Spira 8 (2022) 47-59
molluscat la web oficial de l'ACM
SPIRA
https://molluscat.com/spira/

The first cave-dwelling Hydrocenidae (Gastropoda: Cicloneritida) in Europe, *Hydrocena canttabrica* sp. nov., lives in the Cantabrian Region (Spain)

Carlos E. Prieto[1], Sergio Quiñonero-Salgado[2], Jesús Ruiz-Cobo[3] & Álvaro Alonso[4]

[1] *Departamento de Zoología y BCA, Universidad del País Vasco (UPV/EHU). PO.Box 644, 48080-Bilbao (Spain) / Calle Astarloa 5, 5ºA, 48001-Bilbao (Spain)*
[2] *Associació Catalana de Malacologia, Museu Blau, Plaça Leonardo da Vinci 4-5, 08019 Barcelona (Spain)*
[3] *Instituto Sautuola de Prehistoria y Arqueología, Calle Rio Ebro 8, 39008-Santander (Spain)*
[4] *Calle Infiesto 7, 6º J, 33207-Gijón (Spain)*

Rebut el 7 de setembre de 2022
Acceptat el 31 d'octubre de 2022

Editat per Joaquín López-Soriano

Key words:
Hydrocena, Cantabria, Spain, troglobiont, new species

Paraules clau:
Hydrocena, Cantàbria, Espanya, troglobi, nova espècie

ABSTRACT

The Cantabrian Region lies, as the Dinaric Region, in the mid-latitude biodiversity ridge in cave fauna, which favours the existence of odd troglobiont taxa. It harbours a rich terrestrial subterranean malacofauna belonging to families Aciculidae, Carychiidae, Azecidae and Papillodermatidae, reaching a dozen species. The finding of a depigmented species with transparent shell belonging to the family Hydrocenidae in Cueva Covallarco and other caves from the Miera-Asón massif allow the description of *Hydrocena canttabrica* sp. nov. The two other extant European species, both epigean, the Dinaric *Hydrocena cattaroensis* (Pfeiffer, 1841) and the Macaronesian *Hydrocena gutta* Shuttleworth, 1852 have been also studied, providing the first data on the anatomy of *Hydrocena gutta*. *H. canttabrica* sp. nov. lives on wet passage walls in the outermost part of caves, in the twilight zone in some cases. Five subterranean terrestrial molluscs have been found in Cueva Covallarco, being the richest Iberian cave for molluscs. In addition, the fossil genus *Schwardtina* Bandel & Riedel, 1994 is proposed as synonym of *Hydrocena,* and *Georissa pilsbryana* Prieto is proposed as *nomen novum* for *Georissa japonica* Pilsbry, 1900.

RESUM

La regió Cantàbrica s'ubica com la regió Dinàrica en la cresta de biodiversitat de la fauna cavernícola de les latituds temperades, cosa que afavoreix l'existència de peculiars taxons troglobionts. Alberga una rica malacofauna terrestre subterrània pertanyent a les famílies Aciculidae, Carychiidae, Azecidae i Papillodermatidae, sumant-ne una dotzena d'espècies. La troballa d'una espècie despigmentada amb conquilla transparent de la família Hydrocenidae a la Cueva de Covallarco i d'altres coves del massís Miera-Asón permet la descripció d'*Hydrocena canttabrica* sp. nov. Les altres dues espècies europees existents, totes dues epigees, la dinàrica *Hydrocena cattaroensis* (Pfeiffer, 1841) i la macaronèsica *Hydrocena gutta* Shuttleworth, 1852 també han estat estudiades, proporcionant les primeres dades sobre l'anatomia de *Hydrocena gutta*. *H. canttabrica* nov. sp. viu a les parets humides de les galeries a la part més externa de les coves, en alguns casos a la zona de penombra. A la Cueva de Covallarco se n'han trobat fins a cinc espècies de mol·luscs terrestres subterranis, tractant-se la cova ibèrica més rica en mol·luscs. A més, es proposa el gènere fòssil *Schwardtina* Bandel & Riedel, 1994 com a sinònim d'*Hydrocena*, i *Georissa pilsbryana* Prieto com *nomen novum* per *Georissa japonica* Pilsbry, 1900.

Introduction

Considering terrestrial cave fauna in Europe, a mid-latitude biodiversity ridge is defined by Culver *et al.* (2006) ranging from the Dinaric region in the east to the Pyrenean-Cantabrian mountains in the west. They base this unit on only two political units: Slovenia with 122 obligate cave species (troglobionts) in 5,600 km^2, and Ariège (France) with 95 troglobionts in 3,000 km^2. Other censuses identified additional putative European hotspots of cave fauna within the Cantabrian region. Galán (2006) listed 104 troglobionts for the province of Gipuzkoa (2,000 km^2, Spain) and Labrada *et al.* (2010) also listed 104 troglobionts for the Autonomous Community of Cantabria (5,300 km^2, Spain). Both catalogues confirm that this biodiversity ridge extends westward beyond of the Pyrenees. Taking into account the number of undescribed taxa, the figures mentioned by Galán and Labrada *et al.* would rise to more than 110 troglobionts, for a suitable area much smaller than the political units. With respect to the aquatic fauna, Achurra *et al.* (2015) considered the Cantabrian region to be a hotspot as diverse as Slovenia, which has the highest stygobiotic species richness in Europe with 21 vs. 28 stygobionts. Apart from the high biodiversity, the Dinaric and Cantabrian regions share a number of supraspecific cave taxa such as oligochaetes (*Delaya* Brinkhurst, 1988), gastropods (*Zospeum* Bourguignat, 1856 vs. *Iberozospeum* Jochum, Kneubühler, Prieto and Neubert, 2022), diplopods (*Mesoiulus* Berlese, 1886), beetles (tribe Leptodirini) and harvestmen (*Ischyropsalis* C.L. Koch, 1839) (Bellés, 1987), but its uniqueness as hotspot is highlighted by relicts such as

*Autor corresponsal.
Adreça electrònica: carlos.prieto@ehu.eus

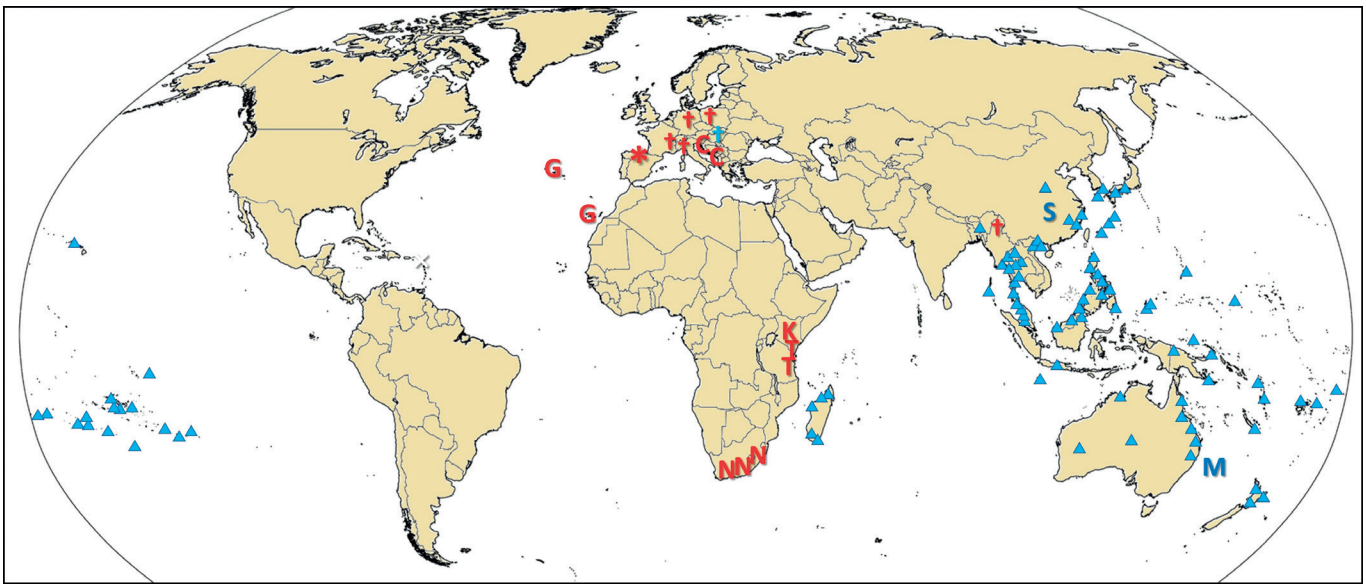


Figure 1. Global distribution of Hydrocenidae taxa. Blue symbols: † *Schwardtina cretacea*, M *Monterissa gowerensis*, S *Sinicena chinensis*, Δ *Georissa* spp.; red symbols: *Hydrocena* spp. (* *canttabrica*, C *cattaroensis*, G *gutta*, K *kenyana*, N *noticola*, T *tanzaniensis*, † fossil spp.). Information for *Georissa* spp. from GBIF.

the polydesmid *Cantabrodesmus lorioli* Mauriès, 1971, the isopod *Cantabroniscus primitivus* Vandel, 1965, the dipluran *Oncinocampa asonensis* Sendra & Condé, 1988 and the carabid *Iberotrechodes spinosus* Faille, Balart-García, Fresneda, Bourdeau & Ribera, 2021 (Faille *et al.*, 2021).

Cave molluscs, a group with an evident high requirement of calcium carbonate for shell construction, also show the highest diversity in the Dinaric karst, where 49 obligate molluscs have been recorded, including the cave clam *Congeria jalzici* Morton & Bilandžija, 2013 (a segregated species from *Congeria kusceri* Bole, 1962 by Bilandžija *et al.*, 2013) and 11 terrestrial gastropods, only from Slovenia (Culver, 2012), and several times that number in the whole Dinaric region, where nine gastropod families harbour troglobiont terrestrial molluscs. In contrast, the Cantabrian region harbours 12 terrestrial obligate cave species belonging to three genera (Prieto *et al.*, in press): *Platyla* Moquin-Tandon, 1856 (Aciculidae), *Iberozospeum* Kneubühler, Jochum, Prieto & Neubert, 2022 (Carychiidae), and *Cryptazeca* Folin & Bérillon, 1877 (Azecidae), plus several *Iberozospeum* species awaiting description (Kneubühler *et al.*, 2022) and an unnamed dwarf species of the slug *Papilloderma* Wiktor, Martín & Castillejo, 1990 (Prieto *et al.*, 2020).

