

ANNALS OF THE SOUTH AFRICAN MUSEUM  
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 65 Band  
July 1974 Julie  
Part 7 Deel



THE STATUS OF THE PLIO-PLEISTOCENE *PANOPEA*  
IN SOUTHERN AFRICA  
(MOLLUSCA, BIVALVIA, HIATELLIDAE)

By  
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Cape Town

Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material  
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid  
van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7-8), 3(1-2, 5, t.-p.i.), 5(1-2, 5, 7-9),  
6(1, t.-p.i.), 7(1-3), 8, 9(1-2), 10(1),  
11(1-2, 5, 7, t.-p.i.), 24(2), 27, 31(1-3), 33

Price of this part/Prys van hierdie deel  
R3,30

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum  
1974

ISBN 0 949940 46 1

Printed in South Africa by  
The Rustica Press, Pty., Ltd.,  
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur  
Die Rustica-pers, Edms., Bpk.,  
Courtweg, Wynberg, Kaap

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By

BRIAN KENSLEY

*South African Museum, Cape Town*

(With 8 figures and 1 map)

[*Ms. accepted 7 August 1973*]

## CONTENTS

	PAGE
Introduction . . . . .	199
Systematic discussion . . . . .	200
Material and measurements . . . . .	203
Southern African localities . . . . .	206
Mediterranean and West African localities . . . . .	209
Description . . . . .	209
Discussion . . . . .	210
Brief ecological observations . . . . .	210
Summary . . . . .	212
Acknowledgements . . . . .	212
References . . . . .	213

## INTRODUCTION

The bivalve genus *Panopea* is represented by about 10 living species in temperate to subtropical seas. All are inhabitants of sand or mud, being buried to depths of 1–2 metres below the substrate surface, in water depths varying from the Low Water of Springs level, to deeper water. The live animal communicates with the overlying water by means of elongate siphons. The North American representative, *P. generosa* Gould, occurs in large numbers in the region of Puget Sound, where, under the name ‘geoduck’, the living animals are eagerly sought after as culinary delicacies (Phillips 1970). Elsewhere, other species are apparently not as common.

As a fossil form, the genus is known from Lower Cretaceous to Recent times, and is represented by numerous species. In South Africa, *P. gurgitis* (Brongniart) is known from the Lower Cretaceous (Neocomian) of Uitenhage and Zululand.

Regarding younger forms from South Africa, Stow (1871), reporting on a raised beach in the Port Elizabeth district, mentioned the presence of a fossil *Panopea*. Earlier, in 1855, Woodward proposed the name *P. natalensis* for a specimen erroneously recorded from Natal but in fact coming from Angola. Since then several more specimens have been recorded from various sites, under a variety of names. Woodward (1855) mentioned the similarity of *P. natalensis* to

the Mediterranean *P. aldrovandi*, while Barnard (1964: 559), using the name *P. aldrovandi* for Pleistocene forms, raised the following question: 'Are there any clear-cut characters apart from minor and inconstant differences in shape due to growth changes, which will serve to differentiate these so-called species?'

Since more Pleistocene specimens have become available, it was thought necessary to establish the systematic position of this species beyond any reasonable doubt. With this in view, the present investigation was carried out. Specimens, both fossil and recent, were obtained from as many sources as possible (Table 1).

It must be noted that the exact age of many of the South African 'beach' deposits, referred to either as early Pleistocene or late Tertiary, is still uncertainly determined, and that the term 'Plio-Pleistocene' is deliberately used in the present work in its broadest sense.

### SYSTEMATIC DISCUSSION

#### Phylum MOLLUSCA

#### Class BIVALVIA

#### Order MYOIDA

#### Family **Hiatellidae**

#### Genus *Panopea* Ménard de la Groye, 1807

Apart from the characteristics of the family, the genus *Panopea* is characterized by the possession of a large ligamental nymph, a wide pallial sinus, and valves gaping at both ends.

#### Subgenus *Panopea*

The subgenus *Panopea* is characterized by a continuous pallial line, and a single cardinal tooth in each valve.

#### *Panopea (Panopea) glycymeris* (Born)

#### SYNONYMY

*Mya glycymeris* was the name first used in a valid description of the present species and is given first in the synonymy.

*Panopea aldrovandi* Ménard, 1807, was the first usage of the valid generic name for the present species (*Mya* and *Glycymeris* both having been pre-occupied), and is given next in the synonymy. This is followed by the correct designation, i.e. *Panopea glycymeris*. As a proliferation of names has been used with reference to the present species, the rest of the synonymy has been given alphabetically, with entries under each name listed chronologically.

*Mya glycymeris* Born, 1778: 10; 1780: 20. Chemnitz, 1782: 33. Gmelin, 1790: 3222. Montagu, 1808: 19. Turton, 1819: 107. Wood, 1825: 13.

