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A new genus and two new species of Hydrobiidae (Mollusca, Caenogastropoda) from the Iberian Peninsula

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Abstract

Two new species of valvatoid hydrobiids are reported from southern and eastern Spain that showed notable similarities with *Horatia* Bourguignat, 1887 species. However, a conchological redescription of *Horatia klecakiana* Bourguignat, 1887, the type species of this Balkan genus, and the study of new characters for the Iberian species suggest differences between the Balkan and the Iberian groups of species. These differences and the large geographical separation between the Balkan and the Iberian populations for species with poor dispersal capacity lead us to introduce a new generic taxon, *Iberhoratia* Arconada and Ramos (this paper), to include the two new species. In the Iberian Peninsula, another two species have been described in *Horatia*, *H. (?) sturmi* (Rosenhauer, 1856) and *H. gatao* Boeters, 1980. The first was recently moved to a new genus, *Boetersiella* Arconada and Ramos, 2001, while the second is here assigned to *Iberhoratia*. The introduction of a new genus for the Iberian Peninsula is another indication of the richness and endemic diversity of the Hydrobiidae in this region.

Keywords: *Gastropoda*, *Hydrobiidae*, *Horatia*, *Iberhoratia* n. g., *Iberian Peninsula*, *Mollusca*, *taxonomy*

Introduction

The genus *Horatia* Bourguignat, 1887, with *H. klecakiana* Bourguignat, 1887 as its type species (Westerlund 1902, non Dollfus 1911), was originally described from the Cetina Valley in Croatia. This was the first nominal genus established for the European valvatiform hydrobiids (Bodon et al. 2001). Bourguignat (1887) included 10 nominal species collected by Letourneux from six localities in Dalmatia, Bosnia, and Albania, distinguishing them by conchological features, such as size and shape of the shell and spire whorls, the width of the umbilicus, and the shape of the aperture. Nevertheless, after the study of the type material of the Bourguignat collection from the Museum of Natural History of Geneva and the rest of the collection of Letourneux, the taxonomic status of the species assigned to *Horatia* s. str. was not clear (Binder 1957; Schütt 1961; Ant 1962). These authors concluded that these species were all synonyms of *H. klecakiana*.

Later, Pollonera (1898) added three species from the Friaul (Italy) to this genus, but included them in the subgenus *Hauffenia*. In the following years, *Horatia* was frequently ignored (Sturany and Wagner 1914; Küscer 1933), their species being included in other genera such as *Valvata* (Müller, 1774), *Pseudamnicola* Paulucci, 1878, *Sadleriana* Clessin 1890, and *Hauffenia* Pollonera, 1898, until it was finally recognized as a valid genus (Thiele 1935; Wenz 1939; Jaeckel et al. 1957).

The distribution area of *Horatia* has been extended to Bosnia, the Caucasus, Spain, north Italy, Greece (Pollonera 1898; Küscer 1933; Hadzisce 1956; Thiele 1963; Radoman 1969, 1983; Gittenberger 1982; Bole and Velkovrh 1986; Boeters 1981, 1988), and even the USA (Walker 1918; Hubricht 1940), though the latter is clearly a misidentification.

Uncertainty in the taxonomic status of several species of this genus has been due to the lack, until recently (Radoman 1966; Boeters 1974; Bodon et al. 2001), of satisfactory anatomical descriptions and illustrations of the type species. For this reason, further descriptions and classifications of new species on the basis of very few and poorly described diagnostic characters has led to historical accumulation of errors. As several authors have pointed out, some of the species previously assigned to this genus are now considered synonyms, and others may be provisionally considered as *Horatia* until exhaustive morphological studies are carried out (Küscer 1936; Binder 1957; Ant 1962; Radoman 1965, 1966; Bodon et al. 2001).

In the Iberian Peninsula, Boeters first recorded this genus in 1980, describing *Horatia gatoa*, a stygobiont species from a cave in Málaga (south of Spain). Several years later this author (Boeters 1988) re-described with uncertainty *Paludina sturmi* (Rosenhauer, 1856) as *Horatia* (?) *sturmi*. This species has recently been studied (Arconada and Ramos 2001) and its complex status clarified, including it in a new genus as *Boetersiella sturmi* (Rosenhauer, 1856). *Horatia gatoa* has been said to be very similar to *H. exilis* (Paladilhe, 1867) from southern France, which has been considered the western European representative of the genus *Horatia* (Schütt 1961; Boeters 1974). This species was described as having only a distal seminal receptacle (Schütt 1961). Subsequently, the discovery of a “cryptic” proximal seminal receptacle (small and tightly attached at the loop of renal oviduct) in the type species forced the re-description of *H. exilis* and its inclusion in a new genus as *Heraultiella exilis* (Bodon, Manganelli, and Giusti 2002) (in Bodon et al. 2001, as *Heraultia exilis*). *Heraultiella exilis* has also been cited in Spain (Granada and Barcelona) (Alonso 1975; Vidal Abarca and Suarez 1985; Bech 1990) but these identifications need to be confirmed.

Recently, two undescribed taxa have been discovered in the Iberian Peninsula that show many morphological similarities with the type species of *Horatia*. Nevertheless, new anatomical characters studied and the geographical distance between the Balkan *Horatia* populations and the Iberian ones suggest that they may belong to a new genus, *Iberhoratia*. At the same time and despite the scarce morphological information available for *Horatia gatoa*, it seems that this species might be also assigned to *Iberhoratia*. In this paper, we follow the assumption of Bodon et al. (2001) and consider the following valid *Horatia* species: *H. klecakiana*, *H. macedonica* (Küscer 1936), and *H. novoselensis* Radoman 1966, all from the Balkans, for comparison with the Iberian *Iberhoratia* species (Figure 1).

Material and methods

The methodology for field collections, anatomical studies, and morphometric measurements are described in Ramos et al. (2000). The morphological descriptions follow the

Figure 1. Iberian *Iberhoratia* populations.

terminology from Hershler and Ponder (1998). Scanning electron microscope (SEM) photographs were made with a Philips XL20 following the methodology described in Ramos et al. (2000) and with an environmental scanning electron microscope (ESEM), a Philips Quanta 200 at low vacuum mode, after being cleaned with ultrasound or the periostracum removed by immersion in 5% sodium hypochlorite.

Type material studied for comparisons are: holotype of *Horatia gatoa* Boeters, 1980 (RMNH 55467) from the Nationaal Natuurhistorisch, Leiden collection and topotypes of *Horatia klecakiana* from the Naturhistorisches Museum of Vienna (NHM-WIEN, 17.683).

Localities are listed according to the code: spring name, municipality, province, UTM coordinates (Universal Transverse Mercator System for geographical coordinates), collection date, collector's initials, museum catalogue number and preservation conditions (see abbreviations below). Locality names and UTM coordinates were taken from the official Army Geographical Service map (1:50,000 series).

All statistics (mean value, standard deviation and coefficient of variation) were calculated using Statview for Macintosh, and standardized in order to avoid the effect of the measurement scale. A discriminant function analysis (DFA) was performed on nine shell measurements (no ratios) and the number of spire whorls with Statistica v.6 for Windows.

Normality was tested both for metrical univariate distributions and for multivariate distribution. Missing data were replaced by the estimated values using regression. The significance of the overall discriminatory power of the analysis was tested using Wilk's Lambda. Canonical correlation was used to measure interpopulation and interspecific variation. Classification functions were computed for each group (population or species) to determine, with the highest probability, which case belonged to which population or species. Cases were assigned to the group with the highest classification score.

Abbreviations used in the text, tables and figures

Shell, operculum characters and statistics. AH, aperture height; AL, aperture length; AW, aperture width; LBW, length of body whorl; NL, length of opercular nucleus; NW, width of opercular nucleus; NSW, number of spire whorls; OL, operculum length; OLWL, length of the last whorl of the operculum; OLWW, width of the last whorl of the operculum; OW, operculum width; SL, shell length; SW, shell width; WAW, width of the antepenultimate whorl; WBW, width of the body whorl; WPW, width of the penultimate whorl; CV, coefficient of variation; SD, standard deviation.

