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Contributions to the nomenclature and phylogeny of Boettgeria O. Boettger, 1863, with description of Loosjesiella n. subgen. (Gastropoda: Pulmonata: Clausiliidae) [1]

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The species of the clausiliid genus *Boettgeria* O. Boettger, 1863, are re-evaluated and a hypothesis concerning their evolution and radiation on the Madeira Archipelago is forwarded. As a result, the genus is subdivided in two subgenera, one of which is herein described (*Loosjesiella* n. subgen.). A cladogram summarizing the hypothetical evolution of the group is presented. The geological background and the mutual implications are discussed.

Key words: Gastropoda, Pulmonata, Clausiliidae, *Boettgeria*, taxonomy, phylogeny, Madeira.

INTRODUCTION

The Madeira Archipelago is inhabited by seven Recent species of the clausiliid genus *Boettgeria*; another species is only known as a fossil. It was reviewed by Groh & Hemmen (1983) who also gave an account of the then known literature. H. Nordsieck (1979) created the tribus Boettgeriini for this genus and added the monotypic *Euxinella* H. Nordsieck, 1973, from Macedonia. An investigation of the internal structure of the epiphallus of the latter genus revealed major differences compared to *Boettgeria*; the genus has to be excluded from this tribus (Neubert, in prep.). H. Nordsieck (pers. comm.) and Groh & Hemmen suggested a closer relationship of *Boettgeria* and the East African species of *Macroptychia* O. Boettger, 1877. A detailed investigation of shell morphology and genital anatomy of two *Macroptychia* species from Arabia (*M. schweinfurthi* v. Martens, 1889 and *M. sumarana* Connolly, 1941) showed that these species are indeed allied to *Boettgeria* and other African taxa of (non-alopiine) Clausiliidae (Neubert, in press).

This work was stimulated by the results of a collection trip conducted by Groh, Hemmen and Gerber during the summer of 1985. This enterprise yielded a considerable amount of additional material, in particular from the hitherto poorly known Ilhas Desertas. A careful re-consideration of both shell material and genital organs, revealed the necessity of subdividing the genus into two subgenera.

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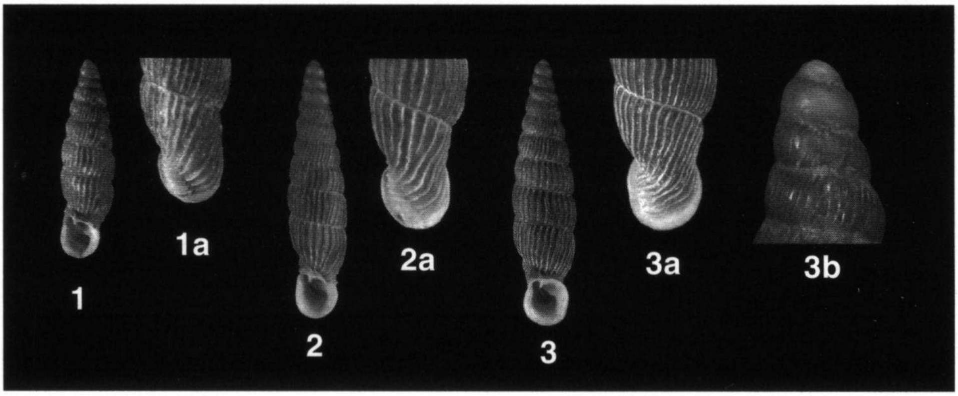
[1] Beiträge zur Kenntnis des Madeira-Archipels, Nr. 15. Nr. 14: Five new species of Cypraeidae from the Middle Miocene ("Vindobonian") of Porto Santo, Madeira Archipelago. – Arch. Molluskenk. 127 (in press).



Figs. 1-3. Shells of *Boettgeria* species; x 3 (frontal view), x 5 (dorsal view), and x 10 (protoconch). 1. *Boettgeria* (*B.*) *deltostoma*, coll. Bronn ex L. Pfeiffer (SMF 304395). 1, frontal view; 1a, dorsal view. 2. *Clausilia deltostoma* var. beta *crebristriata* Lowe, 1854, topotypes, northern part of Deserta Grande (SMF 68215). 2, frontal view; 2a, dorsal view. 3. Boettgeria (B.) jensi n. sp., holotype (SMF 311400). 3, frontal view; 3a, dorsal view; 3b, protoconch. All photos by E. Neubert.

Abbreviations: MRP, Musculus retractor penis; NNM, Nationaal Natuurhistorisch Museum, Leiden; SMF, Senckenberg Museum, Frankfurt; H= height, D= diameter, PH= peristome height, PD= peristome diameter, W= number of whorls, R_1= number of ribs on one millimetre of the last whorl.