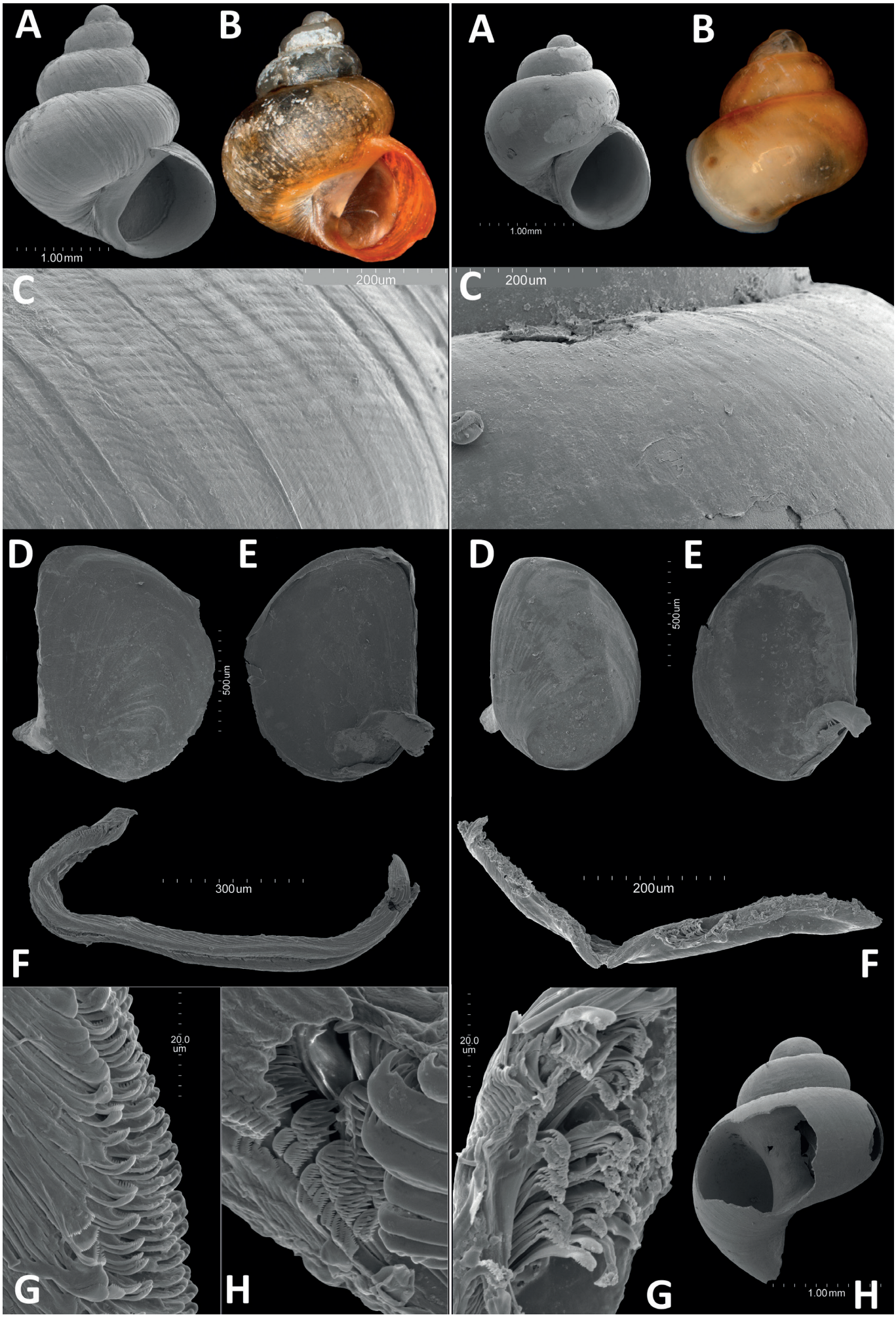
Five years ago, many empty shells of an unknown short-spired species with very convex whorls and thick test were discovered by the first author inside the Cueva de La Puntida, in the eastern part of the Autonomous Community of Cantabria, in northern Spain. Although they were found on fallen blocks covered by stalagmitic concretions, they were supposed to be an aquatic species dragged somehow. Similar shells had previously been found in other caves and in spring sediments from Cantabria, which were classified by the authors as a presumably unknown troglobiont species of the genus *Hydrocena* Troschel, 1844. We decided to await finding live specimens that would allow a more complete study and ensure their correct systematic placement.

The subclass Neritimorpha Golikov & Starobogatov 1975, to which *Hydrocena* belongs, is an old clade including four superfamilies: the marine Neritopsoidea Gray, 1847; the Helicinoidea Férussac, 1822, including a family of subtidal, underground or freshwater aquatic snails and three other terrestrial families; the Neritoidea Rafinesque, 1815, including deep-sea, tidal, mangrove and freshwater genera in two families; and the monotypic terrestrial Hydrocenoidea Troschel, 1857 (Kano *et al.*, 2002; Uribe *et al.*, 2016). The divergence time between the related Hydrocenoidea and Neritoidea was estimated at around 180 Mya (Uribe *et al.*, 2016). The family Hydrocenidae is currently composed by four extant genera (Figure 1): *Hydrocena* Küster, 1844 from South and East Africa, Macaronesia and southern Europe; *Georissa* W.T. Blanford, 1864, having the widest distribution including Madagascar, Southeast Asia, Australia, New Zealand and Pacific Islands (Auffenberg, 1999; Verdcourt, 2004; Haase & Schilthuizen, 2007), and only dubious records from the Americas; and two monotypic genera, *Monterissa* Iredale, 1944 from Lord Howe Island and *Sinicena* Egorov, 2003 from China (Kang, 1986; Egorov, 2003). The fossil record of Hydrocenidae was restricted to the European Palaeocene/Pliocene, until Yu & Neubauer (2021) described *Hydrocena praecursor*, the oldest representative of the family from mid-Cretaceous Burmese amber. Hydrocenids are associated with shady biotopes with a high degree of humidity, such as tropical and subtropical forests, in the soil, on trunks or the vertical surface of wet rocks or gorges, and even species from cave habitats have been described (Haase & Schilthuizen, 2007; Vermeulen *et al.*, 2015).

The family has not been revised since Pfeiffer (1876), more than 140 years ago, and its systematics is based solely on conchological traits. Species have small conical shells, rarely reaching 4 mm high, with few and convex whorls, large body whorl with generally rounded aperture, sharp-edged peristome and umbilicus covered by a thick callus; the calcareous operculum has concentric striae to the nucleus, which has a curved and prominent apophysis on its inner side; the internal septa of the shell, except for the last whorl, have been reabsorbed, so the body of the animal is bag-shaped and occupies the wide interior cavity; the thick shell is ornamented by a conspicuous radial and spiral sculpture, especially in *Georissa*, but it is tenuous in *Hydrocena* (Thompson & Dance, 1983; Barker, 2001; Khalik *et al.*, 2018). First data for the radula were provided by Troschel (1857), for soft parts by Blanford (1869), and for anatomy based on histological sections by Thiele (1910), but afterwards anatomical descriptions have been scarce (Kang, 1986; Bernasconi, 1995; Haase & Schilthuizen, 2007).

According to the fossil record, in Europe the family presents a residual distribution, with two extant species: *Hydrocena cattaroensis*

Figure 2. *Hydrocena cattaroensis* (L. Pfeiffer, 1841) from Clissura Cave (Kotor, Montenegro). A-B, complete shells; C, shell microsculpture; D-E, operculum in outer and inner view; F, complete radula; G-H, radular teeth.
Figure 3. *Hydrocena gutta* Shuttleworth, 1852 from São Miguel Island (Açores, Portugal). A-B, complete shells; C, shell microsculpture; D-E, operculum in outer and inner view; F, complete radula; G, radular teeth; H, opened window in shell.


A
B
1.00mm
C
200um
D
E
500um
300um
F
G
20.0 um
H
A
B
1.00mm
C
200um
D
E
500um
200um
F
G
20.0 um
H
1.00mm

(Pfeiffer, 1841) from the Dinarides (Welter-Schultes, 2012) and *Hydrocena gutta* (Shuttleworth, 1852) from laurel forests in the Azores and the Canary Islands (Backhuys, 1975; Núñez & Núñez, 2010). Thus, the herein described taxon is the only European subterranean species of this genus.

Material and methods

The studied material of *Hydrocena cattaroensis* from Kotor (Montenegro) comprised a few dried snails obtained from Conchology Inc. (https://www.conchology.be); the material of *Hydrocena gutta* was provided by A.M. Frias Martins (Universidade dos Açores) from two sites from Sao Miguel Island (Pico dos Bodes and Pico da Praia). The material of the new species, indicated in the appropriate section in the descriptive part, has been sampled by the authors mostly by direct sampling at sight on relevant sites within caves; in a few instances, empty shells were obtained by sieving sediments from karstic springs.

Samples for SEM were sputter-coated with a 15nm layer of gold in a EMITECH K550X metallizer and B/W photographs were taken using a HITACHI® S-3400 N SEM from the Analytical and High-Resolution Microscopy Service in Biomedicine, located at the Faculty of Medicine and Nursing of the University of the Basque Country (EHU-UPV). Colour photographs and measurements and photographs were obtained using a NIKON® SMZ 1500 stereomicroscope and the associated image analysis equipment. The stacked images were produced with the HELICON® Focus 7.6 software. Drawings were made through drawing tubes coupled to a NIKON® SMZ 1500 stereomicroscope or a NIKON® Optiphot microscope.

For the anatomical study, snails preserved in 70º alcohol were removed by shell breaking and dissected under a stereomicroscope. Handling has been difficult due to the minute and weak structures, and it is possible that some of the smaller organs could not be recognised or found. The fully anatomical description of Barroso *et al.* (2012) of the neritid *Neritina zebra* (Bruguière, 1792) was used for comparison.

Abbreviations:
AA / CAA, Álvaro Alonso / AA personal collection
CP, Carlos E. Prieto
HRC, Han Raven collection
JRC / CJRC, Jesús Ruiz-Cobo / JRC personal collection
MNCN, Museo Nacional de Ciencias Naturales (Madrid, Spain)
SQS / CSQS, Sergio Quiñonero-Salgado / SQS personal collection
ZUPV, Cave Fauna Collection of the Departamento de Zoología y Biología Celular Animal, Universidad del País Vasco (UPV/EHU, Bizkaia, Spain)

Results

Systematics

Family Hydrocenidae F.H. Troschel, 1857
Genus *Hydrocena* Kuster, 1844
Type species: *Cyclostoma cattaroensis* L. Pfeiffer, 1841

Hydrocena cattaroensis (L. Pfeiffer, 1841) **(Figure 2)**
Cyclostoma cattaroensis L. Pfeiffer, 1841, *Arch. Naturg. Berlin.* 7 (1): 225

Material. Spiljara Clissura, Kotor (=Cattaro), Montenegro; ex-coll. Beckmann, 20/05/1984 (5 s.). Other shells from this collection are figured at http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/picture?id=5113

Measurements (n=5). Shell height 2.68-3.11 mm, mean 2.85; shell width/height ratio 0.77-0.86, mean 0.827; body whorl/shell height ratio 0.695-0.745, mean 0.721; number of whorls 3.25-3.6, mean 3.5.

Description. The shell is about 3 mm high and sharply conical, with spire formed by 3½ very convex whorls separated by deep sutures; body whorl relatively large, not reaching ¾ of shell height. Aperture almost circular, with a thick columellar callus joining the columellar edge almost at a right angle. Protoconch of 0.45 x 0.3 mm. Operculum of 1.2 x 0.9 mm with short, thick internal peg, without obvious base. Microsculpture consisting of irregularly wavy spiral striae (6 by 0.1 mm). Shell reddish-brown, especially the body whorl. Studied shells were profusely covered by patches of calcareous concretions, especially in the apical area.

Radula (extracted from a dried snail body) of 1.2 mm length. It has not been possible to study the anatomy, other than the radula, which was meticulously described by Troschel (1857) and Thiele (1910), thus being the only anatomical contribution for this species; although Berry (1965) described the genital anatomy of *Hydrocena monterosatiana* Godwin-Austen & G. Nevill, 1879, which currently is placed in the genus *Georissa*.

Geographical distribution. The species ranges along the Dinaric region, from Croatia to Montenegro (Gittenberger & Maassen, 1980) and Albania (Gittenberger, 2015), from the coast to up to 800 m a.s.l. inland. Bernasconi (2014) considers it a relict from the Tertiary.

