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Annotated check-list of the South East Asian Phaedusinae, with the description of new taxa (Gastropoda, Pulmonata, Clausiliidae)

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A revised check-list of the Phaedusinae from South East Asia (Himalayan countries, Further India, Malaya and Indo-Australian archipelago) is presented. The changes of the current system are discussed in annotations. The following genus taxa are described as new: *Loosjesia* gen. nov. (type species *Clausilia cambojensis* L. Pfeiffer), *Cylindrophaedusa* (*Montiphaedusa*) subgen. nov. (*Clausilia ioes* Benson), *Dautzenbergiella* (*Mansuyia*) subgen. nov. (*Clausilia mansuyi* Dautzenberg & Fischer), *Hemiphaedusa* (*Dendrophaedusa*) subgen. nov. (*Clausilia lemyrei* Bavay & Dautzenberg), *Juttingia* (*Pseudohemiphaedusa*) subgen. nov. (*Hemiphaedusa excurrens* Loosjes, non Martens). The following species is described as new: *Hemiphaedusa* (*Selenophaedusa*) *bavayi* spec. nov. For *Hemiphaedusa excurrens* Loosjes, non Martens, a replacement name is given: *Juttingia loosjesi* nom. nov.

Key words: Gastropoda, Pulmonata, Clausiliidae, Phaedusinae, taxonomy, new taxa, South East Asia.

INTRODUCTION

After the revision of the Phaedusinae of Taiwan (Nordsieck, 1997), the Japanese Islands (Nordsieck, 1998b) and mainland China (Nordsieck, 2001) a revised list of the Phaedusinae of the remaining Asian countries is presented. The region concerned comprises the Himalayan countries (northernmost Pakistan, Himalayan states of India, Nepal, Sikkim, Bhutan), Burma, Thailand, the Indochinese countries (Vietnam, Laos, Cambodia), the Malay Peninsula and the Indo-Australian archipelago (Indonesia, North Borneo, some Philippine islands). The revision of the Indo-Australian and Malayan species is based on the work of Loosjes (1953, 1963, 1965), that of the Himalayan countries and parts of Burma on my own papers (Nordsieck, 1973, 1974). As regards the Indochinese Phaedusinae all taxa which were described mainly by Mabille (1887), Fischer (1898), Bavay & Dautzenberg (1899a, b, 1900, 1903, 1909, 1912, 1915), Dautzenberg & Fischer (1905, 1908), and Möllendorff (1898, 1901) were examined, the species and their synonyms are listed, and the species are classified. If available, the types of the species taxa were examined. The system used is that of the revision of the Phaedusinae of the Japanese Islands (Nordsieck, 1998b: 23-24) and of mainland China (Nordsieck, 2001: 27-29).

The respective material is in the collections of the following institutions (with abbreviations used): British Museum (Natural History), London [BM(NH)]; Instytut Zoologii Polska Akademia Nauk, Warszawa (IZPAN); Muséum National d'Histoire Naturelle, Paris (MNHN); Nationaal Natuurhistorisch Museum, Leiden (NNM); Senckenberg-Museum, Frankfurt am Main (SMF); Természettudományi Múzeum Állattára, Budapest (TMA); United States National Museum, Washington (USNM); Zoölogisch Museum, Amsterdam (ZMA).

SYSTEMATIC LIST

In the following systematic list all known species of South East Asian Phaedusinae are recorded. Type species are underlined. Names in brackets are regarded as synonyms or subspecies names, if added to a species. The species of which the shell was examined by me are marked with *, those in which also the inner lamellae endings were studied are marked with °. The species which were anatomically examined were listed by Loosjes & Loosjes-van Bemmel (1973) and Nordsieck (1973, 1974); since then no results of anatomical work on South East Asian Phaedusinae have been published. Nomenclatural changes are discussed in Nordsieck (1998a).

Phaedusinae A.J. Wagner, 1922
Megalophaedusini Zilch, 1954:

Oospira Blanford, 1872 (note 1):

Oospira (*Oospira*) (*Pseudonenia* O. Boettger, 1877; *Acrophaedusa* O. Boettger, 1877; *Macrenoica* A. J. Wagner, 1920) (note 1):
abstrusa (Szekeres, 1970)* (note 2); *alticola* (Martens, 1892); *arakana* (Stoliczka, 1872)*; *asaluensis* (Blanford, 1872)*; *blanfordi* H. Nordsieck, 1998° [= *monticola* (Blanford, 1872) non Stabile]; *bolovenica* (Möllendorff, 1898)°; *bouddah* (Bavay & Dautzenberg, 1912)°; *brachyptycta* (Loosjes, 1953)*; *brevior* (L. Pfeiffer, 1868)* [= *abbreviata* (Martens, 1867) non Rossmässler] [*mentaweiensis* (Ehrmann, 1928)]; *bulbus* (Benson, 1863)*; *cornea* (Küster, 1844)°; *coudeini* (Bavay & Dautzenberg, 1899)° (note 2); *decollata* (Likharev, 1962)°; *dextrogyra* (Bavay & Dautzenberg, 1909)*; *eregia* (Szekeres, 1969)* (note 2); *ferruginea* (Blanford, 1872)*; *fornicata* (Loosjes, 1963); *fruhstorferi* (Möllendorff, 1897)*; *fusiformis* (Blanford, 1865)*; *gouldiana* (L. Pfeiffer, 1857)*; *gracilenta* (Loosjes, 1953); *insignis* (Gould, 1844)° [*gracilior* (Hanley & Theobald, 1870) non Mousson]; *jacobsoni* (Loosjes, 1953)° (note 2); *javana* (L. Pfeiffer, 1841)°; *johorensis* (Tomlin, 1939); *junghuhni* (Küster, 1844)*; *loosjesi* (Zilch, 1954)*; *loosjesiana* (Ray & Roychoudhuri, 1968)*; *loxostoma* (Benson, 1836)°; *mairei* (Bavay & Dautzenberg, 1909)°; *malaisei* H. Nordsieck, 1973*; *miranda* (Loosjes & Loosjes-van Bemmel, 1973)* (note 2); *nubigena* (Möllendorff, 1897)*; *ovata* (Blanford, 1872)*; *orientalis* (L. Pfeiffer, 1842)*; *penangensis* (Stoliczka, 1873)°; *philippiana* (L. Pfeiffer, 1847)°; *salacana* (O. Boettger, 1890)* [*aenigmatica* (Sykes, 1893)]; *scalariformis* (Loosjes, 1953); *schepmani* (Möllendorff, 1897)*; *semipolita* (Bavay & Dautzenberg, 1899)° (*mansonensis* (Möllendorff, 1901)*, *flaveola* (Bavay & Dautzenberg, 1915)*); *stoliczkana* (Sykes, 1893)*; *suluana* (Möllendorff, 1894)*; *sumatrana* (Martens, 1864)*; *thrausta* (Loosjes, 1953)*; *vanbuensis* (Bavay & Dautzenberg, 1899)° [*pocsi* (Szekeres, 1969)*, *umbratica* (Szekeres, 1970)*] (note 2); *vespa* (Gould, 1859)*; *wuellerstorfi* (Zelebor, 1867)*.