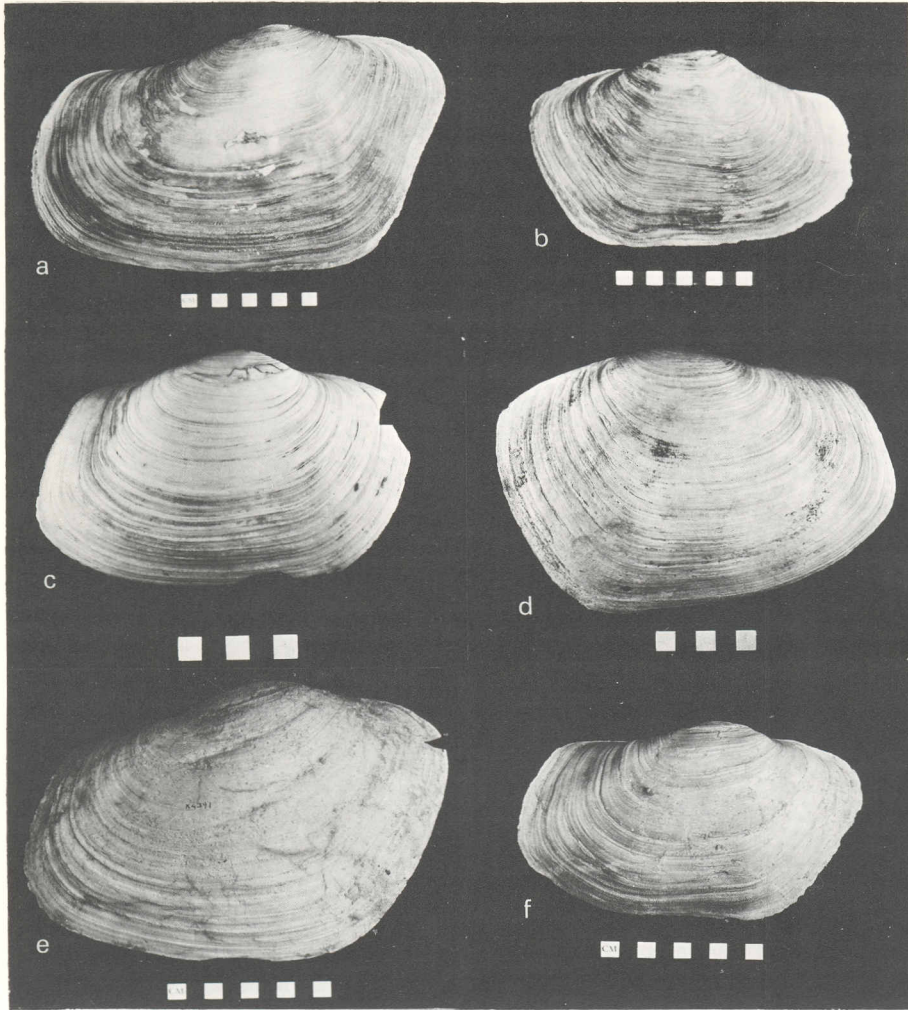


Fig. 1. *Panopea glycymeris*: External view.

a. Sicily; b. Portugal; c. Moçâmedes; d. Baia dos Tigres; e. Velddrif; f. Klein Brak River.

*Panopea aldrovandi*, Ménard, 1807: 136; 1808: 464. Nicklès, 1950: 228. Franca 1960: 37. Barnard, 1964: 557.

*Panopea glycymeris*: Lamy, 1925: 267. Thiele, 1935: 924. Imperatori, 1961: 141. Ghisotti & Steinmann, 1969: Sheet 78-Ac-01. Treatise, 1969: N700.

*Glycymeris aldrovandi*: Pallary, 1900: 410; 1920: 94.

*Glycymeris glycymeris*: Gray, 1847: 189. Tryon, 1869: 60. Malatesta & Nicosia, 1955: 177.

*Glycymeris rugosa*: Bosc, 1802: 5. Adams & Adams, 1856: 350.

*Glycymeris aldrovandi*: Fischer, 1880-1887: 1125.

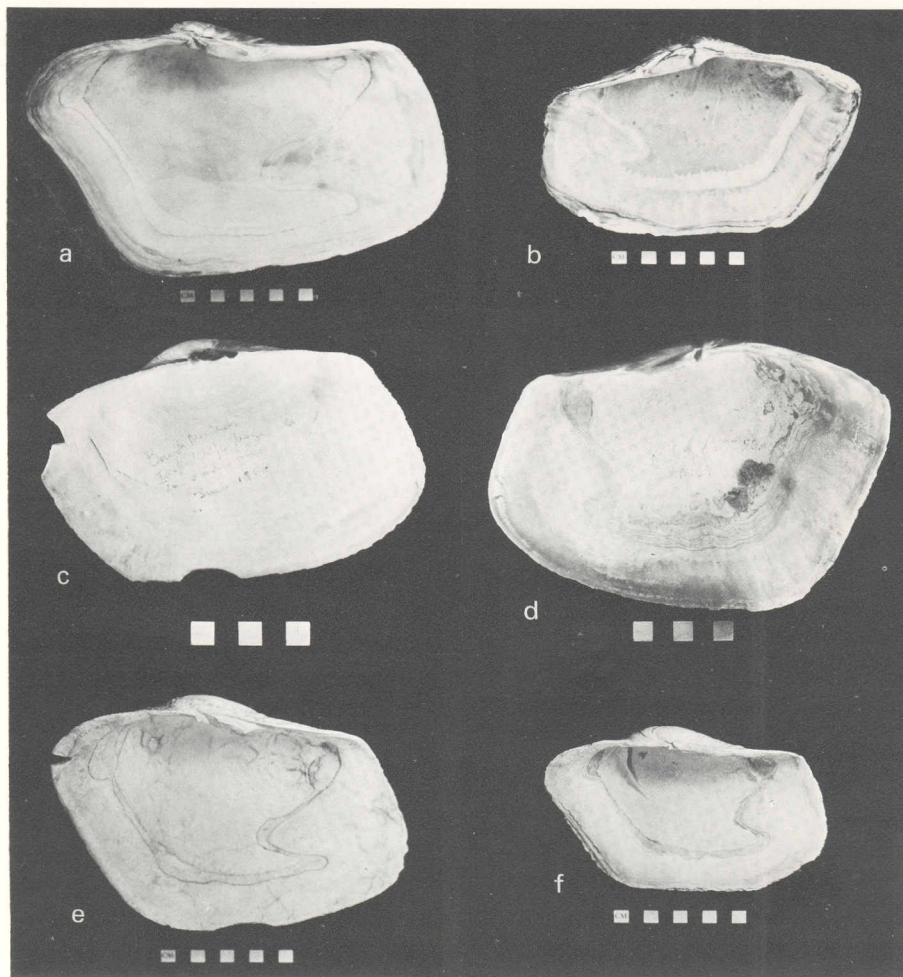


Fig. 2. *Panopea glycymeris*: Internal view.

