

Differentiation of small limnic European caenogastropods by characters of the intestine

HANS D. BOETERS

Karneidstrasse 8, D 81545 München, Germany; boeters@online.de

Among the European Hydrobiidae and Moitessieriidae characters of the intestine can be useful for a differentiation of taxa at the levels of sexes, species, subgenera, genera and even families. These characters often reflect different nutritive habits.

Key words: Caenogastropoda, Hydrobiidae, Moitessieriidae, intestine, differentiation of taxa, dependence on food supply.

INTRODUCTION

It is difficult to distinguish closely related species of Hydrobiidae and Moitessieriidae (Caenogastropoda) conchologically. Based on Troschel's "Das Gebiss der Schnecken zur Begründung einer natürlichen Classification" (1856-63) attempts have been made to distinguish closely related species by characters of their radula, but only occasionally with success. For example, Arconada et al. (2007: 142) distinguished two species of *Alzoniella* (*Navarriella*) Boeters, 2001, by characters of the rachidean tooth. As regards soft parts, Seibold (1904) described the anatomy of *Bythiospeum quenstedti* (Wiedersheim, 1873) already early in

the 20th century, Bregenzer (1916) that of *Bythinella dunkeri* (Frauenfeld, 1857), and Robson (1922) that of *Ecrobia ventrosa* (Montagu, 1803), but these authors did not compare the species with close relatives. A comparative approach was introduced by Krull (1935). Radoman (1955) was the pioneer in describing small limnic prosobranchs using features of their reproductive organs in addition to conchological characters. Since Radoman it has become usual to describe the copulatory organs of males and the female reproductive tract.

Features of the reproductive organs, even if in combination with conchological characters, do not always allow a clear distinction of related species (Haase et al., 2007: 1). This led Boeters (1971) to examine other organs as well, including the digestive tract. Usually, Hydrobiidae such as *Ecrobia* Stimpson, 1865, and *Bythinella* Moquin-Tandon, 1856, have an intestinal loop between the stomach and the wall of the mantle cavity (see Robson, 1922; Bregenzer, 1916). Boeters's interest in intestinal characters dates from 1971 when he found that, in *Bythiospeum* Bourguignat, 1882, there are two intestinal loops, the usual loop and a second one behind the wall of the mantle cavity in its roof (1971: 169, 171 figs 6, 10b). The second loop had already been figured by Seibold (1904: pl. 6 fig. 3) but had not received any attention. Even

Radoman never illustrated the intestinal tract. However, Hershler & Longley (1986) described *Phreatodrobia rotunda* and anatomical characters of this species, and later on Hershler & Ponder (1998) referred to this description in stating that coiling of the intestine at the dorsal side of the style sac is known for few hydrobioids (such as the mentioned species), and appears to be correlated with minute size and/or with living in caves or phreatic environments.

In the same year Boeters (1998: 45, legend to figs 3-11) demonstrated that characters of the intestine can be useful for a differentiation of the sexes, and at the levels of species, genera and even families. This observation will be dealt with in greater detail here.