Oospira (*Siphonophaedusa*) Lindholm, 1924 (note 3):
grangeri (Bavay & Dautzenberg, 1899)°.

Oospira (*Atractophaedusa*) Ehrmann, 1927 (note 3):
kebavica (Möllendorff, 1901)*; *pyknosoma* Gittenberger & Vermeulen, 2001°; *rhopaloides* (Möllendorff, 1901)°.

Juttingia Loosjes, 1965 (note 4):

Juttingia (*Juttingia*):
fucosa (Loosjes, 1963)°; *schlueteri* (O. Boettger, 1879)*.

Juttingia (*Pseudohemiphaedusa*) subgen. nov. (note 5):
?*excurrens* (Martens, 1864); *loosjesi* nom. nov.*.

Lindholmiella Ehrmann, 1927 (note 4):
aciculata (Bavay & Dautzenberg, 1909)*.

Loosjesia gen. nov. (note 4, 6):
cambojensis (L. Pfeiffer, 1861)°.

Liparophaedusa Lindholm, 1924 (note 4):
auregani (Bavay & Dautzenberg, 1903)°; *freyi* (Bavay & Dautzenberg, 1899)*; *pseudauregani* (Dautzenberg & Fischer, 1908)*; *ruminiformis* (Mabille, 1887)°.

Dautzenbergiella Lindholm, 1924 (note 4, 7):

Dautzenbergiella (*Dautzenbergiella*):
duella (Mabille, 1887)° (*grangeri* sensu Möllendorff, 1901*).

Dautzenbergiella (*Mansuyia*) subgen. nov.:
mansuyi (Dautzenberg & Fischer, 1908)°.

Leptacme Ehrmann, 1927 (note 4):
sykesi (Bavay & Dautzenberg, 1899)°.

Cylindrophaedusa O. Boettger, 1877 (note 4, 8):

Cylindrophaedusa (*Montiphaedusa*) subgen. nov.:
annandalei (Preston, 1915)*; *bacillum* (Hanley & Theobald, 1870)°; *farooqi* (Auffenberg & Fakhri, 1995)*; *ioes* (Benson, 1852)°; *kathmandica* (H. Nordsieck, 1973)°; *martensiana* (H. Nordsieck, 1973)°; *waageni* (Stoliczka, 1872)*.

Cylindrophaedusa (*Cylindrophaedusa*):
cylindrica (L. Pfeiffer, 1846)° (*turritella* (G. Sowerby II, 1875)).

Hemiphaedusa O. Boettger, 1877 (note 9):

Hemiphaedusa (*Synprosphyma*) A. J. Wagner, 1920:

suilla group:
acrostoma (Bavay & Dautzenberg, 1909)° (*rudis* (A. J. Wagner, 1922)*); *auricoma* (Bavay & Dautzenberg, 1899)*; *babeensis* (Bavay & Dautzenberg, 1899)*; *cervicalis* (Bavay & Dautzenberg, 1909)*; *fistulata* (Bavay & Dautzenberg, 1909)*; *gastrodes* (Möllendorff, 1901)°; *gastrum* (Möllendorff, 1901)*; *moirati* (Bavay & Dautzenberg, 1909)*; *suilla* (Bavay & Dautzenberg, 1909)°.

Hemiphaedusa (*Selenophaedusa*) Lindholm, 1924:

porphyrostoma group:
callistoma (Bavay & Dautzenberg, 1899)*; *chiemhoaensis* (Sykes, 1902)* (*lavillei* (Dautzenberg & Fischer, 1905)*); *ophthalmophana* (Mabille, 1887)° (*cazioti* (Bavay & Dautzenberg, 1909)*); *porphyrostoma* (Bavay & Dautzenberg, 1909)°; *thatkheana* (Bavay & Dautzenberg, 1899)°.

diplochilus group:
diplochilus (Möllendorff, 1901)°.

billeti group:
bavayi spec. nov.°; *billeti* (Fischer, 1898)° (*falcifera* (Bavay & Dautzenberg, 1899)*, *callistomella* (Bavay & Dautzenberg, 1900)*).

Hemiphaedusa (*Dendrophaedusa*) subgen. nov.:
lemyrei (Bavay & Dautzenberg, 1899)°.

Hemiphaedusa (*Notoptychia*) Ehrmann, 1927:
polydona (Mabille, 1887)° (*gisota* (Bavay & Dautzenberg, 1899)*, *falciformis* sensu Möllendorff, 1901*).

Hemiphaedusa (*Margaritiphaedusa*) H. Nordsieck, 2001:
margaritifera (Bavay & Dautzenberg, 1909)°.

