

TOWARD A SYSTEMATIC REVISION OF BROODING FRESHWATER
CORBICULIDAE IN SOUTHEAST ASIA (BIVALVIA, VENEROIDA):
ON SHELL MORPHOLOGY, ANATOMY AND MOLECULAR PHYLOGENETICS
OF ENDEMIC TAXA FROM ISLANDS IN INDONESIA

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ABSTRACT

The Indonesian island of Sulawesi, with its central zoogeographical position within the so-called “Wallacea”, harbors a large number of endemic faunal elements, rendering this region a biodiversity hotspot. The present paper shows that this holds also true for limnic molluscs of the family Corbiculidae. Although less species-rich than previously assumed, we document here that the Indonesian corbiculids exhibit more anatomical and life-history variation than in the rest of their collective Old World distribution.

As a first step toward a comprehensive revision of the Southeast Asian corbiculids, morphological characters and molecular genetics are studied in the various taxa described from Sulawesi and Sumatra. Based on morphological studies of materials collected recently, especially in the central lakes on the island of Sulawesi and supplemented by historical museum collections, we conclude that *Corbicula* is represented on Sumatra by at least one and on Sulawesi by four endemic taxa. *Corbicula javanica* (Mousson, 1849), known from several islands of Indonesia, and *C. moltkiana* Prime, 1878, sampled in lakes Singkarak and Manindjau on Sumatra are similar in their anatomical characters and the mode of brooding to the widely distributed Asian *C. fluminea* (Müller, 1774), but differ from the latter in shell form and sculpture. The distinctness of *C. linduensis* Bollinger, 1914, restricted to the basin of the Palu River in North Sulawesi is confirmed in finding a peculiar mode of ovoviviparous reproduction, that is, incubation of embryos in the gills until juveniles are 1.3 mm long. *Corbicula matannensis* P. Sarasin & F. Sarasin, 1898, and *C. loehensis* Krümel, 1913, both occurring within the Malili lake system on Sulawesi, as well as *C. possoensis* P. Sarasin & F. Sarasin, 1898, endemic to Lake Poso, all release small larvae, a reproductive mode similar to *C. fluminea*, but they differ from the latter in having broad siphons with slit-like apertures. *Corbicula loehensis* differs from *C. matannensis* in its very delicate sculpture and hinge, whereas *C. possoensis* is distinguished from other species in having big posterior adductors and especially broad inhalant siphon. In addition, only *C. possoensis* broods in both demibranchs, whereas all other known brooding corbiculids incubate in the inner demibranch only. Monoflagellate spermatozoa were observed in all studied Indonesian taxa except *C. javanica*, in which sperm structure remains unknown.

Phylogenetic analyses of COI sequences (MP and NJ) including now five Indonesian taxa studied herein show distinct clades occurring (i) on Sumatra, identified as *C. moltkiana*, and (ii) on Sulawesi with two separate lineages of *C. possoensis* from Lake Poso being most distinct from *C. matannensis* and *C. loehensis* from the Malili lake system. The analyses also suggest a close relationship of *C. javanica* to the Korean *C. fluminea* within an Asian cluster, including also the Australian corbiculid. Systematic, biogeographical and evolutionary implications of these results are discussed.

Key words: freshwater Bivalvia, *Corbicula*, ovoviviparity, anatomy, systematics, biogeography, endemics, Sulawesi.

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INTRODUCTION

Limnic bivalves of the family Corbiculidae are widespread in tropical and subtropical regions of the Old and New worlds. The genus *Corbicula* is also widely distributed and abundant in fresh and brackish waters of Africa, the southern parts of Asia, extending from Turkey and Israel in the west to China, the Malayan Peninsula and the Sunda Archipelago, New Guinea and eastern Australia. Members of the genus were also introduced to both Americas and Western Europe (reviews: Morton, 1986; Araujo et al., 1993; Pfenninger et al., 2002).

Comprising brackish-water and freshwater species and, therefore, representing different stages of adaptation to freshwater environments, renders *Corbicula* an important model organism for evolutionary and ecological studies not only among molluscs. However, its taxonomy and systematics is far from being resolved and many aspects are still disputable. A great number of species were described, especially from Southeast Asia (e.g., Martens, 1897; P. Sarasin & F. Sarasin, 1898; Kruimel, 1913; reviews: Prashad, 1930; Morton, 1979), resulting in a plethora of named taxa. To date a comprehensive revision of these corbiculids is lacking.

While an earlier review (Prashad, 1930) dealt exclusively with conchological characters, recognizing many congeneric morphospecies, some later investigations focused on anatomy (Britton & Morton, 1979; Harada & Nishino, 1995) and particularly on reproductive biology (Morton, 1979, 1986), resulting in greatly reducing the number of species considered valid. For example, Morton (1986) recognized only two species, namely *C. fluminalis* Müller, 1774, and *C. fluminea* Müller, 1774. According to this author, *C. fluminalis* more frequently inhabits estuaries, tolerates higher salinity (thus, basically being a brackish-water representative) and releases free-swimming veliger larvae. In contrast, *C. fluminea* occurs in pure freshwater only and incubates embryos in the gills, which are not released before the foot of the juveniles is well developed. Summarizing the available biological data, Morton (1986) concluded that both *Corbicula* species are distributed throughout the range of the genus and include a great variety of conchological forms with overlapping characters.

A different taxonomic concept of *Corbicula* is accepted in Japan (Harada & Nishino, 1995). The estuarine, non-incubating species is re-

ferred to as *C. japonica* Prime, 1864, and the local freshwater incubating form as *C. leana* Prime, 1864, and *C. fluminea* is reported from several Japanese localities (Harada & Nishino, 1995; Komaru et al., 1998). Komaru et al. (1998) provided morphological characters to distinguish *C. leana* from *C. fluminea*. In addition, *C. sandai* Reinhardt, 1878, is recognized as an endemic species restricted to Lake Biwa in Japan.

To further complicate corbiculid systematics, new insights into the genetic structure of Asian *Corbicula* are salient to any taxonomic revision. As shown first by Okamoto & Arimoto (1986), Japanese taxa have different karyotypes, with *C. japonica* and *C. sandai* being diploid (with $2n = 38$ and 36 , respectively), whereas *C. leana* is triploid ($3n = 54$). Recently, polyploidy has also been discovered in several taxa from Korea (Park et al., 2000) and in two color forms of *C. fluminea* from China, Sechuan Province (Qiu et al., 2001). It has been repeatedly reported that polyploidy is associated with peculiar biflagellate spermatozoa and ameiotic reproduction, resulting in clonality (Komaru & Konishi, 1996, 1999; Komaru et al., 1997, 2000; Konishi et al., 1998; Siripattawan et al., 2000; Qiu et al., 2001; Lee et al. 2002). For example, those investigations of the reproductive biology of *Corbicula* showed that biflagellate spermatozoa observed in *C. leana* from Japan and *C. fluminea* from China and Taiwan are non-reductional, and that these molluscs reproduce by means of androgenesis, that is, the elimination of the mother's genome from eggs and development of embryos from the genome of spermatozoon only. Similar biflagellate spermatozoa were reported for the *C. fluminea* samples from Thailand, Korea and the exotic forms introduced into the USA. Thus, apparently this taxon is a heterogeneous assemblage of variably polyploid and ameiotic clonal lineages (Siripattawan et al., 2000). Spermatozoa of the Australian *C. australis* (Lamarck, 1818) are also biflagellate (Byrne et al., 2000), therefore indicating a clonal structure for this taxon as well (Siripattawan et al., 2000).

All these clonal lineages, to our present knowledge, lack sexually reproducing parental taxa and, therefore, greatly complicate the meaningful application of specific names. Consequently, the name *C. fluminea* has been applied to multiple genetically distinct clonal lineages of unknown parentage in recent studies on European and introduced North American populations. In contrast, there is only one

documented sexual species of freshwater *Corbicula*, *C. sandai*, endemic to the "ancient" Lake Biwa (Hurukawa & Mitsumoto, 1953). Interestingly, at the same time only *C. sandai* has monoflagellate spermatozoa, thus allowing to correlate reproductive mode with sperm morphology (Konishi et al., 1998; Siripattawan et al., 2000). In addition, *C. sandai* is also the only known gonochoric freshwater *Corbicula*, whereas all other taxa appear to be hermaphroditic (Komaru & Konishi, 1996; Byrne et al., 2000; Siripattawan et al., 2000).

Surprisingly, only diploid karyotypes were reported for the two introduced European *Corbicula* morphotypes, traditionally identified as *C. fluminalis* and *C. fluminea* (Pfenninger et al., 2002). In the absence of direct evidence of clonality in these morphotypes, hybridization between those two morphotypes, which was discovered in this molecular study, might indicate sexual reproduction. Accordingly, clonality is widely distributed, especially among most Asian taxa, albeit not the universal feature among freshwater *Corbicula*. Therefore, the genetic structure of these limnic clams needs further investigation.

Furthermore, not only these new data on genetics, polyploidy and reproduction disagree with the two-species concept of Asian *Corbicula* as suggested by Morton (1979, 1986). Preliminary data from mitochondrial DNA sequences utilizing the COI gene (Siripattawan et al., 2000; Lee et al., 2002) indicate that *C. leana*, *C. japonica* and *C. sandai* are distinct lineages alongside *C. fluminea*, whereas two North American morphotypes (forms A and B) might have different origin, with the first (form A) being closer related to Japanese *C. leana* and the second (form B) to *C. fluminea* from Korea. This analysis, as well as a later one that included samples from China, Israel and Europe (Pfenninger et al., 2002), demonstrated that all studied freshwater *Corbicula* form one single clade with poorly resolved relationships, though, with the exception of *C. madagascariensis* Smith, 1882, from Madagascar (erroneously referred to as *C. africana* from "Africa" in the latter paper as well as in GenBank). The modest levels of genetic divergence demonstrated for the freshwater lineages suggested evolutionary recent common origin (Siripattawan et al., 2000; Pfenninger et al., 2002).

Despite these accounts, to date many regions remain poorly investigated with respect to *Corbicula* diversity and distribution, in par-

ticular islands of the Sunda Archipelago, such as the Indonesian islands of Sumatra and Sulawesi. This island chain is among the biologically most diverse regions in the world, representing one of the major hot spots of biodiversity, areas exceptionally rich in endemic species and harbouring rare and threatened species (Myers et al., 2000; Mittermeier et al., 2000; Reid, 1998). Due to its biogeographically central position within the so-called "Wallacea", in the heart of the complex crossroads of two continents Asia and Australia, Sulawesi not only harbours a number of unique and endemic faunal elements, but recently also figured prominently in palaeogeographical research providing new geological insights (Whitmore, 1981; Hall & Blundell, 1996; Metcalfe et al., 2001). Consequently, this region became a central focus of biogeographic interest again (Whitmore, 1987; Hall & Holloway, 1998; Metcalfe et al., 2001).

Although molluscs have unfortunately only rarely been considered in biogeographic research (Davis, 1982), especially limnic gastropods from the Sunda region were recently utilized as models in an approach to synthesize systematic and geological patterns (overview: Glaubrecht, 2000). For example, based on the known distributional pattern found in the constituent taxa for the mainly viviparous Pachychilidae which are widely distributed throughout the mainland of Southeast Asia and the Indo-Malayan Archipelago, reaching as far east as the Philippine Islands and Sulawesi, it has been hypothesized that the biogeography of these limnic snails (i) find their explanation in palaeogeographical events that go back to the Cretaceous and early Cenozoic instead of explaining the distribution as correlated to the forming of the so-called Sunda- and Sahulland, respectively, and (ii) that it implies vicariance over dispersal as causation (Glaubrecht, 2000; Köhler et al., 2000; Köhler & Glaubrecht, 2001, 2003; Glaubrecht & Rintelen, 2003).

In contrast, according to Siripattawan et al. (2000) and Pfenninger et al. (2002), the known patterns of distribution and genetic divergence in *Corbicula*, based on data for continental Southeast Asia, Japan and Australia, suggest rather dispersal than vicariance scenario for these freshwater bivalves. Therefore, it is promising to test the mentioned scenario by extending the data set, and to compare the patterns of morphological and genetic divergence among Indonesian bivalves with that of the sympatric pachychilid snails. In this context,

the corbiculid bivalves provide a second model group that inhabits the same limnic environments in this crucial biogeographic region and, with them incubating eggs and embryos in their gills, also share a similar reproductive strategy with the ovoviviparous and viviparous pachychilid gastropods.

However, any zoogeographical evaluation has to be based on solid systematic knowledge. Unfortunately, any modern revision of the Corbiculidae is still lacking. For example, from Sulawesi a total of nine endemic corbiculid species have been described, especially from its ancient central lakes (Martens, 1897; P. Sarasin & F. Sarasin, 1898; Kruimel, 1913; Bollinger, 1914). In contrast, Prashad (1930) recognised only two endemic species on Sulawesi, assigning all lacustrine taxa to *C. subplanata* Martens, 1897. In his revision of the corbiculids from Sulawesi, Djajasasmita (1975, 1977) recognised four taxa – three endemic species living in lakes in addition to *C. subplanata* as the only riverine form. He also reported on one widely distributed Asian species, *C. javanica* (Mousson, 1849), as occurring on Sulawesi. From Sumatra, also a total of nine endemic species of *Corbicula* have been described (Prime, 1878; Clessin, 1887; Martens, 1897, 1900), of which Djajasasmita (1977) recognized four as valid – *C. moltkiana* Prime, 1878, *C. gustaviana* Martens, 1900, *C. sumatrana* Clessin, 1887, and *C. tobae* Martens, 1900, and, in addition, recorded four widely distributed Asian species on the island, viz. *C. javanica*, *C. pullata* Philippi, 1851, *C. rivalis* (Philippi, 1850), and *C. tumida* Deshayes, 1854.

However, none of these studies provided any sufficiently distinctive characters for the individual species. Although shell proportions, angle between lateral teeth, position of beaks, shell thickness and sculpture are usually used, the intraspecific variability of these characters remained largely unknown and, therefore, the taxonomic decisions appeared as being highly arbitrary. Consequently, Morton (1979, 1986) tentatively suggested conspecificity of the Indonesian species reviewed by Prashad (1930) and Djajasasmita (1975, 1977) with *C. fluminea*, synonymizing the species names listed above with the latter taxon. However, Morton did not discuss in detail the taxonomy, nor did he provide any new data on the morphology or biology of these Indonesian corbiculids. Thus, not only is the systematics and phylogenetic relationships of the presum-

ably endemic insular Corbiculidae unknown, but the anatomy and reproductive biology of any of the disputable species from this region has remained undescribed.

The recent discovery of an endemic genus of Corbiculidae from Lake Poso with its unique cemented mode of life (Bogan & Bouchet, 1998) shows that the molluscan fauna at least of this lake on Sulawesi is much more specific than assumed earlier. This stimulated the present study of other Corbiculidae, namely species of the genus *Corbicula* inhabiting Poso and neighbouring lakes, as was suggested by Bogan & Bouchet (1998). Accordingly, we here integrate shell characters, new data on the anatomy, especially the reproductive biology, and molecular genetics (sequences of COI mitochondrial gene fragment) for six nominal taxa of *Corbicula* from Indonesia, namely *C. javanica*, *C. moltkiana*, *C. linduensis*, *C. matannensis*, *C. loehensis* and *C. possoensis*, based on recent sampling by the authors on Sumatra and Sulawesi, and we compare with historical material deposited in the museum collections. In addition, we report for the first time for any Indonesian *Corbicula* principal features of sperm morphology, as well as presence and localization of larvae in gills. We also provide a preliminary evaluation of the status and affinities of the studied taxa, but any final taxonomic decision is postponed until more molecular data on the diverse morphotypes from lacustrine and riverine habitats in the area are available. Some other taxa described by Martens (1897, 1900) from Sumatra and Sulawesi are also awaiting revision. However, because no fresh material on these taxa was available, these are beyond the scope of our current study. Nevertheless, we document here that the corbiculids endemic to the region (Fig. 1), although less species-rich than assumed before, exhibit more anatomical and life-history variation than in the rest of their collective Old World range.

MATERIALS AND METHODS

Material Studied

The material at hand (Fig. 1) was collected during two field trips to Sulawesi in August 1999 and March 2000 by M. G. and T. v. R., and on Sumatra in April 2000 by Frank Köhler and Sabine Schütt. It is housed in the Malacological collection of the ZMB, voucher material is also

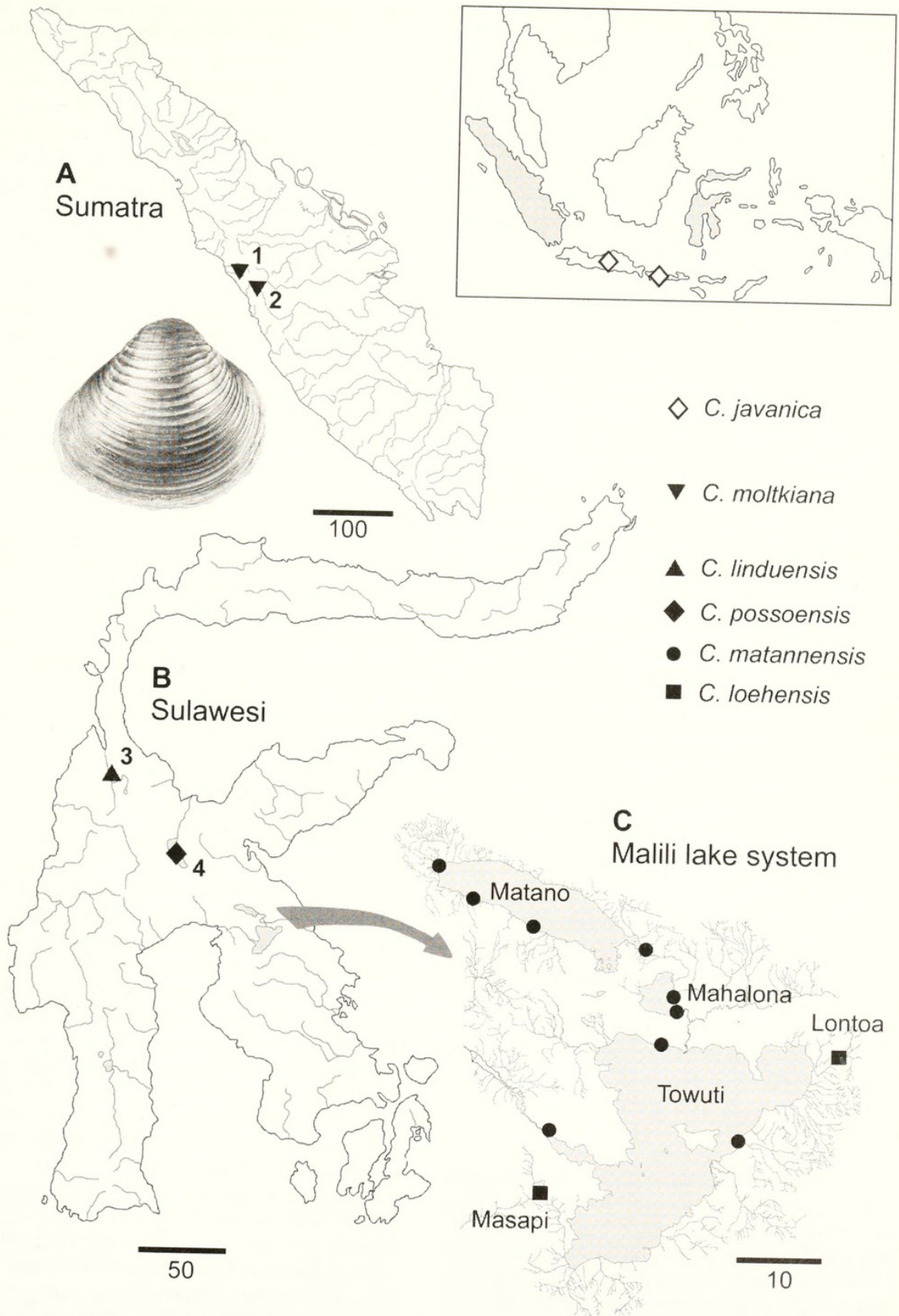


FIG. 1. The occurrence of freshwater bivalvia of the genus *Corbicula* on Indonesian islands based only on material examined in the present study; details are given for *C. moltkiana* on Sumatra (A) and four taxa on Sulawesi (B) and the Malili lake system (C), respectively. Numbers refer to the following locations: 1 - Lake Maninjau, 2 - Lake Singkarak, 3 - Palu River, 4 - Lake Poso. Scale bars given in km.

provided to the Zoological Museum in Bogor.