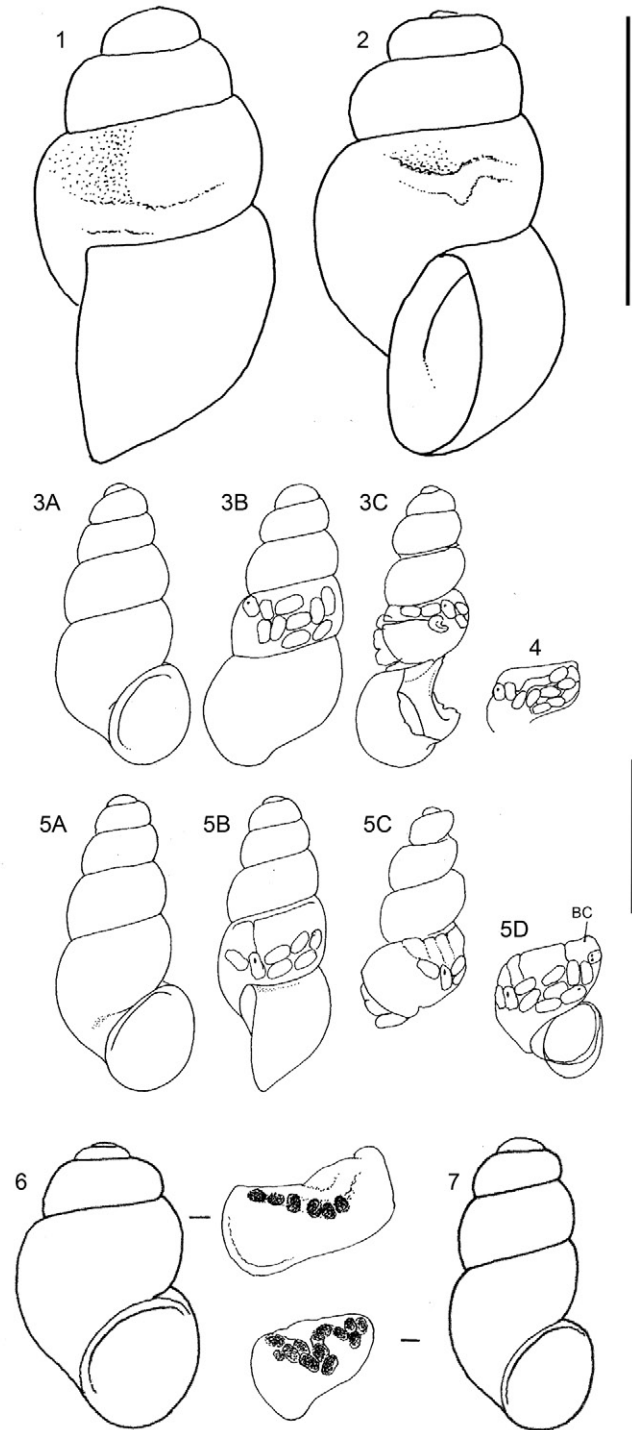
MATERIALS AND METHODS

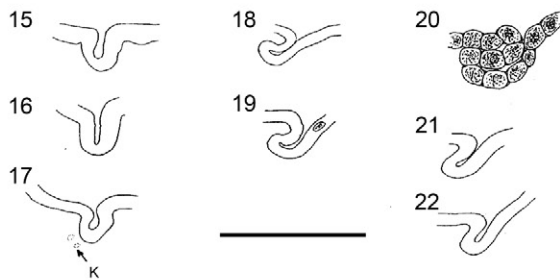
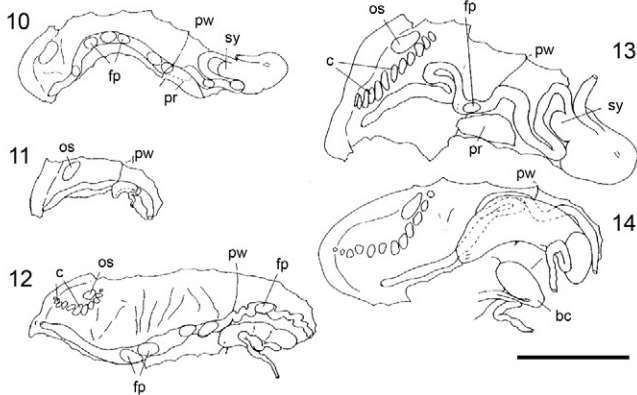
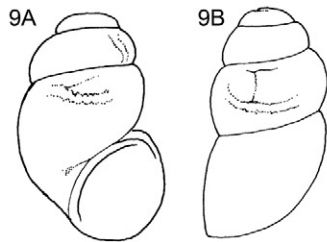
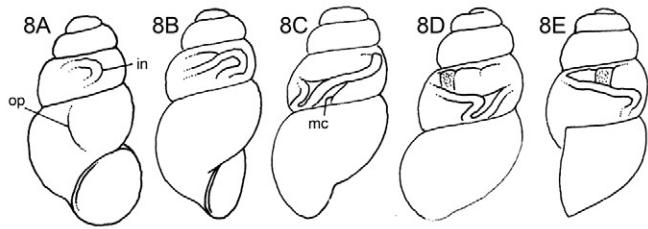
Specimens from the following species and localities were used (BOE = collection Boeters):

