

**Reconsidering the generic position of the species once classified in  
*Carinigera*, *Isabellaria* and *Sericata*  
(Gastropoda, Pulmonata, Clausiliidae, Alopiinae)**

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On the basis of molecular and distributional data, and a new interpretation of morphological data, the generic and/or subgeneric position of the species once classified with *Carinigera*, *Isabellaria* or *Sericata* is revised. *Sporadhia* subgen. nov. of *Carinigera*, and *Inchoatia* gen. nov. and *Vallatia* gen. nov. are introduced.

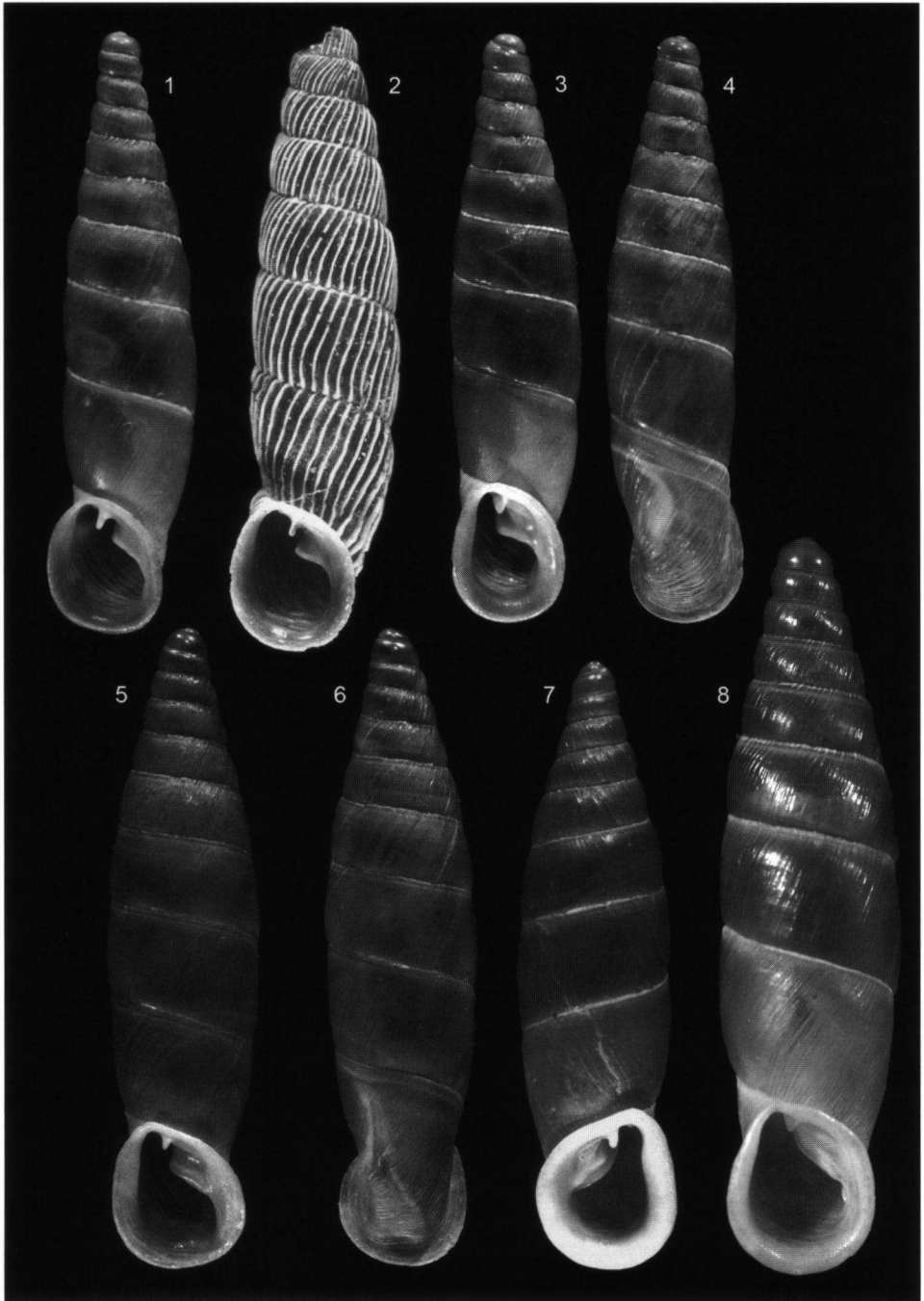
Key words: Gastropoda, Pulmonata, Clausiliidae, Alopiinae, Medorini, taxonomy, new taxa, DNA, distribution, Bulgaria, Greece, Makedonija, Serbia.

