

**The genus *Avenionia* Nicolas, 1882, redefined
(Gastropoda, Prosobranchia, Hydrobiidae)**

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Anatomical study of specimens of the type species of *Avenionia*, *Avenionia vaysseri* Nicolas, 1882 (junior synonym of *Paulia berenguieri* Bourguignat, 1882, currently *A. brevis berenguieri*), from southern France, revealed characters different from those known in the available literature and prompted the redefinition of *Avenionia*. The other *Avenionia* species from France and nearby countries of central-western Europe are tentatively left in this genus, whereas taxa from Italy which were included in *Avenionia* on formerly available evidence will have to be assigned to another genus.

Key words: Gastropoda, Prosobranchia, Hydrobiidae, *Avenionia*, France, Europe, taxonomy.

INTRODUCTION

The type species of *Avenionia*, *Avenionia vaysseri* Nicolas, 1882, junior synonym of *Paulia berenguieri* Bourguignat, 1882 (Boeters, 1967; Kabat & Hershler, 1993), was unknown anatomically so that the diagnosis of the genus was based on allegedly related taxa from central-western Europe. The recent finding of living specimens closely matching the

lectotype selected by Boeters (1967) in a site near the type locality, prompted anatomical study which revealed characters different from those reported for the species/genus (Boeters & De Winter, 1983; Boeters, 1998).

This paper redescribes the type species, redefines the genus *Avenionia* and analyses the relationships between the French, central-western European and Italian taxa hitherto included in this genus.

MATERIALS AND METHODS

Shells and live specimens were collected with a net and by sorting sediment from a subterranean spring. Shells and radulae (obtained by dissecting out buccal bulbs and washing in distilled water) were mounted on copper blocks with conductive glue, sputter-coated with gold and photographed using a Philips 515 SEM. All dimensions (shell height, shell diameter, aperture height and aperture diameter) were measured using a micrometer lens on the light microscope (Wild M5A). Unrelaxed material preserved in 80% ethanol was studied by light microscopy (Wild M5A). Bodies were isolated after crushing the shells and were dissected using very fine pointed watchmaker's forceps. Images of the whole body and isolated parts of the genitalia were drawn using a Wild camera lucida.

The material studied is deposited in the following collections: Museo Zoologico de "La Specola" (Sezione del Museo di Storia Naturale dell'Università di Firenze, Firenze, Italy; MZUF), F. Giusti (Dipartimento di Biologia Evolutiva dell'Università, Siena, Italy), M. Bodon (Via delle Eriche 100/8, Genova, Italy), S. Cianfanelli (P.le Porta Romana 13, Firenze), and H. Girardi (Montfavet, France).

REDESCRIPTION AND TAXONOMIC STATUS OF *AVENIONIA VAYSSIERI* NICOLAS, 1882, A JUNIOR SYNONYM OF *PAULIA BERENGUERI* BOURGUIGNAT, 1882

