

# KOREAMYA ARCUATA (A. ADAMS, 1856) GEN. NOV. (GALEOMMATOIDEA: MONTACUTIDAE), A COMMENSAL BIVALVE ASSOCIATED WITH THE INARTICULATE BRACHIOPOD *LINGULA ANATINA*

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*Abstract* We describe the shell, soft anatomy, and reproduction of the montacutid bivalve, *Koreamya arcuata* (A. Adams, 1856) gen. nov. Contrary to most montacutids the outer demibranch has been preserved, although in a reduced state. The species is a protandrous consecutive hermaphrodite which stores sperm in a groove-shaped ctenidial seminal receptacle. The particular type of sperm receptacle and the presence of a lithodesma in *Koreamya* indicate an affinity to *Montacutona Yamamoto & Habe, 1959*, but the shells of the two differ widely in shape and proportions. The species is a commensal, and lives permanently attached to the valves near the shell gape of *Lingula anatina* at several Korean intertidal flats. It is also known from the Philippines, SE India and W Australia.

*Key words* *Koreamya arcuata*, *Galeommatoidea*, morphology, systematics, commensalism, distribution.

## INTRODUCTION

Commensal bivalves of the superfamily Galeommatoidea are a diverse group which often displays a number of remarkable morphological adaptations to their particular life style. The groups that serve as hosts comprise benthic and often burrowing invertebrates such as anthozoans, irregular sea urchins, sea cucumbers, sipunculans, polychaetes, and various malacostracans. The host-commensal associations have been reviewed by Boss (1965) and, for the Hong Kong area, by Morton (1988) and Morton & Scott (1989). Only one species of bivalve has been recorded to live commensally with a brachiopod, namely *Pythina arcuata* A. Adams (A. Adams 1856; Fernando & Fernando 1983), a species which is clearly identical with *Mysella* sp. (Savazzi 2001) and an unidentified montacutid species (Yamashita 2004; Sato *et al.* 2004; Hong *et al.* 2007). This bivalve is found to be associated with the burrowing inarticulate brachiopod *Lingula anatina* Lamarck at several Korean tidal flats along the Yellow Sea. The species has never been adequately described, whence we have undertaken to study its biology and morphology in more detail. The findings presented in this paper have resulted in the species' transfer from *Pythina* (family Lasaeidae) to a new genus, *Koreamya*, tentatively grouped with the family Montacutidae.

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## MATERIAL EXAMINED

- 1) Syntype material consisting of five dried shells and one dried valve (Natural History Museum, London, BMNH 1967995)
- 2) Bivalves attached to *L. anatina* at the following Korean tidal flat in the middle intertidal level, sand mud bottom: Okbong-ri, Okseo-myeon, Gunsan City, Jeollabuk-do (35° 55' 55" N, 126° 36' 15" E); Simpo-ri, Jinbong-myeon, Gimje City, Jeollabuk-do (35° 50' 37" N, 126° 40' 21" E); Gaehwa-ri, Gaehwa-myeon, Buan-gun, Jeollabuk-do (35° 47' 11" N, 126° 37' 09" E); Yubu-do Island, Seocheon-gun, Chungcheongnam-do (36° 00' 20" N, 126° 37' 55" E); Hajeon tidal flat, Gomso Bay, Jeollabuk-do (35° 30' 30" N, 126° 30' 50" E). The bivalves of a large number of brachiopods were either dislodged or, still in situ, preserved in 70 % ethanol. Some of these bivalves are deposited in the Zoological Museum, University of Copenhagen.
- 3) Several other bivalves associated with *L. anatina* collected at Yubu-do Island, Seocheon-gun, Chungcheongnam-do (26 September 2006) and Dokkyo tidal flat, Incheon, Korea (4 November 2006) and preserved in 5 % formaldehyde in sea water.
- 4) Photos of two dried shells, SL 5.6 and 6.3 mm, labelled "*Pythina arcuata*, Ostindien, det. Lischke" (Aquazoo Löbbecke-Museum No. LMD/LÖB 12806a-b, Düsseldorf, Germany).

5) One shell on each of two *Lingula* sp. from Cowrie Cove, Burrup Peninsula, Dampier, Western Australia, July 2000 (Natural History Museum, London).

## METHODS

Several bivalves were decalcified in Bouin's fluid. A few had the mantle and/or gills removed to display the organization of the mantle cavity. Twelve specimens (Shell length (SL) 1.6-7.2 mm) were embedded in Paraplast or Araldite. The Paraplast-embedded bivalves were cut into 8- $\mu$ m thick serial sections that were stained with hematoxylin and eosin (H+E). The Araldite-embedded bivalves were cut into 2- $\mu$ m thick sections and stained with toluidine blue. SH and SB mean shell height and breath.

## DESCRIPTION

Galeommatoidea J. E. Gray, 1840

Montacutidae Clark, 1855

*Koreamya* gen. nov.