Type and other historical material representing *Corbicula* species from Sulawesi and Sumatra, including the type specimens of *C. subplanata* Martens, *C. celebensis* Martens, *C. lacustris* Martens, *C. possoensis* P. Sarasin & F. Sarasin, and *C. matannensis* P. Sarasin & F. Sarasin, also housed in the ZMB, were studied for comparison. This is supplemented by the relevant type materials recovered in other museums, including the lectotype of *C. fluminea* designated by Araujo et al. (1993), as well as type lots of *C. javanica* and *C. sumatrana*. Comparative alcohol material of *C. fluminea* was kindly provided by C. Ituarte (collected near Buenos Aires, Argentina).

Shell Morphology and Anatomy

All newly collected material was fixed in 70% ethanol after cracking the shells of some specimens per sample; this material is given as w = wet material in the Material sections below. Shell measurements were made with a caliper to a precision of 0.1 mm; size of adductor scar was measured as the distance between its uppermost point and junction with mantle line. Dissections were made under a Leica MZ 9.5 stereomicroscope, and anatomical structures illustrated using a camera lucida. Pieces of mantle for the study of musculature were stained by eosine (water solution) and mounted in Canada Balsam.

Sperm Morphology

Sperm was obtained from gonads of ethanol-fixed specimens. Its morphology was studied by means of interference contrast optics (DIC) and scanning electron microscopy (SEM), in the latter case applying hexamethyldisilazane (HMDS) following the procedure described by Nation (1983).

Molecular Genetics

DNA was purified from about 1–2 mm³ of foot tissue by CTAB extraction (Winnepenninckx et al., 1993). Polymerase chain reaction (PCR) was used to amplify a region of ~710 bp at the 5'-end of the cytochrome oxidase subunit I gene (COI). PCR was performed in 25 µl volumes containing 1X Taq buffer, 1.5 mM MgCl₂, 200 µM each dNTP, 1–2.5 U Taq polymerase, approximately 100 nM DNA and ddH₂O up to volume on a Perkin Elmer GeneAmp 9600 or

2400 thermocycler. After an initial denaturation step of 3 min at 94°C, cycling conditions were 35 cycles of 1 min each at 94°C, 45–53°C, and 72°C, with a final elongation step of 5 min.

Primers used were LCO 1490 [5' GCTCAA CAAATCATAAAGATATT 3'] and HCO2198 [5' TAAACTTCAGGGTGACCAAAAAATCA 3'] (Folmer et al., 1994). PCR products were purified with QiaQuick PCR purification kits (Qiagen) following the standard QiaQuick PCR purification protocol. Both strands were cycle sequenced with the original primers using ABI Prism BigDye™ terminator chemistry and visualized on an ABI Prism 377 automated DNA sequencer. The resulting sequence electropherograms of both strands were corrected manually for misreads and merged into one sequence file using BioEdit Version 5.0.1 (Hall, 1999). Sequences were aligned manually and checked by translating the DNA sequences into amino acids in DAMBE 4.0.75 (Xia & Xie, 2001) using the genetic code for invertebrate mitochondrial DNA. The sequences obtained by this study were analyzed together with *Corbicula* sequences published by Siripattawan et al. (2000) and Pfenninger et al. (2002); the latter included samples from Hong Kong, which is near to the type locality (Canton) of *C. fluminea*, and from Israel (presumably *C. fluminalis*).

Polymesoda caroliniana (Bosc, 1801) and *Neocorbicula limosa* (Maton, 1809) were used as outgroups. The latter taxon needs a nomenclatorial commentary. As pointed out by Parodiz (1996: 265), the generic name *Cyanocyclas* Blainville, 1818, is a senior subjective synonym of *Neocorbicula* Fisher, 1887, and, therefore, should have priority. Understanding that this taxon is in need of a taxonomic revision and possibly formal decision of the ICZN, we for the time being will use here the latter generic name, as done in recent molecular literature (e.g., Siripattawan et al., 2000; Pfenninger et al., 2002). GenBank accession numbers of all sequences used and ZMB catalogue numbers for original material are provided in Table 1.

Aligned sequences were processed with PAUP* 4.0b10 (Swofford, 1998). Corrected sequence divergence levels were calculated by using a General Time Reversible model, to obtain the matrix comparable with that of Siripattawan et al. (2000). Phylogenetic trees were reconstructed using neighbor joining (NJ, Saitou & Nei, 1987) and maximum parsimony (MP) methods as implemented in PAUP*. NJ

TABLE 1. Sources of the corbiculid material utilized in this study for COI sequence data analyses; numbers in brackets refer to analyses of sequence data as given in Table 4 and Figs. 18 and 19.

Taxon	Locality data	Museum catalog no.	GenBank accession no.	Reference
<i>Corbicula javanica</i> (Mousson, 1849)	Bogor, Java	ZMB 106449	AY275668	This study
<i>C. moltkiana</i> Prime, 1878 (1)	L. Singkarak, Sumatra	ZMB 103024	AY275660	This study
<i>C. moltkiana</i> (2)	L. Singkarak, Sumatra	ZMB 103034	AY275659	This study
<i>C. moltkiana</i> (3)	L. Manindjau, Sumatra	ZMB 103025	AY275657	This study
<i>C. moltkiana</i> (4)	L. Manindjau, Sumatra	ZMB 103032	AY275658	This study
<i>C. matannensis</i> Sarasin & Sarasin, 1898 (1)	L. Matano, Sulawesi	ZMB 103002	AY275663	This study
<i>C. matannensis</i> (2)	L. Matano, Sulawesi	ZMB 103003	AY275664	This study
<i>C. matannensis</i> (3)	L. Mahalona, Sulawesi	ZMB 103009	AY275665	This study
<i>C. loehensis</i> Kruimel, 1913 (1)	L. Lontoa, Sulawesi	ZMB 103033	AY275667	This study
<i>C. loehensis</i> (2)	L. Masapi, Sulawesi	ZMB 103011	AY275666	This study
<i>C. possoensis</i> Sarasin & Sarasin, 1898 (1)	L. Poso, Sulawesi	ZMB 190024	AY275661	This study
<i>C. possoensis</i> (2)	L. Poso, Sulawesi	ZMB 103028	AY275662	This study
<i>C. fluminea</i> (Müller, 1774)	Thailand	UMMZ 266691	AF196270	Siripattrawan et al., 2000
<i>C. fluminea</i>	Korea	UMMZ 266690	AF196269	Siripattrawan et al., 2000
<i>C. fluminea</i>	Hong Kong	-	AY097292	Pfenninger et al., 2002
<i>C. leana</i> Prime, 1864	Japan	UMMZ 266668	AF196268	Siripattrawan et al., 2000
<i>C. sandai</i> Reinhardt, 1878	L. Biwa, Japan	UMMZ 266689	AF196272	Siripattrawan et al., 2000
<i>C. fluminalis</i> ?	Israel	-	AY097299	Pfenninger et al., 2002
<i>C. australis</i> (Lamarck, 1818)	NSW, Australia	UMMZ 266662	AF196274	Siripattrawan et al., 2000
<i>Corbicula</i> "form A"	Michigan, USA	UMMZ 266693	AF196280	Siripattrawan et al., 2000
<i>Corbicula</i> "form B"	Utah, USA	UMMZ 266695	AF196278	Siripattrawan et al., 2000
<i>C. madagascariensis</i> Smith, 1882	Madagascar	UMMZ 255293	AF196275	Siripattrawan et al., 2000
<i>C. japonica</i> Prime, 1864	Japan	UMMZ 266688	AF196271	Siripattrawan et al., 2000
<i>Neocorbicula limosa</i> (Maton, 1809)	Argentina	UMMZ 265500	AF196277	Siripattrawan et al., 2000
<i>Polymesoda caroliniana</i> (Bosc, 1801)	Florida, USA	UMMZ 265499	AF196276	Siripattrawan et al., 2000

analyses were conducted using the random initial seed option to break ties. The robustness of inferences was assessed through bootstrap resampling (1000 replicates) (Felsenstein, 1985). In the MP analyses, the heuristic search algorithm was employed with 10 random additions of taxa and tree bisection-reconstruction (TBR) branch swapping. All other settings were left at default values. Support for nodes was estimated by bootstrap resampling (500 replicates) with one random addition per replicate.

Abbreviations Used in Figures

aa – anterior adductor, es – exhalant siphon, is – inhalant siphon, mc – concentric mantle musculature, mp – papillae, mr – radial mantle musculature, p – papillae, pa – posterior adductor, pss – presiphonal suture, sr – siphonal retractor.

Museum Acronyms

MLP – Museo de La Plata, Buenos Aires, Argentina; MZB – Zoological Museum Bogor, Indonesia; SMF – Senckenbergsmuseum, Frankfurt/Main, Germany; UZMC – Universitetets Zoologisk Museum, Copenhagen, Denmark; ZMA – Zoological Museum Amsterdam, The Netherlands; ZMB – Museum für Naturkunde, Humboldt University, Berlin, Germany (formerly Zoological Museum Berlin); ZMZ – Zoologisches Museum, Universität Zürich, Switzerland.

SYSTEMATIC ACCOUNT

Species from the Sunda Islands

Corbicula javanica (Mousson, 1849)
Figs. 2A–C, 3D–F

Cyrena orientalis var. *javanica* Mousson, 1849: 86, pl. 15, fig. 2.

Corbicula ducalis Prime, 1862: 274; Martens, 1897: 114.

Corbicula javanica – Martens, 1897: 111; Prashad, 1930: 203, pl. 25, figs. 7–20; Djajasasmita, 1977: 6.

Type Locality: Tikojia (probably an error for Tjikoya), Java.

Type Material: Lectotype ZMZ 532199 (Fig. 2A) from Tjikoya, Java, leg. Zollinger, ex. coll. Mousson; corresponding to the specimen fig-

ured by Mousson (1849: pl. 15, fig. 2) with the following measurements: L = 39.5, H = 33.0, W/2 = 11.9 mm (present designation, to fix the status of this specimen as the sole name bearing type). Paralectotypes (2 specimens) from the same original lot, ZMZ 532199a. Paralectotypes ZMZ 532200 (2 specimens), the same locality and collector.

Other Material Examined: Java: Tjiponnas near Garut (ZMB Moll. 103054w; leg. M. Schmidt 1902); Bogor (ZMB Moll. 106459; leg. T. v. Rintelen, May 2002). Lombok: Narmada (ZMB Moll. 75535w; leg. Rensch, Sunda Expedition). Sulawesi: Lake Tempe (ZMB Moll. 103024; leg. Max Weber; originally identified as *Corbicula ducalis* Prime, 1862).

Taxonomic Remarks: In respect to the discrepancy of the spelling of the type locality for this taxon, we follow here Djajasasmita (1977), who interpreted it as Tjikoya. The latter author also synonymized *C. ducalis* Prime, 1862, which was reported earlier on as a valid species from several Indonesian islands (Martens, 1897; Prashad, 1930) with *C. javanica*. Our revision of specimens from Sulawesi originally identified by Martens as *C. ducalis* is consistent with this point of view, although some minor differences to the typical *C. javanica* are discernable. Specimens from Lombok included in this study (Fig. 2C) also correspond well to the published descriptions (Prashad, 1930) and revised type specimens of *C. javanica* (Fig. 2A, B).

Description

Shell: Oval or broad triangular, without angles, somewhat inequilateral, convex. Beaks broad, protruding, markedly shifted anteriorly. Periostracum yellow to brown, shiny. Internal coloration usually white or pale blue, with purple pattern at lateral teeth. Concentric sculpture coarse and widely spaced (8–11 ribs per 1 cm), ribs usually not sharp (wave-like). Hinge plate relatively narrow; cardinal teeth small; anterior lateral teeth long, arched. Specimens from Lombok and Sulawesi up to 20 mm long; Javanese specimens much larger, up to 50 mm long.

Anatomy: Adductors small, oval. Posterior adductor diameter about 0.13 length of shell (Table 2). Presiphonal suture not elongated, length equal to breadth of inhalant siphon. Siphons conical, with thick walls (when contracted) and circular or short oval apertures, both narrow; inhalant siphon with about 30

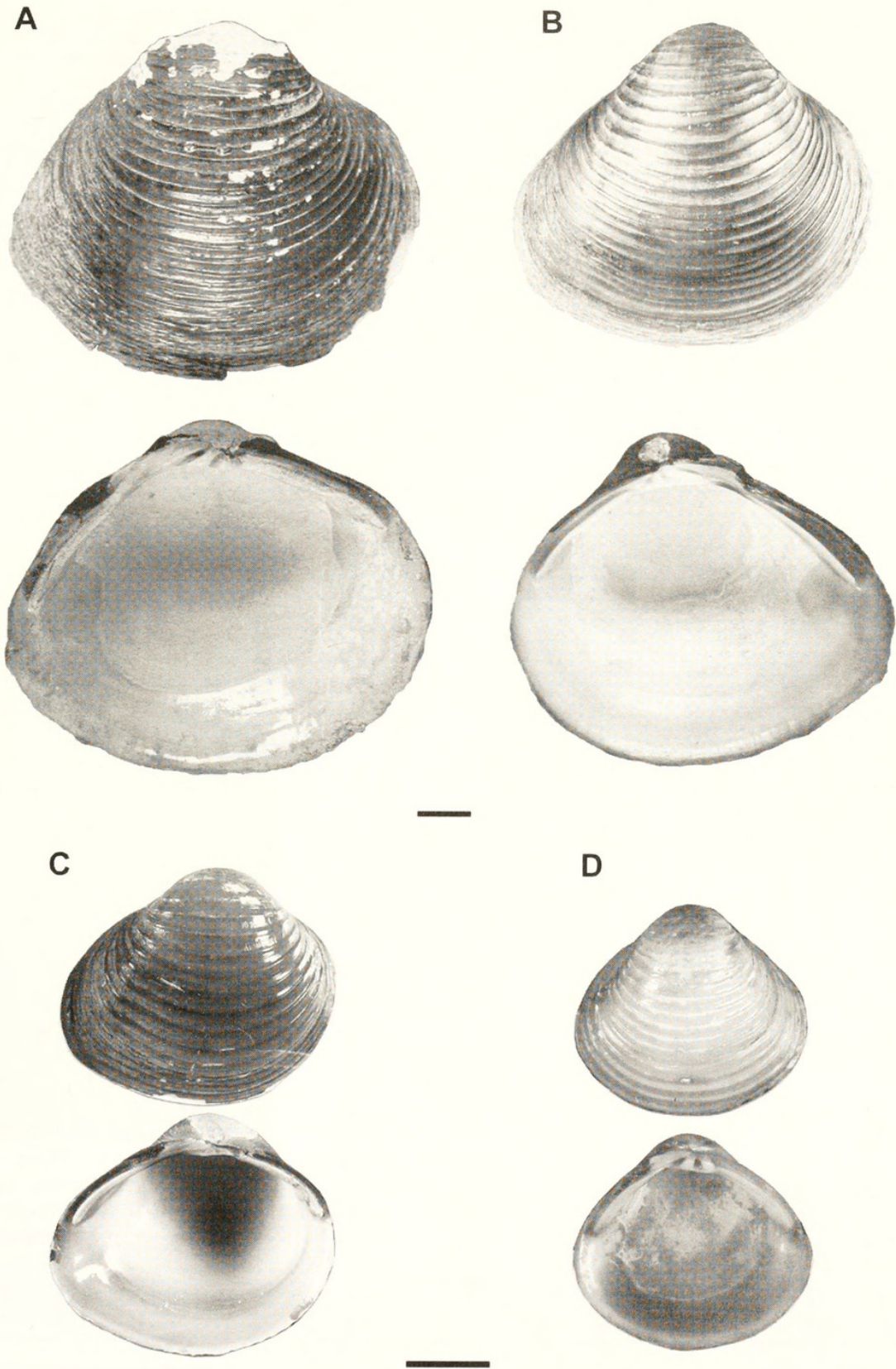


FIG. 2. Shells of *Corbicula javanica* in comparison with *C. fluminea*: A. *C. javanica*, Java, lectotype (ZMZ 532199); B. *C. javanica*, one of the paralectotypes (ZMZ 532200); C. *C. javanica*, Lombok (ZMB Moll.75535); D. *C. fluminea*, China, lectotype (UZMC). Scale bars = 5 mm.

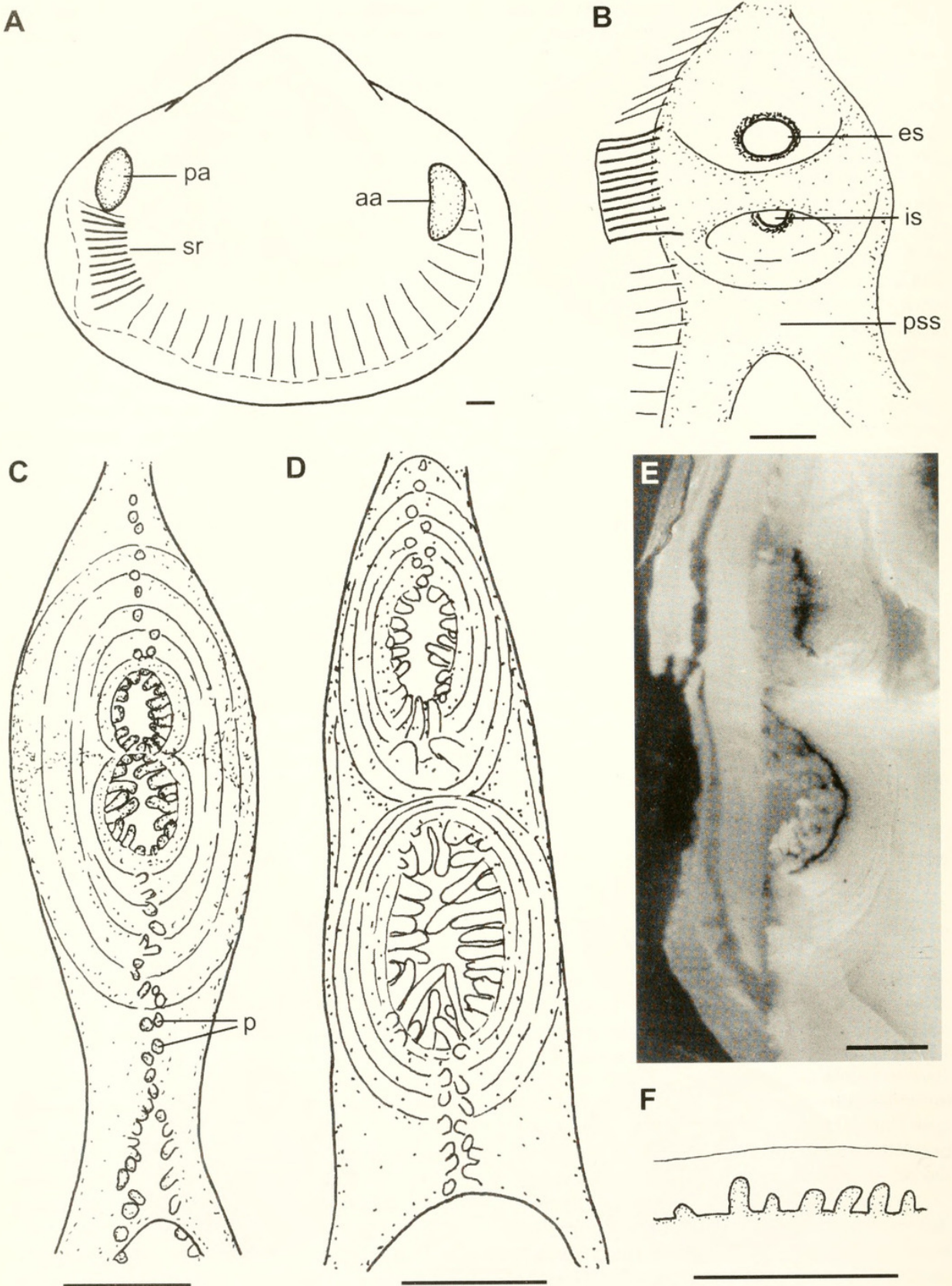


FIG. 3. Anatomy of *Corbicula fluminea*, Argentina (MLP 5329) (A–C) and *C. javanica*, Lombok (ZMB Moll. 75535) (D–F): A. Habitus of soft body; B. Siphons from inside; C, D. Siphons from outside; E. Section of siphons; F. Marginal mantle papillae. Scale bars = 1 mm.