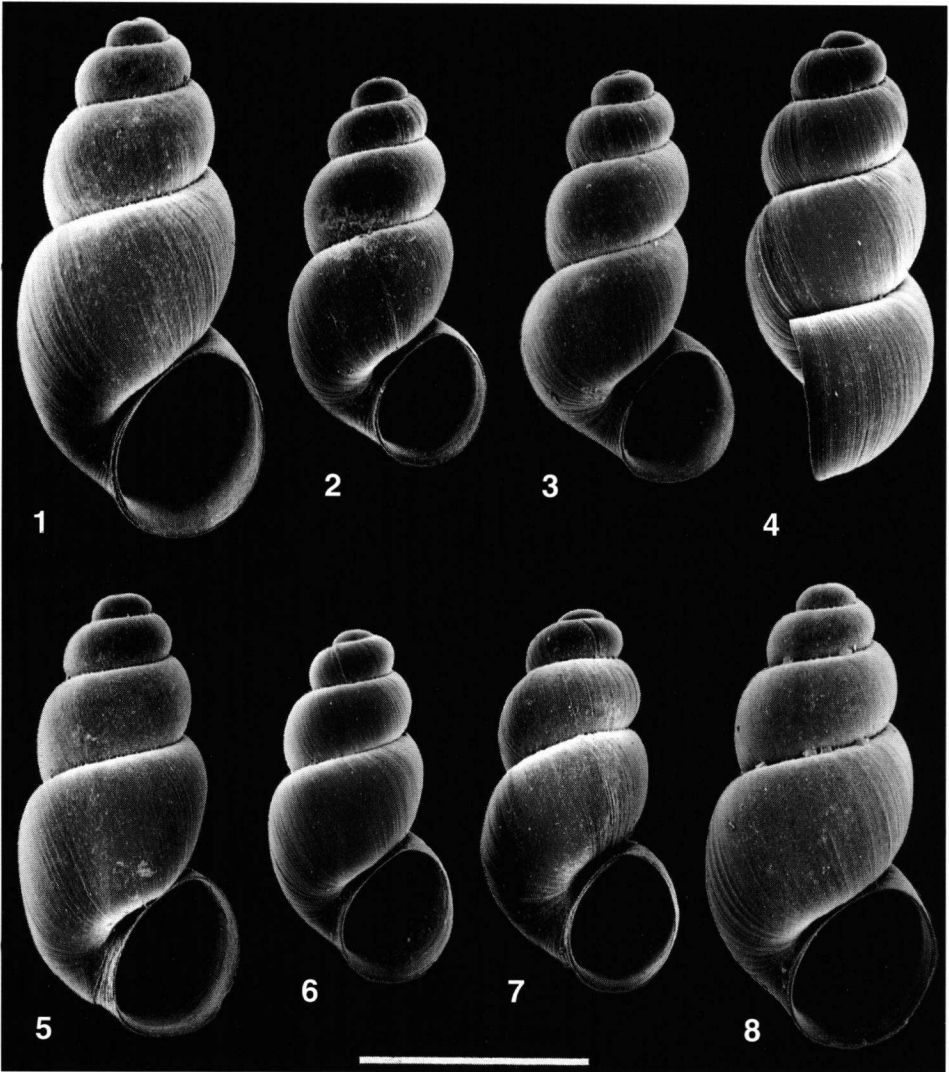
Description. — Shell (figs 1-11) very small, cylindro-conical, bythinelloid, waxy, whitish and translucent when fresh; apex rather acute; spire consisting of $3\frac{3}{4}$ -4 $\frac{3}{4}$ convex whorls; last whorl wide, $\frac{2}{3}$ - $\frac{3}{4}$ of shell height; sutures very deep; aperture rather small, oval and slightly oblique; peristome thin, continuous, adhering to last whorl or slightly detached, not reflected and not sinuous, but sometimes very slightly concave (in lateral view) at upper external margin; umbilicus variably narrow, slit-like; surface of protoconch finely malleated; surface of teleoconch rather smooth, with more or less evident growth lines and very finely malleated on the first whorls.

Dimensions. — Shell height, 1.55-2.89 mm; shell diameter, 0.81-1.29 mm; aperture height, 0.62-0.97 mm; aperture diameter, 0.46-0.75 mm.

Operculum (fig. 12). — Corneous, paucispiral, thin, pale yellowish in colour, yellowish-orange at centre, with subcentral nucleus and without projection or thickening on inner side.

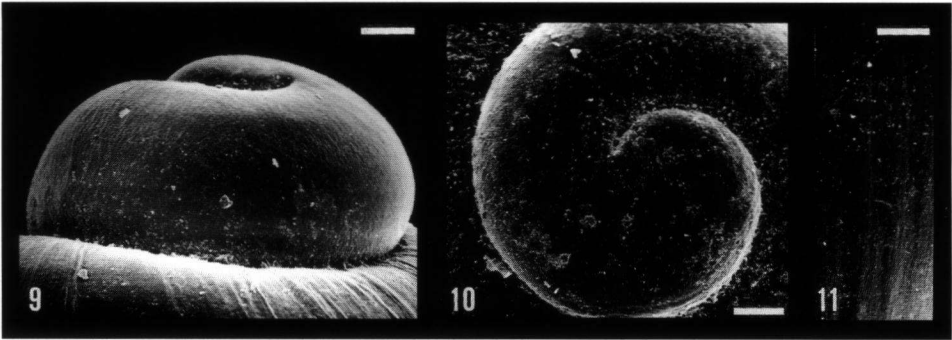
Body (fig. 13). — Almost unpigmented, traces of pigment only on walls of visceral sac; eye spots small; pallial tentacle absent. Sparse whitish granules in walls of body and foot; group of whitish granules behind base of eyes; buccal mass, body and base of tentacles intensely pink coloured (all these details are visible only in living specimens).

Male genitalia (figs 14-18). — Testis near apex of visceral sac, with many lobes;



Figs 1-8. Shells of *Avenionia brevis berenguieri* (Bourguignat, 1882), collected in the spring of the fountain of St Victor-la-Coste (Gard, France). Scale bar 1 mm.

vas efferens thick, functioning as seminal vesicle; prostate gland elongated, its distal portion bulging slightly into pallial cavity; vas deferens thin, arising from anterior side of prostate gland, crossing body wall, entering base of penis and running (as penial duct) all along right (outer) side of penis to end at tip of penis proper; penis unpigmented, bent upon itself inside pallial cavity, squat, with sides wrinkled near base; penis with apex bifid, divided into very large subapical lobe and slender tip of penis proper; subapical



Figs 9-11. Microsculpture of surface of protoconch (fig. 9, lateral view; fig. 10, upper view) and teleoconch on the last whorl (fig. 11) of *Avenionia brevis berenguieri* (Bourguignat, 1882), collected in the spring of the fountain of St. Victor-la-Coste (Gard, France). Scale bar 50 μ m.

lobe with three glandular swellings along its border, one short, the others long, band-like and sinuous; another very small, glandular lobe on dorsal side of penis close to base of subapical lobe; tip of penis proper conical, slender and pointed, about as long as penial lobe.