a. Sicily; b. Portugal; c. Moçâmedes; d. Baia dos Tigres; e. Velddrif; f. Klein Brak River.

*Panopae aldrovandi*: Lamarck, 1818: 457.

*Panopaea aldrovandi*: Blainville, 1825-27: 571. Deshayes, 1832: 698; 1835: 67. Philippi, 1836-44: 6, 7. Valenciennes, 1839: pl. 1. Deshayes, 1843: 133. Potiez & Michaud, 1844: 259. Forbes & Hanley, 1853: 178. Woodward, 1855: 218. Sowerby, 1873: pl. 1. Debeaux, 1884: 510. Clessin, 1895: 46. Dautzenberg, 1910: 148; 1912: 99.

*Panopaea attenuata* Sowerby, 1893: pl. 3; 1889: 156. Clessin, 1895: 45.

*Panopaea australis* Valenciennes, (*non* Sowerby), 1839: 3, 34; 1843: pl. 8, pl. 12. Woodward (*non* Sowerby), 1855: 220.

- Panopaea cyclopana* Di Monterosato, 1889: 26. Locard, 1892: 256.
- Panopaea faujasii*: Philippi, 1836-44: 6, 7. Valenciennes, 1843: pls. 2, 3, 4, 6. Wood, 1853: 283. Chenu, 1862: 27. Sowerby, 1873: pl. 2. Clessin, 1895: 51.
- Panopaea glycimera*: Locard, 1886: 384.
- Panopaea glycimera*: Brown, 1827: pl. 10. Deshayes, 1843: 5. Brown, 1844: 112. Petit de la Saussaye, 1869: 33. Mayer, 1870: 24, 39. Di Monterosato, 1875: 19; 1878: 75. Crosse, 1884: 191. Petersen, 1888: 159. Moncharmont Zei, 1960: 184. Di Monterosato, 1889: 26. Nobre, 1938-40: 712. Ruggieri, 1943-44: 99; 1948: 70; 1949: 92.
- Panopaea glycymeris*: Turton, 1822: 42. Brown, 1827: pl. 10. De Gregorio, 1929: 5. Ekman, 1953: 84. Priolo, 1966: 669.
- Panopaea glycymeris faujasi*: Chiesa, 1932: 171.
- Panopaea natalensis*: Woodward, 1855: 220. Smith, 1906: 294. Schwarz, 1910: 115. Barnard, 1951: 167.
- Panopea dreyeri* Van Hoepen, 1940: 186.
- Panopea glycymeris*: Winckworth & Winckworth, 1935: 162. De Stefani, 1941: 274.
- Panopea glycymeris* var. *rugosa* Lamy, 1925: 269.
- Panopea natalensis* Woodward, 1855: 220. Smith, 1903: 399. Lamy, 1925: 271. Barnard, 1962: 187.
- Panope faujasii* Ménéard, 1807: 115.

#### MATERIAL AND MEASUREMENTS

A complete list of the material examined is given in Table 1. Only shell characters were used for comparative purposes. These characters include hinge structure, muscle and pallial scars, and general proportions. For the comparison of general proportions, the following measurements were used:

- greatest diagonal length (a)
- umbo to ventral margin (b)
- umbo to antero-dorsal corner (c)
- umbo to postero-ventral corner (d)

Figure 3 illustrates these dimensions, which were taken for all measurable specimens. In the case where both valves of the shell are preserved, only one valve was measured. Figure 5 illustrates the scatter resulting from the plotting of diagonal length against the distance from the umbo to the ventral margin. Figure 6 illustrates the scatter obtained from a comparison of the distance from the umbo to the antero-dorsal corner with the distance from the umbo to the postero-ventral corner. (Because of the very gradual curve of the postero-dorsal margin, umbo to postero-dorsal corner is difficult to measure, and was not used.)

