

PAPHIA (PROTAPES) (BIVALVIA: VENEROIDEA) IN THE ARABIAN SEA, WITH THE DESCRIPTION OF A NEW SPECIES

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Abstract: The genus *Paphia* in the Arabian Sea contains taxa belonging to the subgenera *Protapes* and *Paratapes*. The species of *Protapes* and *Paratapes* are revised using shell morphometric analysis. Five taxa are recognised of which four are distinguished at the species level with the fifth given sub-species status only. A new species, *Paphia* (*Protapes*) *thamphodes* is described from the coast of Oman and the Arabian Gulf. *Paphia* (*Protapes*) *gallus* is regarded as distinct from *P. (P.) sinuata*, the former not extending north of the Malabar coast and absent from the Arabian Sea. A new subspecies *P. (P.) gallus bombayana* is recognised from NW India and hypothesised to be a result of clinal and ecological influences. The remaining taxon, *P. (P.) cor* is tentatively retained in the genus *Paphia*.

Key words: Taxonomy, Bivalvia, Tapetinae, Arabian Sea.

INTRODUCTION

Venerid clams are a predominant component of inter-tidal and sub-littoral sand and mud flats. They have been widely used as food and are a major part of prehistoric shell middens in the Gulf region. The most common inter-tidal species in the Arabian Sea are *Circeiina callipyga* (Born, 1798), *Amiantis umbonella* (Lamarck, 1819), *Marcia flammea* (Gmelin, 1791) and a species of Tapetinae with affinity to *Paphia* subgenus *Protapes*. It is this latter species that formed the impetus for this research for not only did it appear to be undescribed it brought into question the number and identity of *Paphia* species in the Arabian Sea.

Early lists (Melvill & Abercrombie, 1893; Melvill & Standen, 1907; Melvill, 1928) suggest that five species with affinity to *Paphia* are present: *Venus textile* Gmelin, 1791; *Venus undulata* Born, 1780; *Venus malabarica* Chemnitz, 1782 = *V. gallus* Gmelin, 1791; *Venus cor* Sowerby, 1853 and *Venus sulcosa* Philippi, 1847. In the only revision of the Tapetinae, Fischer-Piette & Métivier (1971) indicate under the genus *Paphia* the following species from Arabian waters, *P. textile*, *P. undulata*, *P. malabarica* and *P. cor*. They believe that *P. sulcosa* is limited to eastern Australia and synonymise it with *P. crassisulca* (Lamarck, 1818). They do not state which species the Arabian records of *P. sulcosa* should be referred to but Oliver (1992) referred all Aden material present in the Shopland collection to *P. gallus*.

The conception of the subgenus *Protapes* being monotypic (type species = *V. gallus*) is widespread, only Matsakuma (1988) referring more than a single species to *Protapes*. This suggests that the original definitions of *Paphia* and *Protapes* do not encompass the degree of variation shown by the critical characters such as outline, sculpture and proportions of the pallial sinus. Consequently this study not only revises species level taxonomy but reviews the generic diagnoses.

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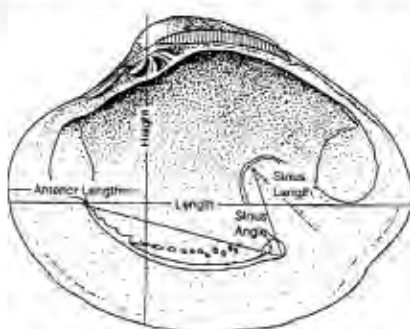


FIG. 1. Internal view of the shell of *Paphia (Protapes) sinuata* showing the parameters used in the morphometric analyses.

METHODS

The discrimination of species based on subjective morphological analysis of shell characters is not a satisfactory method for most bivalves. In the vast Indo-West Pacific province geographic (clinal) variation can be significant and is further compounded by ecophenotypic effects. Morphometrics can add objectivity but ideally should be combined with molecular or genetic methods. This has not been possible here because of the unavailability of material. Our conclusions therefore will remain partly unsubstantiated until future research is possible.

Little attention has been given to the constancy of shell characters. In epifaunal taxa shape can be greatly influenced by spatial constriction (Seed 1980). Variation amongst infaunal bivalves is little studied but it is predictable that growth would be affected by physio-chemical conditions and food availability. Details of sculpture and external features such as the lunule and escutcheon may be less variable than shell shape. Internal anatomical features are probably more constant than shell shape or sculpture (Lam, 1980). Thus, shell characters, such as muscle scars, that reflect anatomy may be useful. In our study we place least emphasis on minor differences in shell outline, more on sculpture and most on muscle scars.

Shell measurements were made using digital vernier callipers accurate to two decimal places or from an image analyser (ImprovisionTM). These were transferred to Statview 4.0TM for statistical analyses.

Shell parameters used in the morphometric analyses are given in Figure 1. To compare measurements between species of differing shapes a standard orientation is needed. This was achieved by fixing a horizontal axis formed by the line joining the bases of the two adductor scars. Sculptural density was measured with the image analyser. The measurement used was the distance between individual concentric lirae at a fixed point on the midline below the umbo (20mm).

GENERIC DIAGNOSES

Detailed diagnoses of the genus *Paphia* are lacking. Fischer-Piette & Métévier (1971) concentrate on hinge characters to separate the genera within the Tapetinae. They note that the most significant character of *Paphia* is the ascending pallial sinus. The definition of an "ascending pallial sinus" is unclear, as there are considerable differences between the species

mentioned by Fischer-Piette, for example *P. gallus* and *P. cor*. There are also differences in the depth of the sinus between *P. undulata* and *P. alapapilionis*. Shell shape is also highly variable ranging from elongate/compressed in *P. alapapilionis* to subovate in *P. gallus* to rotund/ovate and inflated in *P. cor*. Sculpture varies from smooth in *P. undulata* to strongly ridged in *P. crassisulca*.

Matsukuma (1988) appears to give diagnoses for *Paphia* and *Protapes* but these refer specifically to the type species of each. As a consequence the presence of radial rows of brown spots cannot be part of the generic diagnoses as only *P. alapapilionis* has them. From his discussion however it is clear that he regarded all the short, tumid, posteriorly twisted forms as belonging to *Protapes*.

Dall (1902) erected the subgenus *Protapes* defining it on the more ovate outline and ridged sculpture. Stoliczka (1870) erected the genus *Paratapes* as a replacement for *Textis* with the type species *V. textile* Linnaeus. Kuroda and Habe (1971) erected the subgenus *Neotapes* for *P. undulata* defining it on the short pallial sinus and weak sculpture. As *V. textile* and *V. undulata* are clearly sister species if not synonymous *Neotapes* should be regarded as a junior synonym of *Paratapes*. Considering the large amount of variation exhibited by the genus *Paphia* its definition must be rather broad.

Superfamily Veneroidea

Subfamily Tapetinae

Genus *Paphia* Röding, 1798

Type species: *Paphia alapapilionis* Röding, 1798

Tapetinae ranging in outline from elongate to roundly-subovate, compressed to tumid. Sculpture smooth, lirate or concentrically ridged. Pallial sinus ascending never confluent with pallial line, short to very deep. Subgeneric definitions can then be given as follows:-

Subgenus *Paphia* Röding, 1798

Type species: *Paphia alapapilionis* Röding, 1798

Plate 2.1-2.2. Text fig. 2

Outline elongate, with no posterior twist. Pallial sinus deep, ascending steeply. Sculpture undulating to coarsely ridged.