Female genitalia (figs 19-21). — Ovary near apex of visceral sac, lobed; short gonadal oviduct, ending where gonopericardial duct enters gonadal oviduct and renal oviduct begins; renal oviduct adhering to pallial oviduct, wide, twisted on itself to form short loop; two seminal receptacles: proximal seminal receptacle (RS2) arising beyond end of loop, larger than distal and with evident, slender duct; distal seminal receptacle (RS1) small, without evident duct, arising very close to where duct of bursa copulatrix enters oviduct, but situated rather close to proximal one; bursa copulatrix very large, shaped like an oblong sac, anterior (distal) side of which adheres closely to posterior (proximal) side of albumen gland portion of pallial oviduct and posterior (proximal) portion of which extends far beyond site of proximal seminal receptacle (inside visceral sac); bursa copulatrix duct very short, anteroventral; pallial oviduct bulging well into pallial cavity and consisting of albumen and capsule glands, its opening (female gonopore) small, situated not far from pallial margin; ventral side of pallial oviduct with ventral groove.

Radula (figs 22-27). — Taenioglossate consisting of many rows of seven teeth, each with the following formula: $C = 6 + 1 + 6 / 1 + 1$; $L = 5 + 1 + 5 - 6 = 11-12$; $M1 = 27-30$; $M2 = 22-25$. Central tooth trapezoidal with long slender lateral wings; body extended to form basal tongue wedged in concave apex of adjacent central tooth; apical margin V-like, with row of 13 denticles, central longer than laterals; one basal cusp arising between base of each lateral wing and body of tooth. Lateral teeth with body elongated; anterior margin with 11-12 denticles, central longer than laterals. Inner marginal teeth rake-like, with elongated body and long apex with row of 27-30 denticles along anterior margin. Outer marginal teeth spoon-shaped, with 22-25 denticles on outer lateral margin of apex.

Stomach and intestine (figs 14, 19). — Stomach with rudimentary gastric caecum. First portion of intestine running adjacent to wall of style sac before forming U-like loop

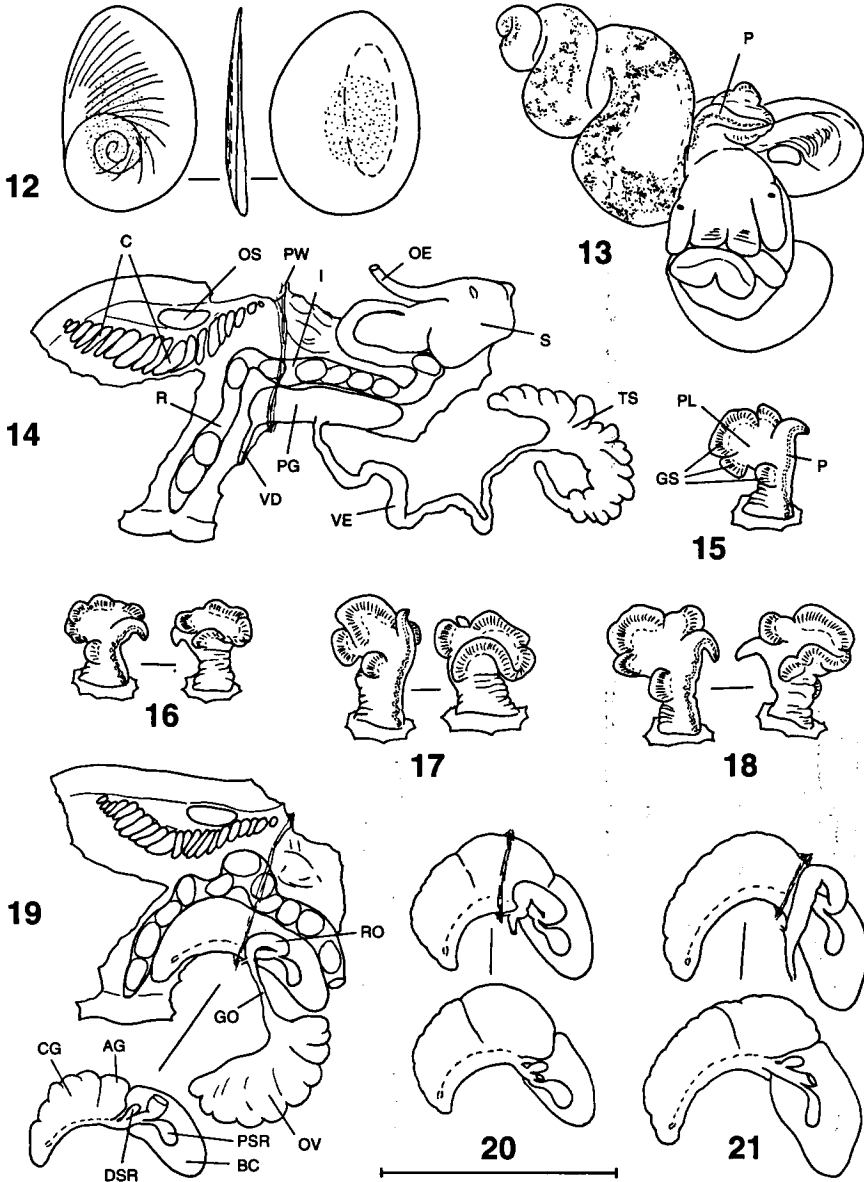
near stomach; loop on pallial wall absent or poorly defined; rectal portion of intestine straight; anus at pallial margin.