Phaedusini:

Phaedusa H. & A. Adams, 1855:

Phaedusa (*Phaedusa*) (*Calcariclavis* Lindholm, 1924):
angkanensis (Loosjes, 1950)° (note 10); *bhutanensis* H. Nordsieck, 1974*; *borneensis* (L. Pfeiffer, 1854)*; *burmanica* (Gude, 1914)*; *ceylanica* (Benson, 1863)*; *cochinchinensis* (L. Pfeiffer, 1841)*; *corticina* (L. Pfeiffer, 1842)°; *dichroa* (Bavay & Dautzenberg, 1899)* (*duporti* (Bavay & Dautzenberg, 1915)*); *dorsoplicata* Loosjes, 1953; *eupleura* (Bavay & Dautzenberg, 1899)*; *filialis* (Martens, 1903) (note 10); *filicostata* (Stoliczka, 1873)° (*lucens* Loosjes, 1953*) (note 10); *inanis* (Bavay & Dautzenberg, 1909)°; *kelantanensis* (Sykes, 1902)* (note 10); *?lemani* (Gude, 1914); *lypra* (Mabille, 1887)° [*houssayi* (Fischer, 1898)*, *backanensis* (Bavay & Dautzenberg, 1899)*, *hamonvillei* (Bavay & Dautzenberg, 1899)*]; *pahangensis* Laidlaw, 1929* (note 10); *paviei* (Morlet, 1892)°; *phongthoensis* Loosjes & Loosjes-van Bemmel, 1949*; *shanica* (Godwin-Austen, 1888)*; *stenothyra* Möllendorff, 1901*; *stenotrema* Thompson & Dance, 1983*; *theobaldi* (Blanford, 1872)°; *theristica* (Mabille, 1887)° [*vatheleti* (Bavay & Dautzenberg, 1899)*, *gereti* (Bavay & Dautzenberg, 1900)*].

Renschiphaedusa Loosjes & Loosjes-van Bemmel, 1973 (note 11):
cumingiana (L. Pfeiffer, 1845)*; *moluccensis* (Martens, 1864)°; *recondita* (Sykes, 1894)*.

Paraphaedusa O. Boettger, 1899 (note 11):
bonthainensis (P. & F. Sarasin, 1899); *celebensis* (E. A. Smith, 1896)*; *makassarensis* (Sykes, 1897)° (*pyrrha* (Sykes, 1897)); *minahassae* (P. & F. Sarasin, 1899); *schwaneri* (Martens, 1867)*; *subpolita* (E. A. Smith, 1896)°; *usitata* (E. A. Smith, 1896)*.

NOTES

Note 1. *Pseudonenia* (+ *Oospira*) and *Acrophaedusa* sensu Loosjes (1953) are united as *Oospira* (Nordsieck, 1973: 66-67, 78-80) because their differences in shell shape and colour and some features of the aperture (cf. Loosjes, 1965: 32) are of little taxonomic value. All species with a steeply ascending inferior lamella and normal (narrow) clausilium plate, the lunellar of which consists of plicae without or with only a slight tendency to develop a lunella, are classified with this genus (Nordsieck, 1997: 13; 2001: 29, 32).

Note 2. *Euphaedusa abstrusa* Szekeres (1970: 81, figs 3-4) (paratype, TMA) has a steeply ascending inferior lamella and distinct palatal plicae and is therefore classified with *Oospira*. Until now, no species of *Euphaedusa* has been found south of China.

The same applies to *Leptacme eregia* Szekeres (1969: 314, figs 2-4) (holotype, colln. Szekeres). Because of the development of the lunellar (lowest palatal plica not connected with the lower one) classification with *Leptacme* is out of the question, as it is for other dextral species of *Oospira* (e. g. *O. dextrogyra*).

Formosana (*Dextroformosana*) *miranda* Loosjes & Loosjes-van Bemmel (1973: 292-295, figs 3-4, pl. 1 figs 1-6) (paratypes, IZPAN) is classified with *O.* (*Oospira*) because the parietal (inner) part of its subcolumellar lamella is fully developed. The same is the case in *Clausilia coudeini* Bavay & Dautzenberg (lectotype, MNHN) which was taken for a *Formosana* species by Ehrmann (1927: 10-11). Until now, no species which should be placed in *O.* (*Formosana*) O. Boettger was found in the Indochinese countries. *Formosana* species with fully developed inner part of the subcolumellar lamella which occur in mainland China and Taiwan are classified with this subgenus because they are closely related to species with reduced inner part (Nordsieck, 2001: 32).

Pseudonenia jacobsoni Loosjes (1953: 100-103, fig. 28) (paratypes, NNM) from the island of Simalur = Simeulue has an inferior lamella and a clausilium plate like the Phaedusini and could therefore be classified with this tribe if its appearance and lunellar would not correspond with that of *Oospira*. It is the question if this species is ovoviviparous like the Phaedusini.

Phaedusa pocsi Szekeres (1969: 313, fig. 1) and *P. umbratica* Szekeres (1970: 81, figs 1-2) (paratypes, TMA) belong to one and the same species and can at best be separated as subspecies. This species, however, is not identical with *Phaedusa paviei*, as Loosjes & Loosjes-van Bemmel (1973: 296-298, fig. 6) meant, but belongs to *O.* (*Oospira*) and has already been described as *Clausilia vanbuensis* Bavay & Dautzenberg (1899a: 38, pl. 2 fig. 1) (lectotype, MNHN). This species which was collected by Bavay near Van Bu, Tonkin, was later on also confounded with *P. paviei* by its authors (Bavay & Dautzenberg, 1909: 84). It differs from *P. paviei* by the development of the inferior lamella (more steeply ascending), the lunellar (plicae more distinct) and the clausilium plate (narrower).

Note 3. *Siphonophaedusa* and *Atractophaedusa* which were affiliated to *Liparophaedusa* by Ehrmann (1927: 17, 23-24) have, contrary to that genus, a lunellar with only a minor tendency to develop a lunella and thus correspond with *Oospira*. Therefore, these are considered subgenera of this genus.

