

**SPECIES DISCRIMINATION IN SEVEN SPECIES OF *BARBATIA*
(BIVALVIA: ARCOIDEA) FROM THAILAND WITH A REDESCRIPTION OF
B. GRAYANA (DUNKER, 1858)**

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ABSTRACT. – Seven species belonging to the genus *Barbatia* were collected from the Kungkrabaen Bay region of southeastern Thailand: *B. foliata* (Forsskål, 1775), *B. decussata* (Sowerby, 1833), *B. trapezina* (Lamarck, 1819), *B. grayana* Dunker, 1867, *B. fusca* (Bruguière, 1789), *B. virescens* (Reeve, 1844), and *B. bistrigata* (Dunker, 1866). Soft tissue colouration of the living animal is found to be a reliable taxonomic character and this is supported by the anatomical characters of the gut looping and anal papilla. Using anatomical characters to confirm shell characters allowed a review of the *foliata/decussata* complex resulting in the recognition of three species: *B. foliata*, *B. decussata* and *B. trapezina*. A lectotype is selected for *B. trapezina*. *Barbatia grayana* is redescribed and a neotype is selected; it is considered not to be part of the *foliata/decussata* complex and most closely resembles *B. multivillosa* (Iredale, 1939). The nomenclature of all species is reviewed and the name *B. fusca* (Bruguière) is retained in preference over *B. amygdalumtostum* (Röding, 1798). *Barbatia signata* (Dunker, 1868), although not found during the workshop, is described as it has been confused with both *B. bistrigata* and *B. grayana*.

KEYWORDS. – Arcidae, morphology, anatomy, taxonomy, systematics.

INTRODUCTION

The genus *Barbatia* in the Indo-Pacific is currently represented by at least 50 nominal species and includes at least 16 nominal subgenera or generic synonyms (OBIS, 2006). Some species are common components of rocky and coralline biotopes in the intertidal and shallow subtidal zones and amongst these are taxa referred to as *B. foliata* (Forsskål, 1775), *B. decussata* (Sowerby, 1833), *B. lima* (Reeve, 1844), and *B. trapezina* (Lamarck, 1819). This group of species, which will here be referred to as the “*foliata/decussata* complex”, has a long and confused nomenclatural history as first evidenced by Lamy’s (1907) revision in which extensive lists of nominal taxa and citations were reviewed. In his time, the non-binomial names of Chemnitz (1784) were still in use and there was acceptance of pan-Atlantic/Indo-Pacific species. Prashad (1932) was next to give extensive synonymy lists and the nomenclatural confusion was summarised by Iredale (1939), but he did not resolve this and only introduced further confusion by creating new nominal species for the Great Barrier Reef material that he was studying.

Oliver (1992) recognised two species in this complex—*B. foliata* and *B. decussata*—in the Red Sea but later Dekker & Orlin (2000) synonymised *B. decussata* with *B. trapezina*. For the Australian fauna, Lamprell & Healy (1998) recognised *B. foliata* but synonymised *B. decussata* with *B. grayana* (Dunker, 1867) and retained *B. trapezina* as a third species in the group. These citations amply indicate the continuing confusion within this complex of species. Concerning the genus *Barbatia* in the Gulf of Thailand, this continuing uncertainty is evidenced by comparing the taxa and illustrations presented by Swennen et al. (2001) with those of Robba et al. (2002).

The International Marine Bivalve Workshop, Kungkrabaen Bay, Thailand, 2005, presented an opportunity to examine living arcids in their natural habitats. Anatomical characters and habitat preferences could be added to the traditional suite of shell characters used in all previous studies. During the workshop, a number of *Barbatia* species were found in the intertidal and shallow sublittoral and a further species was found in fishermen’s net trash from offshore. Included were

forms attributable to the *foliata/decussata* complex, thus presenting an opportunity to revisit this problem in particular. This study has the aim of recognising morphological characters and ecology that are reliable in distinguishing species of *Barbatia* found in the Gulf of Thailand.

Caution might be needed in any application of these findings to species discrimination in other geographic areas. We strongly recommend that similar studies at other locations be undertaken to confirm that the characters hold true in species that have a wide Indo-Pacific range.

This study does not attempt to revisit previous studies and especially cannot revise the lengthy synonymies given by Lamy (1907) and Prasad (1932). We do, however, attempt to give the taxa recognised here correct nomenclature and in doing so revisit some of the issues surrounding the earliest available names.

This study will also not comment on the generic nomenclature contained within the concept of *Barbatia* sensu lato. It suffices to state that we are aware that this large complex of species probably contains a number of genera, and indeed, that none of the species included here might be congeneric with the type species of *Barbatia*, *Arca barbata* Linnaeus, 1758, from the Mediterranean Sea.

MATERIALS AND METHODS

All of the observations on living material were made on specimens collected during the International Marine Bivalve Workshop, Kungkrabaen Bay, Thailand, 2005. This material is now deposited in the National Museum of Wales, Cardiff.

All literature citations have been taken from the original texts, which are present in the Tomlin Library in the National Museum of Wales. Many of these volumes contain annotations by Winckworth or Tomlin on the dates of publication, and pagination is taken from them.

Living material was collected in the field, where habitat (substratum, tidal level, exposure, and orientation) was recorded before removing the material to the laboratory. The valves were separated by inserting a scalpel in the byssal gape and cutting through the adductor and byssal retractor muscles close to the shell. The exposed soft tissues were then recorded for colour pattern, relative size of organs, and degree of mantle folding. The digestive system was examined by dissection from the left side to reveal the shape and course of the alimentary canal and stomach. All dissections were recorded by digital colour photography with the addition of line drawings of the gut.

Shell characters included those of the periostracum, general outline and radial ribbing. As all species included are epibyssate, they can be variable in outline due to influence from the substratum to which they are attached. All species have the habit of adding riblets between the primary ribs or

display splitting of the primary ribs as they increase in size. This makes rib number difficult to use as a character when examining shells of different sizes. Ribbing is shown as an overall pattern of expression and micro-sculpture in shells in which the periostracum has been removed by soaking in bleach. The resulting white shells were then blackened with ink before coating with ammonium chloride (NH₄Cl) sublimate to enhance the topography of the sculpture.

Similar issues arise when examining the number of teeth and number of ligament chevrons. Both increase in number with growth, with that of the ligament often being allometric. Tooth number can decrease in gerontic shells by erosion of the hinge plate through transgression of the ligament.

Abbreviations used in this paper are:

Institutional: BMNH, The Natural History Museum, London; MNHN, Museum National d'Histoire Naturelle, Paris; NMW and NMWZ, National Museum of Wales; ZMB, Zoological Museum, Berlin; ZMUC, Zoological Museum, University of Copenhagen.

Material: sh., shell of both valves; ex., live-collected specimen complete with soft tissues; v., unpaired valve.

Anatomical: DDD, digestive diverticula ducts; HG, hindgut; MG, midgut; OE, oesophagus; S, stomach; SS/MG, combined style sac and midgut.

TAXONOMY

Barbatia Gray, 1842

Type species. – *Arca barbata* Linnaeus, 1758.

Diagnosis. – Shell small- to medium-sized, compressed. Outline inequilateral, beaks towards anterior; subtrapezoidal with medium-sized byssal sinus. Hinge taxodont, teeth numerous. Ligament in cleft dorsal area; chevrons numerous. Sculpture mostly subcancellate. Periostracum lamellose, mostly with radial arrays of bristles. Byssus strong. Habit epibyssate.

The *foliata/decussata* Complex

Barbatia foliata (Forsskål, 1775)

(Figs. 1a–d, 4c, 5c, 6a–b, 7a)

Arca foliata Forsskål, 1775: xxxi.

Arca nivea maris rubri Chemnitz, 1784: 191, Tab. 54, Fig. 538.

Arca ovata Gmelin, 1791: 3307.

Arca scaphaciunacula Meuschen, 1781: 274, #1174, Tab. 18, Fig. 7.

Arca nivea Röding, 1798: 174.

Byssosarca velata Sowerby, 1833: 18.

Material examined. – Type material: Lectotype, 1 v. (see Kilburn & Rippey, 1982: 215–216; for image, see Yaron et al., 1986:

196–197, Fig. 47) (ZMUC), Red Sea, coll. Forsskål; syntypes of *Byssoarca velata* Sowerby, 3 sh. (BMNH 1969238), Lord Hood's and Chain Islands.

Other material examined. – 1 ex. (NMWZ.2005.21.16), off Chong Saba Island, Gulf of Thailand, among coral, 4 m; 5 ex. (NMWZ.2005.21.167), off Him Tamae, outside of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°32.862'N 101°57.831'E, among coral, 6 m; 6 ex. (NMWZ.2005.21.166), Koh Nom Sao Island, Laem Singha district, Gulf of Thailand, Thailand, 12°27.90'N, 102°01.39'E, extreme low water mark to 1 m among coral; toptotypical material of *Barbatia foliata*, many ex. (various lots in NMW collection), Bay of Safaga, Red Sea.

Diagnosis. – Shell (Figs. 1a–d, 4c): Large, our material to 88 mm in length. Outline initially trapezoidal (Fig. 1c) becoming trigonal in larger specimens (Fig. 1a); posterior greatly expanded, with beaks at about one-third of length from anterior in smaller shells, becoming more central in larger shells. Median sulcus flat or weakly concave. Byssal sinus

variable but byssus massive. Sculpture (Fig. 4c) of numerous radial riblets (maximum 85) intersected by equally dense but less deep commarginal grooves, to give overall subcancellate sculpture. Anterior riblets distinctly larger (Fig. 4c/v), more widely spaced than on posterior, especially in larger shells. Shell colour white.

Periostracum (Fig. 5c): Very thick, of commarginal fringes with pointed bristles between ribs, longer at posterior angle.

Soft tissue colouration (Fig. 6a): Anterior mantle edge orange, anterior mantle white; posterior mantle and inner fold velvet black with bluish iridescence; this colour in outer epithelium only, easily damaged. Middle and outer folds orange pink (anterior) to dark red (posterior). Foot mostly white, with reddish tinge along byssal groove. Ctenidia grey, posterior filaments and free part of gill axis becoming black as in mantle. Posterior mantle edge weakly undulating.