Table 1

Specimen	Locality	Valves	Greatest diagonal length mm	Umbo to ventral margin mm	Umbo to antero-dorsal corner mm	Umbo to postero-ventral corner mm
Paris Museum	Mediterranean	L & R	247	127	105	170
Paris Museum	Sicily	L & R	272	146	114	189
Paris Museum	Portugal	L	211	120	104	131
British Museum	Malta	L & R	246	132	106	170
S.A. Museum	Mediterranean	R	173	88	71	115
Lisbon	Baia dos Tigres	L	204	126	96	121
Lisbon	Moçâmedes	R	167	92	72	112
Geological Survey	Velddrif	R	240	132	112	154
S.A. Museum						
K4391	Velddrif	L & R	234	133	95	159
K4390	Velddrif	L & R	244	133	112	158
K4393	Velddrif	L & R	202	109	87	137
K4394	Velddrif	L & R	198	114	88	129
K4395	Velddrif	L & R	228	131	100	155
A2139	Velddrif	L & R	209	111	82	150
Geological Survey	Klein Brak River	L & R	185	95	84	121
National Museum						
D2010a	Klein Brak River	R	205	116	83	143
D2010b	Klein Brak River	R	194	103	84	128
D2010c	Klein Brak River	L	178	95	75	117
D2010d	Klein Brak River	R	183	99	74	125
D2010e	Klein Brak River	L	155	84	61	104
D2010f	Klein Brak River	L	162	92	71	113
D2010g	Klein Brak River	R	209	104	90	133
S.A. Museum						
K4385	Klein Brak River	L & R	183	99	77	122
K4389	Klein Brak River	L & R	165	93	71	112
K4384	Klein Brak River	L & R	180	98	71	125
K4383	Klein Brak River	L	197	118	83	134
K4386	Klein Brak River	L & R	168	83	65	115
K4388	Klein Brak River	L	184	103	76	132
3486	Klein Brak River	L & R	157	91	68	119

The following material, being damaged, could not be measured:

- S.A. Museum. Velddrif L & R, L, R
- Geological Survey. Velddrif 2 fragments
- Paris Museum. Dakar L

The possibility was considered that shell proportions changed differently with growth in the different populations. With this in mind, 2 individuals were selected from each of the Mediterranean, Velddrif and Klein Brak populations, and 6 growth lines traced on each of these. The length/height ratios were plotted for each of these growth lines and are shown in Figure 7. These dimensions are given in Table 2. In each case, the final length/height set represents the total dimensions of the specimen. For convenience, height was measured, not from the umbo, but from the most dorsal point of the shell as illustrated in Figure 4.



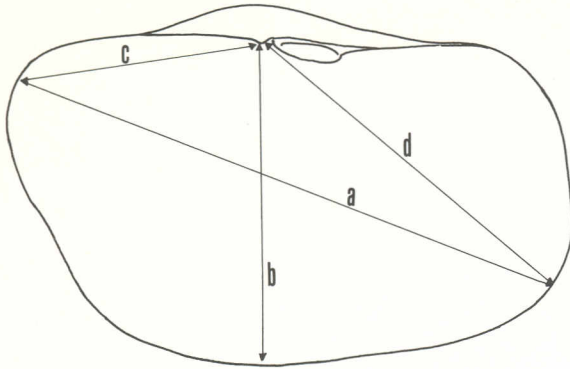


Fig. 3. Diagram to illustrate dimensions used.

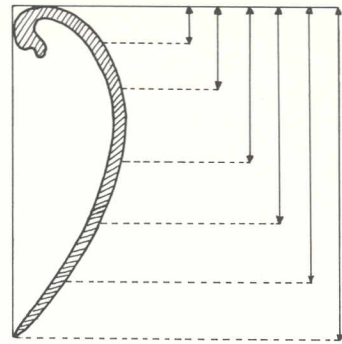


Fig. 4. Diagram to illustrate method of growth-line measurement.