RESULTS

NOMENCLATURE

The nomenclature of the species of *Boettgeria* was confused right from the beginning, when Lowe (1831) published his first contribution to the flora and fauna of Madeira. Under the name *Clausilia deltostoma*, he published the description for a mixture of similar species with the variety names 'alpha' from 'Portu S^{to}.' and 'beta' from 'Madera'. The next author to mention *C. deltostoma* was L. Pfeiffer in 1848, but his text is too vague and his material came from Madeira and from Porto Santo (the only place where *B. lowei* is living) and thus cannot be accepted as first revising author (Groh & Hemmen, 1984: 8). Meanwhile, parts (?) of his material could be traced in the collection of Bronn, which was recently discovered and is now housed in the Senckenberg Museum (SMF 304395/2). Bronn exchanged material with his colleagues and also had two specimens of *B. deltostoma* ex coll. Pfeiffer in his private collection (fig. 1). These specimens represent *B. deltostoma* as understood here.

The first to recognize that there was a different species living on Porto Santo was Albers in 1852, who created the name *lowei*. Later, in 1854, Lowe added several new forms of Clausiliidae. One of them was *Clausilia deltostoma* var. alpha *raricosta* subvar.

1 *portosanctana*, which disregards the earlier Albers name and consequently has to be relegated to the synonymy of *lowei*. At the same time, he founded *Clausilia deltostoma* var. alpha *raricosta* subvar. 2 *maritima* from Madeira. The original label of *maritima* reads '*Clausilia deltostoma* var. alpha subvar. 2 *maritima*; ex R. A. MM. Exeter ex Lowe; evidently a Caniçal (Piedade) spec. on comparison with ex.s of 1827-51. Orig. fig. Tr. Cambr. ph. Soc. IV, T. 6 Fig. 38'.

The designation of a lectotype of *Clausilia deltostoma* and of the same specimen as a lectotype of var. alpha *raricosta* subvar. 2 *maritima* Lowe by Groh & Hemmen in 1984 was rejected by F. Naggs (in litt., 2. IV. 1985) arguing, that *maritima* as an infrasubspecific name is beyond the scope of the rules. This is true regarding this infrasubspecific name *maritima* (ICZN § 1 and § 45). Nonetheless, the text on the *maritima* label clearly proves the identity of the specimen discussed as the original of fig. 38 on plate 6 from 1831. Thus, it cannot be the type of *B. maritima* but it actually is the type specimen of *B. deltostoma* var. beta!

Another problem arises from the fact, that authors like Lowe, Férussac and others normally used the varietas alpha to name the nominate form, which consequently has to bear the original name. In this case, Lowe and all subsequent authors used *B. deltostoma* var. alpha for *B. lowei* and *B. deltostoma* var. beta for *B. deltostoma*. Although this is inconsequent, this usage should be retained for the sake of stability of nomenclature. Otherwise, the species *B. lowei* must be named *B. deltostoma*, and what was hitherto *B. deltostoma* has to bear the next available name *B. maderensis* Charpentier, 1852. As this would perpetuate the chaotic situation, the authors propose to preserve the long-lasting use of the var. beta for *deltostoma*.

The situation concerning infrasubspecific names has also to be adopted for *Boettgeria depauperata*. As a consequence of the situation explained above, *Clausilia deltostoma* var. beta *crebristriata* subvar. 2 *depauperata* Lowe, 1854 is invalid. In 1863, Lowe used *C. depauperata* on subspecific level of *C. deltostoma* [*Clausilia deltostoma* var. delta *depauperata*] For this reason, the correct publication date and author for this species is Lowe, 1863 and not Lowe, 1854.

TAXONOMY

The most difficult taxonomical problem within *Boettgeria* is the differentiation between *B. deltostoma* and *B. jensi* n. sp. The latter species was already recognised by Groh & Hemmen while working on their material collected on the islands of Deserta Grande and Bugio in 1985. A re-evaluation of the topotypes of *Clausilia deltostoma* var. beta *crebristriata* [subvar. 1 *normalis*] Lowe, 1854 (SMF 68215/3 coll. O. Boettger ex G. Fitz-Gerald, locus typicus restricted by Groh & Hemmen, 1984: Deserta Grande, figured 1984: pl. 1 fig 2) revealed, that they are identical with *B. deltostoma* and thus do not interfere with *B. jensi*. For a better understanding, they are here re-figured (fig. 2). In fact, both species live sympatrically on the island of Deserta Grande as is shown by a lot collected from the northern part of the island in August 1985.

Boettgeria (Boettgeria) jensi n. sp. (fig. 3)

1993 *Boettgeria* n. sp. [= *jensi*, name used on p. 15] Neubert & Groh in Neubert, Systematik der Unterfamilie Clausiliinae: 14-15, pl. 2 fig. 4, text-fig. 11, Diss. FB Biol., TH Darmstadt [published on microfiche].