TABLE 2. Morphometric indices (mean and standard deviation provided) calculated from measurements of shells and siphon structure of the *Corbicula* species studied: L - shell length; H - shell height; W - shell thickness (two valves); U - distance from beak to anterior end; HH - hinge plate length; A - diameter of the posterior adductor scar; S - breadth of siphons. Note that for the last two taxa only range is given for siphons.

Species	No. of measured specimens (dry/wet)	H/L	W/H	U/L	HH/H	A/L	S/L
<i>C. fluminea</i> (lectotype)	1	0.93	0.80	0.48	0.100	0.14	not measured
<i>C. javanica</i> ZMZ 532199, 532200 (type lot)	5/0	0.83 ±0.059	0.75 ±0.066	0.43 ±0.017	0.059 ±0.005	0.14 ±0.012	not measured
<i>C. javanica</i> ZMB 75535	3/0	0.82 ±0.035	0.81 ±0.022	0.39 ±0.021	0.057 ±0.006	0.13 ±0.009	not measured
<i>C. javanica</i> ZMB 106459	10/5	0.89 ±0.041	0.73 ±0.020	0.42 ±0.018	0.069 ±0.004	0.12 ±0.013	0.12 ±0.010
<i>C. moltkiana</i> ZMB 54370, 103058	10/2	0.78 ±0.056	0.68 ±0.020	0.47 ±0.022	0.080 ±0.016	0.14 ±0.007	0.24 ±0.05
<i>C. moltkiana</i> SMF 5994 (paratypes of <i>C. sumatrana</i>)	10/0	0.95 ±0.049	0.73 ±0.065	0.46 ±0.047	0.099 ±0.007	0.18 ±0.020	not measured
<i>C. moltkiana</i> ZMB 170000-01 (syntypes of <i>C. lacustris</i>)	6/0	0.94 ±0.126	0.80 ±0.033	0.44 ±0.069	0.111 ±0.016	0.18 ±0.043	not measured
<i>C. moltkiana</i> ZMB 103024	5/4	0.91 ±0.029	0.69 ±0.039	0.47 ±0.040	0.079 ±0.004	0.17 ±0.015	0.18 ±0.013
<i>C. moltkiana</i> ZMB 103032	7/4	0.84 ±0.049	0.69 ±0.039	0.50 ±0.032	0.073 ±0.008	not measured	0.19 ±0.030
<i>C. linduensis</i> ZMB 103016	10/4	0.77 ±0.022	0.63 ±0.039	0.49 ±0.029	0.081 ±0.007	0.14 ±0.015	0.18 ±0.033
<i>C. matannensis</i> ZMB 103002	10/6	0.84 ±0.043	0.64 ±0.035	0.42 ±0.022	0.098 ±0.005	0.15 ±0.010	0.24 ±0.015
<i>C. matannensis</i> ZMB 103009	9/7	0.83 ±0.045	0.59 ±0.041	0.39 ±0.031	0.96 ±0.013	0.13 ±0.017	0.26 ±0.034
<i>C. matannensis</i> ZMB 103006	4	0.96 ±0.050	0.70 ±0.090	0.42 ±0.052	0.111 ±0.016	0.15 ±0.016	not measured
<i>C. loehensis</i> ZMB 103010	5	0.88 ±0.028	0.68 ±0.034	0.44 ±0.011	0.078 ±0.015	0.14 ±0.023	not measured
<i>C. loehensis</i> ZMB 103011	8/3	0.88 ±0.040	0.68 ±0.026	0.47 ±0.046	0.075 ±0.011	0.12 ±0.010	0.32 ±0.032
<i>C. loehensis</i> ZMB 103033	3/2	0.87 ±0.047	0.60 ±0.040	0.44 ±0.026	0.070 ±0.014	0.12 ±0.004	0.27–0.33
<i>C. possoensis</i> ZMB 103028	10/7	0.93 ±0.028	0.65 ±0.033	0.41 ±0.033	0.115 ±0.007	0.23 ±0.019	0.32 ±0.022
<i>C. possoensis</i> ZMB190024	3/2	0.89 ±0.070	0.75 ±0.037	0.31 ±0.010	0.120 ±0.012	0.21 ±0.022	0.30–0.31

papillae usually arranged in one row (Fig. 3D), sometimes with additional row of short papillae. Black pigment concentrated in rings internally at base of both siphons (Fig. 3E); outer surface of siphons white or with pale

brown pigment (in specimens from Lombok). Larger papillae of inhalant siphon with dark rings. Siphonal muscles strong, arranged in broad bands. Papillae on outer surface of presiphonal suture arranged in two rows (Fig.

TABLE 3. Comparative morphological characteristics of *Corbicula* taxa from Indonesia; ranges are given for indices in brackets (compare to Table 2).

Characters	<i>C. javanica</i>	<i>C. moltkiana</i>	<i>C. linduensis</i>	<i>C. matannensis</i>	<i>C. loehensis</i>	<i>C. possoensis</i>
Shell form	Oval or broad triangular, without angles	Triangular or tetragonal, with pronounced posteroventral angle	Oval, with rounded posteroventral angle	Tetragonal, with obtuse posteroventral angle	Round, with obtuse posteroventral angle	Triangular or tetragonal, with posterior keel
Beaks	Broad, anterior	Narrow, central or subcentral	Narrow, central	Narrow, subcentral or anterior	Narrow, subcentral	Narrow, anterior
Sculpture	Wave-like ribs, 8–11 per 10 mm	Sharp ribs, 9–12 per 10 mm	Wave-like ribs, 10–12 per 10 mm	Sharp ribs, 15–20 per 10 mm	Delicate ribs, 30–40 per 10 mm	Delicate ribs, 25–30 per 10 mm
Hinge (HH/H index)	Narrow (0.05–0.07)	Moderately broad to broad (0.07–0.13)	Moderately broad (0.08–0.09)	Moderately broad to broad (0.07–0.13)	Moderately broad (0.07–0.08)	Broad (0.09–0.13)
Adductor size (A/L index)	Small (0.10–0.14)	Small (0.13–0.21)	Small (0.12–0.17)	Small (0.11–0.18)	Small (0.10–0.15)	Large (0.20–0.27)
Siphons form (S/L index)	Conical, narrow (0.11–0.13)	Conical, somewhat broadened (0.15–0.25)	Conical, somewhat broadened (0.14–0.22)	Cylindrical, broad (0.22–0.32)	Cylindrical, broad (0.24–0.34)	Cylindrical, broad (0.29–0.35)
Inhalant siphon papillae	About 30, in one row	30–80, in two rows	About 50, in two rows	55–70, in two rows	About 50, in two rows	60–70, in two rows
Internal pigmentation of siphons	Dark rings	Dark rings and patches	Pale rings or absent	Entirely pigmented	Entirely pigmented	Entirely pigmented
Siphonal muscles	Strong, broad	Strong, broad	Strong, broad	Weak, narrow	Weak, narrow	Weak, narrow
Marginal mantle papillae	Numerous	Numerous	Numerous	Scarce	Scarce	Scarce
Radial mantle musculature	Strong, bundles not separated	Strong, bundles in large specimens separated	Strong, anterior bundles separated	Weak, bundles separated	Weak, bundles separated	Weak, bundles separated
Spermatozoa (type and head length)	Unknown	Monoflagellate, 11–12 μ m	Monoflagellate, 8–9 μ m	Monoflagellate, 11–12 μ m	Monoflagellate, 9–10 μ m	Monoflagellate, 10–11 μ m
Location of brood	Inner demibranchs	Inner demibranchs	Inner demibranchs	Inner demibranchs	Inner demibranchs	Both demibranchs
Larval size	Small (final size unknown)	Small (0.25–0.35 mm)	Large (up to 1.5 mm)	Small (0.30–0.33 mm)	Small (about 0.25 mm)	Small (0.26–0.30 mm)

3D). Marginal mantle papillae well developed, densely arranged (Fig. 3F). Radial mantle muscles strong, arranged in band, individual bundles not separated.

Reproductive Biology: Only eggs were found in all dissected specimens, therefore sperm morphology remained unknown. One specimen from Java contained in its inner demibranchs several hundred small larvae (0.13–0.15 mm long) with uncalcified shells. Since these larvae were apparently not fully developed, the final size of released young remains unknown. Other studied specimens were not brooding.

Distribution and Ecology: According to Djajasasmita (1977), this taxon is widely distributed in Southeast Asia, from the Malay Peninsula to Timor and Aru Islands, as well as to the Philippines. It occurs in several different types of lentic and lotic habitats, that is, rivers, creeks and irrigation canals as well as lakes and ponds (Djajasasmita, 1977).

Remarks: This taxon is recognizable as a distinct morphotype, differing from the typical form of *C. fluminea* in its inequilateral shell, anterior shift of beaks, and relatively narrow hinge plate (Fig. 2, Table 3). Anatomical characters described here well agree with those reported for *C. fluminea* (Britton & Morton, 1979; Harada & Nishino, 1995) and observed in specimens of the latter species studied here for comparison (Fig. 3A–C), with the only difference of a darker pigmentation of the outer surface of siphons. In fact, we anticipate that *C. javanica* might probably just be a variety of *C. fluminea*. However, this supposition should be confirmed by investigating the reproductive biology and molecular genetics of the relevant forms in more detail.

Corbicula moltkiana Prime, 1878

Figs. 4–6, 7A, B, 8A, B

Corbicula moltkiana Prime, 1878: 43, pl. 2, fig. 2a, b, c; Prashad, 1930: 200, pl. 25, figs. 17–22; Djajasasmita, 1977: 4.

Corbicula sumatrana Clessin, 1887: 78, pl. 3, fig. 7; Prashad, 1930: 198, pl. 25, figs. 1–8; Djajasasmita, 1977: 7.

Corbicula verbecki Clessin, 1887: 79.

Corbicula moltkeana [sic] Prime – Martens, 1897: 111, pl. 7, figs. 1–6.

Corbicula lacustris Martens, 1897: 118, pl. 7, figs. 20–24.

Type Locality: “Sumatra”, not exactly specified.

Type Material: Type specimens of *C. moltkiana* Prime located in UZMC are presumed to be lost (T. Schiötte, pers. comm.). Presumably syntypes (although catalogued as paratypes) of *C. sumatrana* Clessin, “Lake Singkarak” [sic!], leg. Verbeck 1880 (SMF 5994, 5995). Holotype of *C. verbecki*, Clessin, same locality data (SMF, not numbered). Syntypes of *C. lacustris* Martens, Lake Singkarak, leg. Weber (ZMB Moll. 170000, 170001, 170002).

Other Material Examined: Sumatra: Lake Manindjau (ZMB Moll. 54370w, 103058, 103059; leg. Max Weber; originally identified as *C. moltkiana* by E. v. Martens); Lake Manindjau, at shore near Manindjau (ZMB Moll. 103024, 103034; leg. Köhler & Schütt, April 2000); Lake Singkarak (0°32.89'S, 100°31.92'E) (ZMB Moll. 103025, 103032; leg. Köhler & Schütt, April 2000) (Fig. 1).

Taxonomic Remarks: We have at our disposal one alcohol lot and two dry lots coming from the collection of Eduard von Martens, bearing his identification. Obviously, the specimens are those cited in Martens' (1897) monograph as “*moltkeana*” (evidently a misspelling of Prime's original name). While characters of these specimens (Fig. 4E) well agree with the original description and figures of Prime (1878), we retain the original identification as *C. moltkiana*. Comparison of type specimens of the three taxa described from Lake Singkarak, namely *C. sumatrana* Clessin (Fig. 4B), *C. verbecki* Clessin, and *C. lacustris* Martens (Fig. 4C), as well as recent collections of *Corbicula* from this lake (Fig. 4D) with the available figures and material of *C. moltkiana* did not provide convincing distinctive characters and, thus, suggests that these taxa are conspecific.

Description

Shell: Variable in shape, but usually triangular or trapezoid, from high to markedly elongated, compressed. Posterior margin somewhat truncate, with characteristic posteroventral right or obtuse angle. Beaks narrow, central or somewhat shifted anteriorly, not protruding. Periostracum yellow, dark green or dark brown to black, shiny. Internal shell surface from white to dark purple. Concentric sculpture of variable spacing (9–12 ribs per 1 cm), ribs sharp. Hinge plate moderately broadened to broad (Table 2, 3). Cardinal teeth well developed; anterior lateral teeth thick, straight or slightly arched. Up to 30 mm long.

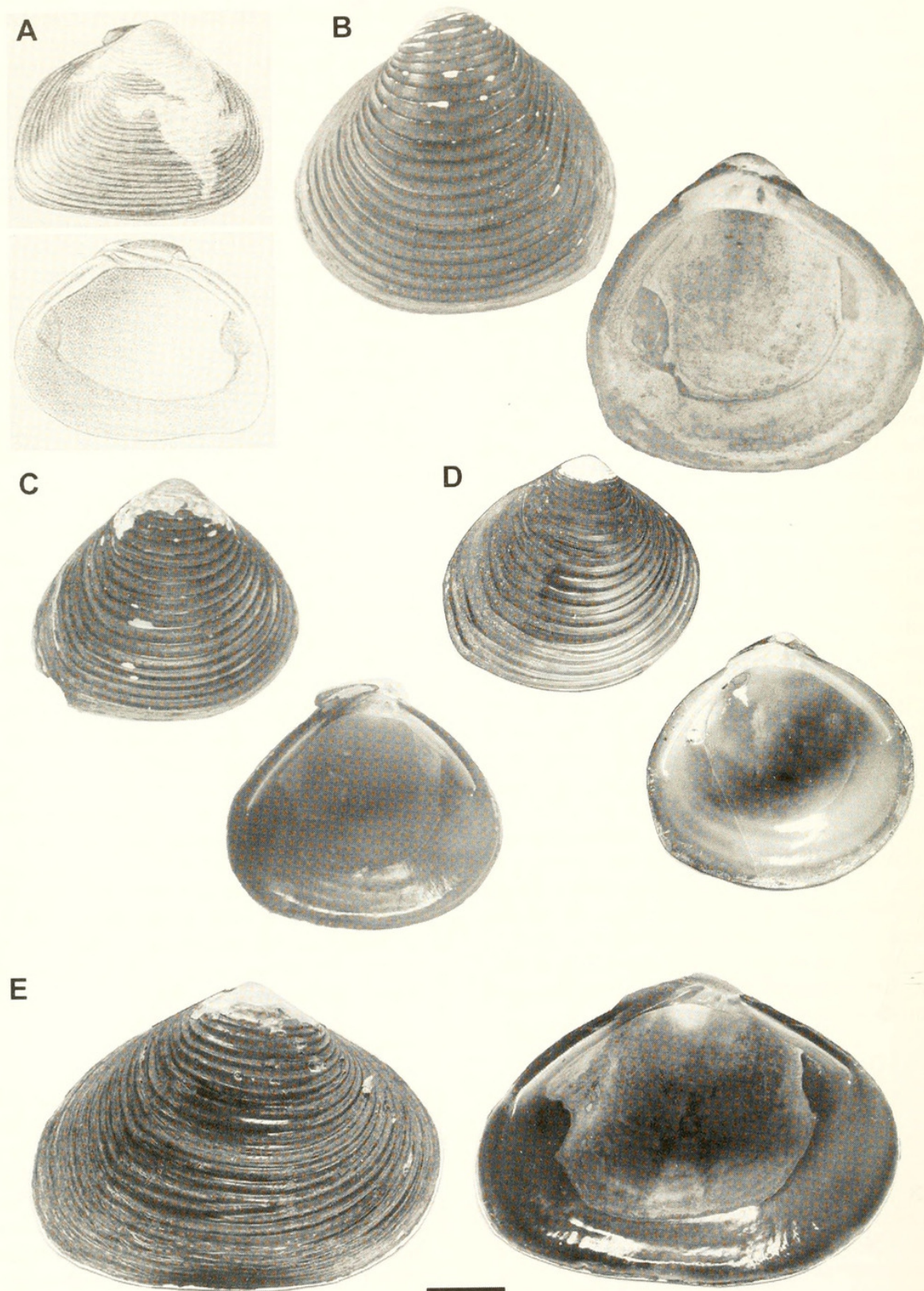


FIG. 4. Shells of *Corbicula moltkiana* from Sumatra with synonyms as suggested in the present paper: A. Original figure from Prime (1878), locality unknown (not to scale); B. One of the syntypes of *C. sumatrana*, Lake Singkarak (SMF 5995); C. One of the syntypes of *C. lacustre*, Lake Singkarak (ZMB Moll. 170000); D. *C. moltkiana*, Lake Singkarak (ZMB Moll. 103024); E. *C. moltkiana*, Lake Manindjau (ZMB Moll. 54370). Scale bar = 5 mm.

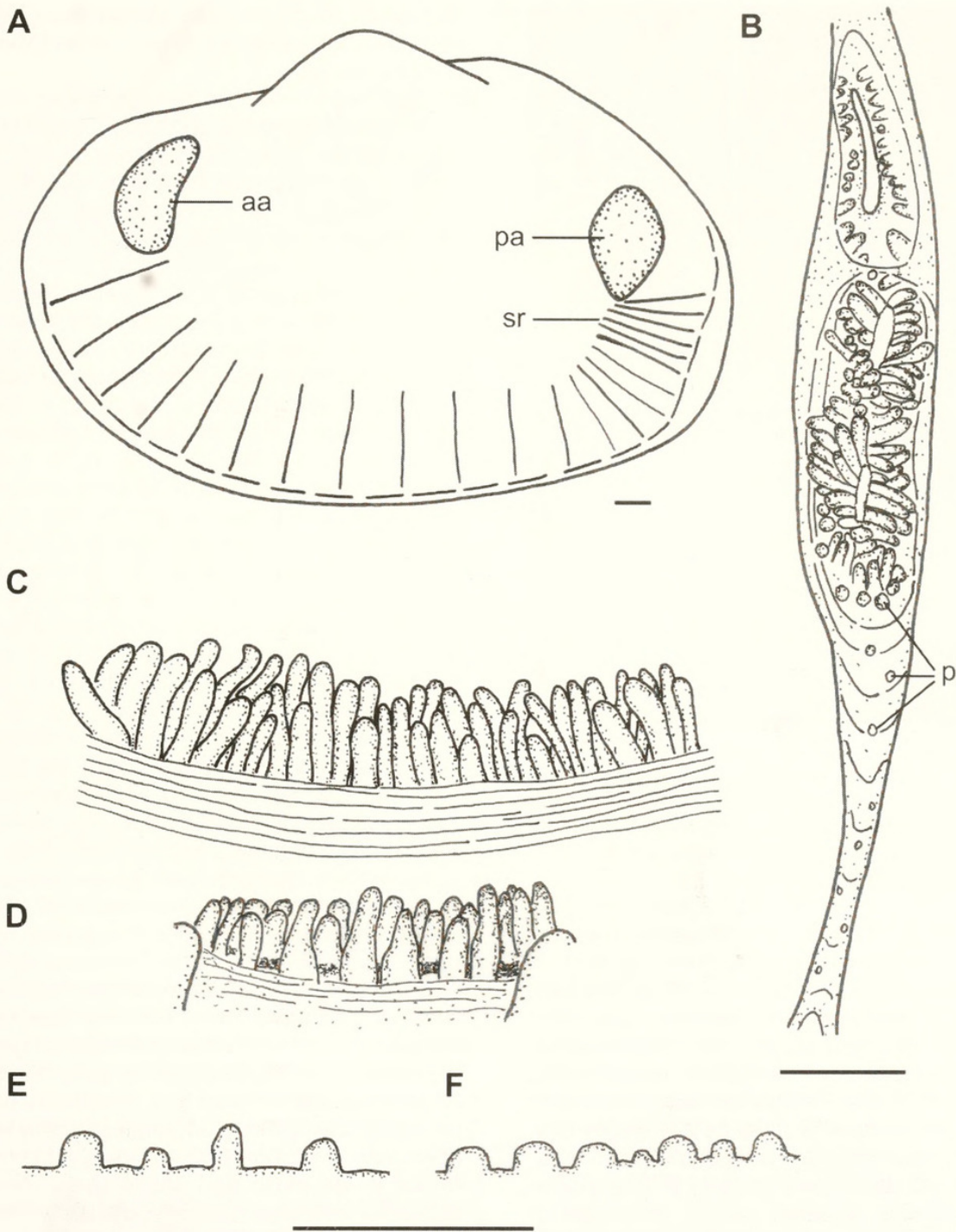


FIG. 5. Anatomy of *Corbicula moltkiana*, Sumatra, Lake Maninjau: A. Habitus of soft body; B. Siphons from outside; C–D. Papillae of inhalant siphon (C - ZMB Moll. 54370, D - ZMB Moll. 103034); E–F. Marginal mantle papillae (E - ZMB Moll. 54370, F - ZMB Moll. 103034). Scale bars = 1 mm.