INTRODUCTION

During several decades now, by far the most impressive contributions to our knowledge of the taxonomy of the pulmonate family Clausiliidae were made by Nordsieck in a large series of papers dealing with morphology and classification. Meanwhile, DNA sequencing has become an additional, valuable tool in particular for cases where morphology brings no unequivocal results, so that, as a consequence, the opinions of the authors diverge. Here we deal with one case of such divergence, viz. the delineation of the nominal genera *Carinigera*, *Isabellaria* and *Sericata*.

Contrary to Nordsieck (1999: 1) we do not consider it "a remarkable fact" that molecular methods usually support the results based on morphological data. In agreement with Schilthuizen & Gittenberger (1996), in a paper that was misinterpreted by Nordsieck (1999: 1), we do not suppose on the one hand that shell characters have (Nordsieck, 1999: 1) "a minor importance", but on the other hand we cannot accept as a dogma that "the relationships of the species can be judged by shell characters, and species groups as phyletic units can be defined by such characters". Schmidt (1868: 4) already emphasized more than once that (translated from German) "a single criterion, how decisive it generally may be, may become meaningless in particular cases". Nordsieck (1972) can also be cited here, emphasizing that the nominal genera *Albinaria* Vest, 1867, *Carinigera* Moellendorff, 1873, *Cristataria* Vest, 1867, and *Sericata* O. Boettger, 1878, cannot always be distinguished conchologically, whereas some species of *Isabellaria* Vest, 1867, can be recognized only because of their so-called G type of the clausilial apparatus (= CA). Finally, there is no reason whatsoever to assume that sibling species do not occur among clausiliid snails.

The nominal genera *Carinigera*, *Isabellaria* and *Sericata* of the tribus Medorini (sensu Uit de Weerd & Gittenberger, 2004a, b) have hitherto been distinguished after only the type of the CA and the structure of the male part of the genitalia, in particular the penial



appendix or papilla. In some cases striking similarities in other conchological characters were acknowledged but interpreted as local, intergeneric, convergent evolution, whereas the mosaic distributional patterns and disjunctions in the ranges of these alleged genera were explained as vicariance resulting from competitive interactions (Nordsieck, 1974). Yet, it has been clearly demonstrated that the two basic types of CA should not be given too much weight in classifications, since obviously the so-called G type has evolved from the N type several times. With Nordsieck (1963: 91, 92) we too “do not think that only on the basis of this type of CA a group can be distinguished as a separate genus” [translated from German]. What remains as most important then is the presence of either a penial papilla, which may be perforated, or an appendix. Dealing in more detail with these structures in *Albinaria*, Kemperman (1992: 72) reported that appendix and papilla are mutually exclusive in general, but may characterize different subspecies of even a single species. Obviously, additional data are needed to achieve a classification in natural, monophyletic taxa that are founded more convincingly. Molecular data, as provided by Uit de Weerd, Gittenberger & Piel (2004) and Uit de Weerd, Piel & Gittenberger (2004) may serve that goal.