Anatomical characters. Ag, albumen gland; Bc, bursa copulatrix; Cg, capsule gland; dBC, duct of the bursa copulatrix; Os, osphradium; P, penis; Pl, penial lobe; Po, pallial oviduct; Pr, prostate; Ro, renal oviduct; SR1, distal seminal receptacle; SR2, proximal seminal receptacle; Ss, style sac; St, stomach; Vc, ventral channel of capsule gland; L, length; W, width. The concentration of the nervous system was determined by the "RPG" ratio (Davis et al. 1976): length of right pleural-supraoesophageal commissure/lengths of right pleural ganglion, supraoesophageal ganglion, and commissure.

Collections. MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; NNM, Nationaal Natuurhistorisch, Leiden, The Netherlands; NHM-WIEN, Naturhistorisches Museum, Vienna, Austria.

Collectors. B. A., B. Arconada; D. M., D. Moreno; M. O., M. Oteo; E. R., E. Rolán.

Systematic description

***Iberhoratia* Arconada and Ramos new genus**

Type species. *Iberhoratia morenoi* new species.

Etymology

The name *Iberhoratia* refers to the similarities found with the type species of the genus *Horatia*.

Diagnosis

Shell minute, dextral and valvatiform; operculum without peg; central tooth with one basal cusp on each side; stomach without gastric caecum; penis slender and cylindrical in a transverse section, with a non-glandular penial lobe located on its middle inner edge; female genitalia with an ovary as a simple mass, a well-developed bursa copulatrix and two

seminal receptacles, a distinct distal seminal receptacle (SR1) arising from an unpigmented renal oviduct and a proximal seminal receptacle (SR2) difficult to distinguish and tightly lying over the widened part of the renal oviduct.

***Iberhoratia morenoi* new species**

(Figures 2–4)

Type locality

Spring in Prado del Rey, Cádiz, UTM: 30STF8160.

Material examined

Type material. Holotype: MNCN 15.05/46980 (SEM preparation, Figure 2A). Paratypes: MNCN 15.05/46980 (SEM preparation, ethyl alcohol and frozen material).

Other populations examined. This species was found in the provinces of Cádiz, Sevilla, and Málaga (Figure 1). Populations in Almería and Huelva have tentatively been assigned to this species as *Iberhoratia* cf. *morenoi* until new specimens are studied. Localities are the following: spring in Prado del Rey, Cádiz (type locality), UTM: 30STF8160, E. R., MNCN 15.05/46980 (ethyl alcohol, SEM preparation); B. A., 16 April 1998, MNCN 15.05/46981 (ethyl alcohol, SEM preparation, frozen material); Benamahoma, Cádiz, UTM: TF87, 18 October 1998, E. R., MNCN 15.05/46982 (ethyl alcohol); spring Los Palominos, Zahara, Cádiz, UTM: TF87, 18 April 1998, E. R., MNCN 15.05/46983 (ethyl alcohol); spring El Cañajoso, Coripe, Sevilla, UTM: 30STF848928, 24 April 1992, D. M., MNCN 15.05/46984 (dried material); 16 April 1998, B. A., MNCN 15.05/46985 (ethyl alcohol, SEM preparation); Casarabonela, Málaga, UTM: 30SUF3572, E. R., MNCN 15.05/46986 (ethyl alcohol, SEM preparation); spring Matiaña, El Chorro, Málaga, UTM: 30SUF4386, 14 April 1998, B. A., MNCN 15.05/46520 (ethyl alcohol, frozen material, SEM preparation); spring La Quemona, Málaga, UTM: 30SUF0581, E. R., MNCN 15.05/46987 (ethyl alcohol), 15 April 1998, B. A., MNCN 15.05/46988 (ethyl alcohol, frozen material); spring El Valentín, Alozaina, Málaga, UTM: 30SUF3366, 14 April 1998, B. A., MNCN 15.05/46989 (ethyl alcohol).

Iberhoratia cf. *morenoi*: spring in Bérchul, Félix, Gador mountains, Almería, UTM: 30SWF298813, E. R., MNCN 15.05/46503 (ethyl alcohol and SEM preparation); 26 March 1998, B. A., MNCN 15.05/46504 (ethyl alcohol, frozen material, SEM preparation); El Marchal de Antón López, Almería, UTM: 30SWF3383, 11 October 1992, E. R., D. M.; 26 March 1998, B. A., MNCN 15.05/46502 (ethyl alcohol, frozen material); spring las Mimbreras, Zufre, Huelva, UTM: QB39, 2 August 2002, B. A., M. O., MNCN 15.05/46990 (frozen material).

Material examined for morphometry. Shell measurements (Table I) correspond to the following populations: *Ib. morenoi* from Prado del Rey (type locality) and *Ib. cf. morenoi* from Félix. Operculum measurements (Table II) to: *Ib. morenoi* from Prado del Rey (type locality) and *Ib. cf. morenoi* from Félix and El Marchal de Antón López. Anatomical measurements (Tables III, V–VII) to: *Ib. morenoi* from Prado del Rey (type locality), Casarabonela, Setenil, and El Chorro, and *Ib. cf. morenoi* from Félix and El Marchal de Antón López. Radular measurements (Table IV) belong to type locality specimens. Males

and females studied and measured were collected in the following months: March, April, October, and November.

Etymology

Dedicated to Dr. Diego Moreno, for his contribution to field collection and study of Iberian Hydrobiidae.

Diagnosis

Shell valvatiform (rarely planispiral); operculum almost circular without peg; the oesophagus makes a loop near the cerebral commissure; rectum strongly U-shaped; male genitalia with a slender penis having a non-glandular penial lobe located in a medial position; female genitalia with a well-developed bursa copulatrix and two seminal receptacles; distal seminal receptaculum elongated and proximal one lying over the widened part of the renal oviduct; central tooth of the radula with one basal cusp on each side.

Description

Shell shape valvatiform (Figure 2A–C, E, G; Table I), sometimes planispiral in Félix and Casarabonela populations, with less than 3.5 whorls (Figure 2J, K); shells from type locality are completely transparent making it possible to follow the position of the intestine; body whorl well-developed measuring 6/7 of total shell length; 1.5 protoconch whorls, total width and nucleus width are 316 and 142 µm, respectively (Figure 2L–N); pitted or malleated protoconch microsculpture (Figure 2O–Q); wide umbilicus, 0.4 mm in diameter (Figure 2H, I); outer peristome simple, thin, and straight (Figure 2D, F).

Operculum thin, pliable, corneous, paucispiral, circular with a large and central nucleus (Figure 3A–G; Table II); its muscle attachment area is rounded.

Body: head scarcely pigmented (Figure 4F); tentacles with scarce black pigmentation around the eyes until the middle part of the tentacles; snout about as long as wide, parallel-sided, with a medium distal lobation; buccal mass can be seen by transparency; ciliary fields located in the pallial edge (Figure 3K).

Nervous system (Figure 4A, B) with a very short suboesophageal and a mid-sized supraoesophageal connective; the oesophagus makes a complete loop posterior to the cerebral commissure; nervous system measurements are: length of the right cerebral ganglia: 0.19 mm; length of the right pleural ganglion: 0.06 mm; length of the left pleural ganglion: 0.06 mm; length of the supraoesophageal ganglion: 0.04 mm; length of the suboesophageal ganglion: 0.06 mm; length of the pleurosuboesophageal connective: 0.01 mm; length of the pleurosupraoesophageal connective: 0.06 mm. RPG ratio is 0.36.

Ctenidium with 6–12 well-developed lamellae (Figure 4C), occupying three-quarters of the length of the pallial cavity; osphradium 50–60% of ctenidium length, bean-shaped, two to three times longer than broad (Table III).

Posterior stomach chamber smaller than the anterior one (Figure 4D; Table V); style sac protrudes anteriorly to the intestinal loop; rectum strongly U-shaped (Figure 4E) but tending to S-shaped in Almería populations.