Anatomy: Adductors small, oval (Fig. 5A, Table 2). Presiphonal suture longer than aperture of inhalant siphon. Siphons conical, narrow in small specimens and rather broad in full grown ones, with thick walls and circular or oval apertures; number of inhalant siphon pa-

pillae varies from 30 to about 80, arranged in one or two rows (Figs. 5B–D, 6B), in largest specimens additional row of small papillae may appear. Black pigment concentrated in rings at base of papillae in both siphons, but patches of pigment also seen around siphons

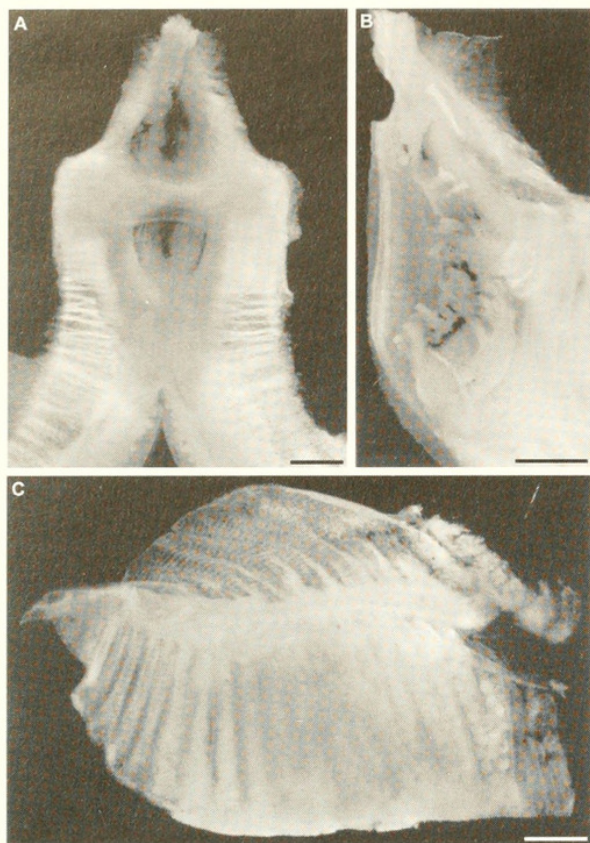


FIG. 6. *Corbicula moltkiana*, Sumatra, Lake Singkarak (ZMB Moll. 103025), view of mantle and gill: A. Siphons from inside, B. Section of siphons; C. Gill with incubated larvae, from inside. Scale bars = 1 mm.

(Fig. 6A, B), in some specimens internal surface of siphons almost entirely pigmented. Some papillae of inhalant siphon with dark rings. In specimens from Martens' collection pattern of pigmentation indistinguishable. Siphonal muscles strong, arranged in broad bands (Fig. 6A). Papillae on outer surface of presiphonal suture arranged in single row, sometimes in two rows. Marginal mantle papillae well developed, densely arranged. Radial mantle muscles strong, arranged in band, their bundles indistinguishable in smaller specimens but distinct in large animals (Fig. 7A, B).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa (Fig. 8A–B) monoflagellate; head length $11.5 \pm 0.58 \mu\text{m}$ ($n = 7$). Eight out of 15 specimens collected in Lake Singkarak (ZMB Moll. 103026) were brooding and their inner demibranchs contained several hundred larvae of approximately equal size (0.25–0.3 mm long). The only gravid

specimen found in Lake Manindjau (ZMB Moll. 54370) contained larger larvae (about 0.35 mm long).

Distribution and ecology: To date known from several localities on Sumatra and the Malay Peninsula, according to Djajasasmita (1977). Material revised by this study was collected in lakes only (Fig. 1A), but the species was also recorded in rivers and ditches (Djajasasmita, 1977).

Remarks: This species is remarkably variable both in shell and anatomical characters. Specimens from Lake Manindjau differ from those collected in Lake Singkarak (type locality of *C. sumatrana* and *C. lacustris*) in their narrower hinge plate and densely arranged ribs. Moreover, the old lots from Lake Manindjau are distinguished from the new collections from the same lake by their elongated shells, broadened siphons, and weaker mantle muscles; anatomical differences might be associated with the larger size of animals collected by Weber, in comparison with those from our collections (26–28 and 15–18 mm, respectively). Furthermore, the purple form found in both sampled lakes (stored separately as ZMB Moll. 103032, 103034) alongside the yellow one (ZMB Moll. 103024, 103025) showed also somewhat more delicate ribs and darker internal pigmentation of siphons. The form described as *C. lacustre* is characterized by smaller size (up to 18 mm), high, thick-walled shell, and especially coarse sculpture; it is probably a deep water variety of the same species (Djajasasmita, 1977). While differences between the extreme forms from the localities discussed here are rather pronounced (Fig. 4), intermediate forms could be also found. All forms assigned here to *C. moltkiana* can be recognized by their angulate compressed shell, narrow not protruding beak, relatively broad hinge plate and sharp ribs. These characters distinguish it from the widely distributed Southeast Asian taxon, *C. javanica* (Table 3), as well as from the typical form of *C. fluminea*. The differences from *C. javanica* in shell elongation and convexity, position of beaks, and relative breadth of hinge plate (Table 2) were significant at $p < 0.05$. Noteworthy, one specimen of *C. javanica* was found in Weber's lot from Lake Manindjau (ZMB Moll. 103.058), being well distinguishable from the sympatric *C. moltkiana* by its protruding beak, narrow hinge and widely spaced smoothened ribs.

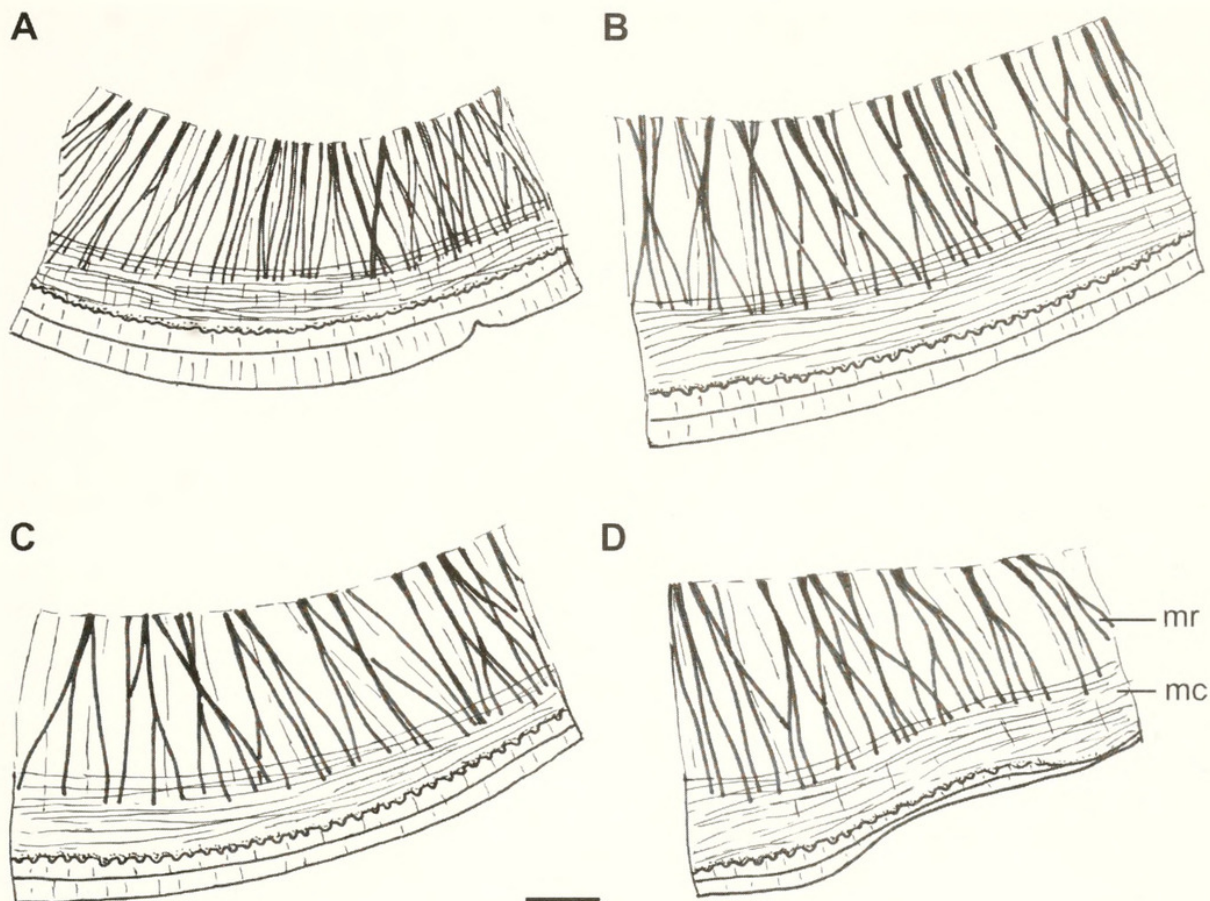


FIG. 7. Mantle musculature of Indonesian *Corbicula*: A. *C. moltkiana*, Sumatra, Lake Singkarak (ZMB Moll. 103024); B. *C. moltkiana*, Sumatra, Lake Maninjau (ZMB Moll. 54370); C. *C. matannensis*, Sulawesi, Lake Matano (ZMB Moll. 103002); D. *C. possoensis*, Sulawesi, Lake Poso (ZMB Moll. 103028). Scale bar = 1 mm. mc - concentric musculature, mr - radial musculature.

Large specimens of *C. moltkiana* are similar in some anatomical characters (form of siphons and patterns of mantle musculature) to the lacustrine taxa from Sulawesi (*C. matannensis* and *C. loehensis*). Dark rings of pigment seen at base of both siphons in *C. moltkiana* are similar to those of *C. fluminea* (Britton & Morton, 1979; Harada & Nishino, 1995), but the internal pigmentation of siphons in the former taxon is generally more intense than in the latter.

Sperm and eggs were not found in the same animal. We understand as functional males those animals producing sperm, while we did not find the relatively large eggs when inspecting the gonad. Although the exact expression of sexuality in this species remains to be verified by detailed seasonal observations and histological study of gonads, we anticipate that *C. moltkiana* is not a simultaneous hermaphrodite. In this aspect, it might

be similar to *C. sandai* from Lake Biwa, but apparently differs from the other freshwater taxa studied so far (Konishi et al., 1998; Byrne et al., 2000; Qiu et al., 2001). It should be stressed again here, that our finding of monoflagellate sperm in this taxon provides an indication of meiosis and sexual reproduction (Siripattrawan et al., 2000).

Species from Sulawesi

Corbicula linduensis Bollinger, 1914
Figs. 8C, 9A, B, 10, 11

Corbicula moltkiana var. *linduensis* Bollinger, 1914: 575, pl. 18, fig. 12.

Corbicula linduensis Bollinger – Djajasasmita 1975: 84, fig. 1.

Corbicula lindoensis [sic!] Bollinger – Djajasasmita, 1977: 4.

Type Locality: Lake Lindu, Sulawesi.

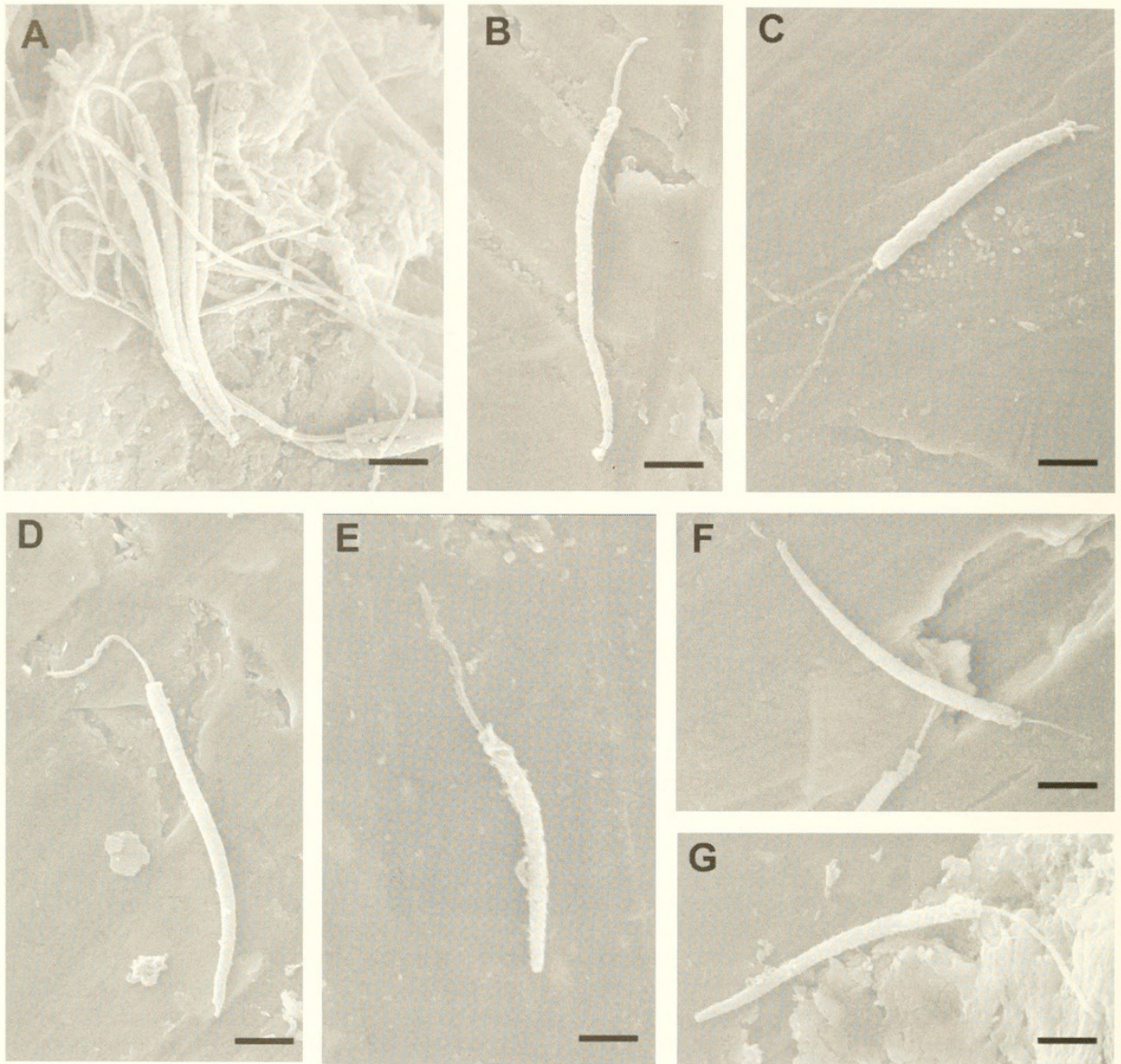


FIG. 8. Sperm morphology (SEM) of Indonesian *Corbicula* exhibiting monoflagellate spermatozoa: A, B. *C. moltkiana* (ZMB Moll. 103024); C. *C. linduensis* (ZMB Moll. 103016); D. *C. matannensis* (ZMB Moll. 103003); E. *C. loehensis* (ZMB Moll. 103010); F, G. *C. possoensis* (ZMB Moll. 103028). Scale bars = 2 μ m.

Type Material: Syntypes deposited at the Natural History Museum Basel (Switzerland) are reported to be lost (U. Wüest, pers. comm.).

Material Examined: Sulawesi: river at the road from Palu to Gimpu, basin of the Palu River (01°13.75'S, 119°56.69'E) (ZMB Moll. 103016w; leg. Brinkmann & Rintelen, March 2000) (Fig. 1).

Description

Shell: Oval, usually markedly elongated, with rounded posteroventral angle (Fig. 9A, B).

Periostracum yellow to brown. Internal coloration white or purple. Beaks central, narrow and not protruding. Surface sculpture with widely spaced, low ribs ($n = 10-12$ ribs per 1 cm); pronounced folds of periostracum noticeable between ribs. Hinge plate moderately broad. Cardinal teeth delicate; lateral teeth relatively short, straight. Largest specimen available for this study was 17 mm long. According to the literature, the specimens from Lake Lindu were on average 23 mm long.