Type-material. — Madeira Archipelago, Ilhas Desertas, Bugio, southern part: Holotype SMF 311400/1 ex Groh. Paratypes: SMF 311401/3 ex Groh; NNM Reg.No. 56839 ex Groh (3); coll. E. Neubert ex Groh (2); coll. J. Gerber (29 and 12 preserved, 7 non-type fragments); coll. K. Groh (10 and 11 preserved); coll. J. Hemmen (17); coll. T. E. J. Ripken ex Groh (3). All 29.-31.VII.1985 leg. Gerber, Groh & Hemmen.

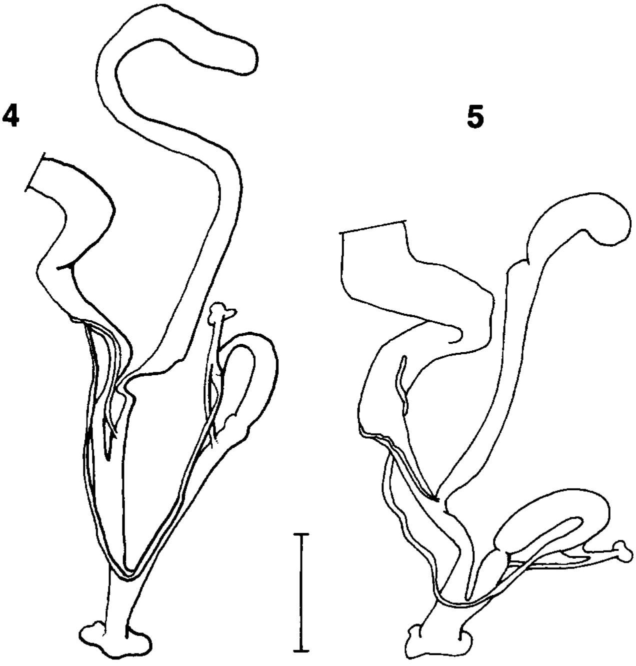
Further referred material. — Madeira Archipelago, Ilhas Desertas, Deserta Grande, southern part: coll. J. Hemmen (4 and 4 preserved); coll. J. Gerber (4, 4 preserved, non vidi, fide Gerber). All 1.-5. VIII. 1985 leg. Gerber, Groh & Hemmen.

Madeira Archipelago, Ilhas Desertas, Deserta Grande, northern part: coll. K. Groh (3); coll. J. Gerber (71, 2 preserved, non vidi, fide Gerber); coll. T.E.J. Ripken ex Groh (8, non vidi Neubert). All 1.-5. VIII. 1985 leg. Gerber, Groh & Hemmen.

Deserta Grande: coll. Hemmen ex Pieper ex Erber (1).

Description.- The fusiform shell is deep brown. The protoconch is acute conical and consists of 2.5 finely granulated whorls. The whorls of the teleoconch are gently convex and covered by acute and evenly spaced ribs. The suture is of medium depth. The last whorl is somewhat broadened with a rounded basal keel and a nearly inconspicuous dorsal keel. There is a shallow furrow between both keels.

The aperture is well rounded with a shallow basal canal. The apertural rim is white and disconnected from the last teleoconch whorl, the lip is flared and recurved. Palatally, there is a broad subrectangular callus which sometimes elongates basally. Parallel to the basal canal, a thick callus may be present reaching towards the interior of the shell and often fused to the elongated palatal callus.



Figs. 4-5. Genital organs of *Boettgeria (B.) jensi*. 4, subadult specimens (= Neubert, 1993: fig. 11); 5, adult specimens. Scale bar 1 mm.

The lunellar lies dorsally or is somewhat shifted dorsolaterally towards the aperture. The principalis is narrow and long. A short interior upper palatalis is connected to the lunella, which is a sharp fold in its upper part and broadens basally where it elongates again to the interior to form the strong subclaustralis.

The upper lamella and the spiralis are connected. The lower lamella is obliquely truncate and may form two small nodes. The subcolumellaris is thin filiform and runs above the basal canal. It does not reach the apertural rim and cannot be seen by perpendicular view into the aperture. The clausilium plate is broad and subtriangular, its surface is somewhat granulated.

Genital morphology (paratypes, figs. 4-5). — The penis is short and somewhat bulbous. The big penial papilla fills the proximal lumen of the penis. The epiphallus reaches the same length as the penis. The MRP is bipartite with the epiphallial part connected to the proximal part of the epiphallus, the penial part attaching proximally at the distal penis part. A flagellum could not be found.

The vagina hardly reaches the length of the penis. The diverticulum is extremely thin. It branches off from the pedunculus at a basal point close to the vagina.

Measurements (holotype SMF 311400). — H= 11.8; D= 2.8; PH= 2.45; PD= 2.05; W= 11, R_1= 4.