*Type species* *Pythina arcuata* A. Adams, 1856

*Diagnosis* Shells equivalve, subequilateral, outline elongately triangular with rounded anterior and posterior margins. Ventral margin slightly incurved. Subumbonal triangular resilifer, ligament amphidetic, with lithodesma. Periostracum brownish, often worn away in older parts of shell. Right valve with an anterior elongate lateral and a posterior cardinal, left valve with an elongate anterior tooth and a posterior hooked tooth. Labial palps large, broadly leaf-shaped. Gills with a complete inner demibranch and a smaller outer demibranch of descending filaments only. Sperm receptacle a groove in the fused ascending lamellae of inner demibranch.

*Etymology* From "Korea" the country of collection and "myax", Greek, meaning a marine bivalve.

*Koreamya arcuata* (A. Adams, 1856)

*Lectotype* The largest (SL and SH 8.4 and 4.5 mm) of five shells and one valve is designated as

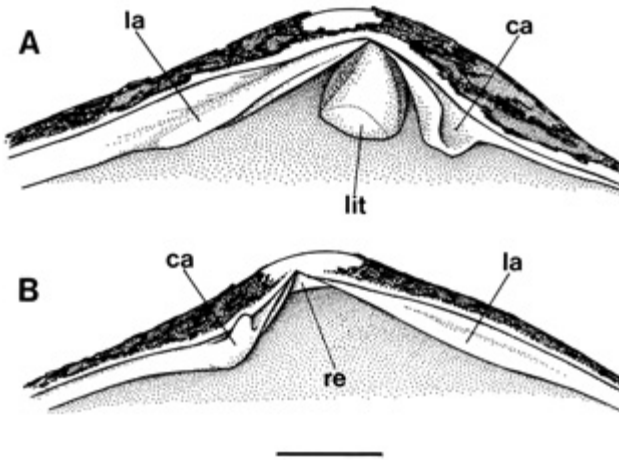


**Figure 1** *Koreamya arcuata*. Dorsal view of two bivalves in situ on the host, *Lingula anatina*. Simpori, Jinbong-myeon, Gimje City, Jeollabuk-do, Korea, 18.08.02.

a lectotype. Natural History Museum, London, BMNH 1967995, H. Cuming Collection.

*Type locality* Cebu Island, the Philippines.

*Shell* (Figs. 1-3) The shell reaches 8.4 mm in length and 4.5 mm in height (through umbo). It is equivalve, relatively inflated, elongately triangular with gently rounded anterior and posterior margins, subequilateral, the anterior end longer. The ventral margin may be more or less insinuated. Smaller specimens generally have higher shells and less insinuated ventral margins. The shell is broadest behind umbo. In a small (1.6 mm) and non-corroded specimens, a 510  $\mu$ m long prodissoconch 2 could be distinguished. A typical adult specimen measures 6.7 mm in SL, 3.7 mm in SH and 2.8 mm in SB. The smallest specimens seen measured 450 x 390 and 555 x 500  $\mu$ m (SL x SH). The umbo is low, the ventral margin is always more or less incurved and near the middle left and right opposed margins recede a little to form a small shell gape to accommodate the prominent byssus. The periostracum is relatively thick, coloured in various shades of brown. The sculpture consists of many close-set and stout radial riblets and weaker commarginal growth lines. Distinct growth checks are absent. All shells are heavily corroded dorsally and in the centre (Fig. 1), whence the prodissoconch can be traced only exceptionally. In addition, parts of the shell often have a coating of a rusty or black, prob-

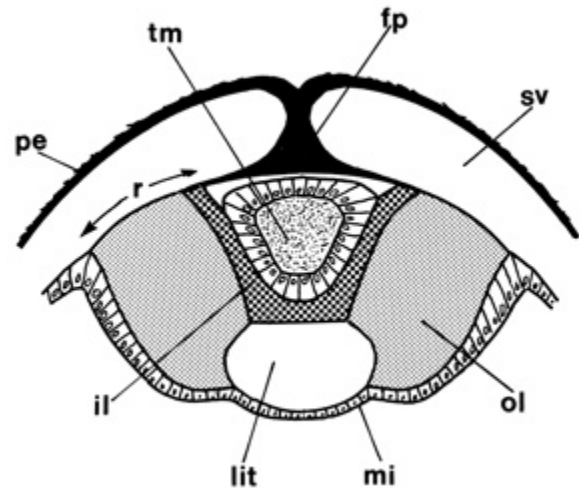


**Figure 2** *Koreamyia arcuata*. Hinge of right (A) and left (B) valve. Ligament present in A, removed in B. ca, cardinal tooth; la, lateral tooth; lit, lithodesma; re, resiliifer. Scale bar: 500  $\mu$ m.

ably ferrous, deposit. The prominent ligament is amphidetic, dumbbell- or butterfly shaped in ventral view, and a lithodesma is present. The resiliifer is triangular and placed immediately below the beak. Hinge (Fig. 2): The right valve has an anterior elongate lateral tooth which is centrally elevated to form a triangular protruding crest and a posterior slightly hollowed cardinal tooth with a thickened anterior crest. The left valve has an elongate low ridge-shaped anterior tooth which fits in between the shell margin and the lateral of the opposite valve, and a posterior cardinal ending in a rounded knob, which locks into the hollow of the cardinal of the opposite valve.