Anatomy: Adductors small, round (Fig. 10A, Table 2). Presiphonal suture not elongated,

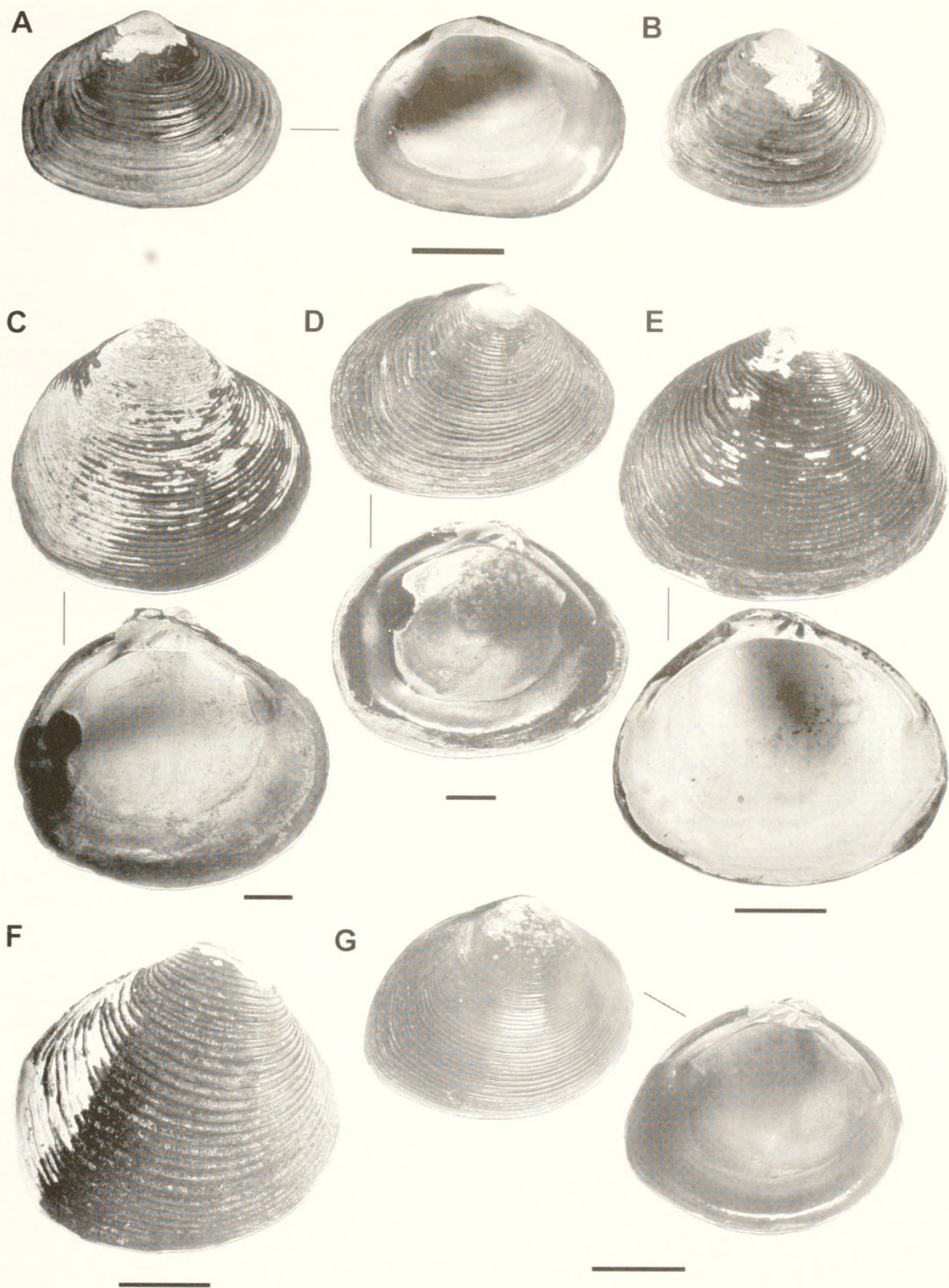


FIG. 9. Shells of *Corbicula* taxa from Sulawesi (right valve from outside, left valve from inside): A, B. *Corbicula linduensis*, Palu River system (ZMB Moll. 103016); C. Syntype of *C. matannensis*, Lake Matano (ZMB Moll. 50799); D. *C. matannensis*, Lake Matano (ZMB Moll. 103002); E. *C. matannensis*, Lake Mahalona (ZMB Moll. 103009); F. *C. matannensis*, Lake Towuti (ZMB Moll. 103006); G. Juvenile specimen of the same species from Lake Towuti (ZMB Moll. 103007). Scale bars = 5 mm.

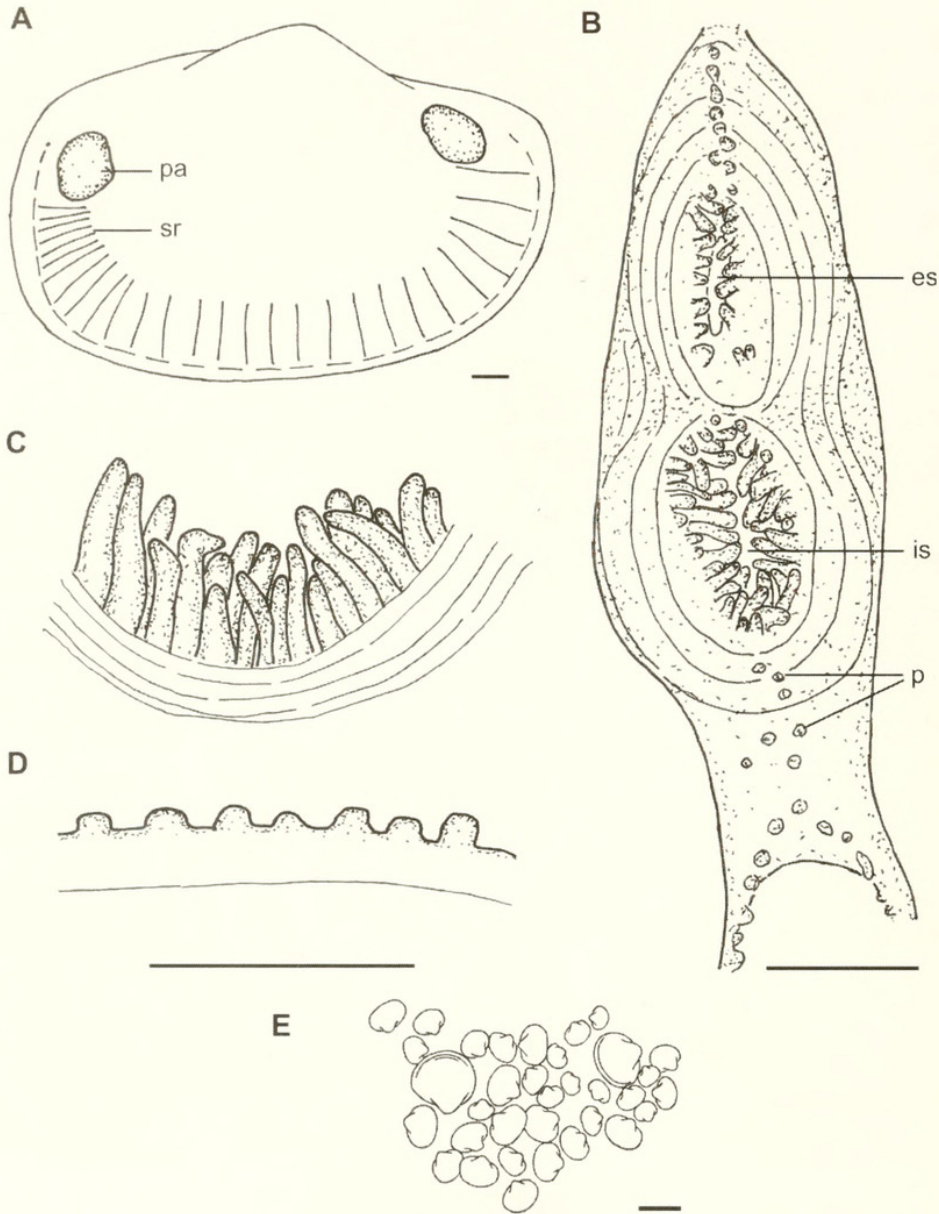


FIG. 10. Anatomy of *Corbicula linduensis*, Sulawesi (ZMB Moll. 103016): A. Habitus of soft body; B. Siphons from outside; C. Inhalant siphon papillae; D. Marginal mantle papillae; E. Clutch of juveniles from a gill. Scale bars = 1 mm (C and D to same scale).

length equal to diameter of inhalant siphon. Siphons conical, thin-walled, apertures circular or short oval, both somewhat broadened; inhalant siphon with about 50 papillae arranged in two rows (external row with shorter papillae) (Figs. 10B, C, 11A, B). Internal pigmentation of siphons weak, but pale internal ring sometimes noticeable around exhalant siphon. Papillae not pigmented. Siphonal muscles rather strong, arranged in broad bands. Papillae on outer surface of presiphonal suture arranged in two uneven rows (Fig. 10B). Marginal mantle papillae well

developed, densely spaced (Fig. 10D). Radial mantle muscles strong, arranged in band, with only anterior bundles distinct, separated from each other.

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa (Fig. 8C) monoflagellate, relatively small (head length $8.8 \pm 0.27 \mu\text{m}$, $n = 7$). Eight of 12 studied specimens were brooding. Some of them contained several hundred larvae of usual size for *Corbicula*. However, most of the gravid animals carried in each inner demibranch 10 to 35 juveniles

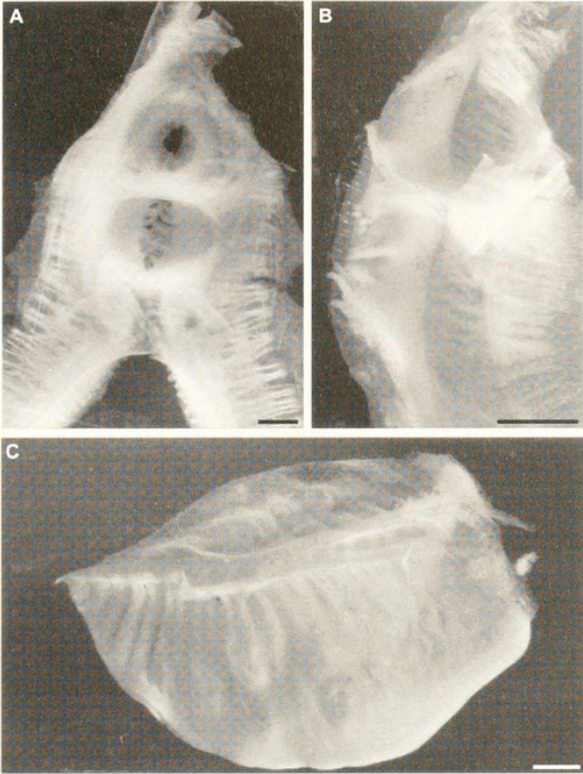


FIG. 11. View of mantle and gills of *Corbicula linduensis*, Sulawesi (ZMB Moll. 103016): A. Siphons from inside; B. Section of siphons; C. Gill with incubated larvae, from inside. Scale bars = 1 mm.

with up to 1.5 mm long shells (Fig. 10E, 11C).

Distribution and Ecology: Apparently restricted to the lake and river of the Palu basin. To date only known from lacustrine habitats (Djajasasmita, 1975, 1977). Our recent findings extend the known distribution from the lake proper to the Palu valley, though, since the specimens studied here were collected in a small river, on muddy bottom with vegetation.

Remarks: This species is similar in its elongated shell to some forms of *C. moltkiana*. However, the sculpture (smoothened ribs) and siphonal characters of *C. linduensis* are more similar to that in *C. fluminea* and *C. javanica* (Table 3). Sperm and eggs were not found in the same animal. Taking into account the monoflagellate type of sperm, we suggest that this species is meiotic, similarly to *C. moltkiana*. It is distinguished from the other taxa studied by the significantly smaller spermatozoa ($p < 0.01$, t-test). Characteristics of its brooding process, i.e. having

the largest incubated juveniles known, are unique among *Corbicula* species. According to Djajasasmita (1975) the population from Lake Lindu has dramatically decreased since 1950, thus rendering conservation strategy for this unique bivalve an urgent task.

Corbicula matannensis P. Sarasin &
F. Sarasin, 1898
Figs. 7C, 8D, 9C–G, 12, 13

Corbicula matannensis P. Sarasin & F. Sarasin, 1898: 92, pl. 11, figs. 158–160; Kruimel, 1913: 231; Djajasasmita, 1975: 84, fig. 3; Djajasasmita, 1977: 4.

Corbicula towutensis Kruimel, 1913: 231, pl. 4, fig. 3.

Corbicula mahalonensis Kruimel, 1913: 231, pl. 4, fig. 4.

Corbicula subplanata (partim) Martens – Prashad, 1930: 203, pl. 26, figs. 7–9, 13.

Type Locality: Lake Matano, Sulawesi.

Type Material: Syntype of *C. matannensis* P. Sarasin & F. Sarasin (ZMB 50799), from Lake Matano (Fig. 11A). Syntypes of *C. towutensis* Kruimel and *C. mahalonensis* Kruimel (ZMA) [vidi].

Other Material Examined: Sulawesi: Lake Matano: S shore, small bay (02°28.04'S, 121°14.04'E) (ZMB Moll. 103000w; leg. Glaubrecht & Rintelen, 15 August 1999); S shore (02°28.44'S, 121°15.78'E) (ZMB Moll. 103001w; leg. Glaubrecht & Rintelen, 15 August 1999); E bay, at outlet of Petea River (02°32.06'S, 121°28.50'E) (ZMB Moll. 103002w; leg. Glaubrecht & Rintelen, 16 August 1999); S shore, at Salonsa (02°30.49'S, 121°19.96'E) (ZMB Moll. 103003w; leg. Glaubrecht & Rintelen, August 1999); NW shore (2°26.01'S, 121°13.03'E) (ZMB Moll. 103004w; leg. Glaubrecht & Rintelen, 11–12 August 1999). Lake Towuti: W shore, bay at outlet of Larona River (02°46.09'S, 121°21.57'E) (ZMB Moll. 103006; leg. Glaubrecht & Rintelen, 18 August 1999); N shore, swamp W of Mahalona inlet, lake side of sand-bar (02°40'S, 121°31.8'E) (ZMB Moll. 103007w; leg. Bouchet, 1991). Lake Mahalona: at mouth of outlet (02°36.88'S, 121°30.98'E) (ZMB Moll. 103008; leg. Glaubrecht & Rintelen, 24 August 1999); E shore, cape (02°35.58'S, 121°30.68'E) (ZMB Moll. 103009w; leg. Glaubrecht & Rintelen, 24 August 1999) (Fig. 1).

Taxonomic Remarks: Comparison of the available material of *C. matannensis* to the

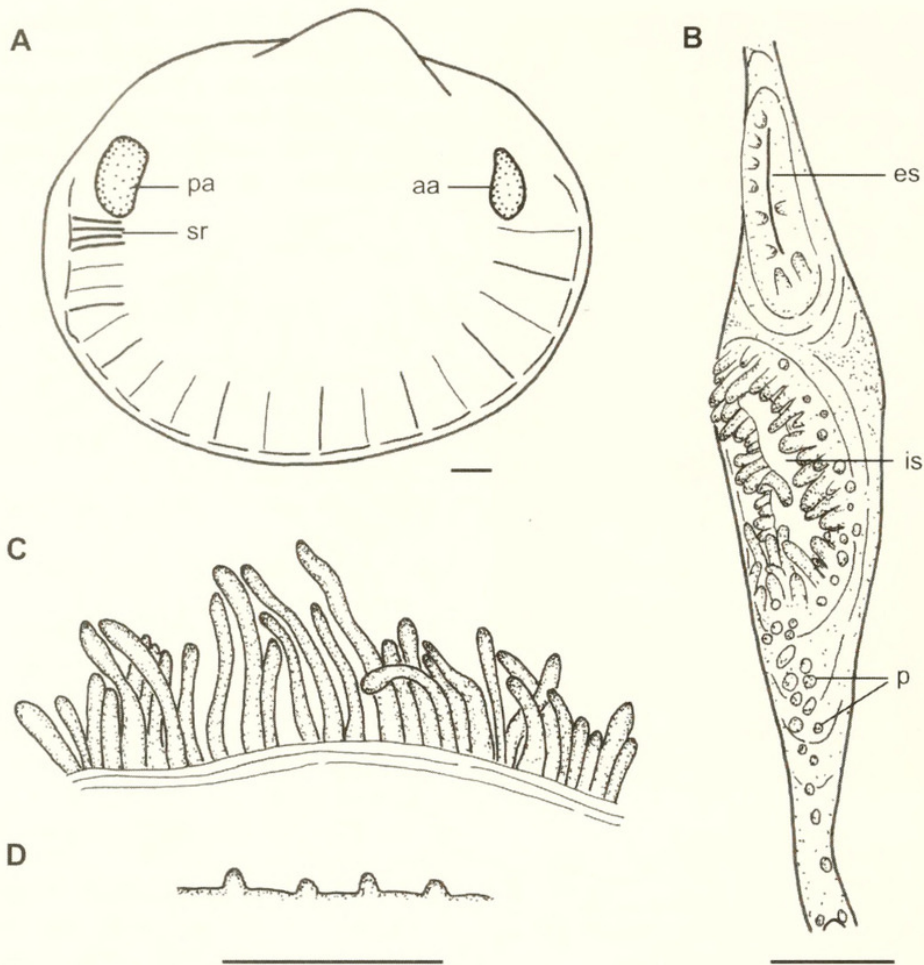


FIG. 12. Anatomy of *Corbicula matannensis* from Sulawesi, Lake Matano (ZMB Moll. 103002): A. Habitus of soft body; B. Siphons from outside; C. Papillae of inhalant siphon; D. Marginal mantle papillae. Scale bars = 1 mm (C and D to the same scale).

syntypes of *C. subplanata* Martens, 1897 (ZMB Moll. 103017, from Minralang River, near Tempe, Sulawesi), confirmed the differences in patterns of sculpture between these taxa mentioned by Djajasasmita (1975). However, the status of the latter taxon remains unclear, until its soft parts are available for anatomical and molecular study. Given that the differences between the respective taxa concern only shell proportions, which proved to be variable in *Corbicula* (Morton 1979, 1986; Harada & Nishino 1995), we accept here the synonymization of *C. mahalonensis* and *C. towutensis* under *C. matannensis* as suggested by Djajasasmita (1975).

Description

Shell: Circular in young specimens and tetragonal in fully grown ones, with obtuse postero-

ventral angle (Fig. 9C–G). Periostracum from pale yellow to dark violet in small shells and usually black in large ones, dull. Internal coloration from white to deep purple, usually darker on outer margin. Beaks central in young shells but markedly shifted forward in adults, narrow, not protruding. Concentric sculpture pronounced, densely spaced (15–20 ribs per 10 mm), ribs sharp. Hinge plate usually broad; cardinal teeth well developed; lateral teeth straight. Length up to 32.5 mm (syntype from Lake Matano).

Anatomy: Adductors small, oval (Fig. 12A, Table 2). Presiphonal suture relatively long. Siphons cylindrical, thin-walled, with broad slit-like apertures; inhalant siphon somewhat broader than exhalant, with 55 to 70 papillae arranged in two rows (internal row of long, external of short papillae) (Figs. 12B, C, 13A–C). Both inner and outer surface of siphons

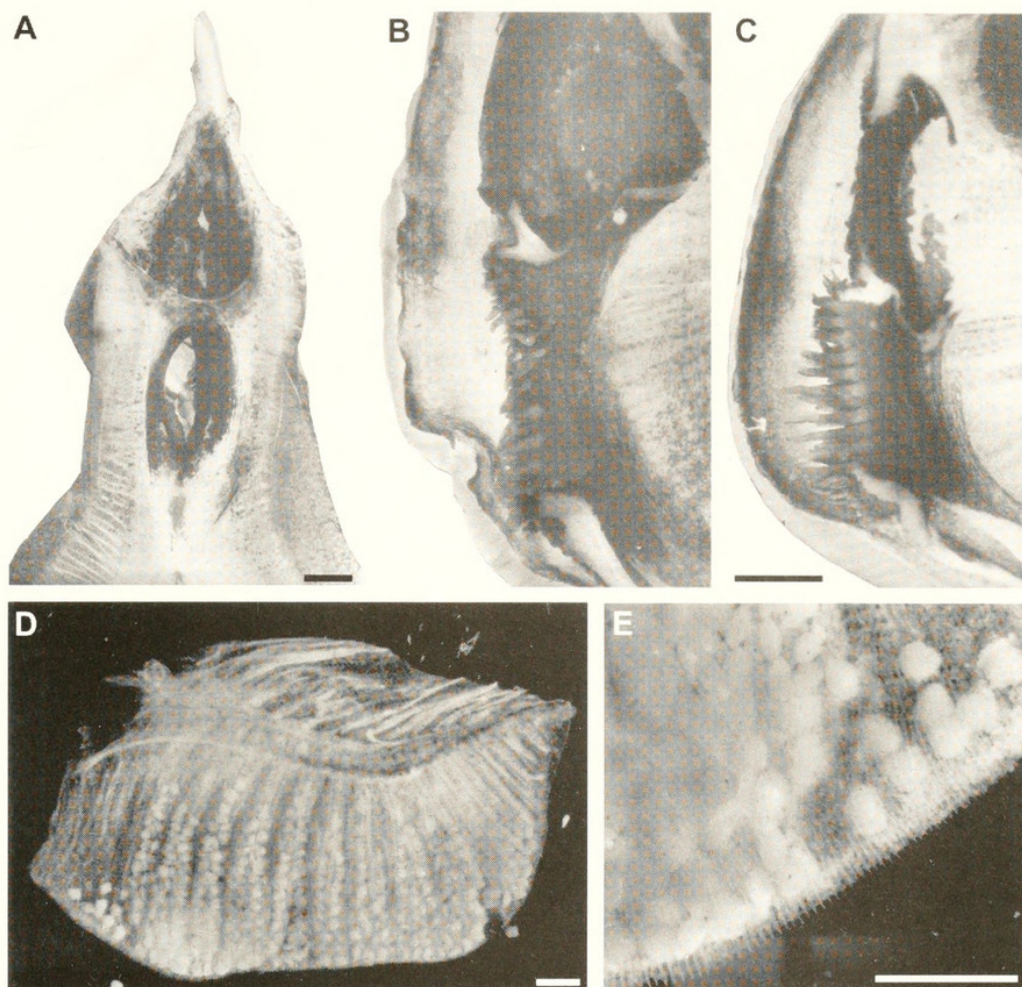


FIG. 13. *Corbicula matannensis* from Sulawesi, view of mantle and gill: A. Siphons from inside, Lake Matano (ZMB Moll. 103002); B. Section of siphons from specimen of the same locality; C. Section of siphons, Lake Towuti (ZMB Moll. 103006); D, E. Gill with incubated larvae, Lake Matano (ZMB Moll. 103002). Scale bars = 1 mm.

and papillae densely pigmented; with dark median internal stripe along presiphonal suture. Siphonal muscles weak, forming two narrow bands and dispersed fibers below and above these bands (Figs. 12A, 13A). Arrangement of papillae on outer surface of presiphonal suture variable: sometimes arranged in several rows, sometimes in single row or dispersed (Fig. 12B). Marginal mantle papillae small, widely spaced (Fig. 12D). Radial mantle muscles weak, forming separate bundles (Fig. 7C).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length $11.1 \pm 0.30 \mu\text{m}$ ($n = 7$). Brooding specimens were found in three samples (two from Lake Matano and one from Lake Mahalona),

representing a total of eight gravid specimens out of 30 specimens dissected. Numerous larvae (0.30–0.33 mm long) were located only in inner demibranchs (Fig. 13D, E).