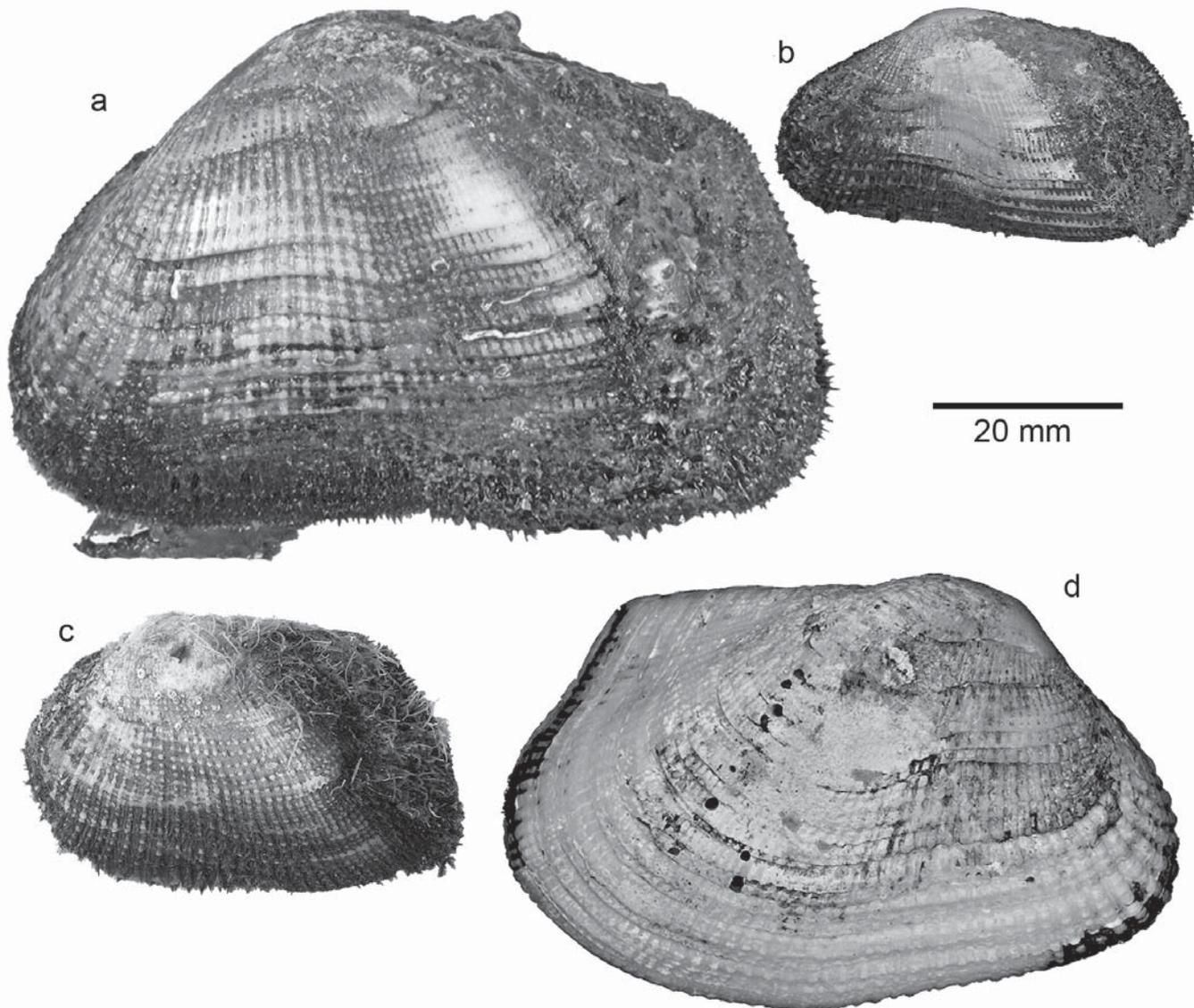


Fig. 1. *Barbatia foliata* (Forsskål), Kungkrabaen Bay, Thailand: a–c, variations, NMWZ.2005.21.166/167; d, right valve with periostracum removed, NMWZ.2005.21.16.

Anal papilla (Fig. 6b): Narrow and curved; white in colour contrasting with surrounding black mantle.

Palps: With 18 sorting ridges, grey in colour.

Gut (Fig. 7a): Midgut with simple but tight, double-S-shaped loop, not extending far anteriorly or dorsally.

Habitat. – Restricted to coral reefs, deeply embedded in living or dead coral.

Remarks. – The mantle colouration of this species is very distinctive with the contrasting velvet black and pink/red posterior mantle. Small and large examples can now be recognised revealing the shell to have coarse, rather widely spaced, anterior ribs with a tendency for the outline to rapidly become triangular with size. The periostracum is very thick especially over the posterior and is foliose rather than spicate.

Given these shell characters and after examination of the types, *Byssoarca velata* Sowerby is considered here to be a junior synonym. The names *Arca nivea* Chemnitz or *A. nivea* Röding (Bolten) have been widely used to include many of the species within the *foliata/decussata* complex (Lamy, 1907). From Chemnitz (1784: 191), it can be seen that he regarded his *Arca nivea maris rubri* and Forsskål's *A. foliata* to be the same species. Therefore, *A. nivea* is an unambiguous junior synonym of *A. foliata* Forsskål (see also Yaron et al., 1986). Furthermore, *A. ovata* Gmelin is also based on *A. nivea* of Chemnitz and is, therefore, a junior synonym of *A. foliata*.

Iredale (1939: 254) mentioned *Arca scaphaciuncula* Meuschen as part of the *foliata/decussata* complex and reference to the illustration by Gronovius (1781) confirms this. This figure is regarded here to represent a shell of *Barbatia foliata*. Meuschen's (1781) index has now been considered unavailable for nomenclatural purposes and that should negate further enquiry (ICZN, 1954: Op. 261). However, Gmelin (1791: 3315) introduced *A. scapha* and cited a figure by Gronovius (1781: tab. 18, Fig. 7). Unfortunately, the cited figure is that of *A. scaphaciuncula* Meuschen and not that of *A. scapha* Meuschen. It can be presumed that Gmelin made a lapsus calumni in his citation and indeed *A. scapha* Meuschen has always been considered part of the *Anadara antiquata* complex (Lamy, 1907). For nomenclatural stability, it is preferable to maintain *A. scapha* Gmelin as part of the *antiquata* complex and we have not included it as a junior synonym of *B. foliata*.

***Barbatia trapezina* (Lamarck, 1819)**

(Figs. 2a–f, 4b, 5b, 6e–f, 7c)

Arca trapezina Lamarck, 1819: 41.

Arca lima Reeve, 1844: Pl. XV, sp. #101.

Material examined. – Type material: Lectotype, herein designated, 1 sh. (Fig. 2a) (MNHN 20000), Timor, coll. Lamarck; paralectotypes, 5 sh. (as lectotype; a sixth paralectotype is here considered to be a

shell of *Barbatia decussata* Sowerby, 1833, see discussion below) (MNHN 20001); syntypes of *Arca lima* Reeve, 1844, 2 sh. (BMNH 1969253), the Philippines.

Other material examined. – 3 ex. (NMWZ.2005.21.168), Laem Ban Tha Klaeng, northern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°35.22'N 101°53.05'E, attached to rocks on lower shore, 23 Aug.2005; 4 sh. (NMWZ.2005.21.138), Laem Ban Tha Klaeng, northern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°35.22'N 101°53.05'E, from shell midden, 23 Aug.2005; 2 ex. (NMWZ.2005.21.170), Hin Tamae Nok, Gulf of Thailand, Thailand, 12°32.28'N 101°53.86'E, patch reef, rubble zone, 10 m, 30 Aug.2005; 3 ex. (NMWZ.2005.21.169), Laem Ban Kung Kraben, southern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°34.932'N 101°53.147'E, attached to coral rubble, extreme low water mark, 30 Aug.2005; 2 ex. (NMWZ.2005.21.66), Koh Nom Sao Island, Laem Singha district, Gulf of Thailand, Thailand, 12°27.90'N 102°01.39'E, among coral rubble lower shore, 2 Sep.2005.

Diagnosis. – Shell (Figs. 2a–f, 4b): Medium-sized, our material to 45 mm in length. Beaks one-quarter of length from anterior margin. Outline trapezoidal, posterior margin sloping, almost straight, creating angled posterior ventral junction; anterior margin rounded, more vertical. Median sulcus flat to slightly concave, byssal sinus weak. Sculpture (Fig. 4b) of numerous riblets intersected by equally numerous, weaker commarginal grooves creating overall subcancellate appearance. (Although the sculpture is subcancellate, the nodules on the ribs are relatively weak except on every third or fourth intersection where the nodules are larger, this expressed as evenly spaced commarginal ridges; Fig. 4b/iv). Primary ribs on posterior slope (four or five in number) deeply cut, widely spaced (Fig. 4b/iii). Shell colour totally white.

Periostracum (Fig. 5b): Frequently worn with little remaining; of commarginal laminae each with weak bristles arising from grooves between ribs; posterior slope with widely spaced, erect, narrow, pointed bristles.

Soft tissue colouration (Fig. 6e): Mantle edge yellow with reddish-brown spots, larger and more dense over posterior area. Foot cream with brown streaks. Ctenidia reddish-brown.

Anal papilla (Fig. 6f): Long, thin, curved, coloured as surrounding mantle.

Palps: With 22 sorting ridges, yellow in colour.

Gut (Fig. 7c): Midgut loop extending anteriorly and dorsally, simple without tight coils.

Habitat. – Found attached under rocks or coral rubble, low in the intertidal and subtidal zones.

Remarks. – This species, along with *Barbatia decussata*, accounts for most of the confusion created in the *foliata/decussata* complex. Lamy (1904), Prashad (1932), and Iredale (1939) recognised that Lamarck's syntypic series of *Arca trapezina* is a mixture of two species. Lamy (1904, 1907) regarded *A. trapezina* as a synonym, in part, of *A. decussata*,

whereas Prashad (1932) also regarded it as a synonym in part of *A. decussata* and in part of *A. decussata* var. *lima*. Lamprell & Healy (1998) treated *B. trapezina* as a valid species and regarded *A. lima* as a synonym of *B. foliata*, and *Byssoarca decussata* as a synonym of *Barbatia grayana*. Throughout this long history of confusion, no one designated a lectotype to fix a definite concept for *A. trapezina*.