**Anatomy (Figs 3-6)** The adductor scars are subequal and joined by a diffuse pallial line which lies well inside the shell margins. The anterior combined byssus and foot retractor scar is adjacent to the corresponding adductor scar, whereas the posterior foot retractor scar is distinctly separated from the posterior adductor scar.

**Ligament and lithodesma (Figs. 3, 5A, B).** The primary ligament consists of a thick inner (fibrous) and a thinner outer (lamellar) layer lying beneath a dorsal secondary ligament of fused periostracum. A calcareous lithodesma lies in the central region of the inner ligamental layer and between the secondary ligament and the mantle isthmus which secretes it. A con-

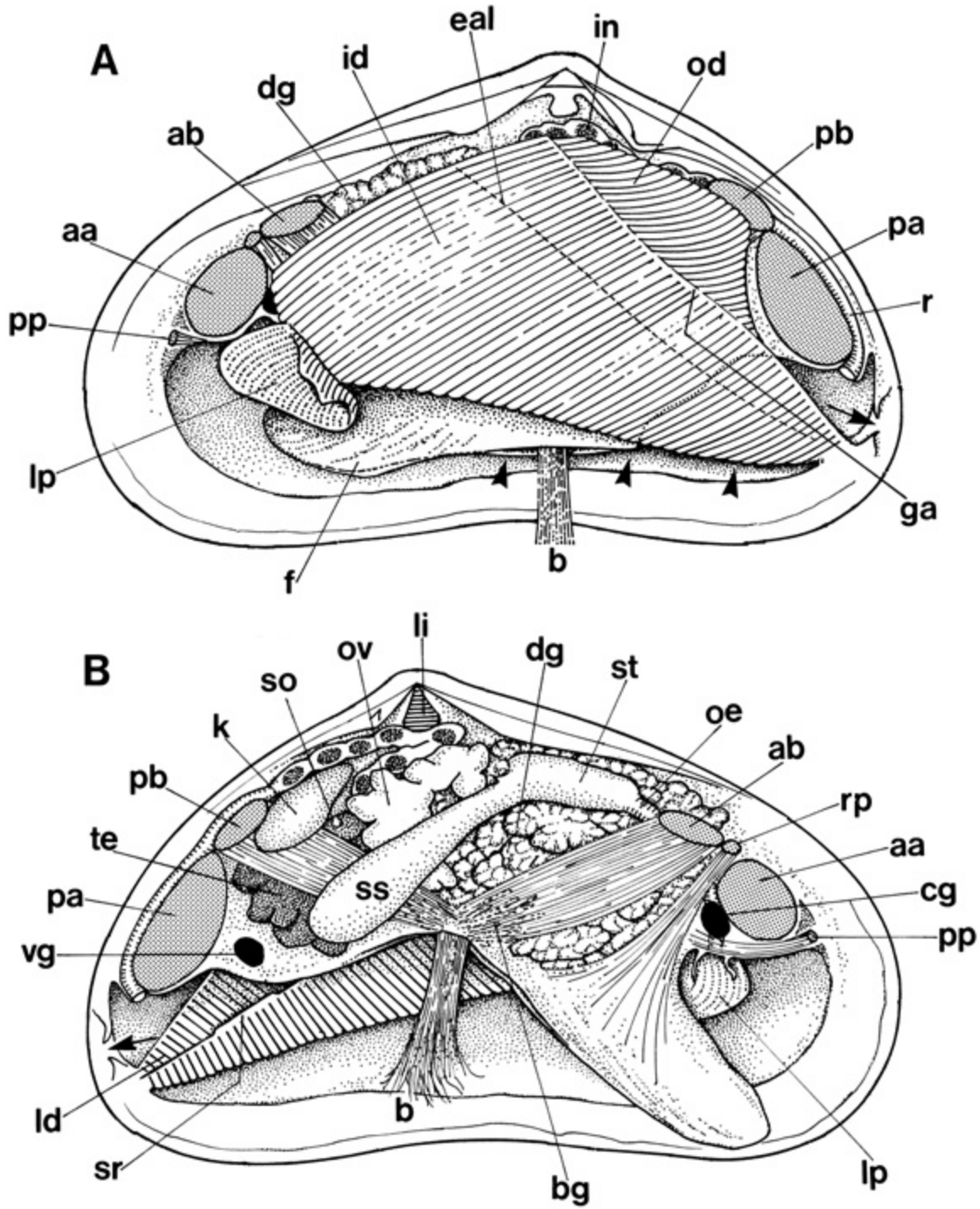


**Figure 3** *Koreamyia arcuata*. Diagrammatic representation of transverse section through ligament. fp, fused periostracum (secondary ligament); il, inner layer of primary ligament; lit, lithodesma; mi, mantle isthmus; ol, outer layer of primary ligament; pe, periostracum; r, resiliifer; sv, shell valve; tm, tongue of mantle bounded by epithelium and with connective tissue internally.

nective tissue tongue of the mantle extends far backward into the ligament and is bounded by an epithelium which secretes the fused periostracum dorsally, the outer layer of the primary ligament ventrally, and the inner calcareous layers of the valves laterally. The lithodesma is relatively better developed in smaller than in larger specimens.

