

The Iberian *Pyrenaearia cantabrica* (Hidalgo, 1873) clade: elucidation of the type localities of its taxa (Gastropoda, Pulmonata, Hygromiidae)

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Within the genus *Pyrenaearia* P. Hesse, 1921, *Pyrenaearia cantabrica* (Hidalgo, 1873), from the NW Iberian Peninsula, is the species with the widest distribution and variability. Herein we discuss the taxa included within the *P. cantabrica* clade sensu Elejalde et al. (2009), including photographs of types and live specimens, and we identify the correct type localities of the alpine taxa *P. schaufussi* (Kobelt, 1876), *P. oberthuri* (Ancey, 1884) and *P. daanidentata* Raven, 1988. For *P. cantabrica*, *P. schaufussi* and *P. oberthuri* lectotypes are designated. This provides a solid basis for further study of this clade. It is shown that some specimens used in past molecular studies of *Pyrenaearia* were attributed to a wrong taxon.

Key words: *Pyrenaearia*, Gastropoda, Hygromiidae, Spain, distribution.

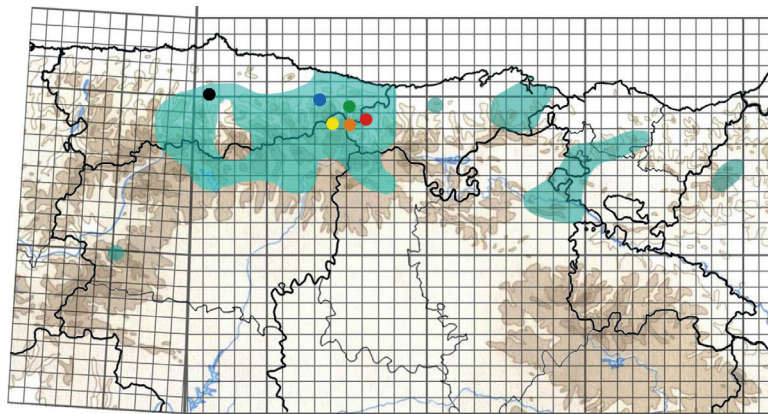
INTRODUCTION

Pyrenaearia cantabrica (Hidalgo, 1873) is a gastropod of the family Hygromiidae Tryon, 1866, with rounded, depressed shell, and present in a substantial part of the NW Iberian Peninsula. Within the genus *Pyrenaearia*, it is the species with the widest geographical distribution (Fig. 1) and also the largest altitudinal range. At low altitudes, it inhabits limestone rock faces and ridges; at higher altitudes it is also present in rocky slopes and karst areas. It is consid-

ered a polytypic species, with several local forms that were described as species, recently synonymised by Elejalde (2008) and Elejalde et al. (2009), with the exception of *P. daanidentata* Raven, 1988. The latter is an alpine taxon only known from a very small area. For all alpine taxa (*P. daanidentata*, *P. schaufussi* (Kobelt, 1876) and *P. oberthuri* (Ancey, 1884)) further study is required to determine their taxonomic status (species or subspecies; Elejalde et al., 2009). In some recent papers (Cadevall & Orozco, 2016; Bank & Neubert, 2017) these taxa are maintained as separate species. *Pyrenaearia velascoi* (Hidalgo, 1867), also from the NW Iberian Peninsula, is excluded from this review, as it belongs to a different clade (Elejalde et al., 2009).

In the literature (Elejalde et al. (2009), Cadevall & Orozco (2016) and previous papers) there is confusion about all three alpine taxa, due to uncertainty about the precise type localities of these. As a consequence, in the molecular studies of *Pyrenaearia* some taxa have been represented by specimens of another taxon, which could invalidate some of the conclusions. A systemic and multidisciplinary revision was undertaken of *P. cantabrica*, the synonymised taxa *P. cantabrica* var. *covadongae* Ortiz de Zárate López, 1956 and *P. poncebensis* Ortiz de Zárate López, 1956, and the alpine taxa *P. schaufussi*, *P. oberthuri* and *P. daanidentata*. In this study several taxonomic details are presented and the precise type localities of *P. schaufussi*, *P. oberthuri* and *P. daanidentata* are presented which, due to various mistakes, had not been located or had been misplaced. Additionally, the first photographs of several types (holotypes, paratypes, lectotypes, topotypes; Figs 2-18), live specimens (Figs 34-39) and their habitat (Figs 22-33) are presented.