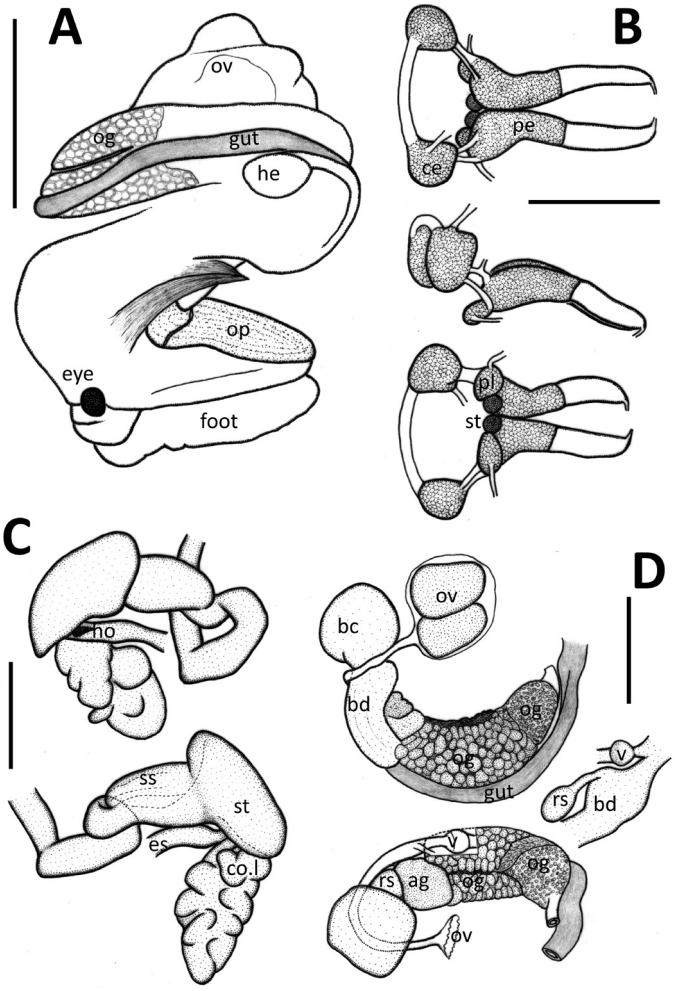


Figure 4. Anatomy of *Hydrocena gutta* Shuttleworth, 1852 (Sao Miguel Island, Azores). A, body after shell removal (di digestive gland, he heart, og oviducal gland, op operculum, ov ovary). B, nerve ring in dorsal, lateral and ventral views (ce cerebral ganglion, pe pedal ganglion, pl pleural ganglion, st statolith). C, stomach in lateral views (co.l columellar lobe of digestive gland, es esophagus, ho hole left by the removed digestive gland, st stomach, ss style-sac). D, female genital system in dorsal and ventral views (ag, albumen gland, bc *bursa copulatrix*, bd *bursa copulatrix* duct, og oviductal glands, ov ovary in two masses, rs *receptaculum seminis*, v valve of the gonoduct). Scale bars: A, 1 mm; B-D, 0.5 mm.

Hydrocena gutta Shuttleworth, 1852 **(Figures 3-4)**

Hydrocena gutta Shuttleworth, 1852, *Mitt. Naturforsch. Ges. Bern.* 1852 (241/242): 145. A photograph of a syntype is provided by Neubert & Gosteli (2005: pl. 6 fig. 1)

Material. Pico da Praia, Agua d'Alto, São Miguel I., Azores; 24/10/1974, A.M.F. Martins *leg.* (5 s.). Pico dos Bodes, E of Furnas, São Miguel I., Azores; 18/03/2004, A.M.F. Martins *leg.* (5 s.).

Measurements (n=8; two subadult damaged shells have not been considered). Shell height 2.11-2.45 mm, mean 2.33; width/height ratio 0.85-0.91, mean 0.864; body whorl/height ratio 0.79-0.835, mean 0.812; number of whorls 2.75-2.95, mean 2.84.

Description. The shell is almost 2.5 mm high, with convex conical profile, spire formed by 2¾ very convex whorls. Body whorl very large, greater than 4/5 of the height of the shell. Aperture vertically ovate, with a thick columellar callus joining the columellar edge in a wide-open angle. Protoconch, 0.51 x 0.36 mm. Operculum of 1.1 x 0.8 mm, with a short internal peg 0.1 mm wide, without obvious basal callus. Microsculpture of the teleoconch imperceptible. Shell yellowish brown, with body whorl quite transparent; upper whorls frequently corroded by humic acids.

Anatomy. Eyes are bulbous, large and conspicuous (Figure 4A). Radula 0.7 mm long (Figure 3F). Nerve ring as in Figure 4B, with large pedal ganglions having a posterior part of distinct aspect. Stomach as in Figure 4C, with arising gut attached to the style-sac; digestive gland divided in two lobes, a smaller inferior one that occupies the columellar cavity of the shell and a larger upper one adjoining the gonad. Female genital system as in Figure 4D; it is very caked resulting in difficult interpretation: gonad with two compact masses in a common bag and a duct ending in a valve-like structure, a globose *bursa copulatrix* with wide duct, a *receptaculum seminis* and a multiglandular oviduct (according its different colors and textures).

Geographical distribution. The species is restricted to the Macaronesian archipelago of Açores, where it is very common and has been recorded from all islands (Backhuys, 1975; Cunha *et al*., 2010; Martins, 2011), and Canaries, where it has been recorded only from the four westernmost islands (Groh & García, 2004; Núñez & Núñez, 2010) where remnants of laurel forest remain.

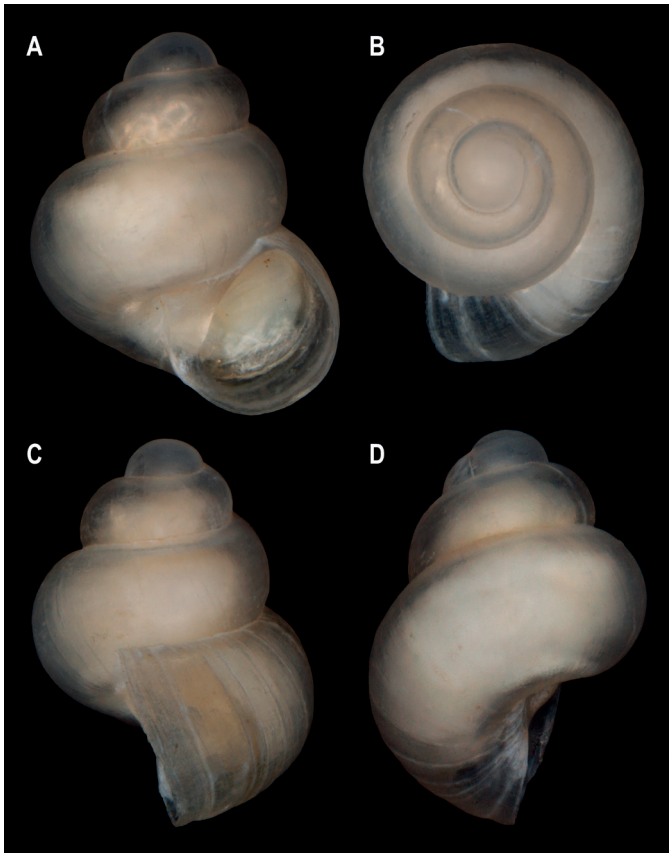


Figure 5. Holotype of *Hydrocena canttabrica* sp. nov. [MNCN·15.05/200202H, ex-col. ZUPV]. Cueva de Covallarco (San Roque de Riomiera, Cantabria, Spain). Shell height, 2.18 mm. Note that the top of the shell is tilted towards the bottom at D.

Hydrocena canttabrica sp. nov. **(Figures 5-10)**

Type locality: Cueva de Covallarco (Cantabria: San Roque de Riomiera: Merilla; 30TVN4041289565, 402 m a.s.l.)

Type material:

Holotype: a fixed snail, supposedly male, 2.18 mm high (Figure 5). MNCN·15.05/200202H, ex-coll. ZUPV-5122.

Paratypes (all samples come from the Autonomous Community of Cantabria, Spain):

Cueva de Covallarco (San Roque de Riomiera: Merilla); 18/06/2016, CP, Jon Fernández *leg*. [ZUPV·3992: 3 s.]; 19/07/2016, CP, SQS & JRC *leg*. [ZUPV·4065: 8 s.] [CSQS·1415: 50 s.] [CAA·0636-C: 20 s.]; 09/03/2018, CP & JRC *leg*. [ZUPV·5122: 659 s.]; [ZUPV·5123: 55 s.]; [MNCN·15.05/200202P, ex-col. ZUPV-5122: 20 s.]; 26/03/2018, AA leg. [HRC-L3223: 3 s.]; 02/06/2019, H. Raven leg. [HRC-L3224: 69 s.]. Cueva de La Puntida (Miera: Ajanedo); 12/10/2015, CP & Alfonso Calvo *leg*. [ZUPV·3031: 115 s.]. Cueva de Las Montosas (Soba: Valdició); 20/02/2016, Alfonso Calvo *leg*. [ZUPV·3626: 14 s.]. Sima PO-153 (San Roque de Riomiera: Porracolina); 08/10/2016, Marta Gutiérrez *leg*. [ZUPV·4183: 17 s.]; 12/11/2016 CP, Marta Gutiérrez & J.A. Noriega *leg*. [ZUPV·4198: 33 s.] [ZUPV·4199: 63 s.] [ZUPV·4204: 8 s.] [ZUPV·4205: 5 s.]. Cueva de Las Cascajosas (San Roque de Riomiera); 09/03/2018 CP, JRC [ZUPV·5157: 14 s.]. Torca de la Rabia (Arredondo: Bustablado); 11/05/2019 CP & A. Calvo *leg*. [ZUPV·5510: 33 s.].

Other material: Cueva de San Juan de Socueva (Arredondo: Socueva); 12/04/2017, CP, SQS, JRC & AA *leg*. [ZUPV·4721: 45 s.]. Abrigo de La Cubija (Ruesga: Matienzo: Valle de La Cubija) [CSQS·1380: 2 old s.]. Cueva de la Carretera (or Fuente Encalada; Miera: Mortesante) [CSQS·1381: 12 s.]

Previous to cited samples, all from 2016 or later, Han Raven (pers. comm.) found a single shell in a drinking trench 0.8 km NE of Puerto de las Alisas [HRC-L2616] but he did not realize to which family this

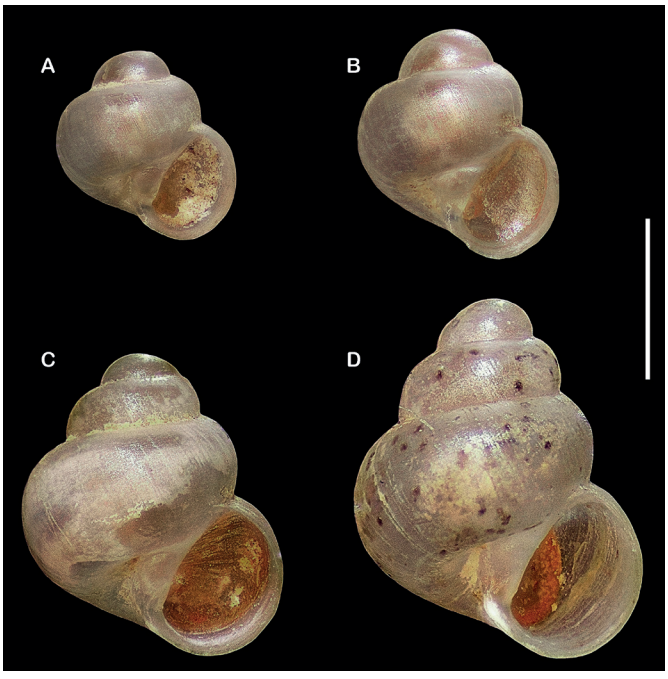


Figure 6. Paratypes of *Hydrocena canttabrica* sp. nov. [CSQS·1415]. Cueva de Covallarco. A-B, two immature shells at different stages of growth (A, 1.16 mm; B, 1.41 mm). C, a subadult shell, 1.87 mm. D, an adult shell, 2.22 mm. Scale bar, 1 mm.