The foot (Fig. 4) has a small heel. A long groove extends from just in front of the heel almost to the rounded tip of the foot. *K. arcuata* is attached to the shell of the host by means of a byssus composed of a tuft of numerous threads, which when leaving the byssus gland form a tight rope, up to 300  $\mu$ m across. Just in front of the heel of the foot, the byssus groove is excavated to a conspicuous cavity with many narrow deep glandular infoldings that reach far into muscle fibers of the byssus retractor muscles. Attachment of the byssus to the host shell may result in a distinct blackening of its periostracal layer. Such black patches besides an attached bivalve reveal the earlier presence of a detached partner.

The anterior adductor is smaller than the posterior. The anterior foot retractor is completely divided into a very large and thick byssus retractor muscle and a smaller retractor pedis



**Figure 4** *Koreamyxa arcuata*. Anatomy of a 4.0 mm long hermaphrodite. **A**, left valve and mantle removed to show disposition of gills and labial palps. **B**, right valve, mantle and gills removed to show the musculature and structure of the organs of the visceral mass. aa, anterior adductor muscle; ab, anterior byssus retractor; b, byssus; bg, byssus gland; cg, cerebral ganglion; eal, edge of ascending lamella of inner demibranch (id); dg, digestive gland; f, foot; ga, gill axis; in, intestine; k, kidney; ld, left inner demibranch; li, ligament; lp, labial palp; od, outer demibranch; oe, oesophagus; ov, ovary; pa, posterior adductor muscle; pb, posterior byssus retractor; pp, protractor pedis muscle; r, rectum; rp, retractor pedis muscle; so, sexual opening; sr, seminal receptacle in fused ascending lamellae of inner demibranch; ss, style sac; st, stomach; te, testis; vg, visceral ganglion. Arrows show water exiting from the exhalant aperture, arrowheads water entering along the posterior part of the pedal/inhalant aperture. Scale bar: 1 mm.

muscle. The posterior byssus retractor is of the same magnitude as the anterior byssus retractor, and most of its fibers terminate in the byssus gland. The well developed byssus musculature is related to the strong development of the byssus in this species. A diminutive protractor pedis muscle attaches ventral to the adductor muscle and runs along the adductor's ventral margin to join the anterior retractor pedis muscle below and behind the cerebral ganglia (Fig. 5D).

The outer fold of the mantle edge forms a sheet-like extension of the mantle margin. The inner fold is not particular muscular except where the two sides are fused for a very short distance far behind to separate a large combined pedal and inhalant aperture from a minute posteriorly directed exhalant, not siphonate aperture. The inner fold is protruding and heavily ciliated just anterior to the end of the pedal/inhalant aperture to form a rejection tract but otherwise forms a narrow glandular ridge.

The labial palps are very large and broadly leaf-shaped. Their opposed surfaces have up to 20 transverse sorting ridges between which project the anterior end of the inner demibranch. The gills are flat, homorhabdic and non plicate. There are few inter-filamentar junctions and much fewer and very thin inter-lamellar junctions. Both demibranchs are present in *K. arcuata*, but the outer demibranch is much smaller and shorter and comprises a single lamella alone, which is reflected backwards (Figs. 4A, 5C).