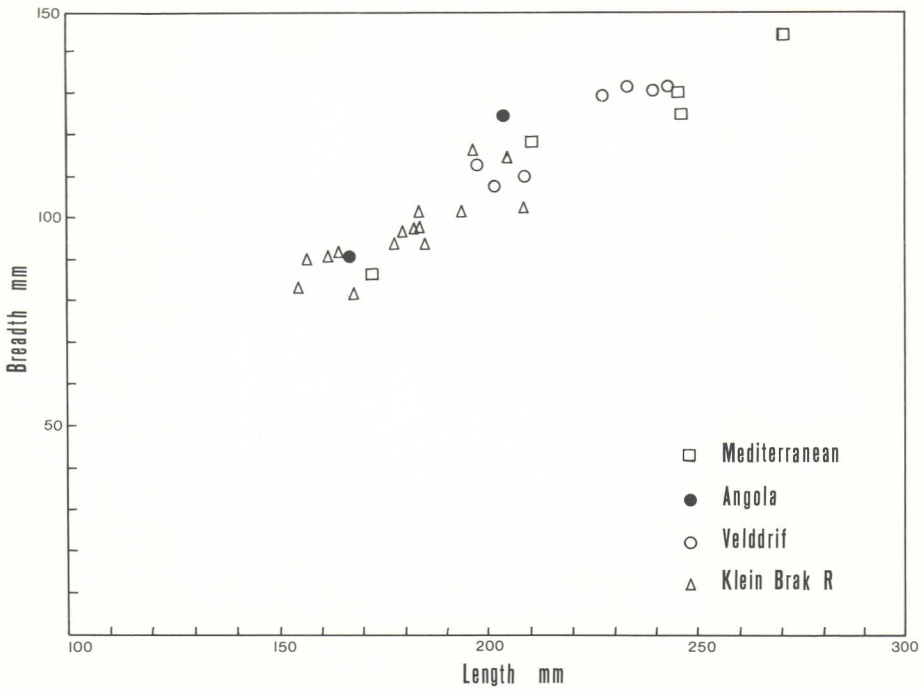


Fig. 5

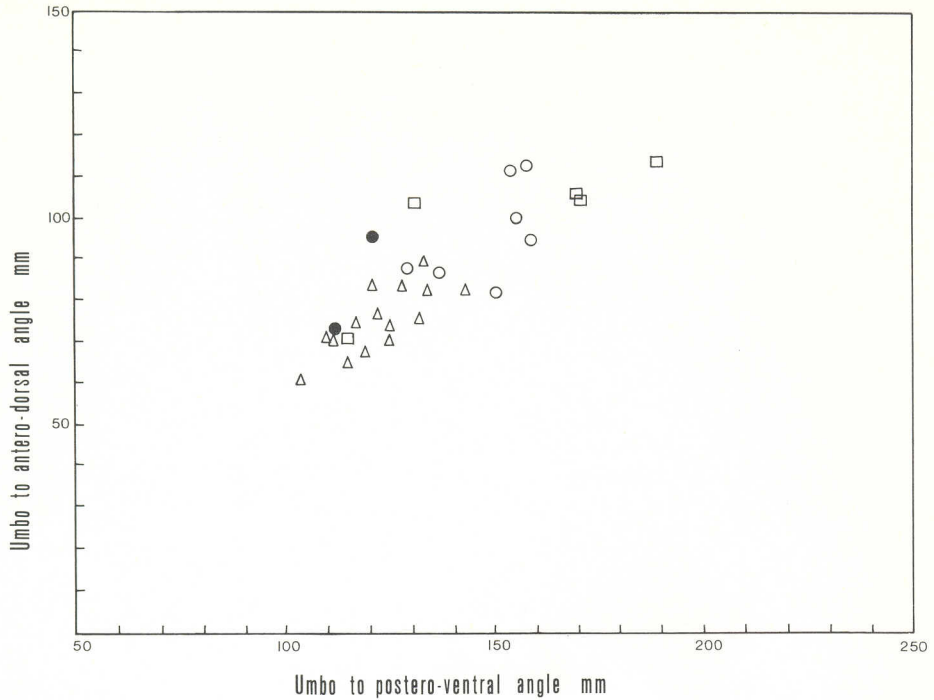


Fig. 6

Table 2

Specimen	Locality	Growth-line Measurements: Length × Height mm					
Paris Museum	Sicily	48 × 31	102 × 65	165 × 100	197 × 118	236 × 145	272 × 159
British Museum	Malta	24 × 16	78 × 46	113 × 75	177 × 109	200 × 122	246 × 144
Geological Survey S.A. Museum	Klein Brak River	41 × 25	75 × 46	109 × 64	141 × 84	170 × 93	185 × 103
K4385	Klein Brak River	27 × 16	59 × 38	95 × 58	147 × 88	167 × 98	183 × 102
K4391	Velddrif	52 × 31	109 × 66	147 × 87	182 × 109	210 × 128	234 × 145
K4390	Velddrif	56 × 34	88 × 58	121 × 76	189 × 114	213 × 135	244 × 145

## SOUTHERN AFRICAN LOCALITIES (See map)

*Zwartkops, Port Elizabeth*

Originally designated as Pliocene or Post-Pliocene (Stow 1871) it has been suggested that these formations are of Pleistocene age (Schwarz 1910).

*Klein Brak River, Mossel Bay* (Rogers 1906; Schwarz 1910)

These deposits have a similar age to the previous locality, i.e. Plio-Pleistocene.