We have examined the syntypic series of *Arca trapezina*, *A. lima* and *Byssoarca decussata* and conclude that two species are present. The syntypic series of *A. trapezina* is a mixture of two different species and it is noted that none of the shells match that figured by Delessert (1841: Pl. 11 Figs. 13a–c).

The larger specimen (Fig. 3d) of the series is considered to match the types of *Byssoarca decussata* but the shell

is aberrant with a double hinge and ligament. The other specimens are considered to match the type of *Arca lima* (Fig. 2f). Although there is considerable variation in the outlines of the shells of the type series, *A. trapezina* and *A. lima* both share the critical sculptural and periostracal characters given here, and this is the basis for our synonymy. It is possible that with molecular data and anatomical observations, the variation in outline could prove to be significant, but the known ecophenotypic variation in outline among many species of *Barbatia* suggests a cautious approach at this time.

In order to fix a single concept for *Arca trapezina*, a lectotype designation is proposed (Fig. 2a). The larger aberrant specimen is disregarded here because it does not make a suitable type specimen and it is the only one of its form in the series. A consequence of this decision is that

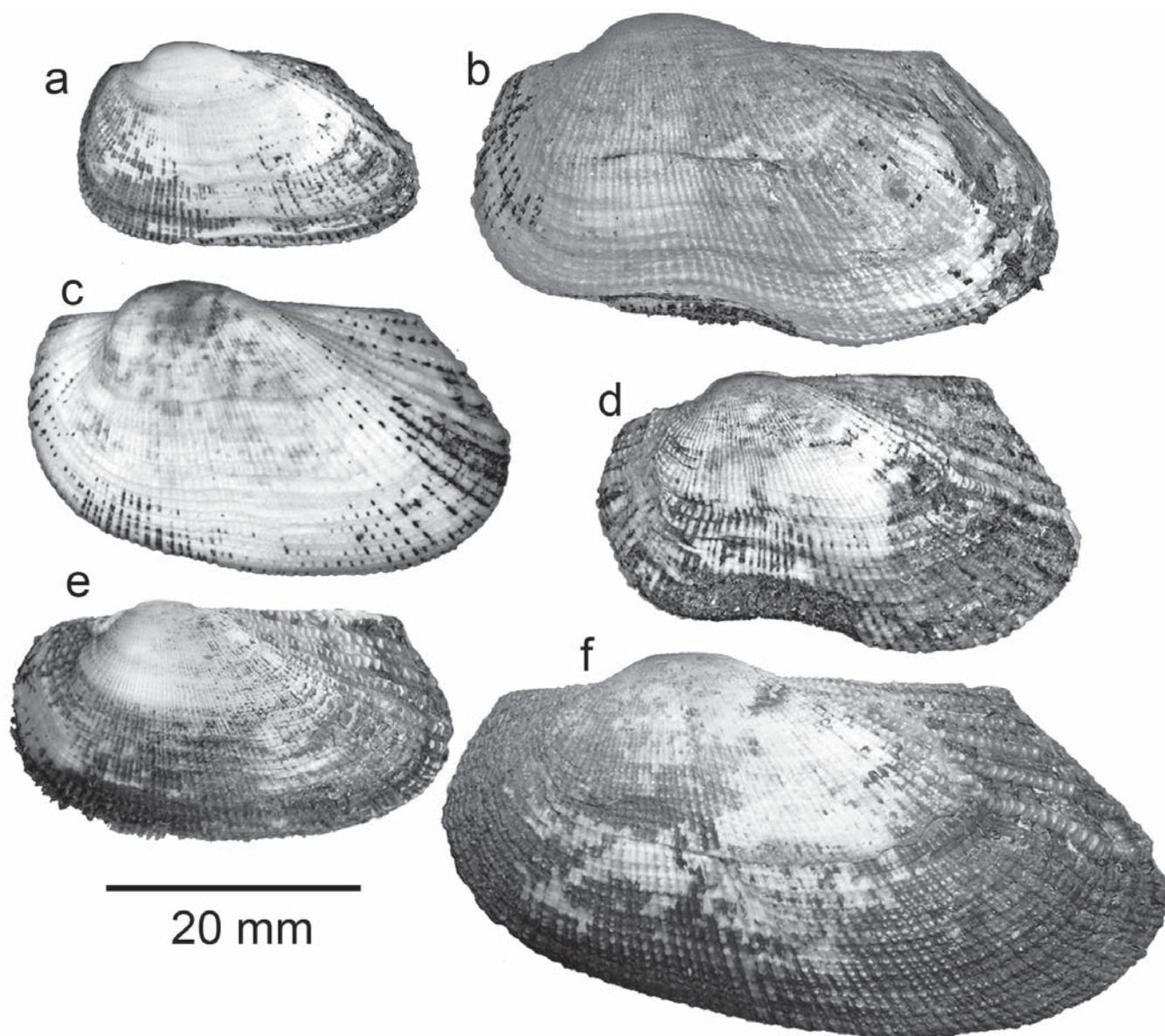


Fig. 2. *Barbatia trapezina* (Lamarck): a, Lectotype, MNHN 20000; b–e, variations from Kungkrabaen Bay, Thailand, NMWZ.2005.21.138/170; f, figured syntype of *Arca lima* Reeve, BMNH 1969253.

Barbatia decussata and *B. trapezina* are here considered two separate species. Choosing one of the remaining shells has the consequence of making *B. trapezina* a valid species with *A. lima* as a junior synonym.

Barbatia trapezina is therefore distinguished from *B. decussata* not only by the soft tissue colouration (compare Figs. 6c, e), but also by the periostracal bristles, which are spicate and erect rather than blunt and adpressed. The shell is generally more rectangular compared to the more anteriorly reduced shell of *B. decussata*. The posterior riblets number only four or five and remain deeply cut throughout life and widely spaced and the remaining riblets are narrow and weakly nodulose. In terms of habitat, *B. trapezina* is found from low in the intertidal to offshore, whereas *B. decussata* is confined to the intertidal and here ranges into the upper zone.

***Barbatia decussata* (Sowerby, 1833)**
(Figs. 3a–g, 4a, 5a, 6c–d, 7b)

Byssoarca decussata Sowerby, 1833: 18.

Material examined. – Type material: Syntypes, 3 sh. (Figs. 3a–c) (BMNH 1969232), Lord Hood’s Island.

Other material examined: 1 sh. (part of the paralectotypic series of *Barbatia trapezina*) (MNHN 20001), Timor, coll. Lamarck; 20+ ex. (NMWZ.2005.21.011, .101 & .171), Laem Ban Tha Klaeng, northern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, attached to rocks and under rocks on upper to mid shore, 12°35.22’N 101°53.05’E, 23 Aug.2005; 5 ex. (NMWZ.2005.21.172), Laem Ban Kung Kraben, southern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, attached to and under rocks on upper to mid shore, 12°34.932’N 101°53.147’E, 30 Aug.2005.

Diagnosis. – Shell (Figs. 3a–g, 4a): Medium-sized, our material to 55 mm in length. Beaks in front of midline approximately one-third of length from anterior margin. Outline trapezoidal, with anterior and posterior margins rounded. Median sulcus slightly concave; byssal sinus clearly defined. Sculpture of dense, evenly sized, low, radial riblets intersected by equally dense commarginal grooves giving overall nodulose, subcancellate appearance (Fig. 4a). Five to seven ribs on posterior area low; interspaces quickly developing secondary riblets (Fig. 4a/i) (Although the sculpture appears primarily radial, the anterior and posterior riblets are distinctly nodulose; Fig. 4a/ii). Shell colour white.

Periostracum (Fig. 5a): Of dense commarginal fringes, each with short, adpressed, pointed bristles between riblets.

Soft tissue colouration (Fig. 6c): Anterior mantle edge and mantle beige, tinged pink by haemoglobin in tissues; posterior mantle reddish-brown with mantle edge of deeper shade of red-brown. Foot pale, streaked with brown. Ctenidia brown-yellow to dark brown; gill axis heavily streaked with brown. Posterior mantle edge with many undulations.

Anal papilla (Fig. 6d): Short and triangular, yellow in colour.

Palps: With 28–32 sorting ridges, yellow in colour.

Gut (Fig. 7b): Midgut loop rising with three tight coils.

Habitat. – Attached to the undersides of rocks and coral rubble from high in the littoral zone to mid-shore.

Remarks. – The nomenclature of *Barbatia decussata* has been largely clarified within the discussion on *B. trapezina*, above. The belief that this name is preoccupied by *Arca decussata* Linnaeus, 1758, as stated by Lamprell & Healy (1998) is mistaken, because Sowerby introduced the name under the genus *Byssoarca* and not *Arca*. The same authors synonymised *B. decussata* with *B. grayana* (see under the latter, below).

Morphological comparisons with *B. trapezina* are made above under that species discussion.

***Barbatia grayana* Dunker, 1867**
(Figs. 4e, 5d, 6g–h, 7d, 8a–e)

Barbatia grayana Dunker, 1867: 92, Pl. 31 Figs. 5–7.

Barbatia signata Dunker, 1868 – Rabba et al., 2002: 55, Pl. 1 Fig.10.

Barbatia sp. – Swennen et al., 2001: 65, Fig. 025.

NOT *Barbatia grayana* Dunker, 1858 – Lamprell & Healy, 1998: 46, Fig. 55.

Material examined. – Type material: Neotype, herein selected, 1 ex. (Fig. 8b) (NMWZ.2005.21.173), Pak Nam Khem Nu, Gulf of Thailand, Thailand, 12°32.3’N 101°57.0’E, from debris in fishermen’s nets on quay side, 1 Sep.2005.

The original shell described by Dunker could not be located. It was stated by Dunker (1867) to be part of the Museum Godeffroy and this collection was largely incorporated into the Zoological Museum, University of Hamburg. It is likely that along with much of the dry molluscan collection, the type was destroyed during World War II. The collections in the Zoological Museum, Berlin, and The Natural History Museum, London, were also checked because Dunker types are also located in these museums. With the lack of original material, a neotype designation is made here. This course of action is taken because the original figure (Fig. 8a) clearly shows the fine radial sculpture and broad periostracal bristles typical of the new material at hand, giving confidence to the application of the name *B. grayana*. The type locality given by Dunker is simply “Ex Indiis misit clar. Gräfe”, which translates as “from [east] Indies sent by Gräfe” and consequently selecting a neotype from Thailand does not contradict the original description. The original type was 35 mm in length and rather smaller than the majority of specimens collected in Thailand.