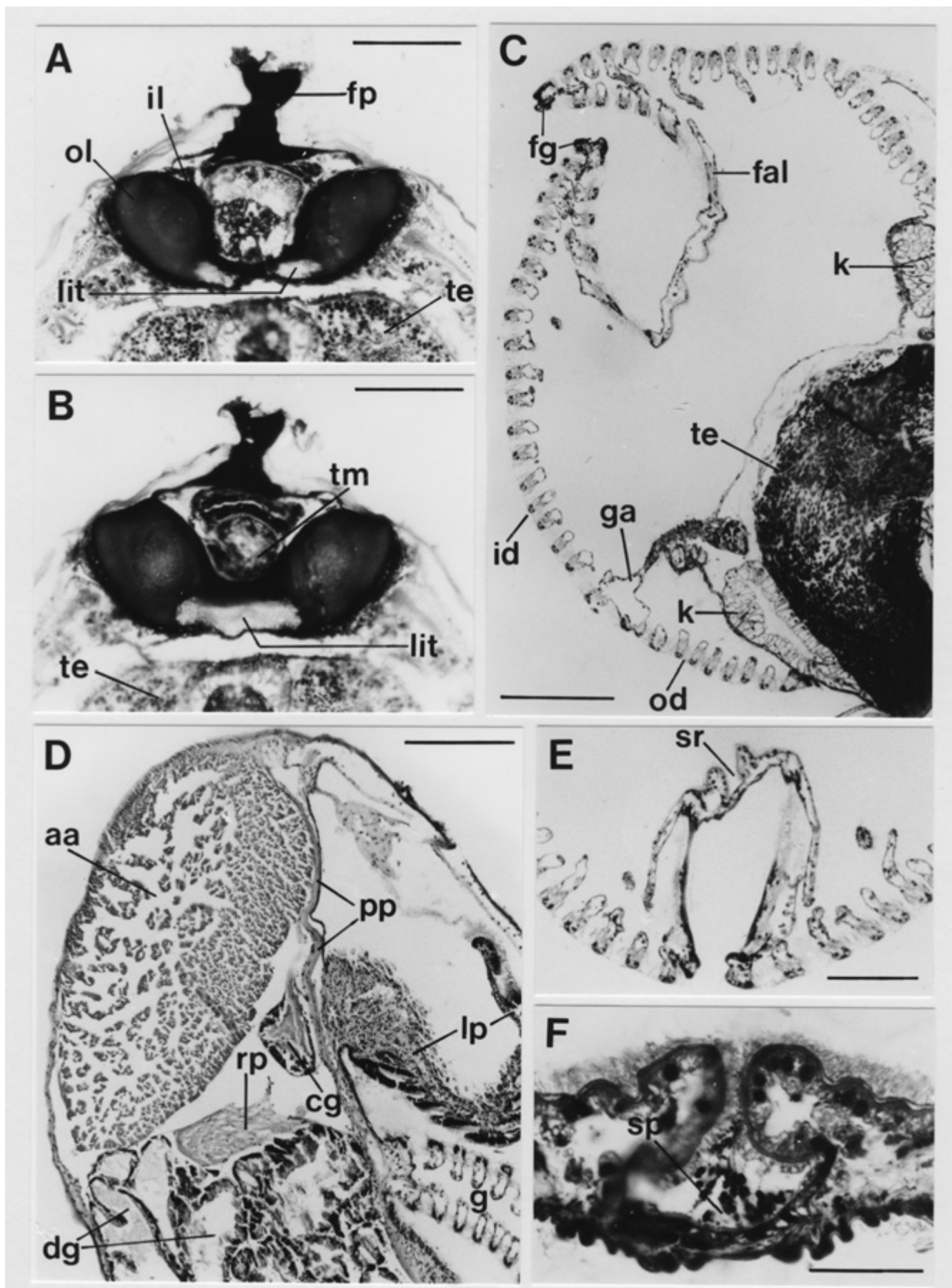
Only the inner demibranch has a food groove along the ventral edge and probably the ciliary currents of the outer demibranch beat towards the gill axis from where particles are transported onward upon the the inner demibranch. Behind the foot, the ascending lamellae of the left and right inner demibranchs are joined in the median plane and the interior surface of the area of fusion is modified to an elongate seminal receptacle (Fig. 4B). While the ascending lamella of the inner demibranch attaches to the visceral mass by tissue fusion, the descending lamella of the outer demibranch is intimately applied to, but not fused with, the visceral mass (Fig. 5C). The gill axis with the inner demibranch is fused ventrally to the mantle where the fused inner folds of the mantle separate the inhalant and exhalant apertures.

The alimentary canal is of ordinary structure

(Fig. 4B). The stomach is rather flattened in most specimens. The style sac forms a wide posterior continuation of the stomach. It is large and elongated, tilted ventrally and backwards, and situated to the far right side of the visceral mass, the wall of which it bulges out. After having left the stomach, the intestine runs backwards, descends to underlie the style sac and then loops forward and dorsally to continue backwards into a long rectum which passes over the posterior adductor and finally opens into the anus close to the exhalant aperture. The intestine in most specimens contained a series of many rounded excrement pellets. The digestive gland is located ventral to and around the stomach and esophagus and extends forwards and ventrally to the anterior retractor pedis muscle. The only identifiable food particles in the stomach and intestine comprised bivalve larvae and diatoms.

The sexual organs are located between the other organs (rectum, style sac, kidney, and posterior byssus retractor) of the hind part of the visceral mass. In mature specimens it is rather voluminous. Small specimens (SL 1.6 and 2.8 mm) are males, larger ones females (SL 5.0, 5.1, 5.3, 5.4, 5.9, 6.8, 7.2 mm), and a few of intermediate size were hermaphrodites (SL 3.7, 3.7, 4.0, 4.0 mm). The gonad consists of numerous lobules that lie close together. In the hermaphrodites the testis dominates the posterior part of the ovotestis. In those parts that are predominantly female, the oocytes are placed peripherally in the lumen of the lobules with male cells in all stages of spermatogenesis occupying the central lumen. The sexual openings are placed on small papillae in the posterior part of the suprabranchial chamber. The species is a brooder and the ova are preferentially retained in the suprabranchial chamber formed by the inner demibranchs, with only a smaller number being present within that of the outer demibranchs. Ethanol-preserved early embryos measure 70-75  $\mu\text{m}$  in diameter and full-grown veligers extracted from the suprabranchial chamber measure 145-160  $\mu\text{m}$  in SL and 118-122  $\mu\text{m}$  in SH (Fig. 6B). Two brooding females, both from August 16, were 5.1 and 7.2 mm.

In males, hermaphrodites and females, a seminal receptacle was present in the shape of a longitudinal groove between two ciliated ridges of the inner surface of the fused ascending lamellae of



the inner demibranchs (Figs. 5E, F, 6A). The bottom of the groove is unciliated but provided with a distinct microvilli border. If sperm cells were present, they were arranged with the heads facing the groove's walls and the flagellae protruding into its space which communicates with the posterior part of the suprabranchial chamber. By apposition of its ciliated walls, the groove could be nearly closed. No sperm were found in the receptacle in the males (N= 2) and the hermaphrodites (N=4), but were present in two of six 5.0-7.2 mm long females that were sectioned. In two of the hermaphrodites (3.7 and 4.0 mm) clouds of free sperm cells extended from one of the sexual openings far backwards into the room above the seminal receptacle without entering it.