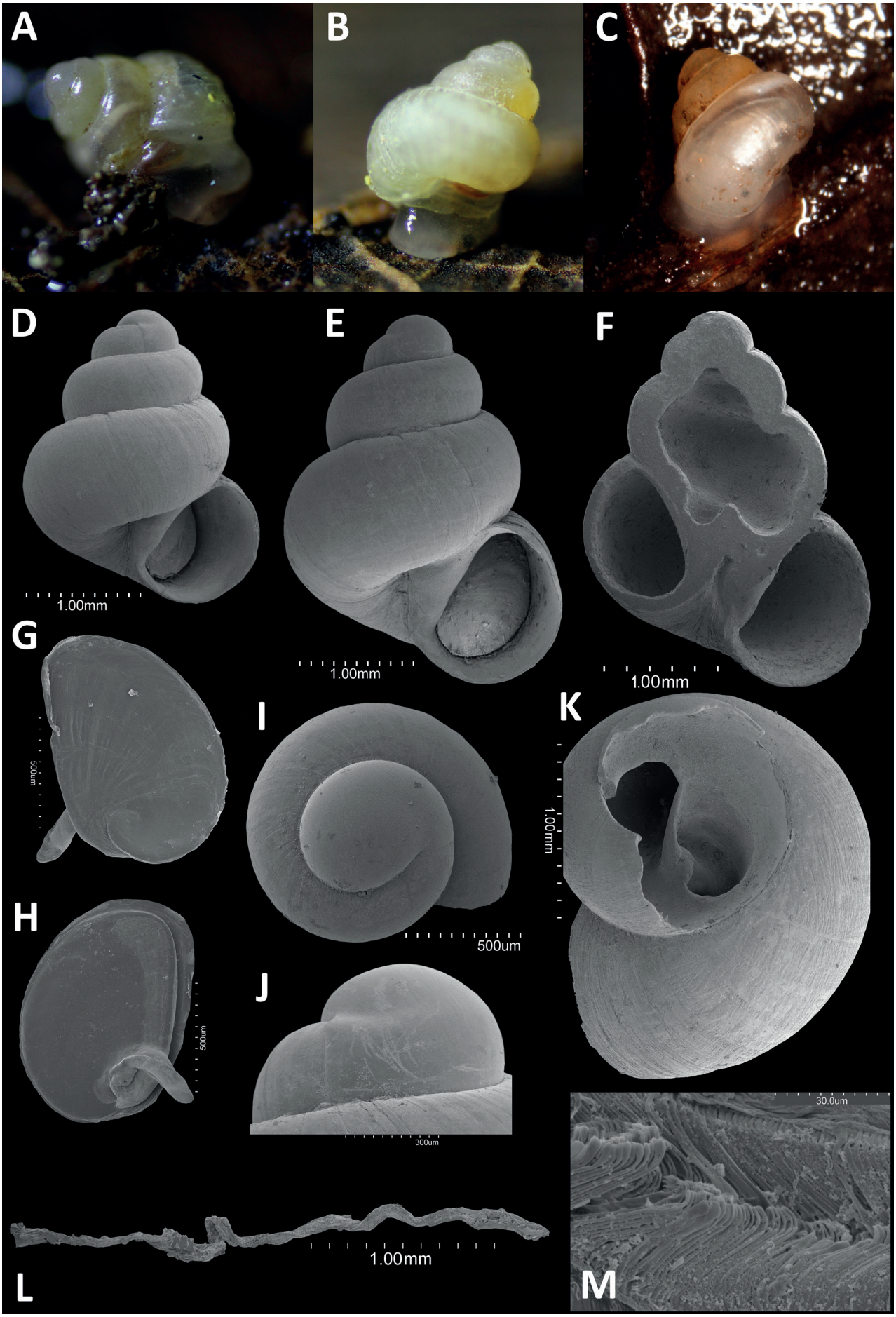


Figure 7. *Hydrocena canttabrica* sp. nov. A-C, live snails (note in C the minute eyes and the rectum filled with dark faeces); D-F, shells (note in F the shell thickness); G-H, operculum (outer and inner view); I-J, protoconch and apical whorl; K, broken shell showing columellar cavity and widening of the septum; L-M, complete radula and radular teeth. [A-B, D, F, I: Cueva de Covallarco; C, G: Torca de la Rabia; E, H, J, L-M: Sima PO-153; K: Torca de las Montosas]

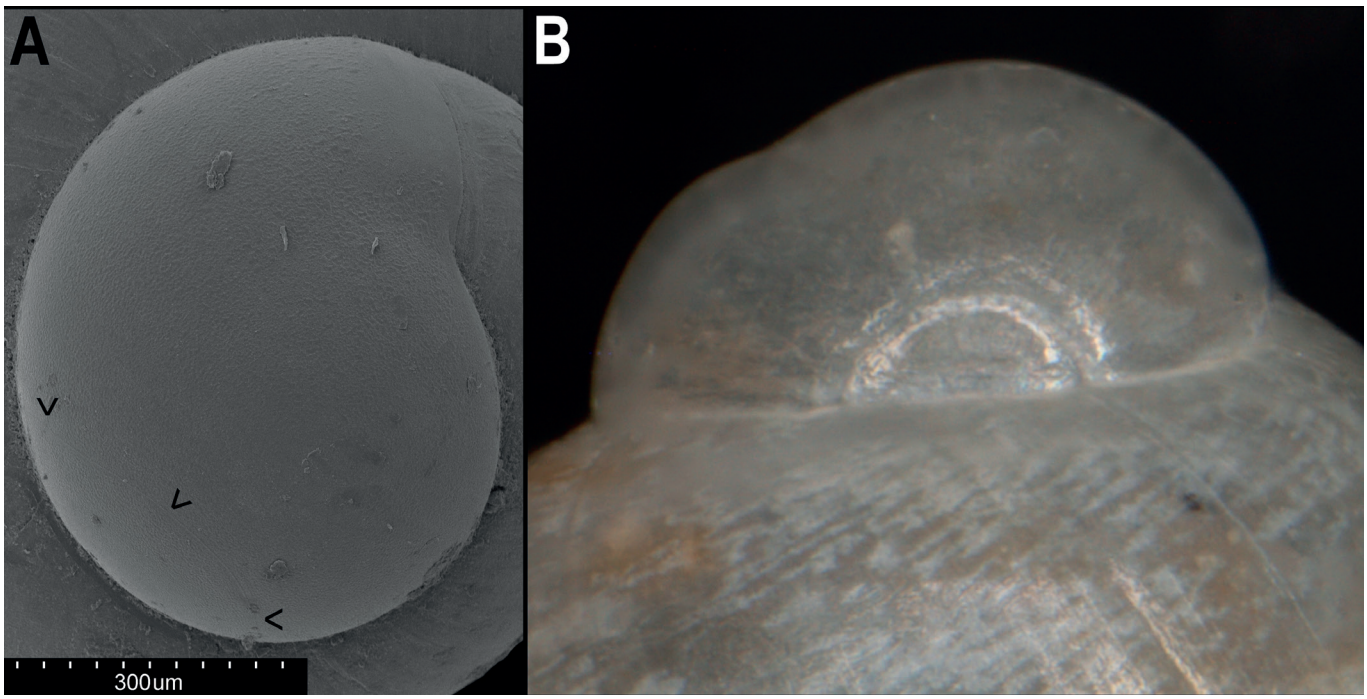


Figure 8. Circular shell cap in the protoconch of *Hydrocena canttabrica* sp.nov. A. Upper view of a juvenile shell (head arrows indicate the shell cap). B. Lateral view of the protoconch and first whorl of a shell. [A: Cueva de Covallarco; B: Cueva de Las Cascajosas].

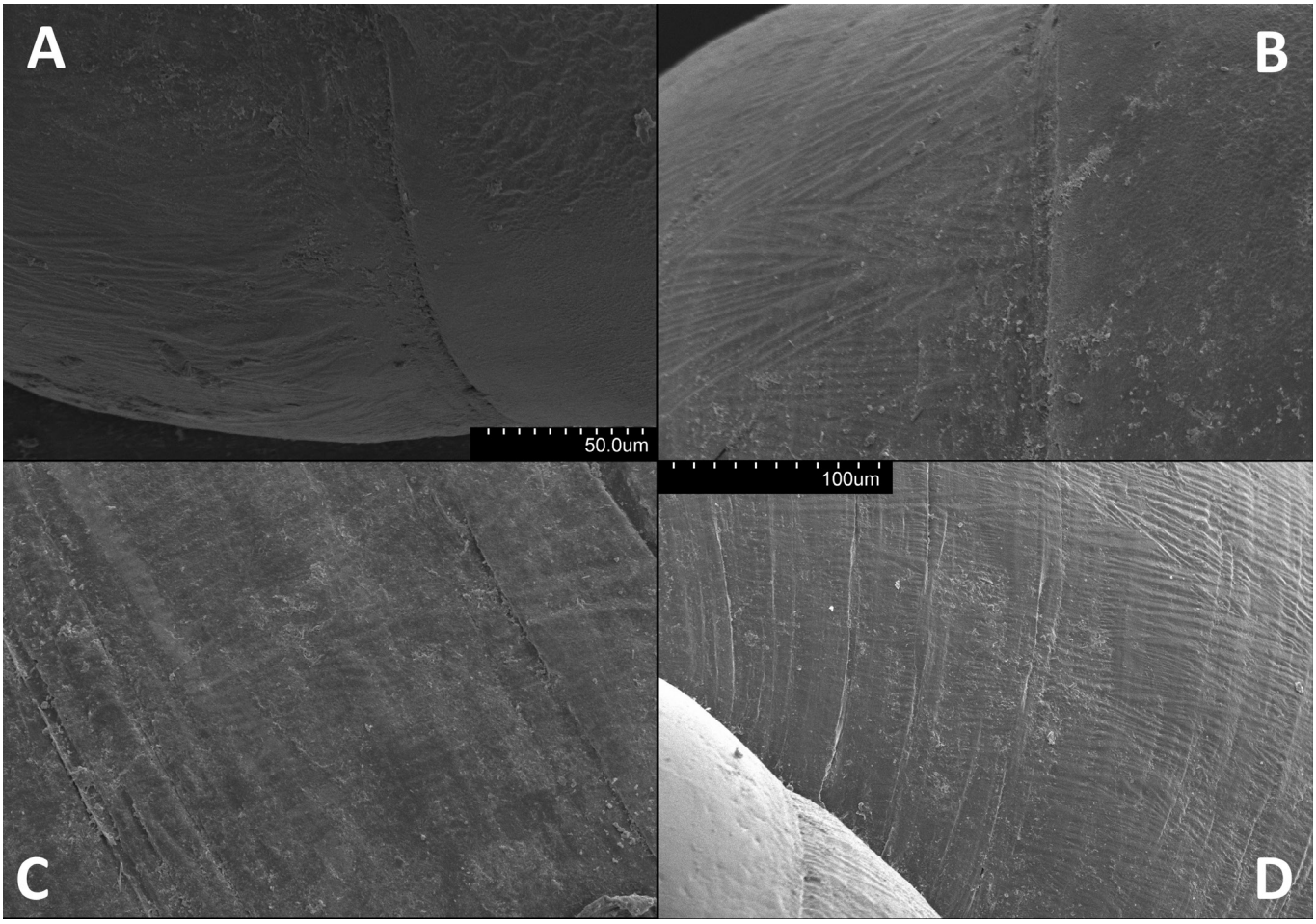


Figure 9. Shell microsculpture of *Hydrocena canttabrica* sp.nov. A-B, protoconch (rigth) /teleoconch transition; C-D, teleoconch of the 2nd whorl. Scale in A for A-C. [A: Cueva de Covallarco; B-C: Sima PO-153; D: Torca de la Rabia].