Bythiospeum acicula (Held, 1838). Germany, Upper Bavaria, between Wallgau and Obernach, valley of Obernacher Ache, Oskar-von-Miller-Institut für Wasserbau der TU München, area "Helgoland", pipe about 7 m deep; Boeters leg. 7.viii.1982; BOE 1094.

Belgrandiella saxatilis (Reyniès, 1844). France, Tarn-et-Garonne, Reyniès-sur-le-Tarn, well chamber downhill of Chateau; Boeters leg. 4.ix.1972; BOE 0511.

Figs 1-7. *Bythinella* and *Bythiospeum* spp. 1-2, *Bythinella* (*B.*) *batalleri* Bofill, 1925. Spain, Tarragona, Alfara, Fuente del Masca; BOE 1241; 1, ♀ and 2, ♂, each with intestine seen through shell wall; scale 2 mm. 3-5, *Bythiospeum acicula* (Held, 1838). Germany, Upper Bavaria, Obernacher Ache (interstitial); BOE 1094; 3-4, ♂♂ (shell partially removed for 3C to show penis under second to last faecal pellet, and completely removed for 4); 5, ♀ (shell removed for 5C and 5D; BC = bursa copulatrix); scale 1 mm. 6, *Bythinella* (*B.*) *syntricus* Boeters & Falkner, 2008. France, Ariège, Moulis, L'Eros; BOE 2595 ex 1063; ♂ (shell and lateral view of last body whorl with intestine in front of mantle skirt); scale 2 mm. 7, *Bythinella* (*B.*) *rouchi* Boeters & Falkner, 2008. Locality as for fig. 6; BOE 2597 ex 1063; ♂ (shell and lateral view of last body whorl); scale 2 mm.





Alzoniella cantabrica (Boeters, 1983). Spain, Santander, San Vicente de la Barquera, at right side of road from Treceno to La Revilla, ditch; Boeters leg. May/June 1974; BOE 0582.

A. perrisii (Dupuy, 1851). France, Pyrénées-Atlantiques, Bayonne, St. - Pierre-d'Irube, Cantegril, several neighboured springs; Boeters leg. 28.ix.1968; BOE 0193.

A. pyrenaica (Boeters, 1983). France, Pyrénées-Atlantiques, Tardets-Sorholus, Grotte de Suhare; Lescher-Moutoue don. 23.iv.1975; BOE 0754.

Bythinella (*B.*) *batalleri* Bofill, 1925. Spain, Tarragona, Alfara, Fuente del Masca; Hinz leg.; iv.1984; BOE 1291.

B. (*Thibynella*) *collingi* Boeters, 2009. France, Lozère, between Balsièges and Bramonas vis-à-vis Le Villaret 8.5 km WSW of Mende, source downhill of sentier and 50 m W of Ravin de la Charbonnière; Boeters leg. 15.ix.2008; BOE 2948.

B. (*B.*) *moulinsii* (Dupuy, 1849). France, Lozère, between Balsièges and Bramonas vis-à-vis Le Villaret 8.5 km WSW of Mende, source downhill of sentier and 50 m W of Ravin de la Charbonnière; Boeters leg. 15.ix.2008; BOE 2947.

B. (*B.*) *rouchi* Boeters & Falkner, 2008. France, Ariège, Moulis, L'Eros, spring 300 m S of Source-La-Marte; Boeters leg. 2.vii.1981; BOE 2597 ex 1063.

