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A remarkably rich prosobranch fauna endemic to the French Pyrenees

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This article describes a remarkably rich fauna of freshwater prosobranchs endemic to the French Pyrenees, which comprises three new (sub)species, viz. *Moitessieria nezi* spec. nov., *Palaospeum bessoni rebenacqensis* subspec. nov. and *(?)P. nanum* spec. nov., and *Alzoniella junqua* Boeters, 2000. These four endemic species can be found sympatric with two species of *Bythinella* which have a larger distribution in the Pyrenees.

Key words: Gastropoda, Prosobranchia, Moitessieriidae, *Moitessieria*, *Palaospeum*, Hydrobiidae, *Alzoniella*, *Bythinella*, France, Pyrenees, taxonomy, biogeography.

I. SPECIATION AND ITS TOPOGRAPHICAL AND GEOLOGICAL ASPECTS

1. Topographical and geological aspects

In the Pyrénées-Atlantiques, the Gave d'Ossau rises in the area of the Pic du Midi d'Ossau, flows past Gabas, Laruns and Arudy, and finally into the Gave d'Oleron at Oleron about 5 km southwest of Pau. At Arudy, the Gave d'Ossau butts against a moranic wall (Delfaud et al., 1980: figs 7-13) deposited on a layer of the Early Cretaceous period (crétacé inférieur) which is overlaid in the south by a layer of the Later Cretaceous period (crétacé supérieur) (Delfaud, 1980: fig. O-8). Where it butts against the moranic wall about 390 m above sea level, the Gave d'Ossau loops westwards from its original south-north direction. To the south of this wall, the small river Nez has cut its bed into the Later Cretaceous layer and flows in a south-north direction towards Pau, joining the Gave de Pau at Jurançon opposite Pau. The main source of the Nez is L'Oeil du Nez, a large karstic spring 315 m above sea level only 4 km distant from the loop of the Gave d'Ossau at Arudy. L'Oeil du Nez is used for the water supply of Pau. L'Oeil du Nez is about 75 m lower than the loop of the Gave d'Ossau at Arudy. The large karstic spring is supplied by water trickling away from the Gave and making its way through the karst (Bauer et al., 1992).

L'Oeil du Nez is the main source of the Nez, but it is associated with a number of smaller springs. An examination of three of these smaller springs has revealed that karstic waters of the Vallée du Nez are inhabited by the following six prosobranchs, the first four of which are characteristic of this valley and can be regarded as endemic: *Moitessieria nezi*

spec. nov.; *Palaospeum bessoni rebenacqensis* subspec. nov.; (?) *Palaospeum nanum* spec. nov.; *Alzoniella junqua* Boeters, 2000; *Bythinella servainiana* (Paladilhe, 1870); *Bythinella* cf. *utriculus* (Paladilhe, 1874).

The four representatives of *Moitessieria, Palaospeum* and *Alzoniella* are stygobionts. The number of six taxa of the Moitessieriidae and Hydrobiidae is remarkable in view of the fact that the waters of the best-known karstic spring in France, the Source du Lez north of Montpellier, are not inhabited by more than seven species of these two families: *Moitessieria rolandiana* Bourguignat, 1863; *Paladilhia pleurotoma* Bourguignat, 1865; *P. conica* Paladilhe, 1867; *Arganiella exilis* (Paladilhe, 1867); *Bythiospeum bourguignati* (Paladilhe, 1866); *Belgrandia gibba* (Draparnaud, 1805); *Bythinella eutrepha* (Paladilhe, 1867).

2. Speciation

Gorthner & Meier-Brook (1985) stressed the following three factors as being essential for speciation resulting in endemism in freshwater molluscs in Lake Ochrid: (1) a great age (Lake Ochrid is dated as Late Pliocene); (2) low temporary fluctuation of abiotic factors; (3) the presence of various ecological niches.

In 1991 Boeters & Müller discussed whether these factors could also explain the origin of the rich subterranean prosobranch fauna of the Rhône basin if this basin is roughly understood as a lake-like subterranean area. They came to the conclusion that factors (1) and (2) do not apply to the Rhône basin and that the subterranean prosobranchs of the Rhône basin might have invaded the valley from the neighbouring karst.

As regards the subterranean prosobranchs of the Nez, the following can be concluded.

Factor (1). In view of the fact that the waters of the Nez originate from karst of the Cretaceous period in a region which has not been covered by marine waters any more (Delfaud, 1980), it can be assumed that this aquatic habitat exists for a very long time already.

Factor (2). Even under the assumption that the area of the loop of the Gave d'Ossau at Arudy was covered by ice during periods of glaciation, it cannot be excluded that the karstic labyrinth of the Nez was not constantly, entirely frozen and remained at least partly inhabitable for freshwater organisms. Reference is made to *Bythiospeum* spec. living at a temperature of 4.5°C (in May) at the cave Angerloch (Upper Bavaria) supplied at least during the cold season by melted snow (Boeters, 1984: 144).

Factor (3). For Lake Ochrid Gorthner & Meier-Brook (1985) described ecological niches for two species of *Gyraulus*. *G. lychnidicus* lives, for example, on rocky limestone bottoms of the littoral zone at a depth of not more than 1 m, whereas *G. trapezoides* lives on soft bottoms covered by *Chara* beds at a depth of 6 to 15 m.

As regards subterranean prosobranchs, we are not yet in a position to characterize their ecological niches adequately. In such a situation it seems logical to refer to observations published for subterranean animals other than molluscs. Bou (1968: 469) examined the subterranean fauna of water bodies and reported differences between populations of springs emerging from the water bodies and of artificial pipe wells bored into these water bodies:

"Si nous considérons les stations les plus riches ... nous remarquons que les espèces sont inégalement réparties. Les genres *Salentinella, Microcharon, Stenasellus,* et *Bathynella* sont abondants dans la nappe des puits tubés alors que *Niphargus gineti* et *Asellus albigensis* se rencontrent essentiellement dans les sources, sur la périphérie des nappes." Notenboom (1986: 81) found *Haploginglymus* and *Pseudoniphargus* species together in some hyporheic habitats in the lower course of a river but added: "In the river system of

