johns in 300–540 m (NMSA C9698) does in fact closely resemble a series of *N. tumidula* from 300–500 m off Norway (NMSA K2932: K. W. Ockelmann), although there is less resemblance to the figures in Salas (1996: figs 4–6). Much more material is needed.

Nucula (Nucula) subluxa sp. n.

Figs 7–10

Nucula sp.; Turton 1932: 214, pl. 55, no 1487.

Diagnosis: Shell trigonal-ovate, umbo high, slightly flattened, posterior end truncate, posteroventral margin slightly angular; externally with close concentric ridges, radial crystalline elements present, but no surface radial sculpture; inner ventral margin finely crenulate; hinge-plate thick, its ventral edge sinuous anteriorly, tooth line



Figs 7–10. *Nucula (Nucula) subluxa* sp. n. 7–8. Holotype NMSA V6720/T1599, Knysna lagoon, 1.95 x 1.75 mm, interior of LV and exterior of RV, SEM. 9–10. Prodissoconch (270 x 222 µm), with sculpture magnified (scale line = 50 µm).

dislocated, the two series directed at a slight angle, 3–5 posterior teeth, 6–8 anteriorly; chondrophore moderately oblique, resilium oblong teardrop-shaped; white with a silky iridescence, under a glossy corneous periostracum. Maximum length about 2.4 mm.

Description: Shell somewhat translucent, relatively tumid (but d/l varying from 0.49–0.73); outline trigonal-ovate, h/l 0.82–0.92, with a high, recurved umbo, which is slightly flattened, and situated at about 0.25–0.40 from posterior end; posterior end truncate (occasionally obliquely convex), posteroventral margin slightly angulate, ventral margin evenly convex, anterodorsal margin moderately convex, anteroventral end strongly rounded to slightly angular.

Externally with a silky iridescence, sculptured by close concentric ridges, usually slightly narrower than their intervals, sometimes irregular; structural crystalline rods convey illusion of radial threads and form fine crenules on inner ventral margin. White, periostracum a glossy, corneous film, sometimes stained with orange oxides at anterior end. No escutcheon, lunule only faintly demarcated.

Hinge-plate thick and flat, its ventral edge convex posteriorly, sinuous anteriorly; tooth-line dislocated, no primary teeth in adult, posterior series nearly twice length of

anterior ones, secondary teeth thick, slightly chevron-shaped, in adults 3–5 teeth in posterior series, of which the middle ones are largest; anterior series 6–8, progressively weaker towards median, outer one also smaller than adjacent teeth; chondrophore moderately projecting, fairly oblique, resilium narrowly inverted-pyriform.

Prodissoconch (Figs 9–10) oblong-ovate, dorsal margin gently convex, surface irregularly and densely punctate, dimensions 270 x 222 µm, 279 x 214 µm.

Holotype: length 1.95 mm, height 1.75 mm, total depth 1.05 mm; largest paratype: length 2.43 mm, height 2.33 mm, total depth 1.50 mm.

Distribution: Eastern Cape region, from Knysna Lagoon to Kowie estuary.

Type material: Holotype NMSA V6729/T1599, Knysna Lagoon, washed up near beds of *Zostera capensis* Setchell, dd, J. P. Marais. Paratypes NMSA S9433/T1598, same data, 20 dd; B336/T1597, Summerstrand, Algoa Bay, in sand in base of algal turf, LST, 7 lve + 1RV, F. Graeve.

Notes: This tiny, inconspicuous species has previously escaped detection, but will probably prove to be abundant in eastern Cape estuaries. Like the following species it broods its eggs; one empty shell from Knysna contained about 24 prodissoconchs.

Turton (1932: 214, pl. 55, no 1488) recorded (but did not describe) a second small (1.8 mm) *Nucula* sp. from Port Alfred, of which two further worn valves from the same locality have been examined (NMSA D4685: J. Hutt). These valves differ in shape from *N. subluxa* and *N. planiculmen*, but it is possible that they will prove to be juveniles.

Etymology: *sub* (slightly) + *luxus* (dislocated), Latin, referring to the tooth line.

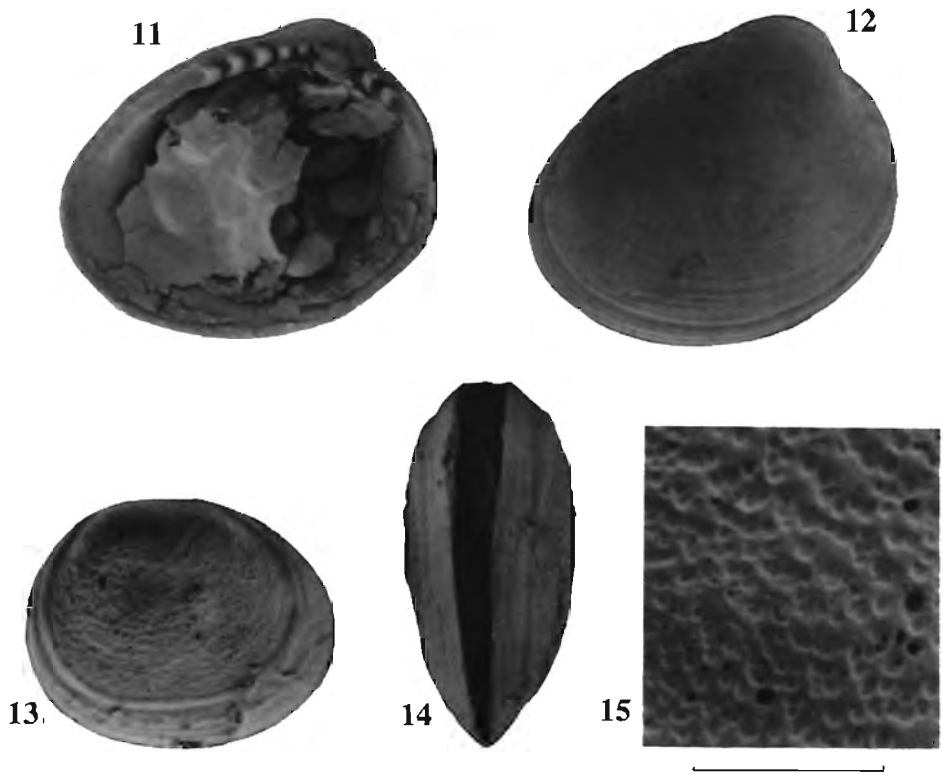
Nucula (Nucula) planiculmen sp. n.