*Habitat* The host of *K. arcuata* inhabits sandy mud bottoms or mud bottoms from the upper middle intertidal zone to the low intertidal zone of the Yellow Sea coasts of Korea between Incheon and Gomsu Bay. A total of six populations of *L. anatina* with *K. arcuata* were found. Very large populations exist in the Saemangeum area, in which three localities (Okbong-ri, Simpori and Gaehwa-ri) have been destroyed by the Saemangeum Reclamation Project (Hong *et al.* 2007). The percentage of *L. anatina* with *K. arcuata* were recorded at 3-12 % (Kai *et al.* 2006) and 0-37.5 % (Hong *et al.* 2007), but vary according to localities and populations.

At Simpo-ri we recorded the following data concerning 18 specimens of *L. anatina*, which had a total of 37 *K. arcuata* (average 2.1) attached: One bivalve per host occurred in six cases, two bivalves in eight cases, three bivalves in one case, and four bivalves in three cases. Twenty-three bivalves attached to the pedicle (ventral) valve, 14 to the brachial (dorsal) valve. Almost all of the bivalves attached to the distal margins of the

shell gape and equally often to the left or right sides. Smallest size of *K. arcuata* at this locality was 3.0 x 1.2 mm, with the majority measuring ca. 3.5 x 1.5 mm.

Bivalves very similar to *K. arcuata* were also sometimes found attached to *Lingula adamsi* Dall at the Wordo tidal flat, SW Korea (Sato *et al.* 2004). The size of these bivalves is generally smaller, the shell thinner and its shape more rounded than in *K. arcuata*.

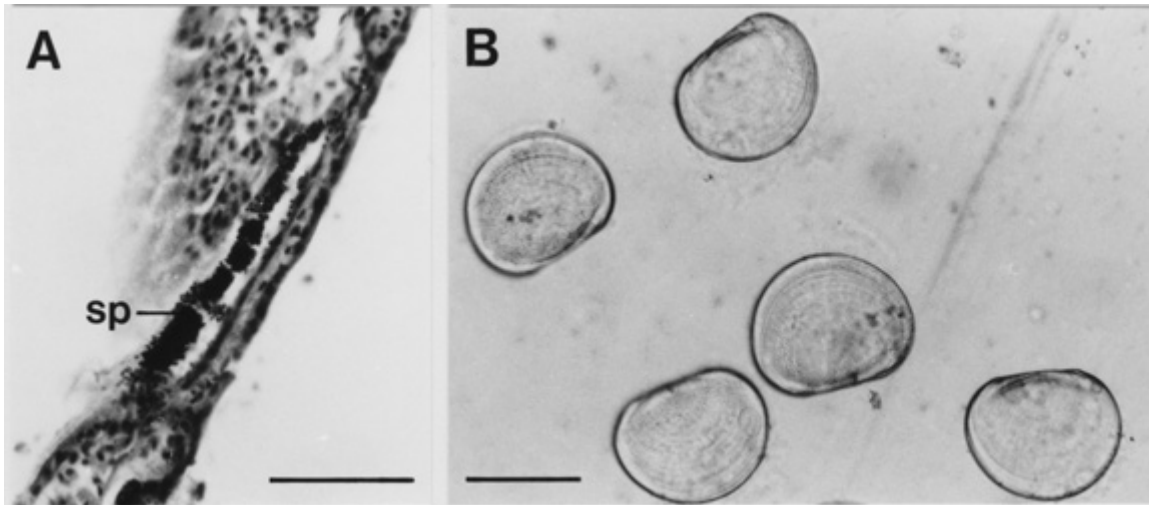
## DISCUSSION

### SYSTEMATICS

Details of shell outline and hinge in our material exactly matches those of the type specimens. Maximum SL in our material is surpassed only by the lectotype which measures 8.4 mm. The comparatively large width relative to height may help the bivalve not to become dislodged when the host moves in its burrow or reburrows in the substrate. Savazzi (2001) did not record the size of his Philippine shells, but the largest illustrated one (Fig. 7G) is ca. 6.4 mm long.