In previous literature no sharp differentiation has been made between the taxa of *Pyrenaearia* living at higher altitudes. For example, Elejalde (2008: 46), citing Faci (1991: 509) described the scree between 1820-2060 m inhabited by *Pyrenaearia navasi* (Fagot, 1907) as 'alpine', whereas in



- Type locality of *P. cantabrica*
- Type locality of *P. cantabrica* var. *covadongae*
- Type locality of *P. poncebensis*
- Type locality of *P. oberthuri*
- Type locality of *P. schaufussi*
- Type locality of *P. daanidentata*

Fig. 1. Known distribution of *Pyrenaearia cantabrica* s.l. (light blue-green shaded areas) on map with provincial borders, topography and UTM grid. The type localities of the various taxa here reviewed are indicated by coloured dots.

the same paper (Elejalde, 2008: 131) several *Pyrenaearia* taxa with a heterogeneous altitudinal range (including *P. navasi* and *P. velascoi* (600–1500 m) or *P. daanidentata* (only known from 2100 m)) are considered to be ‘sub-alpine’. We recognise that the use of terms ‘alpine’ and ‘subalpine’ is a simplification as even in the Alps, where these zones were first defined, their ranges may vary several hundreds of meters (García Codron, 2011). Herein we use the term ‘alpine’ for the taxa *schaufussi*, *oberthuri* and *daanidentata* which occur above 1700 m. This is based on the vegetation and landscape of their habitat (Figs 26–31), which is well above the tree limit and fully matches the description of the alpine zone in García Codron (2011: 16), even though its mean temperature would suggest a sub-alpine level (Rivas-Martínez, 1990). Actually, these taxa typically only occur in microhabitats with lower temperatures (fissures and scree). We also repeatedly observed specimens of these collected alive to become active at low temperatures (even below 0° centigrade).

MATERIAL AND METHODS

The current paper is based on a careful revision of the bibliography (including the original descriptions of all taxa) and the cartography, including the maps of the Instituto Geográfico Nacional (2002a, 2002b) and the Adrados maps covering the Picos de Europa (Adrados (1990, 1993)). Relevant type material was reviewed. This was complemented with extensive field sampling, including several field trips to mountain ranges above 2000 m.

Abbreviations

AA = collection Alvaro Alonso Suárez, Gijón, Spain; MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain; MVHN = Museu Valencià d’Història Natural, Valencia, Spain; NBC = Naturalis Biodiversity Center, Leiden, The Netherlands; R = collection J.G.M. Raven, Den Haag, The Netherlands; RBINS = Royal Belgian Institute of Natural Sciences, Brussel, Bel-

gium; RMNH = Rijksmuseum van Natuurlijke Historie, now part of NBC; SNF = Senckenberg Naturmuseum, Frankfurt am Main, Germany; sp. = specimen(s)

RESULTS

Superfamilia Helicoidea Rafinesque, 1815

Familia Hygromiidae Tryon, 1866

Subfamilia Leptaxinae C.R. Boettger, 1909

Tribus Cryptosaccini Neiber, Razkin & Hausdorf, 2017

Genus *Pyrenaearia* P. Hesse, 1921

Pyrenaearia cantabrica (Hidalgo, 1873)

Figs 1–4, 19, 22–23, 34

Helix cantabrica Hidalgo, 1873: 358–359. “Peña Abis, aux environs de Caldas de Oviedo (Asturies).”

Type series. — Syntypes: MNCN collection Hidalgo, 15.05/3317 (5 sp.), 15.05/2687 (1 sp.); MNCN collection Azpeitia 15.05/3318 (1 sp.), all leg. Hidalgo.

According to Puente (1994), Elejalde (2008), Elejalde et al. (2009), Alonso & Raven (2019) and unpublished data, this species occurs throughout the NW Iberian Peninsula (Fig. 1), inhabiting limestone cliffs and rocky areas between 100 and 1600 m altitude. Several forms were described as separate taxa (Ortiz de Zárate López, 1956; Puente, 1994; Elejalde, 2008). Based on molecular studies the taxa *poncebensis*, *oberthuri*, *schaufussi* and *covadongae* were included in the synonymy of *cantabrica*, whilst the status of *daanidentata* remained to be confirmed (Elejalde, 2008; Elejalde et al., 2009).