Figs 11–15

Diagnosis: Shell obliquely oblong-ovate, umbo moderately high, beaks flattened, posterior end broadly rounded, posteroventral margin not angular; externally smooth, except for growth lines which may develop into concentric ridges in adults, radial crystalline elements present, but no external radial sculpture; inner ventral margin finely crenulate; hinge-plate thick, its ventral edge evenly concave anteriorly, tooth line forming an almost unbroken arc, 3–4 posterior teeth, 6–8 anteriorly; chondrophore moderately oblique, teardrop-shaped; white with glossy corneous periostracum. Maximum length 2.5 mm.

Description: Shell thin and slightly translucent to fairly thick, relatively tumid (d/l 0.50–0.61); outline obliquely oblong-ovate, h/l 0.82–0.96, with a moderately high, recurved umbo, which is distinctly flattened, and situated at about 0.27–0.43 from posterior end; posterior end broadly rounded (not distinctly truncate), posteroventral margin more sharply rounded, ventral margin evenly convex, anterodorsal margin moderately convex, anteroventral end strongly to fairly sharply rounded; neither lunule nor escutcheon demarcated.

Externally somewhat glossy, juveniles sculptured by growth lines only, in adults (i.e. towards ventral margin) sometimes strengthening into close, irregular concentric ridges; structural crystalline rods convey illusion of faint radial threads and finely



Figs 11–15. *Nucula* (*Nucula*) *planiculmen* sp. n. 11–12. Holotype, NMSA V6879/T1579, Onrus River, intertidal, 2.40 x 2.05 mm. 11. RV interior (with incubated prodissoconchs *in situ*). 12. LV exterior, SEM. 13–15. Prodissoconch. 13. RV exterior, dimensions 373 x 304 µm. 14. Ventral view, length 360 µm. 15. Sculpture of fig. 13 magnified (scale line = 50 µm); SEM.

crenulate inner ventral margin. White, periostracum a corneous film, sometimes stained or encrusted with orange oxides; umbonal region often eroded in adult. No escutcheon, lunule faint or absent.

Hinge-plate thick and flat, its ventral edge convex posteriorly, evenly concave anteriorly; tooth-line forming an almost continuous arc (interrupted only by the chondrophore), no primary teeth visible in adult, posterior series nearly twice length of anterior ones, secondary teeth thick, slightly chevron-shaped, in adults 3–4 teeth in posterior series, of which the middle ones are largest; anterior series 6–7, progressively weaker towards median, outer one also smaller than adjacent teeth; chondrophore moderately oblique, weakly to distinctly projecting, resilium fairly oblique, narrowly inverted-pyriform.

Prodissoconch (Figs 13–15) similar to that of *N. subluxa* but larger (exceeding 360 µm in length, examples 373 x 304 µm, 380 x 280 µm).

Holotype: Length 2.40 mm, height 2.05 mm, total depth 1.40 mm; largest paratype 2.50 mm, height 2.35 mm, total depth 1.48 mm.

Distribution: Southwestern Cape, from Paternoster/Cape Columbine to the Hermanus area, in coarse, more or less muddy sand in low tide rock pools and down to 4 m.

Type material: Holotype NMSA V6879/T1579, Onrus River mouth (34°25'S; 119°11'E), c. 5 km W. of Hermanus, in sand in sheltered rock pool, J. P. Marais. Paratypes: **Atlantic Cape**: NMSA V6727/T1580, Jacobs Bay, Cape Columbine area, in coarse muddy sand among rocks in large sheltered pool, 30 lve, J. P. Marais; NMSA V5720/T1595: Britannia Bay, Cape Columbine area, in coarse, slightly muddy sand under rocks in pool, 8 lve + 1LV, J. P. Marais. **Overberg**: NMSA S2613/T1596, same data as holotype, 1 lve, J. P. Marais; NMSA E6695/T1594, off Hawston, near Hermanus, in kelp forest in 2–4 m, 1 lve, D. G. Herbert.

Other material from Cape Columbine area: Jacobs Bay, in coarse muddy sand among rocks in large sheltered pool, NMSA V5729, numerous, J. P. Marais; Paternoster, under intertidal rocks and stones, NMSA E6264, 2 lve, D. G. Herbert.

Notes: *Nucula planiculmen* appears to replace *N. subluxa* in cold temperate waters–the Hermanus area is characterised by seasonal upwelling of cold water, supporting a biota with some degree of Atlantic coast affinity. Unlike *N. subluxa*, *N. planiculmen* does not seem to be associated with algal turf or grassflats. Under ideal conditions it may form extremely dense populations, the Jacobs Bay sample containing several hundred individuals, and it has presumably been overlooked solely on account of its small size. *N. planiculmen* is superficially very similar to *N. subluxa* in characters, but is more ovate in outline, with a flatter umbo, develops concentric ridges only as an adult, and has a less dislocated hinge-line (the two series of teeth being aligned on either side of the chondrophore in an even curve).

Like *N. subluxa, N. planiculmen* is incubatory: the mantle cavity of a dry specimen of length 2.3 mm from Onrus contained approximately 30 juveniles; no trace of a pericalymna remains on any. This appears to be the first report of internal brooding in the Nuculidae, although Knudsen (1979) concluded that direct development occurred in several species of *Nucula*; Drew (1901) described brooding within an external mucus sac in *N. delphinodonta* Mighels & Adams, 1842.

N. planiculmen and, to a lesser extent *N. subluxa*, have a flattened, well-demarcated prodissoconch, but this is not conspicuously hat-shaped as in *Condylonucula* Moore, 1977.

Etymology: *planus* (flat) + *culmen* (summit), Latin.

Subgenus *Lamellinucula* Schenck, 1944

Lamellinucula Schenck, 1944: 97.