Radula taeniaglossate, long (0.4%) relative to maximum shell dimension; its central tooth has one basal cusp on each side (Figure 3H; Table IV); distance between internal

Figure 2. Shells of *Iberhoratia morenoi* (A, B, D, I, L, O) and *Ib. cf. morenoi* (C, E–H, J, K, M, N, P, Q). (A, B, D, I, L, O) Shells from Prado del Rey; (C, F, G, H, M, P) shells from Félix; (E, J, K, N, Q) shells from El Marchal de Antón López. (A) Holotype; (L–N) protoconch; (P, Q) detail of the microsculpture from the protoconch and teleoconch. Scale bar: 500 µm (A–K).

cusps is 8.3 µm, approximately; its central denticle is long and tapered, followed on each side by four long and tapered denticles in decreasing order of size; basal tongue V-shaped; lateral teeth with three to six denticles on each side of the central one; denticles from the

Table I. Shell measurements (in mm) of *Iberhoratia* species.

	1 (n=11)	2 (n=15)	3 (n=14)	4 (n=25)	5 (n=15)	6 (n=26)
SL	0.95±0.06; 0.06 (1.06–0.82)	0.78±0.09; 0.12 (1.08–0.68)	1.20±0.13; 0.11 (1.50–1.04)	1.05±0.06; 0.05 (1.15–0.94)	1.02±0.07; 0.07 (1.21–0.90)	1.10±0.08; 0.07 (1.34–0.94)
SW	1.53±0.09; 0.06 (1.68–1.36)	1.25±0.11; 0.09 (1.60–1.11)	1.48±0.04; 0.04 (1.56–1.40)	1.55±0.09; 0.06 (1.78–1.40)	1.51±0.07; 0.04 (1.64–1.43)	1.55±0.06; 0.04 (1.70–1.47)
SL/SW	0.62±0.02; 0.04 (0.67–0.57)	0.62±0.05; 0.08 (0.77–0.54)	0.81±0.09; 0.11 (1.03–0.68)	0.67±0.05; 0.07 (0.81–0.59)	0.68±0.05; 0.07 (0.75–0.60)	0.71±0.06; 0.08 (0.89–0.60)
AH	0.73±0.04; 0.06 (0.82–0.66)	0.60±0.04; 0.07 (0.73–0.53)	0.79±0.04; 0.05 (0.84–0.72)	0.77±0.04; 0.05 (0.85–0.70)	0.74±0.04; 0.05 (0.83–0.67)	0.80±0.03; 0.03 (0.85–0.75)
LBW	0.84±0.06; 0.07 (0.96–0.74)	0.69±0.08; 0.12 (0.95–0.61)	1.02±0.13; 0.12 (1.32–0.84)	0.93±0.05; 0.05 (1.03–0.84)	0.88±0.07; 0.08 (1.05–0.75)	0.93±0.09; 0.09 (1.18–0.77)
WBW	0.98±0.08; 0.08 (1.16–0.88)	0.80±0.07; 0.09 (1.05–0.71)	1.05±0.05; 0.05 (1.16–1.00)	0.97±0.05; 0.05 (1.08–0.88)	0.98±0.06; 0.07 (1.10–0.91)	1.01±0.06; 0.06 (1.18–0.90)
AL	0.64±0.04; 0.06 (0.70–0.56)	0.52±0.03; 0.05 (0.60–0.48)	0.76±0.05; 0.07 (0.86–0.70)	0.67±0.05; 0.07 (0.78–0.57)	0.65±0.05; 0.08 (0.74–0.53)	0.75±0.03; 0.04 (0.81–0.68)
AW	0.64±0.04; 0.06 (0.70–0.58)	0.53±0.03; 0.06 (0.61–0.48)	0.66±0.04; 0.06 (0.72–0.60)	0.65±0.02; 0.04 (0.71–0.60)	0.65±0.04; 0.06 (0.71–0.57)	0.71±0.04; 0.06 (0.81–0.64)
WPW	0.35±0.12; 0.33 (0.50–0.12)	0.30±0.07; 0.23 (0.53–0.21)	0.52±0.03; 0.06 (0.56–0.46)	0.44±0.04; 0.09 (0.50–0.35)	0.47±0.02; 0.05 (0.51–0.43)	0.49±0.04; 0.07 (0.57–0.43)
WAW	0.16±0.03; 0.21 (0.22–0.12)	0.12±0.04; 0.34 (0.23–0.06)	0.21±0.03; 0.12 (0.24–0.16)	0.17±0.02; 0.15 (0.24–0.14)	0.19±0.04; 0.19 (0.27–0.14)	0.19±0.02; 0.12 (0.23–0.14)
NSW	3.42±0.12; 0.03 (3.5–3.25)	3.00±0.00; 0.00 (3.0–3.0)	3.51±0.07; 0.02 (3.75–3.40)	3.38±0.12; 0.03 (3.50–3.25)	3.41±0.12; 0.03 (3.50–3.25)	3.47±0.08; 0.02 (3.50–3.25)

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); *Iberhoratia* cf. *morenoi*: 2, Félix, Almería; *Iberhoratia aurorae*: 3, spring between Hervás and Jerte, Cáceres (type locality); 4, Roturas, Cáceres; 5, Sierra de Altamira, Cáceres; 6, Béjar, Salamanca. Measurements are given as mean±SD; CV (maximum–minimum).

Table II. Operculum measurements (in mm) of *Iberhoratia* species.

	1	2	3	4
OL	0.59 ± 0.03; 0.05 (0.64–0.56) [n=6]	0.47 ± 0.03; 0.07 (0.54–0.40) [n=12]	0.44 ± 0.03; 0.06 (0.52–0.42) [n=9]	0.62 ± 0.06; 0.10 (0.72–0.54) [n=5]
OW	0.51 ± 0.03; 0.07 (0.56–0.46) [n=6]	0.41 ± 0.03; 0.07 (0.48–0.37) [n=12]	0.40 ± 0.03; 0.08 (0.46–0.36) [n=9]	0.49 ± 0.03; 0.07 (0.53–0.45) [n=5]
OLWL	0.16 ± 0.03; 0.19 (0.21–0.14) [n=4]	0.15 ± 0.02; 0.16 (0.21–0.13) [n=9]	0.13 ± 0.01; 0.12 (0.16–0.12) [n=5]	0.27 ± 0.05; 0.18 (0.32–0.22) [n=3]
OLWW	0.15 ± 0.03; 0.18 (0.18–0.12) [n=4]	0.13 ± 0.02; 0.18 (0.19–0.11) [n=9]	0.11 ± 0.01; 0.07 (0.12–0.10) [n=5]	0.18 ± 0.01; 0.07 (0.18–0.16) [n=3]
NL	0.32 ± 0.01; 0.04 (0.33–0.31) [n=4]	0.23 ± 0.03; 0.12 (0.26–0.19) [n=9]	0.22 ± 0.02; 0.11 (0.26–0.20) [n=5]	0.25 ± 0.03; 0.11 (0.28–0.23) [n=3]
NW	0.36 ± 0.01; 0.03 (0.37–0.35) [n=4]	0.25 ± 0.02; 0.10 (0.30–0.22) [n=9]	0.25 ± 0.02; 0.10 (0.29–0.23) [n=5]	0.30 ± 0.03; 0.08 (0.32–0.29) [n=3]
OL/OW	1.15 ± 0.05; 0.04 (1.21–1.09) [n=6]	1.15 ± 0.05; 0.04 (1.24–1.05) [n=12]	1.14 ± 0.04; 0.04 (1.21–1.08) [n=9]	1.27 ± 0.05; 0.04 (1.34–1.20) [n=5]

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); *Iberhoratia* cf. *morenoi*: 2, Félix, Almería; 3, El Marchal de Antón López, Almería; *Iberhoratia aurorae*: 4, spring between Hervás and Jerte, Cáceres (type locality). Measurements are given as mean ± SD; CV (maximum–minimum).

internal marginal teeth approximately equal in size to those of the external marginal teeth (Figure 3I, J).