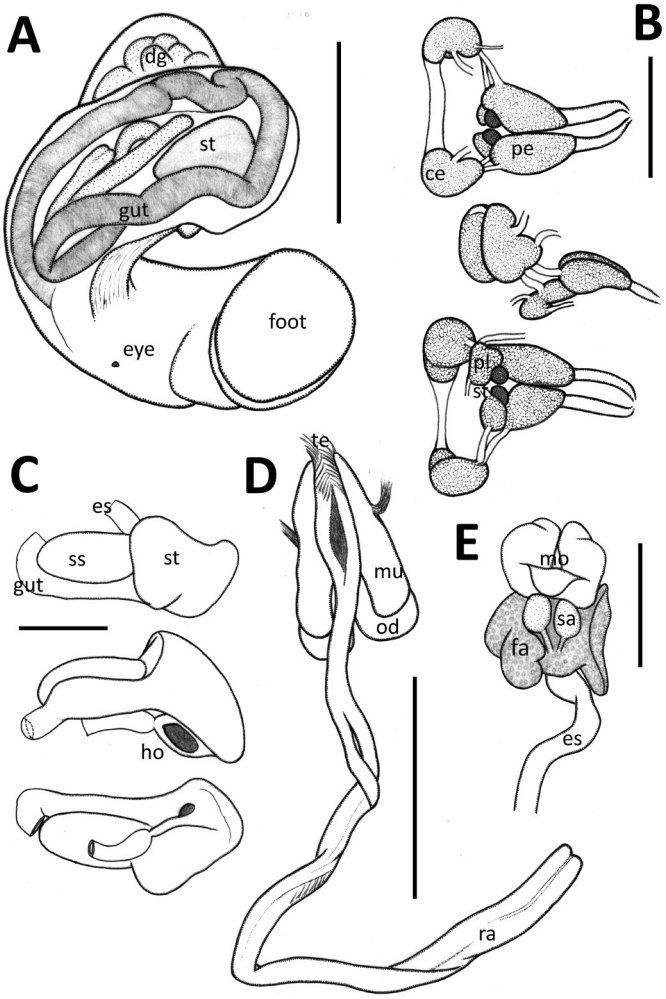


Figure 10. Anatomy of *Hydrocena canttabrica* sp.nov. (Sima PO-153, San Roque de Riomiera). A, body after partial removal of body wall (dg digestive gland, st stomach). B, nerve ring in dorsal, lateral and ventral views (ce cerebral ganglion, pe pedal ganglion, pl pleural ganglion, st statolith). C, stomach in dorsal, lateral and ventral views (es esophagus, ho opening towards digestive gland, st stomach, ss style-sac). D, radular sac (mu muscular mass, od odontophore, ra radular sac, te distal teeth). E, roof of buccal mass in ventral view (es esophagus, fa faringeal gland, mo mouth, sa salivary gland). Scale bars: A,D, 1mm. B,C,E, 0.5 mm

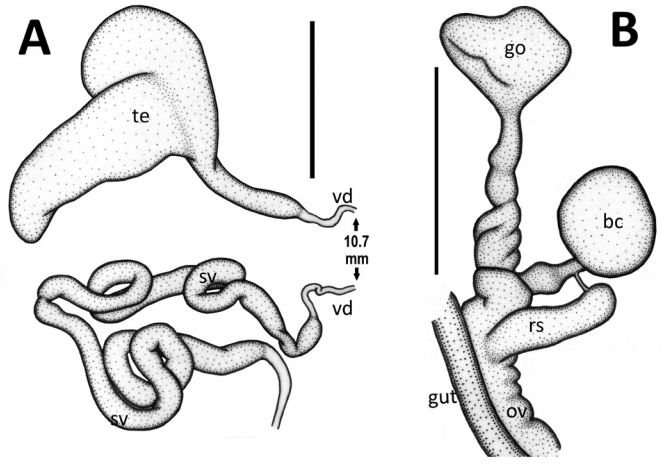


Figure 11. Anatomy of *Hydrocena canttabrica* sp.nov. A, male genital system (sv seminal vesicle, te testis, vd vas deferens 10.7 mm long). B, female genital system (bc, bursa copulatrix, go gonad, ov oviduct, rs receptaculum seminis). [A: Sima PO-153; B: Torca de la Rabia]. Scale bars: A, 0.5 mm; B, 1 mm.

shell belonged to, until its discovery at Cueva de Covallarco. That finding could be placed at coordinates 30TVN4794.

Etymology: The name *canttabrica* refers to the Cantabrian mountains, the Iberian region where the species has been found. The additional "t" is a little literary licence to highlight its affinity with the other two European *Hydrocena* species, which also have a double "t" in their names.

Description: Shell small and conical, 2-3 mm high in fully grown shells, spire with 2¼ -3 very convex whorls, apparently smooth, separated by a deep suture (Figures 5, 6, 7 A-F). Test transparent in living snails (Figures 5 and 7 A-C) and thick, especially in the upper part of the shell (Figure 7 F). As can be seen in broken shells, inner septa, except that of last whorl, are resorbed (Figure 7 F), while the umbilical space, covered by the umbilical callus, is available for internal organs (Figure 7 K). Protoconch 0.67 x 0.52 mm (Figure 7I) with poorly defined teleoconch border and surface apparently smooth, but under high magnification numerous irregularly disposed small depressions can be seen; a protoconch nucleus, indicated by a very subtle circular line 0.37 mm in diameter (Figure 8), can be seen at the opposite side to the start of the suture. Teleoconch microsculpture (Figure 9) weakly developed as fine spiral lines, crossed evenly by oblique lines and radial growth lines. Last whorl large, its width representing 69-91% of shell height and its height 73-81% of shell height, rounded, although ovate in cross section.

Aperture nearly semicircular, barely oblique, with peristome acute and not reflected (Figures 7 D-F); parieto-columellar area lined by a thick, almost straight callus, wider in the middle and curved onto the umbilical depression without filling it completely; the callus reaches the parieto-palatal corner.

Operculum ovate (Figures 7 G-H), 1.0 x 0.7 mm, calcareous inside, externally a proteinaceous layer extends all over, showing an open spiral arising from the nucleus and growth lines; calcareous side with a thick callus in the parieto-columellar area from which a curved apophysis 0.3 mm in length and 0.1 mm in thickness protrudes obliquely.

Shell rather strong due shell thickness, 0.05 mm at minimum, being thickest in the upper part where it can reach 0.2 mm (Figure 7 F), but variable among individuals according to their age. Internal septa and columella resorbed until the last half whorl (Figure 7 K); inner umbilical space kidney-shaped in apical view due to a ridge that deepens reaching the bottom of the umbilical space, behind the apertural callus.

The holotype (a male) is 2.18 mm high, 1.80 mm wide, having 2.9 whorls, body whorl 1.66 mm high and aperture 0.98 mm high by 0.73 mm wide.

Anatomy (Figures 10-11). Visceral sac completely transparent. Eyes inconspicuous, small, apparently ovate, 70 x 90 μm (Figure 10 A). Buccal mass with odontophore 0.5 mm length (Figure 10 D) and a large pharyngeal gland and two small salivary glands (Figure 10 E). Radular sac very long (up to 3 mm) and pleated in visceral sac (Figure 10 D), with a longitudinal groove disjoining the hemiradulae. Stomach as in Figure 10 C, with arising gut attached to the style-sac; digestive gland divided into two lobes, a smaller inferior one occupying the columellar cavity of the shell and a larger upper one adjoining the gonad. Nerve ring as in Figure 10 B, with large pedal ganglions having a narrower distinct posterior part. Male genital system (Figure 11 A) with a large bilobular gonad and a long curly *vas deferens*, more than 10 mm long, leading into a long seminal vesicle; distal parts not discerned. Female genital system as in Figure 11 B (interpretation caution): gonad with a compact mass and a duct with no obvious distal valve, a globose *bursa copulatrix* with distal wide duct, which connects by a thin duct with the *receptaculum seminis*; the oviduct (likely immature) without glands of different coloration.

Shell measurements. See Table 1, and also Figure 12. They have been made on what we interpret to be adult shells, but because the peristome does not reflect or form a callus, it is not possible to ascertain whether a specimen has actually become adult. Obvious

Table 1. Shell measurements of some populations of *Hydrocena canttabrica* sp. nov. For each cell, the mean plus standard deviation (top line), and minimum and maximum values (bottom line) are given.

	shell height	shell width	body wh. height	aperture height	aperture width	no. of whorls	shell w /shell h	body wh. / shell h
Covallarco	2.12 ± 0.13	1.75 ± 0.11	1.61 ± 0.10	0.99 ± 0.06	0.70 ± 0.04	2.82 ± 0.16	0.82 ± 0.03	0.75 ± 0.02
n=18	1.96 – 2.18	1.57 – 1.81	1.49 – 1.66	0.91 – 1.00	0.64 – 0.73	2.50 – 2.90	0.77 – 0.87	0.71 – 0.81
Las Montosas	2.48 ± 0.18	2.04 ± 0.14	1.91 ± 0.12	1.15 ± 0.08	0.83 ± 0.07		0.82 ± 0.01	0.77 ± 0.01
n=8	2.20 – 2.79	1.82 – 2.33	1.69 – 2.12	1.01 – 1.32	0.73 – 0.93		0.79 – 0.84	0.75 – 0.79
PO–153	2.57 ± 0.17	2.00 ± 0.11	1.93 ± 0.10	1.17 ± 0.06	0.80 ± 0.04	2.69 ± 0.26	0.77 ± 0.03	0.75 ± 0.01
n=9	2.34 – 2.93	1.81 – 2.25	1.76 – 2.14	1.06 – 1.32	0.72 – 0.88	2.50 – 3.00	0.74 – 0.84	0.73 – 0.78
La Puntida	2.50 ± 0.17	2.09 ± 0.11	1.96 ± 0.12	1.19 ± 0.07	0.86 ± 0.05	2.71 ± 0.13	0.83 ± 0.02	0.78 ± 0.02
n=18	2.22 – 2.83	1.92 – 2.29	1.66 – 2.12	1.07 – 1.31	0.75 – 0.95	2.50 – 2.95	0.78 – 0.87	0.74 – 0.81
La Rabia	2.27 ± 0.19	1.91 ± 0.12	1.76 ± 0.12	1.12 ± 0.08	0.75 ± 0.05	2.70 ± 0.18	0.84 ± 0.03	0.77 ± 0.02
n=16	1.94 – 2.65	1.77 – 2.10	1.58 – 2.01	1.03 – 1.25	0.64 – 0.87	2.30 – 2.95	0.79 – 0.91	0.74 – 0.81
Las Cascajosas	2.09 ± 0.10	1.76 ± 0.06	1.62 ± 0.04	1.01 ± 0.03	0.70 ± 0.02	2.65 ± 0.12	0.84 ± 0.02	0.77 ± 0.02
n=12	1.93 – 2.24	1.66 – 1.87	1.55 – 1.68	0.96 – 1.07	0.65 – 0.73	2.45 – 2.90	0.80 – 0.88	0.74 – 0.82
ALL POPULAT.	**2.31 ± 0.24**	**1.91 ± 0.17**	**1.78 ± 0.18**	**1.10 ± 0.10**	**0.77 ± 0.08**	**2.73 ± 0.17**	**0.82 ± 0.03**	**0.77 ± 0.02**
n=81	**1.93 – 2.93**	**1.57 – 2.33**	**1.49 – 2.14**	**0.91 – 1.32**	**0.64 – 0.95**	**2.30 – 3.00**	**0.74 – 0.91**	**0.71 – 0.82**

juvenile shells (less than 2 whorls) have not been measured; it has been considered that maturity is reached with 2¼ whorls or 2 mm high.

According to the limited number of shells we measured, *H. cattaroensis* and *H. gutta* clearly differ in shell size, *H.cattaroensis* being wider and higher. *H. canttabrica* sp. nov. presents a wider morphological range showing differences between populations; individuals of the topotypical population from Covallarco do not reach 2.5 mm in height, and those of the population from Las Cascajosas are even smaller. The individuals of populations from PO-153, La Puntida and Las Montosas are notably larger, having a mean height of around 2.5 mm with the largest reaching 2.8 mm.