Distribution and Ecology: Occurring in the larger lakes of the Malili system, that is, Lake Matano, Mahalona and Towuti. This species is known from lacustrine habitats only so far.

Remarks: This species is distinguished from *C. subplanata*, as described by Martens (1897), by its sculpture. *Corbicula matannensis* has much more densely placed ribs, and they are narrower and more sharp; because spacing between ribs in *Corbicula* increases with age, equally sized specimens should be compared. The latter taxon is also characterized by rather peculiar anatomical

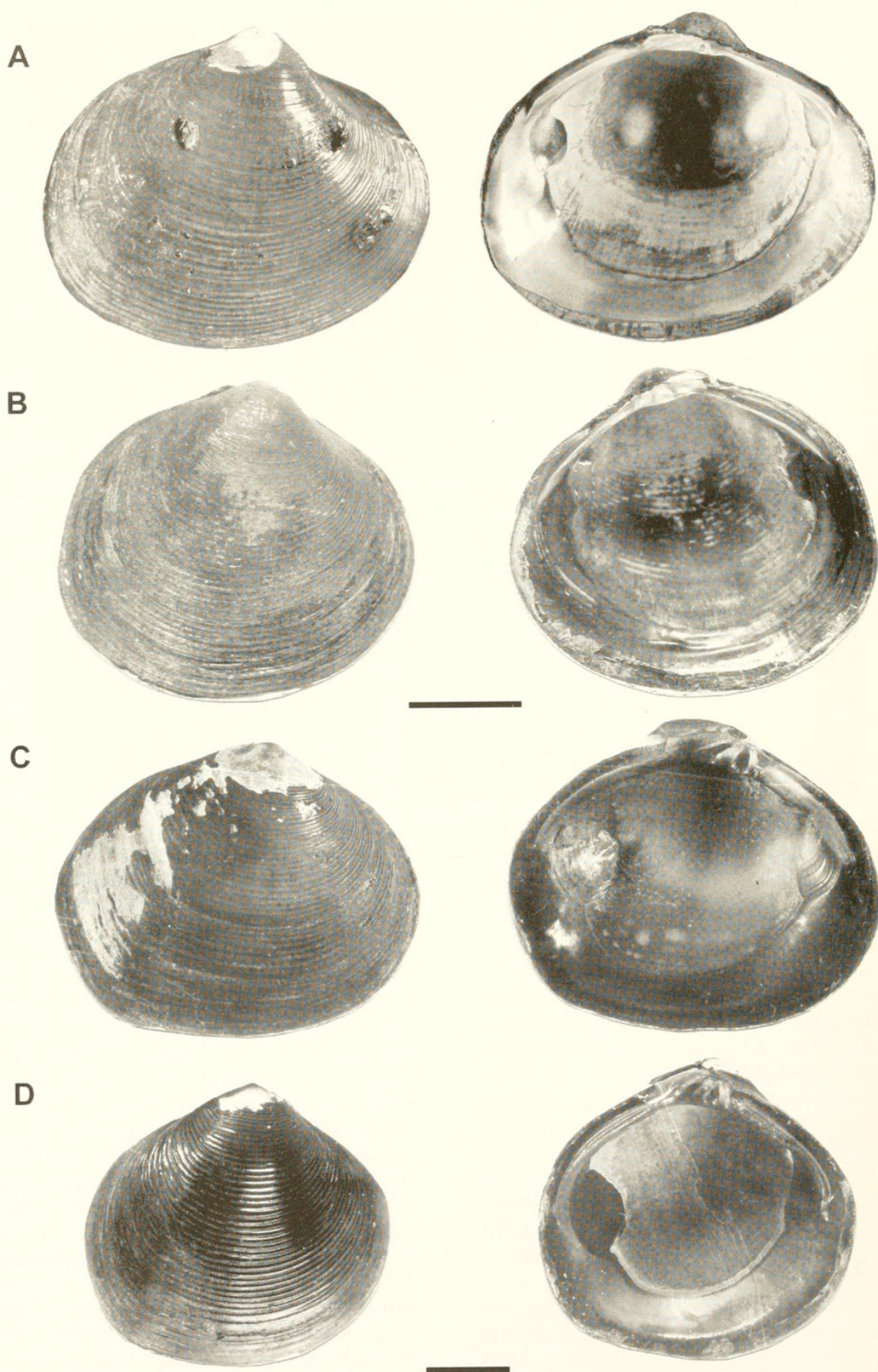


FIG. 14. Shells of *Corbicula* from Sulawesi: A. *C. loehensis*, Lake Masapi (ZMB Moll. 103010); B. *C. loehensis*, Lake Lontoa (ZMB Moll. 103005); C. Syntype of *Corbicula possoensis*, Lake Poso (ZMB Moll. 50798; D. *Corbicula possoensis*, Lake Poso (ZMB Moll. 190024). Scale bars = 5 mm.

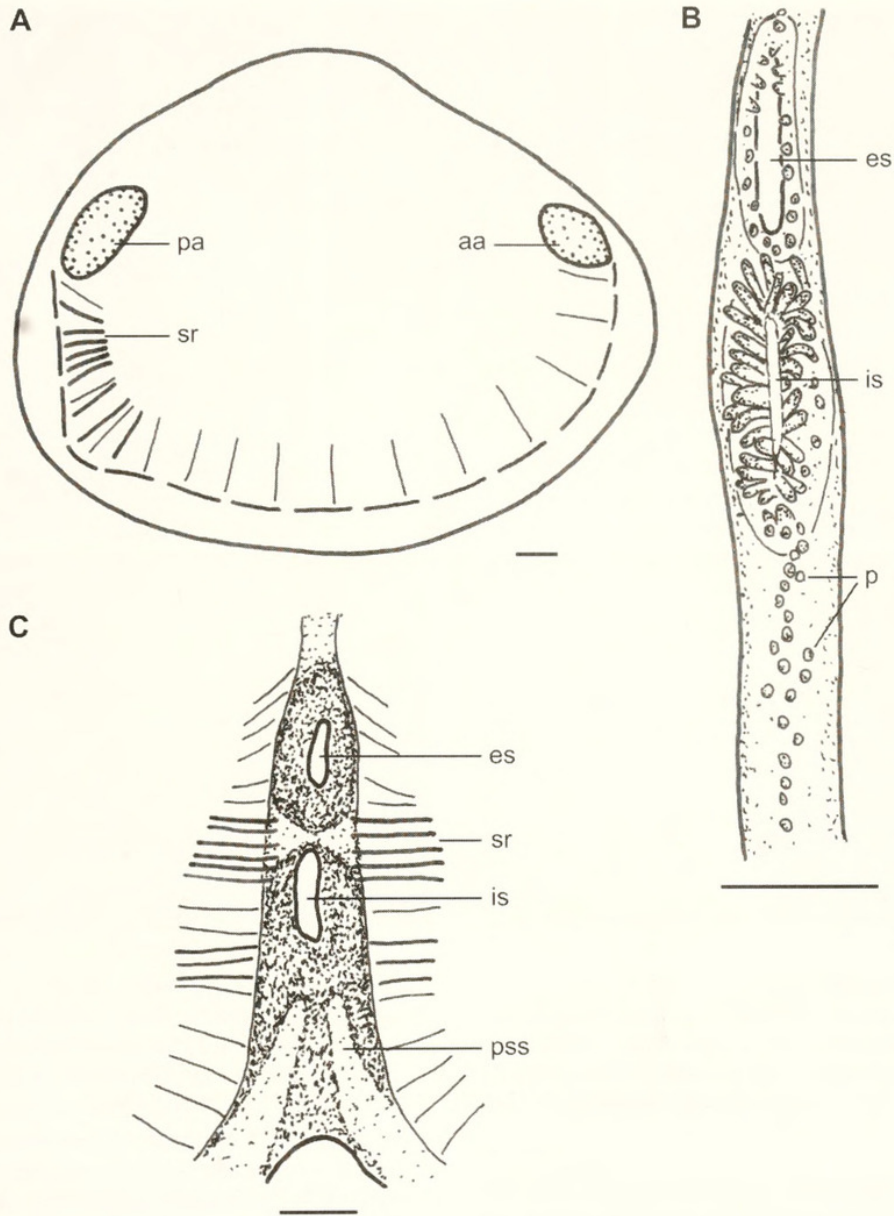


FIG. 15. Anatomy of *Corbicula loehensis*, Lake Masapi (ZMB Moll. 103010): A. Habitus of soft body; B. Siphons from outside; C. Siphons from inside. Scale bars = 1 mm.

characters (broad siphons with strong inside pigmentation, and widely spaced marginal papillae of mantle). One sample from Lake Towuti contained small shells (up to 16 mm long) with delicate sculpture (Fig. 9G) that show some similarity to *C. loehensis* (see below). However, none of these specimens were brooding, therefore, we conclude that all of them were young and could represent *C. matannensis*, in which juveniles have more delicate sculpture than adults. Noteworthy, the doubtful specimens from Towuti were similar to young *Corbicula* from Lake Matano and dis-

tinguished from *C. loehensis* of Lake Masapi and Lake Lontoa (older name: Wawontoa) by their broad hinge plate. The shells from Lake Matano are the largest (length up to 35 mm) characterised by well developed sculpture ($n = 14-16$ ribs per 10 mm in the middle and about 12 at the outer margin, near the beaks ribs are fine) and strong hinge. The specimens from Lake Towuti are very similar to that from Lake Matano, but they never reach such a large size (largest specimen found was 23 mm long) and are more round and convex (Fig. 11D, Table 2). This form is similar to

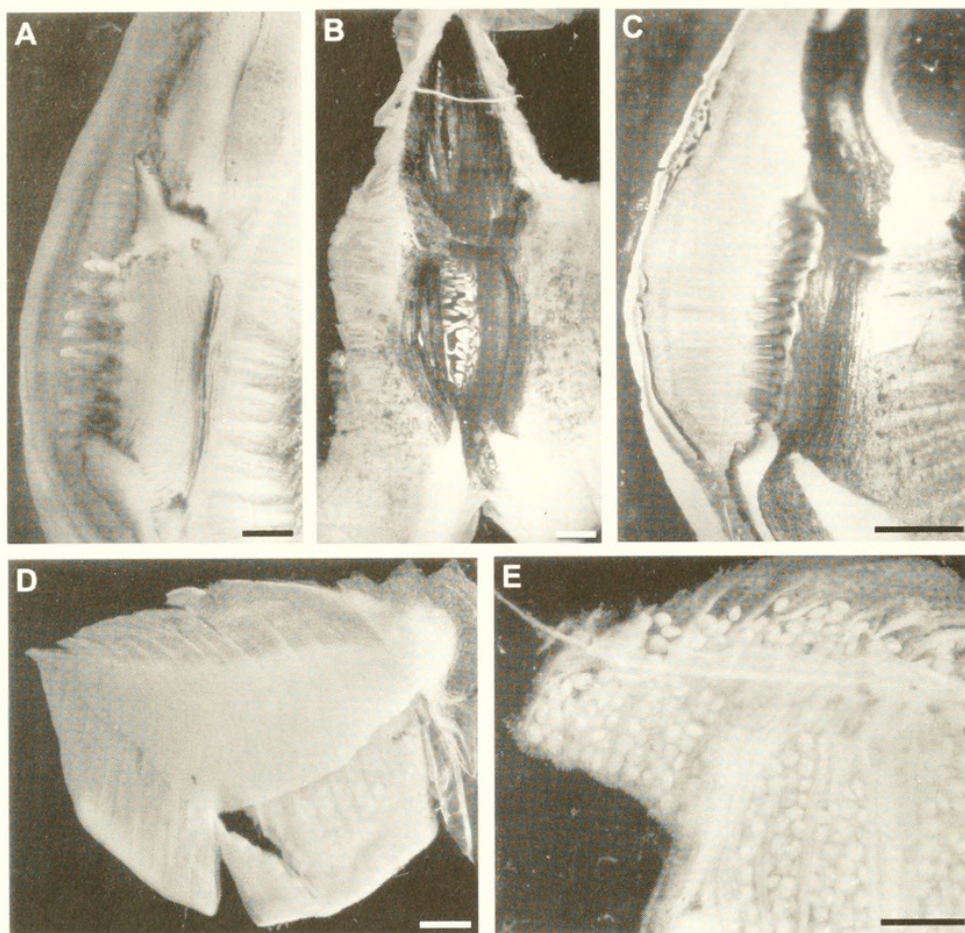


FIG. 16. *Corbicula loehensis* and *C. possoensis*, view of siphons and gills: A. *C. loehensis*, Lake Lontoa (ZMB Moll. 103005), section of siphons; B. *C. possoensis*, (ZMB Moll. 190024), siphons from inside; C. *C. possoensis* (ZMB Moll. 190024), section of siphons; D. *C. loehensis*, Lake Masapi (ZMB Moll. 103010), gill with incubated larvae from outside; E. *C. possoensis* (ZMB Moll. 190024), anterior portion of gill from inside (inner demibranch partly removed). Scale bars = 1mm.

small specimens of *C. possoensis*, but can be readily distinguished by the size of the adductors (see below). The corbiculids from Lake Mahalona are more elongated (especially posterior part) and flat (see Fig. 9E, Table 2). However, variation within one and the same lake (Matano) is also considerable (Fig. 11C, D, Table 2).

In features of reproductive biology (i.e., in presence of sperm and eggs in different animals, sperm morphology and mode of brooding) this species is similar to *C. moltkiana* from Sumatra.

Corbicula loehensis Kruimel, 1913
Figs. 8E, 14 A, B, 15, 16 A, D

Corbicula loehensis Kruimel, 1913: 232, pl. 4, figs. 2, 3; Djajasasmita, 1975: 84, fig. 3; Djajasasmita, 1977: 4.

Corbicula masapensis Kruimel, 1913: 232, pl. 4, fig. 1.

Corbicula subplanata Martens (part.) – Prashad, 1930: 203, pl. 26, figs. 11-12.

Type Locality: SE shore of Loeha Island, Lake Towuti.

Type Material: syntypes ZMA [vidi].

Other Material Examined: Sulawesi: Lake Masapi: S shore (02°50.84'S, 121°21.09'E) (ZMB Moll. 103011w; leg. Brinkmann & Rintelen, 30 March 2000); Lake Masapi, locality not specified (ZMB Moll. 103010w; leg. Bouchet, 1991). Lake Lontoa (= Wawontoa): SW shore (02°39.6'S, 121°44.8'E) (ZMB Moll. 103005w; leg. Bouchet, October 1991); W shore (02°39.90'S, 121°43.46'E) (ZMB Moll. 103033w; leg. Brinkmann & Rintelen, Mar 2000) (Fig. 1).

Taxonomic remarks: Djajasasmita (1975) synonymised *C. masapensis* with *C.*

loehensis. This point of view is tentatively accepted here, but we suggest to study Lake Towuti populations carefully before a final decision on the taxonomic status of the forms under consideration is possible. Identity of the form present in Lake Lontoa to *C. loehensis* was first shown by Djajasasmita (1975).

Description

Shell: Round to ovate, with somewhat obtuse posterior edge (Fig. 14A, B). Periostracum yellow in specimens from Lake Masapi and dark violet in those from Lake Lontoa, with silky glitter. Internal coloration white and purple, respectively. Beaks subcentral. Sculpture very fine, formed by delicate ribs (30–40 per 1 cm). Hinge plate moderately broad; cardinal teeth delicate; laterals relatively short, straight. The largest examined specimen was 18 mm long, but according to literature data the species may reach a length of 25 mm (Djajasasmita, 1975).

Anatomy: Adductors small, oval (Fig. 15A, Table 2). Siphons cylindrical, rather thin-walled, with broad oval apertures, inhalant siphon somewhat broader than exhalant, with about 50 papillae arranged in two rows. Internal surface of siphons, papillae and presiphonal suture usually strongly pigmented (Figs. 15B, C, 16A). Marginal mantle papillae small, widely spaced. Mantle musculature weak, muscle bundles well distinguishable and separated.

Reproductive biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length $9.1 \pm 0.21 \mu\text{m}$ ($n = 7$). The largest of the studied specimens was brooding. Larvae located in its inner demibranchs (Fig. 16D) were about 0.24 mm.

Distribution: Recorded ashore in Lake Towuti (Kruimel, 1913; Djajasasmita, 1975) and its satellite lakes Masapi and Lontoa.

Remarks: Anatomical characters of *C. loehensis* and *C. matannensis* are similar (Table 3), as well as are juvenile shells. However, the characters of juvenile shells in the former species (very fine sculpture and delicate hinge) are also retained in more advanced individuals of the latter species, which might indicate distinct developmental trends. Differences in coloration between the shells from Lakes Masapi and Lontoa are also noteworthy.

This species is similar in features of reproductive biology (structure of gonads, sperm type and mode of brooding) to *C. moltkiana* and *C. matannensis*, but differs in having significantly smaller spermatozoa ($p < 0.001$).

Corbicula possoensis P. Sarasin & F. Sarasin, 1898

Figs. 7D, 8F–G, 14C, D; 16B, C, E; 17

Corbicula possoensis P. Sarasin & F. Sarasin, 1898: 92, pl. 11, figs. 161–162; Kruimel, 1913: 231.

Corbicula subplanata Martens (part.) – Prashad, 1930: 203, pl. 26, figs. 10, 17–20.

Corbicula matannensis P. Sarasin & F. Sarasin (part.) – Djajasasmita, 1975: 84; Djajasasmita, 1977: 4.

Type Locality: Lake Poso, Sulawesi.

Type Material: syntype ZMB Moll. 50798 (Fig. 14C).