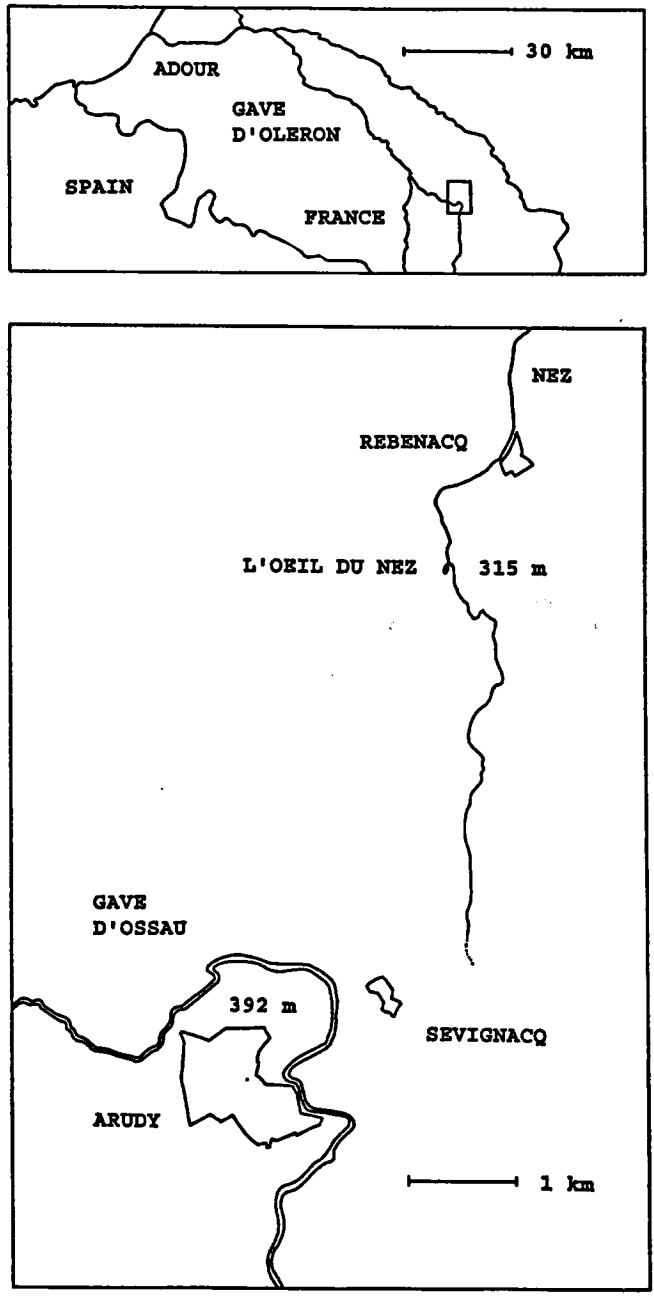


Fig. 1. Map of southwestern France (top), with an enlarged detail.

the Rio Deva (Picos de Europa) which was investigated at several localities, *Haploginglymus* shows a preference for the upper courses, while *Pseudoniphargus* prefers the lower courses." These observations show at least indirectly that even subterranean waters may offer different niches for speciation.

II. MOITESSIERIIDAE AND HYDROBIIDAE IN THE VALLÉE DU NEZ

As far as the Vallée du Nez has been examined, the valley is inhabited by three representatives of the Moitessieriidae and three species of Hydrobiidae: *Moitessieria nezi* spec. nov., *Palaospeum bessoni rebenacqensis* subspec. nov., (?) *Palaospeum nanum* spec. nov., *Alzoniella junqua* Boeters, 2000, *Bythinella servainiana* (Paladilhe, 1870), and *Bythinella* cf. *utriculus* (Paladilhe, 1874). Details of these species are given below.

Abbreviations used for collections: BOE, colln H.D. Boeters, München; MNHN, Muséum national d'Histoire naturelle, Paris; RMNH, Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden.

Moitessieria nezi spec. nov. (fig. 34)

Material. — France, Pyrénées-Atlantiques, spring below the farms Hiqueres and Junqua, 1.35 km WSW. of the center of Rébénacq [UTM YN18]; Boeters leg. 20.ix.2000 (MNHN holotype ex BOE 1483, shell; BOE 1483/2, shells) and 3/4.vi.1998 (BOE 1446/1, shell).

Shell. — Shell cylindro-conical. Spire with 6.25 convex whorls, separated by a deep suture. The first three whorls of about the same size; the following ones, up to the aperture, gradually increasing in size. Rows of pits form a spiral sculpture (21 rows above the edge of the aperture). The last whorl ascends very slightly on the shell wall. The aperturral lip is very slightly thickened, indicating that shell growth has been completed. The lip makes merely point contact with the shell wall and does not close the umbilicus. Aperture ovoid and slightly oblique. Viewed from the side, the edge of the aperture is curved like a question mark. Height and width of shell 2.35 and 0.8 mm, height and width of aperture 0.6 and 0.5 mm (holotype).

Anatomy. — Unknown.

Differentiating features. — *Moitessieria nezi* spec. nov. occurs close to *Moitessieria lescherae* Boeters, 1981, in the west, and *Moitessieria simoniana* (Saint-Simon, 1848) in the east. The shell of *M. lescherae* differs by a partially scalaroid last whorl and closely arranged spiral ridges. (Closely arranged spiral ridges are also shown by two samples of *Moitessieria* spec. from the Pyrénées-Atlantiques, both collected by Bertrand, at Tardets in deposits of the Saison and at Alcay). As regards *M. simoniana*, Bodon & Giusti (1991) have published a biometric analysis of six shells of this species from deposits of the Garonne at Toulouse and found the ratios 3.3-3.6 for 'total height:width of second to last whorl' and 1.4-1.5 for 'height of last whorl:width of second to last whorl'. For the holotype of *M. nezi* spec. nov. these ratios are 3.3 and 1.5. The data for *M. nezi* spec. nov. show that the size of the whorls scarcely increases before the fourth whorl. Further, according to photographs of four of the shells examined by Bodon & Giusti (1991: 3, fig. 1A-D), the height of the shell in *M. simoniana* is only 1.55-1.85 mm and never reaches 2.35 mm. These fin-

dings agree with a shell height of 1.65 mm of another specimen from deposits of the Garonne at Toulouse which might be a syntype of *M. simoniana* (Boeters, 1988: pl. 1 fig. 1; SMF 307268, ex colln Charpentier, Lausanne).

Habitat. — Known from only a single spring, where it occurs sympatrically with *Palaospeum bessoni rebenacqensis* subspec. nov., (?) *P. nanum* spec. nov. and *Alzoniella junqua* Boeters, 2000.

Distribution. — France, Pyrénées-Atlantiques, subterranean waters feeding the Nez which flows into the Gave de Pau at Jurançon.

Derivatio nominis. — The epithet *nezi* is derived from the river Nez. It should be mentioned that the Carte Topographique 1546ET (1:25,000) designates the river in question "Nez" whereas Bauer et al. (1992) speak of "Neez".

Palaospeum bessoni (Bernasconi, 1999)

Paladilhia bessoni Bernasconi, 1999: 385.