Habitat. *Hydrocena canttabrica* sp. nov. lives in extremely humid places located a short distance from the entrances of the cavities, requiring water that slides down the surface of the wall or rocks, where they feed on the organic particles dragged from the outside by the circulating water. In Sima PO-153, snails are more abundant on the walls of a pit that are obscured by organic matter washed away by seepage water. In Cueva de Covallarco, snails are abundant in a cone of debris located under the collapse of the entrance gallery, where leaves and other plant debris fall, and where there is an intense dripping. In Torca de la Rabia, the snails occurred on the eastern slope of the huge cone of debris located under the entrance of the sinkhole; there, in a twilight zone, the molluscs are found preferably on rotting branches and wood soaked in water.

Geographical distribution (Figure 13). All known localities of *Hydrocena canttabrica* sp. nov. are concentrated in the calcareous mountains around the Miera and Asón valleys, the largest karstic massif in Spain.

The area indicated by the ten sites where the species has been located forms the centre of the wide karst that makes up the territories of the Miera and Asón valleys; it is located in the southeastern corner of the Cantabrian region. All this area is connected by layers with high karstification capacity and most of it is made up by the massive limestone of the Upper Aptian (Lower Cretaceous) Reocín marine facies, formed by reefs. It houses some of the best developed and most complex karstic systems on the Iberian Peninsula, such as the Alto Tejuelo (or Cuatro Valles) system, the Mortillano system and the Gándara system, all three having more than 100 km of development (AER 2014; Degouve-de-Nuncques, 2014; Martínez-Cedrún *et al*., 2014; Simmonot, 2014; Sosa-Bravo *et al*., 2014). In the karst area of Miera, the species has appeared in cavities located from its lower zone (below 200 m a.s.l.: Cueva de La Carretera) and especially in the core sector of the karst (between 300 and 500 m a.s.l: Cueva de Las Cascajosas, Cueva de Covallarco or Cueva de La Puntida) and continues in the higher territories, above 700 m a.s.l, to the south of

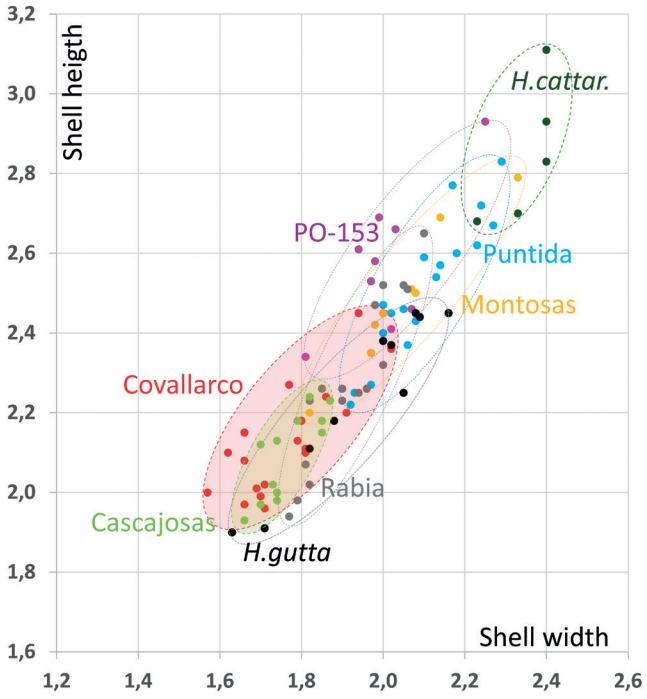


Figure 12. Graphical representation of main conchological features (shell height and width) of measured specimens of European species of *Hydrocena*. Colored dots correspond to populations from caves whose names have been colored in the same way. Ellipses enclosing each data set have been created manually.

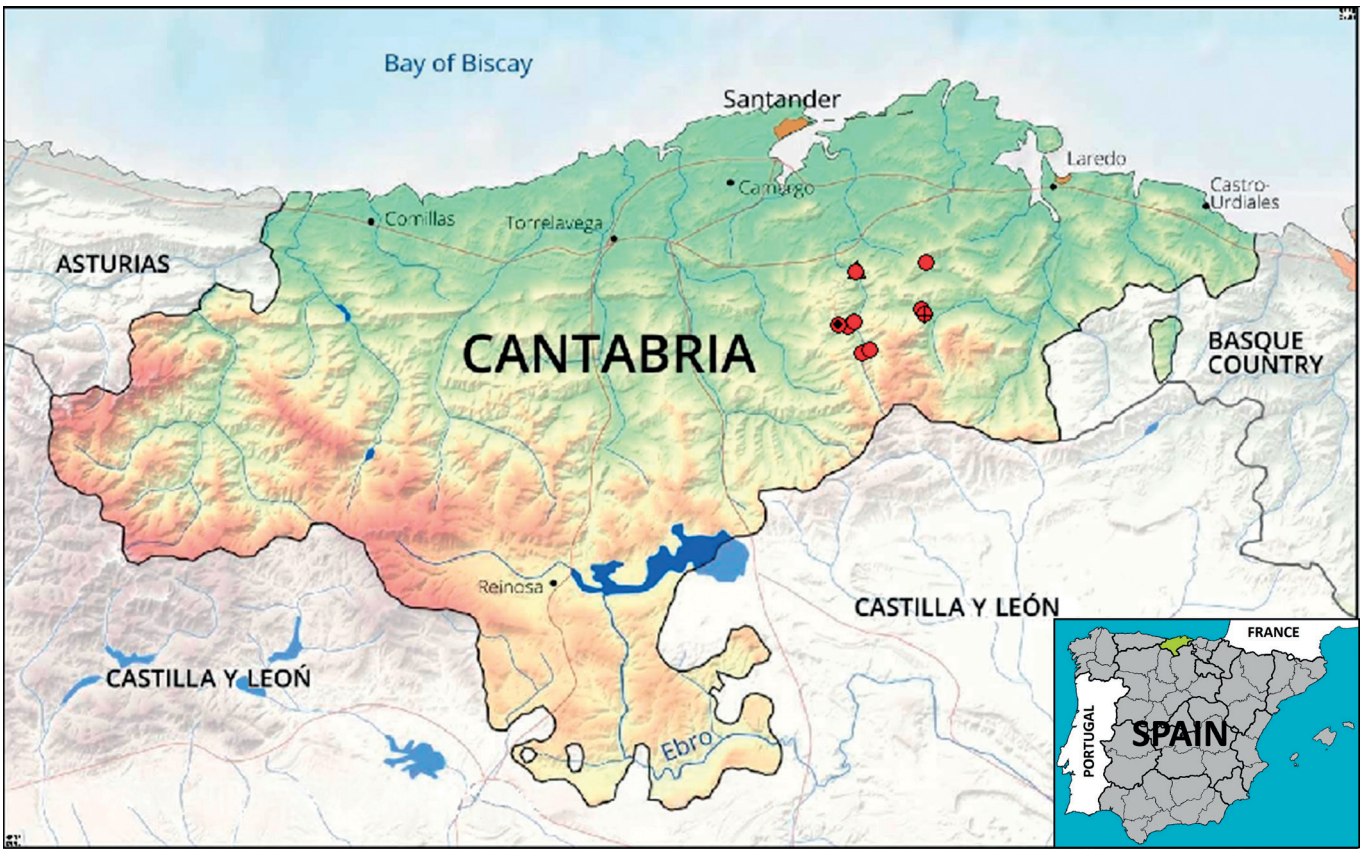


Figure 13. Geographical distribution of *Hydrocena canttabrica* sp. nov. Caves, red dots (the black spot denotes the type locality; the plus sign denotes fossil shells); springs, triangle. Inset, the Autonomous Community of Cantabria in northern Spain.

the area (Cueva de Las Montosas). The locations of the Asón valley are on the northern flank of the karst, at medium altitudes (Torca de La Rabia and Cueva de San Juan de Socueva).

Characterization of known localities:

Cueva de Covallarco (San Roque de Riomiera: Merilla; 30TVN 4041289565, 402 m a.s.l.). The cave is a relatively large system, 2500 m in length, carved out in massive Aptian limestone, with six entrances (Zubieta-Hyllenius & Noriega-Suárez, 1975; García, 2010). It is a network with active lower levels, frequently flooded, isolating parts of the cavity. The entrance I, oriented to the W, is low and 2 m wide, leading to a descending vestibule that collapses into another gallery after 10 m. Entrance II, located 80 m to the SW, forms a wide vestibule 30 m wide, 30 m deep and a roof that falls sharply towards the bottom, where it continues through a narrow passage currently blocked by sediments. The main *Hydrocena* site is the small cone of debris accumulated under the collapse of the entrance gallery, where plant remains fall from the entrance under a continuous water drip, but they have also been found in a little nook, with oozing water, on the ceiling of the vestibule of the entrance II (currently clogged by sediments), where they live on wet concretions of organic origin.

Cueva de Las Montosas (Soba: Valdició; 30TVN4312086295, 725 m a.s.l.). The entrance, oriented to the W, is 2 m high and 1.5 m wide, has a linear development through a wide gallery with an EW direction and a length of 1070 m, ending in a large room measuring 98 by 45 m (García, 2010). *Hydrocena* shells were provided by a collaborator without precise information about the collecting site.

Cueva de La Puntida (Miera: Ajanedo; 30TVN4233889803, 500 m a.s.l.). Huge fossil spring, open at the base of a cliff and oriented to the W, with an entrance 7 m high and 23 m wide. The entrance gives access to a large gallery full of large blocks, 250 m long and up to 55 m wide; on the right wall, 85 m from the entrance, a narrow gallery opens, through which a lower gallery is accessed, long, narrow and sinuous. Large numbers of *Hydrocena* shells were found on the upper surface of large limestone blocks under intense drip; no transparent shells were found and they could be flushed away empty shells.

Cueva de San Juan de Socueva (Arredondo: Socueva; 30TVN 5022090615, 430 m a.s.l.). Small cave near the rock chapel of San Juan. The cave is entirely fossil, with dry walls. *Hydrocena* shells were recovered from the sediment; all of them are old and frequently colonised by lichens.

Cueva de Las Cascajosas (San Roque de Riomiera; 30TVN 4161889336, 328 m a.s.l.). The main entrance of 4 m (there are two other entrances, the closest one blocked by a rockfall) gives access to a gallery that communicates with a network of wide galleries with a floor formed by stones detached from the ceiling. The *Hydrocena* site is a very humid narrow area with roots, located in the entrance gallery wall.

Abrigo de La Cubija (Ruesga: Matienzo: Valle de La Cubija; 30TVN 5038396533, 264 m a.s.l.). A wide and deep shelter that opens at the base of a cliff in Aptian reef limestones. The entrance is 10 m wide and 4 m high, being a cool and moist cavity, with abundant drip; on the E side there is a 30 m long cat hole leading to a 10 m diameter room (http://matienzocaves.org.uk/descrip/0975.htm).

Sima PO-153 (San Roque de Riomiera: Porracolina; 30TVN 4392886570, 585 m a.s.l.). A poorly developed chasm, with a practically vertical path through short and narrow wells, with walls oozing with water. The *Hydrocena* site is the wall of the second well, covered by a dark crust where snails are abundant and easily visible.

Torca de La Rabia (Arredondo: Bustablado; 30TVN4990591143, 555 m a.s.l.). The spectacular entrance opens at the bottom of a funnel 50 m in diameter, dug into the slope, having 17 x 9 m in its narrowest part and 48 m deep and opened in the SW corner of a large room of 180 by 50-60 m width (http://karstexplo.fr/CuevasAson/CavSecteur1/Rabia.htm). The *Hydrocena* site is in the twilight zone, on the eastern slope of the scree cone below the entrance, under stones.

Cueva de la Carretera (Miera: Mortesante; 30TVN4242795542, 173 m a.s.l.). Cave close to the road located 0.3 km south of Fuente

Encalada and from which a permanent water course flows through a waterfall (Bohigas Roldán & Cousillas Uberti, 1975).

Genus ***Georissa*** Blanford, 1864
Type species, *Hydrocena pyxis* Benson, 1856
Georissa japonica (von Martens, 1886) comb. nov.