For the first time photos of shells (Figs 2–3) and a live specimen (Fig. 34) of *P. cantabrica* from the type locality (Peña Avis, Las Caldas de Oviedo, Asturias, 130 m altitude, UTM 30TTP63150033, Fig. 22) are presented. It has a quite flat, thin shell with wrinkled surface and fine hairs (the

periostracum is missing in the lectotype, but present in the topotype), and occurs in a very limited area, but isolated populations with similar shells occur elsewhere in central Asturias. Herein the specimen MNCN 15.05/2687 (Figs 2, 19) figured by Hidalgo (1879: pl. 24 figs 252-254) is designated as lectotype.

Hidalgo (1873) also described a β variety from Monsacro (Morcín, south of Oviedo, Asturias). We collected specimens (Fig. 4) that agree with the description of Hidalgo ('Testa paulo major, minus rugulosa et impresso-punctata'), at a limestone rock face at 850 m altitude (UTM 30TTP65889370, Fig. 23). The shells are very similar to those from the type locality of *P. cantabrica*. According to Templado et al. (1993: 238) specimen MNCN 15.05/2690 in the Hidalgo collection probably represents this variety, but as it is also reported to be from the type locality it could also be another syntype of *cantabrica*.

Although the typical form of *P. cantabrica* has a very limited distribution, based on phylogenetic analyses Elejalde (2008), Elejalde et al. (2009) and Caro et al. (2019) consider specimens from the entire Cantabrian mountains and Basque mountains (from Asturias to Navarra) to belong to this species.

Pyrenaearia cantabrica* var. *covadongae

Ortiz de Zárate López, 1956

Figs 1, 5, 25, 35

Pyrenaearia cantabrica var. *covadongae* Ortiz de Zárate López, 1956: 44, fig. 14. "Covadonga."

Material used to describe the variety (no formal status). — Leg. Ortiz de Zárate López. MNCN coll. Ortiz de Zárate López, 15.05/44163 (1 sp.); MNCN coll. Cobos 15.05/43471 (1 sp.).

Ortiz de Zárate López (1956) described the specimens from the Covadonga sanctuary (Cangas de Onís, Asturias, 300 m, UTM 30TUN334969, Fig. 25) as a variety (form). Although these specimens are more colourful due to the thicker shell and wider orange lip (Fig. 5), there is little justification for a separate name as *P. cantabrica* is very variable throughout its range. Ortiz de Zárate López (1956) correctly refuted the opinion of Azpeitia (1924), who suggested that the specimens from Covadonga, rather than being *P. cantabrica*, corresponds to *Helix subcantabrica* Fagot, 1888, a species from the Central Pyrenees, currently synonymised with *Xerotracha renei* (Fagot, 1882). We agree with Elejalde (2008) who synonymised this taxon with *P. cantabrica*. The first photos of a shell (Fig. 5) and a live specimen (Fig. 35) from the type locality are presented. Populations of similar specimens occur at various localities (e.g. Desfiladero de los Beyos, Asturias) surrounded by other forms.

***Pyrenaearia poncebensis* Ortiz de Zárate López, 1956**

Figs 1, 6-7, 24, 36

Pyrenaearia poncebensis Ortiz de Zárate López, 1956: 46-48, figs 5, 16, 22-23, 25-27. "En las rocas del margen de la carretera entre Arenas de Cabrales y Puente-Poncebo (Asturias), a unos 3 kilómetros de la primera localidad y aproximadamente a 180 metros sobre el nivel del mar".

Type series. — Leg. Ortiz de Zárate López. Paratypes: MNCN, coll. Ortiz de Zárate López, 15.05/23726 (20 sp.); MNCN coll. Cobos 15.05/43472 (1 sp.); NBC RMNH.MOL.137530 (3 sp.); MVHN 599 (3 sp.). The type series consisted of 80 specimens, but the holotype is reported missing (Villena et al., 1997: 110).