Note 4. *Juttingia* (Loosjes, 1965: 34-35), *Lindholmiella* (Ehrmann, 1927: 25), *Loosjesia* gen. nov. (see note 6), *Liparophaedusa* (Ehrmann, 1927: 22-23), *Dautzenbergiella* (Ehrmann, 1927: 24), *Leptacme* (Ehrmann, 1927: 9-10) and *Cylindrophaedusa* as defined in this paper (Nordsieck, 1973: 64-66, see note 8) have a lunellar with a tendency to develop a lunella,

each in a different manner. Therefore, they are regarded as independent genera, just like the respective oospiroid groups from China (cf. Nordsieck, 2001: 29, 33).

Note 5. The species which was identified by Loosjes (1953: 182-185, 194-195, fig. 55) as *Hemiphaedusa excurrens* (NNM) does neither belong to *Hemiphaedusa* nor is it identical with *Clausilia excurrens* Martens. Its lunellar differs from that of all *Hemiphaedusa* groups; it consists of an upper palatal plica and an oblique lower one, with a weakly developed lunella in between. This lunellar is similar to that of the genus *Juttingia* from the same region, except that the middle palatal plicae are replaced by a lunella. This lunellar may have originated from an ancestral state as in *Juttingia*, comparable to the changes in other groups in which plicae are replaced by a lunella (see note 4). It should be added that until now no *Hemiphaedusa* species has been found south of Tonkin, Vietnam.

The description and figures of *Clausilia excurrens* (Martens, 1867: 378, text-fig. 2, 384, pl. 22 fig. 16) in several essential features contradict the results of the examination of Loosjes' species so that without doubt the latter is a different species for which a new name is proposed. For this species a new subgenus of *Juttingia* is erected.

Note 6. *Clausilia cambojensis* which was described from Cambodia [syntypes, BM(NH)] and recently rediscovered in S.E. Thailand by Brandt (SMF) was classified by Loosjes (1948: 1) and Loosjes & Loosjes-van Bemmel (1973: 291) with *Formosana* and by Szekeres (1969: 314) with *Pseudonenia*. A thorough investigation of the genital apparatus (Nordsieck, 1973: 77-80, fig. 22) made clear that the species differs from both groups and has an isolated systematic position. The proposed classification with *Phaedusa*, however, was premature, because it is not supported by the shell characters. The examination of the clausiliar had the result that *C. cambojensis* is similar to *Liparophaedusa* and other groups from Vietnam. It belongs to those oospiroid groups which differ from *Oospira* by the tendency to develop a lunella (see note 4); in this respect, too, classification with *Formosana* or *Pseudonenia* is not tenable. Therefore, for *C. cambojensis* a new genus is erected.

Note 7. *Dautzenbergiella* (Ehrmann, 1927: 24-25) is that oospiroid group in which the most perfect lunella is developed. This is especially true for *Clausilia mansuyi* Dautzenberg & Fischer (1908: 188, pl. 6, figs 1-3) (syntypes, MNHN) which has a perfect lunella comparable to that of the hemiphaedusoid groups. Because this species differs from the type species *D. duella* in several further characters a new subgenus is erected for *C. mansuyi*.

Note 8. The species from the Himalayan countries and westernmost Burma which were formerly classified with *Hemiphaedusa* (Nordsieck, 1973: 64-66) also represent one of the oospiroid groups which are separated from *Oospira* by the tendency to develop a lunella (see note 4). *Clausilia cylindrica* for which O. Boettger (1877: 64) has erected the section *Cylindrophaedusa* belongs also to this group. Therefore, the group from the Himalayan countries is regarded as the genus *Cylindrophaedusa*. Because the type species differs considerably from the other species (*ioes* group, Nordsieck, 1973) these are separated in a new subgenus of this genus.

Note 9. The genus *Hemiphaedusa* comprises all species with steeply ascending inferior lamella and normally developed (narrow) clausilium plate which have a completely developed lunella, i. e. a lunella in which the plicae from which it originated are no lon-

ger recognizable (Nordsieck, 1998: 24, 2001: 29, 32). The subgenera of this genus differ mainly by the development of the lunellar. A new subgenus is erected for *Clausilia lemyrei* Bavay & Dautzenberg (1899b: 275, pl. 12 fig. 1) (lectotype, MNHN).

Note 10. *Phaedusa* (*Euphaedusa*) *aculus angkanensis* Loosjes (1950: 544-545, fig. 53) from N. W. Thailand (paratypes, USNM) is a separate species which is classified with *Phaedusa*. It differs from *Euphaedusa aculus* (Benson) by the shell colour (greenish-white), the development of the inner lamellae endings (spiral lamella penetrating less deeply than inferior lamella) and the lunellar (more deeply situated, with ± distinct palatal plicae). Until now, no *Euphaedusa* species has been found south of China (see note 2).

The examination of an extensive material of *Phaedusa filicostata* from the Malay Peninsula (coll. Hemmen) showed that the delimitation and subdivision of the species as proposed by Loosjes (1953: 38-53) cannot be maintained. *P. filialis* (Loosjes, 1953: 50-53, fig. 13) from E. Borneo is separated from *P. filicostata* because it differs by the shell shape and the development of the lunellar; this judgement is supported by the occurrence of *P. filialis* far from the range of *P. filicostata*. On the contrary, *P. lucens* (Loosjes, 1953: 35-37, fig. 8) (paratypes, NNM) from Mount Charas is connected with *P. filicostata* via the form from Mount Panching of the same region and is therefore regarded as a subspecies of this species. *P. filicostata tenuicosta* sensu Loosjes (1953: 42-43) comprises forms of several subspecies, among them the nominate subspecies to which *Clausilia filicostata* var. *tenuicosta* of former authors belongs. *P. pahangensis* (Loosjes, 1953: 33-35, fig. 7) from the Cameron Highlands does not much differ from *P. filicostata* and may also be a subspecies of this species. The differences between *P. kelantanensis* (Loosjes, 1953: 53-56, fig. 14) and *P. filicostata* are also slight, but both occur sympatrically without transitions at several places in Kelantan and Pahang so that the species rank of *P. kelantanensis* is out of question.