Locus typicus. — Madeira Archipelago, Ilhas Desertas, southern part of the island of Bugio, leg. Gerber, Groh & Hemmen, 29.-31. VII. 1985.

Etymology. — Named after our colleague and friend Jens Hemmen, Wiesbaden, Germany.

This investigation revealed some interesting information on the value of length ratios of genital organs. It could be observed, that within the paratypic population of *B. jensi*, specimens with full grown shells but two ‘types’ of genital organs are present. One is characterised by white to translucent tissue with extremely thin walls, thin penial and epiphallial pilasters, a tubular bursa copulatrix/pedunculus-complex and an elongate penis. The second type always displays thick-walled and often pigmented organs with well developed pilasters and penial papillae. The penis is much shorter and thickened, while the epiphallus nearly keeps its relative size. The bursa copulatrix/pedunculus-complex is well differentiated, and the vesicle often bears remains of a spermatophore thus reflecting sexual activities. Subsequently, the first type represent full grown but sexually inactive subadult specimens (fig. 4), while the others are fully mature adults (fig. 5). In juveniles, the genital organs are only represented by extremely small lobes of tissue, although even in this case the shell yet may be adult.

This phenomenon could also be observed in specimens of *B. deltostoma* collected at Deserta Grande North, which sample contained only subadult specimens, while from Madeira, full-grown adults were available. This observation indicates, that two generations of these perennial species are living together at the same locality. To avoid errors while discussing character states, the effects of allometric growth have to be considered very carefully (cf. table 2).

The most important differentiating character between *B. deltostoma* and *B. jensi* is the presence of a lunella in the latter species. All lots of *B. deltostoma* housed in the SMF (52 lots) with several hundred specimens were checked, but a lunella is always missing. Other characters as type of ribbing and development of apertural callus are subject to intraspecific variation and thus cannot be used for discrimination between both species.

Within the sympatric population at Deserta Grande North, a niche separation could be observed. Here, *B. jensi* could be found dwelling on the open rock faces while *B.*

deltostoma lived in sheltered places in crevices and under stones. In the material list below, the lots of *B. deltostoma* from the Desertas are listed. It has to be noted, that the lunella of the specimens from Deserta Grande North identified as *B. jensi* is broadening basally, while speciemens from the southern part of the island are very close to those from Bugio.

Material of *B. deltostoma.* — Deserta Grande North: coll. Groh (26); coll. Hemmen (29, 7 preserved). All 1.-5.VIII.1985 leg. Gerber, Groh & Hemmen. Deserta Grande (exact location not specified): coll. J. Hemmen ex Hinterseher, 16. III. 1982 (14).

Boettgeria (Loosjesiella) n. subgen.

Type species. — *Clausilia crispa* Lowe, 1831, is herewith designated type species.

Diagnosis. — A subgenus of *Boettgeria* O. Boettger, 1863, which differs from the nominate subgenus in the form of its subcolumellaris, the shape of the protoconch, the tumidity of the teleoconch whorls, and the fragility of the shells.

Description.- Conchologically, the new subgenus differs from *Boettgeria* s.s. by the form of the subcolumellaris, which is shifted in a basal direction and exhibits a considerable arch. Moreover, it is elongate and runs parallel to the basal canal. This is in marked contrast to *Boettgeria* s.s., where this lamella never enters the basal part of the aperture. Usually, it is short, but when elongate (*B. deltostoma*), it is always a thin thread running close to the lower lamella. The protoconch is short and dome-shaped (more acutely mammillate in *Boettgeria* s.s.). The teleoconch whorls are tumid with a moderately deep to deep suture (whorls flat and suture always shallow in *Boettgeria* s.s.*)*. The labial callus is reduced and the peristome flared (usually heavily thickened in *Boettgeria* s.s.*)*. The teleoconch whorls are finely ribbed and thin-walled (coarse and thick-walled in *Boettgeria* s.s.).