This taxon is characterised by its rather thin and flat shell, with coarse wrinkles and coarse hairs even in adults (Fig. 6-7). Elejalde (2008) and Elejalde et al. (2009) synonymised, based on molecular studies, the taxon with *P. cantabrica*. The local occurrence of specimens with hairs on their shells is explained as adaptation to living on a limestone cliff that is permanently in the shade (Elejalde et al., 2009). The type locality is between Arenas de Cabrales and Poncebos (Cabrales, Asturias, 200 m altitude, UTM 30TUN511936, Fig. 24), but populations of similar specimens have been collected in small areas of the Desfiladero de los Beyos in the West and in the valley of the Cares river including the limestone rocks around the Tito Bustillo cave in Ribadesella (Asturias) at 5 m altitude. Although the explanation by Elejalde et al. (2009) may be correct, it does not explain why the type of hairs and distance between the hair pits is different between these populations and those of typical *P. cantabrica*.

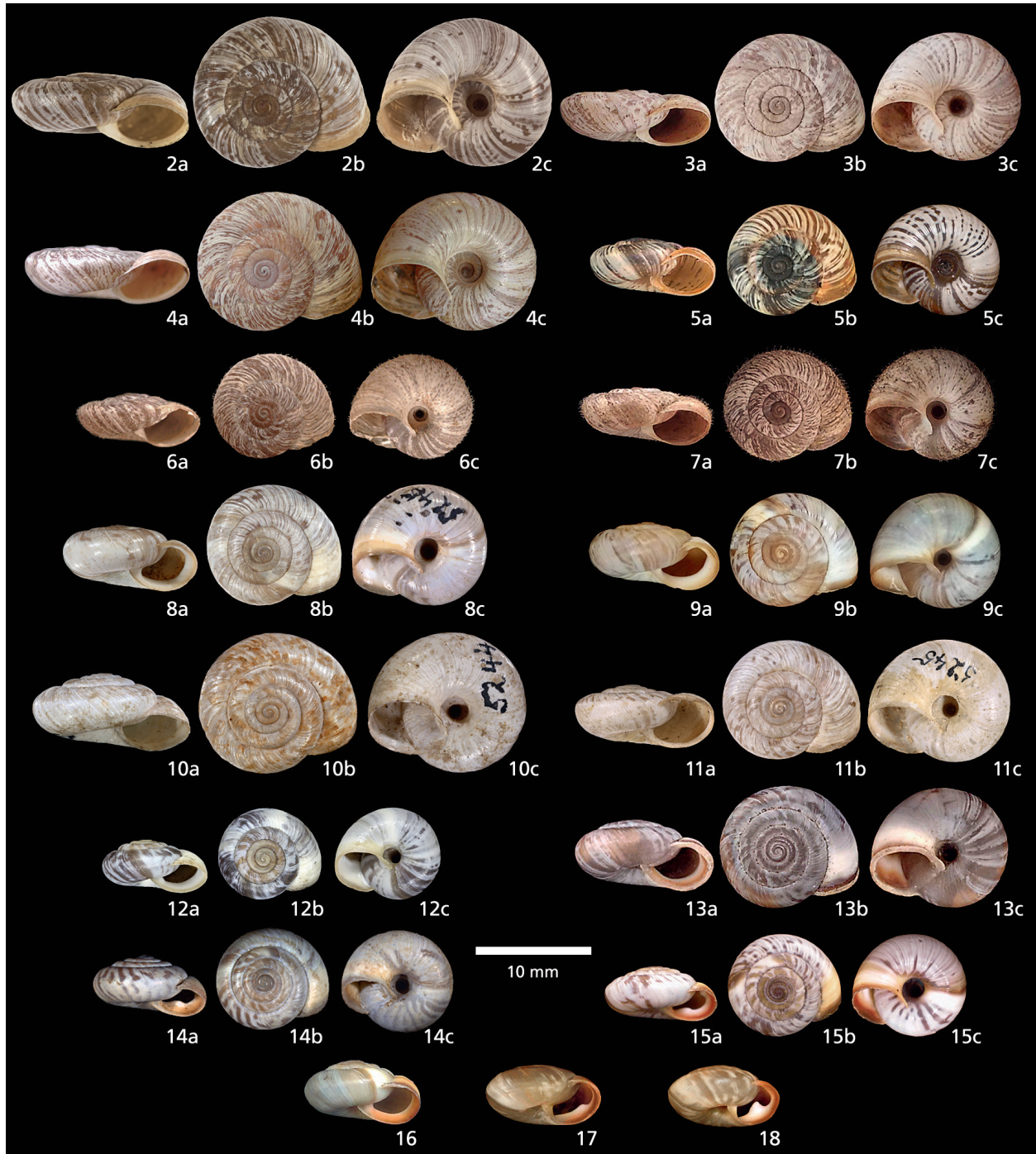
***Pyrenaearia schaufussi* (Kobelt, 1876)**