Pallial organs (figs 14, 19). — Osphradium oval or kidney-shaped, short or slightly elongated; ctenidium consisting of 17-31 lamellae; pallial tentacle absent.

Material examined. — Spring of the fountain of St. Victor-la-Coste (Gard, France) (for a description of the biotope, see Girardi, 1990), M. Bodon, H. Girardi & B. Bomba leg., 29.xii.1998 (7 males, 5 females, many shells and undissected specimens).

Taxonomy. — Stygobiont hydrobiids living in the wells of "Rue de Velouterie, n° 9" at Avignon (Dép. Vaucluse, France) were discovered by M.H. Nicolas in the 1870s. In May 1881, Nicolas gave material of these species to somebody [P. Bérenguier ?] charging him to ask J.R. Bourguignat for an opinion (Nicolas, 1882: 161). In June 1881, Nicolas read a paper at the Académie de Vaucluse on the new genus *Avenionia* (Fischer, 1885: 34). In May 1882, Bourguignat published a paper (Bourguignat, 1882) in which he introduced the new genus *Paulia* Bourguignat, 1882, and two new species (*P. berenguieri* Bourguignat, 1882, and *P. locardiana* Bourguignat, 1882) based on material received from P. Bérenguier, but actually discovered by M. Nicolas. Nicolas heard about this and gave a detailed explanation (Nicolas, 1882: 161, and note 1) of the events which preceded the publication of Bourguignat's paper (1882) claiming never to have renounced his rights to the discovery ("... me réservant, bien entendu, tous les droits que ma découverte m'accordait"). Nicolas's paper, published in the Mémoires de l'Académie de Vaucluse (Nicolas, 1892), contains the description of the new genus *Avenionia* for two new species: *Avenionia vayssieri* Nicolas, 1882, and *A. fabri* Nicolas, 1882. Another species named and described by Bourguignat in his letter to Nicolas, *A. lacordiana* [sic], was added when the paper was already in press (Nicolas, 1882: 167, note 1). Because the paper of Bourguignat results published in May 1882 (see front cover) and that of Nicolas on 15 July 1882 (according to Bourguignat, 1887: 42), Bourguignat's names have priority over those of Nicolas. However, since *Paulia* Bourguignat, 1882, is preoccupied by *Paulia* Gray, 1840 (Echinodermata) and *Paulia* Stål, 1869 (Hemiptera), *Avenionia* must be used as the valid name.

As for the specific taxa, Fischer (1885) regarded *A. vayssieri* as a junior synonym of *P. berenguieri*, *A. fabri* as an uncertain entity based on "un seul individu, en partie brisé, a une forme générale différente de ses congénères et pourrait même, d'après d'auteur, devenir le type d'un genre particulier", and *A. lacordiana* [sic] to correspond to *P. locardiana*. Bourguignat (1887: 42) regarded *A. fabri* as a junior synonym (!) of *Moitessieria lineolata* var. *buteana* Coutagne, 1883. Nicolas (1892: fig. 13^{tris}) and Locard (1893: fig. 95) figured a shell of *P. berenguieri* which looks like that of a species of *Moitessieria*. Germain (1913) was the first to propose synonymy of *P. berenguieri* and *P. locardiana*, and taking the former as the valid name, established the priority of one of the two names published simultaneously. More recently, Boeters (1967) revised the status of these taxa, illustrated the holotype of *P. locardiana*, designated lectotypes of *P. berenguieri* and *A. vayssieri*, confirmed the synonymy of these three nominal taxa and considered *P. berenguieri* as a subspecies of *Avenionia brevis* (Draparnaud, 1805). The status of *A. fabri* (amended to *A. fabrei* by Nicolas, 1892) is still uncertain. Nicolas (1892) stated that Bourguignat was wrong to claim synonymy with *Paladilhia puteana*, Germain (1931: 636) recorded "*A. Fabrei* Nicolas, 1892, p. 44, fig. 13^{bis}" as a synonym of *P. berenguieri*, and Boeters & De Winter (1983) listed "*fabri*", probably instead of "*lacordiana*", together with "*vayssieri*" as a name used by Nicolas (1882) for *A. brevis*.