Subgenus *Protapes* Dall, 1902

Type species: *Venus gallus*, Gmelin, 1791

Outline subovate to roundly-subovate, with a twisted posterior-ventral margin. Pallial sinus deep to very deep, ascending gently to steeply. Sculpture coarsely ridged.

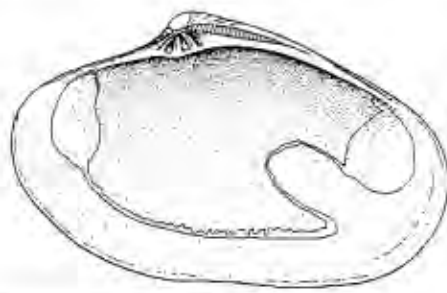


Fig. 2. *Paphia* (*Paphia*) *alapapilionis* Röding. Scale bar = 20 mm.

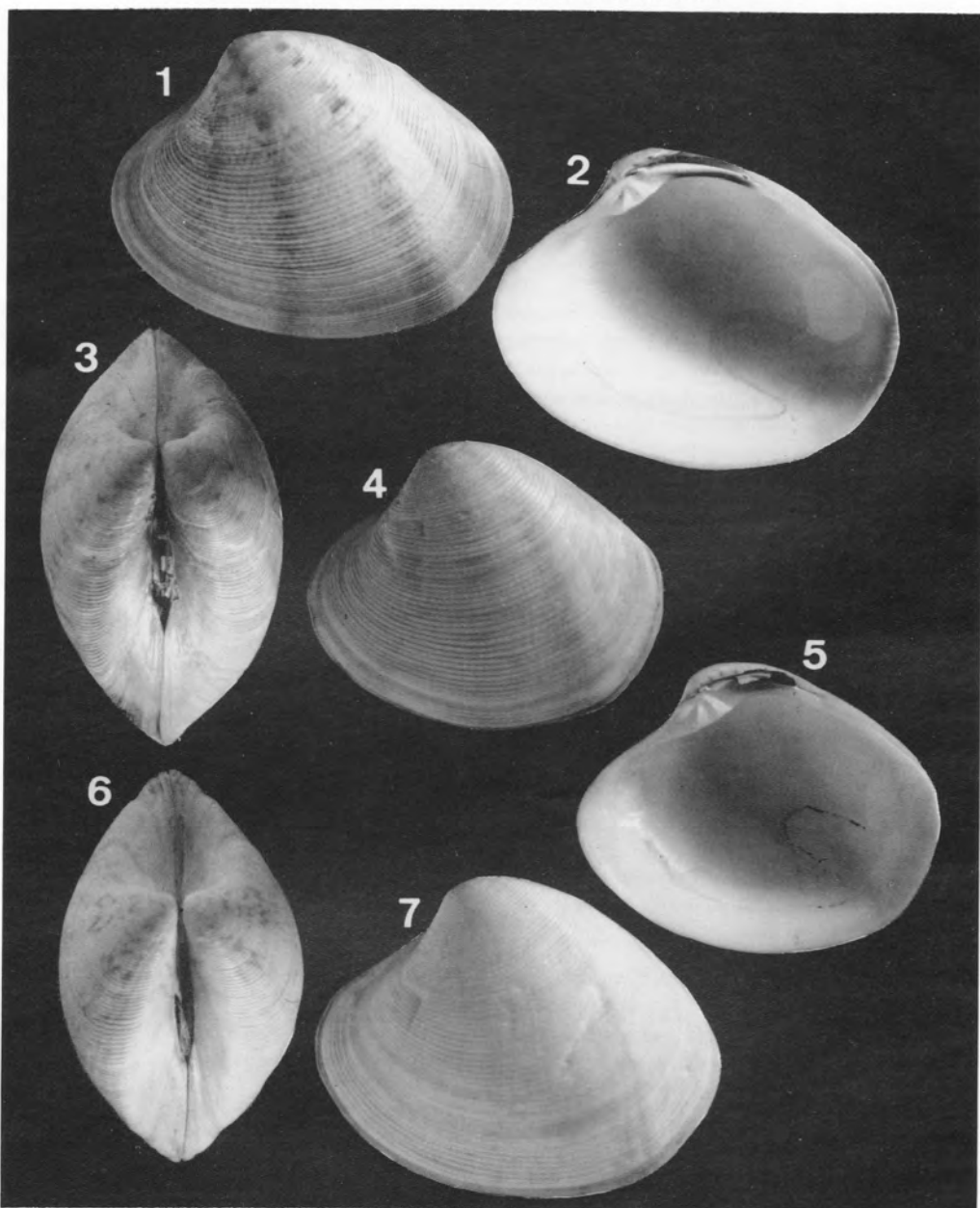


Plate 1. *Paphia (Protapes) rhamphodes* n. sp.:— 1.1–1.3, Holotype, Masirah; Figs. 1.4–1.6, Coloured specimen from Bahrain (NMW.Z. 1993.061.1295); Fig. 1.7, Large white specimen from Bahrain (NMW.Z. 1993.061.1295) All $\times 1.5$.

Subgenus *Paratapes* Stoliczka, 1870

Type species: *Venus textile*, Linnaeus, 1758

Outline elongate with no posterior twist. Sculpture smooth. Pallial sinus short, ascending steeply.

All three subgenera are present in the western Indian Ocean. *Paphia (Paphia) alapapilionis* is restricted to Madagascar, Mauritius and possibly Ceylon and only *Protapes* and *Paratapes* are found in the Arabian Sea. This paper will not consider *P. (Paratapes.) undulatus* further other than to note its widespread occurrence in the Arabian Sea and Arabian Gulf.

SPECIES DESCRIPTIONS

Paphia (Protapes) rhamphodes n.sp.
Plate 1.1–1.7. Text figs. 3a–d.

Paphia cor Sowerby: Ahmed 1975

Protapes n. sp.: Oliver in Dance, 1995, 274, fig. 1230.

Material

Holotype: 1 complete shell (37.8 mm in length \times 29.6 mm in height), Umm Rusays, Masirah, Sultanate of Oman, coll. S.P. Dance, 21.xi.1991, NMW.Z. 1993.061.1303.

Paratypes: 1 shell as holotype NMW.Z. 1993.061.1304; 2 shells as holotype NMW.Z. 1993.061.1305; 10 specimens BMNH 1995082.

Other material examined: Outer Tubli Bay, Bahrain, 20 sh., Coll. H.C.G. Chesney & S. Green, xi. 1992, NMW.Z. 1993.061.1295, 1296; as above but Coll. E. Glover & S. Green 1991, BM(NH): Umm al Qaywayn, United Arab Emirates, 2v, Coll. H.C.G. Chesney, Nov. 1992, NMW.Z. 1993.061. Between As Sib and Muscat 23°41'N 58°11'E to 23°37'N 58°36'E, 2sh., Coll. D. Bosch, 1992, NMW.Z. 1993.061.1301; Muscat 23°37'N 58°36'E, 1sh., Coll. D. Bosch, 1992, NMW.Z. 1993.061.1297; 3sh., NMW.Z. 1993.061.1302; Sur Masirah, Masirah, 20°26'N 56°43'E, 10v., Coll. S. P. Dance, 23.ii.1989, NMW.Z. 1993.061.1299; 4v. (7.ii.1989), NMW.Z. 1993.061.1298; Umm Rusays, Masirah, 20°29'N 58°47'E, 1sh., Coll. S. P. Dance, 21.xi.1991.