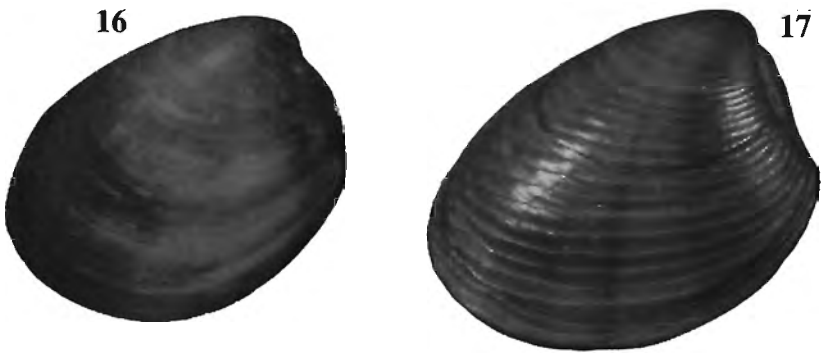
Type species (o.d.) *N. tamatavica* Odhner, 1943.

Diagnosis: Anterodorsal surface (escutcheon area) with transverse ridges or corrugations, which are sometimes also present posteriorly.

Notes: Subgenera of *Nucula* (and sometimes genera) have been defined largely by sculptural details, occasionally supported by degree of projection of chondrophore, valve outline and other minor characters. To a greater or lesser extent each of these could be regarded as stages in transformation sequences, and sometimes even vary intraspecifically. Previously, *Lamellinucula* was defined by the presence of strong commarginal sculpture, a rather subjective character, as intermediary states occur in a number of species. I here use the name for a group of species showing a range of

sculptural states, but all characterised by possession of a set of transverse dorsal ridges (Fig. 22), which cross the ends of any commarginal sculpture that might be present; these presumably serve as ratchet-sculpture, reducing slippage during burrowing. They may even indicate a relationship with *Acila* H. & A. Adams, 1858, as the divaricate ridges characterising that genus terminate dorsally in a similar transverse fashion.

As here redefined, the group is a cosmopolitan one, and apart from those covered here, includes species such as *Nucula sulcata* (Bronn, 1831) of Europe, *N. exigua* Sowerby, 1833, of west central America, and several Japanese species such as *N. dorsocrenata* (Habe, 1977) and *N. gemmulata* Habe, 1953.



Figs 16–17. *Nucula* (*Lamellinucula*) *sultana* (Thiele, 1931), and *N.* (*L.*) *irregularis* Sowerby, 1904. 16. *N. sultana*: Conducia Bay, Mozambique, NMSA H5457, 1.5 x 12.6 mm, LV exterior. 17. *N. irregularis*: off Umlaas Canal, Durban, 35–40 m, 8.3 x 6.5 mm, LV exterior.

Nucula (*Lamellinucula*) *sultana* Thiele, 1931

Fig. 16

Nucula sultana Thiele in Thiele & Jaeckel, 1931:197 (39), pl. 7 (2), figs 41, 41a; Barnard 1964: 364, fig. 1b; Boshoff 1965: 102. Type locality: 5°55.8'S, 39°01.2'E (Zanzibar Channel), 50 m.
Nucula convexa (*non* Sowerby, 1833); Spry 1964: 7, pl. 1, fig. 2.

Diagnosis: Shell obliquely trigonal, l/h 0.77–0.97, d/l 0.54–0.69, posteriorly truncate, umbo strongly recurved, valves thick, with sunken adductor muscle scars; chondrophore strongly oblique, 9–11 posterior teeth, 19–26 anterior ones (in adults of 15–17 mm length); smooth except for coarse growth-lines and faint radial striae toward either end; antero- and postero-dorsal ends with thin transverse ridges that curve umbonally on either side of valve face; periostracum dull brown; attains 17.4 mm in length.

Range: East Africa to southern Mozambique; also subsurface deposits in Durban Bay.

Regional locality data (all NMSA): **Southern Mozambique**: Inhaca Island, Bay of Maputo (9161: R. K.; G8835: P. Boshoff). **Central Mozambique**: Beira (F8661: R. K.). **Northern Mozambique**: Conducia Bay (H5456–7: K. Grosch).

Extinct: **Natal**: Durban Bay (9902: R. K.).

Notes: *Nucula sultana* is a tropical East African–Mozambican species, which I have collected on Inhaca Island living in the muddy silt between the roots of the marine grass *Thalassodendron*, in about 1 m at LST. Although reported from Durban harbour sediments by Barnard (1964), such material is associated with various other

bivalves that are not part of the Recent Durban Bay fauna, and probably dates from the mid-Holocene (ca 4800–4500 bp) hypsithermal event or possibly the last interglacial. Spry (1964) illustrated a specimen from the littoral of the Dar es Salaam area.

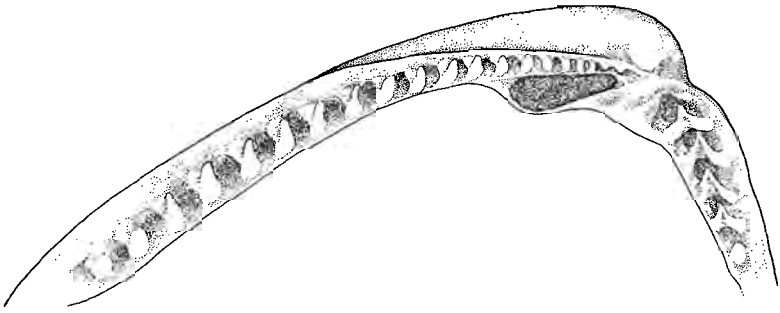


Fig. 18. *Nucula* (*Lamellinucula*) *irregularis* Sowerby, 1904, diagram of RV hinge.

Nucula (*Lamellinucula*) *irregularis* Sowerby, 1904

Figs 17–18

Nucula irregularis Sowerby, 1904: 7, pl. 6, fig. 12; Barnard 1964: 363. Type locality: 'Struis Point, N.W., 15 miles, depth 48 fathoms' [erroneous, here emended to: off Tugela River, 37 fathoms (= 68 m)].

Diagnosis: Shell obliquely ovate-trigonal, h/l 0.88–1.04, d/l 0.49–0.58, posterodorsal margin markedly truncate, posteroventral end angular; lunule concave, well-defined; sculptured by oblique ridges, divaricating posteriorly, dorsally crenulated by transverse riblets; lunule and escutcheon crossed by transverse ridges; chondrophore strongly oblique, moderately projecting, 6–8 posterior hinge teeth, 17–23 anteriorly (in 6–8 mm shells); glossy greenish-brown; attains 9.4 mm in length.