Figs 12-21. Operculum and anatomical details of *Avenionia brevis berengueri* (Bourguignat, 1882), collected in the spring of the fountain of St. Victor-la-Coste (Gard, France). 12: outer surface (left), profile (centre) and inner surface (right) of operculum; 13: body of a male with pallial cavity open to show penis; 14: male genitalia (penis excluded), stomach, intestine and pallial organs; 15-18: penis in four males; 19: genitalia and pallial organs in a female; 20-21: distal portion of genitalia in two other females. Abbreviations: AG = albumen gland; BC = bursa copulatrix; C = ctenidium; CG = capsule gland; DSR = distal seminal receptacle (RS1); GO = gonadal oviduct; GS = glandular swellings; I = intestine; OE = oesophagus; OS = osphradium; OV = ovary; P = penis; PD = penial duct; PG = prostate gland; PL = penial lobe; PSR = proximal seminal receptacle (RS2); PW = posterior wall of pallial cavity; R = rectum; RO = renal oviduct; S = stomach; TS = testis; VE = vas efferens (seminal vesicle). Scale bar 1 mm.

DISCUSSION

As is evident from the above description, the type species of *Avenionia* has a bursa copulatrix and the genus is therefore defined by a combination of anatomical characters different from that described so far in the literature (bursa copulatrix absent according to Boeters & De Winter, 1983, and Boeters, 1998). This implies that the relationships of the genus *Avenionia* and the systematics of at least some of the species included in it, need to be revised.

Relationships. — The combination of anatomical characters distinctive of *Avenionia* (males, penis with glandular lobes; females, renal oviduct with two seminal receptacles and bursa copulatrix) also occurs in other European genera: *Pezzolia* Bodon & Giusti, 1986 (including the type species *Pezzolia radapalladis* Bodon & Giusti, 1986, and other undescribed species), *Fissuria* Boeters, 1981 (including only the type species *Fissuria boui* Boeters, 1981); *Lithhabitella* Boeters, 1970 (including only the type species *Paludinella* (Bythinella) *chilodia* Westerlund, 1886) and *Alzoniella* Giusti & Bodon, 1984 (including the type species *Alzoniella finalina* Giusti & Bodon, 1984, and *A. sigestra* Giusti & Bodon, 1984; other species assigned to this genus are not included here due to their uncertain taxonomical position or their separate distribution) (Bodon & Giovannelli, 1993; Bodon et al., 1992, 2000).

Fissuria and *Pezzolia* can be recognized immediately by their depressed valvatiform shell, but the distinction between *Lithhabitella* and *Alzoniella* is less evident because both have a cylindro-conical, bythinelloid shell very similar to that of *Avenionia* (by virtue of a thin and unreflexed peristome, *Alzoniella* is the more similar). Nevertheless, *Avenionia* can be clearly distinguished from all the above genera by the fact that its type species is defined by the following anatomical characters (table 1):

- subapical lobe of penis very large, with three glandular swellings along border, two of which in form of the sinuous bands (subapical glandular lobe absent in type species of *Pezzolia*; subapical lobe/s small, sessile, glandular in species of *Pezzolia*, *Fissuria* and *Alzoniella*; subapical lobe large, non-glandular on apical border but with 1-4 globular to elongated glandular swellings on lower surface - and on surface of penis close to base of lobe - in *Lithhabitella*);