It should be emphasized that the revised classification proposed in this article cannot simply be considered a molecular one, as opposed to a morphology-based classification. Shell morphology is not neglected but it is used in a less biased way, whereas distributional patterns are also taken into account. Apart from this, there hardly is a prevailing generic nomenclature for the Clausiliidae. During the past decades the (sub)generic classification of several species has changed repeatedly, in particular where the genus-level taxa that were accepted could not be diagnosed conchologically. That resulted in frequent nomenclatorial adaptations whenever the structure of the penial papilla or appendix of a particular species became known. Maybe future molecular analyses of some species that have not yet been investigated with those methods will result in deviations from the views that are presented in this paper. A similar situation counts for many more molluscan species, for example in the former Helicellinae, that have once been described on the basis of shell characters only, without any anatomical data, not to mention a molecular analysis. However, this should not hamper progress in systematics and phylogenetics.

Here we start from the phylogenetic relationships between the various species, as derived from the molecular data produced by DNA sequencing (Uit de Weerd, Gittenberger & Piel, 2004; Uit de Weerd, Piel & Gittenberger, 2004). Several taxa cannot be diagnosed conchologically. In that respect nothing has changed. Convergent and parallel evolution in shell characters are clearly not uncommon. The molecular data show that a typological interpretation of the morphology, rigorously giving decisive weight to a very small set of characters, results in an artificial classification. The species that are referred to below as *Carinigera* (*C.*) *albicosta*, *Isabellaria sericata* and *Inchoatia inchoata*, for example, have shells (figs 2, 16, 21) that strikingly differ at first sight, but the rigid interpretation of few character states once dictated their congeneric classification. Triggered by the molecular data, but not exclusively so, *Inchoatia inchoata* is now classified next to some species that look similar in shell characters and also belong together zoogeographically. The *Carinigera* species from the Sporadhes islands, with shells that look very similar at first sight, used to be classified in two genera but are now united within a single subgenus. In

Fig 1-8. *Carinigera* spec. 1, *C.* (*C.*) *buresi cavallaensis* Brandt, 1962, Makedhonia, Kavala, Kavala town, 100 m alt. (H 15.6 mm); 2, *C.* (*C.*) *albicosta* (O. Boettger, 1877), Makedhonia, Pieria, 10 km WSW. of Litokhoron, 1050 m alt. (H 18.7 mm); 3-4, *C.* (*C.*) *buresi conciliatrix* (Fuchs & Käufel, 1936), Makedhonia, 35 km E. of Serres near Alistrati cave, 200 m alt. (H 15.3 mm); 5-6, *C.* (*Nymphogena*) *lophauchena* (Sturany, 1894), Makedhonia, Kilkis, 16.5 km NW. of Axioupoli, 550 m alt. (H 16.5); 7, *C.* (*N.*) *dextrorsa* (O. Boettger, 1877), Makedhonia, Pella (= Pella), 11.5 km ESE. of Aridaia (= Aridea), NE-side of Theodoraki, 450 m alt. (H 17.4 mm); 8, *C.* (*N.*) *torifera* (O. Boettger, 1885), Thessalia, Trikala, N-side of Theopetra, 250 m alt. (H 14.9 mm).

other cases the revised classification is less compelling from a conchological perspective. The anatomical data, not all of which are easily accessible, should be reconsidered in view of the molecular data. Attention should be drawn to the fact that most species once classified with *Carinigera* s.str. are still kept in *Carinigera* s.str., whereas all the species now considered to belong to *Carinigera* (*Nymphogena*) were earlier considered *Isabellaria* and *Sericata* taxa. The nomenclature presented here differs from that used by Uit de Weerd, Piel & Gittenberger (2004), Uit de Weerd, Schneider & Gittenberger (2005) and Uit de Weerd et al. (2006) in anticipation of the current publication. The taxa *Carinigera*, *Isabellaria* and *Vallatia*, which were considered subgenera of *Isabellaria* in those earlier papers, are here distinguished as separate genera. This classification is preferred by the first author. Anyway, the classification is consistent with the distributional patterns. These patterns are far less of a mosaic nature than hitherto thought.

## SYSTEMATIC PART

### *Carinigera* Moellendorff, 1873

*Carinigera* Moellendorff, 1873. Type species: *C. (C.) eximia* (Moellendorff, 1873).