Description: Shell obliquely ovate-trigonal, h/l 0.88–1.04, posterior end markedly truncate, posterodorsal margin concave, forming a distinct posteroventral angle; d/l 0.49–0.58; lunule concave, well-defined, as is escutcheon. Surface crossed by low, oblique ridges, slightly declivous in cross-section, their dorsal edges sharply defined and feebly pliculated by traces of radial striae; posteriorly, these ridges become closer and divaricate to some extent, terminating at lunular margin; on anterodorsal margin these ridges merge with a series of slightly rugose transverse plicae, a second such series crossing lunule. Radial elements present in shell structure, forming crenules on inner ventral margin. Hinge-plate moderately wide, chondrophore strongly oblique, moderately projecting, resilium curved; tooth-line dislocated, 17–23 teeth anteriorly, 6–8 posteriorly (in adult of 6–8 mm length). Periostracum glossy, moderate olive-brown, nacre sometimes with orange tint. Attains 9.4 x 8.1 mm.

Range: Continental shelf of southern Zululand and Natal, in fine sand (occasionally coarse or slightly muddy sand), in depths of about 30–100 m.

Additional locality data (NMSA: NMDP unless otherwise stated, selected records only): **S. Zululand**: off Cape St Lucia, 76–80 m, coarse sand with mud (E5027, lve); off Richards Bay, 50 m (A1694, A6050: CSIR Water Research); off Port Durnford, 50 m, coarse/medium sand (D8081, E4706, lve); same loc., 75 m, coarse sand

(D8156, lve); SE of Port Durnford, 52 m, coarse sand (E4538, dd); off Tugela Bluff, 50 m, fine sand (E9093, E9036, lve). **N. Natal**: off Sheffield Beach, 60 m, muddy sand (E9562, lve); same loc., 50 m, fine sand (E9619, lve); same loc., 100–105 m, mud (E5052, dead); SE of Sheffield Beach, 50–55m, sandy mud (E5153, dd); off Ballito, 60 m, sandy mud (E5177, dd); 3–5 mi. off Umhlanga Rocks, 15 fath. (A312: R. K. **S. Natal**: off Umlaas Canal, 35–40 m, fine sand (D850); same loc., 50 m, fine sand (D1025); same loc., 40 m, fine sand, lve (D850); same loc., 75 m, muddy sand, lve (D712); same loc., 100 m, muddy sand, lve (D1070); SE of Umzimbazi River, 65 m, fine sand, lve (D3744).

Type material: Two syntypes SAMC 14834, one probable syntype NMWC.

Notes: The obliquely 'concentric' (almost scissulate) sculpture of *N. irregularis* is unusual within the family.

Barnard rightly queried the given type locality of 'Struis Point' (near Cape Agulhas), but his suggestion that the types came from the East London area is equally unacceptable. NMDP samples have yielded no sign of *N. irregularis* from even as far south as Transkei, the southernmost station at which it occurs being just south of Durban. Consequently I have designated a PF station on the Natal/Zululand boundary as the corrected type locality.

Figs 19–22. *Nucula* (*Lamellinucula*) *sculpturata* Sowerby, 1904, NMSA 3917, off Durban, 100 m. 19–20. 8.3 x 2.5 mm, exterior of LV and interior of RV. 21. SEM of concentric sculpture. 22. SEM of 2.5 mm juvenile, showing dorsal ratchet-sculpture.

Nucula (*Lamellinucula*) *sculpturata* Sowerby, 1904

Figs 19–22

?*Nucula pulchra* Hinds, 1843: 97; *idem* 1844: 62, pl. 18, fig. 3. Type locality: 'L'Agulhas Bank, Cape of Good Hope. From seventy fathoms [= 128 m].'

Nucula pulchra [*partim*]; Barnard 1964: 362.

Nucula sculpturata Sowerby, 1904: 7, pl. 6, fig. 11. Type locality: 33°03'S, 27°57'E, 34 fath. [62 m] [doubtful, see below].

Diagnosis: Shell ovate-trigonal, h/l 0.79–0.90, d/l 0.50–0.59, posteriorly slightly angularly rounded, lunule slightly concave, not well-defined; sculptured by low concentric ridges, crenulated dorsally by feeble axial riblets, escutcheon and lunule crossed by wavy transverse ridges; chondrophore very strongly oblique, scarcely projecting, 7–8 posterior teeth, 17–20 anterior ones (in 8–10 mm adults); periostracum glossy, pale yellowish (but usually stained), interior silver. Attains 9.9 mm in length.

Description: Shell ovate-trigonal, h/l 0.79–0.90, posterior end slightly angularly rounded, anterodorsal margin evenly convex, valves fairly thick, rather tumid (d/l 0.50–0.59); lunule slightly concave, neither lunule nor escutcheon well-defined. Sculptured by low concentric ridges, declivous in t/s, dorsal edge of each ridge raised and largely smooth, although appearing as if crenulated by the structural radial rods. Escutcheon and lunule crossed by wavy, rugose transverse ridges. Radial elements in crystalline structure conspicuous, forming crenules on inner ventral margin. Hinge-plate relatively wide; chondrophore very strongly oblique, projecting only slightly from hinge-plate; tooth line dislocated, 7–8 teeth posteriorly, 17–20 anteriorly (in adults of 8–10 mm length). Periostracum glossy, light greyish-yellow, in life usually coated with a film of olive-grey mud; interior silvery. Attains 9.9 x 8.8 mm.

Range: Southern Zululand to Western Transkei, in 26–200 m, rarely as deep as 300 m, mainly in fine muddy sand/sandy mud.