Note 11. The group of *Clausilia cumingiana* which was classified by Loosjes (1953: 105) with *Euphaedusa* and later on separated by Loosjes & Loosjes-van Bemmel (1973: 309) as the subgenus *Renschiphaedusa* differs from *Euphaedusa* by the development of the lunellar (middle palatal plicae absent, occasionally an indistinct lunella present). Also, the genital morphology and the distribution of *Renschiphaedusa* speak against classification with *Euphaedusa*. The genital apparatus (Loosjes & Loosjes-van Bemmel, 1973: 300-301, fig. 9) is characterized by its strikingly small male end ducts which look immature. As to the distribution, until now no *Euphaedusa* species has been found south of China (see notes 2, 10). *Renschiphaedusa* corresponds in the development of the lunellar to *Paraphaedusa* most species of which are distributed within the range of *Renschiphaedusa*. *Paraphaedusa* differs from *Renschiphaedusa* by the absence of sutural papillae and the development of the inferior lamella (becoming high in the interior of the body whorl). *Renschiphaedusa* is therefore placed as a genus of its own near *Paraphaedusa*.

The *cumingiana* group was regarded by Loosjes (1953: 105-122) as a single species *E. cumingiana* (L. Pfeiffer), with four subspecies, *E. c. cumingiana*, *E. c. moluccensis* (Martens), *E. c. simillima* (E. A. Smith), and *E. c. recondita* (Sykes). The examination of these taxa (SMF) shows that they have different rank. While *E. c. moluccensis* and *E. c. simillima* agree largely in shell characters, *E. c. cumingiana* and *E. c. recondita* differ from both by the indistinct sutural papillae, and *E. c. recondita* from the other taxa by the development of the inferior lamella (ascending with a ± stronger spiral). The taxa are therefore regarded as three species, *R. cumingiana*, *R. moluccensis* and *R. recondita*. This judgement is supported by the distribution in fairly separate areas: *R. cumingiana* occurs in Siquijor, Philippine Islands, *R. moluccensis* is distributed in Sulawesi and the Moluccas (and in E. Java, if autochthonous), and *R. recondita* in the lesser Sunda Islands.

SYSTEMATIC DESCRIPTIONS

New genus taxa

Juttingia Loosjes, 1965.

The genus is characterized in comparison with *Oospira* as follows: Lunellar consisting of 2-3 (normal) palatal plicae and an obliquely situated lower palatal plica, separated from or connected with the next middle palatal plica.

The type species, *J. fucosa*, was collected in Tamandjaja, westernmost Java (paratypes, NNM). *J. schlueteri* the type locality of which is unknown has recently been found at Mount Tanggamus, southernmost Sumatra; this form (coll. Hemmen) differs only slightly from the holotype (SMF).

Juttingia (Pseudohemiphaedusa) subgen. nov.

Type species. – *Hemiphaedusa excurrens* sensu Loosjes, 1953 = *J. loosjesi* nom. nov.

Diagnosis. – Lunellar consisting of an upper (normal) palatal plica and an obliquely situated lower palatal plica, with weakly developed lunella in between.

Etymology. – Combined from Gr. pseudo- = wrong and *Hemiphaedusa*.

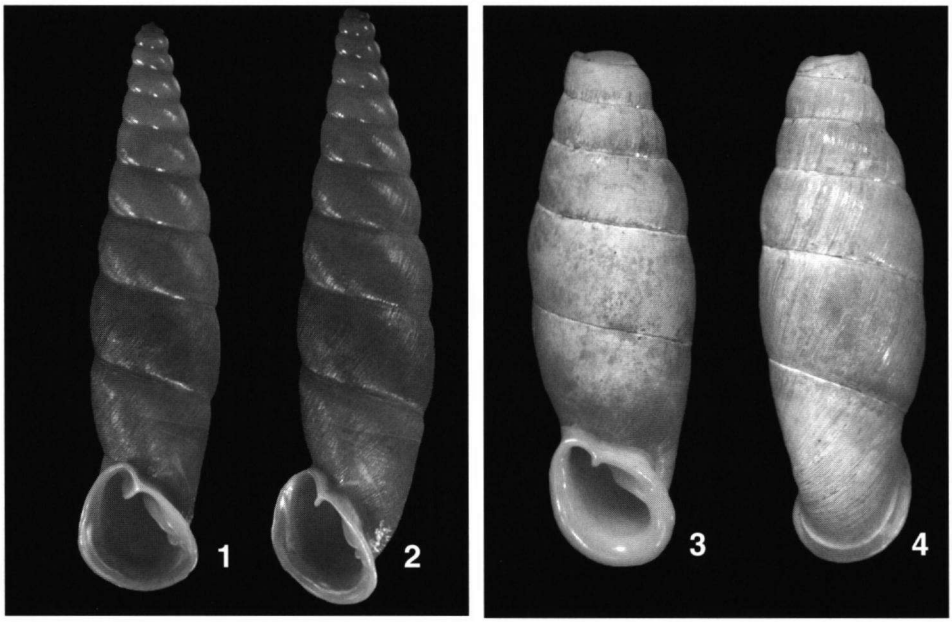
Notes. – The type species which was collected in Pagaralam near Lahat, southern Sumatra, must be given a new name, because it is without doubt another species than *Clausilia excurrens* Martens from Kepahiang in the same region. It differs from this species not only in shell colour (reddish-brown) and the development of the lamellae (superior lamella continuous with spiral lamella; subcolumellar lamella emerging), but also, which was overlooked by Loosjes (1953: 184), in the development of the lunellar. *C. excurrens* has, according to the figure of Martens (1867: 378, text-fig. 2), a lunellar which consists of an upper palatal plica and an obliquely situated lunella, thus being more similar to that of *J. (Juttingia)*. Since type material is not available, the position of this species cannot be specified until it has been rediscovered. The specimen which was figured by Loosjes (1953: fig. 55) as *Hemiphaedusa excurrens* (ZMA) is designated as holotype of ***J. loosjesi*** nom. nov.

Loosjesia gen. nov.

Type species. – *Clausilia cambojensis* L. Pfeiffer, 1861 (figs 1-2).