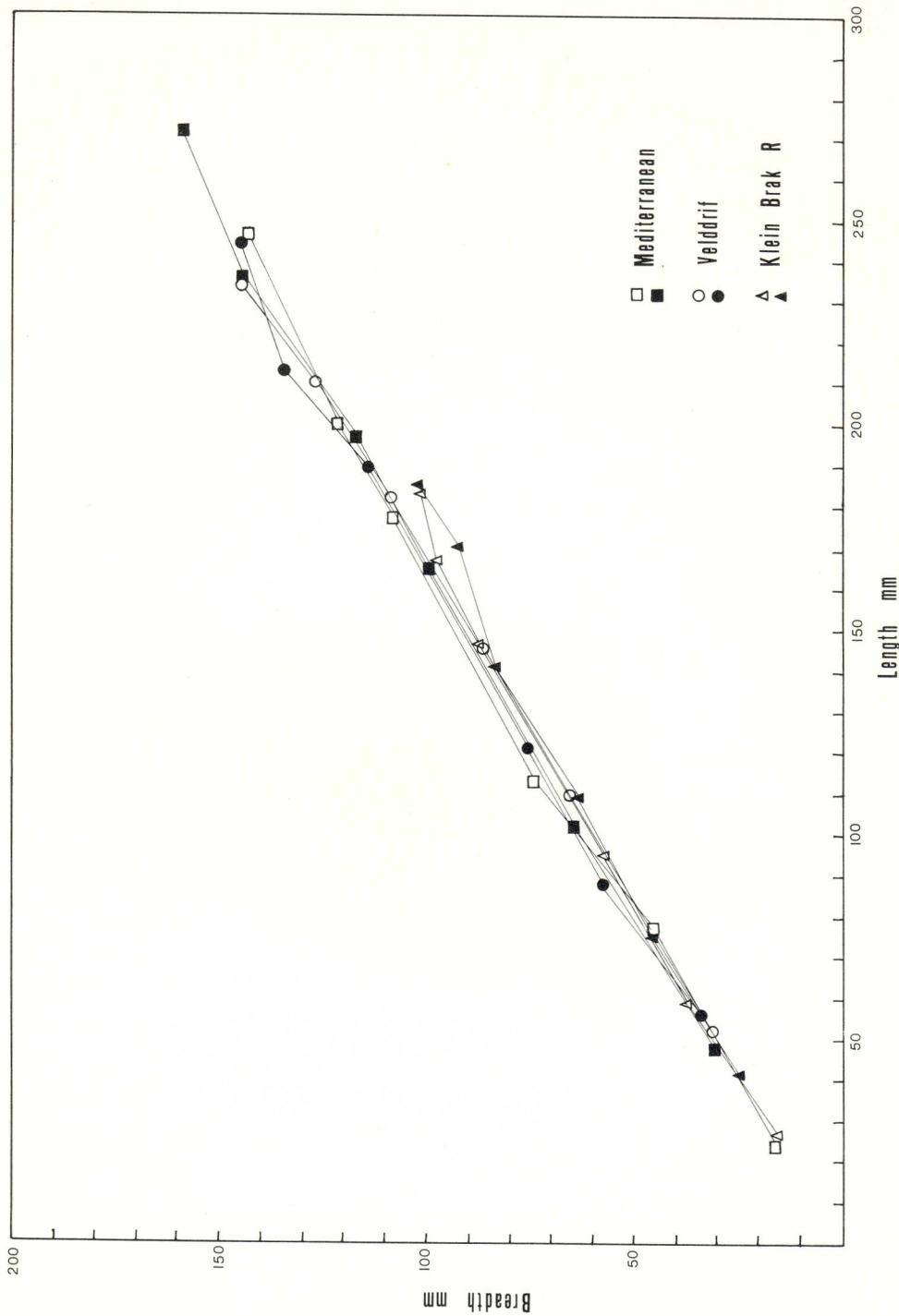
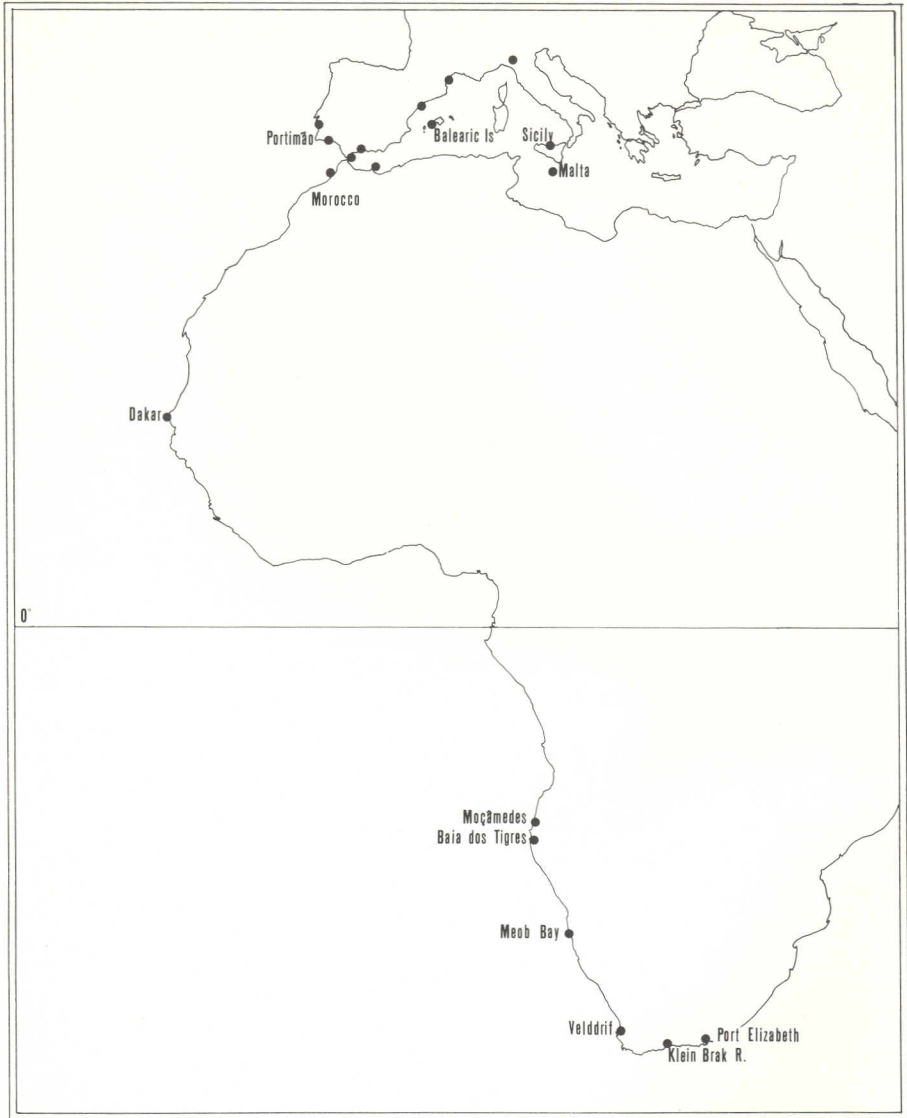


Fig. 7



MAP 1. Locality map for *Panopea glycymeris*.

*Velddrif*

Situated near the mouth of the Great Berg River, the farm 'Kruispad', 8 km from the present seashore on the west coast, has been given a Pleistocene age (Visser & Schoch 1973).

*Meob Bay, South West Africa*

The exact origin of these specimens is uncertain, as they were washed ashore at springtide.

*Baia dos Tigres, Angola* (Franca 1960)

Whether this specimen is from a recently living animal, or a fossil from a raised beach deposit, is difficult to establish. In appearance, state of preservation, it is not unlike some of the material from Klein Brak River.

*Moçâmedes, Angola* (Franca 1960)

This is a valve from a recently living animal, as a portion of the external ligament is preserved.

## MEDITERRANEAN AND WEST AFRICAN LOCALITIES

Atlantic coasts of Portugal and Spain; Mediterranean coasts of Spain, France, Italy, Morocco; Balearic Islands; Sicily; Malta; Port of Dakar, Senegal.