Locality records (NMSA: NMDP, unless otherwise stated, selected records only): **S. Zululand**: off Cape Vidal, 80–100 fath., dd (Barnard 1964); SE of Neill Peak (Cunge), 110–115 m, mud, stones, dd juvs (NMSA E3793); Cape St Lucia, 160–180 m, coarse sand with mud, dd (E3316); off St Lucia Lighthouse, 100 m, mud and pebbles, dd (A5736: CSIR Water Res.); SE of Port Durnford, 120 m, mud, lve (E864). **N. Natal**: off Mvoti River, 200 m, mud, lve (E9120); off Sheffield Beach, 100 m, shell grit, lve (E9476); same loc., 110 m, muddy sand, lve (E9298); off Tongaat Bluff, 150 m, sandy mud, lve (S110); same loc., 240 m, fine soft mud, lve (E9905); same loc., 120 m, sandy mud, lve (E9970); off Umhlanga Rocks, 98 m, fine sand, lve (S262); same loc., 90 m, muddy sand, shell debris, lve (S330); same loc., 105 m, fine muddy sand, lve (S218); off Mgeni River, 92 m, mud, lve (S684), same loc., 96 m, sand, solitary corals, lve (S654). **S. Natal**: off Durban, 30–165 m, numerous lve samples, mostly from grey sandy mud or fine muddy sand (D4197, D3678, D4129, D4024, D4970, D4252, D426, D4165, D3863, D3949, D3917, B5869, B5894); off Umlaas Canal, 50 m, fine sand, dd (D986); off Amanzimtoti, 245–250 m, medium sand, lve (D1666); same loc., 300–305 m, medium sand, lve (D1300). **E. Transkei**: between Mtamvuna and Mzamba rivers, 100 m, sponges,

rubble, lve (C5442); off Waterfall Bluff, 95 m, black mud, dd (C744); off Mbotyi, 45–50 m, mixed mud, sand, gorgonians, some rocks, dd (C380); same loc., 50 m, mixed sand, mud, numerous worm tubes, lve (C1797, C1795, C285); same loc., 60–70 m, mud, dd (C366); off Whale Rock, 58–60 m, mixed sand and mud, dd (C3118). **W. Transkei**: off Mncwasa Point, 74 m, sand and rubble, dd (C2270); off Bulungula River, 60 m, mixed fine sand and mud, dd (V6728).

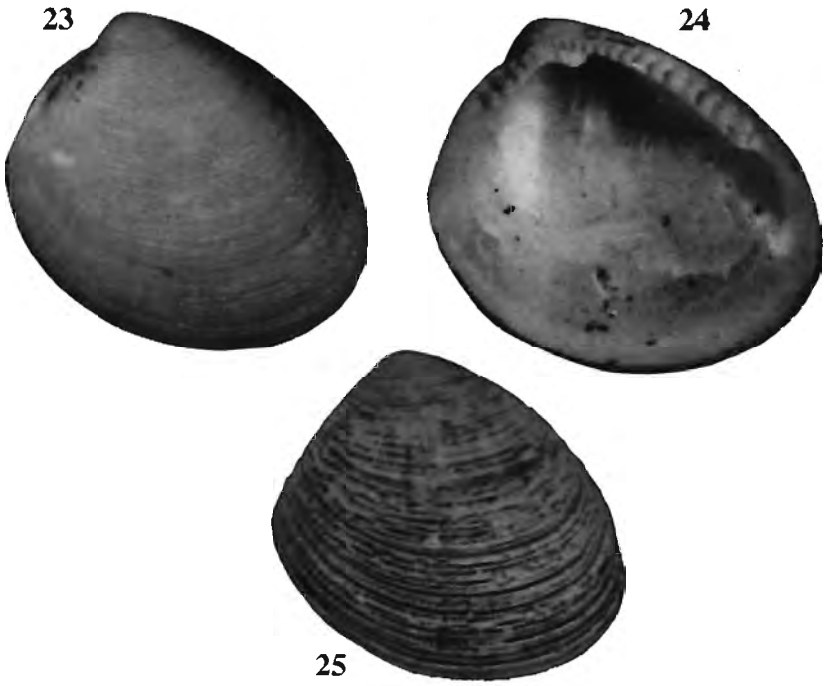
Type material: *N. sculpturata*: 5 syntypes SAMC 14830, f. Barnard 1964 (10 syntype valves f. Giles & Gosliner 1983); one syntype NMWC.

Notes: *Nucula sculpturata* is characteristic of KwaZulu-Natal waters and is very abundant in muddy substrates (one dredge sample contained over 170 adults); consequently only representative data is given above. The southernmost station from which it was collected is situated well within Transkei limits (29°02'E). I therefore believe that both the given type locality (near East London) and Barnard's record from off St Francis Bay require confirmation, and were probably based on material from mislabelled PF stations.

It is indeed possible that *Nucula pulchra* Hinds, 1843, is an earlier name for this species, as claimed by Schenck (1944: 98) and Barnard (1964). However, the holotype of *pulchra* is no longer extant–there is no record of it ever being received by the BMNH with other Belcher material (S. Morris, *pers. comm.*) and it must have been lost soon after description, as it was not available when Hanley monographed *Nucula* in 1859, and Sowerby in Reeve (1871: pl. 5, fig. 38) stated 'Mus.–??'. The original description and figure are not diagnostic enough for its recognition, although the sculpture would fit *N. sculpturata*. On the other hand, Hind's reference to 27–29 'posterior' [presumably = anterior] teeth in his *pulchra* would be greatly excessive for *sculpturata*, in which there occurs a maximum of 20. The type locality is equally valueless, as Belcher's localities are notoriously untrustworthy. No co-ordinates were given, but the Cape species dredged by *HMS Sulphur* are typical central to western Agulhas Bank species, and the dredge hauls in question would probably have been made soon after the ship's departure from Simon's Bay. In contrast, *N. sculpturata* is distinctive of the warmer Transkei-Natal region. On available evidence, therefore, I prefer to reject *Nucula pulchra* as a *nomen dubium*.

As another synonym of *N. pulchra*, Barnard (1964) listed *Nucula rugosa* Odhner, 1919 (*non* Conti di Ferrara, 1864) [= *Nucula tamatavica* Odhner, 1943], from the littoral of Madagascar. However, specimens of *N. tamatavica* from Ifaty Lagoon, Madagascar (NMSA K3144: J. Drivas) have markedly coarser sculpture than *sculpturata* of similar size, and the median area of the lunular region is more projecting; the species also has a much thicker shell and attains more than twice the size of *sculpturata*.

N. sculpturata has a less oblique outline than *N. irregularis* and a chondrophore that is also more strongly inclined. Although the outer surface appears to bear strong radial riblets, this is an illusion caused by the crystalline structure of the shell, although these may produce faint crenulations on the ventral edge of the ridges. *N. sculpturata* does not appear ever to wash ashore, and littoral records (Krauss 1852; Bartsch 1915; Turton 1932) were evidently based on worn specimens of *N. nucleus* with strong growth-lines.