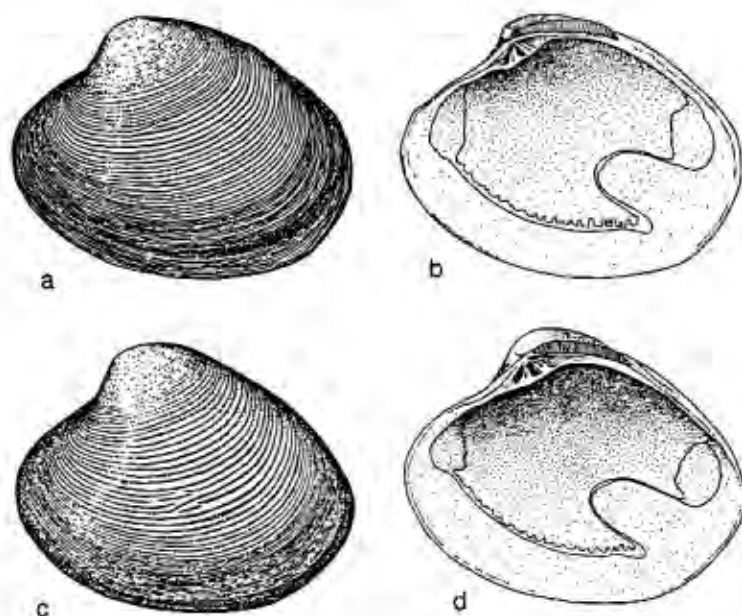


Fig. 3 *Paphia (Protapes) rhamphodes* n. sp. a–b, typical form from Masirah; c–d, Gulf form from Bahrain. Scale bar = 15 mm.

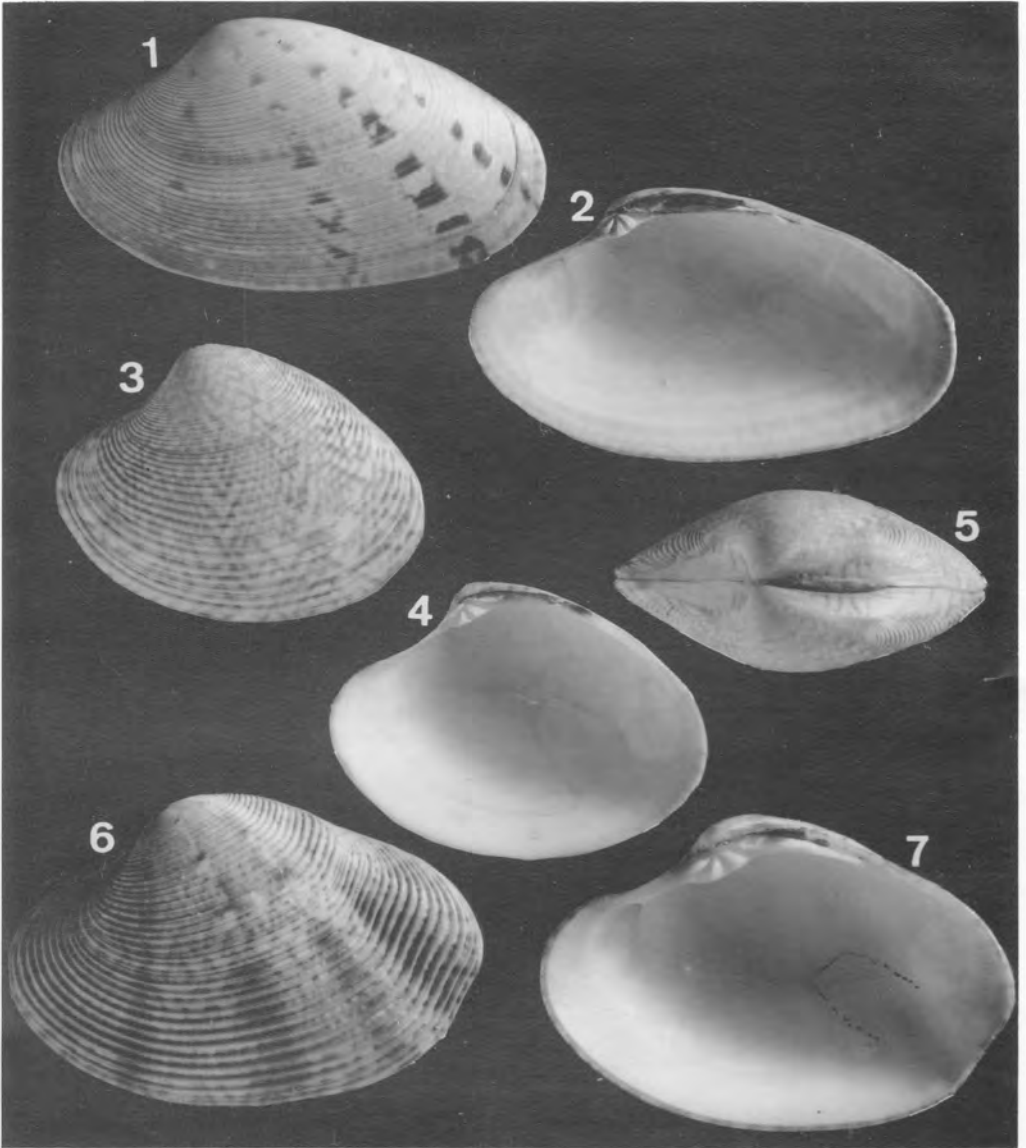


Plate 2. 2.1–2.2, *Paphia (Paphia) alapapilionis*, Indian Ocean (NMW. 1955.158) $\times 0.5$; 2.3–2.5, *Paphia (Protapes) gallus*, Singapore (NMW. 1955.158) $\times 1$; 2.6–2.7, *Paphia (Protapes) sinuosa*, Masirah (NMW.Z. 1993.061.1699) $\times 1$.

Description: Shell to 46 mm in length; shell solid but light, moderately inflated (Length to Tumidity ratio 1.74:1, range 1.55:1–1.98:1). Shell inequilateral, beaks towards the anterior (Anterior Length to Total Length ratio 3.48:1, range 3.18:1–3.82:1), sub-ovate, slightly longer than high (Length to Height ratio 1.25:1 range 1.17:1 to 1.33:1), anterior considerably narrower than posterior; posterior dorsal margin sloping gently, slightly sinuous on posterior margin, which can be sub-truncate. Ventral margin evenly rounded, anterior dorsal margin short, slightly concave, anterior margin sub-acute. Escutcheon weak, shallow, concentric sculpture fading. Lunule narrowly cordate, smooth. Sculpture fine, of

closely spaced concentric lirae (lirae spacing 0.56 mm, range 0.44–0.73). Hinge with three cardinal teeth in each valve, radiating from the beak; RV posterior and middle slightly bifid. LV anterior and middle bifid anterior cardinal thin, often worn. Ligament on long, shallow nymph. Lunule margin with weak sub-marginal groove in RV. LV with longer weak sub-marginal groove. Remainder of inner margin smooth. Adductor scars with posterior slightly rounder and larger than anterior. Pallial sinus moderately deep, sub-quadrate and slightly erect (pallial sinus angle 35°, range 26°–39°). Pallial line associated with discrete accessory pallial muscle scars. Colour background dirty greyish cream with two to four occasional broad radial rays often interrupted near umbo. Rays dull purple-brown in colour.