As defined here, *Carinigera* forms a well supported clade with three subclades in the molecular analysis (Uit de Weerd, Gittenberger & Piel, 2004; Uit de Weerd, Piel & Gittenberger, 2004). The species that are included occur in a well defined area in NE. Greece and somewhat further north. The subclades can be circumscribed geographically. As before (Nordsieck, 1972: 9), the genus cannot be differentiated conchologically. The three subclades are here given subgeneric status. Within the genus, *Carinigera* s.str. is also characterized by the presence of a penial papilla. The *Sporadhia* species are all very similar in shell shape and sculpture. *Nymphogena* Sajó, 1968, cannot be distinguished morphologically. It remains to be investigated whether there are shared derived character states among the various *Carinigera* species that are in congruence with the subdivision in three taxa that is introduced here. The structure of the genitalia for example, which has not been published in detail, should be restudied in the perspective of the new data.

Only the subgeneric classification of *Carinigera thessalonica* is problematic, though its belonging to *Carinigera* is not a matter of dispute. For the moment being we classify it with *Nymphogena* in the absence of a clearly better alternative.

### *Carinigera* (*Carinigera*) Moellendorff, 1873 (figs 1-4)

*Carinigera* Moellendorff, 1873. Type species: *C. (C.) eximia* (Moellendorff, 1873).

*Olympicosta* Nordsieck, 1972. Type species: *C. (C.) albicosta* (O. Boettger, 1877).

*Angiticosta* Nordsieck, 1977. Type species: *C. (C.) superba* Nordsieck, 1977.

Distribution. – The species of *Carinigera* s.str. are known from NE. Greece, Bulgaria, Makedonija and Serbia. Only *C. (C.) albicostata* is found among *C. (Nymphogena)* species. The occurrence of *C. (C.) buresi pharsalica* Nordsieck, 1974, more to the south in central Greece was considered by Uit de Weerd, Schneider & Gittenberger (2004, 2005) a result of human-induced long-distance dispersal southwards.

Notes. – *Carinigera* s.str. cannot be diagnosed on shell characters. A renewed comparison of the anatomical details of the various species might reveal differentiating character

states in addition to the presence of a penial papilla mentioned by Nordsieck (1972: 9) for this taxon. The clade is well supported by the molecular analysis.

All but one of the species classified with *Carinigera* by Nordsieck (1977) are here placed in *Carinigera* s.str. The monotypic, nominal taxa *Angiticosta* and *Olympicosta* (see Nordsieck, 1972: 17; 1977: 83) were introduced for species with attractively ribbed shells, containing a less prominently developed (“abgeschwächt”) CA. The former taxon is supposed to be characterized conchologically also by an erect outer border of the clausilial blade, whereas in the latter the shells are decollated (“dekolliert”: according to the diagnosis of the subgenus) or slightly decollated (“etwas dekolliert”: after the description of the type species). On the basis of our research on Clausiliidae, we conclude that there is a considerable intrageneric variation in shell sculpture, structure of the clausilial blade and decollation among clausiliid species, which implies that the conchological character states used to characterize *Angiticosta* and *Olympicosta* cannot be accepted as convincing autapomorphies.

Nordsieck (1977: 83) suggested that the penial papilla of *Angiticosta* might be derived independently from a penial appendix, as is present in *Sericata* (sensu Nordsieck, 1972, 1977) and referred to the penial retractor muscle in *Angiticosta* as simple, as in *Carinigera* and in some *Sericata* species. *Olympicosta* was supposed to be characterized in genital anatomy by a penial appendix that is shorter than in most of the other so-called *Sericata* species (Nordsieck, 1972: 17), but Uit de Weerd & Gittenberger (2004a, b) found neither an appendix nor a papilla in *C. (C.) albicostata*.

Two conchologically similar and geographically close species that were classified with *Carinigera* by Nordsieck (1972: 9) are transferred to *Inchoatia* gen. nov., viz. *Inchoatia haussknechti* and *I. megdova*.