Other material examined: 6 ex. (live-collected as neotype) (NMWZ.2005.21.174); 7 sh. (NMWZ.2005.21.74), from shell midden close to village of Pak Nam Khem Nu, Gulf of Thailand, Thailand, 12°32.3’N 101°57.0’E, 1 Sep.2005; comparative material of *B. multivillosa*, 8 ex. (NMWZ.1991.121.55), deep water port, Broome, Western Australia, Australia, intertidal, attached to rocks, coll. P. G. Oliver, 29 Jan.1991.

Diagnosis. – Shell (Figs 4e, 8b–e): Medium-sized, to 58 mm length, distinctly compressed, with length:tumidity ratio 2.7:1. Outline trapezoidal, with posterior distinctly more expanded than anterior, beaks about one-third of length from anterior margin. Posterior dorsal area well-defined; posterior margin almost subauriculate. Median sulcus weakly depressed; byssal sinus clearly defined.

Sculpture (Fig. 4d): predominantly of numerous, very fine radial riblets crossed by commarginal grooves giving finely nodulose appearance, but in reality more complex and changing with growth; posterior dorsal area initially with six or seven primary riblets, these becoming progressively indistinct; three or four riblets on posterior carina rapidly widening, bifurcate or trifurcate (Fig. 4d/vi); riblets over

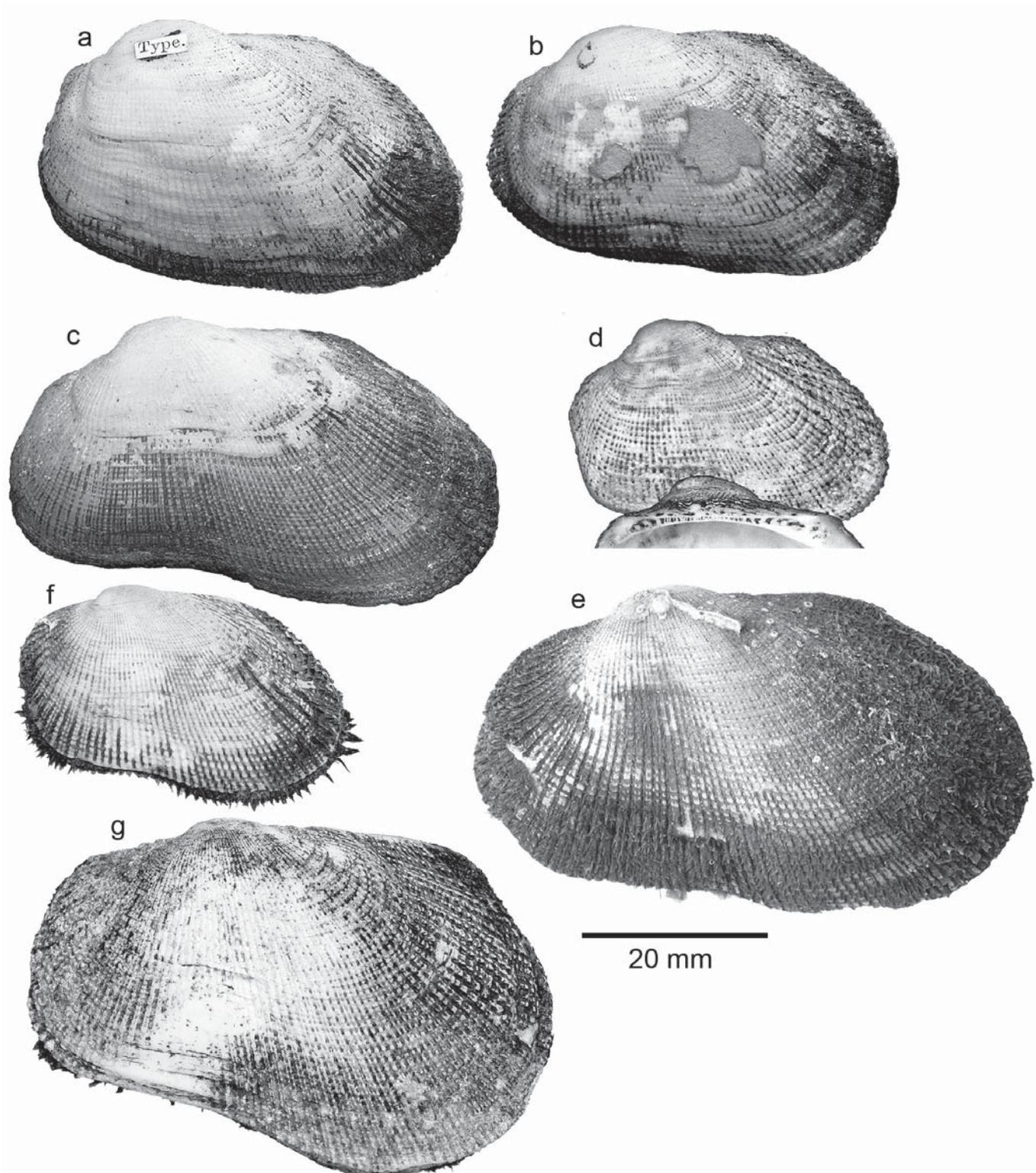


Fig. 3. *Barbatia decussata* (Sowerby): a–c, syntypes of *Byssarca decussata* Sowerby, BMNH 1969232; d, aberrant shell from type series of *Arca trapezina*, MNHN 20001; e–g, variations from Kungkrabaen Bay, Thailand, NMWZ.2002.21.11/171/172.

median area narrow, becoming bifurcate with secondary riblets developing between bifurcations; anterior riblets more broad, often distinctly bifurcate (Fig. 4d/vii). Total rib count at margin ca. 50 in smaller shells (25 mm), increasing in larger (50 mm) shells to ca. 100.

Hinge teeth numerous but variable, rather small, with to 35 teeth in anterior set, 34 in posterior set; posterior set often degraded medially, therefore reduced in number to 16 in some specimens; outer posterior teeth set obliquely, outer anterior teeth less so. Ligament duplivincular with well-developed chevrons set on shallow, cleft dorsal area.

Periostracum (Fig. 5d): Overall of commarginal soft lamellae, very weak, strengthening between ribs to form indistinct bristles, except over posterior carina as few, widely spaced radial rows of large foliate bristles, these with two or three strengthening ridges projecting well beyond shell edge. Rows of foliate bristles lying on wide bifurcate or trifurcate riblets. Anterior bristles also larger than on median area but not so well developed as those on posterior carinal area.

Anatomy: Typical of epibyssate *Barbatia* species in being heteromyarian, with anterior adductor muscle smaller than posterior; byssal retractor muscles large, elongate; foot with

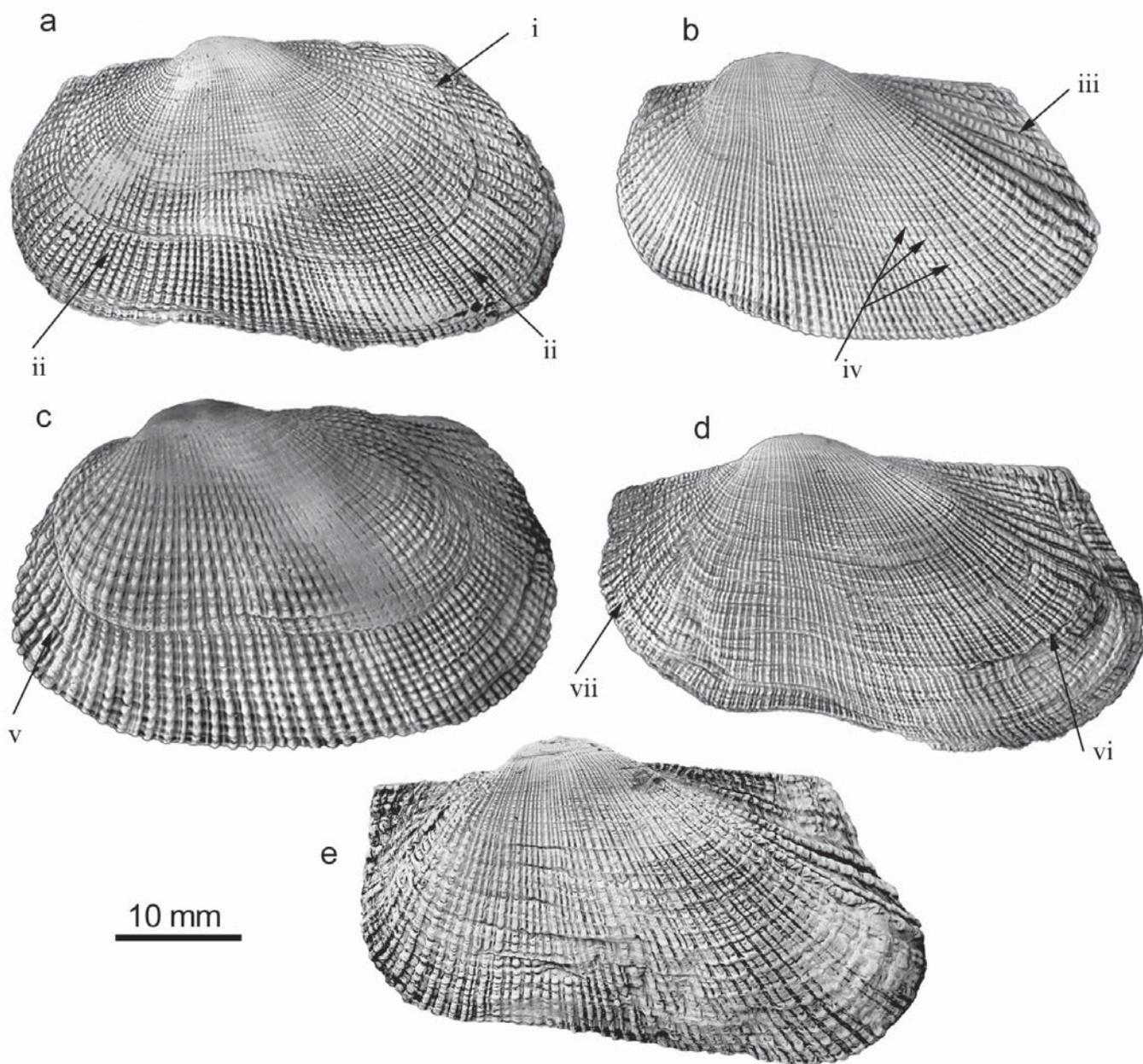


Fig. 4. Left valves of five species of *Barbatia*, periostracum removed, blackened, and coated with ammonium chloride. a, *B. decussata*, NMWZ.2005.21.101; b, *B. trapezina*, NMWZ.2005.21.138; c, *B. foliata*, NMWZ.2005.21.167; d, *B. grayana*, NMWZ.2005.21.74; e, *B. multivillosa*, Broome, Western Australia, NMWZ.1991.121.55. Arrows numbered with Roman numerals refer to characters cited in the text.

wide byssal groove, large toe, small heel. Mantle edges unfused; mantle edge frilled around posterior ventral region. Ctenidia of both demibranchs large; gill axis muscular, extendable.

