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SYSTEMATIC NOTES ON THE MESODESMATIDAE (MOLLUSCA, BIVALVIA), AND DESCRIPTIONS OF A NEW SPECIES AND A NEW SUBSPECIES

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With six text-figures

In 1959, Mr. A. Hoogerwerf obtained a number of small Mollusca from the gizzard of a godwit (*Limosa* spec.) shot near Koerik, West Irian, New Guinea, that eventually came into my hands for identification. Though the specimens clearly belonged to a species of the genus *Mesodesma* (Mactracea, fam. Mesodesmatidae), further identification with any of the known species of this family proved to be impossible. This stimulated me to revise the Mesodesmatidae.

During this revision many species were encountered, that had each been described under several different names. New synonymies in the genera *Ervilia* Turton, 1822, and *Coecella* [1]) Gray, 1853, will be dealt with in the present paper.

Diagnosis of the Mesodesmatidae.

Shell equivalved, small to moderately large (maximum length 3-140 mm) and of ovate to triangular, mostly inequilateral shape. The umbones are generally on the posterior side. The external ligament is short and weak, but there is a stout resilium fitted into a deep resilifer. The hinge is rather solid. Each valve has one cardinal. On the left valve there is one lateral on each side of the umbo fitting between the two opposite laterals of the right valve. The pallial sinus is variously developed, or even absent in some genera.

1) As already pointed out by Heppell (quoted by Beu, 1971: 127), Gray used the spelling *Coecella*. The first reviser (Deshayes, 1855: 333), however, used the spelling *Caecella*, which was followed by almost every author ever since.

Diagnosis of the genus *Mesodesma* [1]) Deshayes, 1832.

The maximum sizes of the shells are very different from one species to another. The umbo is generally on the posterior side, rarely in the middle but never on the anterior side. The shells are white with a yellow to brown periostracum which is often worn off, partly or even completely. The resilifer never points to the posterior side. The pallial sinus is always present.

Mesodesma altenai spec. nov. (fig. 1a-b)

I propose the name *altenai* for this species in dedication to Dr. C. O. van Regteren Altena for the encouraging help he gave me during the revision of the Mesodesmatidae.

Description. — Shell small (maximum dimensions: length 7.5 mm; height 3.5 mm), convex, elongate-ovate, inequilateral, anterior side much produced, anterior : posterior = 5 : 2. The umbo is not produced. The dorso-anterior side is almost straight, the anterior end semicircular, the ventral side slightly curved and the posterior side short and rounded. The white valves are often thin and transparent. The surface, which is covered with a very thin, light brown periostracum, is smooth and glossy, with concentric growth lines only.

Interior. The pallial line is clearly visible, the broad pallial sinus reaches to well beyond the umbo. The muscle scars are spindle-shaped, that of the anterior is more elongated than that of the posterior adductor.

Hinge. The resilifer projects into the shell, making an angle of 20° with the dorso-anterior margin.

Hinge of the left valve. The long anterior cardinal is a plate, curling upwards to the dorsal side. It has a small, posterior appendix, nearly perpendicular to its length lines. The anterior lateral tooth is larger than half the dorso-anterior side. The posterior lateral tooth is short and has a thick dorsal end.

Hinge of the right valve. The straight, long and thin cardinal tooth runs parallel to the dorso-anterior margin. There is a thin lamella, nearly perpendicular to its posterior end, just under the umbo. Because the anterior

1) As already pointed out by Beu (1971: 117), the name *Paphies* Lesson [1831] has priority over *Mesodesma* Deshayes [1832]. As the part of the Encyclopédie Méthodique in which Deshayes published the name *Mesodesma* is dated 1830, this name is almost exclusively used, instead of *Paphies*. Moreover, *Paphies* and *Mesodesma* by many authors are considered different genera, but the only, and therefore type-species in *Paphies*, *P. australe* (Gmelin, 1791), in my opinion belongs to *Mesodesma*. For the sake of stability of nomenclature an application will be made to the International Commission on Zoological Nomenclature to suppress the generic name *Paphies* Lesson [1831] in favour of *Mesodesma* Deshayes [1832]. In accordance with art. 80 of the Code the name *Mesodesma* is maintained for the time being.