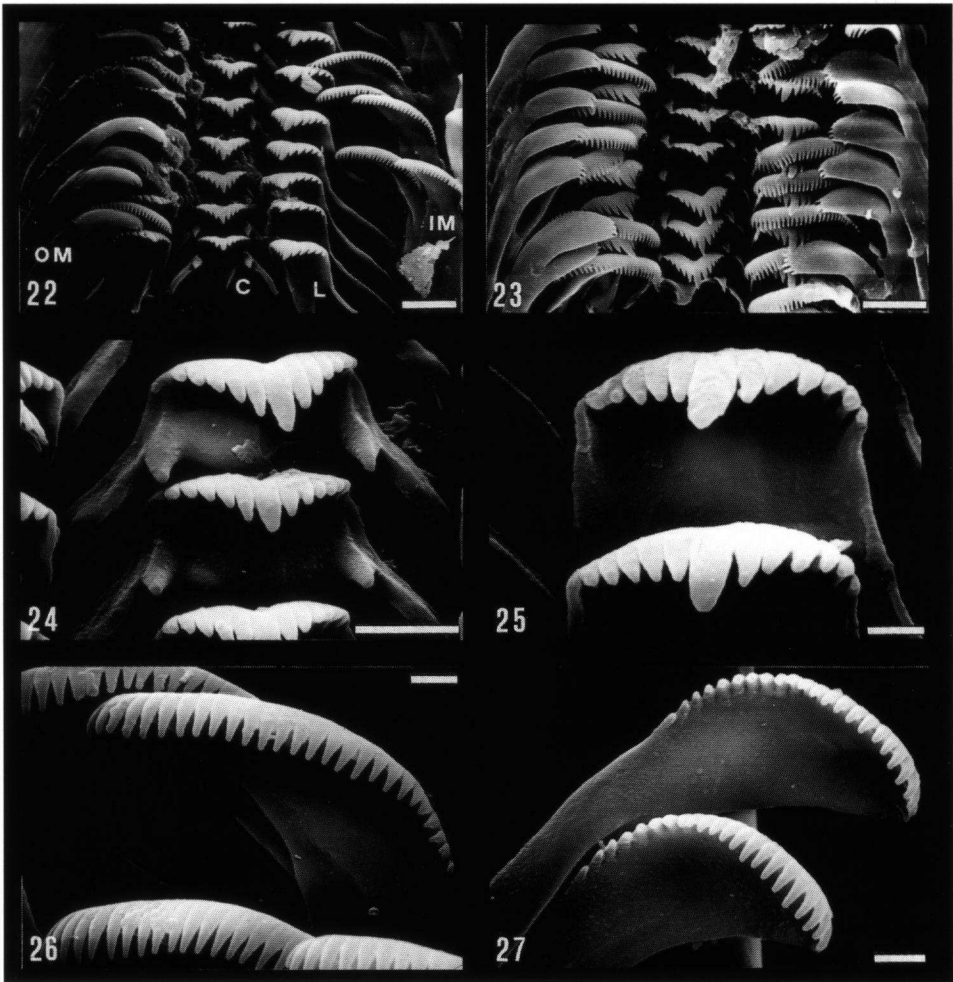
- dorsal glandular lobe of penis small, globular, on dorsal side of penis close to base of subapical lobe (absent in *Lithhabitella*; absent or, if present, on dorsal side of penis near base in *Pezzolia* and *Alzoniella*; absent or, if present, in variable position in *Fissuria*);

- proximal seminal receptacle (RS2) larger than distal and with evident slender duct (proximal seminal receptacle smaller than or equal to distal and without evident duct in *Pezzolia*, *Alzoniella*, *Lithhabitella*, and *Fissuria*; sometimes with short duct in *Fissuria*);

- proximal seminal receptacle (RS2) arising beyond end of loop, close to distal one (proximal seminal receptacle arising at end of loop, far from distal one in *Pezzolia*, *Fissuria*, *Alzoniella* and *Lithhabitella*);

- bursa copulatrix very large, in form of oblong sac, anterior (distal) side of which adheres closely to posterior (proximal) side of albumen gland portion of pallial oviduct and posterior (proximal) portion of which extends (towards inside of visceral sac) far beyond site of proximal seminal receptacle (bursa copulatrix rudimentary or absent in *Pezzolia*, small to rather large, always lying on albumen gland portion of pallial oviduct and not extending proximally beyond site of proximal seminal receptacle in *Fissuria*, *Alzoniella*, and *Lithhabitella*);

- bursa copulatrix duct short, anteroventral (bursa copulatrix duct rudimentary or



Figs 22-27. Radula of *Avenionia brevis berenguieri* (Bourguignat, 1882), collected in the spring of the fountain of St. Victor-la-Coste (Gard, France). 22-23: central portion of radula with central (C), lateral (L), inner marginal (IM) and outer marginal (OM) teeth; 24: central teeth showing one basal cusp on each side; 25: lateral teeth; 26: inner marginal teeth; 27: outer marginal teeth. Scale bars 10 μm (figs 22-23); 5 μm (fig. 24); 2 μm (figs 25-27).

absent in *Pezzolia*, short to long in *Fissuria*, *Alzoniella*, and *Lithabitella*, anterodorsal in *Alzoniella* and *Fissuria*, anterior to posteroventral in *Lithabitella*;

— stomach with gastric caecum rudimentary (stomach without gastric caecum in *Pezzolia*, *Fissuria*, *Alzoniella*, and *Lithabitella*);

— intestine loop on pallial wall absent or poorly defined (well developed pallial loop in *Pezzolia*, *Fissuria*, and *Alzoniella*, absent in *Lithabitella*).