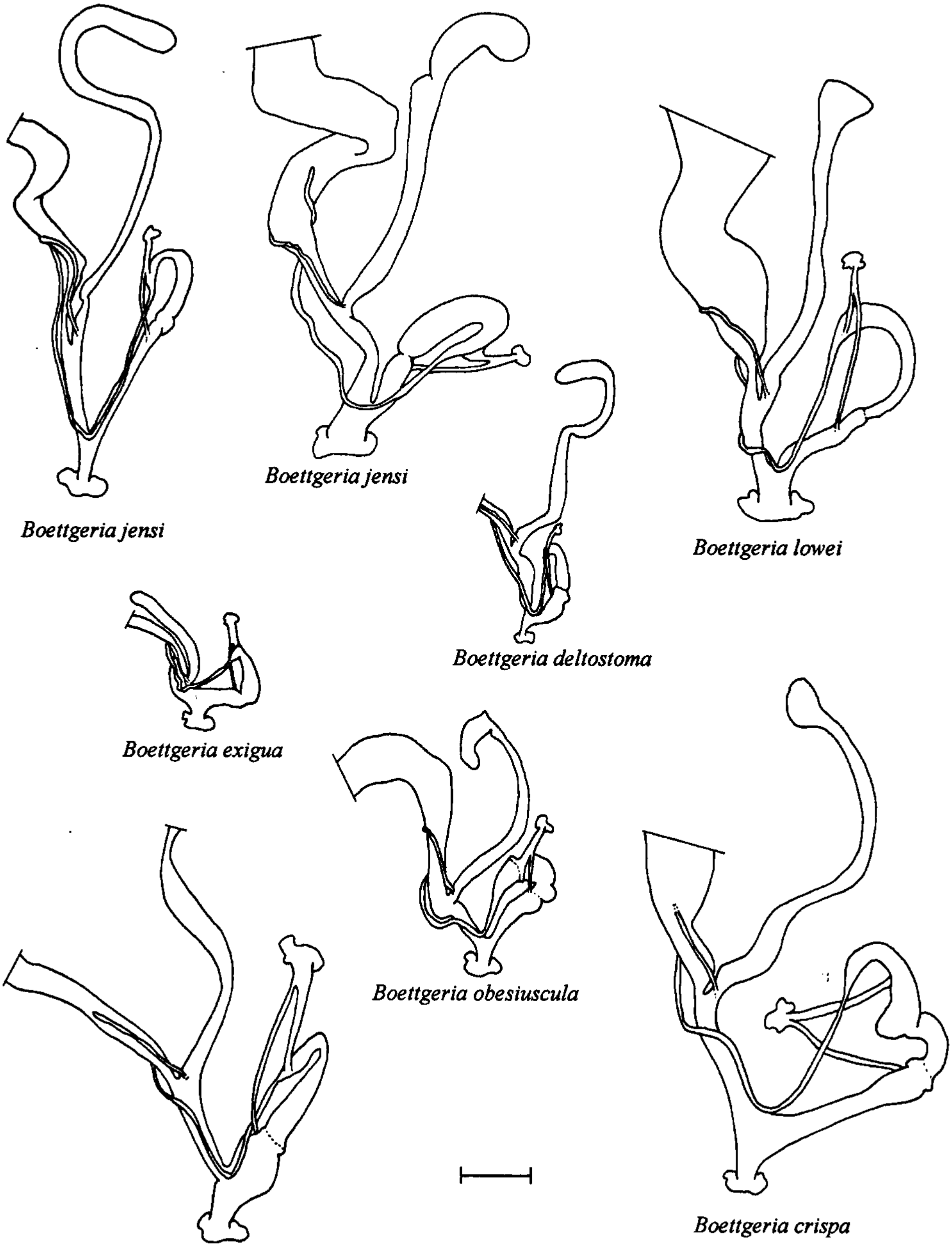
The attachment site of the epiphallial retractor muscle tends to be shifted distally (exception: *B. depauperata*). It is always close to the boundary between epiphallus and vas deferens in *Boettgeria.*

Etymology. — This subgenus is named in honour of F. E. Loosjes for his valuable contributions to malacology and in particular to the knowledge of the Clausiliidae.

The genus is here subdivided as follows (type species in bold): *Boettgeria* s.s.: ***deltostoma*** (Lowe, 1831); *jensi* n. sp.; *lowei* (Albers, 1852). *Loosjesiella* n. subgen.: ***crispa*** (Lowe, 1831); *obesiuscula* (Lowe, 1863); *lorenziana* Groh & Hemmen, 1984; *exigua* (Lowe, 1831); *depauperata* (Lowe, 1863).

PHYLOGENETICAL CONSIDERATIONS (figs. 6, 7)

The development of the closing apparatus within the Clausiliidae was summarized by H. Nordsieck (1982). According to his theory, the presence of a lunella has to be interpreted as an apomorphous stage compared to the so-called 'fold-type' clausiliarian apparatus although the 'lunella-type' was already present in Eocene Clausiliidae. In contrast to the advanced type of the lunella-system, the connected spiralis and upper lamella in *Boettgeria* reflect the persistence of plesiomorphous conditions as can be observed in other genera even outside the Boettgeriini (*Olympicola* Hesse, 1916; partim *Euxinella* H. Nordsieck, 1973). Reductions within the lunella-system of the 'lunella-type' represent a process, which can be observed as occurring in many groups of the Clausiliidae. Thus, the partial or complete loss of this fold system can be used as one indicator, where evolutionary processes within an isolated entity are taking place.