Figs 23–25. *Nucula* (*Lamellinucula*) *rhytidopleura* sp. n. 23–24. Holotype, NMSA D4529/T1623, off Durnford Point, Zululand, RV exterior, LV interior, 6.8 x 5.8 mm. 25. Paratype NMSA E5953/T1609, off Sheffield Beach, N. Natal, 100–105 m, coated RV.

Nucula (Lamellinucula) rhytidopleura sp. n.

Figs 23–25

Diagnosis: Shell trigonal-ovate, h/l 0.83–0.95, d/l 0.52–0.64, posterior end truncate, sometimes strongly so, lunule rather weakly delimited, escutcheon not defined; sculpture of low concentric ridges, narrow and non-declivous, usually interrupted and rugose at each end, intervals crossed by weak radial threads, anterodorsal margin with weak transverse ridges; hinge-plate not declivous in cross-section; chondrophore strongly oblique, moderately projecting; tooth-line strongly dislocated, 5–6 posterior teeth, 15–17 anteriorly (at 6–7 mm in length); periostracum dull olive-brown to pale yellowish, usually stained orange. Attains 7.7 mm.

Description: Shell trigonal-ovate, h/l 0.83–0.98, d/l 0.52–0.64, umbo recurved, posterior end very short and truncate, sometimes rather flattened in adult, posteroventrally forming a rounded angle, lunule rather weakly defined by a groove, no escutcheon, shell rather thick. Sculptured by low concentric ridges, which are narrower than their intervals, non-declivous, with an occasional one stronger than the others, rides at each end more or less interrupted to give a rugose appearance; intervals crossed by thin radial riblets, rendering them somewhat pitted; anterodorsal area with weak transverse corrugations, posteriorly indistinct. Radial elements present internally, forming crenules on inner ventral margin. Hinge-plate moderately wide, chondrophore strongly oblique, moderately projecting from hinge-plate,

resilium rather narrow; tooth-line dislocated, 5–6 posterior teeth, 15–17 anterior ones (in 6–7 mm adults). Periostracum dark greyish-yellow to greyish-yellowish-brown. Dimensions: length 6.8 mm, height 5.8 mm (holotype); largest paratype valve 7.7 x 7.3 mm.

Range: Continental shelf of northern Natal and southern Zululand, 68–150 m, mainly in mud and rubble.

Type material (all NMSA: NMDP, unless otherwise stated): Holotype, D4529/T1623, off Durnford Point, S. Zululand (29°05.2'S, 32°08.6'E), 112 m, lve, dredged A. Connell. Paratypes: **S. Zululand**: E5118/T1608, SE of Mission Rocks, 150 m, broken shell and coral rubble, 1 lve; E3808/T1622, SE of Neill Peak (Cunge), 110–115 m, mud, stones, 1 + 8 LV and 3 RV; D7808/T1601, off Durnford Point, 142 m, mud, 1 lve; E1619/T1607, same loc., 114 m, sandstone rubble, 2 + 2 juvs, lve; D8120/T1600, same loc., 98–110 m, coarse brown sand, 1 + 1 RV; E4591/T1605, SE of Durnford Point, 152 m, mud, stones, 1 dd + 1 RV + 1 LV; E8585/T1606, same loc., 95 m, sponge rubble, 1 lve + 2 RV; E8775/T1604, off Matigulu River mouth, 145 m, mud, shell rubble, 1 lve, 1 LV. **N. Natal**: E5053/T1609, off Sheffield Beach, 100– 105 m, glutinous grey mud, 1 dd +2 RV + 3 LV; E9864/T1608: off Tongaat Bluff, 85 m. coarse sand, 1 RV, 1 LV; D4886/T1603: off Durban, 110–120 m, coarse muddy sand, 4 lve.

Notes: The dorsal corrugations are much weaker than in other South African *Lamellinucula* species, and in live examples the overall sculpture tends to be obscured by the periostracum and adherent mud. This species is superficially similar in form to *Nucula nucleus*, which it appears to replace in the subtropical waters of KwaZulu-Natal, but differs in its relatively strong concentric ridges (which, however, are weaker and more widely spaced than in *N. sculpturata*), more regular radial riblets, more oblique ligament and somewhat fewer posterior hinge teeth (at 6–7 mm length, 8–9 posterior teeth occur in *N. nucleus*, instead of 5–6). *Nucula sumatrana* Thiele, 1931, from S. E. Asia appears to differ in profile of the hinge-plate and in lacking distinctly elevated radial ribs.

Etymology: *rhytido* (wrinkled) + *pleura* (*pleuron* = side or rib), Greek compound noun.

Brevinucula Thiele, 1934

Type species: (monotypy) *Nucula guineensis* Thiele, 1931 [= *Nucula verrilli* Dall, 1886, fide Knudsen 1970].

Diagnosis: Shell deeply triangular and almost equilateral, with a trigonal, vertical chondrophore; inner ventral margin smooth or crenulate.

Notes: *Brevinucula* has been treated occasionally as a subgenus of *Ennucula* or *Nucula*, but most authors accord it full generic status. Although the genus has been diagnosed as having smooth margins, a puzzling sample from off Stony Point, Transkei (32°37.2'S; 28°47.7'E), in 510 m, combines the triangular form of *Brevinucula* with the structural crystalline rods and marginal crenules of *Nucula s. s.* Unfortunately all three available valves are damaged. It appears likely that the triangular shape will prove to be a homoplasy.

Figs 26–27. *Brevinucula aequalitas* (Barnard, 1964), holotype of *Nucula aequalitas*, SAMC A9472, 3.6 x 3.5 mm, exterior and interior of LV.

Brevinucula aequalitas (Barnard, 1964)

Figs 26–27

Nucula aequalitas Barnard, 1964: 365, Fig. 1c. Type locality: off East London, 400–450 fathoms [= 730–820 m].
Brevinucula aequalitas; Knudsen 1970: 18.
Nucula aequalis [sic]; Rhind & Allen 1992: 85.

Diagnosis: See under notes.