Hydrocena japonica von Martens, 1886, described from Tosa (Japan), is currently included in *Hydrocena* (MOLLUSCABASE: http://www.molluscabase.org). Since it was described as "striatula" (a diagnostic character of *Georissa*) and the genus *Hydrocena* is restricted to Europe and continental Africa (see Discussion), the species is herein placed in the genus *Georissa,* together with the four *Georissa* species considered for Japan by Sasaki (2008).

Georissa pilsbryana Prieto *nom. nov.* for *Georissa japonica* Pilsbry, 1900

Georissa japonica Pilsbry, 1900, described from Kashima (Japan), is one of the four hydrocenid species considered for Japan (Sasaki 2008) but it results to be a junior secondary homonymy with *Georissa japonica* (von Martens, 1886). Thus, a new name is here provided for it. Möllendorf (1901) also described another *Georissa japonica* Möllendorf, 1901 from the same locality, whose lectotype was figured by Zilch (1973) under *G. japonica* Pilsbry, 1900; being the same species, it constitutes a curious case of synonymy and homonymy.

Discussion

The classification of the new species within the family Hydrocenidae has no objection because the conchological (shell shape, umbilical callus, resorption of internal septa) and opercular (long inner process) characters agree with features of the family (Barker, 2001). There is also no doubt that it is a new species because it clearly differs from the two species of Europe and Macaronesia (by direct comparison) and from the other species of the family (by comparison of descriptions).

The generic placement, however, is more troublesome. The systematics of the family Hydrocenidae has not been reviewed since Pfeiffer (1876), when he included in that family what he named *Realiea*, including a unique genus *Realia* Gray, 1850 with a mixture of species currently placed in different families from Pupinidae to Cyclophoridae. A modern account of the family (Molluscabase, 2022) includes most species within *Georissa* or *Hydrocena*, although the list also records three monotypic genera, one of them extinct. The two extant genera, *Monterissa* Iredale, 1944 for *M. gowerensis* (Iredale, 1944) from Lord Howe Island (Australia) and *Sinicena* Egorov, 2003, a replacement name for *Lapidaria,* which was created by Kang (1986) for *L. chinensis* Kang, 1986 from Fenghuang (Hunan, China), to resolve the homonymy with the trilobite *Lapidaria* Tjernvik, 1956. The extinct genus *Schwardtina* was erected by Bandel & Riedel (1994) for the fossil *Helix cretacea* Tausch, 1886 from the Late Cretaceous (Santonian) of Hungary.

Many species have been described as belonging to this family but because of the simplicity of the shell, most of them have been based only on a few conchological features, and their descriptions are short and with low diagnostic value. The main difference is the presence of conspicuous spiral sculpture in *Georissa* (lacking in *Hydrocena*), which produces a reticulated pattern where radial sculpture (growth lines) is present (Thompson & Dance, 1983). The genus *Sinicena* presents a conspicuous spiral sculpture like that of *Georissa*; it was mainly based (Kang, 1986) on the existence of a small cavity behind the parieto-columellar callus, occupied by a "conical soft tissue stretch" inserted on it, a very long intestine and a very long radula "without central tooth, consisting of two bands which are grappling with each other" with 7-9 teeth bearing 6-7 cusps on the upper margin.

Diversity and distribution of *Hydrocena* species. The zoogeography of the Hydrocenidae is hampered by a defective taxonomy, but species currently ascribed to *Georissa* are widely distributed in the western Pacific, from the Hawaiian Islands westward to Japan, China, Guam and the Philippines, southward to tropical Queensland and then eastward through the Cook and Society Islands to the Marquesas and Pitcairn Islands (Preece, 1995); moreover, scattered species have been recorded further west, from Vietnam, Myanmar and India, and eleven species from Madagascar (Emberton, 2004).

Formerly, and even today, the genus *Hydrocena* has been used as a catch-all genus and numerous old taxa described within this genus have been transferred to *Georissa*, especially those described from outside Europa and Africa (see below). According to MOLLUSCABASE (consulted January 2022), the genus includes six European extinct species, from the oldest *H. atavina* Stache, 1889 (taxon *inquirendum*) from the early Palaeocene of Italy and Slovenia to two Pliocene species from France (Schlickum, 1979; Harzhauser *et al*., 2015); most of those have smooth shells but *H. moncuccoensis* Harzhauser, Neubauer & Esu, 2015 was described as having a shell sculptured by spiral-threads separated by slightly narrower spiral grooves, which is a typical feature of the genus *Georissa*. Recently, Yu & Neubauer (2021) described *Hydrocena praecursor* from mid-Cretaceous Burmese amber as the oldest representative of the family. Somewhat younger is *Helix cretacea* Tausch, 1886 from the Late Cretaceous (Santonian) of Hungary, for which Bandel & Riedel (1994) erected the genus *Schwardtina*; its generic diagnosis is like that of *Hydrocena* except for a different ornamentation of the protoconch. This statement is not in the diagnosis but only in "Differences", while the different ornamentation with irregular pits and an initial circular shell cap of 120 µm demarcated by a groove, is explained in the redescription of *Schwardtina cretacea.* Bandel & Riedel (1994: 4) also stated that "The columella is not resorbed" as a main difference of *Hydrocena* with respect to *Schwardtina*, but this is incorrect. Since that circular cap is a feature also found in specimens of the new species (Fig. 8), two opposite statements could be considered: that the new species belongs to the genus *Schwardtina,* or that this name must fall within the synonymy of *Hydrocena.* We consider that the circular cap is a sort of primordial nucleus from which the rest of the protoconch is formed, although it is normally not observable. Thus, we propose *Schwardtina* to be considered a junior synonym of *Hydrocena*.

In the systematic reappraisal herein, *Hydrocena* comprises six extant species, all of them distributed in the Western Palaearctic (*H. cattaroensis*, *H. gutta* and *H. canttabrica*) and continental Africa (*Hydrocena noticola* Benson, 1856 from South Africa, *Hydrocena kenyana* Connolly, 1929 and *Hydrocena tanzaniensis* Verdcourt, 2004). Herbert & Kilburn (2004: p.90) provide an excellent photograph of *H. noticola.* With respect to the African species, Verdcourt (2004: p. 301) considers that "The lack of a peg on the operculum suggests that this species [*Hydrocena tanzaniensis* Verdcourt, 2004] and probably *Hydrocena kenyana* Connolly, 1929 are misplaced" but "that the family is correct" because the "minute radula (...) agrees well with the description given for the family (...) with the central area devoid of teeth but numerous imbricate spathulate marginals with about 10 minute cusps". The presence of a peg in the operculum of *H. noticola* allowed Connolly (1939) to confirm its placement within Hydrocenidae; however, the operculum profile, with concentric whorls, basal nucleus and "apophysis on left centre of basal margin", does not fit the opercular structure of European *Hydrocena*, where growth marks, not visible on the inner side, are not concentric, and the apophysis is on the base of a straight left margin.

On the other hand, based on its strong spiral striation, the Australasian species *Hydrocena spiralis* Wiktor, 1998 (MOLLUSCABASE), which was described based on a single empty shell from Padang, Papua New Guinea (Wiktor, 1998), does not belong to *Hydrocena*. Probably it does not even belong to the Hydrocenidae as the profile of the shell does not show the presence of convex whorls separated by deep sutures and especially by the existence of a perforated umbilicus, which implies that there is no umbilical callus nor resorption of the columellar funnel to form an umbilical cavity.

Finally, MOLLUSCABASE also includes *Hydrocena japonica* von Martens, 1886, described from Tosa (Japan). Sasaki (2008) did not record it among the four hydrocenid species he considered for Japan, although he mentioned *Georissa japonica* Pilsbry, 1900 among them. As the original descriptions of these two taxa, both unfigured, depict different species, a shell with 4½ whorls and a height/diameter ratio of 1.55 in the von Martens species and 3¾ whorls and 1.17 ratio in the Pilsbry species (Von Martens, 1886; Pilsbry, 1900), a replacement name is proposed above for Pilsbry's taxon.

Hydrocena canttabrica sp.nov. is the first cave species of the genus and represents an isolated relict. There are other cave species of Hydrocenidae but they belong to the genus *Georissa*, and in most cases live sympatrically with their putative parental epigean species: the cave species *Georissa filiasaulae* Haase & Schilthuizen, 2007 and the epigean species *Georissa saulae* van Benthem Jutting, 1966 in a karstic limestone outcrop in Sabah, Malaysian Borneo (Haase & Schilthuizen, 2007); the cave species *Georissa mawsmaiensis* Das & Aravind, 2021 and the epigean species *Georissa saritta* (Benson, 1851) in a limestone area in Meghalaya, North-East India (Das & Aravind, 2021); the cave species *Georissa silaburensis* Khalik, Hendriks, Vermeulen & Schilthuizen, 2018 and the epigean species *Georissa pyrrhoderma* Thompson & Dance, 1983 at Mount Silabur in Sarawak, Malaysian Borneo (Khalik *et al*., 2020).

Conclusions

In the present article, a new troglobiont species of the genus *Hydrocena* is described, with a relictual distribution in the Cantabrian Mountains. The new species is the only one in its genus living in caves, and possesses a thick, transparent shell, and a very long radular sac.

The Covallarco cave represents a very interesting case, since it hosts a great malacological diversity, with up to five mollusc species living inside: *Iberozospeum* sp., *Iberozospeum costulatum* Prieto & Jochum, 2022, *Papilloderma* sp., *Platyla merillaensis* Quiñonero-Salgado, Ruiz Cobo & Rolán, 2017 and the newly described species. Another remarkable fact is the coexistence of *H. canttabrica* sp. nov. with taxa of the genus *Iberozospeum* Jochum, Kneubühler, Prieto and Neubert, 2022 in all the localities covered in this study.

The finding of a new species in cave habitats highlights the need for further sampling in the hypogean habitats of the northern Iberian Peninsula, still very scarcely studied, which is continuously giving a wealth of new taxa.

Acknowledgments

To Han Raven (The Netherlands) for his collaboration in some speleomalacological sampling trips and for the careful and detailed revision of the manuscript. To Ruud Bank (The Netherlands) for his kind revision of the manuscript and for the suggestions for the incorporation of relevant bibliography. To Antonio Frias Martins (University of Azores) for donating the specimens of *Hydrocena gutta* that have made possible to compare the different European species of the genus.

References

Achurra, A., Rodriguez, P., & Reynoldson, T. B. (2015). Is the Cantabrian region of northern Spain a biodiversity hotspot for obligate groundwater fauna? The case of oligochaetes (Annelida, Clitellata). *Hydrobiologia 745*, 151–166.

A.E.R. (Agrupación Espeleológica Ramaliega) (2014). El Sistema del Mortillano. *Boletín de la Sociedad Española de Espeleología y Ciencias del Karst* 10, 34–41.

Auffenberg, K. (1999). A new species of land snail of the genus *Georissa* (Gastropoda: Hydrocenidae) from the Philippine Islands. *The Nautilus* 112, 109–112.

Backhuys, W. (1975). *Zoogeography and taxonomy of the land and fresh-water molluscs of the Azores*. Backhuys & Meesters. 447 pp.

Bandel, K. & Riedel, F. (1994). The late Cretaceous gastropod fauna from Ajka (Bakony Mountains, Hungary): a revision. *Annalen des Naturhistorischen Museums in Wien* 96*A*, 1–65.

Barker, G.M. (2001). Gastropods on Land: Phylogeny, Diversity and Adaptative Morphology [pp:1-146]. In: G.M. Barker (Ed.) *The Biology of Terrestrial Molluscs*. CAB International Publ. 558 pp.

Barroso, C.X., Matthews-Cascon, H. & Simone, L.R.L. (2012). Anatomy of *Neritina zebra* from Guyana and Brazil (Mollusca: Gastropoda: Neritidae). *J. Conchol.* 41, 49–64.

Bellés, X. (1987). *Fauna cavernícola i intersticial de la Península Ibèrica i les Illes Balears*. Editorial CSIC-CSIC Press.