Other Material Examined: Lake Poso: S shore, Tentena, beach at Hotel “Pamona Indah” (01°45.92’S, 120°38.42’E) (ZMB Moll. 190024w; leg. Glaubrecht & Rintelen, September 1999); at Hotel “Mulia” (02°03.91’S, 120°41.50’E) (ZMB Moll. 103028w; leg. Brinkmann & Rintelen 23 September 2000); SW shore, Matawai (02°02.4’S, 120°38.1’E) (ZMB Moll. 103012w; leg. Bouchet, September 1991); E shore, Tolambo Bay (01°59.8’S, 120°42.1’E) (ZMB Moll. 103013w; leg. Bouchet, 1991); N shore, Saluopa (01°46.6’S, 120°32.9’E) (ZMB Moll. 103014w; leg. Bouchet, 1991) (Fig. 1).

Description

Shell: Triangular or short tetragonal, often with blunt keel at posterior end (Fig. 14C, D). Periostracum dark violet to black, sometimes yellowish in very young specimens, shiny. Internal coloration purple. Posterior margin truncate (diagnostic feature). Beaks markedly shifted forward, in small specimens relatively narrow while in large ones this can not be seen because shells are eroded. Hinge plate relatively broad, even in young specimens. Cardinal teeth well developed; lateral teeth somewhat shortened, straight. Sculpture: 25–30 delicate ribs per 1 cm.

Anatomy: Adductors large, posterior larger than anterior one (Figs. 14, 17A). Diameter of posterior adductor more than $\frac{1}{5}$ length of shell (Table 2). Presiphonal suture relatively short, not exceeding diameter of inhalant siphon.

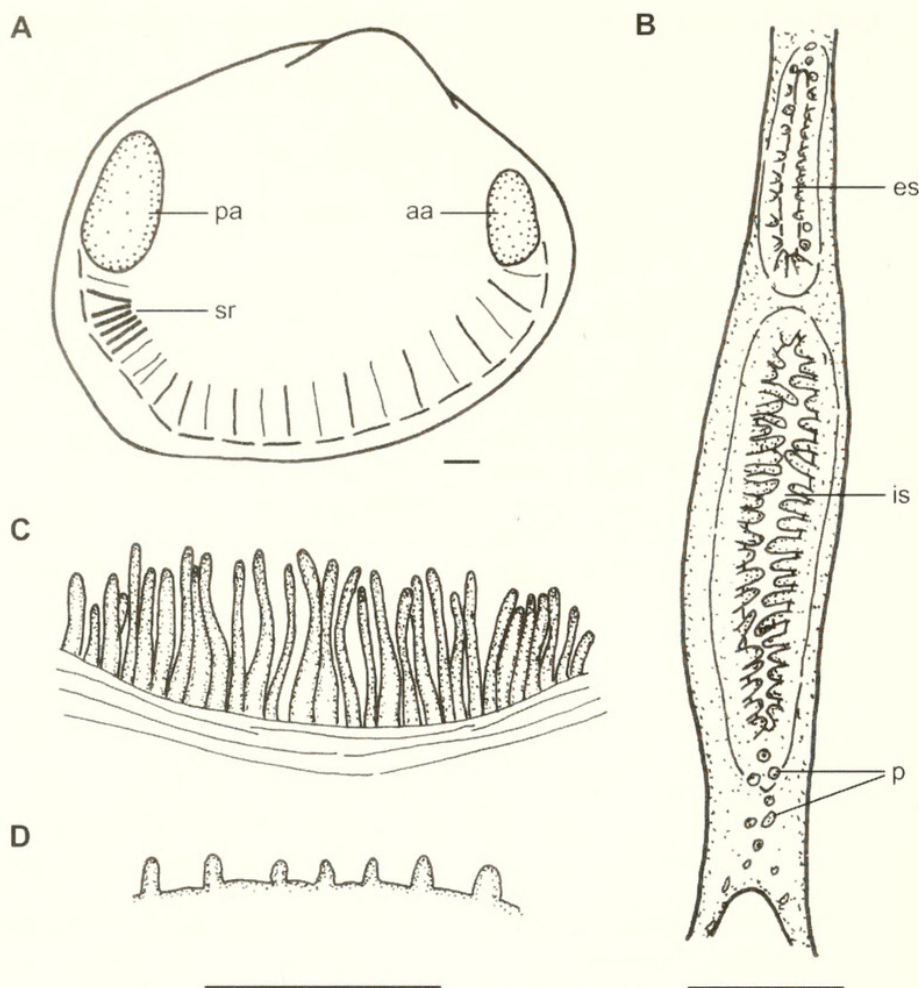


FIG. 17. Anatomy of *Corbicula possoensis*, Lake Poso: A. Habitus of soft body (ZMB Moll. 103014); B. Siphons from outside (ZMB Moll. 190024); C. Papillae of inhalant (ZMB Moll. 190024); D. Marginal mantle papillae (ZMB Moll. 190024). Scale bars = 1 mm (C and D to same scale).

Siphons broad, cylindrical, inhalant siphon markedly broader than exhalant, both with slit-like apertures; inhalant siphon with 60 to 70 papillae (depending on age), arranged in one or two rows (papillae of outer row always relatively smaller) (Figs. 16B, C, 17A, B). Both inner and outer surface of siphons and papillae densely pigmented, presiphonal suture also pigmented internally. Papillae on the outer surface of presiphonal suture scarce, unevenly arranged (Fig. 17B). Marginal mantle papillae small and widely spaced (Fig. 17D). Mantle musculature weak, muscle bundles separated, dispersed (Fig. 7D).

Reproductive Biology: Gonads of the dissected animals contained either sperm or eggs. Spermatozoa monoflagellate, head length $10.7 \pm 0.37 \mu\text{m}$ ($n = 6$). Branchial incubation was observed in two samples contain-

ing larger specimens (exceeding 18 mm); 6 of 15 dissected specimens were brooding and contained larvae in both demibranchs of each gill (Figs. 16E), one gravid specimen had larvae in inner demibranch only, though. Larvae were 0.26–0.30 mm long.

Distribution: Restricted to Lake Poso in Central Sulawesi.

Remarks: Conchologically, this species is distinguished from *C. matannensis* by its truncate posterior edge, fine sculpture (more than 20 ribs per 10 mm) and larger posterior adductor scar (Table 3). Beaks in large shells are somewhat broader and placed more anteriorly than in all previous species; also the hinge plate is relatively higher. *Corbicula possoensis* differs from *C. matannensis* also in having broad siphons extending over about $\frac{1}{3}$ of the body length in the former and $\frac{1}{4}$ in the latter species. Differences in relative

height of hinge plate, adductor size, siphons breadth and number of ribs were confirmed by t-test ($p < 0.001$). These diagnostic characters were consistent among all examined specimens, which is, in concert with our molecular data, the argument against synonymization of *C. possoensis* with *C. matannensis* as was earlier on suggested by Djajasasmita (1975).

Corbicula possoensis differs from other studied congeners in characteristics of brooding, because it is the only *Corbicula* species known that incubates in both demibranchs, instead of only the inner demibranch. Slight but significant ($p < 0.05$) difference in sperm size between this taxon and *C. matannensis* is also noteworthy. Other reproductive features of *C. possoensis* are similar to those shown for the taxa from Sumatra and Sulawesi (Table 3).

MOLECULAR PHYLOGENETICS

Of a total of 614 base pairs included in the final alignment, 103 were parsimoniously informative. Heuristic search recovered 56 most parsimonious trees of 368 steps (CI = 0.742, RI = 0.685). The strict consensus tree (Fig. 18) shows that all newly sequenced taxa included in the present molecular study form a well supported monophyletic clade with those freshwater taxa of *Corbicula* studied earlier, with the exception of *C. madagascariensis*. Within this clade three distinct Indonesian taxa are supported in this study, occurring (i) on Sumatra, identified as *C. moltkiana*, and (ii) on Sulawesi with *C. matannensis* and *C. loehensis* from the Malili lake system. In addition, two different sequences with unresolved relationships were obtained from specimens identified morphologically as *C. possoensis* from Lake Poso. Furthermore, one other of the Indonesian taxa, *C. javanica*, is shown in the parsimony analysis as closely related to *C. fluminea* from Korea and the North American *Corbicula* "form B", a clade that is also well supported. The second sequence attributed to *C. fluminea*, originating from material from Thailand, a sequence of *C. australis* from Australian, and *C. cf. fluminalis* from Israel is also clustering with this clade; however, the bootstrap support for the joint group is weak.

The NJ tree (Fig. 19) is more resolved than the consensus tree recovered by the maximum parsimony analysis, but the clades supported

by high bootstrap values are basically the same in both reconstructions. The two different morphotypes of *C. moltkiana* from Lake Maninjau cluster together, as well as the two different morphotypes from Lake Singkarak, irrespective of the morphological similarity between the corresponding morphotypes found in each of the two lakes; thus, the four samples from Sumatra cluster according to geography instead of morphology. The NJ analysis also indicates an outstanding position of *C. moltkiana* and a sister relationship between *C. loehensis* and *C. matannensis*, although the support of the relevant clades is below the 50% level. Heterogeneity of *C. possoensis* is found in this analysis as well.

Distance analyses show remarkable similarity in COI sequences (divergence levels not exceeding 1%) between the samples from the adjacent lakes Maninjau and Singkarak on Sumatra, as well Matano and Mahalona on Sulawesi (Table 4). The divergence between sequences obtained from different samples in Lake Matano was approximately of the same level as the difference between the samples from Matano and Mahalona. Only minor differences were recovered for *C. loehensis* from Masapi and Lontoa, while divergence level between this taxon and *C. matannensis* reaches 3.5%. The distance between two sequences of *C. possoensis* comprised 3.8%. Most of the pairwise sequence divergence levels calculated for the freshwater *Corbicula* taxa by this study did not exceed the level of 4.1% reported by Siripattrawan et al. (2000); only *C. moltkiana* showed greater distances, especially when compared with *C. possoensis* (up to 5.7%) and *C. australis* (up to 5.2%).

In conclusion, the molecular data agree with the morphological comparisons presented above in showing (i) distinctness of three lacustrine taxa from Sumatra (*C. moltkiana*) and Sulawesi (*C. matannensis* and *C. loehensis*), respectively, (ii) distinctness of these Indonesian taxa with respect to known continental Asian lineages, and (iii) the relationship of *C. javanica* and *C. fluminea*. However, the results concerning *C. possoensis* are equivocal, because no morphological characters correlated with the observed sequence differences were found. Plotting sperm morphology data on the trees based on COI sequence data suggests polyphyletic origin of the biflagellate condition, since no close relationship between the lineages sharing this state could be found.

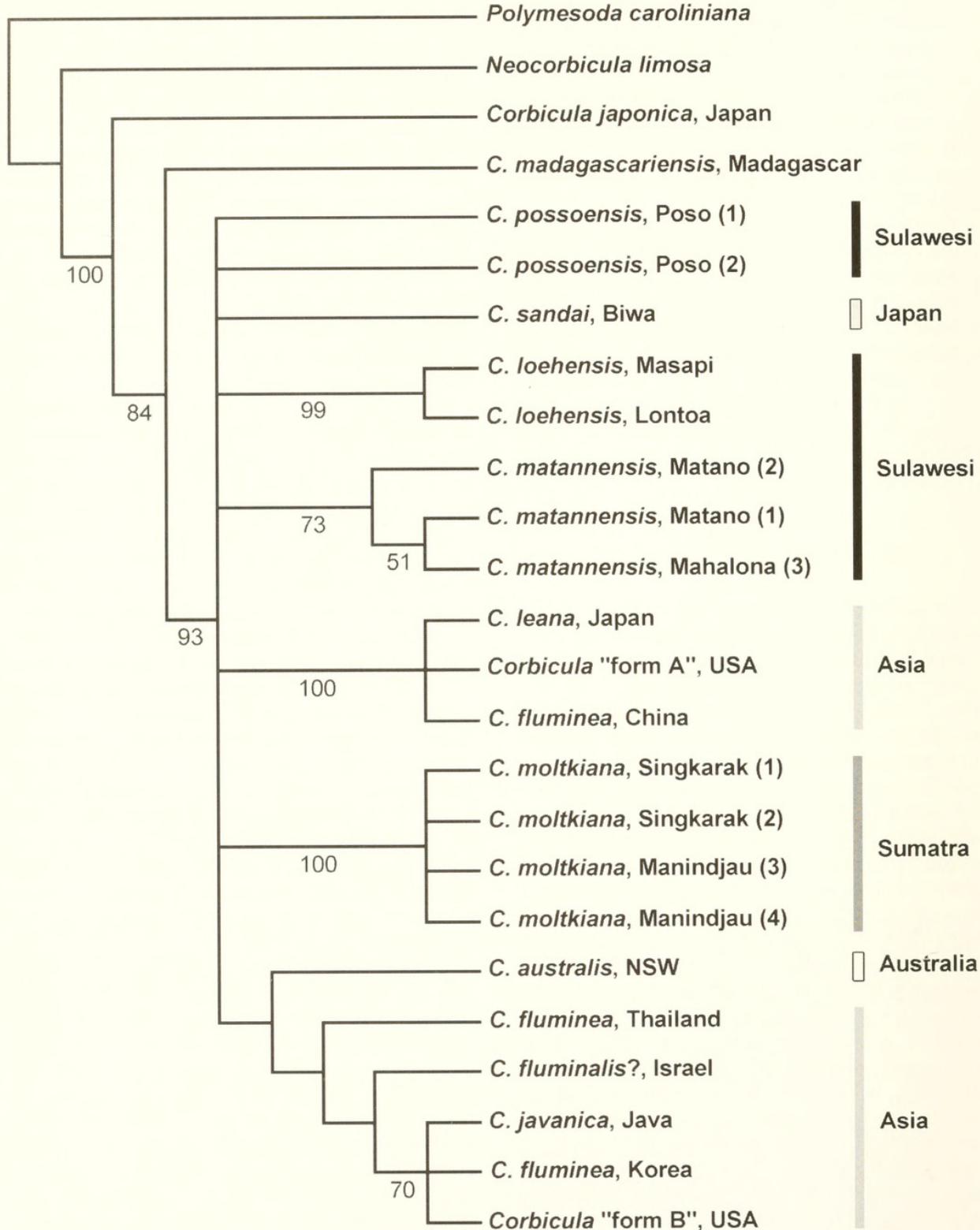


FIG. 18. Strict consensus of 56 maximum parsimony trees (368 steps, CI = 0.742, RI = 0.685) obtained for the corbiculid COI extended dataset. The numbers below branches show bootstrap support (if more than 50%).

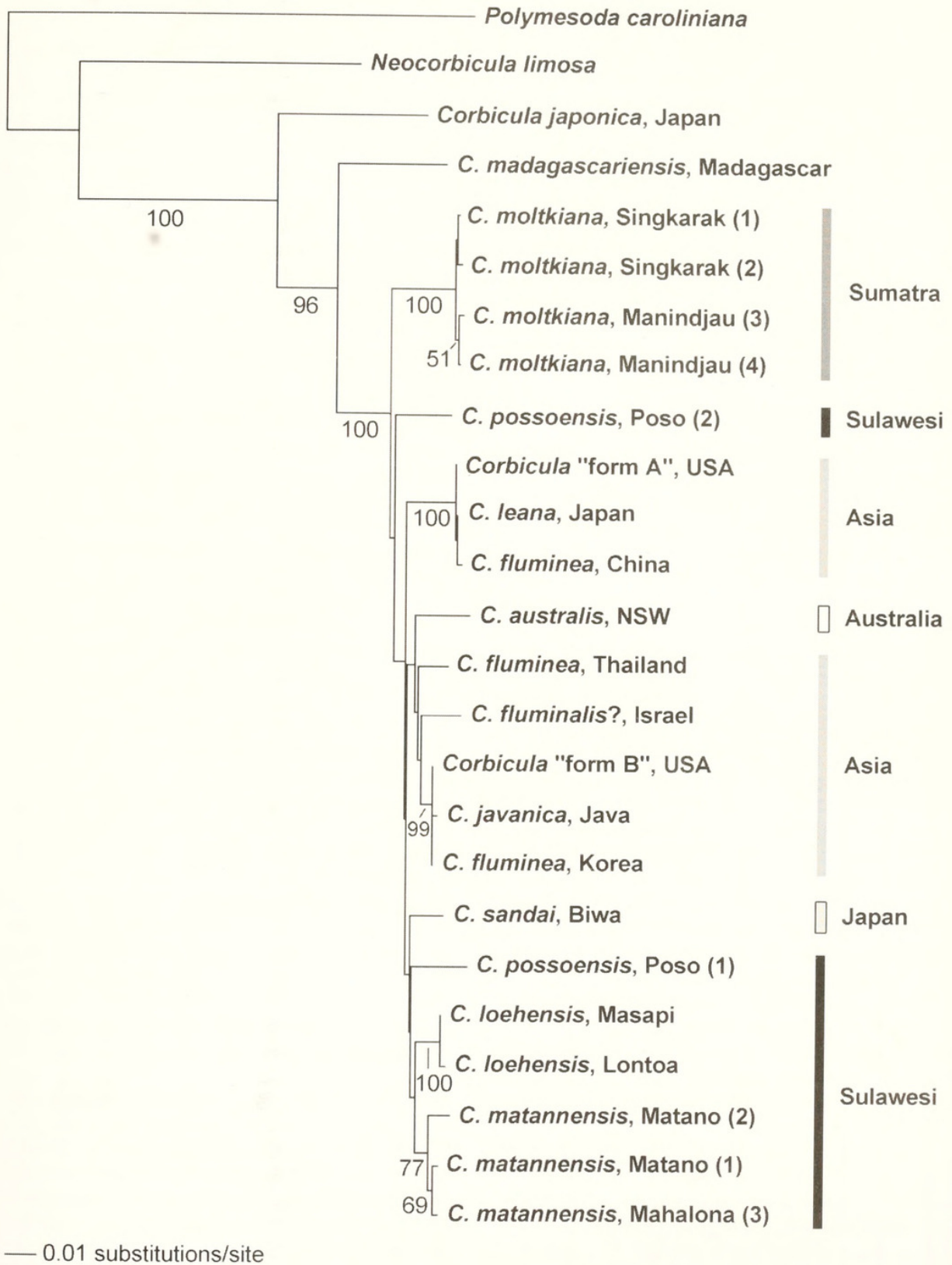


FIG. 19. A neighbor joining tree obtained for the corbiculid COI extended dataset. The numbers below branches show bootstrap support (if more than 50%).