Boettgeria jensi

Boettgeria jensi

Boettgeria lowei

Boettgeria deltostoma

Boettgeria exigua

Boettgeria obesiuscula

Boettgeria crispa

Boettgeria depauperata

Fig. 6. Genital organs of *Boettgeria* spp. Genital organs of adult specimens. Scale bar 1 mm (partly after Neubert, 1993: figs. 5-11).

Starting from this point of view, basic lineages can be observed within *Boettgeria* (fig. 7). The following table contains the characters, which will be used as arguments in the following phylogenetical discussion. As an outgroup, the closely related genera *Macroptychia* O. Boettger, 1887, and *Abbadia* Bourgouignat, 1883, had been used (Neubert, in prep.). A comprehensive illustration of genital organs and lunella-systems of all species is given in figs. 6 and 7.

Number	character	Apomorphous (+)	plesiomorphous (-)
1	subcolumellaris	basal position	lateral position
2	shell wall	Thick	thin
3	lunella	Reduced	retained
4	epiphallial MRP	shifted in distal direction	proximal position
5	ratio epiphallus/penis	High	low
6	basalis	Reduced	retained
7	absolute size	Tall	small
8	dorsal keel	Reduced	present

Table 1. Characters and character states in *Boettgeria*.

(1) The lateral position of the subcolumellaris is a plesiomorphous character state as its general shape and position is close to what is known within the outgroup genera.

(2) A thin shell wall is here considered to be plesiomorphous as this character state is shared with most of the species of the outgroup.

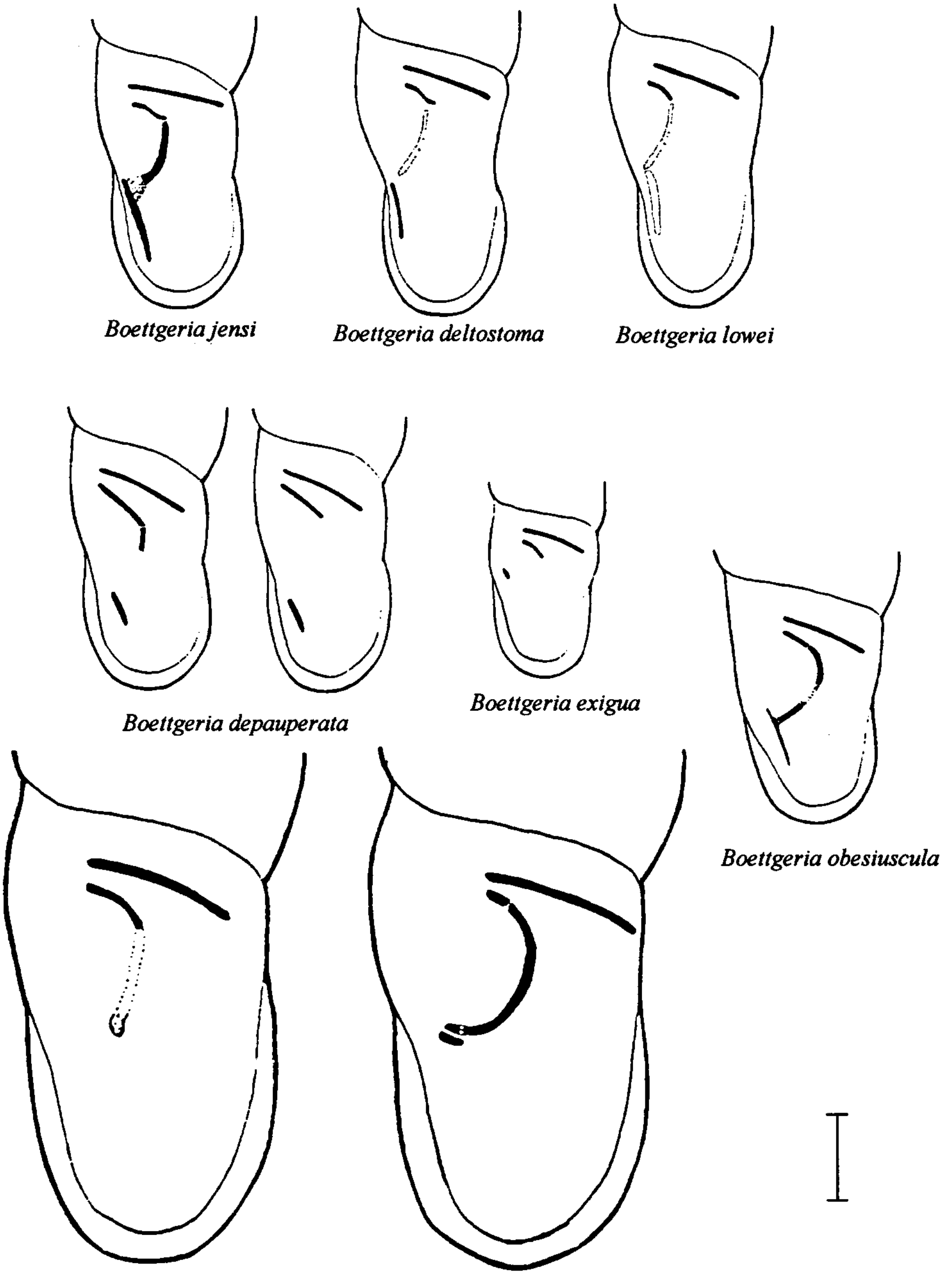
(3, 6) The reduction of the lunella-system can be considered to constitute a general evolutionary process, which can be seen in many subfamilies of the Clausiliidae. This process may follow several pathways. One direction is loss or reduction of the lunella with the basalis retained (*B. deltostoma*). Another is vice versa with reducing the basalis but leaving a lunella (*B. crispa*). Intergrading stages are frequently found leaving no doubt about the general direction of the reduction process.