Soft tissue colouration (Fig. 6g): Mantle margin creamy yellow with brown streaks, these wider and more dense at posterior margin. Foot white, toe with brown streaks. Ctenidia yellow, changing to brown at posterior end.

Anal papilla (Fig. 6h): Very long, thin, with secondary anal papilla; yellow in colour.

Palps: With 29 sorting ridges; yellow in colour.

Gut (Fig. 8d): Midgut loop extending anteriorly, then at right angles vertically, forming double tight coil.

Habitat. – *Barbatia grayana* in the Gulf of Thailand is an offshore species, to date exclusively found attached to a variety of other bivalves, mostly *Spondylus* and *Malleus*. The community appears to be formed on semi-infaunal *Malleus* shells to which cementing and byssate taxa attach, developing a reef-like clump. These clumps become tangled in drift nets and large quantities of debris can be found at and around fishing harbours. The exact locality and depth of the fishing grounds could not be gleaned from the fishermen.

Remarks. – The most distinctive character of *Barbatia grayana* is the soft, foliate periostracum, which is not seen in any of the other species found in the Gulf of Thailand. The outline is also unusual in the almost wing-like posterior area and the subauriculate posterior margin. The closest resemblance is to the Australian species *B. multivillosa* (Iredale, 1939) (Fig. 8f), but in that species the large bristles are more robust but narrower, more erect, and with few, weak strengthening ridges (Fig. 5f). Furthermore, the overall shell sculpture is stronger with fewer and more widely spaced radial riblets (Fig. 4e).

Although some authors (e.g., Robba et al., 2002) have used the name *Barbatia signata* (Dunker, 1868), an examination of the type material (below, Figs. 9f–h) shows this to be an entirely different species. In *B. signata*, the dorsal area is flat, there are only 29 distinctly nodulose ribs, and these ribs especially over the anterior and posterior areas are widely spaced and bifurcate.

Lamprell & Healy (1998) are the only authors to have used the name *Barbatia grayana* in any other than the original context. They used it as the available name for *B. decussata*, which they deemed preoccupied by *Arca decussata* Linnaeus, 1758.

Here we have described *Barbatia decussata* and the characters listed above demonstrate that *B. decussata* and *B. grayana* are not synonymous. Lamprell & Healy (1998) also listed *B. multivillosa* as a synonym but again this study indicates that that species is close to but distinct from *B.*

grayana and consequently is also completely distinct from *B. decussata*.

Species Not Belonging to the *foliata/decussata* Complex

Barbatia fusca (Bruguère, 1789)

(Figs. 5e, 6i–j, 9a–b)

Arca amygdalum frixum five tostum Chemnitz, 1784: 185, t. 54, Fig. 534.

NOT *Arca fusca* Lightfoot, 1786: 42, lot no. 1001 (*nomen dubium*).

Arca fusca Bruguère, 1789: 102.

Arca bicolorata Chemnitz, 1795: 243, t. 204, Fig. 2007.

Arca amygdalumtostum Röding, 1798: 175.

Arca bicolorata Dillwyn, 1817: 231.

Arca cruciata Philippi, 1849: 87, Pl. V, Fig. 7.

Barbatia rodatzki Dunker, 1866: 89, Pl. xxix, Figs. 1–3.

Material examined. – Type material: No shells could be located that relate to either Bruguère's (1789) or Chemnitz's (1784) descriptions; neither could type material of *Arca cruciata* or *Barbatia rodatzki* be found.

Other material examined: 6 ex. (NMWZ.2005.21.13), Laem Ban Tha Klaeng, northern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°35.22'N 101°53.05'E, attached to rocks on mid to lower shore, 23 Aug.2005; 1 ex. (NMWZ.2005.21.177), Laem Ban Kung Kraben, southern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°34.932'N 101°53.147'E, under boulders, lower rocky shore, 30 Aug.2005.

Diagnosis. – Shell (Figs. 9a–b): Medium-sized, our material to 60 mm in length. Outline rounded oblong; beaks about one-fifth of length from anterior margin; median sulcus and byssal sinus indistinct. Sculpture of dense, evenly sized, radial riblets, these intersected by equally dense commarginal grooves, giving overall subcancellate appearance. Shell purplish brown to brown with paler patches, mostly with two white radial rays over umbones.

Periostracum (Fig. 5e): Of dense narrow, erect, pointed bristles, all of similar size except in three or four radial rows on posterior angle where they are longer, slightly wider, with spear-shaped tips.

Soft tissue colouration (Fig. 6i): Posterior mantle grey, densely spotted pale yellow and reddish-brown, these colours more dense on mantle edge; foot creamy yellow with reddish-brown streaks and spots; ctenidia greenish with yellow and red/brown areas along ventral margins.

Anal papilla (Fig. 6j): Narrowly triangular, pointed, coloured as surrounding mantle, greyish-yellow with pale yellow spots.

Palps: With 18–29 sorting ridges, greenish-yellow in colour.

Habitat. – Attached to the sides and undersides of rocks and coral debris low in the intertidal and subtidal zones.

Remarks. – This is one of the most recognisable Indo-Pacific species of *Barbatia*, with its dark colouration and white umbonal rays. Specimens heavily encrusted with epifauna can be confused with *B. setigera* (Reeve, 1844), but that species has no radial white rays and the posterior rows of bristles are much larger and the bristles foliate. *Barbatia setigera* is not recorded from Thailand but the two species co-occur in the western Indian Ocean (Oliver, 1992; Oliver et al., 2004).

In the literature (e.g., Lamy, 1907), this species is most often referred to *Barbatia fusca* but, as pointed out by Iredale (1939), this name is preoccupied by *Arca fusca* Lightfoot, 1786. We confirm this and note that Lightfoot's *fusca* is a true *Arca*, resembling *A. imbricata* as seen in the image by Gualtieri (1742: Fig. 87G). However, the image is insufficient to determine exactly which species was intended and we agree with Rehder (1967: 10–11) that Lightfoot's name is a nomen dubium. Iredale (1939) chose to use *B. cruciata* Philippi as

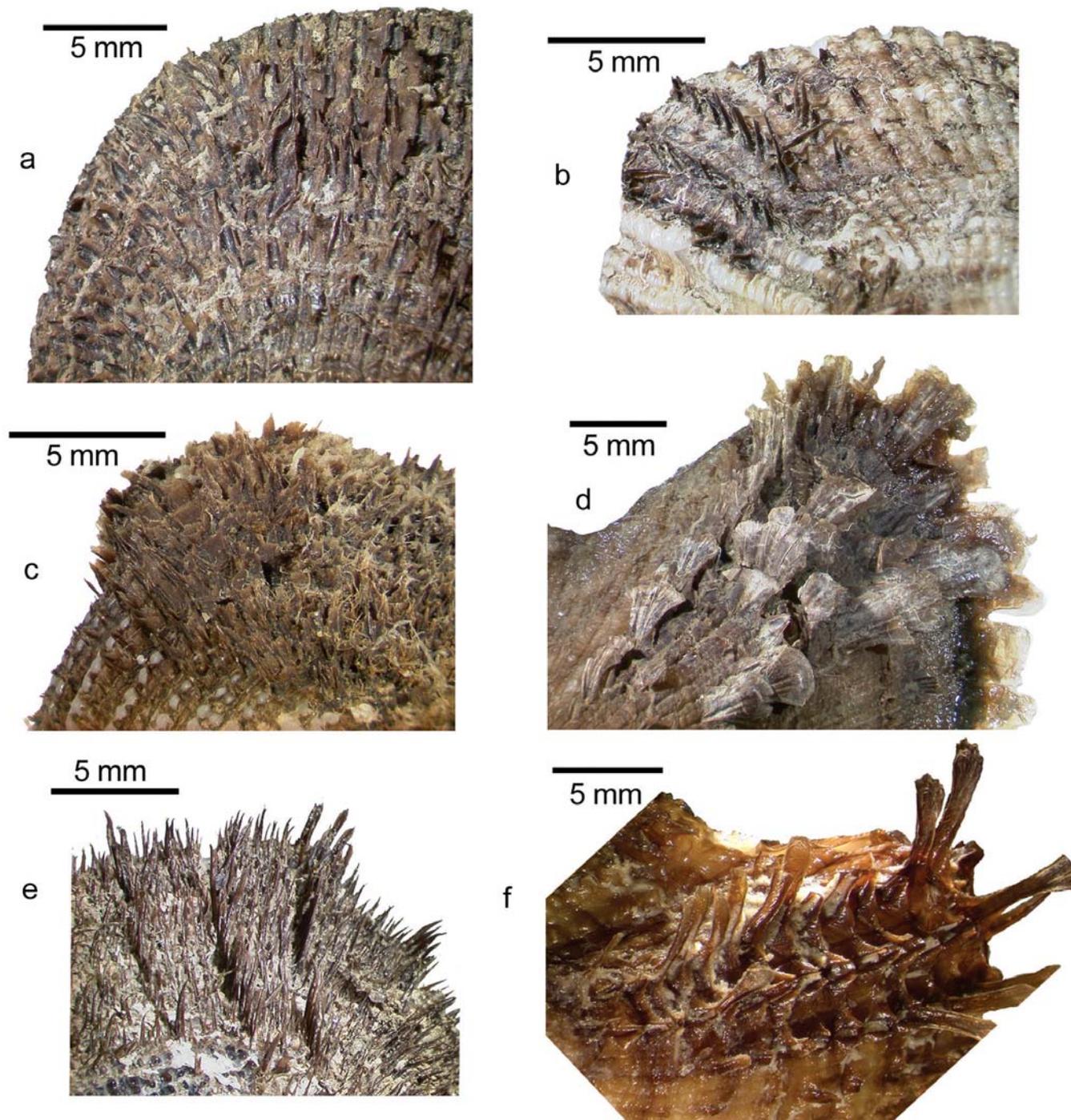


Fig. 5. Periostracum over the posterior angle in six species of *Barbatia*: a, *B. decussata*, NMWZ.2002.21.172; b, *B. trapezina*, NMWZ.2005.21.138; c, *B. foliata*, NMWZ.2005.21.166; d, *B. grayana*, NMWZ.2005.21.173; e, *B. fusca*, NMWZ.2005.21.13; f, *B. multivillosa*, Broome, Western Australia, NMWZ.1991.121.55.