A. Adams never illustrated the species, and only gave a cursory description of the shell and none of the hinge. Prasad (1932, Pl. V, figs. 31, 32) illustrated one of A. Adams's specimens which, from its size, can be identified as the largest specimen of the holotype material. Savazzi (2001) figured several specimens of various sizes. According to Savazzi (2001) the hinge of the right valve shows a well developed, elongated anterior tooth and a somewhat shorter posterior tooth, while the left valve has corresponding, but shorter teeth. Although less detailed, this description corresponds with our observations. This kind of dentition does not resemble that of the type species of *Pythina*, *P. deshayesiana* Hinds

**Figure 5** *Koreamya arcuata*. **A** and **B**, transverse sections through the ligament. **C**, transverse section through the posterior part of the gills. **D**, sagittal section through the anterior part of the body. **E**, transverse section through the fused ascending lamellae of the inner demibranchs with the seminal receptacle. **F**, transverse section through the seminal receptacle containing sperm cells. aa, anterior adductor muscle; cg, cerebral ganglion; dg, digestive gland; fal, fused ascending gill lamellae; fg, food groove; fp, fused periostracum; g, gill; ga, gill axis; id, inner demibranch; il, inner layer of primary ligament; k, kidney; lit, lithodesma; lp, labial palp; od, outer demibranch; ol, outer layer of primary ligament; pp, protractor pedis muscle; rp, retractor pedis muscle; sp, sperm cells; sr, seminal receptacle; te, testis; tm, tongue of mantle bounded by epithelium and with connective tissue internally. Toluidine stained 2- $\mu$ m thick Araldite sections (A-C, E, F) and 8- $\mu$ m thick paraplax sections stained with H+E (D). Scale bars: A, B and E: 100  $\mu$ m, C and D: 200 $\mu$ m, and F: 25 $\mu$ m.



**Figure 6** *Koreamyia arcuata* **A** longitudinal section through the ctenidial seminal receptacle filled with sperm cells (sp). 8- $\mu$ m thick Paraplast section stained with H+E. **B** D-shaped veliger larvae extracted from the brood pouch. Scale bars: A: 50  $\mu$ m, B: 100  $\mu$ m.

1844, in which the cardinals are anterior (not posterior) and the laterals posterior (not anterior), and the laterals of the right valve moreover duplicate (Chavan 1969). The opisthodetic ligamentary pit in *P. deshayesiana* forms an oblique narrow line, while the subumbonal amphidetic ligament in *K. arcuata* is seated in a triangular hollow. For these reasons, A. Adam's inclusion of the species in *Pythina* can not be upheld, and also the other four species of that genus which he described (1856) have since been transferred to other genera (of the family Montacutidae). Thus *P. cumingii* was transferred to *Barrimysia* Iredale 1919 by Habe (1977), *P. triangularis* to *Mysella* Angas 1877 by Morton & Scott (1989), *P. paula* first to *Montacuta* Turton 1822 by Smith (1885), later to *Curvemysella* Habe 1959 by Habe (1959), and *P. peculiaris* synonymized with *C. paula* by Smith (1885). Although recognizing differences in the dentition, Morton & Scott (1989) considered *K. arcuata* to be identical with *C. paula*. This is unlikely for the following reasons: 1) teeth are absent in the left valve of *C. paula* and replaced by the produced dorsal margin which fits into the elongate teeth of the right valve (Smith 1885; Morton & Scott 1989); 2) an outer demibranch is entirely missing in *C. paula* (according to Pelseneer (1911, pl. XV, fig. 6) but present in *K. arcuata*; and 3) in *C. paula* the pedal protractor muscle divides the anterior adductor in two, while in *K. arcuata* it issues ventral of the unpartitioned adductor. The dissimilarity in overall shell shape between *C. paula* and *K. arcuata* is also

obvious when one compares Savazzi's (2001) Fig. 7A-D and E-G of the two species. Robba *et al.* (2002) distinguished between the two species, but followed Morton & Scott (1989) in including *K. arcuata* in *Curvemysella*

Many species of galeommatoid bivalves store sperm in seminal receptacles in the shape of paired or unpaired pouches lying in the visceral mass and opening into the posterior part of the suprabranchial chamber (Lützen *et al.* 2004; Lützen & Kosuge 2006). The ctenidial receptacle of *K. arcuata* is of quite another type and this may offer a clue to its systematic position. An exactly identical sort of receptacle exists in *Montacutona compacta* (Gould 1861), in which it is developed behind the foot in the modified, inner surface of the fused ascending lamellae of the inner demibranchs (Morton 1980). In both species it is represented by a deep furrow walled in between two longitudinal ciliated ridges in which the sperm are oriented with their heads towards the epithelium. A study which we have made of the fused gill lamellae in species of *Montacuta*, *Litigiella*, *Nipponomysella* (all Montacutidae) and *Pseudopythina* (Kellidae) shows that such a structure is absent. The same is true in *Neaeromya rugifera* (Carpenter), as illustrated by Narchi (1969, as *Pseudopythina rugifera*). Therefore, in *K. arcuata* and *M. compacta*, the seminal receptacle probably represents a unique specialization with the function of storing and maintaining sperm. Ctenidial receptacles are also present in another montacutid, namely *Mysella sovaliki*, but in that



species they are paired pouches, each of them being located in the vestigial outer demibranch (Petersen & Lützen, 2008).

The sperm heads of *K. arcuata* and *M. compacta* are small and short, but a detailed comparison is not possible as the fine structure is unknown in both. Species of *Montacutona*, in contrast to the majority of other montacutids but similarly to *K. arcuata*, possess an outer reduced demibranch (Ponder 1971; Morton 1980), and the protractor pedis muscle has the same course as in *K. arcuata*. In *Montacutona* the dentition in each valve consists of an anterior and posterior tooth separated by a triangular ligamental socket as in *K. arcuata*.