Figs 8-22. **8**, *Bythinella* (*Thibynella*) *collingi* Boeters, 2009. France, Lozère, between Balsièges and Bramonas; BOE 2948; ♀ (in = intestine, mc = posterior wall of mantle cavity, op = operculum); scale 1 mm. **9**, *Bythinella* (*B.*) *moulinsii* (Dupuy, 1849). Locality as for fig. 8; BOE 2947; ♀ (shell with intestine seen through shell wall); scale 1 mm. **10-14**, after Bodon & Giusti (1991); c = ctenidium, fp = fecal pellet, os = osphradium, pr = prostate gland, pw = posterior wall of pallial cavity, sy = style sac. **10-11**, *Moitessieria simoniana* (Saint-Simon, 1848). France, Ariège, Moulis. **10**, ♂; **11**, ♀; scale 1 mm. **12**, *Paladilhia pleurotoma* Bourguignat, 1865. France, Hérault, Prades-le-Lez, Source du Lez; ♀; scale 1 mm. **13-14**, *Spiraliix rayi* (Locard, 1882). France, Cote-d'Or, Bèze, Grotte de Bèze. **13**, ♂; **14**, ♀; scale 1 mm. **15-22**, after Boeters 1983 (intestine in mantle roof; fig. 20 shows faecal pellets; K = gill leaflets); scale 1 mm. **15-17**, *Belgrandiella saxatilis* (Reyniès, 1844). France, Tarn-et-Garonne, Reyniès-sur-le-Tarn; BOE 0511. **18-19**, *Alzoniella perrisii* (Dupuy, 1851). France, Pyrénées-Atlantiques, St. Pierre-d'Irube; BOE 0193. **20**, *Alzoniella pyrenaica* (Boeters, 1983). France, Pyrénées-Atlantiques, Tardets-Sorholus; BOE 0754. **21-22**, *Alzoniella cantabrica* (Boeters, 1983). Spain, Santander, between Treceno and La Revilla; BOE 0582.

B. (B.) syntriculus Boeters & Falkner, 2008. France, Ariège, Moulis, L'Eros, spring 300 m S of Source-La-Marte; Boeters leg. 2.vii.1981; BOE 2595 ex 1063.

For the dissection of the animals, see Boeters (1999). The figures are drawn with a ZEISS 45 degree Drawing Prism. The appendix lists species of Moitessieriidae and Hydrobiidae with well examined intestine.

RESULTS

In Hydrobiidae as well as in Moitessieriidae the intestine principally forms a loop like a Z behind the stomach and in front of the mantle cavity. In some cases that loop is followed by a second loop in the roof of the mantle cavity, such as the Z-like second loop in *Bythiospeum*. The following review, with the exception of the notes on the family level, deals only with the curvature of the intestine in the roof of the mantle cavity.

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Male versus female (sexual dimorphism). – If the shell is transparent and the animal weakly pigmented, females can clearly be distinguished from males. In females the intestine runs along the complex of albumen and capsule gland, which occupies more space than the prostate of males. As a consequence, in females (*Bythinella*: Fig. 1; *Bythiospeum*: Fig. 5A-D) the intestine is strongly curved, instead of only slightly so in males (*Bythinella*: Fig. 2; *Bythiospeum*: Figs 3A-3C, 4).

Species level. – The use of characters of the intestine for a differentiation at the species level can be demonstrated by two *Bythinella* species, viz. *B. (B.) syntriculus* Boeters & Falkner, 2008, and *B. (B.) rouchi* Boeters & Falkner, 2008. They represent one of the rare cases of partly co-occurring *Bythinella* species. The shell and the final section of the intestine in the roof of the mantle cavity are illustrated for male individuals of both species (Figs 6, 7). The animals were collected together in a spring in the French department of Ariège. The soft parts of *B. (B.) syntriculus*, which lives mainly in the outflow of the spring, are strongly pigmented. In contrast, *B. (B.) rouchi*, which can be found in the mouth of the

spring, is scarcely pigmented. The latter species may have invaded the interstitial. In *B. (B.) syntriculus* the final section of the intestine follows the prostate with a broad curve, whereas in *B. (B.) rouchi* it has a more irregular, V-like shape. These differences reflect that *B. (B.) rouchi* depends on a comparatively poor food supply in its subterranean or quasi subterranean habitat.