## DESCRIPTION

Shell equivalve, elongate, roughly trapezoidal, gaping at both ends, strongly vaulted. Umbo situated slightly anterior to midpoint, just below dorsal vault. Hinge axis and dorsal margin more or less straight. Anterior margin slightly concave, sloping posteriorly in the ventral region. Antero-dorsal corner evenly rounded. Posterior margin truncate, postero-dorsal and postero-ventral corners smoothly rounded. Hinge bearing slight conical protruding cardinal tooth in each valve, situated just below umbo. Tooth of right valve fitting into hollow anterior to cardinal tooth of left valve. Cardinal tooth bearing a fine mid-dorsal ridge. Posterior to tooth, a stout, solid, elongate roughly rectangular structure. Nymph narrow near umbo, widening posteriorly.

Interior of valves with roughly oval anterior adductor muscle scar, posterior broad, irregular, but always continuous. Pallial sinus variable, triangular to rounded. One to several thin lamellar structures sometimes developed in dorsal half of valve, usually running obliquely from internal dorsal margin, alongside adductor muscle scar, more frequently seen in shells from Klein Brak River, function possibly to give added strength to strongly vaulted shell. Margin of shell often eroded, revealing layered structure; occasionally, perhaps due to injury, more extensive layers of calcareous material becomes separated from rest of surface of shell.

Exterior of valves bearing rounded concentric ridges, smoother and more regular at early growth stages. Ridges and growth lines becoming irregular with age. Overall external surface smoothness varying with individuals. Fine short oblique striae sometimes developed in region of ventral margin.

While the material from the Velddrif area is usually bleached white and often fractured, the material from Klein Brak River usually has a remarkably fresh appearance, and could be mistaken for living, were it not that the localities in the raised beaches are so well recorded. In both these localities, specimens with both valves preserved in the 'living' position are sometimes found.

## DISCUSSION

Comparison of the hinge lines of specimens from the different localities failed to reveal any differences either in size or disposition of the structures (Fig. 8). (Note: the protruding cardinal tooth tends to be broken off.)

The pallial line and pallial sinus both appeared to be variable between individuals from the same locality and therefore of no diagnostic value. From Figures 5 and 6, it would be difficult to separate any populations; indeed, both figures would seem to indicate a single continuous 'population'. The lines obtained from growth-line measurements (Fig. 7) would seem to indicate that the pattern of growth is similar in the Klein Brak River, Velddrif, and Mediterranean populations, especially during the younger stages. With age, individuals may become distorted and display more irregular growth. It is of interest to note that of the 15 Klein Brak specimens, 209 × 104 mm is the maximum size attained, whereas five of the six Velddrif specimens, and four of the five Mediterranean specimens exceed these dimensions, the Mediterranean specimens being, on the average, the largest.

The variety *rugosa* mentioned by Lamy (1925) from the Atlantic coast of Portugal and Morocco, would seem merely to be individuals showing a higher degree of rugosity, several of the Klein Brak specimens being equally rugose. The more pronounced roughness may well be due to the inhabiting of a substrate more prone to shifting by greater water movement, as, for example, on the exposed Atlantic coasts.

*P. dreyeri*, described by Van Hoepen (1940) from the Klein Brak deposits, was separated, as already pointed out by Barnard (1964), on the basis of individual variation.

The Plio-Pleistocene of the Mediterranean has yielded numerous examples of *P. glycymeris*. The fossil form was originally designated as *P. faujasi*, but has long been recognized as being synonymous with the living Mediterranean form (Priolo 1966).

It would seem from the foregoing data, that the same specific name should be applied to the living Mediterranean and West African forms, as well as to the fossils from the Mediterranean, South West Africa and the Cape.

## BRIEF ECOLOGICAL OBSERVATIONS

Ekman (1953, 1967), in discussing the fauna of the Mediterranean, regarded *Panopea glycymeris* as an endemic form. The inaccuracy of this statement was hinted at by Barnard (1962, 1964) and is now confirmed. Discussing the hydrography of the Mediterranean, Ekman (1967: 81) states that the south-east Mediterranean in summer has a temperature of 25–27°C, the rest having a temperature of 20–25°C. In spite of the fact that winter temperatures drop well below these levels, the area may nevertheless be regarded as warm-temperate.