Shells from the Arabian Gulf, notably Bahrain, are different because of their predominantly cream or white shells. Morphometric analysis showed that they were more reduced anteriorly (Anterior Length to Total Length ratio 3.29:1 as opposed to 3.48:1, *t* test significant at $p=0.001$). The sculpture is coarser (0.66, range 0.54–0.88 as opposed to 0.56, *t* test significant at $p=0.001$).

Derivation of name: *rhamphodes* from the Greek "beaked"

Habitat: Recorded from intertidal sandy mud flats at the mid-shore level. In Bahrain a zonation of venerids is apparent (pers. obs. authors); *Circenita callipyga* occurs on the upper shore, with *P. (P.) rhamphodes* and *Amiantis umbonella* confined to mid shore but absent from the sea grass beds which are exposed at extreme low tide. They are shallow burrowers which are often dislodged and found on the surface.

Distribution: Gulf of Oman from Masirah, Muscat and Fujayrah; Arabian Gulf from Ras al-Khaymah (archaeological material only), Umm al-Qaywayn, Bahrain, Kuwait and Shatt al-Arab (Fig. 7a).

Remarks: *Paphia (Protapes) rhamphodes* n.sp. can be distinguished from *P. (P.) sinuosa* and *P. (P.) gallus* by its finer sculpture (Fig. 9A) and shallow semi-erect pallial sinus. From *P. (P.) sinuosa* further by its more rounded, more tumid and more anteriorly reduced outline (Figs. 9B–9D). *Paphia cor* differs in lacking a defined lunule, having a more spherical form and having a very short pallial sinus. All morphometric analysis of these comparisons are significant at the 95% level at *p* values greater than 0.0001. In outline and fine concentric sculpture *rhamphodes* resembles *Paphia (Protapes) irrediviva* Makiyama 1930, an extinct late Pleistocene species from Japan (Matsukuma 1988), but lacks the erect pallial sinus.

Paphia (Protapes) rhamphodes is recorded archaeologically only from Ras al-Khaymah, U.A.E. Fifteen valves were recovered from Julfar, a 13th–16th AD century settlement on a beach north of Ras al-Khaymah township, excavated in 1992. The specimens were found amongst a large collection of venerid clams in a late habitation layer of the site. The shells are evidently the remains of food. The most common species (>90%) are *Marcia* sp, with small numbers (in order of abundance) of *Amiantis umbonella*, *Callista erycina*, *P. (P.) rhamphodes*, and *Circenita callipyga*. One specimen of *P. (P.) rhamphodes* was recovered from archaeological deposits at Rafaq, Ras al-Khaymah, an inland settlement of probably late 1st millennium BC.

There are no earlier records of *P. (P.) rhamphodes* from the Arabian Gulf but the archaeological record is limited. Archaeo-zoological samples from the settlement of Saar, Bahrain, dated to 2000BC, did not contain *P. rhamphodes* although there are great numbers of other intertidal venerids including *Marcia* cf. *flammea*, *Amiantis umbonella* and *Circenita callipyga* (Glover 1995). This result is suggestive of a relatively recent appearance of *P. (P.) rhamphodes* in the Arabian Gulf.

Paphia (Protapes) sinuosa (Lamarck, 1819)

Plate 2.6–2.7. Text figs. 4a–b.

= *Protapes ziczac* (L, 1958)
in Huber, 2010.

Venus sinuosa Lamarck, 1818 p. 604

Tapes lentiginosus Reeve, 1864 pl. 6 fig 25

Tapes sinuosa Lamarck: Römer, 1870 p. 35, pl. 11 fig. 1

Paphia malabarica (Chemnitz) part: Fischer-Piette and Méuvier 1971, p. 39–41 pl. 9 figs 7–10.

Paphia (Protapes) sinuosa (Lamarck, 1818) Matsukuma 1988 p. 413 pl. 2 figs. 3–4.

Material

Syntypes: MNHN, Paris

Other material examined: Kalbar, Masirah, 20°20'N 58°38'E, 1sh., Coll. M. Day, 9.i.1993, NMW.Z. 1993.061.1699; Masirah, 2sh., Coll. D. Bosch, NMW.Z. 1991.103; Sur Masirah, Masirah, 20°26'N 58°45'E, 1sh., Coll. S. P. Dance, 17.ii.1989, NMW.Z. 1993.061.1700; 2sh., 23.vi.1991, NMW.Z. 1993.061.1705; 1sh., 22.xii.1991, NMW.Z. 1993.061.1706; 1sh., Coll. M. Day, 05.ii.1993, NMW.Z. 1993.061.1707; Umm Rusay, Masirah, 20°29'N 58°47'E, 5sh., Coll. M. Day, 6/7.ii.1993, NMW.Z. 1993.061.1701; Muscat, 2sh., Coll. D. Bosch, Hormuz, Massadam, 2v., Coll. K. Smythe, 1.1976, NMW.Z. 1995.008.265; Rams, Ras al Khaymah, 25°45'N 55°55'E, 4sh., Coll. S. P. Dance, 1.1993, NMW.Z. 1993.061.1702; Juffair, Bahrain, 1sh. + 2v., Coll. S. Green, ca.1991, NMW.Z. 1993.061.1703/4; Aden, Coll. Major Yerbury, BM(NH) 4.9.4.9; Muscat, Coll. R. Jayakar BMNH 339; Gulf of Oman, Coll. K. Smythe BM(NH) 2341; Aden, Coll. Dinshau, BM(NH); Aden, Coll. A.J. Peile, BM(NH); Malaya, Coll. R. D. Purchon BM(NH) 2264; Mozambique, Coll. P. M. Reid BM(NH) 2341; Aden, Coll. H. F. Biggs BM(NH) 2258; Tranquebar, India, 6sh., Coll. Spengler, 4sh., Coll. Vedelsby, ZMC.

Description: Shell length to 75 mm. Shell solid, slightly inflated (Length to Tumidity ratio 2.06:1, range 1.67:1–2.37:1). Inequilateral, beaking towards anterior (Length to Anterior Length ratio 2.87:1, range 2.62:1–3.03:1), sub-ovate (Height to Length ratio 1.37:1 range 1.26:1–1.48:1); posterior margin sloping gently, strongly sinuous on posterior margin, sub-truncate, ventral margin slightly sinuous. Anterior dorsal concave, anterior margins sub-acute. Escutcheon weak, shallow, indistinct ridges. Lunule lanceolate, slightly concave, weakly ribbed. Shell sculpture strong concentric ridges (lirae spacing 1.32 mm, range 0.84–1.71) separated by nearly equal grooves. Hinge with three cardinal teeth in each valve, radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid, anterior cardinal thin and often worn. Ligament shallow. Lunule margin LV with sub-marginal groove, RV sub-marginal groove weaker. Remainder of inner margin smooth. Sub-circular posterior adductor scar larger than semi-circular anterior scar. Pallial sinus deep, sub-acute,

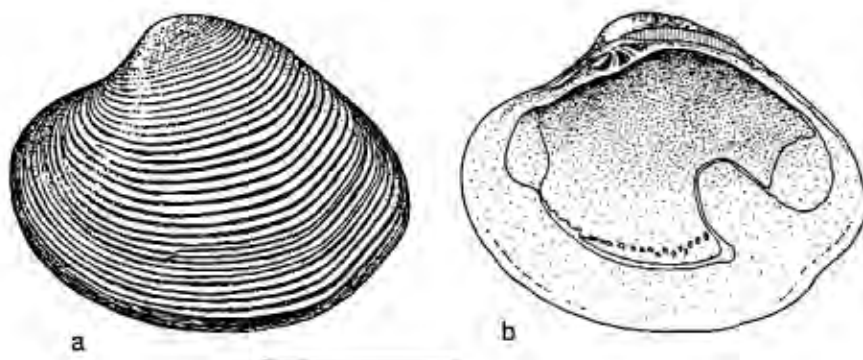


Fig. 4a–b) *Paphia (Protapes) sinuosa* (Lk.) from Masirah. Scale bar = 25 mm.

erect (44° , range 38° – 50°), pallial line associated with accessory pallial muscle scars. Shell colour fawn with four brown rays and zigzag streaks.