Male genitalia with a large, bean-shaped prostate gland (Table VI; Figure 4E); seminal vesicle leans over the posterior chamber of the stomach; penis small, slender, with an unpigmented non-glandular penial lobe located in a medial position (Figures 3L, 4F); the penis is black pigmented near its tip, except for males from Almería populations which have an orangish pigmentation; penial duct runs straight near the outer edge of the penis.

Female genitalia with a renal oviduct making a tight S-shaped circle which leans over the albumen gland (Figure 4G); ovary occupies approximately 75% of visceral mass; more than 50% of the oviduct glands (albumen + capsule glands) (Table III) are located inside the pallial cavity without narrowing; relative size of oviduct can vary between populations: albumen gland is larger than capsule gland in type locality (Figure 4G; Table VII), but smaller in other populations examined; bursa copulatrix large and oval, with a medium-sized narrow duct, protruding posterior to albumen gland; the origin of bursal duct is anteroventral; distal seminal receptacle (SR1) large and elongated with a short stalk protruding from renal oviduct in the middle between the oviduct fold and the point where the bursa copulatrix duct joins the oviduct; proximal seminal receptacle (SR2) difficult to identify as it tightly lies over a widened part of the renal oviduct (Figure 4H), having the characteristic refringent colour when it is full of sperm.

Remarks

This species is distributed over an extended area in which populations are very much fragmented. This wide geographic area may lend itself to intraspecific differences. In this

Figure 3. Opercula, radula, and penis of *Iberhoratia morenoi* (E–G, I, K, L), and *Ib. cf. morenoi* (A–D, H, J). (A, C, H, J) Opercula from Félix; (B, D) opercula from El Marchal de Antón López; (E, F, G, I, K, L) opercula and radula from Prado del Rey; (L) head of a male and penis from El Chorro. (A, B, E) External side of the operculum; (C, D, F, G) internal side of the operculum; (H, I) central teeth; (J) lateral, internal, and external marginal teeth; (K) ciliary fields in the pallial edge. Scale bars: 200 μm (A–G).

way, populations from Almería show more depressed shells, a penis with orangish pigmentation, a rectum loop which looks more S-shaped than U-shaped and smaller digestive and genital organs. Nevertheless, the general shape of anatomical characters for all populations is very conservative. In these populations, it is frequent to find an egg capsule located inside the umbilicus of the shell of both male and female specimens containing an embryo in different developmental stages.

Table III. Oosphradium measurements (in mm) of *Iberhoratia* species.

	1 (<i>n</i> =6)	2 (<i>n</i> =4)	3 (<i>n</i> =3)	4 (<i>n</i> =8)	5 (<i>n</i> =3)	6 (<i>n</i> =6)	7 (<i>n</i> =8)	8 (<i>n</i> =6)
Os L	0.21 ± 0.04; 0.19 (0.27–0.17)	0.20 ± 0.04; 0.19 (0.25–0.16)	0.18 ± 0.01; 0.06 (0.19–0.17)	0.20 ± 0.03; 0.15 (0.24–0.16)	0.25 ± 0.06; 0.24 (0.32–0.21)	0.22 ± 0.04; 0.19 (0.26–0.16)	0.22 ± 0.04; 0.16 (0.26–0.16)	0.22 ± 0.03; 0.12 (0.25–0.18)
Os W	0.10 ± 0.02; 0.24 (0.13–0.07)	0.07 ± 0.02; 0.29 (0.09–0.05)	0.08 ± 0.03; 0.38 (0.11–0.05)	0.08 ± 0.02; 0.29 (0.13–0.05)	0.11 ± 0.03; 0.25 (0.14–0.09)	0.08 ± 0.01; 0.15 (0.09–0.06)	0.07 ± 0.02; 0.28 (0.09–0.05)	0.06 ± 0.02; 0.32 (0.10–0.05)

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); 2, Casarabonela, Málaga; 3, Setenil, Málaga; *Iberhoratia* cf. *morenoi*: 4, Félix, Almería; 5, El Marchal de Antón López, Almería; *Iberhoratia aurorae*: 6, spring between Hervás and Jerte, Cáceres (type locality); 7, Sierra de Altamira, Cáceres; 8, Béjar, Salamanca. Measurements are given as mean ± SD; CV (maximum–minimum).

Figure 4. Anatomy of *Iberhoratia morenoi* from type locality. (A, B) Partial nervous system; (C) osphradium and ctenidium; (D) stomach; (E) prostate and rectum; (F) head of a male and penis; (G) anterior female genitalia; (H) bursa copulatrix and seminal receptacles. Abbreviations in text. Scale bar: 500 μ m.

Table IV. Radula formulae and measurements (in mm) of *Iberhoratia* species from type localities.

	<i>I. morenoi</i>	<i>I. aurorae</i>
Central teeth	4+C+4/1-1	(4)-5+C+4-(5)/1-1
Central teeth width	~7 μm	~5.3 μm
Lateral teeth	4-6+C+3	6-C-4
Internal marginal teeth	≥23 cusps	≥34 cusps
External marginal teeth	≥8 cusps	≥16 cusps
Radula length	~396 μm	0.45 mm
Radula width	~64 μm	~0.08 μm
Number of rows	~60	~75

Iberhoratia aurorae new species
(Figures 5–7)

Type locality

Spring between Hervás and Jerte, Cáceres, UTM: 30TTK551596.

Material examined

Type material. Holotype: MNCN 15.05/46991 (SEM preparation, Figure 5F, H, J, K). Paratypes: MNCN 15.05/46991 (ethyl alcohol).

Other populations examined. This species was found in the provinces of Cáceres, Salamanca, and Toledo (Figure 1). Localities are the following: spring between Hervás and Jerte, Cáceres (type locality), 10 June 1989, E. R., MNCN 15.05/46991 (ethyl alcohol, SEM preparation); stream in Roturas, Cáceres, UTM: 30STJ8482, 30 March 1991, E. R., MNCN 15.05/46992 (ethyl alcohol, SEM preparation); stream in Sierra Altamira, Toledo, UTM: 30SUJ29, 29 March 1991, E. R., MNCN 15.05/46993 (ethyl alcohol); Béjar, Salamanca, UTM: 30TTK6573, 10 June 1989, E. R., MNCN 15.05/46994 (ethyl alcohol).

Material examined for morphometry. Shell measurements (Table I) correspond to specimens from all above populations. Operculum and radular measurements (Table II, IV) correspond to the type locality. Anatomical measurements (Tables III, IV, VI, VII) correspond to the type locality, Roturas, Béjar, and Sierra de Altamira. Males and females studied and measured were collected in March and June.

Etymology

Dedicated to Aurora López, mother of the first author.

Diagnosis

Shell valvatiform; operculum oval without peg; the oesophagus makes a loop near the cerebral commissure; rectum strongly S-shaped; male genitalia with a slender penis having a non-glandular penial lobe located in a medial position; female genitalia with a pallial

Table V. Digestive system measurements (in mm) of *Iberhoratia* species.