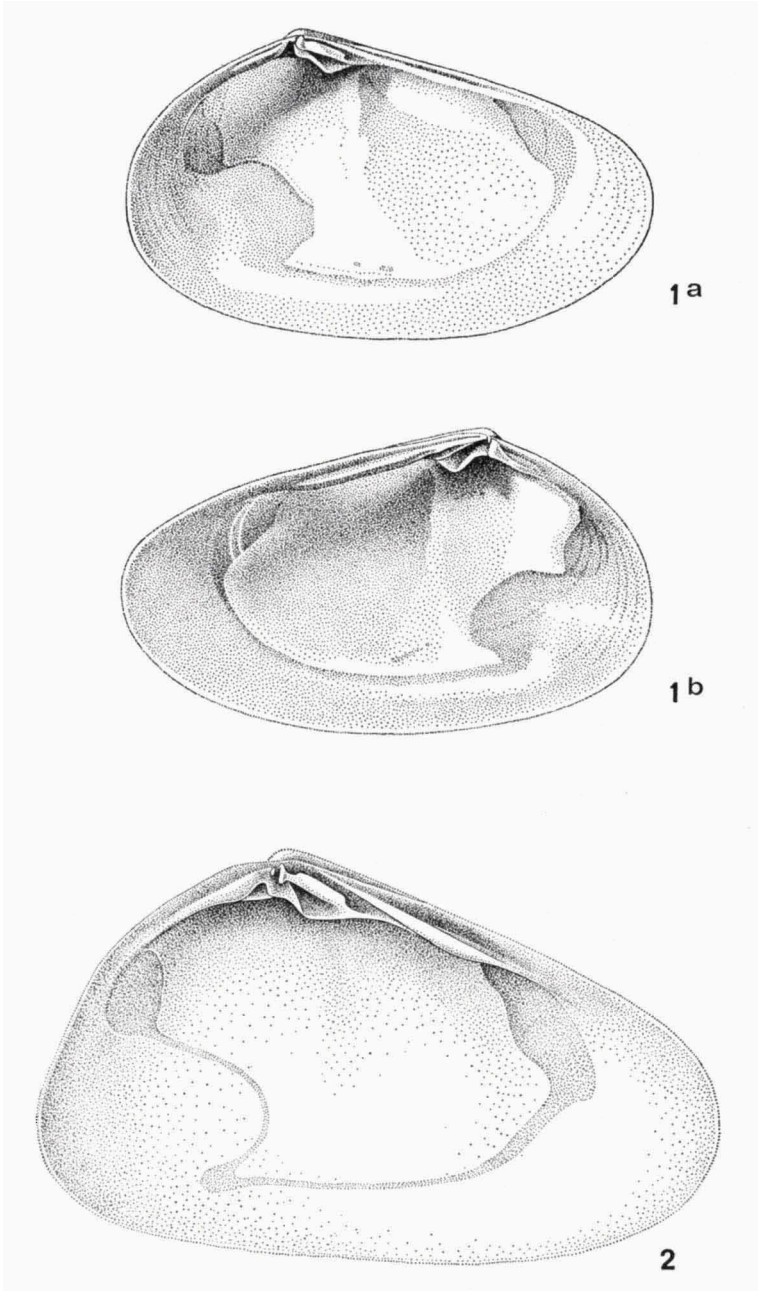

Fig. 1. *Mesodesma altenai* spec. nov. a, left valve of holotype, natural size 5.6 × 3.2 mm; b, same specimen, right valve. W. C. G. Gertenaar del. Fig. 2. *Mesodesma elongatum* Reeve, left valve from Henley Beach, Adelaide, South Australia, natural size 7.0 × 4.8 mm. J. Wessendorp del.

laterals begin at the end of the cardinal, they are shorter than the anterior lateral of the left valve. The short posterior, ventral lateral tooth has a big, thick, wedge-shaped curled anterior origin fitting into a regularly triangular pit at the anterior end of the posterior lateral tooth in the left valve.

Material (from each locality the total number of specimens and single valves is given).

Holotype: length 5.6 mm; altitude 3.2 mm; diameter 2.1 mm.

Holotype + paratypes, 1 + 46, Koerik, from gizzard of *Limosa* spec., 29.x.1959, A. Hoogerwerf.

Paratypes, $^3/_2$, Boeti (village east of Merauke), beach, 25.iii.1955, Exp. L. D. Brongersma; $^1/_2$, Lampoe Satoe (near Merauke), 4.iv.1955, Exp. L. D. Brongersma; $^1/_2$, Merauke, fixed on coral washed ashore, ii.1960, W. Bergmans.