Habitat: Sub-tidal soft substrates.

Distribution: Indo-West Pacific from Mozambique to southern China and Philippines (Fig. 7c.)

Paphia (Protapes) gallus (Gmelin, 1791)

Plate 2,3–2,5, Text fig. 5

Venus malabarica Chemnitz, 1782: p. 323, pl. 31 figs. 324–325.

Venus gallus Gmelin 1791: p. 3277.

Tapes malabarica Chemnitz: Römer, 1870 p. 34 pl. 10 fig. 3

Paphia malabarica (Chemnitz) part: Fischer-Piette and Métévier 1971: 39–40

Paphia (Protapes) gallus (Lamarck, 1818): Matsukuma, 1988 p. 412, pl. 2 figs. 5a–b.

Material

Holotype: not located.

Other material examined: Singapore, 8sh., leg. S. Archer, Coll. Melvill-Tomlin, NMW. 1955.158; Siglap, Singapore, 10sh., Coll. H. Winckworth, 11.vi.1933, BM(NH); Malabar Coast, 4sh., Coll. Melvill-Tomlin, NMW. 1955.158; Malabar Coast, 6sh., Coll. H. Comins, BM(NH); North Queensland, Australia Coll. D. Reid BM(NH); Ennur, Coll. H. Winckworth, BM(NH) 1933 1.2; Penang, Malaysia, 4sh., Coll. H. Winckworth, 14.iii.1933, BM(NH).

Description: Shell length to 65 mm; shell solid but light, not inflated (Length to Turbidity ratio 2.15:1, range 1.57:1–2.47:1). Shell inequilateral, somewhat extended towards anterior (Length to Anterior Length 2.88:1, range 2.64:1–3.13:1), sub-ovate (Height to Length ratio 1.36:1 range 1.24:1–1.44:1), posterior margin sloping gently, straight, weakly sinuous on posterior margin. Anterior dorsal margin concave, anterior margins sub-acute. Escutcheon long, narrow, weakly striated with blunt ridge running from beak towards postero-dorsal. Lunule lanceolate, slightly concave, smooth, with indistinct shallow groove on lunule margin. Shell sculpture low concentric riblets separated by shallow narrower grooves (Irae spacing 1.05 mm, range 0.85–1.36). Hinge plate, thin, with three cardinal teeth in each valve radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid, anterior cardinal thin. Inner margin smooth. Adductor scars sub-circular with posterior scar larger than semi-circular scar. Pallial sinus deep, sub-quadrate, very erect (Pallial sinus angle 52° ,

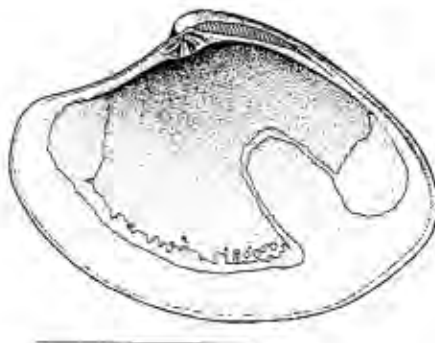


Fig. 2. *Paphia (Protapes) gallus* (Gmelin) from Singapore. Scale bar = 30 mm.

range 45°–59°). Pallial line dorsally associated with discontinuous accessory pallial muscle scars. Colour fawn, with four, more or less, distinct brown rays and/or narrow zigzag streaks.

Habitat: Sub-tidal soft substrates.

Distribution: Indo-West Pacific from Malabar coast of south-west India to Philippines and northern Australia. Apparently absent from greater part of the western Indian Ocean (Fig. 7c).

Paphia (Protapes) gallus bombayana n. subsp.

Plate 3, 1–3.3, Text fig. 6

= *Protapes monstrosus* (Römer, 1870)
in Huber, 2010.

Material

Holotype: Ratnagiri, 1sh., leg. Aitken, Coll. A. J. Peile, BM(NH) 996023.

Paratypes: Ratnagiri, 2sh., leg. Aitken, Coll. A. J. Peile, BM(NH) 2242; Bombay, 2sh. Leg. Abercrombie, Coll. Melville-Tomlin, NMW.1955.158.

Other material examined: Bombay, 4sh., Coll. H. Winckworth, 1.v.1945, BM(NH) 1953.1.2.169–172; Bombay, 6sh., Coll. E. Deakin BM(NH) 1909.9.23.1–6; Karwar, Coll. H. Winckworth, 24.ii.1944, BM(NH) 1953.1.2.173; Khar Beach, Bombay, 3sh. + 1v., Coll. P. Narang viii. 1969, BM(NH); Karachi, 1sh., Coll. A. Salisbury, BM(NH) 2172;

Description: Shell length to 75 mm; shell solid, inflated (mean Length to Tumidity ratio 1.79:1, range 1.61:1–2.00:1). Inequilateral, beaking towards the anterior (Length to Anterior Length ratio 3.04:1, range 2.69:1–3.49:1), sub-ovate (Height to Length ratio 1.23:1 range 1.16:1–1.30:1, anterior narrower than posterior; posterior margin sloping gently, slightly convex. Slightly sinuous on posterior ventral margin. Anterior dorsal margin concave. Escutcheon long, narrow, striated. Lunule broad, lanceolate, slightly concave smooth with indistinct shallow groove on lunule margin. Sculpture of concentric ribs separated by distinct grooves in adult (lirae spacing 1.11 mm range 0.86–1.39). Hinge plate fairly narrow with three cardinals in each valve radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid. Inner margin smooth. Adductor scars sub-circular with posterior scar larger than semi-circular anterior scar. Pallial sinus deep, sub-quadrate very erect (Pallial sinus angle 47°, range 33°–56°) Pallial line with discontinuous

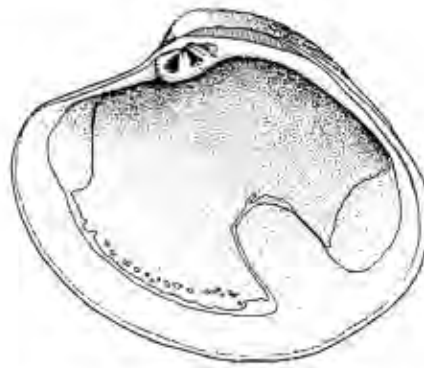


Fig. 6. *Paphia (Protapes) gallus bombayana* n. subsp. from Bombay. Scale bar = 30 mm.

accessory pallial muscle scars. Colour fawn occasionally with brown rays and/or zigzag streaks.

Habitat: Unknown.

Distribution: Eastern Arabian Sea from Karachi to Bombay (Fig. 7d).

Remarks: This variety bears a strong resemblance to the shell figured in Reeve (1864) and labelled as *Tapes turgidula* Deshayes. The true *T. turgidula* of Deshayes is synonymous with *T. turgida* Lamarck 1818.