	1 (<i>n</i> =4)	2 (<i>n</i> =4)	3 (<i>n</i> =4)	4 (<i>n</i> =7)	5 (<i>n</i> =6)	6 (<i>n</i> =4)	7 (<i>n</i> =4)	8 (<i>n</i> =5)
Ss L	0.34±0.09; 0.25 (0.42–0.20)	0.29±0.02; 0.08 (0.32–0.27)	0.28±0.04; 0.13 (0.32–0.24)	0.27±0.05; 0.19 (0.36–0.20)	0.41±0.02; 0.04 (0.43–0.39)	0.28±0.05; 0.17 (0.34–0.24)	0.33±0.02; 0.07 (0.36–0.30)	0.26±0.05; 0.18 (0.33–0.20)
Ss W	0.22±0.03; 0.15 (0.26–0.15)	0.21±0.03; 0.16 (0.26–0.18)	0.21±0.04; 0.18 (0.23–0.15)	0.19±0.04; 0.19 (0.24–0.15)	0.25±0.06; 0.22 (0.35–0.22)	0.18±0.03; 0.16 (0.22–0.15)	0.21±0.03; 0.16 (0.24–0.17)	0.20±0.03; 0.13 (0.24–0.18)
St L	0.41±0.05; 0.12 (0.46–0.27)	0.41±0.05; 0.13 (0.48–0.36)	0.43±0.06; 0.13 (0.48–0.37)	0.41±0.07; 0.18 (0.51–0.27)	0.59±0.07; 0.13 (0.73–0.49)	0.48±0.06; 0.12 (0.56–0.40)	0.54±0.01; 0.02 (0.55–0.53)	0.50±0.05; 0.09 (0.56–0.46)
St W	0.36±0.04; 0.10 (0.45–0.26)	0.32±0.04; 0.13 (0.37–0.28)	0.35±0.08; 0.22 (0.45–0.29)	0.30±0.06; 0.20 (0.40–0.24)	0.42±0.04; 0.11 (0.48–0.35)	0.32±0.04; 0.12 (0.36–0.28)	0.35±0.05; 0.13 (0.36–0.30)	0.33±0.04; 0.11 (0.37–0.28)

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); 2, Setenil, Málaga; 3, Casarabonela, Málaga; *Iberhoratia* cf. *morenoi*: 4, Félix, Almería; *Iberhoratia aurorae*: 5, spring between Hervás and Jerte, Cáceres (type locality); 6, Sierra de Altamira, Cáceres; 7, Béjar, Salamanca; 8, Roturas, Cáceres. Measurements are given as mean ± SD; CV (maximum–minimum).

Table VI. Male genitalia measurements (in mm) of *Iberhoratia* species.

	1	2	3	4	5	6	7	8
Pr L	0.67 ± 0.16; 0.23 (0.84–0.54) [n=3]	0.51 [n=1]		0.58 ± 0.12; 0.20 (0.72–0.41) [n=5]		0.41 ± 0.04; 0.09 (0.44–0.37) [n=3]	0.33 ± 0.02; 0.05 (0.35–0.32) [n=3]	0.35 ± 0.05; 0.12 (0.40–0.31) [n=3]
Pr W	0.25 ± 0.02; 0.06 (0.27–0.24) [n=3]	0.22 [n=1]		0.26 ± 0.07; 0.28 (0.33–0.17) [n=5]		0.18 ± 0.01; 0.07 (0.19–0.17) [n=3]	0.18 ± 0.02; 0.09 (0.19–0.16) [n=3]	0.24 ± 0.03; 0.11 (0.26–0.21) [n=3]
P L	0.57 ± 0.14; 0.25 (0.86–0.44) [n=8]	0.51 ± 0.10; 0.19 (0.61–0.41) [n=3]	0.80 ± 0.22; 0.28 (1.03–0.59) [n=3]	0.55 ± 0.21; 0.38 (0.84–0.28) [n=7]	0.80 ± 0.11; 0.13 (0.86–0.68) [n=3]	0.66 ± 0.07; 0.11 (0.77–0.57) [n=5]	0.62 ± 0.06; 0.09 (0.67–0.56) [n=3]	0.62 ± 0.08; 0.13 (0.70–0.52) [n=4]
P W	0.10 ± 0.03; 0.27 (0.16–0.09) [n=8]	0.11 ± 0.02; 0.16 (0.12–0.09) [n=3]	0.17 ± 0.04; 0.23 (0.21–0.13) [n=3]	0.11 ± 0.03; 0.27 (0.14–0.06) [n=7]	0.16 ± 0.02; 0.13 (0.18–0.14) [n=3]	0.15 ± 0.02; 0.11 (0.17–0.13) [n=5]	0.11 ± 0.02; 0.18 (0.13–0.09) [n=3]	0.15 ± 0.03; 0.18 (0.18–0.12) [n=4]
Pl L	0.09 ± 0.02; 0.25 (0.13–0.06) [n=8]	0.08 ± 0.02; 0.29 (0.11–0.06) [n=3]	0.20 ± 0.03; 0.14 (0.22–0.17) [n=3]	0.08 ± 0.04; 0.51 (0.13–0.04) [n=7]	0.15 ± 0.04; 0.24 (0.17–0.11) [n=3]	0.10 ± 0.02; 0.18 (0.13–0.09) [n=5]	0.12 ± 0.04; 0.36 (0.15–0.07) [n=3]	0.13 ± 0.02; 0.13 (0.15–0.11) [n=4]
Pl W	0.06 ± 0.01; 0.22 (0.08–0.05) [n=7]	0.05 ± 0.01; 0.14 (0.05–0.04) [n=3]	0.13 ± 0.05; 0.40 (0.18–0.07) [n=3]	0.07 ± 0.01; 0.15 (0.09–0.05) [n=7]	0.20 ± 0.04; 0.22 (0.24–0.16) [n=3]	0.07 ± 0.02; 0.27 (0.08–0.04) [n=5]	0.06 ± 0.01; 0.20 (0.07–0.05) [n=3]	0.09 ± 0.01; 0.07 (0.09–0.08) [n=4]
Pl/Head length	1.01 ± 0.15; 0.15 (1.32–0.84) [n=7]	0.79 ± 0.20; 0.25 (1.00–0.62) [n=3]	1.32 [n=1]	0.86 ± 0.14; 0.16 (0.95–0.56) [n=7]	1.10 ± 0.13; 0.12 (1.25–0.98) [n=3]	0.66 ± 0.04; 0.06 (0.70–0.61) [n=4]	0.90 ± 0.06; 0.06 (0.93–0.83) [n=3]	0.80 ± 0.08; 0.10 (0.88–0.69) [n=4]

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); 2, Setenil, Málaga; 3, El Chorro, Málaga; *Iberhoratia* cf. *morenoi*: 4, Félix, Almería; 5, El Marchal de Antón López, Almería; *Iberhoratia aurorae*: 6, spring between Hervás and Jerte, Cáceres (type locality); 7, Sierra de Altamira, Cáceres; 8, Béjar, Salamanca. Measurements are given as mean ± SD; CV (maximum–minimum).

Table VII. Female genitalia measurements (in mm) of *Iberhoratia* species.