Description: Shell moderately thick but slightly translucent, relatively deep (d/l 0.56–0.67), almost equilateral (h/l 0.85–0.97), posterodorsal margin gently and evenly convex, with a large lunule defined by a shallow groove, posteroventral end forming a slight, rounded angle; escutcheon indistinct; anterodorsal margin almost straight, terminating in a broadly rounded anteroventral angle; ventral margin very gently curved, smooth inside; adductor muscles slightly sunken. Hinge-plate thick, chondrophore rounded-trigonal, symmetrical, vertical, projecting only slightly into interior; teeth large, 7–8 posteriorly, 8–9 anteriorly. Exterior with growth-lines, becoming slightly coarser towards ventral margin, periostracum glossy to iridescent, light orange-yellow. Dimensions: length 3.6 mm, height 3.5 mm (holotype); 3.4 x 2.0 mm (NMSA E4775).

Range: Continental slope from eastern Cape region to southern Zululand, mud in about 500–800 m.

Type material: Holotype SAMC A9472.

Additional material: **S. Zululand**: off Durnford Point, 500 m, soft mud, 1 lve (NMSA E4775: NMDP).

Notes: Although Knudsen (1970) did not, as claimed by Rhind & Allen (1992), suggest that '*Nucula aequalis*' from 'off Cape Point' might be a synonym of the predominantly abyssal and North Atlantic *Brevinucula verrilli* (Dall, 1886), no evidence to prove their distinctness can be presented here. According to the tables given by Knudsen for *B. verrilli*, the distinguishing characters proposed by Barnard fall within the range of variation of the latter species. Rhind & Allen (1992: 83, figs

29–32), who describe *B. verrilli* in some detail, quote records from the western Atlantic at depths as shallow as 538 m.

Ennucula Iredale, 1931

Type species (sd Singleton 1932): *Nucula obliqua* Lamarck, 1819.

Diagnosis: Shell as in *Nucula*, but inner ventral margin smooth, reflecting the absent of radial crystalline elements.

Notes: Although several recent workers have with valid reason disputed the taxonomic integrity of a genus based on the absence of crenulate margins, I prefer to maintain it as a provisional 'pigeon-hole' for species such as the two following. I follow Maxwell (1988) and Di Geronimo & La Perna (1997) in utilising the relatively non-controversial *Ennucula* Iredale, 1931, in preference to the earlier names *Nuculoma* Cossmann, 1907, or *Leionucula* Quenstedt, 1930, which were based on fossil types.

Key to southern African species of *Ennucula*

1 Shell translucent (hinge teeth visible from exterior when fresh), periostracum pale greenish-brown or yellowish; valves compressed (d/l 0.40–0.43), posterior end slightly angular; hinge-plate thin ..... **fragilis** (Thiele, 1931)
– Shell not translucent, periostracum greyish-green; somewhat tumid (d/l 0.49–0.51), posterior end somewhat truncate; hinge-plate very thick ..... **oliva** sp. n.

Ennucula fragilis (Thiele, 1931)

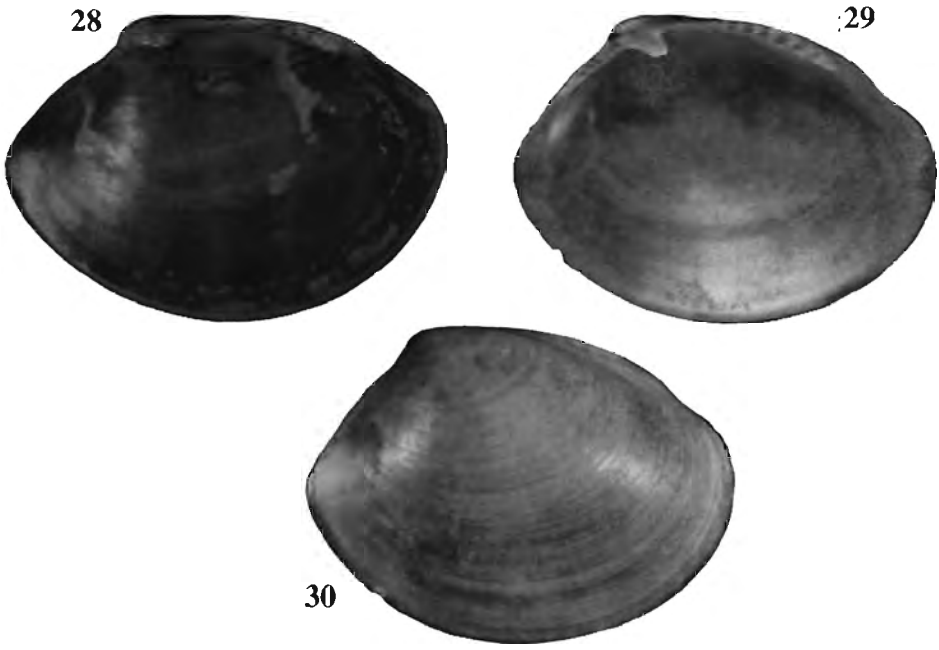
Figs 28–30

Nucula fragilis Thiele in Thiele & Jaeckel, 1931: 195 (37), pl. 2 (7), fig. 36. Type locality: off Dar es Salaam, 404 m.

Nucula fragilis Boshoff, 1968: 95, pl. 8a, text fig. **Syn.n.** Type locality: 29°34'S, 31°39'E [off Tongaat area, northern Natal], 115–118 m, sandy mud.

Diagnosis: Shell thin, translucent, interior rather thinly nacreous, compressed, d/l 0.40–0.43, h/l 0.75–0.80, posterior end somewhat angular; sculptured only by growth-lines; white with thin, pale olive-grey to yellowish periostracum; hinge-plate narrow, chondrophore projecting, 13–20 anterior teeth, 6–7 posteriorly (in adults of 10–13 mm); attains 13 mm.

Description: Shell thin and translucent, nacre thin, no radial elements visible in structure; rather compressed (d/l 0.40–0.43, h/l 0.75–0.80), umbo at about 0.26–0.32 length from posterior end; posterior end rather angularly rounded, dorsal margin convex; escutcheon lanceolate, slightly sunken, but medially raised; anterodorsal margin strongly convex, except near anterior end where there is a slight concavity, lunule feebly defined but strongly elevated medially; exterior glossy, with growth-lines only, periostracum thin, silky, corneous. Hinge-plate narrow, ventral margin concave anterior to chondrophore, on posterior side nearly straight; chondrophore strongly oblique, projecting well beyond hinge margin; tooth line slightly dislocated, teeth rather weak, 6–7 posteriorly, 13–20 anteriorly (in 10–13 mm shells). White with pale olive-grey to yellowish periostracum. Largest regional example 13.5 x 9.8 mm.