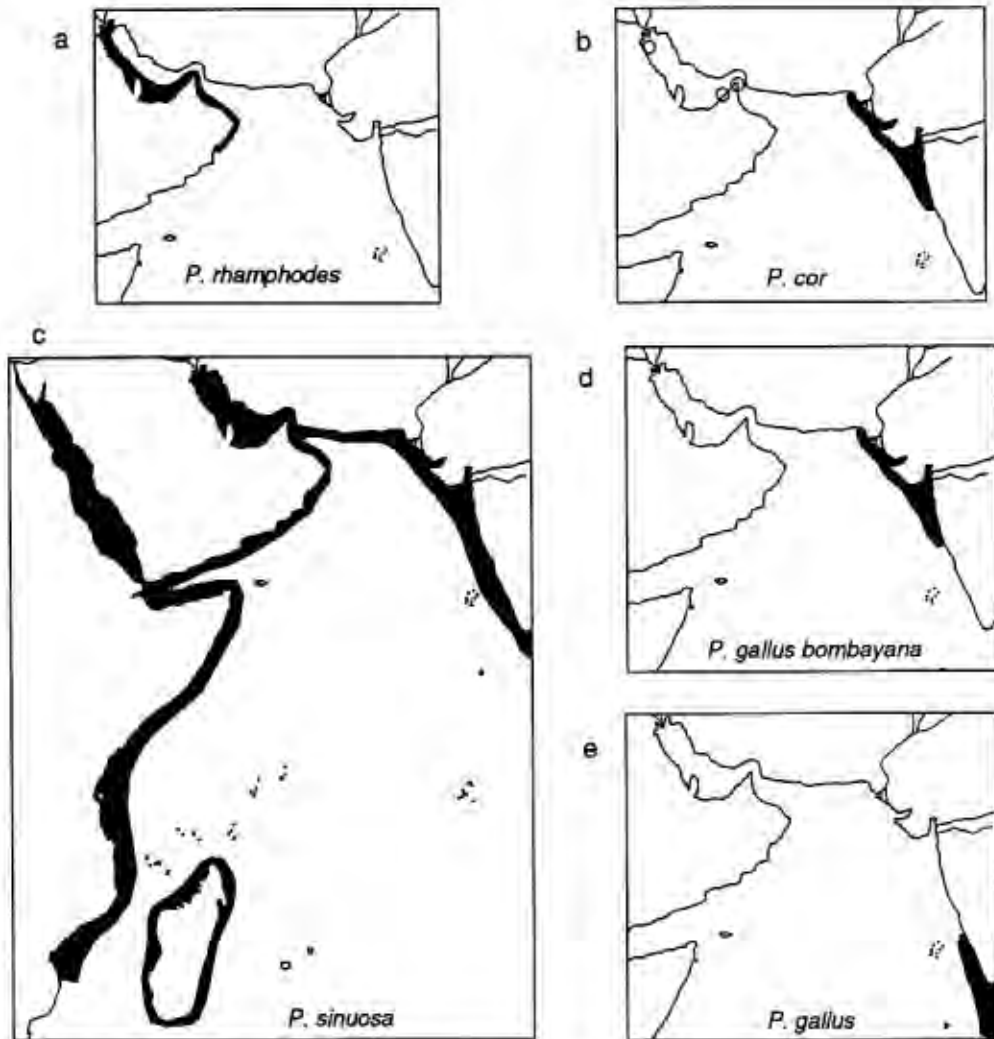
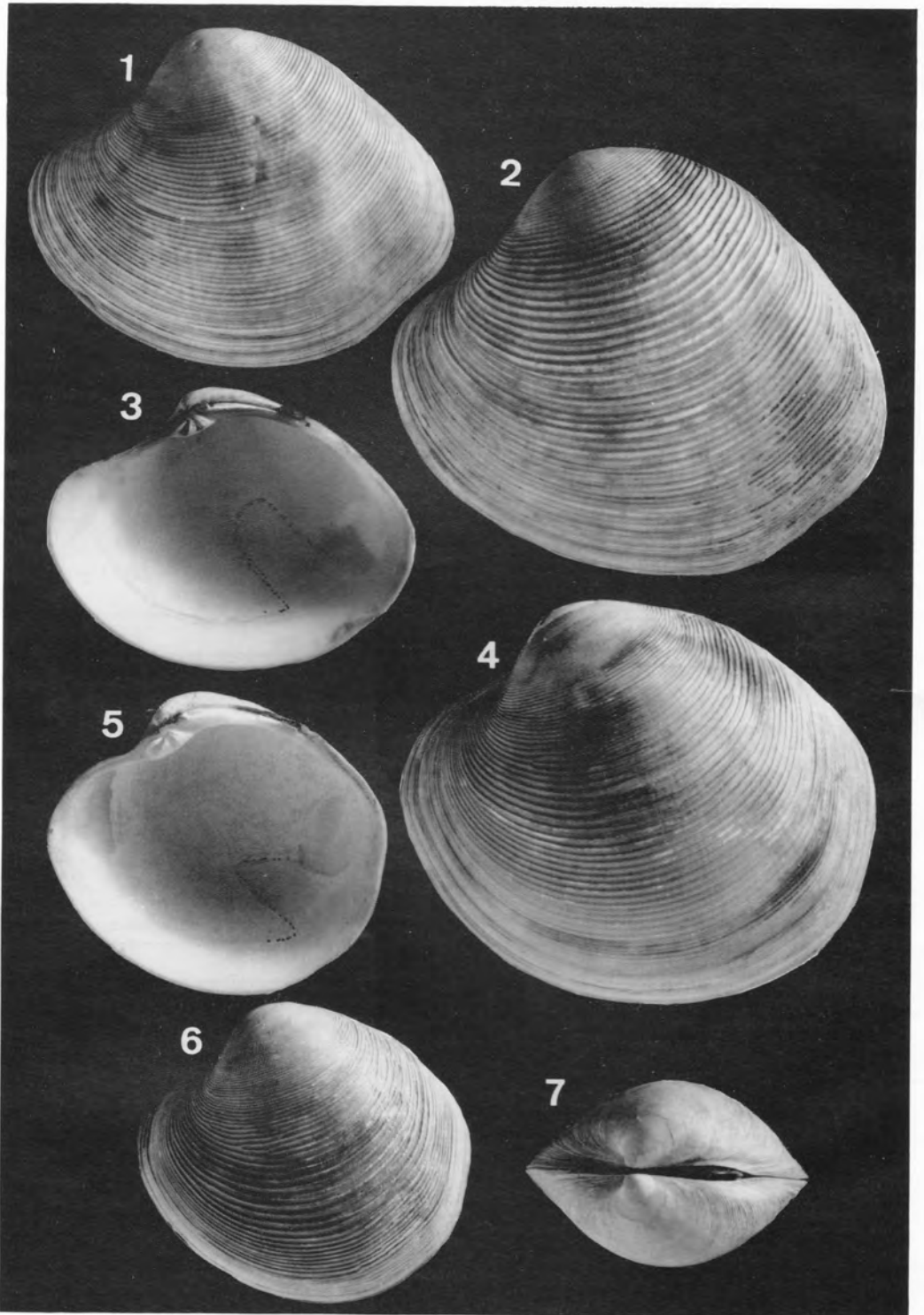


Fig. 7a-e. Distribution maps for five forms of *Protapes* found in the western Indian Ocean. Black areas - living; Open circles - dead shells only



Paphia (Protapes) cor (Sowerby, 1853)

Plate 3.4–3.77. Text figs. 8a–b.