	1	2	3	4	5	6	7	8
Po L	0.62±0.13; 0.20 (0.75–0.51) [n=3]	0.49±0.06; 0.13 (0.55–0.43) [n=3]	0.54±0.06; 0.29 (0.58–0.50) [n=2]	0.56±0.11; 0.19 (0.68–0.47) [n=3]	0.53±0.08; 0.14 (0.59–0.48) [n=2]	0.72±0.07; 0.09 (0.80–0.63) [n=5]	0.72±0.10; 0.15 (0.86–0.61) [n=4]	0.70±0.03; 0.04 (0.73–0.66) [n=7]
Po W	0.35±0.03; 0.08 (0.38–0.32) [n=3]	0.30±0.02; 0.05 (0.32–0.29) [n=3]	0.27±0.04; 0.16 (0.30–0.24) [n=2]	0.23±0.03; 0.25 (0.26–0.21) [n=3]	0.29±0.02; 0.08 (0.31–0.28) [n=2]	0.25±0.04; 0.16 (0.31–0.21) [n=5]	0.25±0.03; 0.14 (0.28–0.21) [n=4]	0.28±0.02; 0.08 (0.31–0.24) [n=7]
Ag L	0.39±0.10; 0.27 (0.46–0.27) [n=3]	0.21±0.06; 0.31 (0.25–0.16) [n=2]	0.27±0.01; 0.04 (0.28–0.26) [n=2]	0.30±0.04; 0.13 (0.34–0.26) [n=3]	0.21±0.00; 0.00 (0.21–0.21) [n=2]	0.23±0.03; 0.13 (0.27–0.19) [n=5]	0.34±0.08; 0.23 (0.45–0.29) [n=4]	0.36±0.07; 0.20 (0.43–0.25) [n=6]
Cg L	0.23±0.07; 0.29 (0.29–0.16) [n=3]	0.31±0.01; 0.04 (0.32–0.29) [n=2]	0.27±0.07; 0.25 (0.32–0.23) [n=2]	0.26±0.07; 0.25 (0.34–0.21) [n=3]	0.32±0.08; 0.24 (0.37–0.27) [n=2]	0.49±0.08; 0.16 (0.61–0.39) [n=5]	0.39±0.08; 0.21 (0.49–0.30) [n=4]	0.36±0.04; 0.11 (0.41–0.32) [n=7]
SR1 L	0.18±0.02; 0.09 (0.19–0.16) [n=3]	0.14±0.03; 0.23 (0.17–0.11) [n=3]	0.11±0.01; 0.13 (0.12–0.10) [n=2]	0.14±0.02; 0.16 (0.16–0.12) [n=3]	0.12±0.00; 0.00 (0.12–0.12) [n=2]	0.07±0.02; 0.26 (0.10–0.05) [n=4]	0.06±0.02; 0.38 (0.09–0.04) [n=4]	0.11±0.03; 0.25 (0.15–0.07) [n=7]
BC L	0.32±0.04; 0.14 (0.35–0.27) [n=3]	0.25±0.05; 0.20 (0.31–0.22) [n=3]	0.25±0.02; 0.09 (0.26–0.23) [n=2]	0.24±0.09; 0.38 (0.36–0.15) [n=4]	0.24±0.08; 0.35 (0.30–0.18) [n=2]	0.27±0.07; 0.24 (0.35–0.21) [n=5]	0.29±0.06; 0.13 (0.35–0.22) [n=4]	0.24±0.03; 0.14 (0.29–0.20) [n=7]
BC W	0.22±0.07; 0.30 (0.29–0.16) [n=3]	0.20±0.04; 0.19 (0.23–0.16) [n=3]	0.17±0.03; 0.17 (0.19–0.15) [n=2]	0.13±0.05; 0.39 (0.19–0.07) [n=4]	0.19±0.03; 0.16 (0.21–0.17) [n=2]	0.19±0.08; 0.40 (0.31–0.11) [n=5]	0.15±0.06; 0.26 (0.30–0.16) [n=4]	0.13±0.07; 0.29 (0.19–0.08) [n=7]
dBC L	0.18±0.02; 0.19 (0.19–0.16) [n=3]	0.25±0.09; 0.37 (0.34–0.16) [n=3]	0.14±0.04; 0.29 (0.17–0.11) [n=2]	0.15±0.06; 0.41 (0.24–0.09) [n=4]	0.15±0.02; 0.15 (0.17–0.14) [n=2]	0.18±0.03; 0.19 (0.23–0.16) [n=5]	0.22±0.06; 0.25 (0.30–0.16) [n=4]	0.30±0.07; 0.23 (0.41–0.24) [n=5]

Iberhoratia morenoi: 1, Prado del Rey, Cádiz (type locality); 2, Setenil, Málaga; 3, Casaraboneal, Málaga; *Iberhoratia* cf. *morenoi*: 4, Félix, Almería; 5, El Marchal de Antón López, Almería; *Iberhoratia aurorae*: 6, spring between Hervás and Jerte, Cáceres (type locality); 7, Béjar, Salamanca; 8, Sierra de Altamira, Cáceres. Measurements are given as mean ± SD; CV (maximum–minimum).

oviduct with a marked narrowing, an oval, well-developed bursa copulatrix and two seminal receptacles; distal seminal receptaculum rounded and proximal one lying over the renal oviduct; central tooth of the radula with one basal cusp on each side.

Description

Shell valvatiform (Figure 5A–F; Table I), with 3.5 whorls, approximately; 1.25 protoconch whorls, total width and nucleus width are 304 and 126 μm , respectively (Figure 5H, I); protoconch microsculpture with granules (Hershler and Ponder 1998, p 4) (Figure 5J, K); some specimens have been found with an eroded protoconch near the varix which separates it from the teleoconch (Figure 5I); umbilicus wide, 0.28 μm in diameter (Figure 5G); aperture rounded-oval; outer peristome simple, thin, and straight (Figure 5D).

Operculum thin, pliable, corneous, paucispiral, oval, yellowish, with a large and central nucleus (Figure 6A, B; Table II); its muscle attachment area is oval, generally submarginal but sometimes almost central.

Body: head unpigmented or scarcely pigmented around the eyes (Figure 7F). Snout about as long as wide, parallel-sided, with a medium distal lobation.

Nervous system with a suboesophageal connective absent and a long supraoesophageal connective (Figure 7B); the oesophagus makes a loop to the right posterior to the cerebral commissure (Figure 7A); nervous system measurements are: length of the cerebral ganglia: 0.16 mm; length of the right pleural ganglion: 0.14 mm; length of the left pleural ganglion: 0.14 mm; length of the suboesophageal ganglion: 0.07 mm; length of the supraoesophageal ganglion: 0.11 mm; length of the pleurosupraoesophageal connective: 0.14 mm; RPG ratio is 0.35.

Ctenidium with 11–13 well-developed lamellae, occupying around two-thirds of the pallial cavity (Figure 7C); osphradium 50–60% of ctenidium length, oval, two to three times longer than broad, located in the opposite middle of the ctenidium (Table III).

Stomach with posterior and anterior chambers approximately equal in size (Figure 7E); rectum strongly S-shaped (Figure 7D); the length of the style sac is around three-fifths of the length of the stomach (Table V).

Radula taeniaglossate (Figure 6C–F; Table IV), long (0.5%) relative to maximum shell dimension; central trapezoidal tooth with one basal cusp on each side; distance between internal cusps is 7 μm , approximately; its central denticle is long and tapered, followed on each side by four to five similar denticles in decreasing order of size; basal tongue V-shaped; cutting edge of the central tooth markedly excavated; lateral teeth with four to six denticles on each side of the central one; marginal teeth with abundant small and sharp denticles.

Male genitalia with a small, bean-shaped prostate gland (Table VI); the anterior lobes of the testis overlaps the posterior chamber of the stomach, sometimes reaching the anterior chamber; penis slender, with distal end tapered, shorter than the head, with an unpigmented non-glandular penial lobe located in a medial position (Figure 7F); the penis is black pigmented near its tip; penial duct runs straight near the outer edge of the penis.

Female genitalia with a renal oviduct making a tight circle which leans over the albumen gland (Figure 7G); bursa copulatrix oval, almost rectangular, protruding posterior to albumen gland, well developed (Figure 7G, H), with a long duct; origin of bursal duct anteroventral; proximal seminal receptacle (SR2) lying tightly over the widened part of the renal oviduct (Figure 7H); most of the females have a large and rounded distal seminal receptacle (SR1), with a very short, or not evident, stalk located at or next to the area where

Figure 5. Shells of *Iberhoratia aurorae*. (A–D, G) Shells from Robladillo de Gata; (E, I) shells from Roturas; (F, H, J, K) shell (holotype) from population between Hervás and Jerte (type locality). (H–K) Protoconch and microsculpture. Scale bar: 500 µm (A–G).

the bursal duct arises from the renal oviduct (Figure 7H); oviduct glands (albumen + capsule glands) slender, with a marked narrowing in its middle part (Figure 7G). This narrowing is produced by the strong folding of the rectum in the pallial cavity constraining the pallial oviduct; capsule gland is larger than the albumen gland (Table VII).

The SR1 appears like an off-white and refringent ball in some populations, while in others it can be observed as a large and almost transparent vesicle inside of which a smaller and off-white vesicle can be distinguished arising from the SR basis.

Figure 6. Operculum and radula of *Iberhoratia aurorae* from type locality. (A) Internal side of the operculum; (B) external side of the operculum; (C) radula; (D) central and lateral teeth; (E) central tooth; (F) lateral and internal marginal teeth. Scale bar: 200 μm (A, B); 100 μm (C).