Types in Rijksmuseum van Natuurlijke Historie, Leiden.

The nearest relative of this new species appears to be *Mesodesma elongatum* Reeve, 1854: pl. 1 fig. 5. *Mesodesma altenai* differs from the latter in the following respects (see figs. 1 and 2):

1) The shell is obviously more convex.
2) The lateral teeth run parallel to the margin of the shell, while in *M. elongatum* they diverge from it.
3) The resilifer points more anteriorly.
4) The part of the posterior ventral lateral near the umbo is triangular; in *M. elongatum* it is ovate.

Ervilia Turton, 1822

Ervilia Turton, 1822: 55. Type-species: *Mya nitens* Montagu, 1808: 165.
Rochefortina Dall, 1924: 88. Type-species: *Rochefortia semele* Dall, 1924: 88.
Spondervilia Iredale, 1930: 402. Type-species: *Ervilia australis* Angas, 1877: 175, pl. 26 fig. 21.

Diagnosis.

Small mesodesmatids (maximum size of recent species: length 15 mm, height 9 mm). The shell is elongate-ovate to triangular, mostly inequilateral. The umbo is on the anterior side. The dorso-anterior side is straight to slightly convex, anterior, ventral, and posterior sides rounded. Some species have white, others coloured shells; the periostracum is nearly always completely worn off. The surface may be smooth and glossy with concentric growth lines only, or it has distinct, concentric ridges. In all species radial sculpture is present, although in some species only on very few specimens. The pallial sinus is deep and the pallial line loops posteriorly on the ventral side of the sinus (see fig. 3).

Systematics. — The genus *Spondervilia* was erected by Iredale, 1930, to accommodate the Australian species described as *Ervilia australis* Angas, because Iredale considered it neither conspecific with the Japanese species *Ervilia bisculpta* Gould (1861: 28), nor bearing much resemblance to the "Palaearctic type-species" of *Ervilia*.

Dall, Bartsch & Rehder (1938: 170) differentiated in a key between *Ervilia* and *Spondervilia* by stating that *Spondervilia* does have anterior radial sculpture, whereas *Ervilia* has none. I have, however, encountered anterior radial sculpture in many specimens of *Ervilia nitens*.

I have studied specimens of the Australian *E. australis* and the Japanese *E. bisculpta* and I have convinced myself that no specific differences can be found; such differences as do occur are no more than individual variations. The same applies to the specimen of *E. bisculpta* figured by Hedley (1906: 479, pl. 36 fig. 8), to which Iredale refers, and Gould's holotype of *E. bisculpta*. *E. australis* Angas and *E. bisculpta* Gould are certainly synonyms, the latter name having priority. A comparison of this species with *E. nitens* (Montagu) reveals the following differences:

Ervilia bisculpta	*Ervilia nitens*
deep radial sculpture both on posterior and anterior sides	if present, radial sculpture mostly only on posterior side, sometimes on anterior side as well
colour white-ivory, seldom with pink, radiating stripes	colour white to pink, surface often shining

They correspond in the typical features which determine the genus *Ervilia*, viz., shape, hinge, characteristic pallial sinus, nature of the concentric and radial sculpture. They evidently belong in the same genus; the generic name *Spondervilia* thereby becomes a synonym of *Ervilia* Turton, 1822.

Dall (1924) described a tiny shell from Oahu, which he placed in *Rochefortina*, a new subgenus of *Rochefortia*, and which he named *R. semele*. In 1938 he synonymized this species with *Ervilia sandwichensis* Smith (1885: 81, pl. 25 figs. 5-5b), thereby raising *Rochefortina* to genus.

The nearest relative of *Rochefortina sandwichensis* is *Ervilia bisculpta*. The differences between these two species are:

Ervilia bisculpta	*Rochefortina sandwichensis*
shell elongate-ovate	shell rounded ovate
very small cavity in the posterior margin near the umbo	cavity near the umbo obvious
radial sculpture only on posterior and anterior sides	radial sculpture all over the shell

They concur in structure of the hinge, characteristic pallial sinus and nature of the concentric and radial sculpture. The essential characteristics which determine the genera in the Mesodesmatidae are the same for these two species. The differences are of the same quality as those between the other *Ervilia* species. Consequently, the two species belong to the same genus, and *Rochefortina* Dall, 1924, becomes a synonym of *Ervilia* Turton, 1822.