The following species are classified with *Carinigera* s.str. (\* = mainly after distribution): *C. (C.) albicosta* (O. Boettger, 1877); *C. (C.) buresi* (A.J. Wagner, 1927); *C. (C.) drenovoensis* (Brandt, 1961); *C. (C.) eximia* (Moellendorff, 1873); *C. (C.) octava* Brandt, 1962; \**C. (C.) pellucida* Dedov & Neubert, 2002; *C. (C.) schuetti* Brandt, 1962; *C. (C.) septima* Brandt, 1962; *C. (C.) superba* Nordsieck, 1977.

#### *Carinigera (Nymphogena)* Sajó, 1968 (figs 5-8)

*Nymphogena* Sajó, 1968. Type species: *C. (N.) praecipua* (Sajó, 1968).

Distribution. – This species group is known from central northern mainland Greece and adjoining southern Makedonija.

Notes. – *Nymphogena* cannot be diagnosed with shell characters, but the clade is well supported in the molecular analysis. A renewed comparison of the anatomical details of the various species might reveal differentiating character states, however. This subgenus differs from *Carinigera* s.str. by the presence of a penial appendix (Nordsieck, 1969: 257; 1972: 8). The various species used to be classified on the basis of their CA type in either *Isabellaria* (G type) or *Sericata* (N type). Uit de Weerd et al. (2004: 92; 2006: 157) also dealt with this subgenus as a separate entity.

The following species are classified with *Carinigera (Nymphogena)* (\* = after distribution and conchological similarity only): \**C. (N.) calabacensis* (Westerlund, 1892); *C. (N.) dextrorsa* (O. Boettger, 1877); *C. (N.) lophauchena* (Sturany, 1894); *C. (N.) praecipua* (Sajó, 1968); *C. (N.) stussineri* (O. Boettger, 1885); *C. (N.) tantilla* (Brandt, 1962); *C. (?N.) thessalonica* (Nordsieck, 1972); *C. (N.) torifera* (O. Boettger, 1885).



Figs 9-12. *Carinigera* & *Vallatia* spec. 9, *Carinigera* (*Sporadhia*) *leucoraphe* (O. Boettger, 1878), Thessalia, Magnissia, Voriai Sporadhes, 4.2 km NNW. of Skiathos village, 150 m alt. (H 18.8 mm); 10-12, *Vallatia val-lata* (Mousson, 1859), Ipiros, Ioannina, Mazia (H 15.0 mm).

#### *Carinigera* (*Sporadhia*) subgen. nov. (fig. 9)

Type species: *C. (S.) leucoraphe* (O. Boettger, 1878).

Diagnosis. – Shells relatively large, not very slender, usually rather pale and fragile, with an obsolete sculpture except for the cervical part of the last whorl where the riblets are still not prominent, however; aperture widely open, roundish with a flaring palatal lip. The clade is well supported in the molecular analysis.

Notes. – The shells of the so-called *Isabellaria* and *Sericata* species of the northern Sporades (= Voriai Sporadhes) are very similar at first sight. Most species have a G type CA, but in *C. (S.) liebegottae* there is an N type. Because of the taxonomic weight given to the CA type, Nordsieck (1974: 131) considered the former ones, i.e. the "*Isabellaria*" species, closely related, and later on (Nordsieck, 1984: 192) the latter, i.e. "*Sericata*" *liebegottae*, generically distinct. The molecular data are unequivocal in contradicting that view. A renewed comparison of the anatomical details of the various species might reveal additional differentiating character states.

The following species are classified with *Carinigera* (*Sporadhia*): *C. (S.) chelidromia* (O.

Boettger, 1889); *C. (S.) leucoraphe* (O. Boettger, 1878); *C. (S.) liebegottae* (Nordsieck, 1984); *C. (S.) praestans* (Westerlund, 1893).