TABLE 4. Corrected pairwise sequence divergences (General Time Reversible model utilized) among the COI haplotypes obtained for autochthonous freshwater *Corbicula* lineages (excluding those introduced to the Americas). Numbers in brackets refer to locality data given in Table 1.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. <i>C. moltkiana</i> , Singkarak (1)	-																			
2. <i>C. moltkiana</i> , Singkarak (2)	0.17	-																		
3. <i>C. moltkiana</i> , Manindjau (3)	0.16	0.34	-																	
4. <i>C. moltkiana</i> , Manindjau (4)	0.33	0.50	0.16	-																
5. <i>C. matannensis</i> , Matano (1)	4.29	4.40	4.48	4.29	-															
6. <i>C. matannensis</i> , Matano (2)	4.64	4.76	4.83	4.64	0.99	-														
7. <i>C. matannensis</i> , Mahalona (3)	4.29	4.40	4.48	4.29	0.33	0.99	-													
8. <i>C. loehensis</i> , Masapi (1)	3.60	3.69	3.78	3.96	1.34	2.02	1.34	-												
9. <i>C. loehensis</i> , Lontoa (2)	3.81	3.90	3.99	4.17	1.52	2.21	1.52	0.17	-											
10. <i>C. possoensis</i> (1)	5.55	5.69	5.74	5.55	2.17	2.86	2.88	2.88	3.08	-										
11. <i>C. possoensis</i> (2)	4.03	4.20	4.22	4.03	3.30	3.65	3.34	3.34	3.55	3.83	-									
12. <i>C. javanica</i>	3.42	3.52	3.60	3.42	2.17	2.52	2.17	2.19	2.38	3.05	3.47	-								
13. <i>C. fluminalis</i> ? Israel	4.28	4.38	4.46	4.28	3.03	3.38	3.03	3.05	3.25	3.55	3.99	1.83	-							
14. <i>C. fluminea</i> , Hong Kong	4.23	4.46	4.43	4.23	2.91	3.27	2.91	2.54	2.72	3.83	4.27	3.09	3.45	-						
15. <i>C. fluminea</i> , Thailand	3.24	3.33	3.42	3.24	2.00	2.34	2.00	2.02	2.21	2.88	3.28	0.16	1.66	2.90	-					
16. <i>C. fluminea</i> , Korea	3.22	3.30	3.40	3.22	2.69	3.04	2.69	2.70	2.91	3.57	3.64	1.49	2.33	3.26	1.32	-				
17. <i>C. leana</i>	4.27	4.37	4.45	4.27	2.70	3.04	2.70	2.37	2.56	3.57	4.01	2.86	3.02	1.75	2.69	3.03	-			
18. <i>C. sandai</i>	3.75	3.85	3.93	3.75	2.00	2.34	2.00	2.01	2.20	2.85	3.27	1.82	3.37	3.45	1.66	2.33	3.37	-		
19. <i>C. australis</i>	5.03	5.16	5.22	5.03	3.38	3.03	3.38	4.41	3.62	3.91	4.37	2.86	3.38	4.05	2.69	2.68	3.75	3.02	-	
20. <i>C. madagascariensis</i>	7.77	7.99	7.98	7.77	7.11	7.47	6.71	6.57	6.80	8.40	7.76	3.36	7.04	6.72	6.16	6.91	6.84	7.30	8.48	-

DISCUSSION

Taxonomy and Systematics

Previous phylogenetic investigations suggested a common, monophyletic origin of all Old World freshwater *Corbicula*, with the estuarine *C. japonica* being the sister taxon (Siripatrawan et al., 2000; Pfenninger et al., 2002). This is confirmed in the present study by the inclusion of new sequence data from Indonesian taxa.

In an attempt to clarify the systematics of these Indonesian corbiculids, mainly of those species inhabiting Sumatra and Sulawesi, five taxa were found to possess specific distinctness and identity, based on shell morphology, anatomy and the features of reproductive biology (including brooding), as well as on molecular data. While the corbiculids studied from Sumatra are identified as *C. moltkiana*, four distinct taxa were identified on Sulawesi: *C. possoensis* (with two distinct lineages revealed in the NJ analysis) endemic to Lake Poso and *C. matannensis* plus *C. loehensis* occurring in the central Malili lake system. Suitable material of the fourth species, *C. linduensis* from the Lindu River, was not available for molecular investigation.

The species distinctness of *C. javanica* from the island of Java remains doubtful in the absence of data on sperm morphology and, thus, there is the possibility of clonality. Remarkable is its close affinity to Asian lineages of *C. fluminea* found in our study. However, the taxonomic status of the latter is also problematic, because it was shown to be an assemblage of several clonal lineages, probably of different origin, that also includes allochthonous populations introduced into North America and Europe (Siripatrawan et al., 2000; Pfenninger et al., 2002). Therefore, any synonymizations in this stage of investigation seem to be premature.

Corbicula taxonomy has historically been plagued by a plethora of nominal taxa described from numerous, at least partly ecophenotypic shell morphs. The occurrence of polyploidy, unisexual reproduction, hermaphroditism, and androgenesis recently reported for certain *Corbicula* populations (see Introduction) suggest that variation observed in these freshwater bivalvia could be the result of clonality and not necessarily imply species level differences, as discussed in Siripatrawan et al. (2000). Because polyploidy is prevalent in

some freshwater molluscs, especially among bivalves, it is assumed to have played an important role in shaping their diversity and can pose significant challenges to reconstruct phylogenetic evolution also in Corbiculidae (Lee et al., 2002).

While the determination of presence or absence of meiosis is a rather laborious task applicable only in adequately fixed material, fortunately in *Corbicula* there is an exceptionally convenient morphological marker to help distinguish clonal forms, since, to the present knowledge, studied ameiotic lineages all have biflagellate spermatozoa (Komaru & Konishi, 1999; Siripatrawan et al., 2000; Qiu et al., 2001). Our preliminary observations suggest that Indonesian corbiculids reproduce sexually and have monoflagellate spermatozoa (with the exception of *C. javanica*, in which sperm structure remains unknown). In this respect, they appear to be similar to *C. sandai* from the "ancient" Lake Biwa in Japan, which is known to be diploid and reproduces sexually with monoflagellate sperm (Hurukawa & Mitsumoto, 1953; Okamoto & Arimoto, 1986). Interestingly, our NJ analysis revealed that *C. sandai* clusters together with the Sulawesi clade, whereas the topology of the MP tree is not resolved in this respect.

Given the notorious variability of morphological characters applied traditionally in *Corbicula* taxonomy, which is also shown in this study, and the incompleteness of data on reproductive biology as well as molecular genetics, any final decision about the systematics and taxonomic status of different forms (morphotypes) distributed across Australasia is still not possible. Uncertainties remain in particular for the Javanese form and the question concerning the existence, distribution and identity of *C. fluminea*. However, several of our systematic conclusions based on the new data on Indonesian taxa are in agreement with some of those already reached in previous revisions, mainly those by Djajasasmita (1975, 1977).

Implications from Morphology

Generally, confirming the presence of endemic taxa in several lacustrine habitats on Sumatra and Sulawesi, this study adds support to the recognition of the following taxa: *C. moltkiana*, *C. linduensis*, *C. possoensis*, *C. matannensis* and *C. loehensis*. The first of these taxa recorded in the lakes on Sumatra is similar to the widely distributed Asian *C.*

fluminea (Britton & Morton, 1979; Morton, 1986; Araujo et al., 1993; Chen et al., 1995; Harada & Nishino, 1995; Komaru et al., 1997, 2000), in anatomical characters and the features of brooding; however, its species status is supported by sperm morphology and COI sequence data.

Taxonomic distinctness of *Corbicula linduensis* from North Sulawesi, first suggested by Djajasasmita (1975), is supported here by characteristics of brooding (limited number of large juveniles incubated in gills) not known in any other *Corbicula*. However, in the absence of molecular data for this taxon, its relationships remain unknown. Noteworthy, brooding in *C. linduensis* seems to be somewhat similar to the South American *Neocorbicula limosa*, as described by Ituarte (1994). Since the latter represents an independent lineage within the family, judging from morphological study (Dreher Mansur & Meier-Brook, 2000) and molecular data (Siripatrawan et al., 2000; Figs. 18, 19), its mode of reproduction has apparently evolved independently.

The taxa inhabiting the Malili lake system on Sulawesi differ from their congeners not only in shell parameters, but also in anatomical characters, for example in the form and pigmentation of siphons. Although diagnostic applications of these characters in *Corbicula* is hindered by the considerable intraspecific variability (see, for example, the description of *C. moltkiana*), in this particular case anatomical differences are supported by molecular data. As shown in this study, the distinctness of *C. matannensis* occurring in Lake Matano and Lake Mahalona (connected through the Petea River; Fig. 1) from *C. loehensis* inhabiting the satellite lakes Masapi and Lontoa of Lake Towuti (but both connected via separate river systems) is in agreement with the taxonomy used by Djajasasmita (1975). Unfortunately, no molecular data are available to date for the latter species from Lake Towuti proper, where both taxa possibly live sympatrically according to Djajasasmita (1975).

The data on *C. possoensis* restricted to Lake Poso are controversial. While morphological observations show similarity of all available lots, molecular data suggest their heterogeneity. Although *Corbicula* from Lake Poso apparently needs further study, the outstanding position of *C. possoensis* in relation to corbiculids inhabiting the Malili lake system found in the present study is consistent with recent results on endemic pachychlid gastro-

pods from Lake Poso, which exhibit a similar isolated position among the *Tylomelania* clade in morphological and molecular phylogenies (Rintelen & Glaubrecht, 1999, 2002; Rintelen et al., submitted).

Some anatomical characters, for example the broad cylindrical (fringe-like) form of siphons and the number and arrangement of the exhalant siphon papillae, which are common in *Corbicula* species inhabiting Lake Poso and the Malili Lakes on Sulawesi were also reported for the Japanese estuarine species *C. japonica* (Harada & Nishino, 1995). However, the internal coloration of siphons and papillae is remarkably similar in all Sulawesi taxa but differ from that of *C. japonica*, which is also very distinct karyologically (Okamoto & Arimoto, 1986), in its non-brooding reproduction (reviewed by Morton, 1986) and its molecular genetics (Siripatrawan et al., 2000). Therefore, any similarity in form of siphons between the freshwater corbiculids in question and their probable estuarine sister taxon are unlikely to be synapomorphic.

Spermatozoan Morphology

The new data on sperm morphology shown here for Indonesian taxa suggest that monoflagellate spermatozoa are more common among freshwater *Corbicula* than assumed in previous studies (Komaru & Konishi, 1996, 1999; Byrne et al., 2000; Siripatrawan et al., 2000). Interestingly, the monoflagellate type is known to occur in species inhabiting lacustrine habitats, such as, for example, Lake Biwa in Japan (*C. sandai*), lakes Singkarak and Maninjau on Sumatra (*C. moltkiana*), Lake Poso (*C. possoensis*) and the Malili lake system (*C. matannensis*, *C. loehensis*) on Sulawesi.

In addition, while all *Corbicula* with biflagellate spermatozoa are simultaneous hermaphrodites (Komaru & Konishi, 1996, 1999; Konishi et al., 1998; Byrne et al., 2000), the Indonesian corbiculids with monoflagellate sperm apparently have a different expression of sexuality. Since monoflagellate sperm is reported for the gonochoric *Corbicula sandai* (Siripatrawan et al., 2000, and literature cited therein), we hypothesize that the Indonesian taxa also have separate sexes.

However, sperm morphology of many riverine corbiculids, especially those occurring on other Sunda Islands, is still not studied; therefore, it is too early to judge on this habitat-sperm mor-

phology correlation. Our phylogenetic reconstruction does also not reveal a close relationship between lineages sharing the biflagellate type of sperm, because the latter occurs in clonal *Corbicula* within both Asian clades found in the analyses (Figs. 18, 19).

The diversity of head size in spermatozoa of *Corbicula* is remarkable, although no correlation between size and the monoflagellate/biflagellate type was found. The biflagellate spermatozoa of the Chinese *C. fluminea* and Japanese *C. leana* are distinguishable by their large size of 16–25 μm (Komaru & Konishi, 1996; Qiu et al., 2001), whereas biflagellate spermatozoa of *C. australis* are relatively small with 9.3 μm on average (Byrne et al., 2000). The latter are, thus, similar in size to the monoflagellate spermatozoa found here for *C. loehensis* (9.1 μm). Biflagellate spermatozoa of another Japanese form, *C. aff. fluminea*, are reported to be also relatively small compared with the sympatric *C. leana* (13.9 μm and 16.9 μm , respectively) (Konishi et al., 1998). Size difference in corbiculid sperm observed in taxa from China was found to be correlated with ploidy (Qiu et al., 2001) and in taxa from Japan with number of mitochondria (Konishi et al., 1998).

Brooding

Observations presented above on reproduction in Indonesian corbiculids agree with the literature data in showing prevalence of brooding among freshwater *Corbicula* (Morton, 1986; Byrne et al., 2000; Siripattawan et al., 2000). To date, within the genus only the estuarine (i.e., brackish-water) sister taxon *C. japonica* is non-brooding and characterized by the development with free-swimming veligers (Byun & Chung, 2001). Among the freshwater corbiculids the endemic *C. sandai* from Lake Biwa with its benthic egg masses with direct developing young (Hurukawa & Mitsumoto, 1953) remains the only known exception of an ovoviparous reproductive mode.

However, we here documented a greater diversity of brooding characteristics in taxa particularly from Sulawesi than was witnessed earlier for the rest of the collective Old World range of *Corbicula*. Remarkable is the presence of large juveniles being incubated in the gills of *C. linduensis* and the brooding utilizing both demibranchs in *C. possoensis*, which is both not known in any other congeners.

Historical Zoogeography

According to the phylogenetic systematics discussed above, two groups of taxa can be distinguished among Indonesian corbiculids. On one hand, there is at least one common widespread clade in Asia that includes populations identified as *C. fluminea* occurring in Korea and Thailand, as well as those populations from the Sunda Islands Java and Lombok assigned here tentatively to *C. javanica* and *C. australis* in Australia.

On the other hand, Sumatra and Sulawesi seem to harbour *Corbicula* species with fairly restricted occurrences that cluster according to their distribution not only on but within these islands. To the present knowledge, all lacustrine forms described herein are endemic to their respective lakes and lake systems with three separate regions to be distinguished (Fig. 1): (i) Northwest Sulawesi with the *graben* or basin of the Palu River and Lake Lindu where *C. linduensis* occurs, (ii) Lake Poso with the endemic *C. possoensis*, and (iii) the central lakes of the Malili system with *C. matannensis* (mainly in Lake Matano and Lake Mahalona) and *C. loehensis* (in the satellite lakes of and in Lake Towuti). Another species, *C. subplanata* was described based on shells only from a fourth region in southwest Sulawesi (area of Minralang), but its specific identity and status remains to be substantiated by anatomical and molecular data. In contrast, sampling on Sumatra is to date too scarce to allow for any solid judgement of an equally restricted occurrence of *C. moltkiana* in lakes Maninjau and Singkarak only. In addition, the specific identity and affinity of *C. tobae* endemic to Lake Toba in northern Sumatra remains unresolved.

The pattern of endemic occurrences of lacustrine corbiculids strongly correlates with the distribution recently studied in detail for pachychilid gastropods of the endemic *Tylomelania* clade on Sulawesi (Rintelen & Glaubrecht, 1999, 2002; Rintelen et al., submitted), as well as with the biogeography of Indonesian Ancyliidae (Glaubrecht, unpub. data), and is, therefore, no artefact of insufficient data on the range of limnic molluscs in Southeast Asia. In case of the evolution of endemic corbiculid bivalves in separate areas within the geologically complex island of Sulawesi, it remains to be tested, based on further sampling and detailed molecular studies, whether this biogeographic pattern finds its historical expla-

nation in the spatial isolation over longer geological time in concert with the composite nature of this odd shaped island that formed by fusion of several microplates (terrane) in Late Miocene-Early Pliocene (palaeogeographical background: Whitmore, 1981; Hall & Bundell, 1996; Metcalfe et al., 2001).

Using other limnic molluscs as models, it has recently been hypothesized that, for example, the phylogeny and biogeography of pachychlid gastropods of *Brotia, sensu lato*, in Southeast and Austral Asia reflect palaeogeographical events since the Cretaceous/Cenozoic rather than more recent geological history (Glaubrecht, 2000; Glaubrecht & Rintelen, 2003; Köhler et al., 2000; Köhler & Glaubrecht, 2001, 2003). The latter comprise, for example, those events related to the formation of Sundaland and its drowning during the Plio-Pleistocene. Accordingly, the distribution of taxa of the *Brotia, sensu lato*, complex might represent an ancient vicariance pattern caused by plate and terrane tectonics that has not been obscured subsequently, presumably due to comparatively restricted dispersal abilities of these viviparous snails in conjunction with ecological factors.

In contrast, the available evidence in case of the East Asian and Australian freshwater corbiculids was regarded incompatible with an ancient vicariance scenario. Above all, an assumed late Cenozoic origin of freshwater *Corbicula* restrict applicability of the studied group as indicator of a long and complex geological history and biogeography within the so-called "Wallacea" (as transitional zone between the Australian and Oriental region). Second, the mitochondrial COI sequences generated for those corbiculids collectively distributed from the Japanese Archipelago to Australia indicated a phylogenetically shallow polytomy, suggesting an evolutionary recent common origin to Siripattrawan et al. (2000) and Pfenninger et al. (2002). Showing rather low levels of genetic distances between different lineages of Asian freshwater *Corbicula*, our analyses including now the Indonesian taxa in general support this scenario of rather late divergence of freshwater lineages. Nevertheless, the higher sequence distances in particular shown by *C. moltkiana* on Sumatra may indicate that this divergence started earlier than Pleistocene age suggested by Pfenninger et al. (2002).

In summary, three statements of biogeographical importance are implied by the present study: (i) presence of distinct and, in

relation to other Asian forms, old taxa on Sumatra and Sulawesi, (ii) a remarkable diversity of *Corbicula* on the island of Sulawesi with at least three distinct lineages and taxa, respectively, and (iii) presumably a relatively late colonization of the Sunda Islands Java and Lombok by *C. javanica* with its strong affinity to *C. fluminea*.

Evolutionary Ecology

The COI sequence data in conjunction with the new finding of exceptional life history and anatomical characteristics, including features of sperm morphology and incubation, presented herein for Indonesian *Corbicula* suggest an evolutionary ecology hypothesis on their origin (theoretical background, reviews: Glaubrecht, 1996; Streit et al., 1997). In particular, the diversity of *Corbicula* in the so-called "ancient" lakes on Sulawesi deserve such an explanation, while there is only one riverine corbiculid which has been collectively assigned to *C. subplanata* (see Introduction).

Accordingly, we anticipate colonization of Sumatra and Sulawesi by an early, sexual reproducing and incubating corbiculid ancestor with monoflagellate spermatozoa and subsequent radiation by speciation of individual corbiculids in situ particularly in Lake Poso and the Malili lake system, respectively, once these special habitats open up and provided new ecological opportunities. A time frame for this process can be given very tentatively only, with an estimated age of Lake Poso and the Malili lakes of about 1–2 myr (Rintelen et al., submitted).

Apparently, local ancient lakes with their temporally stable habitats facilitated an endemic radiation of specialized forms in case of *C. possoensis* in Lake Poso and *C. matannensis* and *C. loehensis* inhabiting the Malili lakes. The latter two lineages might originate from intralacustrine divergence within (at least temporarily) separated lakes and/or independent colonizations of the Malili system. In contrast, this specific intralacustrine speciation in an ancient lake setting is more unlikely in case of *C. linduensis* (for which riverine localities are also reported here for the first time), because Lindu is not known to fulfill the criteria of being an ancient lake. Nevertheless, the outstanding mode of brooding in *C. linduensis* may indicate rather long isolation.

Exceptional cases for lacustrine speciation and adaptive radiation on Sulawesi are pro-

vided by gastropods of known incidences in Pachychilidae (*Tylomelania*), Ancyliidae (*Protancylus*) and Lymnaeidae (*Miratesta*) (P. Sarasin & F. Sarasin, 1898; Rintelen & Glaubrecht, 1999; Rintelen et al., submitted), and among bivalves also by the evolution of the endemic corbiculid genus *Possostrea* in Lake Poso (Bogan & Bouchet, 1998). On a more subdued scale, such a process that involves the evolution of several adaptations unknown for long in other freshwater congeners seems to have occurred only in *Corbicula sandai* of Lake Biwa. Although not brooding but laying benthic eggs masses with direct developing young, this endemic Japanese corbiculid share certain reproductive features (i.e., the monoflagellate sperm) with taxa endemic to Sulawesi, to which also its sequence data exhibit a certain affinity.

CONCLUSION

As shown in the present study, peculiarities of shell morphology, anatomy, sperm morphology and the brooding process, as well as available molecular data support the presence of several endemic *Corbicula* taxa on Sumatra (*C. moltkiana*) and particularly on Sulawesi (*C. linduensis*, *C. possoensis*, *C. matannensis* and *C. loehensis*). These taxa apparently represent relatively old and distinct genetic lineages which show no particularly close relationship to any previously studied *Corbicula* from the Japanese islands, Asian mainland or Australia. In contrast, *C. javanica* that is supposed to be widely distributed across the Sunda Archipelago, appears closely related to a Korean lineage identified as *C. fluminea* within an Asian cluster, and might be a later migrant in this region. Future additional morphological, biological and molecular investigations may provide more decisive information concerning the evolutionary pathways along which *Corbicula* species colonized freshwater habitats in Southeast and Austral-Asia.

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