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The systematic position of the Garnieria and Triptychia groups, two ambiguous phylogenetic branches of Clausiliidae (Gastropoda Pulmonata)

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Due to the limited amount of available information about the *Garnieria* and *Triptychia* groups, their systematic status has been changed frequently. Based on the similarities revealed by conchological analysis of several species and anatomical examination of *Indionenia ardouiniana*, the *Garnieria* group is now proposed to be classified with the subfamily Neniinae, as the tribus Garnieriini. A re-examination of the shell structure and paleontological records of the *Triptychia* group lead to the conclusion that it represents a subfamily, Triptychiinae, of the Clausiliidae.

Key words: Gastropoda, Clausiliidae, *Garnieria*, *Triptychia*, taxonomy, SE. Asia.

Despite the considerable progress that has been made toward the understanding of phylogenetic relationships between the extant representatives of European Clausiliidae, the systematic status of some non-European or fossil suprageneric taxa remained obscure. By introducing new data and clarifying some controversial points of earlier evaluations, this paper re-assesses the position of some of these little-known groups of Clausiliidae.

THE GARNIERIA GROUP

The *Garnieria* group is an archaic phylogenetic branch of Clausiliidae with about 20 extant species, distributed over a very limited, less than 400,000 km^2 , part of Southeast Asia, delimited by southern Guangxi (China), central Burma and southern Laos. The species of the group belong to the following four genera (listed with their type species): *Garnieria* Bourguignat, 1877 [*G. mouhoti* (L. Pfeiffer, 1862)]; *Indionenia* Ehrmann, 1927 [*I. masoni* (Theobald, 1864)]; *Tropidauchenia* Lindholm, 1924 [*T. bavayi* (Lindholm, 1924)]; *Symptychia* Ehrmann, 1927 [*S. orientalis* (Mabille,1887)].

All members of the group have a characteristic shell, with an apostrophic peristome, that clearly distinguishes them from the rest of Southeast Asian Clausiliidae, belonging to the subfamily Phaedusinae.

Apostrophy refers to a special form of detached peristome (Ehrmann, 1927; Nordsieck, 1978). This aperture type, best known from Laminiferinae and South American Neniinae, is associated with a characteristic closing apparatus. The phylogenetic significance of apostrophy was recognized by Ehrmann (1927) who concluded that this trait reflects an early evolutionary partitioning of Clausiliidae. Hence, the family can be divided into two major phylogenetic branches, those of the apostrophic and the non-apostrophic subfamilies, respectively. Accordingly, in subsequent works the *Garnieria* group was classified either as a part of the Neniinae or separated as the subfamily Garnieriinae, including all Southeast Asian genera with an apostrophic aperture or only *Garnieria* (reviewed by Nordsieck, 1978).