Characters of the intestine can also be used to distinguish *Bythinella (Thibynella) collingi* Boeters, 2009, and *B. (B.) moulinsii* (Dupuy, 1851), which represent another rare case of co-occurring *Bythinella* species. They can be observed in the French department of Lozère, in the mouth of springs. *Bythinella (T.) collingi* is a subterranean, blind species that forms a distinct, intestinal, Z-like loop in the roof of the mantle cavity (Fig. 8), whereas in *B. (B.) moulinsii* there is no such loop (Fig. 9).

Genus level. – The use of characters of the intestine for a differentiation at the genus level can be demonstrated by two examples. The relevant characters have been described before, but that had not yet received the attention that it deserves.

Spiralix and *Moitessieria*. – *Spiralix* Boeters, 1972, was described as a subgenus of *Paladilhia* Bourguignat, 1865, with *Lartetia rayi* Locard, 1882, as its type species, on the basis of only shell characters. Bodon & Giusti (1991) described the anatomy not only of the type species of both *Paladilhia* (Fig. 12) and *Spiralix* (Figs 13-14), but also of *Moitessieria* Bourguignat, 1863 (Figs 10-11). They regarded the type species of *Spiralix* as a species of *Moitessieria*. Later on, *Spiralix* was considered a distinct genus, as is reflected, for example, by the description of *Spiralix ovidiensis* Girardi & Bertrand, 2009, and *Spiralix thaisensis* Girardi, 2009. The fact that *Spiralix* forms an intestinal loop in the roof of the mantle cavity, in contrast to *Paladilhia* and *Moitessieria*, where such a loop is lacking, supports this view.

Alzoniella and *Belgrandiella*. – On the basis of the anatomy, Boeters (1983) classified several species into the genus *Belgrandiella* A.J. Wagner, 1928, viz. *B. saxatilis* (Reyniés, 1844) (Figs 15-17), *B. perrisii* (Dupuy, 1851) (Figs 18-19), *B. pyrenaica* Boeters, 1983, (Fig. 20) and *B. cantabrica* Boeters, 1983, (Figs 21-22). Subsequently, based on characters of the female reproductive tract, *B. perrisii*, *B. pyrenaica*

and *B. cantabrica* were attributed to *Alzoniella* Giusti & Bodon, 1984, (Arconada et al., 2007). This revision is supported by characters of the intestine, which in *Alzoniella* forms a loop in the roof of the mantle cavity instead of a simple curve as in *Belgrandiella*.

Family level. – The characters of the intestine are also useful for a differentiation between Hydrobiidae and Moitessieriidae. In Hydrobiidae, in both males and females, the intestine upon leaving the stomach encircles the crystal style sac closely when running back to the distal wall of the stomach and then changes again its direction by turning towards the pallial cavity up to the mantle skirt (Boeters, 1998: 45, Fig. A3; 2003: 37, 20, Fig. 51B). However, in Moitessieriidae, again in both males and females, the intestine upon leaving the stomach runs clearly beyond the crystal style sac before turning back to run parallel with the prostata and the albumen gland, respectively, towards the pallial cavity (Figs 10, 13; Boeters, 1998: 45, Fig. A4).

CONCLUSIONS

Characters of the intestine of small limnic caenogastropods have not yet found adequate attention. They can be a useful tool for a differentiation of sexes and at various taxonomic levels. The differences in the intestine, which imply an elongation of the digestive tract in various taxa, might reflect that for example *Bythinella* (*B.*) *rouchi* depends on a comparatively poor food supply in its subterranean or quasi subterranean habitat. The same applies to *B. (Thibynella) collingi*, which is also mainly a subterranean, blind species, occurring only occasionally in the mouth of springs. *Bythinella (Thibynella) collingi* has a distinct, intestinal, Z-like loop, like the subterranean *Bythiospeum* species and *B. (B.) rouchi* has at least a V-like instead of a flat curved final section of the intestine as is usual in the nominate subgenus. *Bythinella (B.) rouchi* and *B. (Thibynella) collingi* may have secondarily invaded the interstitial since the overwhelming majority of the *Bythinella* species occurs in overground habitats. These differences are in accordance with the fact that *Belgrandiella* species can be found in springs, but *Alzoniella* species rather in subterranean habitats with their poorer food supply.