Remarks

The granulated protoconch microsculpture of *Ib. aurorae* is different from that of *Ib. morenoi* and the rest of the known Iberian Hydrobiidae species. There is very low variability between populations of this species. Comparing the type locality with the other populations

Figure 7. Anatomy of *Iberhoratia aurorae* from type locality. (A, B) Partial nervous system; (C) osphradium and ctenidium; (D) rectum curve; (E) stomach; (F) head of a male and penis; (G) anterior female genitalia; (H) bursa copulatrix and seminal receptacles. Abbreviations in text. Scale bar: 500 μ m (A–H).

examined, shells are smaller and more flattened, thus showing lower values in all shell parameters, except for the ratio of shell length/shell width. Number of whorls is also higher in the type locality. Other anatomical measurements show similar range variability, although very few specimens were available for comparisons. Several females studied from Roturas populations were infected with parasitic trematodes in different larval stages. The bursa copulatrix, pallial oviduct, and seminal receptacle were almost indistinguishable in these specimens. Castration induced by parasites and the role of intermediate hosts in some parasite cycles has already been described in other gastropods (Rothschild 1938; González-Moreno et al. 1994). These parasites have also been found infecting the whole body of females. Shells from the Altamira population are reddish, probably due to external metal deposition. On the contrary, shells from Bejar and Hervás-Jerte populations are transparent.

Iberhoratia gatoa (Boeters, 1980) n. comb.

(Figures 8, 9)

Horatia gatoa Boeters 1980, p 62–64, Figures 5, 7, 8.

Type locality

A cave named Hundedero del Gato, Benaolán, Málaga, UTM: 30SVF003673.

Material examined

Type material. Holotype: (shell and operculum) in the NNM collection (55467). Shell of the holotype, which has the peristome damaged, has been examined (Figure 8A–C). The following paratypes are deposited in different collections but they were not examined: NNM 55468/1 (juvenile shell and operculum), NNM 9079/1 (juvenile in alcohol), Boeters 948/4 (damaged shell with operculum and three genitalia from two males and one female).

Type material excluded from the species. Shell originally included by Boeters into *H. gatoa* (Boeters 1980, Figure 6=Figure 9C, D in this paper), is re-identified as *Milesiana schueleii* (Boeters, 1981) (in Arconada and Ramos 2006).

Description

Original description in Boeters (1980) and redescription (Boeters 1988) (Figures 8A–C, 9A, B, E, F; Table VIII). Anatomical description was based on two males and one female. The following description is based on the original one excluding the shell re-identified as *M. schueleii*, and on the study of the holotype.

Shell shape valvatiform, with 3.5 whorls. The aperture does not ascend or descend near the last whorl. Shell aperture is rounded. Operculum pale yellowish, without any outgrowth. Rectum Z-shaped. Penis with a small lobe located in a medial position. Female genitalia has a well-developed bursa copulatrix, an elongated distal seminal receptacle, and a proximal receptacle lying tightly over a widened part of the renal oviduct.

Remarks

Original illustrations of female genitalia of *Ib. gatoa* (Boeters 1980) show a widened renal oviduct, which may have a seminal receptacle bent and adhered to the renal oviduct as in

Figure 8. Holotype of *Iberhoratia gatoa* (RMNH 55467). Scale bar: 500 µm (A, B).

Ib. morenoi and *Ib. aurorae*, and a distal seminal receptacle (Figure 9F) as is the normal female genital disposition for *Iberhoratia* species.

According to the measurements given by Boeters (1980) in the original description, the shell length varies from 0.8 to 1.5 mm and shell width from 1.3 to 1.5 mm. In the figure caption the holotype width is 1.5 mm and length 1.5 mm. We cannot determine if this variability in shell values indicates that Boeters included in the species description

Figure 9. Original illustrations of *Iberhoratia gatoa* (Boeters 1980, p 63). (A, B) Holotype (RMNH 55467), shell width 1.5 mm; (C, D) paratype (BOE 948), shell width 1.2 mm; (E) penis (paratype BOE 948); (F) anterior female genitalia (paratype BOE 948).

Table VIII. Shell measurements (in mm) of holotype of *Iberhoratia gatoa* (RMNH 55467) and topotypes of *Horatia klecakiana* (NHM-WIEN, 17.683).

	Holotype of <i>Iberhoratia gatoa</i>	Topotypes of <i>Horatia klecakiana</i> ^a
SL	1.50 [n=1]	1.24 ± 0.13; 0.11 (1.40–1.03) [n=14]
SW	1.50 [n=1]	1.58 ± 0.14; 0.09 (1.83–1.33) [n=14]
SL/SW		0.79 ± 0.06; 0.07 (0.89–0.71) [n=14]
AH		0.89 ± 0.09; 0.10 (1.07–0.77) [n=14]
LBW		1.11 ± 0.11; 0.10 (1.25–0.93) [n=14]
WBW		1.09 ± 0.10; 0.09 (1.20–0.90) [n=14]
AL		0.77 ± 0.07; 0.08 (0.93–0.67) [n=14]
AW		0.82 ± 0.06; 0.12 (1.10–0.73) [n=14]
WPW		0.48 ± 0.06; 0.14 (0.60–0.33) [n=14]
WAW		0.22 ± 0.05; 0.22 (0.33–0.17) [n=11]
NSW	2.75 [n=1]	3.23 ± 0.21; 0.06 (3.50–3.00) [n=11]

^aMeasurements are given as mean ± SD; CV (maximum–minimum).

measurements of the other three specimens for which anatomy was studied. Original shell illustrations from the holotype (Figures 8A–C, 9A, B) and paratype of *H. gatoa* (Figure 9C, D) correspond to two specimens, which may not be conspecific. The paratype of *H. gatoa* (BOE 948) has a much flatter shell relative to the holotype, probably corresponding to *Milesiana schuelelei* (Boeters, 1981) (in Arconada and Ramos 2006), a species which is very abundant in the type locality of *Ib. gatoa*. In fact, shell measurements from this paratype (shell width 1.2 mm; length 0.8 mm) correspond to that described for *M. schuelelei*. We can either consider that this paratype is actually a juvenile of *Ib. gatoa*, or that it belongs to *M. schuelelei*. The second hypothesis seems to be more feasible because the growth rate of this shell is greater than that of the holotype. For this reason we have proposed that this specimen might be excluded from the type material (Arconada and Ramos 2006). Nevertheless, the genital illustrations from two other paratypes (one male and one female) with the same collection number (BOE 948) illustrated by Boeters (1980, Figure 9E, F) actually correspond to the typical anatomical scheme of the genus *Iberhoratia*.

Statistical analysis of *Iberhoratia* species

Morphological differences between *Ib. morenoi* and *Ib. aurorae* are based on the shape of the protoconch microsculpture, the loop of the rectum, the length of the supraoesophageal connective, the direction of the loop of the oesophagus posterior to the ganglion complex of the nervous system, the marked narrowing of the pallial oviduct of *Ib. aurorae*, a larger prostate gland in *Ib. morenoi* than in *Ib. aurorae* and the different shape of both the distal seminal receptacle and the bursa copulatrix.

Both species are smaller than European *Horatia* species: *H. klecakiana* (shell length: 1.7–2.7 mm in Radoman (1966) or 1.55–2.14 mm in Radoman (1983), width: 1.8–2.41 mm in Radoman (1966) or 1.81–2.18 mm in Radoman (1983); NSW: 3.25–3.5), *H. macedonica* (shell length: 1.47–1.68 mm, width: 1.64–1.68 mm; NSW: 3.25–3.5), and *H. novoselensis* (in Radoman 1966: shell length: 1.3–1.5 mm, width: 1.3–1.4 mm; NSW: 3–3.25). Anatomical comparisons are difficult due to the lack of data for all species except for the type species (Bodon et al. 2001, p 127). *Horatia klecakiana* is very similar to *Ib. morenoi*, having several differences such as shell characters, the absence of a penial pigmentation, and a long to somewhat short pleurosuboesophageal connective (Bodon et al. 2001, p 130–131). It shows more differences from *Ib. aurorae*, the latter having an S-shaped rectal loop, a globular bursa copulatrix, a very pronounced narrowing in the pallial gland (albumen + capsule gland) and lacking a pleurosuboesophageal connective. *Horatia novoselensis* is the only species described which lacks a ctenidium.