Ervilia nitens (Montagu, 1808) (fig. 3a-b)

Mya nitens Montagu, 1808: 165.
Ervilia nitens; Turton, 1822: 56, pl. 19 fig. 4.
Ervilia concentrica Gould[1]), 1862: 281. [new synonymy].
Ervilia subcancellata Smith, 1885: 80, pl. 6 fig. 2-2b. [new synonymy].
Ervilia maculosa Dall, 1896: 26. [new synonymy].
Ervilia californica Dall, 1917: 414. [new synonymy].
Ervilia rostratula Rehder, 1944: 189, pl. 19 figs. 1-2. [new synonymy].

Diagnosis.

Medium sized *Ervilia* (maximum length 9 mm, heigth 6 mm). Shell ovate to triangular. The appearence of the apex is variable. Sometimes, especially in pink specimens, the outline is rounded, hardly disturbed by the umbo. Sometimes the umbo projects conspicuously. All intermediate forms do occur. Shell white to pink. Concentric ridges occur all over the shell. If radial sculpture is present, it is distinct, but not as deep as the concentric ridges. Radial sculpture is mostly only present on the posterior side, sometimes also on the anterior side.

Remarks. — In literature two species that occur in the Caribbean area are frequently mentioned, viz., *Ervilia nitens* (Montagu) and *Ervilia concentrica* Gould.

Shells are considered to be *E. nitens* when they have most of the following characteristics: pink colour, ovate shape, umbo not produced, dorsal and anterior margins convex, radial sculpture often absent, if present on posterior side only.

Specimens with a white colour, ovate to trigonal shape, a concave dorso-anterior margin, a papilliform umbo, radial sculpture on both posterior and anterior sides are generally named *Ervilia concentrica*. This current concept of *Ervilia concentrica*, however, clearly is at variance with the characters of the type-series of *Ervilia concentrica* Gould, the latter showing all the characteristics of *E. nitens*.

1) Holmes (1860: 44, pl. 6 fig. 10) described a fossil *Ervilia*, and named it *Mesodesma concentrica*. According to Davis (1967) it is conspecific with *Ervilia concentrica* Gould. I do not want to express a definite opinion now, because I have not yet studied the fossils thoroughly, but tend to agree with Davis.

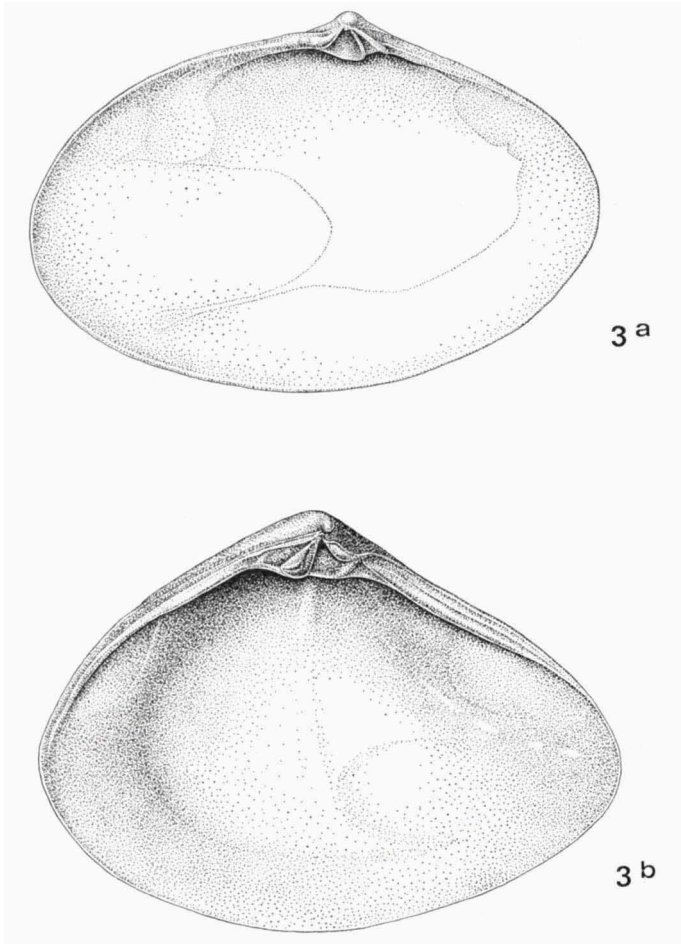

Fig. 3. *Ervilia nitens* (Montagu). a, left valve of lectotype of *E. maculosa* Dall, natural size 4.7 × 3.0 mm; b, right valve of holotype of *E. rostratula* Rehder, natural size 4.7 × 3.3 mm. Both J. Wessendorp del.