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APPENDIX

Species of Moitesseriidae and Hydrobiidae with well examined intestine.

- Moitesseria* Bourguignat, 1863. Intestine in the roof of the mantle cavity curved without loop.
- massoti* Bourguignat, 1863 (Bodon & Giusti, 1991: 15 figs B, E, 22 figs D, P)
- simoniana* (Saint Simon, 1848) (Bodon & Giusti, 1991: 7 figs E, G)
- Paladilhia* Bourguignat, 1865. Intestine in the roof of the mantle cavity curved without loop.
- pleurotoma* Bourguignat, 1865 (Girardi, 2009: 131 fig. 3)
- roselloi* Girardi, 2003 (Girardi, 2003: 74 fig. 3)
- Palaospeum* Boeters, 1999. Intestine in the roof of the mantle cavity curved without loop.
- bessoni* Bernasconi, 1999 (Boeters, 1999: 196)
- Sardopaladilhia* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998. Intestine in the roof of the mantle cavity curved without loop.
- plagigeyrica* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998 (Manganelli et al., 1998 62 figs 18-19):
- Spiralix* Boeters, 1972. With intestinal loop in the roof of the

- mantle cavity.
- rayi* (Locard, 1882) (Bodon & Giusti, 1991: 15 fig. I)
- valenciana* Boeters, 2003 (Boeters, 2003: 22 fig. 55)
- vitrea* (Draparnaud, 1801) (Boeters, 1998: 46 fig. B8)
- Alzoniella* Giusti & Bodon, 1984. With intestinal loop in the roof of the mantle cavity.
- cornucopia* (De Stefani, 1880) (Manganelli et al., 1995: 177 fig. 17)
- fabrianensis* (Pezzoli, 1969) (Manganelli et al., 1995: 179 fig. 29)
- finalina* Giusti & Bodon, 1984 (Giusti & Bodon, 1984: 161 fig. 2H)
- Avenionia* Nicolas, 1882. Intestine in the roof of the mantle cavity curved without loop.
- berenguieri* (Bourguignat, 1882) (Bodon et al., 2000: 192 fig. 14)
- Belgrandiella* A.J. Wagner, 1928. Intestine in the roof of the mantle cavity curved without loop.
- ganslmayri* Haase, 1993 (Haase, 1993: 183 fig. 1)
- saxatilis* Reynies, 1844 (Girardi, 2003: fig. 3.1)
- Bythinella* (*Bythinella*) Moquin-Tandon, 1856. Intestine in the roof of the mantle cavity curved without loop.
- dunkeri* (Frauenfeld, 1857) (Bregenzer, 1916: pl. 16 fig. 3)
- isolata* Boeters, 2006 (Boeters, 2006 : 6 fig. 10)
- Bythinella* (*Thibynella*) Boeters, 2009. With intestinal loop in the roof of the mantle cavity.
- collingi* Boeters, 2009 (Boeters, 2009: 58 fig. 1)
- Bythiospeum* Bourguignat, 1882. With intestinal loop in the roof of the mantle cavity.
- diaphanum* (Michaud, 1831) (Girardi, 2002: figs 4-5)
- gardonense* Girardi, 2009 (Girardi, 2009: 171 fig. 2)
- klemmi* (Boeters, 1969) (Girardi, 2001: 17 fig. 4)
- quenstedti* (Wiedersheim, 1873) (Seibold, 1904: pl. 6 fig. 3)
- Guadiella* Boeters, 2003. With intestinal loop in the roof of the mantle cavity.
- ramosae* Boeters, 2003 (Boeters, 2003: 22 fig. 59)
- Hadziella* Kuscer, 1932. With intestinal loop in the roof of the mantle cavity.