*Vallatia* gen. nov. (figs 10-12)

Type species: *Vallatia vallata* (Mousson, 1859).

Diagnosis. – In *V. vallata*, the only species classified with *Vallatia*, the shell is characterized by a conspicuous cervical thickening, which runs parallel to the apertural border. The species clearly has an isolated position in the molecular analysis and also shows an aberrant geographical distribution.

Distribution. – *Vallatia vallata* has a remarkably disjunct range, with two slightly differentiated subspecies, viz. *V. v. vallata* and *V. v. errata* (Fauer, 1985). There is a distributional gap of about 100 km, occupied by the Pindos mountains. Guided by a geological map W.J.M. Maassen and the first author investigated several limestone-islands along the east side of the Pindos. It turned out that *V. v. errata*, originally only known from the type locality, occurs at a series of localities with limestone rocks at altitudes of 135-750 m, over a distance of 25 km as the crow flies in Thessalia, nomos Karditsa, S-SSE. of Karditsa. The records are as follows (with 1 km square UTM codes): 1 km W. Rousso, 135 m alt., EJ7751; 2.5 km SW. Rousso, 150 m alt., EJ7549; 0.5 km SE. Kalithiro, 170 m alt., EJ7847; 0.4 km NE. Dafnospilia, 210 m alt., EJ8243; 1.5 km NW. Thrapsimi, 450 m alt., EJ8637; 2.1 km N. Loutropigi, 600 m alt., EJ9032; Loutropigi, near graveyard, 750 m alt., EJ9030.

Notes. – Without an explanation, Nordsieck (1974: 131) once considered *Vallatia vallata* a systematically isolated species within the genus *Isabellaria* ("Systematische Stellung isoliert."). Later on (Nordsieck, 1999: 6) that view was not repeated, but it is supported by DNA analysis (Uit de Weerd, Gittenberger & Piel, 2004; Uit de Weerd, Piel & Gittenberger, 2004).

The conspicuous, external white rib shortly behind the aperture, together with a strongly thickened, white apertural lip, narrowing the aperture, is not known from any *Carinigera*, *Isabellaria* or *Inchoatia* species. It is known, however, from a minority of the species in *Cristataria* Vest, 1867. There is also a single subspecies in the speciose genus *Albinaria* Vest, 1867, with a similarly shaped apertural region of the shell, viz. *A. senilis inconstans* (Mousson, 1859). That *Albinaria* subspecies occurs in the same part of Greece where *Vallatia v. vallata* is known from.

*Isabellaria* Vest, 1867 (figs 13-17)

*Isabellaria* Vest, 1867. Type species: *I. isabellina* (L. Pfeiffer, 1842).

*Venusta* O. Boettger, 1877. Type species: *I. venusta* (A. Schmidt, 1868) (= *I. thermopylarum* L. Pfeiffer, 1850).

*Sericata* O. Boettger, 1878. Type species: *I. sericata* (L. Pfeiffer, 1850).

*Euclista* O. Boettger, 1878. Type species: *I. saxicola* (L. Pfeiffer, 1848).