Figs 1, 8-9, 20, 26, 37

Helix schaufussi Kobelt, 1876: 45-46, pl. 109 fig. 1099. "im Liébanathal in den cantabrischen Gebirgen".

Type series. — Leg. Schaufuss. Syntypes: leg. Schaufuss; SNF collection Kobelt, 5244 (1 sp.), 5245 (2 sp.).

According to its original description (Kobelt, 1876) this taxon has a discoid shell, similar to *cantabrica*, but clearly an undescribed species as its shell is robust and glossy, with a much less flattened spire and with a distinctive lip with a white interior callus, strongly thickened, visible from the outside as a yellowish band. Kobelt specifically notes that even juveniles do not have hairs (though almost all taxa have fine hairs on the first 1-3 whorls, only visible with magnification). The type series comprises three specimens (Figs 8, 10-11, 20). As part of his review of the types in the



Figs 2-18. Shells of the taxa included within the *Pyrenaearia cantabrica* clade. **2-3.** *P. cantabrica*, Peña Avis, Las Caldas de Oviedo (Oviedo, Asturias). **2.** Lectotype, MNCN 05.05/2687, 14.3 mm (photos Rafael Araujo, © MNCN). **3.** Topotype, AA 0232-XC-TP, 13 mm. **4.** *P. cantabrica* var. *B. Monsacro* (Oviedo, Asturias), topotype, R L2171/001, 13.9 mm. **5.** *P. cantabrica* var. *covadongae*, Covadonga sanctuary (Onís, Asturias), topotype, AA 0232-XD-TP, 10.5 mm. **6-7.** *P. poncebensis*, La Infiesta, between Arenas de Cabrales and Puente Poncebos (Cabrales, Asturias). **6.** Paratype, MVHN 599, 10.1 mm (photos Martínez Ortí & Uribe, 2006: CC BY-NC 3.0). **7.** Topotype, AA 0232-XE-TP, 11.3 mm. **8-9.** *P. schaufussi*, south of Peña Vieja (Liébana, Cantabria). **8.** Lectotype, SNF 357936, 11.7 mm (photos Sigrid Hof, © SNF). **9.** Topotype, AA 0620-AL-E-TP, 10.8 mm. **10-11.** *P. cantabrica* s.l., from the type series of *P. schaufussi*, Liébana valley (Liébana, Cantabria) (photos Sigrid Hof, © SNF). **10.** SNF 5244, 14.3 mm. **11.** SNF 5245, 11.6 mm. **12-13.** *P. oberthuri*. Rasa de la Inagotable (Liébana, Cantabria). **12.** Lectotype, RBINS MT.1889, 9 mm (photos Yves Samyn, © RBINS). **13.** Topotype, AA 0620-AL-C-TP, 11.6 mm. **14-15.** *P. daanidentata*, Camino del Burro, south of Peña Santa (Valdeón, León). **14.** Holotype, NBC RMNH.MOL.56016, 9.5 mm. **15.** Topotype, AA 0620-B-TP, 9.1 mm. **16.** *Pyrenaearia* sp. from 'Hoyo del Burro', south of Peña Santa (Valdeón, León), AA 0620-AL-D-P4/1, 10.1 mm. **17.** *Pyrenaearia* sp. from 'Canal del Perro', south of Peña Santa (Valdeón, León), AA 0620-AL-D/1, 10 mm. **18.** *Pyrenaearia* sp. from 'Collado del Burro', south of Peña Santa (Valdeón, León), AA 0620-AL-D/2, 9.6 mm.