In the following, this species is described as inhabiting the French Pyrénées-Atlantiques with two subspecies. Their known areas of distribution are about 43 km apart. The nominate subspecies lives in karstic waters of the massiv of the Pic des Vautours. These waters feed the Saison which flows into the Gave de Oleron at Sauveterre-de-Bearn. The new subspecies *P. b. rebenacqensis* subspec. nov. inhabits karstic waters in the Vallée du Nez.

Palaospeum bessoni bessoni (Bernasconi, 1999) (fig. 29)

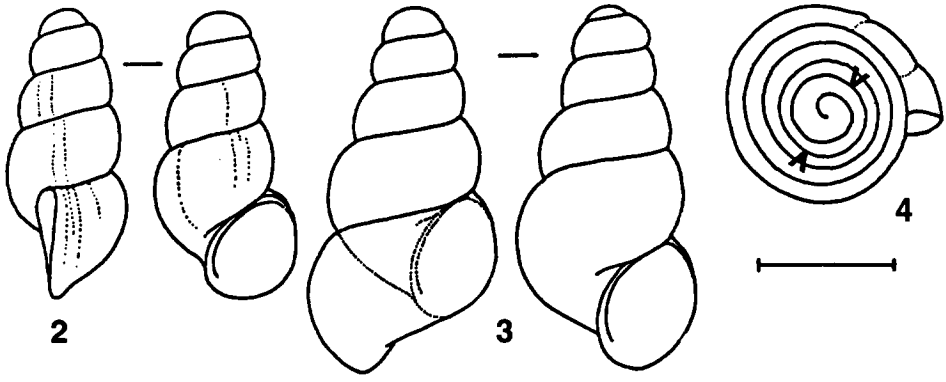
Shell (after Bernasconi, 1999: 387). — Shell conical, with 6.5 weakly convex, regularly increasing whorls, suture deep, apex small and obtuse. Umbilical opening narrow. Aperture oblong, border continuously slightly broadened, outer edge curved. Shell smooth, last whorl sometimes with more or less blurred spiral lines (about 40 to 50 lines per mm longitudinally). Judging from a paratype the number of whorls can be as few as 5.75; cf. below under *B. b. rebenacqensis* subspec. nov.

Differentiating features. — See sub *B. b. rebenacqensis* subspec. nov.

Palaospeum bessoni rebenacqensis subspec. nov. (figs 3-4, 30)

Palaospeum bessoni (Bernasconi, 1999); Boeters, 1999: 193, 194, fig. 3, 195, figs 5-6.

Material. — France, Pyrénées-Atlantiques; (i) spring below the farms Hiqueres and Junqua, 1.35 km WSW. of the center of Rébénacq [UTM YN18]; Boeters leg., 3./4.vi.1998 (RMNH 59396/holotype, shell, 59397/1, shell; BOE 1446/7 [not 2], shells, and BOE 1446/6, animals) and 20.ix.2000 (BOE 1483/12, shells, and BOE 1483/13, animals); (ii) spring in the right embankment between the roadway and the Ruisseaux-de-Nez immediately south of the bridge at Lacoucuré, WSW. of Rébénacq [UTM YN18]; Boeters leg., 1.vi.1998 (BOE 1445/1 [not 6], shell).



Figs 2-4. *Palaospeum* spec., France, Pyrénées-Atlantiques, Rébénacq, below the farms Hiqueres and Junqua. 2, (?) *P. nanum* spec. nov.; 3-4, *P. bessoni rebenacqensis* subspec. nov. 3, two views of a juvenile shell, the left one with a reconstructed dotted frontal view of the same shell with merely 4.0 whorls, for comparison with the shell of fig. 2 with also 4.0 whorls; 4, plan-view of an adult shell with arrows marking the diameter of the first 1 1/2 whorls. Scale bar 1 mm.

Shell. — Shell elongated conical, with 5.0-5.75 whorls, separated by a clearly indented suture. Whorls moderately convex, narrow shouldered, with at most a very weak spiral structure. Last whorl forming half of the total height of the shell. Aperture slightly oblique, ovate, with a sharp edge. The columellar border of the aperture is strongly broadened, it touches the last whorl for only a short distance and forms a broad funnel with the shell wall in the umbilical region. Viewed from the side, the palatal border of the aperture is very slightly curved.

Height 3.0-4.5 mm; width 1.5-2.15 mm (n = 10).

Operculum very pale yellow, nucleus not set off.

Anatomy. — Eyes not detected. A small mantle tentacle is present as in *Paladilhia pleurotoma* Bourguignat, 1865. This observation supplements the description given by Boeters (1999). Grains of black pigment found only at the base of the mantle cavity and in males in the area between the intestine and the prostate. Gill with 16-17 leaflets (n = 2). After leaving the stomach, the intestine surrounds the stile sac at a clear distance and forms a Z-shaped loop, followed by a V-shaped bend. The penis is slim, without any appendices. In females the gonopericardial duct is absent. One of the two receptacula found in females joins the oviduct near the genital opening, the other seems to have a comparatively long pedunculus since its sac can be seen through the shell just below the suture as flanked by the intestine and the most proximal gland of an agglomeration of three glands accompanying the oviduct.

Differentiating features. — The diameter of the first 1 1/2 whorls of shells of *P. b. bessoni* is the same or slightly smaller than that of *P. b. rebenacqensis* subspec. nov., despite the fact that the shells of *P. b. bessoni* are about 25 % higher, as is shown in the following table (measurements in mm). As regards the determination of the diameter of the first 1 1/2 whorls, reference is made to fig. 4.

	B. b. bessoni	*B. b. rebenacqensis* subspec. nov.
	Locus typicus (Bidalunia)	Locus typicus (farm Junqua)
Shell height	3.10-4.47-5.54 (n = 37)	2.95-3.46-3.60 (n = 8)
Whorls	5.75 (n = 1) [1]	5.00-5.75 (n = 3)
Diam. first 1 1/2 whorls	0.60 (n = 1) [1]	0.60-0.62-0.70 (n = 10)
	Uthurbietta	Lacoucur
Shell height	3.70-4.37-5.35 (n = 26)	Could not be examined because
Diam. first 1 1/2 whorls	0.57 (n = 1) [2]	of partial damage

1) Paratype (BOE 1468 ex Bernasconi): Height of shell 4.5 mm, diameter of first 1 1/2 whorls 0.60 mm.
2) Bernasconi, 1999: 389, fig. 9.