Conchological differences between *Iberhoratia* populations and *Horatia klecakiana* topotypes were investigated by a discriminant function analysis (DFA). It was carried out using the nine standard shell measurements on Table I and the number of spire whorls. Five highly significant discriminant functions were found (Wilk's lambda=0.0068, $F(60, 539)=14.279$, $P<0.001$). For the first function that accounted for 54% of explained variance with an eigen value of 6.22, the variables that contributed (the highest weight) were (in order): SL, LBW, and AL. This function mostly discriminates the population corresponding to the type locality of *Ib. aurorae* and the Gador population of *Ib. cf. morenoi*. For the second function that accounts up to 80% of the explained variance with an eigen value of 3.02, the order was: AW, SL, and NSW. This function discriminates *H. klecakiana* from the rest. The first four discriminant functions were highly significant ($P<0.001$). Of the 118 individuals classified, all of the *Ib. cf. morenoi* from Gador, 93% of type locality of *Ib. aurorae* (Hervás-Jerte), 87% of Altamira, 80% of Béjar, 68% of Roturas, and 64% of Cádiz were correctly classified, and finally, all individuals of *H. klecakiana* (100%) were also well classified. On the scatterplot (Figure 10), seven clusters can be observed. *H. klecakiana* separates from the rest, mostly in the proportions of the aperture, which is wider than in the other populations and in the size of the body whorl that is longer and wider than in the others. The population from the type locality of *Ib. aurorae* (Hervás) has less depressed shells than the rest (Table I) and the highest number of spire whorls, which corresponds to variables which have more discriminatory power (SW and NSW).

A second DFA was performed at the species level bringing together all the populations of each species and using the same number of variables (Figure 11). In this analysis only two highly significant discriminant functions were found (Wilk's lambda=0.097, $F(20, 212)=23.212$, $P<0.001$). For the first function that accounted for 63% of explained variance, the variables that contributed (the highest weight) were (in order): AW, NSW, and LBW. For the second function the order was: SL, WBW, and SW. Of the 120 individuals classified, 100% of *H. klecakiana*, 98% of *Ib. aurorae* (78 out of the 80 measured), and 85% of *Ib. morenoi* were correctly classified. Only four of the 26 individuals

of *Ib. morenoi*, those having the largest shells, were classified as belonging to *Ib. aurorae*. Of the 82 individuals of *Ib. aurorae*, one was classified as *Ib. morenoi* and other as *H. klecakiana*. Therefore, the analysis discriminated well between the three species and especially separated *H. klecakiana* from the Iberian *Iberhoratia* species.

Habitat and distribution

Iberhoratia morenoi and *Ib. aurorae* live in springs with clear water and aquatic vegetation. In this typical habitat of Iberian valvatiform Hydrobiidae, they can be found on the roots and leaves of aquatic vegetation, stones, or even in the sand. The unique known population of the stygobiont species *Ib. gatoa* inhabits a cave difficult to access, which has a subterranean river. The conservation status of this population is actually unknown. Populations of *Ib. morenoi* and *Ib. aurorae* are distant from each other, but the distribution area of *Ib. morenoi* overlaps that of *Ib. gatoa*.

Iberhoratia species can be found sharing the same habitat with a wide variety of other freshwater molluscs, such as *Potamopyrgus antipodarum* (Gray, 1843), *Mercuria* sp., *Pseudamnicola* sp., *Milesiana schueleii* (Boeters, 1981) (in Arconada and Ramos 2006), *Lymnaea truncatula* (O. F. Müller, 1774), *Ancylus fluviatilis* (O. F. Müller, 1774), and *Pisidium* spp.

Figure 10. Plot of discriminant scores on the two canonical axes, obtained from DFA of shell measurements for *Iberhoratia* species and topotypes of *Horatia klecakiana* (NHM-WIEN, 17.683). Confidence interval for ellipses: 0.95.

Figure 11. Plot of discriminant scores on the two canonical axes, obtained from DFA of shell measurements for the species *Iberhoratia morenoi*, *Ib. aurorae*, and *Horatia klecakiana*. Confidence intervals for ellipses: 0.95.

Discussion

The existence of an internal seminal receptacle is a novel character seen for the first time in Iberian Hydrobiidae. Traditionally, illustrations of the genitalia of *Horatia* type species (Radoman 1966) describe only one SR1, although they show a significant thickening of the renal oviduct.

Recently, *Horatia* has been re-described as having a “proximal seminal receptacle relatively indistinct, bent to adhere to oviduct level with end of loop” (Bodon et al. 2001). On the other hand, in these two new Iberian species this proximal seminal receptacle rather seems to be an internal organ that protrudes from the wall of the renal oviduct, similar to that described and illustrated by Radoman (1983) for *H. klecakiana*. This author described this character as “rs2 sometimes imbedded in the oviduct tissue itself, where it can hardly be observed”. This character is not similar to the widened renal oviduct described for other Iberian Hydrobiidae species (Ramos et al. 2000), which consists of a strong columnar epithelium that makes longitudinal internal folds and leaves a stretched lumen, instead of an internal receptacle.

Other morphological characters of the Spanish *Iberhoratia* species are rather similar to those of *H. klecakiana*. Morphological differences between them mostly consist of morphometrical characters and relative size of several structures. *Horatia klecakiana* has bigger shells (height=1.55–2.14 mm; width=1.81–2.18 mm); a narrower umbilicus; a smaller capsule gland and correspondingly larger albumen gland in relation to the total size of pallial oviduct. The penis of *H. klecakiana* has one or two relatively small outgrowths while the two species of *Iberhoratia* show one medium-sized lobe. In relation to the nervous

system, the pleuro-suboesophageal connective is always present in *H. klecakiana* (Radoman 1983) and seems to be longer than in *Ib. morenoi*; it is absent in *Ib. aurorae*. There is still no available data about the shape of the oesophagus along the cerebral commissure for *H. klecakiana*, although this might be an interesting characteristic for comparison.

A comparison of the 16S ribosomal RNA gene, partial sequence (503 bp) in GenBank for *Horatia klecakiana* (accession number AY222656) with still unpublished molecular data of several species and genera of Iberian valvatoid hydrobiids (Arconada 2000) was carried out. *Horatia klecakiana* showed a divergence of around 10% with *Iberhoratia* populations, whilst the divergence between congeneric species ranges from less than 4 to 6%. The introduction of the new genus *Iberhoratia* for these Iberian species based on morphological characters is therefore well supported by genetic distances.

Most of the species which were previously considered as belonging to the genus *Horatia* may have to be revised and morphologically studied in detail. From the list of valid and dubious species listed by Bodon et al. (2001), we may have to exclude two of them which were recently re-described and included in two new genera: “*Horatia*” *gasulli* (Boeters, in Gasull 1981) as *Tarraconia gasulli* (Ramos et al. 2000) and *Horatia* (?) *sturmi* (Rosenhauer, 1856) as *Boetersiella sturmi* (Arconada and Ramos 2001). In fact, Bodon et al. (2001) stated that “neither *Horatia sturmi*, nor *Horatia gatoa* belonged to *Horatia*”. In the case of *Horatia sturmi*, main differences are based on the morphology of the penis and the existence of only one seminal receptacle (SR2) (supported by previous data, Ramos et al. 1992, 1995). Oddly, these authors omitted the previously published paper in which the systematics of this species was profusely discussed (Ramos et al. 2000). The second species, *Ib. gatoa*, is defined as having “a wide bursa copulatrix similar to that of species of *Horatia* and female genitalia having a large bursa copulatrix and a distal (or RS1) seminal receptacle” (Bodon et al. 2001). In this paper, the authors did not recognize the existence of a proximal seminal receptacle in the widened part of the renal oviduct, although in the female genitalia originally illustrated by Boeters (1980, Figure 8) this fact is not completely clear. The scarce morphological data available for this species and the fact that its only known population is located within the geographical range of *Ib. morenoi* suggest that it be provisionally assigned to *Iberhoratia* until more specimens are available for study.

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