When studying the types one may group them as follows:
Ervilia nitens group: *E. nitens, E. concentrica, E. maculosa, E. californica.*
Ervilia "concentrica" group: *E. subcancellata, E. rostratula.*

When studying material from many localities a great diversity in shape even in one lot is evident. In some samples the majority of specimens has one of the forms mentioned above; in other samples however, the various characteristics appear in other combinations. This phenomenon has compelled me to consider the species listed above one pluriform species. It even proved to be impossible to find any evidence of differentiation at the subspecific level at the border of the distributional area.

The synonymy of *Ervilia maculosa* Dall with *E. concentrica* Gould, and of *E. rostratula* Rehder with *E. subcancellata* Smith, has also been noticed by J. D. Davis (personal communication).

Material (from each locality the total number of specimens and single valves is given; the number between brackets refers to the number of samples).

Type-material of *E. nitens*, Scotland, $^{4}/_{2}$ (possibly paratypes) (1); *E. concentrica*, coast North Carolina, $^{1}/_{2}$ + $^{6}/_{2}$ (holotype + paratypes) (1); *E. subcancellata*, Bermuda, $^{2}/_{2}$ (syntypes) (badly corroded by chemical influences) (1); *E. maculosa*, Cape Lookout, $^{1}/_{2}$ + 1 + $^{6}/_{2}$ (lectotype + paratypes) (1); *E. californica*, Bridwell, Los Angeles, 1 (holotype) (1); *E. rostratula*, Lake Worth, 1 (holotype) (1).

Scotland, 2 (1); Recife, $^{1}/_{2}$ (1); Fernando de Noronha, $^{7}/_{2}$ (1); Suriname (Dutch Guiana), > 50 (4); Margarita $^{35}/_{2}$ (2); Antilles, > 200 (10); Curaçao, > 350 (5); West Indies, 8 + $^{14}/_{2}$ (5); St. Vincent, 51 + $^{4}/_{2}$ (3); Guadeloupe, 6 + $^{30}/_{2}$ (4); Barbuda, > 130 + $^{130}/_{2}$ (11); St. Martin, > 130 + $^{300}/_{2}$ (4); St. Thomas, 7 + $^{20}/_{2}$ (2); Florida Keys, 7 + $^{19}/_{2}$ (3); Frying Pan Shoal, 15 + $^{7}/_{2}$ (2); Bermuda, $^{50}/_{2}$ (3); New York, $^{6}/_{2}$ (1); unknown, > $^{250}/_{2}$ (10).

Coecella Gray, 1853

Diagnosis.

Medium sized Mesodesmatidae (maximum length 45 mm). Shell elongate-ovate to rounded, generally equilateral. The anterior and posterior sides are rounded, the ventral side is convex to straight. The white valves have a resistant brown periostracum, sometimes partly worn off. The surface is smooth with concentric growth lines only.

Interior. The pallial line has a sinus variable from short in rounded specimens to long, nearly reaching beyond the umbo, in elongate-ovate specimens. Obvious but small muscle scars present.

Hinge. The resilifer points to the posterior side. The short lateral teeth are triangular (see fig. 5). The cardinals have a tendency to become bifid.

Coecella horsfieldi Gray, 1853 (figs. 4-6)

Coecella Horsfieldii Gray, 1853: 43.
Caecella turgida Deshayes, 1855: 333. [new synonymy].
Caecella zebuensis Deshayes, 1855: 334. [new synonymy].
Caecella cumingiana Deshayes, 1855: 334. [new synonymy].
Caecella chinensis Deshayes, 1855: 334. [new synonymy].
Caecella convexa Deshayes, 1855: 334. [new synonymy].
Caecella lata Deshayes, 1855: 334. [new synonymy].
Caecella transversalis Deshayes, 1855: 335. [new synonymy].
Caecella oblonga Deshayes, 1855: 335. [new synonymy].
Caecella zelandica Deshayes, 1855: 335. [new synonymy].
Caecella tenuis Deshayes, 1855: 336. [new synonymy].
Ervilia otsuensis Yokoyama, 1920: 109, pl. 7 figs. 21-22.