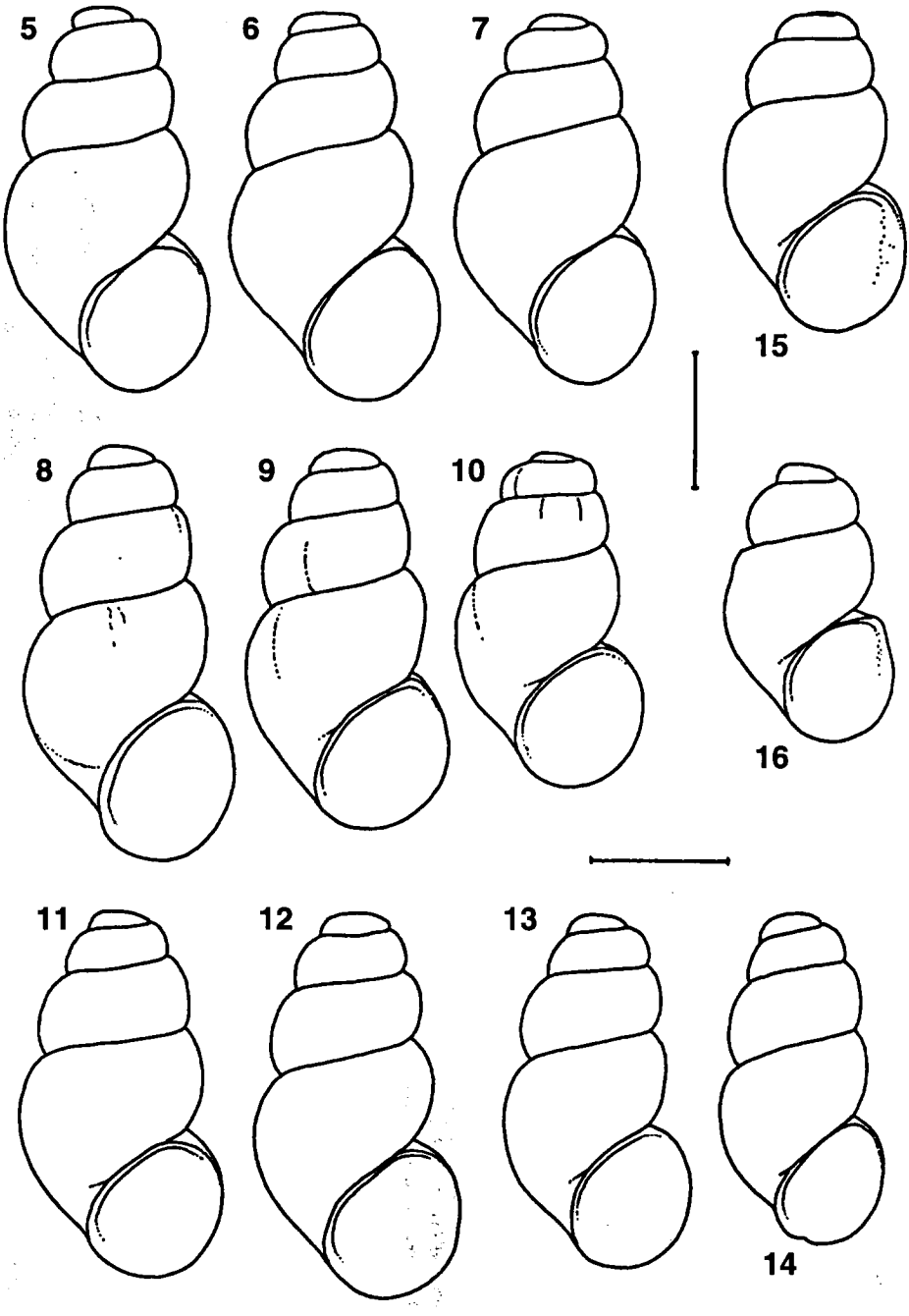
A shell height of only 2.15 mm, instead of at least 2.95 mm, distinguishes (?) *P. nanum* spec. nov. from *P. b. rebenacquensis* subspec. nov.

With a height of up to 5.54 mm *P. b. bessoni* is the largest representative of subterranean prosobranchs known from western Europe. It is not surprising that it has been described from a cave and a karstic spring and not from the interstitial of gravel deposits. While comparatively large prosobranchs have also occasionally been discovered in gravel layers, their shell height has never exceeded about 4 mm (Nicolas, 1891: 20, *Avenionia fabrei* Nicolas, 1891; Boeters, 1973: 65, *Paladilhia pleurotoma* Bourguignat, 1865). It can be assumed that the continuous shifting of gravel deposits does not suit prosobranchs with large shells. Only sedimentation zones, characterized by comparatively smaller particles and a correspondingly smaller pore size, are relatively stable. Therefore, only a karstic environment permits the development of shells of such a size as are characteristic of both subspecies of *P. bessoni*. It follows that populations of the two subspecies cannot have contact with each other across gravel beds of rivers; on the contrary, these gravel beds are a separating factor. In this context it should not be overlooked that a basis for this interpretation can be seen in Bolling's observation (1966: 82, 83) that the variation in shell size of subterranean representatives of another genus, viz. *Bythiospeum*, is related to their habitat: " ... formenbestimmend ist vor allem die Raumgröße des Karstsystems bzw. Korngröße des Kieses, Enge, Weite, Tiefe und Strömungsgeschwindigkeit der unterirdischen Wasserläufe" (p. 82). "Die relativ größte Einheitlichkeit der Prägung des Gehäusecharakters findet sich beim Formenkreis der *acicula* Held. Ob es sich nun um die Zwerge der Bayerischen Schotterebene, des Rheingrabens oder des Untermains handelt oder um Formen des [Karsts] des Neckars, des Tauber-, Kocher- oder Jagst-Gebietes mit ihren wesentlich größeren, ja Riesenstücken, immer haben wir ... [etc.]" (p. 83). If the particle size of gravel, or more exactly its interspaces, is to be understood as a size determining factor, the logical conclusion is that it will lead to local separation of populations and of speciation.

Habitat. — Karstic waters of the Vallée du Nez.

Distribution.— France, Pyrénées-Atlantiques, Vallée du Nez at Rébénacq.

Remarks. — According to Boeters (1999: 196) *P. bessoni* might be a polytypic species. The populations at Alcay and Uthurbietta are 6 km apart, whereas the population at Rébénacq occurs about 43 km distant from these two sites.