Diagnosis. – Shell: Partly decollated; superior lamella continuous with spiral lamella; inferior lamella spirally ascending, low in front, in the interior edge turned up (forming a sack-like structure); lunellar deeply situated, consisting of three (normal) palatal plicae and an obliquely situated lower palatal plica, middle palatal plica next to the lower one short or missing, lower palatal plica connected with this reduced palatal plica or, if this is absent, with the next (normal) palatal plica; clausilium plate relatively broad, with calcar; inner lamellae endings as in *Oospira*, inner part of subcolumellar lamella present. Genital apparatus (Loosjes & Loosjes-van Bemmel, 1973: 292, fig. 2; Nordsieck, 1973: 78-79, fig. 22): Vagina short; most proximal part (= end part) of penis missing, distal part of penis and distal part of epiphallus thick, the latter longer than proximal part.

Etymology. – Named after F. E. Loosjes (1913-1994) who gave valuable information on the shell and genital morphology of the type species.



Figs 1-2. *Loosjesia cambojensis* (L. Pfeiffer, 1861), Thailand, Chanthaburi, Kao Sabab; Brandt leg. (SMF 264421a); H 28.8 mm, W 6.6 mm. 1, front view; 2, view on lunellar.
Figs 3-4. *Dautzenbergiella* (*Mansuyia*) *mansuyi* (Dautzenberg & Fischer, 1908), Vietnam, Tonkin, Quang Huyen Mansuy leg. (syntype, MNHN); H 23.45 mm, W 7.8 mm. 3, front view; 4, view on lunellar.

Note. – The shell of *L. cambojensis* is provided with a clausilium plate with calcar and a correspondingly modified inferior lamella (cf. Loosjes, 1948: figs 1-4). This character complex has also been found in other non-related Phaedusinae species (*Oospira* (*O.*) *vanbuensis*, *O.* (*Formosana*) *longispina* (Heude), *Hemiphaedusa* (*Margaritiphaedusa*) *hensaniensis* (Gredler), *Tyrannophaedusa* (*T.*) *nankaidoensis* Kuroda, *Phaedusa* (*P.*) *paviei*, *P.* (*P.*) *potanini* Möllendorff, cf. Nordsieck, 2001: 29); it has obviously evolved more than once. Possibly, it prevents predators from intruding into the shell via the aperture.

Dautzenbergiella Lindholm, 1924

The genus is characterized in comparison with *Oospira* as follows: Shell decollated; lunellar consisting of three (normal) palatal plicae, a lunella and an obliquely situated lower palatal plica, lunella connected with the (normal) lower palatal plica (= anterior lower palatal plica) and the obliquely situated one (= posterior lower palatal plica); 1-3 anterior upper palatal plicae present, separated from the main palatal plicae.

The characters of the nominate subgenus, including only the type species, are the following: Superior lamella continuous with spiral lamella; spiral lamella and principal plica forming a respiratory tube; subcolumellar lamella emerging; lunella short, connected only with anterior and posterior lower palatal plicae; generally two ore more anterior upper palatal plicae present; inner part of subcolumellar lamella present.

Dautzenbergiella (Mansuyia) subgen. nov.

Type species. – *Clausilia mansuyi* Dautzenberg & Fischer, 1908 (figs 3-4).

Diagnosis. – Superior lamella separated from spiral lamella; spiral lamella and principal plica normally developed (not forming a respiratory tube); subcolumellar lamella immersed; middle (normal) palatal plica continuous with lunella, without anterior part, anterior lower palatal plica deep in position; only one anterior upper palatal plica present; clausilium plate with a distal process at the columellar side; inner part of subcolumellar lamella short.

Etymology. – Named after H. Mansuy who collected the type species (cf. Dautzenberg & Fischer, 1908).

Note. – The anterior lower palatal plica of *D. mansuyi* is situated so deeply that it can be confused with the subcolumellar lamella; the latter is not even visible from outside in oblique view. The comparison of both subgenera shows that the clausiliar of *D. (Mansuyia)* is more derived in all its characters.

Cylindrophaedusa O. Boettger, 1877

The genus is in comparison with *Oospira* characterized as follows: Lunellar consisting of upper palatal plica and lower one, middle palatal plicae ± united by a lunella or missing.

The type species, *Clausilia cylindrica*, differs considerably from the other species of the genus by shell characters as follows (Nordsieck, 1973: 66): Shell decollated; lunellar consisting only of two palatal plicae, lower one shorter, relatively high in position. The species is more farly distributed than other species; it is also the only species which was collected together with other species of the genus at the same place (Murree, with *C. waageni*, cf. Gude, 1914: 338; Darjeeling, with *C. ioes*, SMF). The remaining species (*ioes* group, Nordsieck, 1973: 64-66, figs 2-11) are therefore separated as a new subgenus.

Cylindrophaedusa (Montiphaedusa) subgen. nov.

Type species. – *Clausilia ioes* Benson, 1852.

Diagnosis. – Shell not decollated; lunellar consisting of upper palatal plica and lower one, several short middle palatal plicae ± united to a lunella or only lunella in between, lower palatal plica occasionally ± reduced, upper one occasionally elongated forward.

Etymology. – Combined from Lat. *mons* = mountain and *Phaedusa*.

Notes. – The species of the new subgenus are distributed in the Himalayan countries as follows: *C. farooqi* and *C. waageni* in N.Pakistan, *C. martensiana* and *C. kathmandica* in Nepal, *C. ioes* in Nepal, Sikkim (with Darjeeling), Bhutan and Arunachal Pradesh, *C. annandalei* in Arunachal Pradesh, and *C. bacillum* in some autonomous regions of India, Assam, and the neighbouring part of Burma. In the collection of Godwin-Austen [BM(NH)] further undescribed species from India, Assam, were found (Nordsieck, unpubl.).

Hemiphaedusa O. Boettger, 1877

Hemiphaedusa (Synprosphyma) A. J. Wagner, 1920

This subgenus was newly diagnosed by Nordsieck (2001: 34). All Tonkinese species belong to the group of the type species which is characterized in comparison with the

Chinese species groups as follows:

suilla group: With anterior and posterior lower palatal plicae; inner part of subcolumellar lamella present.