- anti* Schütt, 1960 (Bodon et al., 2001: 121 fig. 65)
- Hauffenia* Pollonera, 1898. With intestinal loop in the roof of the mantle cavity.
- erythropomatia* Hauffen, 1856 (Bodon et al., 2001: 112 figs 20, 25)
- kerschneri* Zimmermann, 1930 (Haase, 1993: 96 fig. 5; Bodon et al., 2001: 185 fig. 219)
- michleri* Kuscer, 1932 (Bodon et al., 2001: 124 fig. 85)
- subcarinata* Bole & Velkovrh, 1987 (Bodon et al., 2001: 191 fig. 234)
- tellini* (Pollonera, 1898) (Bodon et al., 2001: 123 figs 76-77)
- Heideella* Backhuys & Boeters, 1974. Intestine in the roof of the mantle cavity curved without loop.
- andreae* Backhuys & Boeters, 1974 (Bodon et al., 1999: 96 fig. 23)
- Heraulitia* Bodon, Manganelli & Giusti, 2001. With intestinal bulge in the roof of the mantle cavity.
- exilis* (Paladilhe, 1867) (Bodon et al., 2001: 208 fig. 291)
- Islamia* Radoman, 1973. With intestinal loop in the roof of the mantle cavity.
- bomangiiana* Boeters & Falkner, 2003 (Boeters & Falkner, 2003: 15 fig. 1a)
- cianensis* Bodon, Manganelli, Sparacio & Giusti, 1995 (Bodon et al., 1995: 47 fig. 12)
- consolationis* (Bernasconi, 1985) (Bodon et al., 2001: 206 fig. 285)
- emanuelei* Girardi, 2009 (Girardi, 2009: 53 fig. 1B)
- gaiteri* Bodon, Manganelli, Sparacio & Giusti, 1995 (Bodon et al., 1995: 47 fig. 22)
- globulus* (Bofill, 1909) (Bodon et al., 2001: 183 fig. 205)
- minuta* (Draparnaud, 1805) (Bodon et al., 2001: 197).
- Istriana* Velkovrh, 1971. Intestine in the roof of the mantle cavity curved without loop.
- mirnae* Velkovrh, 1971 (Bodon & Giovannelli, 1993: 199 fig. 12)
- Kerkia* Radoman, 1978. With intestinal loop in the roof of the mantle cavity.
- kusceri* (Bole, 1961) (Bodon et al., 2001: 137 fig. 121)
- Lobaunia* Haase, 1993. With intestinal loop in the roof of the mantle cavity.
- danubialis* Haase, 1993 (Haase, 1993: 101 fig. 12)
- Ohrigocea* Hadzisce, 1959. With intestinal loop in the roof of the mantle cavity.
- samuili* Hadzisce, 1959 (Bodon et al., 2001: 146 fig. 148)
- Orientalina* Radoman, 1978. Intestine in the roof of the mantle cavity curved without loop.
- curta* (Küster, 1852) (Bodon et al., 1992: 89 fig. 26)
- Palacanthilhiosis* Bernasconi, 1988. Intestine in the roof of the mantle cavity curved without loop.
- carolinae* Girardi, 2009 (Girardi, 2009: 99 figs 6Ab, 6Bb)
- kuiperi* Girardi, 2009 (Girardi, 2009: 101 figs 8Ed, 8Ef)
- Plesiella* Boeters, 2003. With intestinal loop in the roof of the mantle cavity.
- guipuzcoa* Boeters, 2003 (Boeters, 2003: 22 fig. 60, 27 fig. 85)
- Pseudohoratia* Radoman, 1967. With intestinal bulge in the roof of the mantle cavity.
- ochridana* (Polinski, 1929) (Bodon et al., 2001: 151 fig. 161)
- Sardohoratia* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998. With intestinal loop in the roof of the mantle cavity.
- islamioides* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998 (Manganelli et al., 1998: 66 fig. 42)