Bernasconi, R. (1995). Two new cave Prosobranch snails from Papua New Guinea: *Selmistomia beroni* n.gen. n.sp. (Caenogastropoda: Hydrobiidae) and *Georissa papuana* n.sp. (Archaeogastropoda: Hydrocenidae). (Zoological results of the British Speleological Expedition to Papua New Guinea 1975). *Revue Suisse de Zoologie* 102, 37–386.

Bernasconi, R. (2014). Mollusca [p.1102–1104]. In: J. Gunn (Ed.) *Encyclopedia of Caves and Karst Science*. Taylor & Francis Books, Inc. 1940 pp.

Berry, A.J. (1965). Reproduction and breeding fluctuations in *Hydrocena monterosatiana*, a Malayan limestone archaeogastropod. *Proc. Zool. Soc. London* 144, 219–228. https://doi.org/10.1111/ j.1469-7998.1965.tb05174.x

Blanford, W.T. (1869). On the animal and operculum of *Georissa*, W. Blanf. and on its relations to *Hydrocena*, Parreyss; with a note on *Hydrocena tersa*, Bens., and *H. milium*, Bens. *Ann. Magaz. Nat. Hist.* (Ser. 4) 3, 173–179.

Culver, D.C. (2012). Mollusks. In: *Encyclopedia of Caves* (Second Edition). W.B. White and D.C. Culver eds., Academic Press, 512–517. New York.

Culver, D.C., Deharveng, L., Bedos, A., Lewis, J. J., Madden, M., Reddell, J.R., Sket, B., Trontelj, P. & White, D. (2006). The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography* 29, 120–128.

Cunha, R., Rodrigues, P. & Martins, A.F. (2010). Lista dos Moluscos [pp. 165–177]. In: Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P. & Vieira, V. (eds.) *A list of the terrestrial and marine biota from the Azores*. Princípia, Cascais, 432 pp.

Das, N.K., & Aravind, N.A. (2021). A new species from the genus *Georissa* Blanford, 1864 (Gastropoda, Neritimorpha, Hydrocenidae) from a limestone cave of Meghalaya, Northeast India. *J. Conchol.* 44, 93.

Degouve-de-Nuncques, P. (2014). El Sistema del Gándara. *Boletín de la Sociedad Española de Espeleología y Ciencias del Karst* 10, 22–33.

Egorov, R.W. (2003). *Sinicena*, a new replacement name for *Lapidaria* Kang, 1986 (non Tjernvik, 1956) (Gastropoda: Neritopsiformes: Hydrocenidae). *Club Conchylia Informationen* 35, 75.

Emberton, K.C. (2004). Madagascan *Georissa, Cyclotus, Omphalotropis* and so-called *Chondrocyclus* (Gastropoda: Caenogastropoda: Hydrocenidae, Cyclophoridae, Assimineidae). *Arch. Mollusk.* 133, 69–107.

Faille, A., Balart-García, P., Fresneda, J., Bourdeau, C., & Ribera, I. (2021). A remarkable new genus of Iberian troglobitic *Trechodina* (Coleoptera: Carabidae: Trechinae: Trechini), with a revisited molecular phylogeny of the subtribe. *Annales de la Société Entomologique de France (NS)* 57, 85–106.

Galán, C. (2006). *Conservación de la fauna cavernícola troglobia de Gipuzkoa: contexto general, biodiversidad comparada, relictualidad y endemismo*. Pág. web aranzadi-sciences. org, Archivo PDF.

García, J.L. (2010). *Cantabria Subterránea. Catálogo de las Grandes Cavidades. Actualización 2010*. Vol. 2 (pp. 453–933). Ed. Instituto de Estudios Cántabros y del Patrimonio. http://matienzocaves.org.uk/cantab/cantasub2010-vol2.pdf

Gittenberger, E. (2015). Caving for snails in northern Albania. *Basteria* 79, 23–29.

Gittenberger, E. & Maassen, W.J.M. (1980). *Hydrocena (H.) cattaroensis* (L. Pfeiffer, 1841) (Prosobranchia, Neritacea) und ihre Lebensbedingungen. *Basteria* 44, 9–10.

Groh, K. & García, A. (2004). Mollusca. In: I. Izquierdo, J.L. Martín, N. Zurita & A. Rechavaleta (eds.). *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres),* pp. 149-154. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.

Haase, M. & Schilthuizen, M. (2007). A new *Georissa* (Gastropoda: Neritopsina: Hydrocenidae) from a limestone cave in Malaysian Borneo. *J. Moll. Stud.* 73, 215–221.

Harzhauser, M., Neubauer, T.A., Georgopoulou, E., Esu, D., D'Amico, C., Pavia, G., Giuntelli, P. & Carnevale, G. (2015). Late Messinian continental and Lago-Mare gastropods from the Tertiary Piedmont Basin, NW Italy. *Bollettino della Società Paleontologica Italiana* 54, 1–53.

Herbert, D.G. & Kilburn, D. (2004). *Field guide to the land snails and slugs of eastern South Africa.* Pietermaritzburg: 336 pp.

Kang, Z.B. (1986). Descriptions of eight new minute freshwater snails and a new and rare species of land snail from China (Prosobranchia: Pomatiopsidae, Hydrobiidae; Hydrocenidae). *Arch. Molluskenkd.* 117, 73–91.

Kano, Y., Chiba, S. & Kase, T. (2002). Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. *Proc. R. Soc. Lond., Series B: Biol. Sci.* 269, 2457–2465.

Khalik, M.Z., Hendriks, K., Vermeulen, J.J., & Schilthuizen, M. (2018). A molecular and conchological dissection of the "scaly" *Georissa* of Malaysian Borneo (Gastropoda, Neritimorpha, Hydrocenidae). *ZooKeys* 773, 1–55.

Khalik, M.Z., Bozkurt, E., & Schilthuizen, M. (2020). Morphological parallelism of sympatric cave-dwelling microsnails of the genus *Georissa* at Mount Silabur, Borneo (Gastropoda, Neritimorpha, Hydrocenidae). *J. Zool. Syst. Evol. Res.* 58, 648–661.

Kneubühler, J., Jochum, A., Prieto, C.E. & Neubert, E. (2022). Molecular investigation and description of *Iberozospeum* n. gen., including the description of one new species (Eupulmonata, Ellobioidea, Carychiidae). *Org. Divers. Evol.* 22, 61–92.

Labrada, L., Salgado, J.M. & Luque, C.G. (2010). Fauna invertebrada de las cavidades de Cantabria. *Locustella: Anuario de la Naturaleza de Cantabria* 7, 29–43.

Martens, E. von (1886). Vorzeigungen einiger der von Dr. Gottsche in Japan und Korea gesammelten Land- und Süsswasser-Mollusken. *Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin* 1886, 76–80.

Martínez-Cedrún, P., Flor, G., Flor-Blanco, G. & Fernández-Maroto, G. (2014). Características geológicas y morfologías singulares de la región del Alto Asón (Cantabria). *Boletín de la Sociedad Española de Espeleología y Ciencias del Karst* 10, 4–21.

Martins, A.M.F. (2011). When the Galapagos "finches" are Azorean snails. *Açoreana* supl.7, 209–228.

Neubert, E. & Gosteli, M. (2005). The molluscan species described by Robert James Shuttelworth. II. Polyplacophora, Gastropoda (Caenogastropoda), Bivalvia. *Contributions to Natural History* 5, 1–79.

Núñez, L. & Núñez, J. (2010). Moluscos [p. 182–189]. En: Arechavaleta, M., Rodríguez, S., Zurita N. & García A. (coord.). *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009.* Gobierno de Canarias.

Pfeiffer, L. (1841). Beiträge zur Molluskenfauna Deutschlands, insbesondere der österreichischen Staaten. *Archiv für Naturgeschichte* 7, 215–230.

Pfeiffer, L. (1876). *Monographia pneumonopomorum viventium, accedente fossilium enumeratione: Supplementum tertium monographiae auriculaceorum, parte secunde auctum* (Vol. 2). T. Fischer.

Pilsbry, H.A. (1900). Notices of new Japanese land snails. *Proc. Acad. Nat. Sci. Philadelphia* 52, 381–384.

Preece, R.C. (1995). Systematic review of the land snails of the Pitcairn Islands. *Biol. J. Linn. Soc.* 56, 273–307.

Prieto, C.E., Quiñonero-Salgado, S., Ruiz-Cobo, J. & Alonso, A. (2020). Shells of *Papilloderma* Wiktor, Martin and Castillejo, 1990 (Gastropoda, Eupulmonata, Papillodermatoidea) found in caves reveal an unknown dwarf hypogean species. *J. Conchol.* 43, 641–653.

Prieto, C.E., Gómez-Moliner, B., de Winter, A.J. & Jochum, A. (in press) Terrestrial cave molluscs from mainland Spain. *Encyclopaedia Biospeleologica* (3rd.Ed.)

Sasaki, T. (2008). Micromolluscs in Japan: taxonomic composition, habitats, and future topics. *Zoosymposia* 1, 147–232.

Shuttleworth, R.J. (1852). Diagnosen einiger neuen Mollusken aus den Canarischen Inseln. In: *Mittheilungen der Naturforschenden Gesellschaft in Bern* 241/242, 137–146.

Simmonot, G. (2014). Bustablado: una gran red espeleológica en construcción. *Boletín de la Sociedad Española de Espeleología y Ciencias del Karst* 10, 42–63.

Sosa-Bravo, M., García-González, D., González-Gallego, J. & González-Gallego, M.A. (2014). Sistema Alto del Tejuelo. *Boletín de la Sociedad Española de Espeleología y Ciencias del Karst* 10, 64–83.

Thiele, J. (1910). Über die Anatomie von *Hydrocena cattaroensis* Pf. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 32, 351–358.

Thompson, F.G. & Dance, S.P. (1983). Non-marine mollusks of Borneo II Pulmonata: Pupillidae, Clausiliidae. III Prosobranchia: Hydrocenidae, Helicinidae. *Bull. Fla. State Mus., Biol. Sci.* 29, 101–152.

Troschel, F.H. (1856-1863). *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification* (1857, part 2: 73–112 + pl. 5–8). Vol. 1. Berlin. 252 pp + 20 pl.

Uribe, J.E., Colgan, D., Castro, L.R., Kano, Y. & Zardoya, R. (2016). Phylogenetic relationships among superfamilies of Neritimorpha (Mollusca: Gastropoda). *Mol. Phylogen. Evol.* 104, 21–31.

Verdcourt, B. (2004). New and little known species of terrestrial Mollusca from East Africa and Congo (Kinshasa). *Annales historico-naturales Musei Nationalis Hungarici* 96, 299–315.

Vermeulen, J.J., Liew, T.S. & Schilthuizen, M. (2015). Additions to the knowledge of the land snails of Sabah (Malaysia, Borneo), including 48 new species. *ZooKeys* 531, 1–139.

Welter-Schultes, F. (2012). *European Non-marine Molluscs, a Guide for Species Identification* / *Bestimmungsbuch für Europäische Land- und Süsswassermollusken.* Planet Poster Editions. Gottingen, Germany. 760 pp

Wiktor, A. (1998). Terrestrial gastropods of the Province of Madang in Papua New Guinea I. Terrestrial Prosobranchia. *Arch. Molluskenkd.* 127, 1–20.

Yu, T. & Neubauer, T.A. (2021). The oldest fossil Hydrocenidae found in mid-Cretaceous Burmese amber (Gastropoda: Cycloneritida). *Cretac. Res.* 122, 104765.

Zilch, A. (1973). Die Typen und Typoide des Natur-Museum Senckenberg, 52. Mollusca: Hydrocenidae. *Arch. Moll.* 103 (4/6), 263–272.

Zubieta-Hyllenius, P. & Noriega-Suárez, J. (1975). Exploraciones en el valle medio del río Miera (Santander). II. Exploraciones en la zona de Merilla. *Cuadernos de Espeleología* 8, 17–34.