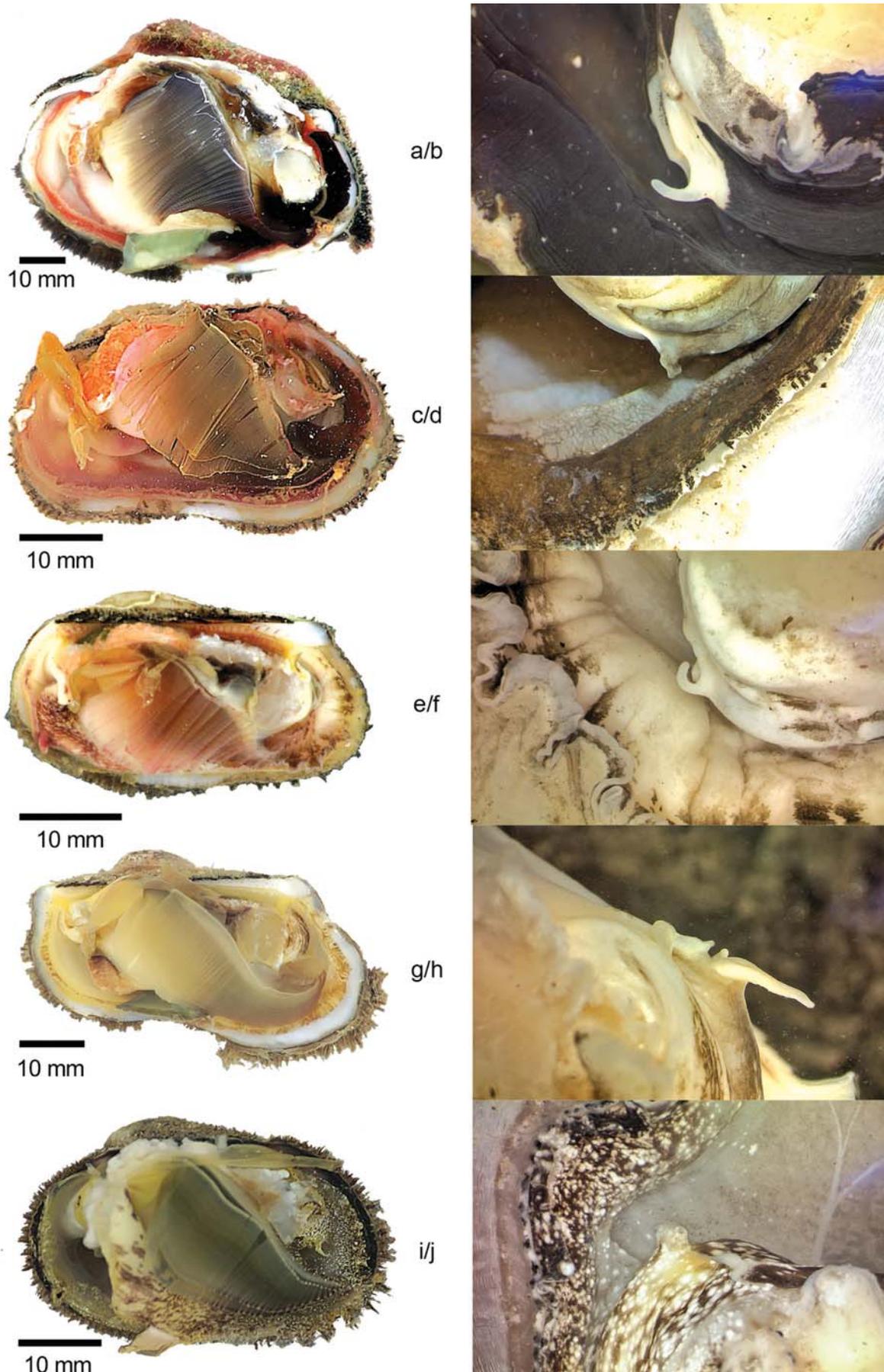


Fig. 6. Soft tissue colouration and details of anal papillae in living material for five species of *Barbatia*, Kungkrabaen Bay, Thailand: a–b, *B. foliata*, NMWZ.2005.21.167; c–d, *B. decussata*, NMWZ.2005.21.172; e–f, *B. trapezina*, NMWZ.2005.21.21; g–h, *B. grayana*, NMWZ.2005.21.174; i–j, *B. fusca*, NMWZ.2005.21.176.

the next available name. The name *Arca amygdalumtostum* (Röding) is older but was rejected by Iredale (1939) because he believed it to be a West Indian species, as did Dall (1921). Röding's *A. amygdalumtostum* is based solely on the figure by Chemnitz (1784: 185, Pl. 54, Fig. 534), which closely resembles the Indian Ocean shell but in the narrative reference is made to shells from the West Indies. Bruguière (1789: 102) cited the same figure by Chemnitz (1784), but also stated that his shells came from Madagascar. The confused range attributed to this taxon is best evidenced by Dillwyn (1817) who cited Barbados, Antilles and Madagascar for *A. fusca*. Neither the original specimen figured by Chemnitz (1784) nor the shells mentioned by Bruguière (1789) could be located, leaving resolution of the geographic origin of the species rather subjective.

Another Chemnitz name is *Arca bicolorata* Chemnitz, 1795; here the illustration is much better and the location (Red Sea) fixes this name to the Indian Ocean taxon. The first valid use of the name was by Dillwyn (1817) and thus predates both Philippi (1849) and Dunker (1866). Habe (1977: 31) adopted *Barbatia bicolorata* Dillwyn but also recognised *B. cruciata* as a separate species. Matsukuma & Okutani (2000: 847) reverted to using *B. fusca* and, similarly recognised *B. cruciata* as a separate species.

The opinion here is that, for nomenclatural stability, the name *fusca* Bruguière, 1789, should be retained. Furthermore, Bruguière's shells came from Madagascar and thus the uncertainty surrounding the shell figured by Chemnitz (1784), and thus the type figure of Röding's *amygdalumtostum*, is avoided. Given the adoption of *Barbatia cruciata* as a separate species by Japanese workers (Matsukuma & Okutani, 2000: 847), it is recommended that neotypes be erected for both taxa should, after revision, they prove to be distinct.

***Barbatia virescens* (Reeve, 1844)**

(Fig. 9c–d)

Arca virescens Reeve, 1844: Pl. 15, sp. #97.

Material examined. – Type material: Syntypes, 2 sh. + 1 v. (BMNH 1969188), Catbalonga, Island of Samar, the Philippines.

Other material examined: 2 ex. (NMWZ.2005.21.175), Laem Ban Kung Kraben, southern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°34.932'N 101°53.147'E, under boulders, mid shore, rocky shore, 30 Aug.2005; 3 sh. (NMW.1955.158.10120), Japan, Melvill-Tomlin Coll.; 3 sh. (NMWZ.1986.80.12), Cape d'Aguilar, Hong Kong, coll. P. G. Oliver, attached to rocks on lower shore, 1986.

Diagnosis. – Shell (Figs 9c–d): Medium-sized (to 50 mm), our material to 18 mm in length, compressed. Beaks in front of midline approximately one-third of length from anterior margin. Outline sub-modioliform, anterior reduced and much narrower than posterior; anterior and posterior margins rounded. Median sulcus almost flat; byssal sinus weakly defined. Sculpture of dense, evenly sized, low, radial riblets, these minutely nodulose but mostly worn smooth. Ligament strong; dorsal area deeply cleft, very narrow. Teeth numerous; anterior set with few, large oblique teeth extending to point below beaks; posterior set with more numerous, large oblique teeth; those beneath ligament small, vertical. Shell white, tinged with green.

Periostracum: Very thick and dense over posterior area, of lamellar bristles lying flat against shell.

Habitat. – Attached to rocks, generally on exposed sites.

Remarks. – Only two small examples were collected during the workshop, the largest being 18 mm in length.