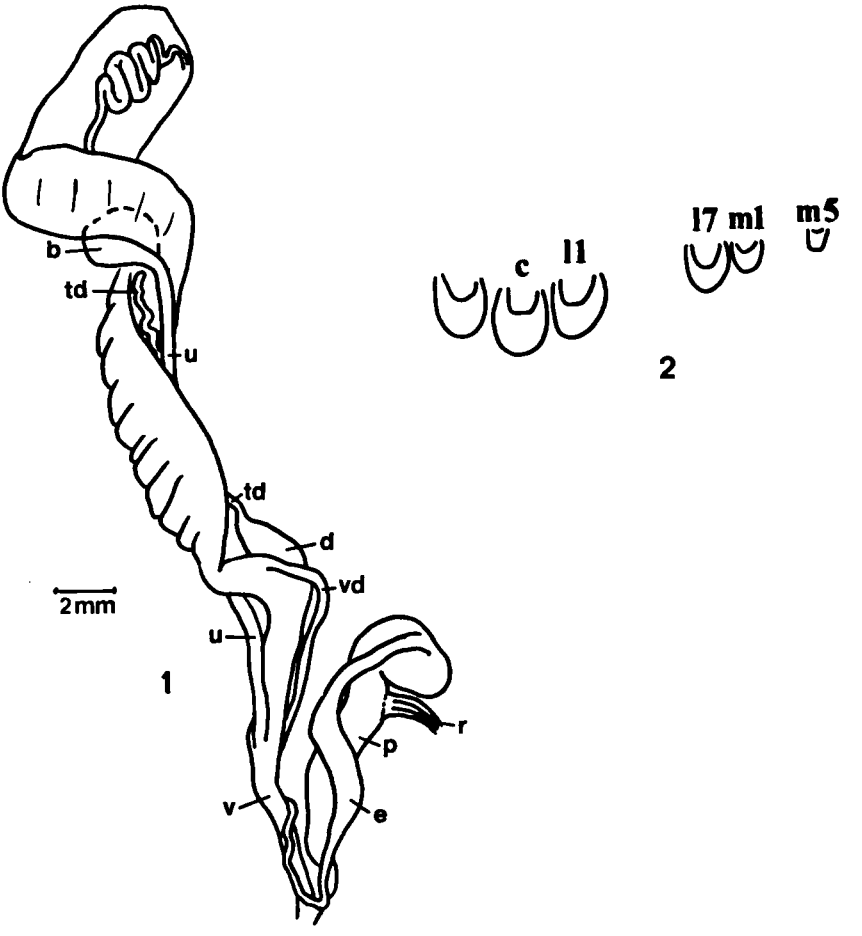
Ehrmann's notion was supported by Nordsieck (1972), who emphasized the improbability that apostrophy would appear through parallel evolution, concluding that all groups with that structure belong to the Neniinae. The first genital morphology and radula analyses (Szekeres, 1969; Loosjes & Loosjes-van Bemmel, 1973a) carried out on a representative of the *Garnieria* group, *Tropidauchenia proctostoma* (Mabille, 1889), provided further insight into the relationships between the various apostrophic Clausiliidae. It was established by Loosjes & Loosjes-van Bemmel (1973a) that, in addition to an apparent similarity in shell characters, *Tropidauchenia* also resembles certain South American Neniinae (Loosjes & Loosjes-van Bemmel, 1966) by having a radula with crescent-shaped teeth (like those of *Gracilinenia* Polinski, 1922, and *Peruinia* Polinski, 1922) arranged in angular rows (as in *Ehrmanniella* Zilch, 1949, *Andiniella* Weyrauch, 1958, *Gracilinenia,* and *Peruinia*). Similar radulae were not observed in any other taxa of Clausiliidae. In the light of these data, Loosjes & Loosjes-van Bemmel (1973b) accepted Ehrmann's view that all apostrophic groups belong to a single, distinct, evolutionary branch within the Clausiliidae.

In 1978 a comprehensive evaluation of the clausiliid subfamilies was published by Nordsieck. He separated the apostrophic groups of South America (Neniinae) from those of Southeast Asia (Garnieriinae), also indicating that all species of the latter belong to only two genera, viz. *Garnieria* and *Tropidauchenia.* Nordsieck claimed that the Asiatic and the South American groups of apostrophic Clausiliidae must have arisen by parallel evolution and that the similarities of the radulae demonstrated by Loosjes & Loosjes-van Bemmel are merely the result of convergent evolution. Discussing the genital morphology, he indicated the distinguishing features of each subfamily. He argued that only in the Garnieriinae, the retractor penis is exclusively attached to the penis, whereas a direct insertion of the diverticulum at the free oviduct is presented as a unique character of certain Neniinae.

Recently I studied the genital and radula structure of *Indionenia ardouiniana* (Heude, 1882), collected near Hong Gai, Vietnam. A comparison of the genital system (fig. 1) to that of *Tropidauchenia* is given in table 1.

	Indionenia	*Tropidauchenia*
penis	thicker than epiphallus, with papilla	as thick as epiphallus, with papilla
insertion of musculus retractor penis	at $^1/_2$ penis length	at $^1/_3$ from distal penis end
vagina	half penis length	same length as penis
pedunculus	longer than diverticulum, with distal lumen	wide, shorter than diverticulum
diverticulum	thread-like with basal lumen; insertion at free oviduct, far from base of pedunculus	tapers gradually towards tip; insertion at base of pedunculus

Table 1. Genital structures of *Indionenia* and *Tropidauchenia*



Figs. 1-2. *Indionenia ardouiniana* (Heude, 1882); Hong Gai, Vietnam; László Drimmer leg. (Colln. Szekeres). 1, genital organs; 2, radula teeth (central, first and seventh lateral, and first and fifth marginal tooth). Abbreviations: b, bursa of the bursa copulatrix; d, diverticulum (basal part with lumen); e, epiphallus; p, penis; td, thread-like upper part of the diverticulum; u, pedunculus; v, vagina; vd, vas deferens.

The radula (fig. 2) consists of 66 wedge-shaped rows of crescent-like teeth. It has the following formula: c/1 + 7l/1 + 9-12m/1.