(4) The attachment site of the epiphallar arm of the MRP in both, *Macroptychia* and *Abbadia*, is close to the boundary between epiphallus and vas deferens. A distally shifted position of this muscle thus has to be considered an apomorphous character.

(5) The relative length of the penis compared to the epiphallus can only be taken into account, when definitely adult specimens are investigated and the genital organs attained their final shape. To the authors' experience, shrinking during preservation has only a minor effect. Moreover, as exclusively the ratio of epiphallus to penis length is used here, the danger of misinterpretation is reduced as shrinking would effect both organs. A low ratio indicates an equilibrium in length of the organs and is here considered to represent the plesiomorphous condition as the outgroup genera show similar ratios.

(7) Size usually should be used very carefully in this context, but both species concerned are so close in their general appearance and other details, that it can be used here within *Loosjesiella*.

In fig. 8 a cladogram is presented summarising the arguments for a subdivision of the genus and for interspecific relationships. Herein, the reduction of some or almost all parts of the lunellar is a considered a product of convergent evolution, which occurs in many not closely related taxa within the Clausiliidae. Reduction of the penis in



Boettgeria jensi

Boettgeria deltostoma

Boettgeria lowei

Boettgeria depauperata

Boettgeria exigua

Boettgeria obesiuscula

Boettgeria lorenziana

Boettgeria crispa

Fig. 7. Lunella-systems of *Boettgeria* spp. Scale bar 1 mm (partly after Groh & Hemmen, 1984: fig. 3).

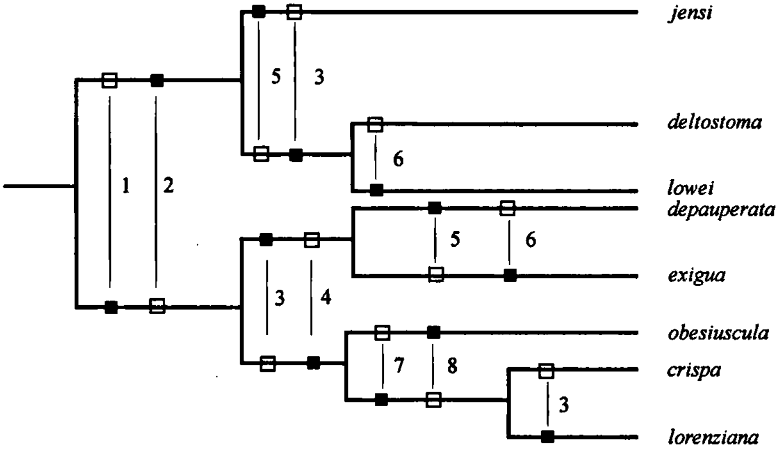


Fig. 8. Cladogram of *Boettgeria* spp. ■ apomorphous character state; □ plesiomorphous character state. Numbers refer to explanations in the text.

relation to the epiphallus is another convergent autapomorphy, which occurred twice, once in each subgenus (*B. jensi* and *B. depauperata*).

Compared to the conchological characters, the genital organs are less significant concerning their value for phylogenetical considerations. In particular, the two conchologically basic types within the subgenera differ considerably in respect of the length of epiphallus and penis (table 2).

Name	epiphallus (mm)	penis (mm)	ratio epiphallus/penis
B. jensi (adult)	2.33	1.33	2.5:1
B. jensi (subadult)	1.66	2.13	0.8:1
B. exigua	2.46	1.46	1.7:1
B. deltostoma	1.53	1.13	1.4:1
B. lowei	3.33	1.73	1.9:1
B. depauperata	1.73	0.93	2.8:1
B. obesiuscula	2	1.66	1.2:1
B. crispa	4.53	2.53	1.8:1

Table 2. Measurements and length ratios of male genital organs of *Boettgeria* spp.