Savazzi (2001) noted a calcified component within the ligament, but did not consider it a true lithodesma. However, the arrangement of the histological elements of the ligament compare well to that occurring in the Anomalodesmata (Yonge & Morton 1980) and, in particular, in the Lyonsiidae. The much shorter primary ligament of *Koreamya* has also been displaced ventrally and been separated from the secondary ligament by a tongue of tissue (compare Fig. 3 with Yonge & Morton 1980, Fig. 1C). A notable difference, however, is that this tongue of tissue is directed backwards in *Koreamya*, while it is directed forwards in the Lyonsiidae, which shows that the structure of the two ligaments are convergent. A lithodesma exists also in *Montacutona* (Morton 1980) but has not been recorded from other galeommatooids except for *Halcampicola tenacis* Oliver 1993. The structure in *M. compacta* differs from that in *K. arcuata* in that a tongue of tissue is absent if this is not in fact represented by the "fibrous material" occupying the centre of the outer ligamental layer in that species.

#### REPRODUCTION

Relations between sex and size indicates that *K. arcuata* is a protandric consecutive hermaphrodite which changes sex from male to female when 3-5 mm long. Shedding of sperm in two hermaphrodites shows that they may function as males and, moreover, that the spawned sperm is not encapsulated in any kind of sperm balls, spermatophores or the like. Morton (1980) believed that small, male *M. compacta* store sperm in the ctenidial seminal receptacle and that they are retained here to autofertilize the

ova when the individual later changes to female. This is not the case in *K. arcuata*, since the seminal receptacle never contained sperm in the males or hermaphrodites. Rather in this species, sperm are exchanged between bivalves sitting together on a host. The high frequency of solitary bivalves could explain the absence of sperm in four of the females. In incubating *M. compacta*, Morton (1980, Fig. 8) noted the presence in the base of the gill filaments of glandular cells richly packed with basophilic droplets. He suggested that their function was to nourish the ova and embryos. No such cells were ever noted in brooding *K. arcuata*

#### HOST RELATIONS

Savazzi (2001) observed that live *K. arcuata* at intervals extends the foot toward the host's mantle opening and he believed that the bivalve in this way samples mucous or detritus trapped in mucous secreted by the host. The diatoms found in the gut of some specimens may have been taken in by this means. The large filtering and sorting area of the gills and labial palps plus the normally developed ctenidial food groove are strong indications that filtration of sea water plays an important role in the feeding. Most of the bivalves were positioned at the lateral parts of the gaping valves where water is being sucked into the host's mantle cavity. While Savazzi (2001) observed the bivalves he studied to be indifferently distributed on either valve of the host, we noted a preference for an attachment to the pedicle valve.

At the Korean collecting sites the average number of bivalves per host is usually two, but the presence on the host shells of marks produced by the byssus of dislodged bivalves besides still attached ones show that in reality more than one occur often. Savazzi (2001) observed the hosts he collected to normally carry one or two, rarely three and in one case four bivalves. When more than one bivalve were present, we and Savazzi observed them to sit tightly together and, with one exception, on either the brachial or the pedicle valve. Although in this position they will have to compete for food, an obvious advantage is that it facilitates the transfer of sperm between the individuals.

Savazzi (2001) found that *K. arcuata* is preferentially associated with larger hosts, which he

moreover believed belonged to the second of the two year classes, he thought to have identified. This is probably an underestimation of the host age since Chuang (1961) documented a much higher longevity (up to 12 years) of *L. anatina* at another tropical site (Singapore). At the area which we studied, maximum life span of *L. anatina* is estimated at 3.45 years based on the growth coefficient from length data (Park *et al.* 2000). Provided the bivalves settle upon hosts that are one year old, this allows for a life expectancy of at least two years. From severed byssuses left behind the bivalves, Savazzi (2001) concluded that the bivalves slowly advance along the host shell as it grows in order to remain in close communication with the host's shell gape.

The difference in size between prodissoconch 1 and 2, and the roughly same size of prodissoconch 2 and the smallest specimens found indicate that settling on the host follows immediately after a larval planktonic life of some length.

*Distribution and hosts* The original material was from Cebu Island, the Philippines (A. Adams 1856), which is also from where Savazzi (2001) got his material (tidal flat off Poor Clare Monastery, Tayud). In both instances, the shells were attached to their brachiopod host, *L. anatina*. The species is further known from off Porto Novo, SE India where thousands of *L. translucida* Dall 1921 were cast ashore during a summer cyclonic storm in 1979, many with the bivalves still attached (Fernando & Fernando 1983). Robba *et al.* (2002) identified shells of *K. arcuata* in the Holocene deposits in Thailand. We extend the species' known distribution to Korea and W Australia. The population of several Korean localities are endangered because of extensive reclamation of the tidal flats (Hong *et al.* 2007), but at present there are still live populations at Yubu-do Island and Hajeon tidal flat. Two shells (host connections unknown) from an unspecified locality in The East Indies in the Aquazoo Löbbecke-Museum probably belong to *K. arcuata*, although the umbos are placed only very slightly behind the middle and the ventral insinuation is very weakly developed.

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