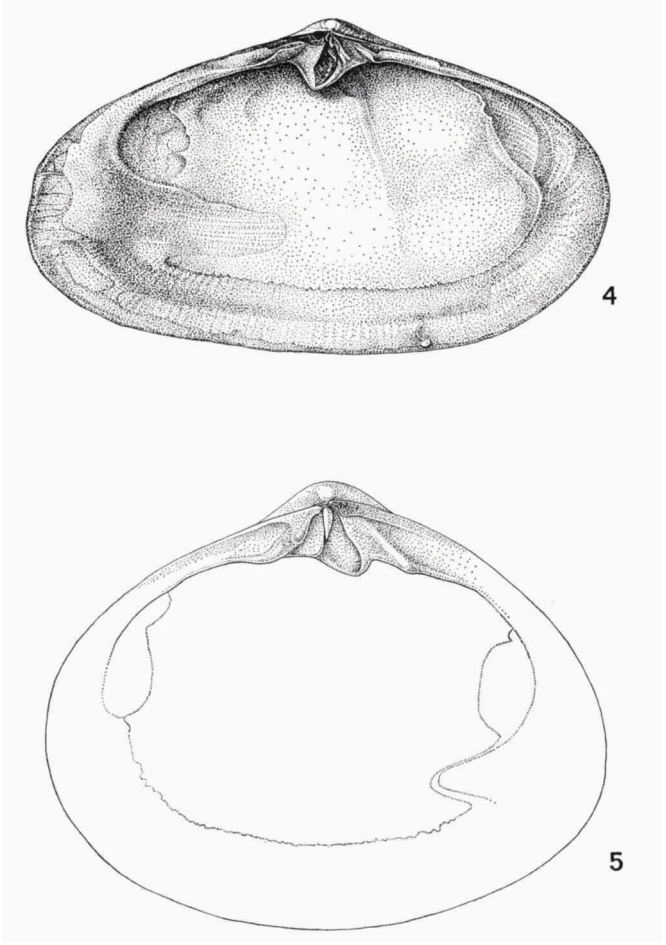

Fig. 4. *Coecella horsfieldi horsfieldi* Gray, left valve, Singapore, fishmarket, natural size 41.7 × 23.5 mm. Fig. 5. *Coecella horsfieldi chinensis* Deshayes, right valve, Awaji, natural size 23.4 × 17.4 mm. Both J. Wessendorp del.

Remarks. — When studying the type-specimens of all the species in this genus it proved to be difficult to differentiate between the various species. Considering the type-specimens only, they can be divided into two groups according to the shape of the shell and the form of the pallial sinus. The features of the hinge, sculpture of the surface, periostracum, and shape of the muscle scars are identical in all these specimens.

The holotype of *C. horsfieldi*, type-species of the genus, is an elongate-ovate, slightly truncated valve. The holotype of *C. transversalis* differs only in being more elongate and having a deeper pallial sinus. The lectotype of *C. cumingiana* has the same elongate shape as the type-species, but is not truncated.

The lectotypes of *C. turgida, C. zelandica* and *C. oblonga* are merely smaller specimens. The pallial sinus in *C. oblonga* is somewhat deeper than that in the other two. The shell of the holotype of *C. tenuis* is thinner.

The lectotypes of *C. chinensis, C. zebuensis,* and the holotypes of *C. convexa* and *C. lata* are rounded-ovate, but cannot be distinguished from each other. *C. lata* is slightly bigger than the other three.

Since Deshayes had at his disposal only a small number of specimens, he described all samples as separate species. When studying larger samples, however, the differences observed and described by Deshayes, prove merely to depend on individual variations. It turned out that specimens corresponding with the various types do occur in the same sample, together with all intermediates. This convinced me that all these specimens are representatives of one polymorphic species. I intend to publish photographs of the holo- and lectotypes in a revision of the Mesodesmatidae, now in preparation.

There appears to be a certain predominance of shape in various geographic areas. The rounded-ovate shape of the specimen described by Deshayes as *C. chinensis* dominates in the Japanese and Philippine regions. Very elongate shells are found predominantly in the Western part of the distributional area. I want to preserve a certain differentiation by distinguishing between three subspecies, *C. horsfieldi horsfieldi* Gray, 1853, *C. horsfieldi chinensis* Deshayes, 1855, and *C. horsfieldi formosae* subspec. nov., described below.