Venus cor G. Sowerby 1853: p. 727 pl. 160 fig. 184

Tapes cor Sowerby: Römer, 1870 p. 103 pl. 40 fig. 4

Paphia cor Sowerby: Fischer-Piette & Métivier, 1971: p. 39.

Material

Holotype: BM(NH), Coll Mus. Cuming, Karachi.

Other material examined: Gulf of Kutch, 4sh. + 1v., Coll. H. Fedden, NMW. 1894.15; Baba Island, Karachi, 3sh., Leg. H. Winckworth, 6.x.1928, Coll. Melvill-Tomlin, NMW. 1955.158; 10sh., Coll. Winckworth, BM(NH) 1838; Dubai, 2v., Coll. H. Kauch, NMW.Z. 1993.061.1708; Hormuz, 1v., Coll. K. Smythe, NMW.Z. 1995.008.266; Arrakan, Burma, 2sh., Coll. H. Fedden, NMW. 1894.15; Pondicherry Coll. McAndrew BM(NH).

Description: Shell length to 75 mm; shell relatively solid, well inflated (Length to Tumidity ratio 1.50:1, range 1.36:1–1.62:1). Inequilateral, beaking towards anterior (Length to Anterior Length ratio 3.34:1 range 3.13:1–3.52:1). Shell broadly sub-ovate; anterior narrower than posterior, posterior dorsal margin rounded somewhat sinuous on posterior margin, which can be sub-truncate. Ventral margin well rounded; anterior dorsal margin short, concave, anterior margin sub-acute. Escutcheon very weak, shallow, ribbed. Lunule indistinct, ridged. Shell sculpture of many strong, concentric ridges separated by nearly equal grooves (lirae spacing 0.74 mm, range 0.52–1.01). Hinge with three cardinal teeth in each valve; RV posterior and middle bifid; LV anterior and middle bifid; anterior cardinal thin, curved. Ligament on long shallow nymph. Lunule margins with shallow groove; remainder of inner margin smooth. Adductor scars, posterior sub-circular larger than semi-circular anterior. Pallial sinus fairly deep, only slightly erect, sub-truncate (angle 24°, range 16°–30°). Occasional accessory pallial muscle scars. Colour light fawn, slightly darker near umbo. No rays.

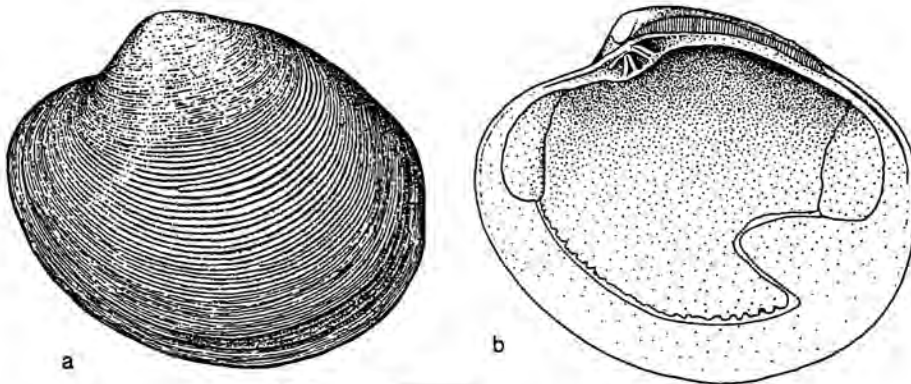


Fig. 8. *Paphia (Protapes) cor* (Sow.) from Karachi. Scale bar = 30 mm.

← Plate 3. 3.1 & 3.3, *Paphia (Protapes) gallus bombayana* n. subsp. Bombay (BM(NH) 1953.1.2.169/70; 3.2, *Paphia (Protapes) gallus bombayana* n. subsp. Holotype Ratnagiri (BM(NH) 996023; 3.4, *Paphia (Protapes) cor*, Karachi (NMW. 1955.158); Figs. 3.5–3.7, *Paphia (Protapes) cor*, Arrakan (NMW. 1894.15)

Habitat: Unknown but locality data suggests that it is restricted to estuarine or brackish embayments.

Distribution: Eastern Arabian Sea from Karachi to the Gulf of Kutch and as dead shells from Kuwait and Hormuz in the Arabian Gulf (Fig. 7b) and Bay of Bengal (Pondicherry and Arrakan).

DISCUSSION

The morphometric analyses presented here give statistical credence to our conclusion that there are five separate morphological groups within *Protapes* in the western Indian Ocean. These can be distinguished on a combination of shell characters; outline as expressed by the ratios of length to height, anterior length to total length and length to tumidity; pallial sinus length and angle of ascent and external sculpture. Comparisons of these parameters are illustrated by the box plots in Figure 9A–F and the bivariate scattergrams in Figure 10.

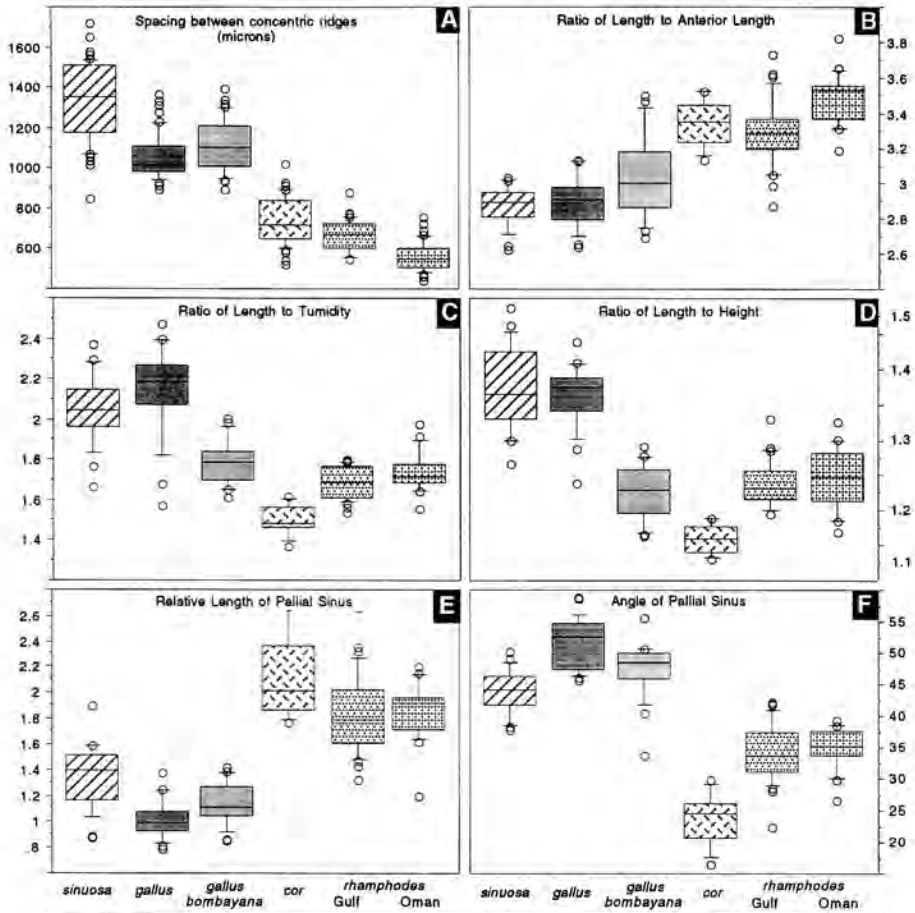
Paphia (Protapes) cor is the most divergent and separates on nearly all characters. It is the most rounded, most tumid, has the shallowest pallial sinus and with the least angle of ascent. The posterior twisting is very slight and the lunule is not defined. The latter characters bring into doubt the placing of this species in *Paphia* s.l. In museum collections the genus *Hemitapes* is often given for *cor* but this is not correct as this name is a synonym of *Marcia* (Dall, 1902). We are reluctant without a much wider ranging review of the Tapetinae to give an alternative generic placement and follow Fischer-Piette & Métivier in retaining it in *Paphia*.