Hemiphaedusa (Selenophaedusa) Lindholm, 1924

In comparison with the other subgenera this subgenus is characterized as follows:

Without neck keel; upper palatal plica continuous with lunella, anterior and posterior lower palatal plicae present; spiral lamella penetrating more deeply than or as far as inferior lamella, inner part of subcolumellar lamella present to reduced.

The Tonkinese species of the subgenus are not as uniform as those of *Synprosphyma*. The following groups are distinguished:

porphyrostoma group: Shell not decollated; anterior lower palatal plica continuous with posterior one and separated from lunella; inner part of subcolumellar lamella present.

diplochilus group: Shell decollated; lower palatal plicae connected with lunella; inner part of subcolumellar lamella present.

billeti group: Shell smaller than that of the other groups, not decollated; anterior lower palatal plica connected with lunella, posterior one connected with or separated from lunella; inner part of subcolumellar lamella present to reduced.

Hemiphaedusa (Dendrophaedusa) subgen. nov.

Type species. – *Clausilia lemyrei* Bavay & Dautzenberg, 1899 (figs 5-6).

Diagnosis. – Shell decollated, without neck keel; peristome adnate; inferior lamella receding, with curved lamella on its upper side; upper palatal plica continuous with lunella, anterior lower palatal plica missing, posterior one connected with lunella; clausilium plate relatively broad, triangular, with lamella on the outside.

Etymology. – Combined from Gr. *dendros* = tree, because of the robust appearance, and *Phaedusa*.

Hemiphaedusa (Notoptychia) Ehrmann, 1927.

This subgenus was diagnosed by Ehrmann (1927: 20-21). The lunellar consists of upper palatal plica and anterior lower palatal plica, a weakly developed lunella in between; clausilium plate distally with a curved tip.

Hemiphaedusa (Margaritiphaedusa) H. Nordsieck, 2001.

This subgenus was diagnosed by Nordsieck (2001: 34).

New species

Hemiphaedusa (Selenophaedusa) bavayi spec. nov. (figs 7-8)

Material. – Holotype (SMF 30332): Vietnam, Tonkin, Pac Kha, leg. Messager, ex coll. Ehrmann ex Preston; paratypes (SMF 62176/2, 85415/1): same data, ex coll. Dautzenberg, ex coll. Käufel, ex Dautzenberg, respectively; paratypes (MNHN/9): Bac Kan, leg. Messager, ex coll. Denis and coll. Letellier. Further material with the localities Bac Kan, That Khé and Muong Kang, leg. Messager (SMF, MNHN, IZPAN).

Figs 5-6. *Hemiphaedusa* (*Dendrophaedusa*) *lemyrei* (Bavay & Dautzenberg, 1899), Vietnam, Tonkin, Than Moi; Fruhstorfer leg. (SMF 30343a); H 25.35 mm, W 7.3 mm. 5, front view; 6, view on lunellar.

Diagnosis. – A *Selenophaedusa* species with small shining shell with both lower palatal plicae clearly connected with the lunella.

Description. – Shell with a conical or somewhat attenuated apical part; yellowish-brown; teleoconch whorls indistinctly rib-striated, shining, sculpture on the neck scarcely coarser; neck rounded, basal keel indistinct or missing, peristome indistinctly doubled; aperture oval or piriform, detached, peristome (inner lip) somewhat thickened; superior lamella continuous with spiral lamella, lamellae at the connection ± lowered, spiral lamella relatively high; inferior lamella medium in position, steeply ± s-like ascending, ± high inwards, in front with an indistinct thickening, ± continued on the columellar edge to the peristome, occasionally also across the columellar edge, thus indistinctly forked; subcolumellar lamella emerging to the lip edge, in an oblique view in the aperture visible far inwards, occasionally a further peristome fold developed; lunellar nearly dorsally situated, occasionally more dorsolaterally, principal plica ending nearly laterally or laterally; upper palatal plica continuous with lunella by a wide curve, lunella connected with both lower palatal plicae, posterior lower palatal plica short to nearly missing, anterior one differently long; clausilium plate in an oblique view in the aperture visible, rarely only partly, distally somewhat pointed.

Spiral lamella penetrating less deeply than or as far as inferior lamella, subcolumellar lamella penetrating less deeply than spiral lamella, inner part short to very short (three specimens examined).

Measurements. – Holotype: Shell height = H 15.7 mm, shell width = W 3.5 mm, W/H 0.223, aperture height 3.6 mm, aperture width 2.6 mm; whorls 10¼ Paratypes: Pac Kha: H / W: 13.9 / 3.5; 14.6 / 3.35; 14.8 / 3.4 mm; whorls 9½-10¼ Paratypes Bac Kan: H / W: 13.4 / 3.4; 13.9 / 3.9; 14.3 / 3.5; 14.3 / 3.6; 14.6 / 3.4; 14.7 / 3.4; 14.9 / 3.5; 14.9 / 3.5; 16.9 / 4.0 mm; whorls 9-10¼

Etymology. – Named after A. Bavay, who described, together with P. Dautzenberg, most known Tonkinese clausiliid species.

Notes. – The samples of the new species which all were collected by Messager were determined by Bavay & Dautzenberg as *Clausilia falcifera* or *C. callistomella* and thus confused with *C. billeti* H. Fischer (1898: 15, pl. 18, figs 28-31) (syntype, MNHN). This species was described once more by Bavay & Dautzenberg as *C. falcifera* (1899b: 290, pl. 12 fig. 10) (lectotype, MNHN) and *C. callistomella* (1900: 446, pl. 10 fig. 7) (lectotype, MNHN).