The basic autapomorphies of *Boettgeria* and its relationship to the other genera within the Boettgeriini will be discussed elsewhere (Neubert, in prep.). Within the genus, the basic autapomorphy for *Boettgeria* s.s. is its thickened shell (2+), while in *Loosjesiella*, the shells are considerably more fragile and compare well to the African Boettgeriini. The autapomorphous character of that group is the basally shifted position of the subcolumellaris and the fact, that this lamella is strongly arched (1+). The shortening of the penis is considered apomorphous for *B. jensi*, although a definite lunella is still present (5+, 3-). It broadens and decreases in size (3+) while retaining the basalis (*B. deltostoma*) and finally, the lunella and basalis are completely lost which is accompanied by a shortening of the upper palatalis (*B. lowei*) (6+).

In *Loosjesiella* the reduction of the lunella can also be observed within the *B. depauperata/exigua* group (3+), while this system is almost completely retained in the remaining three species. The short penis can be used to characterize *B. depauperata* (5+) in contrast to *B. exigua*, where the reduction of the lunella-system is almost finished by loss of the basalis. In the remaining group, the dorsal keel is almost completely lost in *B. obesiuscula* (8+), while the group of *B. crispa/lorenziana* is characterized by their size (8+), which is an outstanding feature within *Boettgeria*. Within this group, the lunellar of *B. lorenziana* shows a tendency to reduction, the lunella is present, but very thin, whereas the shortened basalis is still retained (3+).

GEOGRAPHICAL IMPLICATIONS CONCERNING THE MADEIRAN TERRESTRIAL MOLLUSC FAUNA

The existence of an 'island' or terrestrial habitat in the area of what is the Madeiran Archipelago today can be considered for a pre-Vindobonian time level, as there is a terrestrial snail recorded from this middle-Miocene epoch. This specimens was confined to *Caseolus* (*Leptostictea*), a genus of Recent terrestrial molluscs of the Madeiran archipelago (Groh, 1985). Although this identification was doubted by Gittenberger & Ripken (1985: 405), who proposed *Keraea* Gude, 1911, as a more appropriate genus for this fossil, its presence illustrates the availability of suitable conditions for a terrestrial malacofauna in general. Moreover, the malacofauna was then quite well established in the Late Miocene of the Canary Islands, but referring to Groh & Ripken (in prep.) does not show so many relations to the Recent as lined out by Gittenberger & Ripken (1985). Comprising *Pupoides*, *Zootecus* and two helicids close to *Eremina*, it is more likely related to the Recent fauna of the Cape Verde Islands (cf. Groh 1983, 1984).

The age of the fossiliferous Tertiary coastal sediments with their rich marine tropical fauna cannot precisely allocated (Mitchell-Thomé, 1976; Lorenz & Groh, in press), but an age between 13 and 20 my BP. seems to be appropriate. It is likely that the islands of the Ilhas Desertas south-east of the main island Madeira represent an even older part, as was already noted by Mitchell-Thomé (1976: 126: 'Deserta Grande and Bugio are the older islands, and all three [the third is the northernmost Ilhéu Chão] show geological similarities to eastern Madeira, and are to be considered as an SE extension of the main island.').

Summarizing these data it can be hypothesised, that the ancestral form of *Boettgeria* already could have dwelled upon the 'Vindobonian'-land. This theory of an early invasion by Clausiliidae is supported by the observation, that in Madeira no Buliminidae can be found which are abundant on the Azores and the Canary Islands. Also no Clausiliidae are known from these islands. This can be explained by occupation of comparable niches. For example, fossil Buliminidae are found with many other representatives of the Recent Canarian fauna most probably in the Late Miocene of Fuerteventura (Groh & Ripken, in prep.) and surely in the Early Pliocene of Gran Canaria (Hutterer & Groh, in prep.).

Boettgeria s.s. is known from all islands (*B. jensi* on Ilhas Desertas, *B. deltostoma* on the northern part of Deserta Grande and Madeira, *B. lowei* on Porto Santo and surrounding islets). In contrast to these findings, *Loosjesiella* lives exclusively on Madeira. For this reason, the hypothesis is forwarded, that the ancestor of *Boettgeria* s.s. lived on a 'Vindobonian' land located in the area of Recent eastern Madeiran Archipelago. Geological events may have split this land mass into islands subdividing the gene pool in independent subgroups, which subsequently could develop into separate species. The fact, that *B. deltostoma* (as the only species!) lives on Madeira, Ilhéu Chão and Deserta Grande supports this idea, although an introduction by human settlement in the last centuries cannot be excluded. *Loosjesiella* represents a second radiation within *Boettgeria*, which must have taken place much later. Species of this group were not able to invade the other island. Obviously, the rich microhabitat structure of the main island of Madeira offered the possibility to exploit niches which had not been used by the older *B. deltostoma.*

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