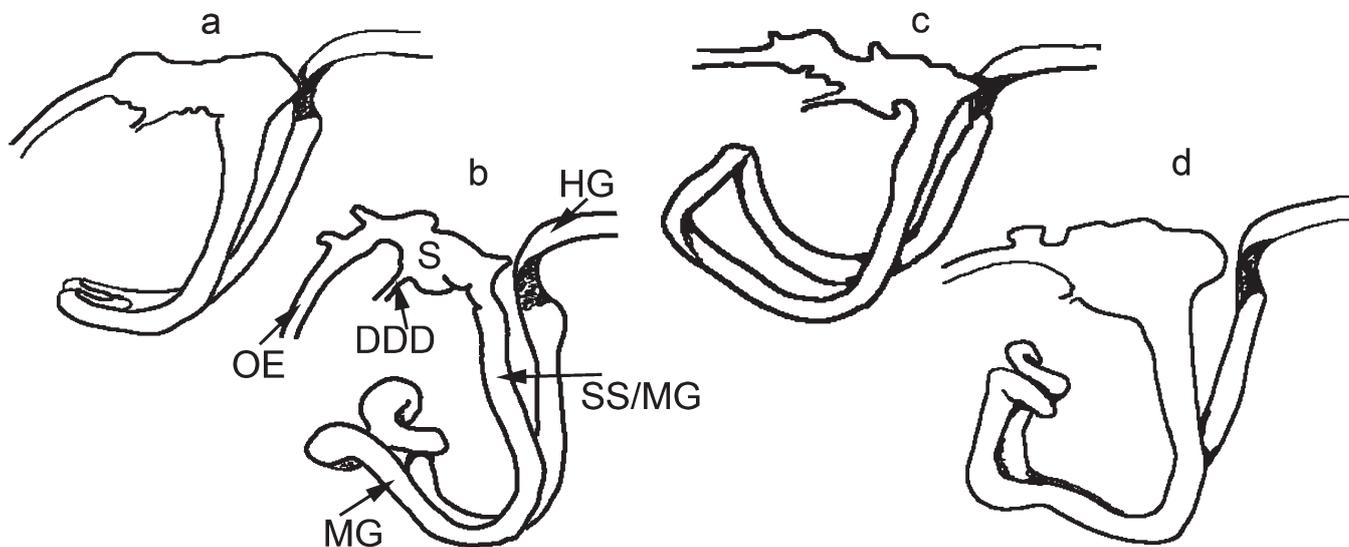


Fig. 7. Composite drawings of the stomach and gut of four species of *Barbatia*, Kungkrabaen Bay, Thailand. All dissected from the right side with oesophagus to the left: a, *B. foliata*; b, *B. decussata*; c, *B. trapezina*; d, *B. grayana*. Not to same scale. DDD, digestive diverticula; HG, hindgut; MG, midgut; OE, oesophagus; S, stomach; SS/MG, combined style sac and midgut.

This compares to shells in collections exceeding 50 mm in length. Due to the small size of the available specimens, no anatomical study was made.

***Barbatia bistrigata* (Dunker, 1866)**
(Fig. 9e)

Arca bistrigata Dunker, 1866: 87, Pl. 30, Figs. 4–6.

Hawaiarca bistrigata (Dunker, 1853) – Robba et al., 2002: 55, Pl. 1, Fig. 11.

Barbatia sp. – Swennen et al., 2001: 65, Fig. 025.

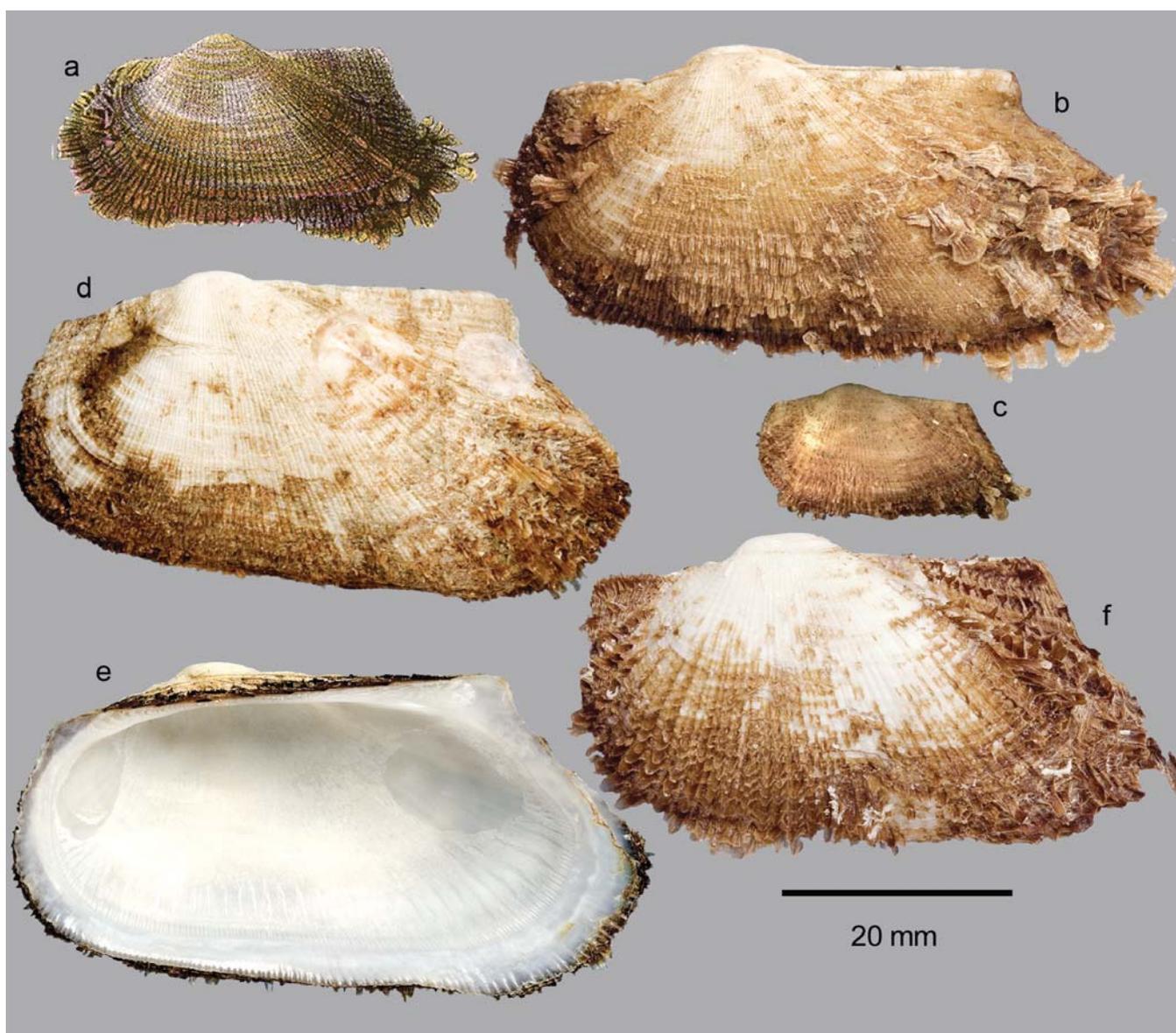
Material examined. – Type material: Syntypes, 2 sh. + 1 v. (BMNH 1969242), Bombay.

Other material examined: 1 ex. (NMWZ.2005.21.176), Laem Ban Kung Kraben, southern opening of Kungkrabaen Bay, Gulf of Thailand, Thailand, 12°34.932'N 101°53.147'E, on dead

coral, extreme low water mark, rocky shore, 30 Aug.2005; 7 v. (NMW.1955.158.10041), Bombay, India, coll. Abercrombie, Melvill-Tomlin Coll.

Diagnosis. – Shell (Fig. 9e): Medium-sized (to 40 mm), our material 10 mm in length. Beaks in front of midline approximately one-third of length from anterior margin. Outline subrectangular, becoming slightly expanded posteriorly in larger shells. Median sinus shallow; byssal gape very small. Sculpture initially of ca. 30 flat-topped ribs, with anterior and median sets becoming bifurcate in large shells; five to seven ribs over posterior angle remaining undivided, becoming distinctly wider than others. Dorsal area narrow. Hinge plate straight with numerous small teeth. Shell white with scattered greenish-brown maculations.

Periostracum: Of fine erect bristles arising from between ribs.



Figs. 8. *Barbatia* spp. *Barbatia grayana* Dunker: a, original figure reproduced from Dunker (1867); b, neotype, Pak Nam Khem Nu, Thailand, NMWZ.2005.21.173; c, small specimen for comparison with original figure, Pak Nam Khem Nu, Thailand, NMWZ.2005.21.174; d–e, external and internal views of a large worn shell, Pak Nam Khem Nu, Thailand, NMWZ.2005.21.174. *Barbatia multivillosa* (Iredale): f, Broome, Western Australia, NMWZ.1991.121.55.

Habitat. – Attached to rocks, coral debris, and other shells, mostly offshore.

Remarks. – Only a single small specimen was found during the workshop (10 mm in length) and consequently no anatomical data is presented. A larger and more typical shell was figured by Robba et al. (2002: Pl. 1, Fig. 11).

***Barbatia signata* (Dunker, 1868)**
(Fig. 9f–h)

Arca signata Dunker, 1868: 112-113, Pl. 38 Figs. 3–5.

Arca signata Dunker, 1858-1870 – Lamy, 1907: 78–79, Pl. 1 Figs. 1–2.

Arca signata Dunker, 1858-1870 – Lyngge, 1909: 110–111, Pl. 1 Figs. 14–15.

? *Barbatia bistrigata* Dunker – Swennen et al., 2001: 65, Fig. 023.

Material examined. – Type material: Holotype, 1 sh. (ZMB 16462), no locality.

Other material examined: 2 sh. (fide Lamy, 1907: 78) (MNHN), Amoy, coll. Jousseume; 1 sh. (fide Lamy, 1907: 78) (MNHN), China, coll. Gaudichaud; 5 sh. (NMWZ.1990.79.1–3), Burma, coll. Burma Pearl Fisheries, ca. 1920; 9 sh. (NMW.1955.158.10108), Singapore, coll. Archer, Melvill-Tomlin Coll.