On the basis of the current praxis in the taxonomy of the hydrobiids, *Avenionia*, *Alzoniella*, *Fissuria*, and *Pezzolia*, having such different anatomy, may be considered distinct valid genera (for *Pezzolia*, see Bodon & Giusti, 1986, and Bodon et al., 2000; for *Fissuria*, see Boeters, 1981, and Bodon et al., 2000; for *Alzoniella*, see Giusti & Bodon, 1984, Bodon, 1988, and Boeters, 1999; for *Lithhabitella*, see Bole, 1971, Radoman, 1983, and Bodon et al., 1999).

No extra-European taxon shows the same combination of anatomical characters as *Avenionia*. Some genera of North America, such as *Nymphophilus* Taylor, 1966, *Pyrgulopsis* Call & Pilsbry, 1886, and *Cincinnatia* Pilsbry, 1891, include species whose males have a penis with glandular swellings in the form of sinuous bands. Their females, however, always have only one seminal receptacle (Davis & Mazurkiewicz, 1985; Hershler, 1985, 1998; Hershler & Landye, 1988; Hershler & Thompson, 1987).

The species of *Avenionia*. — In central-western Europe *Avenionia* includes two species, each with two subspecies: *A. brevis brevis*, distributed from the Jura to the Côte d'Or and nearby Lyon (France), *A. brevis berenguieri*, distributed in the Rhone basin south of Lyon, in the French departments of Ardèche, Gard and Vaucluse (Boeters & De Winter, 1983); *A. bourguignati bourguignati* (Locard, 1883), from the department Aube (France) and *A. bourguignati roberti* Boeters, 1967, in the Low Countries and nearby Germany (Boeters, 1998). All these taxa were first considered to be subspecies of *A. brevis* (Boeters, 1967; Boeters & De Winter, 1983).

Their shell is always cylindro-conical, bythinelloid, and has a thin peristome, not reflexed and not sinuous at the external margin (Boeters, 1967, 1998; Notenboom & De Winter, 1983). Anatomical data is scarce. Only the penis of *A. brevis brevis* is known, having a wide subapical lobe with glandular, globular and band-like swellings, and a dorsal glandular lobe very similar to those described herein for *A. brevis berenguieri* (Boeters & De Winter, 1983, fig. 2; Boeters, 1998, fig. G 2). *A. bourguignati bourguignati* and *A. bourguignati roberti* also have a penis with a subapical lobe and glandular swellings (usually more than two), however neither is band-like (as in the case of two of the swellings in *A. brevis brevis*), but globular to finger-like (Altena, 1946, figs a-b; Boeters & De Winter, 1983, figs 4-9; Boeters, 1998, fig. G 4, 6-7). Female genitalia have only been summarily figured and described in *A. bourguignati roberti* and have a very short renal oviduct and proximal seminal receptacle (RS2) larger than distal (RS1); the bursa copulatrix is described as absent (Boeters & De Winter, 1983, fig. 1; Boeters, 1998, fig. G 8).

It is clearly impossible to comment on generic and specific taxonomy with such incomplete anatomical data. The fact that they all have a penis with a subapical lobe and glandular structures, and that "*A. brevis roberti*", the northernmost entity has seminal receptacles located and shaped like those of the type species, supports the hypothesis that they all belong to *Avenionia*. If this is true it becomes possible to accept the most recent opinion of Boeters (1998) according to which there exist two distinct *Avenionia* species, characterized by the different structure of the penis: *A. brevis* (penis having a subapical lobe with at least two band-like glandular swellings) and *A. bourguignati* (penis having a subapical lobe with only globular or finger-like glandular swellings).

The Italian taxa assigned to *Avenionia*. — The fact that *Avenionia* was believed to have female genitalia characterized by a renal oviduct with two seminal receptacles and without bursa copulatrix led to some species from central-northern Italy being assigned to it (Giusti & Bodon, 1981; Bodon et al. 1995). This was logical because *Avenionia ligustica* Giusti & Bodon, 1981 and *Avenionia parvula* Giusti & Bodon, 1981 (Liguria and nearby Italian regions) have a shell similar to that of *A. brevis* and *A. bourguignati* (cylindro-

conical, peristome thin, not reflexed and not sinuous at external margin) and a penis with a glandular subapical lobe (the simpler structure and smaller size of the lobe were seen as indicating a distinct species) and sometimes (*A. ligustica*) also with a globular, glandular lobe on the dorsal side near the base (maybe corresponding to that situated close to the base of subapical lobe in *A. brevis*).

The present study nevertheless revealed that these assignments are incorrect when the current practice to distinguish the hydrobiid genera is applied. In fact, apart being characterized by a penis which has a different subapical lobe, *A. ligustica* and *A. parvula*, are now obviously distinguished by the fact that they actually do not have a bursa copulatrix (there may be a vestigial one in *A. ligustica*; Giusti & Bodon, 1981, fig. 2 H). This and the fact that they also differ by a proximal seminal receptacle (RS2) situated at the end of the loop and never larger than the distal receptacle (RS1), a stomach lacking even rudiments of the gastric caecum and the intestine loop well developed on the pallial wall (Giusti & Bodon, 1981; personal unpublished data), indicate that the two Italian species will have to be included in a generic taxon different from *Avenionia* (Wilke et al., in preparation).