Paphia (Protapes) rhamphodes is distinguished by its small size, fine sculpture, relatively shallow pallial sinus and the narrow beaked anterior area. The statistical significance of these characters in comparison to *P. (P.) gallus* and *P. (P.) sinuosa* are very high, all above the 95% confidence limits.

The remaining groups, described above as *P. (P.) sinuosa*, *P. (P.) gallus* and *P. (P.) gallus bombayana* all show more overlap in the morphometric analyses. *Paphia (Protapes) sinuosa* can be separated from *P. (P.) gallus* because of its shallower and less acute pallial sinus and the coarsest sculpture of all in the *Protapes* species discussed here.

Although colour is seldom reliable all *P. (P.) sinuosa* from the Arabian Sea show some radial maculations in shades of brown over a buff background. *Paphia (Protapes) gallus* is recognisable by its compressed, approximately triangular outline with a very deep, steeply ascending pallial sinus. *Paphia (Protapes) sinuosa* and *P. (P.) gallus* can be regarded as separate species as there is considerable overlap in their geographic range without any indication of intermediate forms. Neither clinal nor ecophenotypic variation are plausible explanations for the morphometric differences expressed by these taxa. This conclusion is in keeping with that of Matsukuma (1988) but conflicts with Fischer-Piette & Métivier (1971) who synonymised these names.

Paphia (Protapes) gallus bombayana n. subsp. described here is problematic not only in terms of its relations but also because it highlights the frailty of relying on shell morphometrics alone. It is distinguishable from typical *P. (P.) gallus* primarily by its large size, more triangular outline, increased tumidity and coarse sculpture and may be equivalent to some of the monstrose forms described by Römer (1870). The form lies at the extreme western end of the range of *P. (P.) gallus* s.l. and apparently does not overlap with the typical form which does not extend beyond the Malabar coast. We have little habitat data for this subspecies but we can note that there is an increasing influence of freshwater run off as one moves north culminating at the Indus Delta. Both clinal and ecological barriers are therefore possible explanations for the appearance of this variety. Those characters which reflect internal



	Spacing between concentric ridges				Ratio of Length to Anterior Length				Ratio of Length to Turidity			
	Count	Mean	Std. Dev.	Std. Err.	Count	Mean	Std. Dev.	Std. Err.	Count	Mean	Std. Dev.	Std. Err.
a	50	742.64	116.21	16.43	8	3.341	.135	.048	8	1.501	.080	.028
b	50	1327.47	187.60	26.53	25	2.875	.113	.023	25	2.056	.170	.034
c	50	1111.61	131.12	18.54	19	3.042	.233	.054	19	1.791	.115	.027
d	50	1055.08	118.71	16.78	25	2.889	.142	.028	25	2.150	.217	.043
e	50	562.77	68.53	9.69	17	3.481	.149	.036	17	1.743	.102	.025
f	50	664.90	75.72	10.70	29	3.289	.193	.036	29	1.686	.078	.014

	Ratio of Length to Height				Relative Length of Pallial Sinus				Angle of Pallial Sinus			
	Count	Mean	Std. Dev.	Std. Err.	Count	Mean	Std. Dev.	Std. Err.	Count	Mean	Std. Dev.	Std. Err.
a	8	1.159	.021	.008	8	2.116	.341	.120	8	23.673	4.181	1.478
b	25	1.376	.062	.012	25	1.346	.240	.048	25	43.671	3.536	.707
c	19	1.227	.039	.009	19	1.139	.165	.038	19	47.391	4.584	1.052
d	25	1.361	.042	.008	25	1.009	.145	.029	25	51.698	4.118	.824
e	17	1.247	.046	.011	17	1.862	.233	.057	17	34.830	3.441	.835
f	29	1.239	.033	.006	29	1.840	.306	.057	29	34.098	4.488	.833

a. *Protapes cor*; b. *P. sinuosa*; c. *P. gallus bombayana*; d. *P. gallus*; e. Oman *P. rhamphodes*; f. Gulf *P. rhamphodes*.

Fig. 9a-f, Box plots for comparison of morphometric analyses of six shell characters in *Protapes* from the Indian Ocean.

anatomy such as pallial sinus angle and length are not significantly different from the typical *gallus* and therefore we are reluctant to assign full species status to this morphological group without further study.

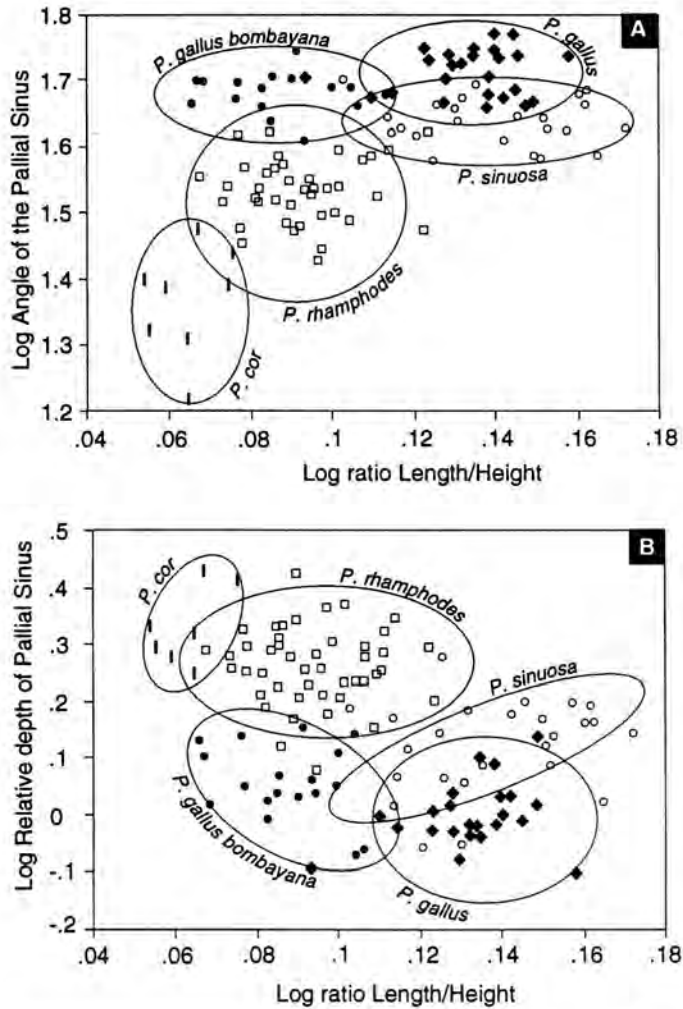


Fig. 10. Bivariate plots of outline (Length to Height Ratio) and pallial sinus characters (Angle and Depth) for five forms of *Protapes* from the Indian Ocean.

INSTITUTIONAL ABBREVIATIONS

BM(NH): British Museum (Natural History) now Natural History Museum
 NMW National Museum of Wales before 1970
 NMW.Z. National Museum of Wales after 1970
 MNHN Museum of National d'Histoire Naturelle, Paris
 ZMC Zoological Museum, Copenhagen

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