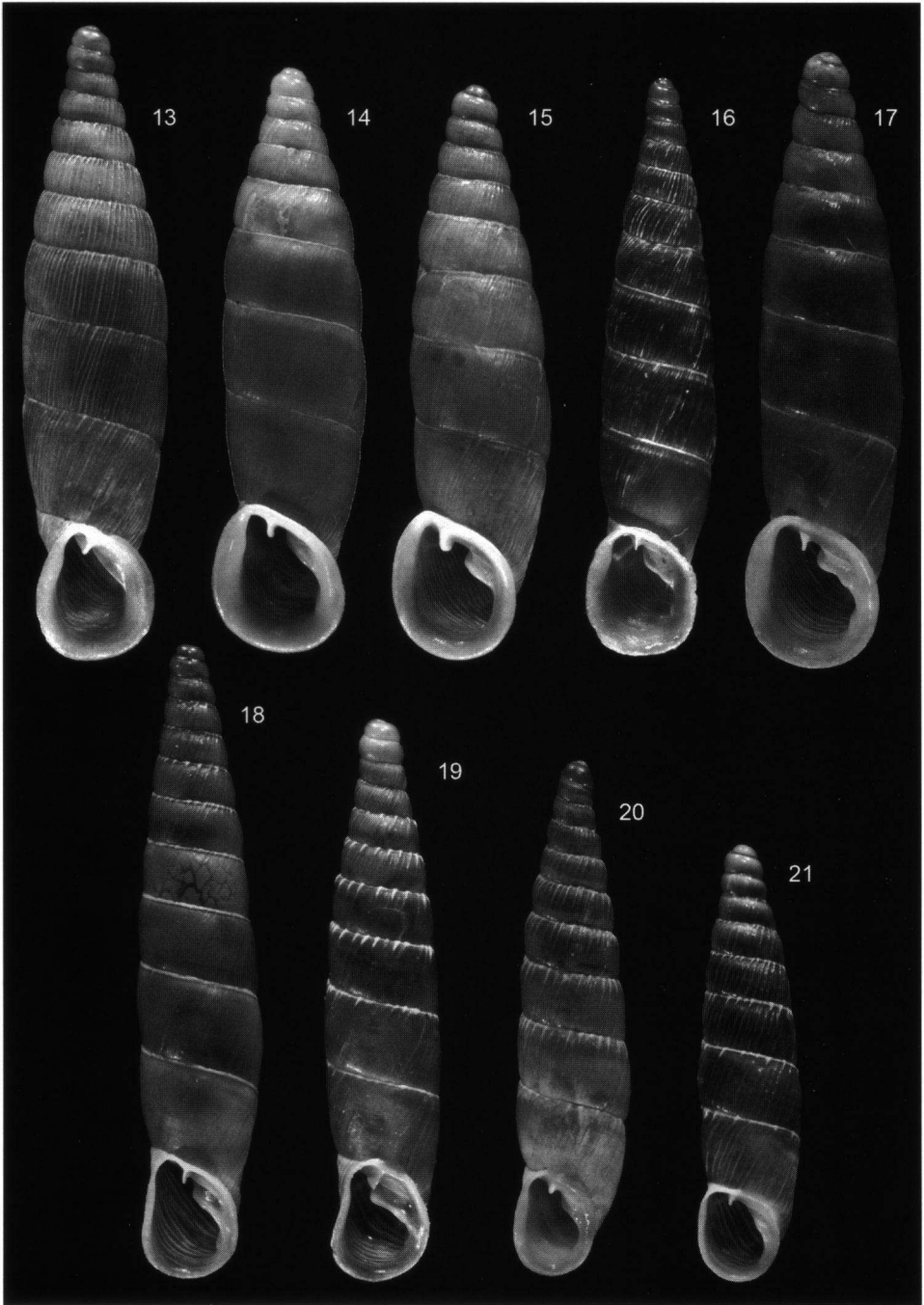
*Bathyclista* O. Boettger, 1885. Type species: *I. bathyclista* (O. Boettger, 1879).

*Charites* Westerlund, 1901. Type species: *I. bathyclista* (O. Boettger, 1879).

*Protalbinaria* A.J. Wagner, 1923. Type species: *I. sericata* (L. Pfeiffer, 1850).

Distribution. – The various *Isabellaria* species are concentrated in SE. Greece.

Notes. – The fact that five synonyms of *Isabellaria* can be listed illustrates the confusing nomenclatorial history of the taxa dealt with in this paper. *Isabellaria* cannot be diagnosed with shell characters anymore because of the devaluation of the CA type as a prime character, but the clade is well supported in the molecular analysis. A renewed compari-





son of the anatomical details of the various species might reveal differentiating character states, but not enough details have been published in the literature to enable such an approach.

Without adding any new data or considerations, *Sericata*, once considered a genus by Nordsieck (1972: 7), was lowered in rank to a subgenus of *Albinaria*.