In northern Italy (Liguria and nearby areas), in sites close to where the two supposed *Avenionia* species live, at least two species of the genus *Alzoniella* Giusti & Bodon, 1984 (*A. finalina* Giusti & Bodon, 1984, and *A. sigestra* Giusti & Bodon, 1984) are also known. Although *Alzoniella finalina*, the type species, has similar male genitalia, it differs from "*Avenionia*" *ligustica* and "*Avenionia*" *parvula* by female genitalia with a large bursa copulatrix and two seminal receptacles, whereas *Alzoniella sigestra*, has a very small bursa copulatrix.

All this suggests that all the species in the western part of northern Italy belong to the same genus, variable in one of the characters of its female genitalia (bursa copulatrix from rather large to absent), but constant in others such as the location and relative dimensions of the seminal receptacles (the latter characters are rather different from those of *Avenionia* from France; table 1). However, this hypothesis has been disproven by genetic studies based on DNA sequencing (Thomas Wilke, personal communication,

CHARACTERS		<i>Avenionia brevis</i> <i>berangeri</i>	<i>Alzoniella finalina</i> <i>Alzoniella sigestra</i>	" <i>Avenionia</i> " <i>"A." parvula</i>	<i>Limnithella chiodi</i>	<i>Pezomachus</i>	<i>Pezomachus</i> <i>radepallatus</i> <i>Pezomachus</i> spp.
Shell	Shape	Cylindro-conical	Cylindro-conical	Cylindro-conical	Cylindro-conical	Valvetiform	Valvetiform
	Peristome	Not reflected	Not reflected	Not reflected	Reflected	Not reflected	Not reflected
Penis	Subapical lobe	Very large, with three glandular swellings on its apical border, one globular and two long, band-like	Small, sessile, globular to club like, glandular	Small, sessile, globular, glandular	Large, not-glandular on its apical border but with 1-4 globular to elongated glandular swellings on lower surface (and on that of penis close to base of lobe)	Two or three lobes, small, sessile, globular, glandular	Absent or one or two lobes small, sessile, globular, glandular
	Dorsal glandular lobe	Small, globular, on dorsal side of penis close to base of subapical lobe	Absent or, if present, small, globular, on dorsal side of penis near base	Absent or, if present, small, globular, on dorsal side of penis near base	Absent	Absent or, if present, small, globular, on dorsal or lateral side of penis in variable position	Absent or, if present, small, globular, on dorsal side of penis near base
Female	Proximal seminal receptacle	Larger than distal With slender duct Beyond the end of the loop	Smaller than distal Without evident duct At the end of the loop	Smaller than distal Without evident duct At the end of the loop	Smaller than distal Without evident duct At the end of the loop	Not larger than distal Without or with short duct At the end of the loop	Not larger than distal Without evident duct At the end of the loop
	Bursa copulatrix	Very wide Beyond albumen gland Protruding posteriorly	Small to wide Lying on albumen gland Not protruding posteriorly	Absent (inapplicable)	Wide Lying on albumen gland Not protruding posteriorly	Small to wide Lying on albumen gland Not protruding posteriorly	Rudimental or absent Lying on albumen gland Not protruding posteriorly
	Bursal duct	Short Anteroventral	Short to medium Anterodorsal	(inapplicable)	Medium Anterior to posteroventral	Short to long Anterodorsal	Rudimental or absent (inapplicable)
Stomach	Gastric caecum	Rudimental	Absent	Absent	Absent	Absent	Absent
Intestine	Pallial loop	Absent or rudimental	Well developed	Well developed	Absent	Well developed	Well developed

Table 1. Comparison of the various genera discussed in the present paper.

27.02.2000). The Italian species currently assigned to *Avenionia* (taxa examined: *A. ligustica* and *A. sp.*) will have to be included in a genus different from *Avenionia* (taxa examined: *A. brevis berengueri*), and also from *Alzoniella* (taxa examined: *A. finalina* and *A. sigestra*). Pending the results of genetic studies and research into morphological characters that could be used for traditional diagnoses, we abstain from introducing new taxa. In the meantime, we refer to the supposed Italian species of *Avenionia* simply as “*Avenionia*”.

ACKNOWLEDGEMENTS

Our thanks are due to B. Bomba (Cadenet, France) for help in collecting the material, M. Ulivi (Florence, Italy) for technical assistance, and H. Ampt (Siena, Italy) for revising the English.

The research was partly financed by grants from MURST (40% and 60% funds) and Museo Zoologico de “La Specola” (Firenze).

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