Diagnosis of *Coecella horsfieldi horsfieldi.*

Elongate-ovate *Coecella.* Length: height > 1.45. Pallial sinus variable. Cardinal of the left valve grooved.

The type-specimens of *C. horsfieldi, C. turgida, C. cumingiana, C. transversalis, C. oblonga, C. zelandica* and *C. tenuis* all belong to this subspecies.

Diagnosis of *Coecella horsfieldi chinensis.*

Rounded-ovate *Coecella.* Length: height between 1.25 and 1.55. Pallial sinus small and sharp. Cardinal of the left valve grooved.

The type-specimens of *C. chinensis, C. zebuensis, C. convexa, C. lata* and *Ervilia otsuensis* show these features.

I have chosen the name *chinensis* for the rounded subspecies because it is used by most of the authors for *Coecella*'s of this shape.

Material.

C. horsfieldi, Madras, ½ (probably holotype) (1); *C. turgida,* Philippines, $^2/_2$ (lectotype + paratype) (1); *C. cumingiana,* Luzon, $^5/_2$ (lectotype

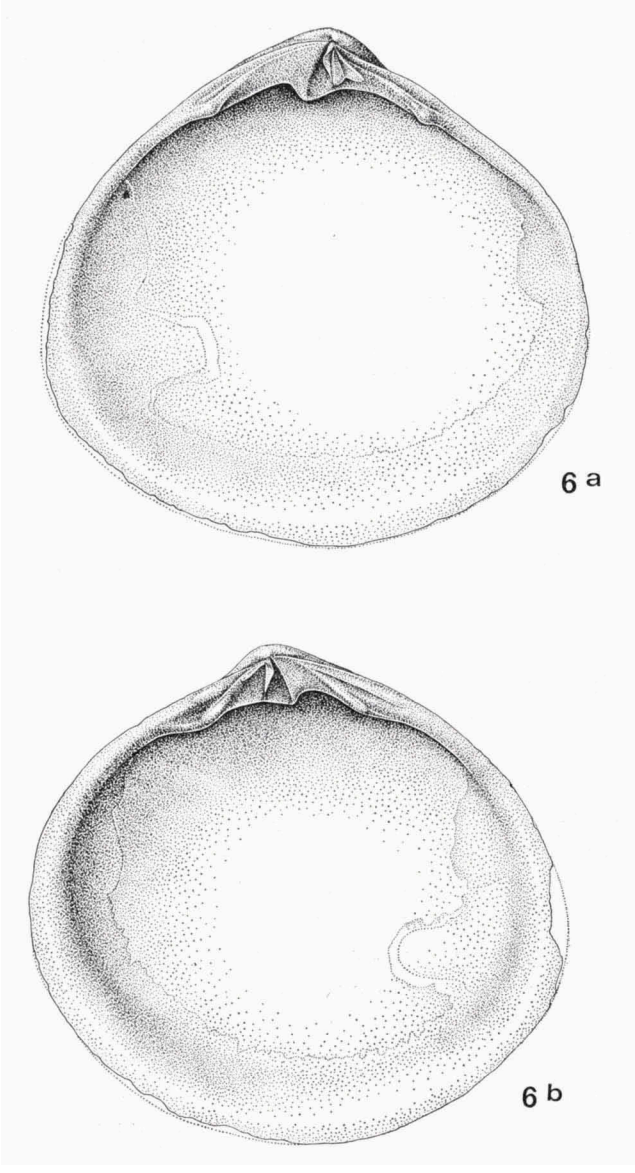

Fig. 6. *Coecella horsfieldi formosa* subspec. nov. a, left valve of paratype, natural size 16.3 × 14.3 mm; b, right valve of holotype, natural size 15.7 × 14.5 mm. Both J. Wessendorp del.

+ paratypes) (1); *C. transversalis*, origin unknown, 1 (holotype) (1); *C. oblonga*, China seas, 1 (holotype) (1); *C. zelandica*, New Zealand, $^3/_2$ (lectotype + paratypes) (1); *C. tenuis*, Loay, Isle of Bohol, 1 (holotype)

(1); *C. chinensis*, China seas, 3 (lectotype + paratypes) (1); *C. zebuensis*, Cebu, 3 (lectotype + paratypes) (1); *C. convexa*, origin unknown, 1 (holotype) (1); *C. lata*, China seas, 1 (holotype) (1); *E. otsuensis*, Otsu, 2/2 (1) (fossil?).