The following species are classified with *Isabellaria* (\* = after distribution and conchological similarity only): *I. abyssoclista* (O. Boettger, 1883); *I. almae* (O. Boettger, 1889); *I. bathyclista* (O. Boettger, 1879); *I. clandestina* (Rossmässler, 1857); *I. isabellina* (L. Pfeiffer, 1842); *I. lutracana* (Nordsieck, 1977); \**I. parnassia* O. Boettger, 1888; *I. perplana* (O. Boettger, 1877); *I. riedeli* Brandt, 1961; *I. saxicola* (L. Pfeiffer, 1848); *I. sericata* (L. Pfeiffer, 1850); *I. thermopylarum* (L. Pfeiffer, 1850).

### *Inchoatia* gen. nov. (figs 18-21)

Diagnosis. – Shell slender to very slender, elongated spindle-shaped with straight sides; with a white, narrow, sutural line and sutural papilla, which may be elongated as axial riblets. Aperture slightly or not at all protruding; in the latter case sometimes interrupted parietally. Since the penis may be provided with either a papilla or an appendix, the species have been classified before in *Carinigera* and *Sericata*, respectively. The clade is well supported in the molecular analysis.

Distribution. – The genus is known from western mainland Greece (Uit de Weerd, Gittenberger & Piel, 2004: 56, fig. 4.3; 66, fig. 4.9 A; Uit de Weerd, Piel & Gittenberger, 2004: 535, fig. 2B; 539, fig. 5A).

Notes. – The conspicuous conchological similarity between *I. inchoata* and *I. haussknechti*, as well as their distributions, suggest that these species are closely related. This was mentioned by Nordsieck (1974: 127), who considered the similarity a result of convergent evolution, and classified the two species with *Sericata* and *Carinigera*, respectively, on the basis of the structure of the male part of the genital organs, with either a papilla or an appendix. The ranges of the various species are quite disjunct, which makes it even more subjective than usual to judge upon the species versus subspecies status of the various forms that can be recognized.

The following species are classified with *Inchoatia*: *I. haussknechti* (O. Boettger, 1886); *I. inchoata* (O. Boettger, 1889); *I. megdova* (Nordsieck, 1974); *I. regina* (Nordsieck, 1972).

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Figs 13-21. *Isabellaria* & *Inchoatia* spec. 13, *Is. isabellina isabellina* (L. Pfeiffer, 1842), Peloponnisos, Korinthos, 1 km W. of Katakali, 100 m alt. (H 16.4 mm); 14, *Is. thermopylarum thermopylarum* (L. Pfeiffer, 1850), Sterea Ellas, Fokis, 5 km SSW. of Gravia (H 18.9 mm); 15, *Is. bathyclista* (O. Boettger, 1879), Sterea Ellas, Evia, 0.1 km E. of Limni, 110 m alt. (H 14.9); 16, *Is. sericata sericata* (L. Pfeiffer, 1850), Sterea Ellas, Evia, NW-side Steni Dirphios, 400 m alt. (H 21.1 mm); 17, *Is. clandestina clandestina* (Rossmässler, 1857), Thessalia, Magnissia, 4 km WSW. of Marathia, 15 m alt. (H 15.8 mm). 18, *Inchoatia regina* (Nordsieck, 1972), Ipiros, Arta, 17.5 km NE. of Arta, 180 m alt. (H 16.5 mm); 19, *In. megdova tavropodiensis* (Fauer, 1993), Sterea Ellas, Evritania, 11.5 km WNW. of Karpenisi, 370 m alt. (H 15.0 mm); 20, *In. haussknechti alticola* (Nordsieck, 1974), Sterea Ellas, Evritania, 4 km N. of Karpeniso, Mt. Timfristos, 1900 m alt. (H 13.4 mm); 21, *In. inchoata inchoata* (O. Boettger, 1889), Ipiros, Prevesa, 21.5 km NNW. of Prevesa, 650-725 m alt (H 11.3 mm).

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