The port of Dakar, situated on the bulge of Africa, lies within an area where

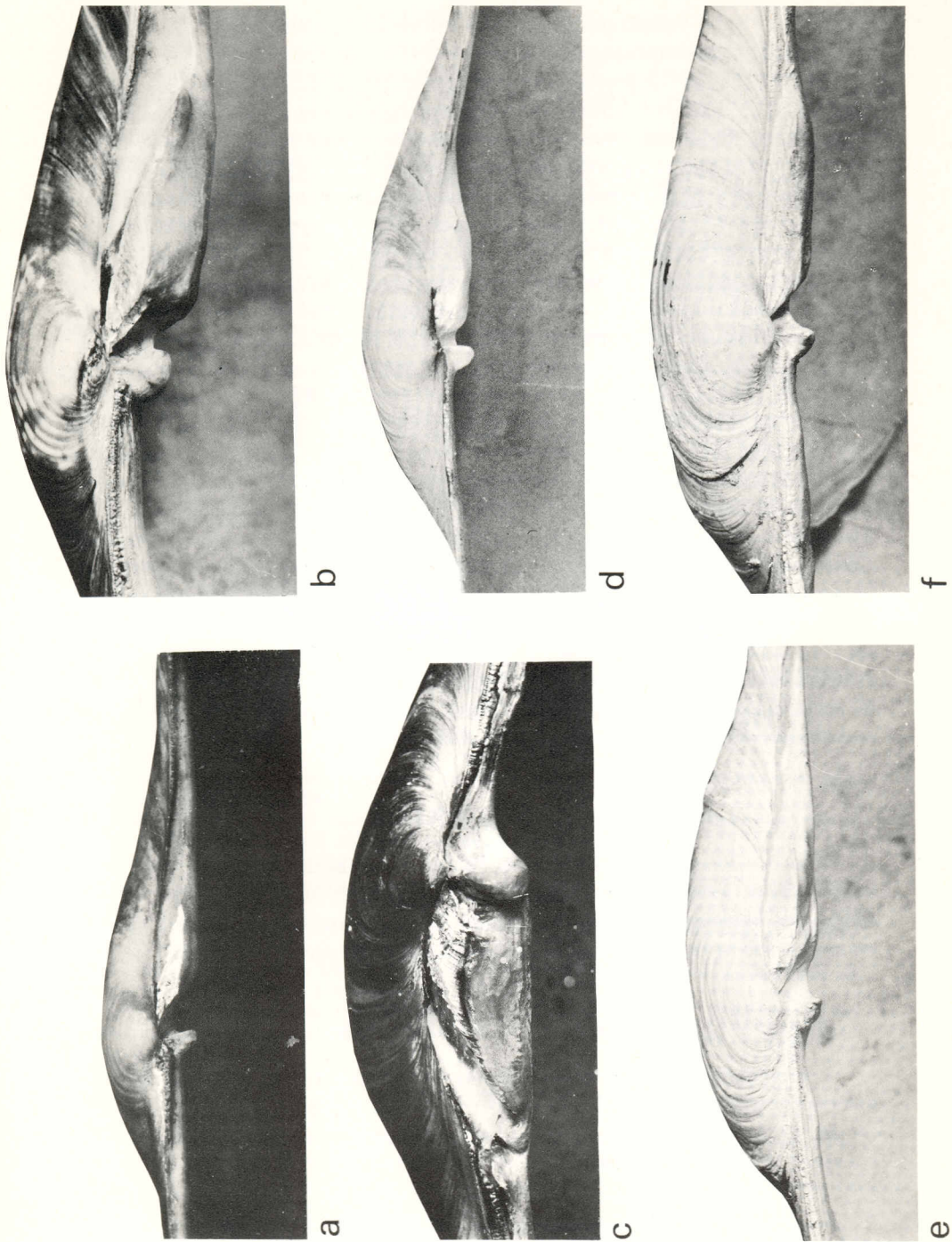


Fig. 8. *Panopea glycymeris*: Hinge lines.  
a Mediterranean; b Sicily; c Portugal; d Moçâmedes; e Velddrif; f Klein Brak River.

the surface water temperature is usually above 20°C, although at 100 m depth the annual mean temperature is 18° or 19°C (Ekman 1967: 56).

In contrast to the present-day cold-temperate conditions of the sea off the west coast of southern Africa, and the only slightly warmer conditions off the south coast, Plio-Pleistocene conditions must have been rather different. It has been suggested that along both the west and south coasts of South Africa, warmer water than that of the present supported a characteristically warm-water fauna (Carrington & Kensley 1969; Visser & Schoch 1973) during part of the Pleistocene. The presence of *Panopea* in the Plio-Pleistocene deposits is yet another indication of warmer conditions in the past. With the change to the present cold-water regime, *Panopea* apparently died out at the southern end of its range, probably due to the inability of either the juvenile forms or the adults to adapt physiologically to the changed conditions. It is of interest to note that amongst the sediments removed from between valves of *Panopea* from the Velddrif area, valves of the small bivalve *Nuculana bicuspidata* were found. This species, which has also been recorded from the marine terraces of the Cape Cross area, has a present-day distribution from Angola to Mauritania (Nicklès 1950). The sediments from between valves of the Klein Brak deposits yield, amongst a large assortment of molluscs, numerous examples of the small trochid gastropod *Cantharidus fultoni* (now only occurring alive from Moçambique northwards along the East African coast), and a species of the bivalve *Diplodonta* provisionally recorded by Barnard (1962) as *senegalensis*, but which would appear to be very similar to *D. diaphana*, recorded from the Quaternary of Benguela, Angola, and living from Angola to Mauritania. These isolated examples would all seem to point to the existence of warmer water conditions along the west and south coast of South Africa during the Pleistocene.

#### SUMMARY

The Plio-Pleistocene specimens of *Panopea* from South Africa are compared with shells of living material from the Mediterranean and West Africa. As no differences between the various specimens could be found, it is decided that all belong to the same species, viz. *Panopea (Panopea) glycymeris* (Born).

#### ACKNOWLEDGEMENTS

I should like to thank the following individuals for making the loan of material possible: Mrs K. M. Way of the British Museum (Natural History); Dr M. de L. Paes da Franca of Lisbon; Mlle A.-M. Testud of the Muséum National d'Histoire Naturelle, Paris; the Director of the National Museum, Bloemfontein; Drs P. J. Roussouw and J. N. Theron of Geological Survey; Mr A. Tankard and Mr M. R. Cooper of the South African Museum for useful criticism.



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Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.

*Style manual for biological journals*. Washington: American Institute of Biological Sciences.

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*Examples* (note capitalization and punctuation)

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To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

*Example*

*Scalaria coronata* Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.