Figs 19–21. Labels of type specimens. 19. Label of the specimen of *P. cantabrica* figured by Hidalgo, here designated as lectotype (photo Rafael Araujo, © MNCN). 20. Labels of the type series of *P. schaufussi* (photos Sigrid Hof, © SNF). 21. Labels of the type series of *P. oberthuri* (photos Yves Samyn, © RBINS).

Senckenberg Museum, Zilch designated a specimen with thin callus and large hair pits (even on the last whorl) as lectotype (SNF 5244, Fig. 10), which made the two other specimens (SNF 5245) paralectotypes, one with thick apertural callus (Fig. 8) and one almost adult that did not yet form the callus (Fig. 11). As this was never formally published (pers. comm. Ruud Bank), all three specimens are syntypes. The specimen Zilch selected closely resembles the one figured (Kobelt, 1876: 1099), but on the plate it is explicitly identified as *Helix cantabrica*. Apparently the plates were made before Kobelt decided his type series represented a different taxon. The description Kobelt made was based on more specimens than those in the type series as he states that Schaufuss for a long time sent specimens (mostly juveniles) from this locality under the name *cantabrica*. ICZN (1999) recommendation 74B states: “Preference for illustrated specimen. Other things being equal, an author who designates a lectotype should give preference to a syntype of which an illustration has been published.” As the specimen SNF 5245 with thick callus best fits Kobelt’s description, with all characteristics Kobelt mentions to differentiate it from *cantabrica*, we designate the thick-lipped specimen from lot SNF 5245 (Fig. 8) as lectotype of *P. schaufussi*. It will be stored as SNF 357936.

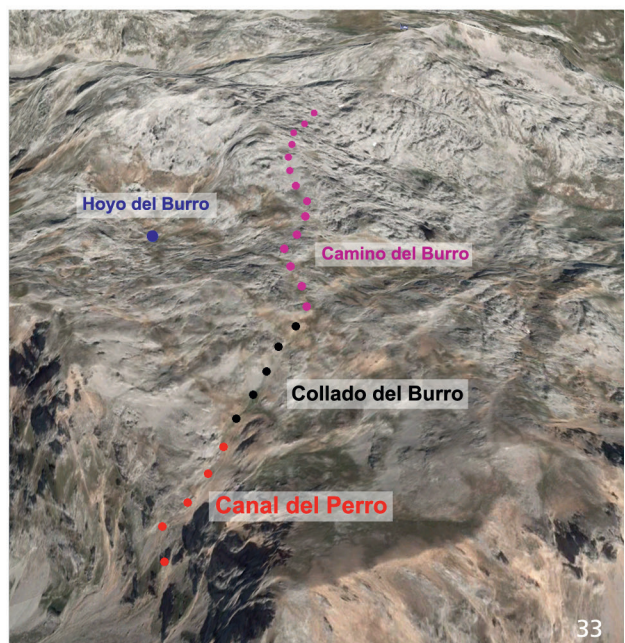
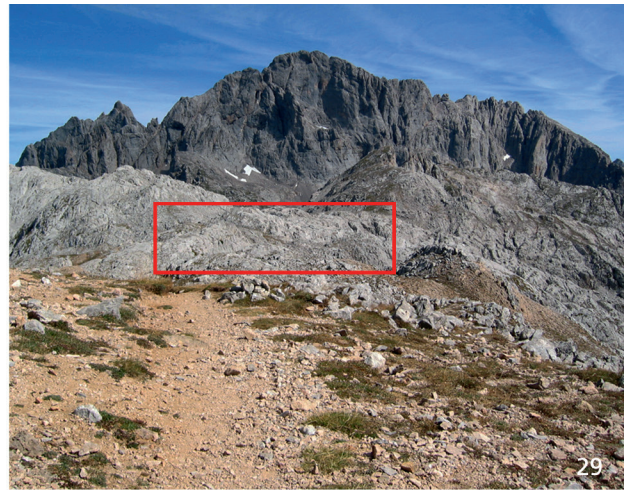
The type locality was vaguely identified as ‘Valle de Liébana’, a valley about 15 km long between Potes and Fuente Dé, flanked by a steep limestone cliff to the North, with a difference in altitude of about 1 km, forming the south-

ern edge of the Central and Eastern massifs of the Picos de Europa. A better definition of the type locality is essential as the limestone cliff has alpine forms living at high altitude, whereas non-alpine taxa may live at its base (remarkably, since Schaufuss nobody has collected *Pyrenaea* at low altitudes in this valley, probably due to the attraction of high mountains, both to tourists and naturalists). Kobelt undoubtedly describes an alpine form, with a thick shell and conspicuous apertural callus (as in the assigned lectotype), but SNF 5244 (which Zilch selected) certainly originated from a lower altitude.