Diagnosis. – Shell (Figs. 9f–h): Medium-sized, to 45 mm in length. Beaks in front of midline, approximately one-third of

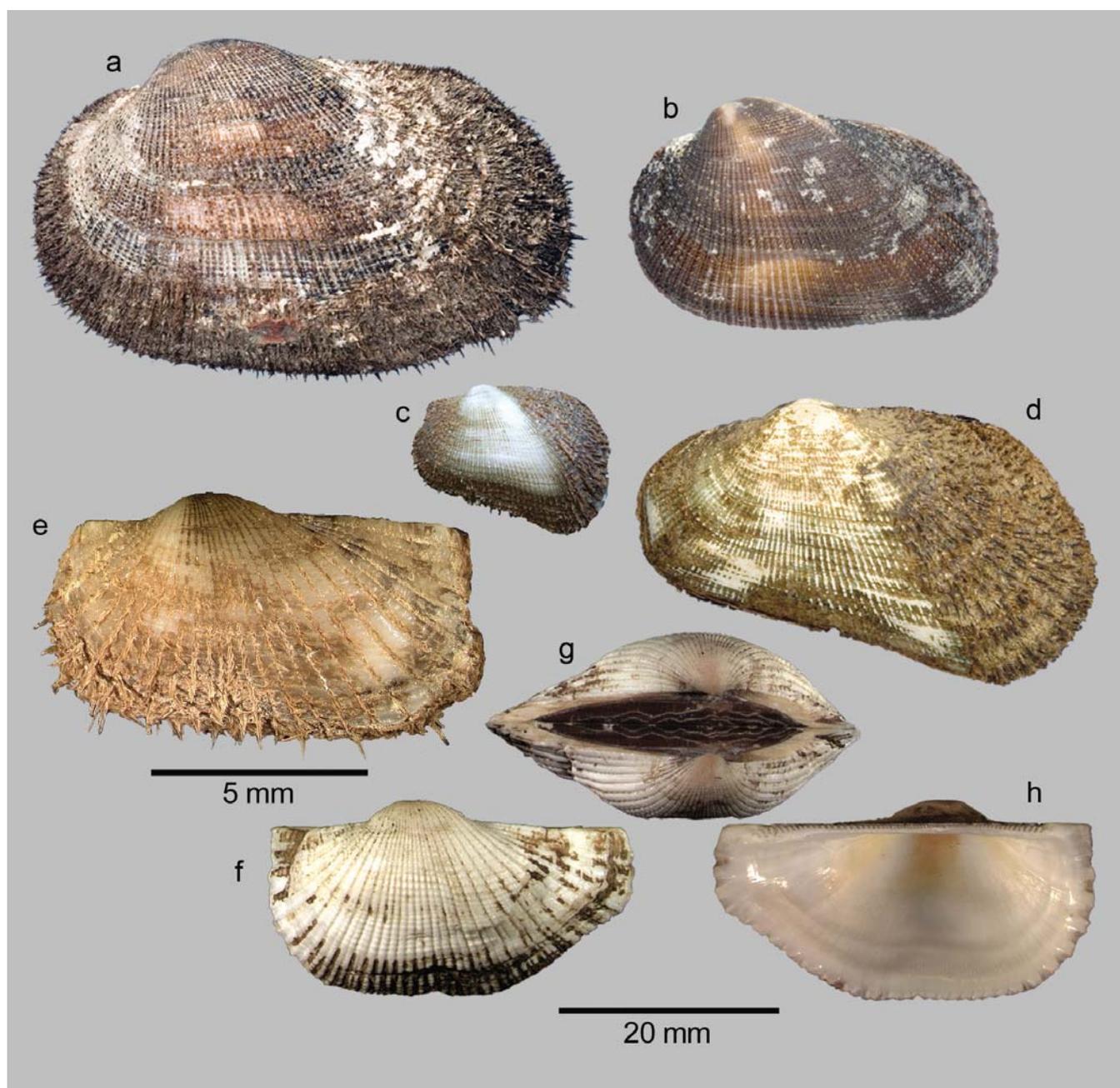


Fig. 9. *Barbatia* spp.: a, b, *Barbatia fusca* (Bruguère), Kungkrabaen Bay, Thailand, NMWZ.2005.21.13; c, d, *Barbatia virescens* (Reeve) [c, Kungkrabaen Bay, Thailand, NMWZ.2005.21.175; d, Japan, NMW.1955.158.10120]; e, *Barbatia bistrigata* (Dunker), Kungkrabaen Bay, Thailand, NMWZ.2005.21.176; f–h, *B. signata* (Dunker), holotype, ZMB 16462.

length from anterior margin. Outline subrectangular; anterior margin curved; posterior margin truncate; ventral margin straight or convex; dorsal area long, wide, remaining flat. Sculpture of ca. 30 radial ribs, all distinctly nodulose, all bifurcating with growth; ribs on anterior and over posterior angle wider and less bisected than median ribs. Hinge plate long, very narrow, with numerous, small, almost vertically oriented teeth. Shell white with occasional brownish blotches and orange flush over umbones best seen internally over umbonal cavity.

Periostracum: Of flimsy lamellae overall, with short, erect bristles between ribs on posterior angle and anterior areas.

Remarks. – No examples of this species were collected during the workshop. However, due to its occurrence in the Gulf of Thailand and confusion with both *Barbatia grayana* and *B. bistrigata*, a description of the shell is given here.

This species is unusual in that the aspect of the hinge and ligament are more akin to that of *Arca* than *Barbatia*. Robba et al. (2002) noted a superficial similarity with *B. bistrigata* (as *Hawaiarca bistrigata*), but that species does not have a wide and flat ligamental area. Lamprell & Healy (1998) went as far as synonymising the two species and placing them in the subgenus *Nipponarca*, but it is doubtful whether the two species are at all related. This discussion further illustrates the widespread confusion concerning subgenera of *Barbatia*. Lamy (1907: 78) considered the type specimen to be abnormal but other specimens examined here also display a contracted posterior ventral margin and the type specimen is adequately representative of the taxon.

Lamy (1907: 79) stated that he believed *Arca adamsiana* Dunker, 1866 (p. 88, Pl. xxix, Figs. 4–6) to be the juvenile of *A. signata*. This has not been sufficiently researched here but as it seems likely that Lamy was correct, then *A. adamsiana* would take precedence over *A. signata*. On a contradictory note, Stevenson (1972: 195) believed that *A. adamsiana* was a small *B. bistrigata*.

DISCUSSION

This study indicates that soft tissue colouration is a consistent character useful for distinguishing species of *Barbatia* at least in a local context. Other anatomical characters, especially the coiling of the gut, were also of value in confirming that different species existed. Using soft-tissue patterns allowed a more rigorous assessment of shell characters indicating that although ecophenotypic variation can be high, certain characters are consistent. The periostracum appears especially useful, as does the overall pattern of the ribbing. Numerical data such as rib number, teeth number and ligament chevron number are unreliable if used in comparisons of shells of different sizes or ages.

The presence of three distinct species within the *foliataldecussata* complex is well-supported by this study. All

three, *B. foliata*, *B. trapezina* and *B. decussata*, have wide geographic ranges and the soft-tissue colouration remains to be tested for consistency over their entire ranges. The ranges stretch from the Red Sea to, probably, Hawaii, and other related taxa could be present. The taxa described by Dall et al. (1938) under the subgenus *Abarbatia* probably all belong to this complex, as do *Arca parvillosa* Iredale, 1939, and *Arca prolatens* Iredale, 1939, from Queensland. This study has disagreed in a number of issues with Lamprell & Healy (1998) and a further study on the Australian species is warranted.

Barbatia grayana is probably not part of the *foliataldecussata* complex and, along with *B. multivillosa*, could constitute another group.

Concerning *Barbatia fusca*, its nomenclature remains finally unresolved as does the distinction, if any, between *B. fusca* and *B. cruciata*. Similar synonymy problems remain with *B. virescens* and the nominal taxa *Arca obtusa* Reeve, 1844, *A. obtusoides* Nyst, 1848, *B. decurvata* Dunker, 1882, and *A. sinensis* Philippi, 1851.

This study does indicate that, with care, species with such ecophenotypically pliable shells can be distinguished. *Barbatia* sensu lato contains very many other taxa that require similar investigation and, with many more species included, a better idea of the number of distinct morphological groups will emerge. These then need to be included in a molecular analysis to assess both their integrity and their relationships. Until this is done, any further generic revision or creation of new genera is unwarranted.

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THAI ABSTRACT

ผู้วิจัยได้ทำการศึกษากายวิภาคของหอยสองฝาในสกุล *Barbatia* จำนวนทั้งสิ้น 7 ชนิด จากอ่าวคุ้งกระเบน ในจังหวัดจันทบุรี คือ *B. foliata* (Forsskål, 1775) *B. decussata* (Sowerby, 1833) *B. trapezina* (Lamarck, 1819) *B. grayana* Dunker, 1867) *B. fusca* (Bruguère, 1789) *B. virescens* (Reeve, 1844) และ *B. bistrigata* (Dunker, 1866) และพบว่าสีของเนื้อเยื่อลำตัว ขณะที่หอยยังมีชีวิตอยู่สามารถใช้เป็นลักษณะในการจำแนกชนิดได้เป็นอย่างดี โดยพิจารณาพร้อมกับลักษณะทางกายวิภาคอื่น ๆ เช่น ลักษณะการขีดไปมาของลำไส้และคุ่มบริเวณทางเปิดของทวารหนัก การใช้ลักษณะค้ำงอเพื่อยืนยันลักษณะรูปร่างของเปลือก ทำให้ผู้วิจัยสามารถทบทวนการจัดจำแนกชนิดของหอยสองฝาในสกุลนี้ โดยเฉพาะกลุ่มที่มีปัญหาทางอนุกรมวิธานคือกลุ่ม *foliata/decussata* และยืนยันชื่อสกุลและชนิดทั้งสิ้น 3 ชนิดคือ *B. foliata*, *B. decussata* และ *B. trapezina* ผู้วิจัยได้คัดเลือก lectotype สำหรับ *B. trapezina* และบรรยายลักษณะของ *Barbatia grayana* เพิ่มเติมพร้อมทั้งคัดเลือก neotype หอยชนิดนี้ล่าสุดนี้ไม่ถือว่าเป็นส่วนหนึ่งของหอยกลุ่ม *foliata/decussata* และมีลักษณะคล้ายกับ *B. multivillosa* (Iredale, 1939) ผู้วิจัยได้ทบทวนและสรุปชื่อวิทยาศาสตร์ของหอยในสกุลนี้ทุกชนิด และตัดสินใจคงไว้ซึ่งชื่อ *B. fusca* (Bruguère) แทนที่ชื่อ *B. amygdalumtostum* (Röding, 1798) ส่วนหอย *Barbatia signata* (Dunker, 1868) ซึ่งไม่พบในการเก็บตัวอย่างภาคสนามในครั้งนี้ ก็มีการทบทวนและบรรยายถึงลักษณะใหม่เพื่อไม่ให้เกิดความสับสนในการจำแนกหอยสองฝาชนิดนี้จากหอย *B. bistrigata* และ *B. grayana*

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