Figs 5-16. *Bythinella* spec. 5-14, *B. servainiana* (Paladilhe, 1870), France, Pyrénées-Atlantiques (5-7, between St. Jean-de-Luz and Hendaye at farm Haicabia (BOE 357) (5 = 24 and 7 = 25); 8-10, Rébénacq, 150 m E. of Mairie (BOE 1487); 11-12, Buzy at Arudy (BOE 1485); 13-14, Louvie-Soubiron at Laruns (BOE 1482); 15, *Bythinella reyniesii* (Dupuy, 1851), France, Hautes-Pyrénées, Bagnères-de-Bigorre, Parc des Thermes (BOE 195). 16, *B. darrieuxii* (Folin & Bérillon, 1877), France, Pyrénées-Atlantiques, Arnéguy (BOE 1491, Falkner ded.). Scale bars 1 mm.

(?) **Palaospeum nanum** spec. nov. (figs 2, 31)

Material. – France, Pyrénées-Atlantiques, spring below the farms Hiqueres and Junqua, 1.35 km WSW. of the center of Rébénacq [UTM YN18]; Boeters leg., 20.ix.2000 (RMNH 82617, holotype, shell; BOE 1483/1, shell).

Shell. – Shell elongated conical, with only 4.0 moderately convex whorls, separated by a clearly incised suture. The last whorl accounts for about 63 % of the total height of the shell. The contour of the aperture rather resembles a blunted right-angled triangle, with the blunted acute angles connected by its columellar border. The border of the aperture is slightly broadened, more clearly its columellar section which touches the shell wall over a short distance and forms a narrow funnel with the shell wall of the umbilical region. Viewed from the side, the palatal border of the aperture is only very slightly Z-shaped. Height, 2.15 mm; width, 1.08 mm (n = 1).

Operculum unknown.

Anatomy. – Unknown.

Differentiating features. – The shell height in (?) *P. nanum* spec. nov. is about 2/3 that of *P. b. rebenacqensis* subspec. nov.; shells of the former species have merely 4.0 instead of 5.0-5.75 whorls.

Habitat and distribution. – Found in a single spring sympatrically with *Moitessieria nezi* spec. nov., *Palaospeum b. rebenacqensis* subspec. nov. and *Alzoniella junqua* Boeters, 2000.

Remarks. – Since anatomical data are not yet available, the question of whether this species really belongs to *Palaospeum* is still open.

Derivatio nominis. – The epithet *nanum* is based on the Latin *nanus* for gnome.

Alzoniella junqua Boeters, 2000 (figs 32-33)

Alzoniella (Alzoniella) junqua Boeters, 2000: 155, figs 4-5, 20-21, 27.

This species is eyeless. It has been found in two different springs of the Vallée du Nez. In one spring sympatrically with *Moitessieria nezi* spec. nov., *Palaospeum b. rebenacqensis* subspec. nov. and (?) *Palaospeum nanum* spec. nov.; in the other one together with *Bythinella servainiana*.

Bythinella servainiana (Paladilhe, 1870) (figs 5-14, 22-25)

Paludinella servainiana Paladilhe, 1870: 205 [39]. Type localities: "Des environs de Saint-Jean-de-Luz (Basses-Pyrénées) ... aussi dans le département de l'Hérault, dans une fontaine près de Gignac."

Paludinella companyoi Paladilhe 1870: 204 [38]. Type localities: "Bourassol [= Burrassol], près de Toulouse (Haute-Garonne)[partim], et Salces (Pyrénées-Orientales) [locus typicus restr.; cf. Bernasconi, 2000: 100]."

Material. – France. Landes: Mont-de-Marsan, spring in left bank of Midouze, about 150 m W. of former railway bridge [UTM YP06], Boeters leg., 27.v.98 (BOE 1440).

France, Pyrénées-Atlantiques: Between St. Jean-de-Luz and Hendaye, about 200 m S. of the sea and N. of N10c, spring on farm Haicabia [UTM XP00], Boeters leg., 18.ix.70 (BOE 357); Ascain, spring at

wash-house W. of the church [UTM XP10], Boeters leg., 27.ix.68 (BOE 192); Arnéguy, well (iron pipe) about 300 m NE. of the church and to the right of the road leading to St. Jean-Pied-de-Port [UTM XN37], Boeters leg., 21.ix.70 (BOE 362); Arnéguy, well (iron pipe) about 1.3 km NE. of the church and to the right of the road leading to St. Jean-Pied-de-Port [UTM XN37], Boeters leg., 21.ix.70 (BOE 363); St. Jean-Pied-de-Port, spring on farm Mitchadoy about 800 m NW. of the railway station [UTM XN48], Boeters leg., 16.ix.70 (BOE 351); to the right of the road from St. Jean-Pied-de-Port towards Caro, Fontaine-de-Santé [UTM XN47], Boeters leg., 16.ix.70 (BOE 352); St. Jean-Pied-de-Port, spring to the right of D301 about 3.3 km SE. of the railway station [UTM XN47], Boeters leg., 16.ix. 70 (BOE 353); Louvie-Soubiron at Laruns, wash-house [UTM YN16], Boeters leg., 15.ix.00 (BOE 1482); Buzy at Arudy, overflow of water reservoir [UTM YN07], Boeters leg., 19.ix.00 (BOE 1485); Rébénacq, spring 150 m E. of Mairie [UTM YN18], Boeters leg., 20.ix.00 (BOE 1487).

The only taxa of *Bythinella* with a type locality in Pyrénées-Atlantiques are *Paludinella darrieuxii* Folin & Berillon, 1877, and *Paludinella servainiana* Paladilhe, 1870, from the surrounding of St. Jean-de-Luz at the French Atlantic coast. Paladilhe, however, also described his species from Hérault, from a spring at Gignac in the bank of the river Hérault. Here it is assumed that the "fontaine près de Gignac" is the Fontaine de Jourmac about 2.5 km southwest of Gignac, since this spring is represented in Paladilhe's collection with a sample of *Belgrandiella* spec. Bernasconi (2000: 25) treats *Paludinella servainiana* as synonym of *Paludinella eurystoma* Paladilhe, 1870. This view can, however, hardly be accepted despite the fact that one of the type localities of *Paludinella servainiana*, i.e. that in Hérault, is not more than about 5 km distant from that of *B. eurystoma*. As regards these two taxa, Bernasconi supplies no anatomical data on samples from Hérault nor from Pyrénées-Atlantiques, but only on samples from Aude and Ariège.

An examination of a sample from the type locality of *Paludinella eurystoma* ["la fontaine de Girard à Saint-Jean-de-Fos (Hérault)" (BOE 114)] has revealed that the species from the Vallée du Nez is different. It is also found in the area of the only type locality of *Paludinella servainiana* in Pyrénées-Atlantiques, viz. on the farm Haicabia between St. Jean-de-Luz and Hendaye. Shells from the farm Haicabia correspond to the syntypes of *Paludinella servainiana* Paladilhe, 1870, as photographed by Bernasconi (2000: 100). Consequently, that species will here be designated *Bythinella servainiana*. It is widespread in Pyrénées-Atlantiques and Landes. A syntype of *Paludinella companyoi* Paladilhe, 1870, photographed by Bernasconi (2000: 100), belongs to *B. servainiana*, which implies that it is distributed eastwards up to Haute-Garonne. *B. servainiana* can also be found in the valley of the Gave d'Oleron which feeds the karstic springs of the Vallée du Nez.