Figs 28–30. *Ennucula fragilis* (Thiele, 1931). 28. Lectotype of *Nucula fragilis*, ZMHB, 13.3 x 9.2 mm, LV interior. 29–30. Off Tongaat Bluff, N. Natal, 235 m, NMSA S47, 11.3 x 8.8 mm, LV interior and exterior.

Range: Tanzania to western Transkei, outer continental slope and upper slope in sandy mud or mud, 80–400 m.

Regional locality data (all NMSA, NMDP unless otherwise indicated, selected records only): **N. Zululand**: off Leven Point, 250 m, coarse sand, lve (S9330). **S. Zululand**: SE of Neill Peak (Cunge), 320–340 m, sandy mud, lve (E4007); off Cape St Lucia, 160–180 m, coarse sand with mud, lve (E3314); off Richards Bay, 110 m, muddy sand (D1541: A. Connell); off Durnford Point, 310–340 m, glutinous sandy mud, lve (E3226); SE of Durnford Point, 215 m, glutinous sandy mud, lve (E3142). **N. Natal**: off Glenton Reef, 200–210 m, sandy mud, live (S469); SE of Sheffield Beach, 100–105 m, glutinous grey mud, lve (E5055); same loc., 75–80 m, glutinous grey mud, lve (E4614); off Tongaat Bluff, 300 m, fine soft mud, live (E9622); off Durban, 270 m, fine sandy mud (B5957). **E. Transkei**: off Mgazi River, 140–145 m, glutinous black mud (C9292); same loc., 190 m, glutinous black mud (C8769); same loc., 250 m, muddy sand (C8919).

Type material: *N. fragilis* Thiele, 1931: 3 syntypes (1 LV, here des. lectotype, one damaged, one juvenile) in ZMHB. *N. fragilis* Boshoff, 1968: holotype SAMC A30212, present location of paratype unknown.

Notes: It is presumably coincidental that Boshoff chose for his species the very name already given to it by Thiele. Both authors were clearly struck by the relatively fragile shell, which is so transparent in live-taken shells that the hinge teeth are visible from without. Boshoff (textfig.) incorrectly illustrated the tooth-line as a

uninterrupted arc. The adult complement of 19–20 anterior teeth is only achieved at a length of about 12 mm. Regional material agrees well with Thiele's types.

Figs 31–32. *Ennucula oliva* sp. n., holotype, NMSA C2113/T1581, off Rame Head, Transkei, 380 m, LV exterior and interior.

Ennucula oliva sp. n.

Figs 31–32

Diagnosis: Shell oblong-ovate, valves rather deep, d/l 0.49–0,51, h/l 0.74–0.77, valves fairly thick, nacreous inside; posterior end somewhat truncate; hinge-plate fairly thick, in adult 7–8 teeth posteriorly, 13–15 anteriorly (in 8 mm adults); periostracum glossy greyish-olive colour, prodissoconch pale and well-defined; length 7.9 mm.

Description: Shell oblong-ovate and rather deep (h/l 0.74–0.77, d/l 0.49–0.51), umbo at about 0.20 length from posterior end, valves rather thick, interior nacreous; posterior end projecting slightly but somewhat truncate, anterior end strongly rounded, flattened above, anterior dorsal margin strongly convex: neither escutcheon nor lunule distinctly defined, not strongly raised medially. Hinge-plate relatively thick, chondrophore strongly oblique, moderately projecting, resilium elongately teardrop-shaped; tooth line dislocated, teeth relatively strong, somewhat chevron-shaped in section, teeth of posterior series becoming markedly stronger admedially, 7–8 teeth posteriorly, 13–15 anteriorly (at a length of about 8 mm). Posterior adductor muscle scar slightly smaller and more oval than anterior one; pallial line with strong medial embayment. Periostracum light greyish-olive to greyish-olive, sometimes darker towards ventral margin, prodissoconch pale.

Dimensions: length 7.9 mm, height 6.1 mm (holotype); length 8.4 mm, height 6.2 mm (largest paratype).

Prodissoconch ovate, slightly angular at each end, 0.85 x 0.65–0.70 mm.

Range: Continental slopes of Transkei and southern Zululand/northern Natal, 300–520 m.

Type material (all NMSA: NMDP): Holotype, C2113/T1581, off Rame Head, Transkei (31°57.3'S, 29°25.5'E), 380 m, coarse sand, old shell debris. Paratypes: **E. Transkei**: C9774/T1584, off Mtentu River, 450 m, smooth black rocks, sand, 1 lve; C8844/T1590, off Mgazi, 350 m, glutinous black mud, stones, 1 RV; C2014/T1582, off Rame Head, 410–430 m, stones, some sand, 2 lve; E7544/T1589, same data, 1 lve; C8879/T1591, off Whale Rock, 430–450 m, fine muddy sand, 1 lve. **W.**

Transkei: C9012/T1593, off Mbashe River, 450–500 m, coarse sand, some mud, 1 lve; C5008/T1583, off Mendu Point, 405–420 m, fine sand, 2 lve; C7030/T1592, off Sandy Point, 450 m, muddy sand, stones, 1 lve, 1 dd; C4064/T1586, off Qolora River, 440–446 m, fine sand, old *Dendrophyllia* corals, 1 lve. **N. Natal**: E9647/T1585, off Tongaat Bluff, 300 m, fine soft mud, 1 dd. **S. Zululand**: E8729/T1587, off Matigulu River, 520 m, mud with clay lumps, 1 LV; E4774/T1588, SE of Durnford Point, 500 m, soft mud, 3 lve.

Notes: This species is not rare in the relatively barren sediments of the Transkei continental slope, but few specimens were dredged further north. It varies little in shape, and is easily recognised by its very shiny, grey-green periostracum. Juveniles are paler than adults, and the prodissoconch is contrastingly paler than the dissoconch; the lunular and escutcheon areas are usually caked with mud. There appears to be some resemblance to *Ennucula siberutensis* (Thiele, 1931) from Indonesia, but that is more trigonal and the resilifer does not project as a chondrophore.

Etymology: *oliva* = fruit of olive tree, Latin.

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