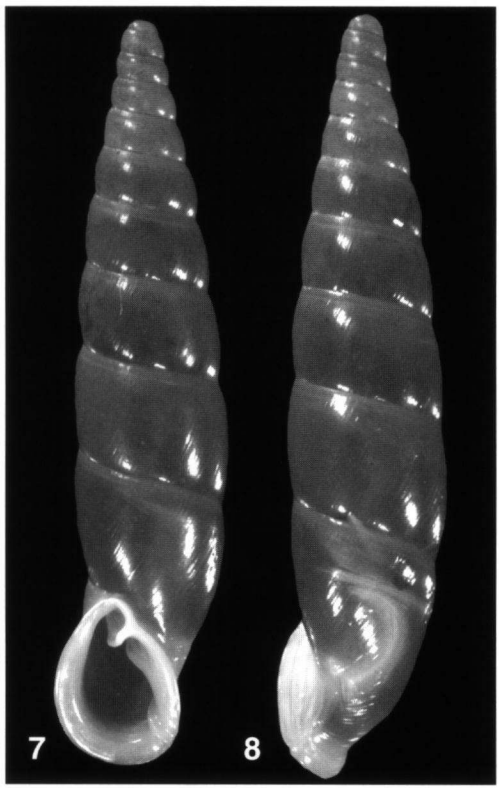
Hemiphaedusa billeti differs from *H. bavayi* spec. nov. by the following characters: Neck sculpture coarser; inferior lamella more straightly (not s-like) ascending; upper palatal plica continuous with lunella ± by an angle, anterior lower palatal plica short or nearly missing, posterior one ± connected with or separated from lunella; inner part of subcolumellar lamella fully developed to short. As is proved by mixed samples both species were collected by Messager in Bac Kan and That Khé; in these samples they can easily be distinguished by an examination of the lunellar.

DISTRIBUTION AND PHYLOGENY OF THE PHAEDUSINAE

The overall preliminary revision of the Phaedusinae enables me to make some concluding remarks on the distribution and phylogeny of the Phaedusinae.

Because the centre of origin of the Clausiliidae may be in the western Palaearctic (cf. Nordsieck, 1986: 98, fig. 4) the Phaedusinae may have originated from a group which in the Upper Cretaceous spread along the southern margin of pre-collision Asia to eastern Laurasia. The absence of clausiliids in the former parts of Gondwana (Indian subcontinent, Australia with New Guinea) speaks in favour of this dispersal route. The occurrences of Phaedusinae species in Sri Lanka (*Phaedusa ceylanica*) and western New Guinea (*Paraphaedusa minahassae*) may be secondary. The species from Sri Lanka is so similar to species from Burma that an origin from there by air transport (wind, birds?) is probable. The species from New Guinea is according to Loosjes (1956: 227-229) the same which occurs in Sulawesi.

The dispersal of the Phaedusinae in S.E. Asia continued eastwards to the eastern Indo-Australian islands and northwards to South Korea and northern Japan. The Philippine Islands were only reached at the northern end by some species of *Zaptyx* Pilsbry (cf. Loosjes, 1950), on a minor island by a *Renschiphaedusa* species and at the southern end by an *Oospira* species (cf. Loosjes, 1953). The connection of the Phaedusinae range with that of the western Palaearctic Clausiliidae which existed in the region of present-day Iran and Afghanistan was probably interrupted by the increasing aridity of this region. The closest relatives of the Phaedusinae (Serrulininae, *Laeviphaedusa* Likharev & Steklov) are still present with several species in the Hyrcanian region of northern Iran (cf. Nordsieck, 1995).



Figs 7-8. *Hemiphaedusa* (*Selenophaedusa*) *bavayi* spec. nov., Vietnam, Tonkin, Pac Kha; Messager leg. (holotype, SMF 30332); H 15.7 mm, W 3.5 mm. 7, front view; 8, view on lunellar.

The stem form of the Phaedusinae may have been close to the genus *Oospira* which has only plesiomorphic characters in the development of the clausiliar (cf. Nordsieck, 1998: 24; 2001: 27). This genus is distributed from Assam in the west to Java and the Sulu Islands in the east and to central China in the north; the genus *Megalophaedusa* O. Boettger which represents *Oospira* in the Japanese Islands reaches Hokkaido in the north. Thus, the distribution of both genera covers nearly the whole of the clausiliid range in Asia. The numerous oospiroid groups with modified plicae-type of the lunellar which are distributed within the range of *Oospira* and partly beyond it (Himalayan countries, *Cylindrophaedusa*, high mountains of Sichuan, *Serriphaedusa* H. Nordsieck) may have originated from different groups of *Oospira* (cf. Nordsieck, 2001: 29, this paper). The same may be true for the hemiphaedusoid groups which by the development of a perfect lunella now have a better closing device for the shell aperture; they are distributed mainly in the subtropical part of the *Oospira-Megalophaedusa* range. From these groups dwarf insular groups (zaptychoid groups) and the G-groups of the Japanese Islands originated (cf. Nordsieck, 1998: 24, 26). All groups which may have evolved from the *Oospira* stem form (oospiroid and hemiphaedusoid groups) are included in the tribe Megalophaedusini.

The remaining groups of the subfamily which are characterized by ovoviviparity and

correlated shell characters (cf. Nordsieck, 1998: 24, 2001: 28) are assembled in the tribe Phaedusini. They may have evolved from a stem form which was close to the genus *Phaedusa* which in the development of the clausiliar has only plesiomorphic characters (except those which are correlated with ovoviviparity). This genus has an extensive distribution which like that of *Oospira* + *Megalophaedusa* covers nearly the whole of the Phaedusinae range. The other groups of the Phaedusini the lunellar of which is only slightly modified (among them also a G-group from the Japanese Islands) are distributed within the range of *Phaedusa* and go beyond it only in the east (Sulawesi, Moluccas, *Renschiphaedusa, Paraphaedusa*) and in the north (South Korea, Hokkaido, *Euphaedusa*).

In central and north-eastern Asia the limit of the clausiliid distribution is marked by the high Himalaya mountains, the high mountains of Sichuan, northern central China, South Korea and Hokkaido. This limit may be caused by climatic stress, aridity and (or) cold winter conditions. Favoured by the warm stream east of the Japanese Islands (Kuroshio) the range of the Phaedusinae in the east extends much further to the north than in the west.

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