Shell.— Shell elongated conical with a flattened apex and 4.0 whorls. The whorls are quite convex and separated by a deep suture. The aperture is slightly slanted ovate. Its columellar border touches the last whorl over a long distance and is faintly reflected below the umbilical slit. Height, 2.53-2.85-3.12 mm; width, 1.40-1.49-1.56 mm (n = 3, BOE 1487); and 2.80-2.94-3.00 mm and 1.48-1.53-1.60 mm, resp. (n = 4, BOE 357).

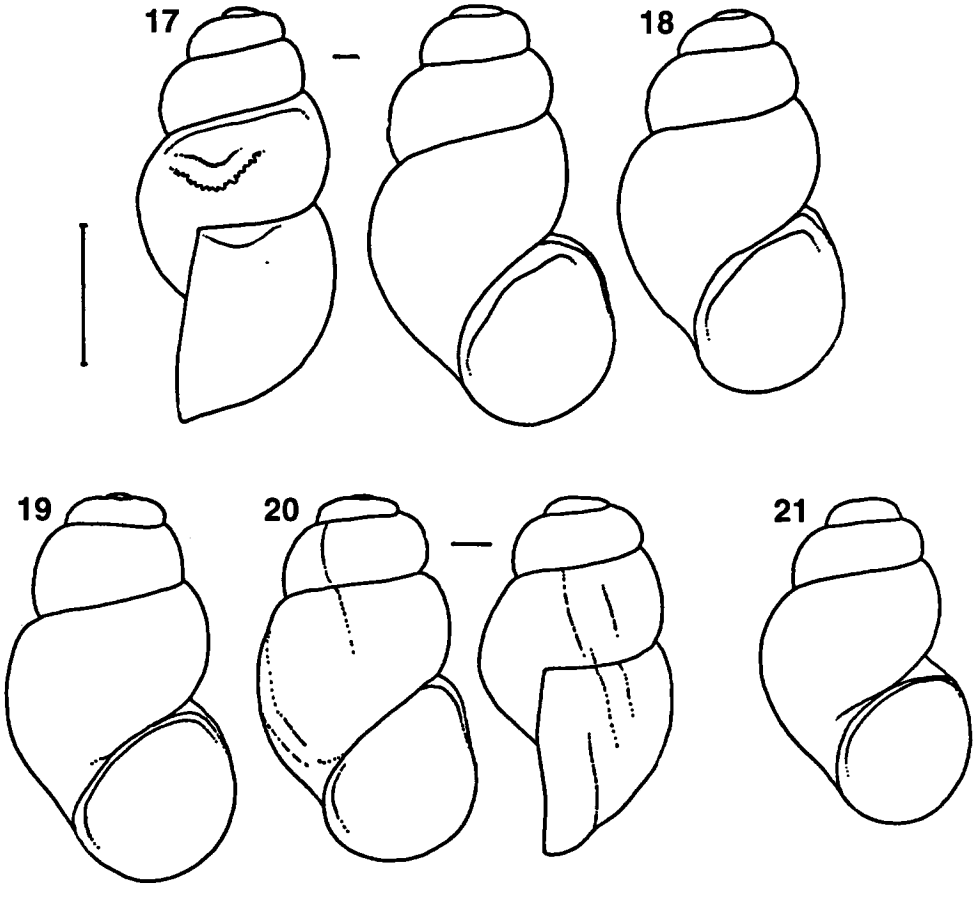
Anatomy. — Eyes present. With the exception of its snout, the head is weakly blackish pigmented. Apart from the white margin, the mantle is strongly pigmented black. Male copulatory organ: in its inactive state, the penis is slightly longer than its accessory organ (n = 2, BOE 537). Female sex tract: length of the tube-shaped bursa about 2/3 of its pedunculus. A single receptaculum present.

Differentiating features. — The shell of *Bythinella eurystoma* (Paladilhe, 1870) differs from that of *B. servainiana* by a thickened umbilical, apertural border (figs 17-18), which can be seen on the border of the aperture immediately under the suture when viewed

from the side through the shell wall. The shell of *B. darrieuxii* (Folin & Bérillon, 1877) is clearly smaller and its last whorl shows a weakly concave profile (fig. 16). The shell of *B. reyniesii* (Dupuy, 1851) has a less conical, but rather prolonged ovate contour (fig. 15). In males the penis is shorter than its accessory organ and not longer as in *B. servainiana*.

Habitat. – Springs; in the Vallée du Nez in a single spring sympatrically with *Alzoniella junqua* Boeters, 2000, at a distance of merely about 900 m downhill of the second *Bythinella* species of this valley, described below.

Distribution. – Known from the catchment area of the Adour in Landes and Pyrénées-Atlantiques and its coastal region. Eastwards quite likely up to Haute-Garonne.



Figs 17-21. Bythinella spec. 17-18, B. eurystoma (Paladilhe, 1870), France, Hérault, vis-à-vis St. Jean-de-Fos, Mas Girard (BOE 114) (17 = 27 and 18 = 28); 19-20, B. cf. utriculus (Paladilhe, 1874), France, Pyrénées-Atlantiques, Lacoucuré N. of Rébénacq (BOE 1445); 21, B. utriculus (Paladilhe, 1874), France, Ariège, 2 km W. of LaBastide-de-Sérou (BOE 1492).

Bythinella cf. *utriculus* (Paladilhe, 1874) (figs 19-20)

Paludinella utriculus Paladilhe, 1874: 29. Type localities: "dans les environs de la bastide [sic] de Sérou (Ariège), et ... le voisinage de Audinac".