These results raise some questions about the system proposed by Nordsieck (1978) because they demonstrate that both the versatile structure of the diverticulum (Nordsieck, 1978), and its insertion at the free oviduct may occur in both the *Garnieria* group and the South American Neniinae. Likewise, the radula with wedge-shaped rows of crescent-type teeth is another characteristic feature shared by only these two groups of Clausiliidae. Also considering the apostrophic shell aperture and the remarkable similarity of the closing structures, it appears extremely unlikely that all these common

traits would have appeared through convergent evolution. Furthermore, some of the distinguishing features mentioned by Nordsieck may only have limited systematic impact. His statement on the position of the lamella subcolumellaris of the South American Neniinae should be viewed in in the light of the great morphological diversity of these clausiliids. And although the attachment of the retractor muscle at the penis is restricted to the *Garnieria* group, its evolutionary precedent could well have been the divided structure, having both a penis and an epiphallus arm, which is present in the apostrophic *Laminifera* Boettger, 1863, and a few other genera (e.g. *Boettgeria* Boettger, 1863), as well as the South American *Zilchiella* Weyrauch, 1957, and *Bequaertinenia* Weyrauch, 1964.

The conchological and anatomical data mentioned above seem to indicate a close relationship between the apostrophic Clausiliidae of South America and those of Southeast Asia, supporting the hypothesis that clausiliids of this type were widely distributed following their appearance in the late Paleocene (Nordsieck, 1972; Loosjes, 1978). Thus, the Southeast Asian group may be classified most appropriately as Garnieriini, a tribus of Neniinae, indicating the phylogenetic relationship with the rest of the subfamily, the Neniini. It has to be emphasized, however, that the main point here is not the status of the *Garnieria* group as a subfamily or tribus, but the fact that this taxon is most closely related to the other apostrophic Clausiliidae.

THE TRIPTYCHIA GROUP

Members of this group are abundant fossil clausiliids throughout the Neogene of Western and Central Europe. Based on their characteristic shell structure, in particular the strongly reduced closing apparatus and the peristome with a narrowly pointed sinulus, they were separated by Wenz (1923) and Zilch (1959) as a subfamily, Triptychiinae, after *Triptychia* Sandberger, 1874, within the family Clausiliidae.

In a systematic re-evaluation Nordsieck (1972) argued in favour of placing this group within the subfamily Phaedusinae. In his assessment the formation of both the neck and the sinulus attests to a close relationship between the *Serrulina* and *Triptychia* groups, whereas the strong reduction of the closing structure in the latter does not warrant their separation at the subfamily level. By contrast, in 1976 Nordsieck came to believe that formerly unrecognized shell features of *Triptychia* differ substantially from those of all other clausiliids. In particular, he referred to the presence of a columellar lamella reaching to mid-height of the shell. Such a lamella had not been found in other Clausiliidae, except for some members of the *Serrulina* group where it is present in the juvenile shell. He also mentioned periodically formed lunella-like bands, the last of which lies in the penultimate whorl. He concluded that these characteristics indicate an independent evolution of the *Triptychia*-type closing apparatus, thereby necessitating the establishment of a distinct family, Triptychiidae.

The reliability of the systematic evaluation given by Nordsieck (1976) depends on whether the shell structures mentioned can convincingly exclude a common phylogenetic origin with other groups of Clausiliidae. Although the columellar lamella of the *Serrulina* group disappears in adult specimens, its presence at the juvenile stage may be seen as recurrence of an ancestral character. More importantly, it has been shown by Nordsieck (1985) that a similar columellar lamella also occurs in the *Eualopia* Boettger, 1877, and *Rillya* Fischer, 1883, groups, fossil Clausiliidae of the Paleogene. On the other hand, formation of the lunella-like folds can be a unique feature of the *Triptychia*

group which may have evolved following the reduction of the closing apparatus.

Some other conchological and phylogenetic aspects are also worth considering. Several species of *Triptychia* have a typical clausiliid appearance, i.e. a sinistral, spindle-shaped, often ventricose shell with a characteristic costate surface, as well as a distinct peristome with a sinulus. It is difficult to conceive that such an extent of similarity could arise by parallel evolution. Paleontological data cast further doubt on the separate development of *Triptychia* and the Clausiliidae. According to fossil records, the first representatives of the Clausiliidae appeared in the late Cretaceous, whereas the *Triptychia* group is much younger, confined to a period between the late Oligocene and the late Pliocene (Zilch, 1959, 1960). By adopting the theory of independent development, one has to accept that *Triptychia* is left without ancestral taxa in the relatively well known Paleocene and Eocene periods.

On the basis of the above considerations, the *Triptychia* group is considered here a highly specialized branch of the Clausiliidae, which became extinct following the climatic changes at the end of the Neogene. Their conchological characteristics suggest that they are descendants of archaic clausiliid groups known from the Paleogene. Therefore, their most likely systematic status is that of a distinct subfamily, Triptychiinae, within the Clausiliidae.

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