C. horsfieldi horsfieldi: New Caledonia, 3 (2); Oceania, 2/2 (1); Geelvinkbaai, 3 (2); Borneo, 1 (1); Philippines, > 4 + 25/2 (6); Bohol, 1/2 (1); Siam, 3 (1); Bintang, 1 (1); Singapore, > 100 (4); Penang, 1 + 1/2 (1); Ceylon, 2 (2); Kon Kan coast, 3 (1); Bombay, > 50 (7); Aden, 2 (2).

C. horsfieldi chinensis: New Caledonia, 19 + 5/2 (6); Oceania, 1 (1); Philippines, > 25/2 (2); Manilla, 1 (1); Luzon, 2 + 1/2 (1); Japan, 10 + 7/2 (6); Cochinchina, 2 (1); Nagasaki, 10 (3); Yukiura, Nagasaki, 5 (1); Yamada, 7 (1); Hiroshima, 7 (2); Awaj, 4/2 (1); Otaru, 1 (1); South Manchuria, 9/2 (1); Wei Hai Wei, 3 (1); China seas, 5 + 3/2 (3); Ceylon, 1/2 (1); Aden, 11 + 14/2 (10); Red Sea, 4 (1).

Coecella horsfieldi formosae subspec. nov.

Dr. Habe of the National Science Museum of Tokyo sent me a lot of seven valves of a species from Formosa, belonging to the Mesodesmatidae, which he could only identify as *Coecella* spec. They appeared to be *C. horsfieldi* s.l., but they are so different from the two above-named subspecies, that I am inclined to consider them to belong to a new subspecies. Since the *Coecella*'s and especially these specimens, bear a strong resemblance to *Mactra*'s there is a possibility this subspecies has already been described as a *Mactra* species, although I have not found evidence of this. Therefore I here give a description of the valves of this formosan subspecies.

Description. — Small *Coecella* (maximum dimensions: length 20 mm, heigth 18 mm), convex, rounded, subequilateral. The umbo protrudes towards the anterior side. The dorso-anterior side passes straight into the round anterior end. The ventral side is rounded. The posterior side is sometimes rounded, sometimes slightly truncated, forming an angle with the ventral side. The white valves bear remnants of a brown periostracum.

Interior. The pallial line is clearly visible. The pallial sinus is small and rounded. The small muscle scars are ovate.

Hinge. Characteristic *Coecella* hinge. The bifid cardinal tooth of the left valve is rather broad.

Holotype. Right valve, length 15.8 mm; altitude 14.7 mm. Holotype + paratypes, 7 valves, Kosan, Shinchikusyn, Formosa. Holotypes + 4 paratypes in National Science Museum, Tokyo; 2 paratypes in Rijksmuseum van Natuurlijke Historie, Leiden.

This subspecies differs from the other subspecies in the following respects:

1) The shell is obviously higher than the highest relative, length: height $\leqslant$ 1.15.
2) The umbo points to the anterior side.
3) The resilifer projects less deeply into the shell.
4) The pallial sinus is rounder.
5) The cardinal is distinctly bifid, instead of inclined to be bifid.

Discussion

In comparing the genera *Coecella* and *Ervilia* it is clear that they differ in the following important features:

Ervilia	*Coecella*
cardinal of the right valve drop-shaped	cardinal of the right valve Λ-shaped
cardinal of the left valve a thin plate	cardinal of the left valve thick and bifid
long laterals	short laterals
broad pallial sinus	narrow pallial sinus
radial and concentric sculpture	concentric growth lines only
very thin periostracum	thick periostracum

Because the features of the hinge are important in the systematics of the Bivalvia, they prove, that within the family *Ervilia* and *Coecella* are widely separated. Comparing the hinges of all the genera in the Mesodesmatidae I am inclined to think, that *Coecella* is more related to *Anapella* and *Mesodesma* than to *Ervilia*. This matter will be discussed in more detail in a revision of the Mesodesmatidae.

The characteristic sculpture and pallial line of *Ervilia* isolate this genus in the family. A conjunction of the genera *Ervilia* and *Coecella* in the subfamily Erviliinae, as proposed by Dall (1895: 213), followed in this respect by modern authors (Keen, 1969: N610; Beu, 1971: 127), is in my opinion unjustified.

Acknowledgement

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