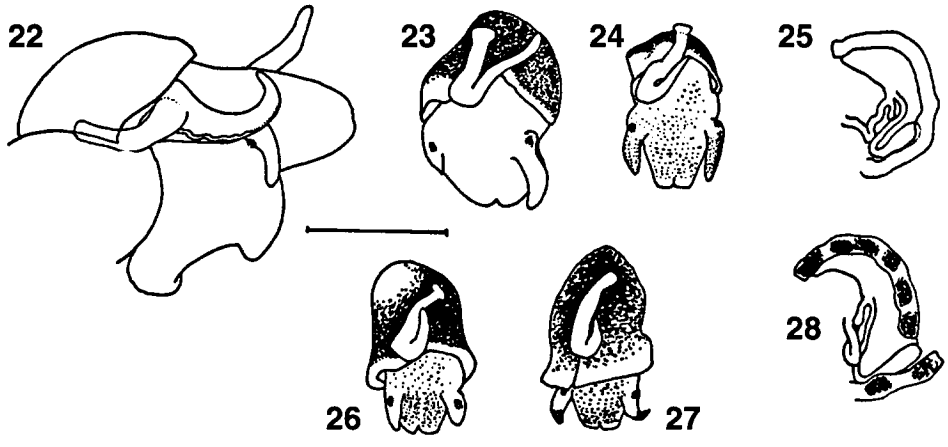
Bythinella utriculus (Paladilhe, 1874); Bernasconi, 2000: 26, 47, 101, 120.

Material. – France. Ariège: La Bastide de Sérou, spring 2 km W. of the village [UTM CH76], Bertrand leg., xi.2000 (BOE 1492). Pyrénées-Atlantiques: Serres at Ascain, eastern of two springs on farm Pascoulin [UTM XP10], Boeters leg., 19.ix.70 (BOE 358); Rébénacq, spring in right embankment between the roadway and the Ruisseau-de-Nez immediately south of the bridge at Lacoucuré, WSW. of Rébénacq [UTM YN18], Boeters leg., 01.vi.1998 (BOE 1445).

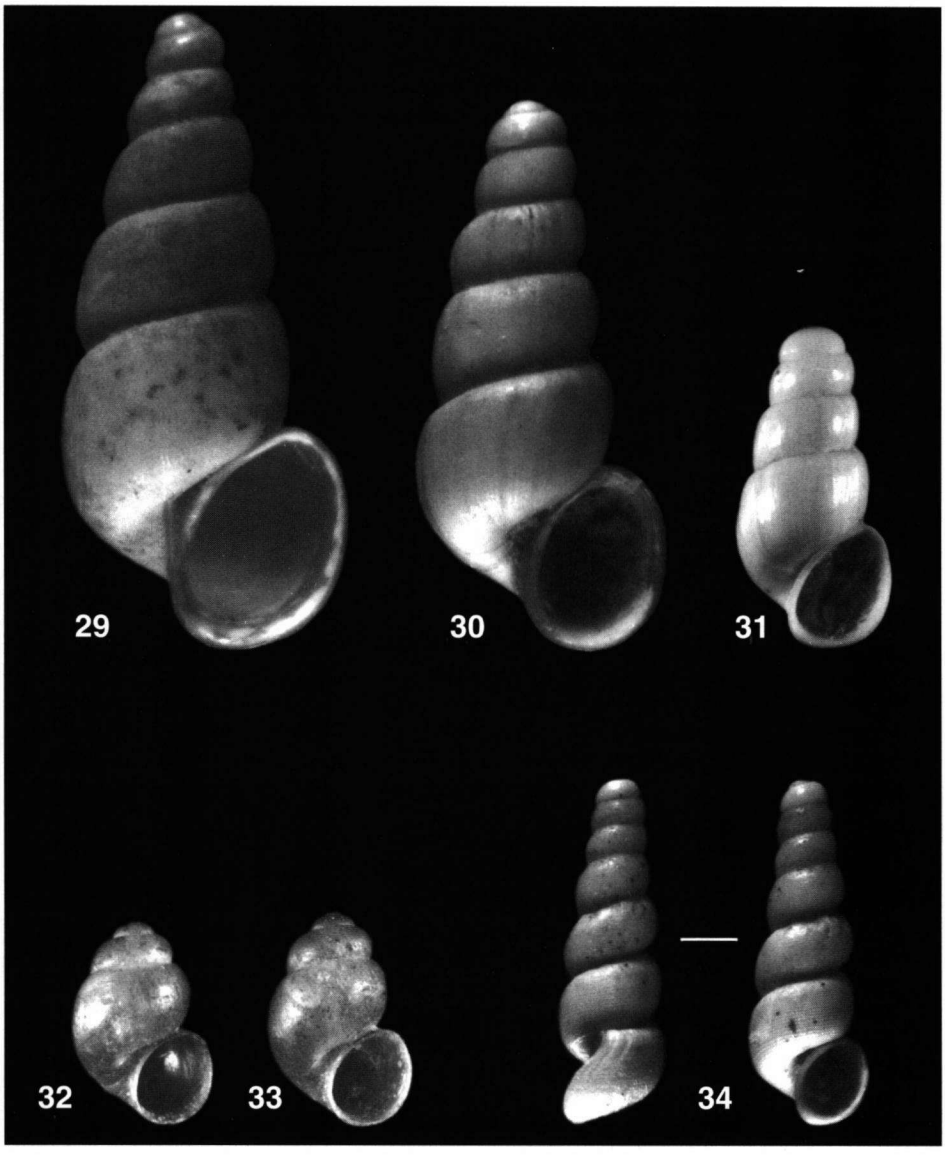
Shell. – The shell is ovoid with a flattened apex. Bernasconi (2000: 101) supplies a photograph of a syntype.

Anatomy. – Drawn from Bernasconi (2000: 120, fig. 21) the penis seems to be as long as its accessory organ. The bursa is not shaped like a tube but rather ovate. A single receptaculum is present.

Differentiating features. – The shell of *Bythinella* cf. *utriculus* differs from that of *B. servainiana* in a more ovoid shape. It is even more ovoid than shells of *B. darrieuxii* (Folin & Berillon, 1877) which, in addition, are smaller and have a narrower aperture (fig. 16); height/diameter of *B. darrieuxii* (lectotype) 1.85 compared to 1.41 for *B. utriculus* (2 syntypes).



Figs 22-28. Anatomical details of the male copulatory organ and of the female sex tract of *Bythinella* spec. 22-25, *B. servainiana* (Paladilhe, 1870), France, Pyrénées-Atlantiques, between St. Jean-de-Luz and Hendaye at farm Haicabia (BOE 357). 22, stretched male; 23-24, head of males with copulatory organs exposed by cutting the mantle (24 = 5); 25, partial view of female sex tract (25 = 7). 26-28, *B. eurystoma* (Paladilhe, 1870), France, Hérault, vis-à-vis St. Jean-de-Fos, Mas Girard (BOE 114). 26-27, head of males with copulatory organs exposed by cutting the mantle; 28, partial view of female sex tract (27 = 17 and 28 = 18). Scale bar 1 mm.



Figs 29-34. Prosobranchs from France, Pyrénées-Atlantiques. 29, *Palaospeum b. bessoni* (Bernasconi, 1999), Bidalunia (BOE 1468, Bernasconi ded.), height 4.45 mm. 30-34, four sympatric prosobranch species from Rébénacq, Vallée du Nez, spring below the farms Hiqueres and Junqua. 30, *Palaospeum bessoni rebenacqensis* subspec. nov., holotype (RMNH 59396), height 3.9 mm; 31, (?) *Palaospeum nanum* spec. nov., holotype (RMNH 82617), height 2.15 mm; 32-33, *Alzoniella junqua* Boeters, 2000 (BOE 1483), height 1.4 and 1.5 mm, respectively; 34, *Moitessieria nezi* spec. nov., holotype (MNHN), height 2.35 mm.

Habitat. — Found in a spring sympatrically with *Palaospeum b. rebenacqensis* subspec. nov.

Remarks. — The attribution of these specimens to *B. utriculus*, takes Bernasconi (2000: 27) into consideration. Bernasconi attributes a sample from Louvie-Juzon to *B. utriculus*, the type locality of which is 150 km distant. Louvie-Juzon lies in the valley of the Gave d'Oleron and not more than 8 km uphill of Rébénacq. We have not been able to examine this sample for this publication, but the data given by Bernasconi do not exclude the assumption that the population of the Vallée du Nez belongs to the same species as that of Louvie-Juzon. Measurements in mm are shown below:

	Louvie-Juzon (n = 10)	Rébénacq (n = 2)
Height	2.63	2.77
Diameter	1.61	1.60
Height/diameter	1.63	1.73

For shells collected 2 km west of La Bastide de Sérou, the type locality of *Paludinella utriculus* Paladilhe, 1874, Bernasconi (2000: 27) mentions a height of 2.42 mm and a width of 1.56 mm (n = 20). Since the shells from the Vallée du Nez at Rébénacq are larger, it is still an open question whether the *Bythinella* from the Vallée du Nez really belongs to *Bythinella utriculus*.

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REFERENCES

BAUER, J., G. OLLER & R. SABRIER, 1992. Pertes du Gave d'Ossau et naissance du Neez (Vallée d'Ossau, Pyrénées Atlantiques). — Karstologia 19: 19-22.

BERNASCONI, R., 1999. *Paladilhia bessoni* n. sp. (Gastropoda Prosobranchia Hydrobiidae) des eaux souterraines karstiques de la Haute Soule (Pyrénées Atlantiques, France). — Revue Suisse de Zoologie 106: 385-392.

—, 2000. Révision du genre *Bythinella* (Moquin-Tandon, 1855) (Gastropoda Prosobranchia Hydrobiidae: Amnicolinae Bythinellini). — Documents Malacologiques, hors série 1: 1-126.

BODON, M., & F. GIUSTI, 1991. The genus *Moitessieria* in the Island of Sardinia and in Italy. New data on the systematics of *Moitessieria* and *Paladilhia* (Prosobranchia: Hydrobiidae) (Studies on the Sardinian and Corsican Malacofauna, 9). — Malacologia 33: 1-30.

BOETERS, H.D., 1973. Französische Rissoaceen-Aufsammlungen von C. Bou. — Annales de Spéléologie 28: 63-67.

—, 1984. Gedanken zu einer Revision der Gattung *Bythiospeum* in Deutschland. — Mitteilungen der deutschen malakozoologischen Gesellschaft 37: 142-171.

—, 1988. Moitessieriidae und Hydrobiidae in Spanien und Portugal (Gastropoda: Prosobranchia). Westeuropäische Moitessieriidae, 2 und Westeuropäische Hydrobiidae, 7. — Archiv für Molluskenkunde 118 [1987]: 181-261.

—, 1999. *Palaospeum* n. gen. (Gastropoda Prosobranchia: Moitessieriidae). Unknown West European Prosobranchia, 10. – Basteria 63: 193-197.

—, 2000. The genus *Alzoniella* Giusti & Bodon, 1984, in France. West European Hydrobiidae, 9. – Basteria 64: 151-162.

—, & D. MULLER, 1992. The Rhone Basin - Thoughts on the speciation of subterranean prosobranchs.– Proceedings of the 10th International Malacological Congress Tübingen 1989, 1 [1991]: 133-136.

BOLLING. W.. 1966. Beiträge zum Problem des Genus *Bythiospeum* Bourguignat (Mollusca - Hydrobiidae). – Bericht der naturforschenden Gesellschaft Bamberg 40: 21-102.

BOU, C., 1968. Faune souterraine du sud-ouest du Massif Central, 2. Contribution à la connaissance de la faune des eaux souterraines de l'Albigeois. – Annales de Spéléologie 23 (2): 441-473.

DELFAUD, J., 1980. Introduction. In: J. DELFAUD, J. DEL VALLE & G. LE POCHAT, Le Bassin d'Aquitaine et sa marge pyrénéenne. – Bulletin des Centres de Recherches Exploration et Production. Elf-Aquitaine. Mémoires 3: 81-86.

—, J. NEURDIN, P. PAILHE & G. THOMAS, 1980. La vallée d'Ossau; traversée des Pyrénées béarnaises. In: J. DELFAUD, J. DEL VALLE & G. LE POCHAT, Le bassin d'Aquitaine et sa marge pyrénéenne. – Bulletin des Centres de Recherches Exploration et Production. Elf-Aquitaine. Mémoires 3: 106-112.

GORTHNER, A., & C. MEIER-BROOK, 1985. The Steinheim Basin as a paleo-ancient lake. In: U. BAYER & A. SEILACHER , eds, Sedimentary and Evolutionary Cycles: 322-334. Berlin, Heidelberg, New York & Tokyo.

NICOLAS, H., 1891. Compléments monographiques des genres *Lartetia, Moitessieria, Bithinella* [sic], *Avenionia* et *Acme*: 24 pp., 1 pl. Lyon [preprint of 1892. – Annales de la Société d'Agriculture, Histoire naturelle et Arts utiles de Lyon (6) 4: 27-50].

NOTENBOOM, J., 1986. The species of the genus *Pseudoniphargus* Chevreux, 1901 (Amphipoda) from northern Spain. – Bijdragen tot de Dierkunde 56: 75-122.

PALADILHE, A., 1870. Prodrome à l'histoire malacologique de la France. Étude monographique sur les paludinidées françaises. – Annales de Malacologie 1: 167-244. Separatum: 1-78.

-, 1874. Monographie du nouveau genre *Peringia* suivie de descriptions d'espèces nouvelles de Paludinidées françaises. – Annales des Sciences naturelles, Zoologie 47 [= (6) 1] (3): (Article 2) 1-38.