Fagot (1888: 33) contributes a key information by specifying that Schaufuss ‘found it [...] south of Peña Meja’. After a detailed cartographic study, no ‘Peña Meja’ was found anywhere in the Liébana area. As this name should refer to a remarkable geographical feature, we believe it is a misspelling of Peña Vieja, one of the main peaks in the area. The altiplane south of this peak, now easily accessible by the Fuente Dé cable car, already was a relatively accessible alpine zone at the time of Schaufuss’ visit, due to the existence of several mines, which were accessed from Sotres or Espinama, ascending through Puertos de Áliva or through a zigzag trail from Fuente Dé. Confirming our conclusions, the specimens we collected at this locality (at eight points between 1850 and 2200 m altitude along the southern and western flanks of Peña Vieja) fit the description of Kobelt. We identify the slopes south of Peña Vieja (near La Vuel-



Figs 22-27. Type localities of various *Pyrenaearia* taxa. **22.** Peña Avis, Las Caldas de Oviedo (Oviedo, Asturias), type locality of *P. cantabrica*. **23.** Limestone rock face at El Monsacro (Morcín, Asturias), locality of the β variety of Hidalgo of *P. cantabrica*. **24.** La Infiesta, between Arenas de Cabrales and Poncebos (Cabrales, Asturias), type locality of *P. poncebensis*. **25.** Sanctuary of Covadonga (Onís, Asturias), type locality of *P. cantabrica* var. *covadongae*. **26.** Rocky slopes south of Peña Vieja (Liébana, Cantabria), type locality of *P. schaufussi*. **27.** Rasa de la Inagotable (Liébana, Cantabria), type locality of *P. oberthuri*.



Figs 28-33. Various localities on the southern slope of Peña Santa (Valdeón, León). **28.** Canal del Perro. **29.** Collado del Burro (foreground), Camino del Burro (red frame) and Peña Santa (background). **30.** Camino del Burro, type locality of *P. daanidentata*. **31.** Hoyo del Burro. **32-33.** area comprising the type locality of *P. daanidentata*, with the most relevant toponyms highlighted with dots: Canal del Perro (red), Collado del Burro (black), Camino del Burro (purple) and Hoyo del Burro (blue) superimposed on a map (IGN 1944; MTN-50) and a 3D view from the South (Google Maps).

tona, 1900 m, UTM 30TUN526810, Fig. 26) as the type locality of *P. schaufussi*. Also the lot MNCN 15.05/43556 from Puer-tos de Áliva fully consists of specimens that are very similar. Specimens SNF 5244 (Fig. 10) and the subadult SNF 5245 (Fig. 11) must have been collected at much lower altitude along one of the access routes to the Peña Vieja. They are similar to the specimens living locally in the Desfiladero de la Hermida, north of Potes. They are herein considered not to represent *schaufussi*, but *cantabrica* s.l. (closest to *ponce-bensis*). That renders erroneous practically all subsequent records of *schaufussi*, the description of which eventually contradicted that of Kobelt.

In his monograph on the genus *Pyrenaearia*, Ortiz de Zárate López (1956) states that Zilch sent three photographs of the holotype (sic) of *P. schaufussi* and that it has a weakly thickened lip. As indicated above, that specimen is not *schaufussi* as defined herein. Ortiz de Zárate López also claimed that Azpeitia (1924) cited it from the Desfiladero de la Hermida (Cantabria) and attributed a single specimen from the Gorbea massif (Vizcaya and Álava) to this species. He did not provide a figure of any of these shells. Azpeitia (1924), however, clearly mentioned he did not have material from the type locality of *schaufussi* and identified his material from La Hermida as *P. cantabrica*. Prieto (1986) and Elejalde (2008) followed Ortiz de Zárate López's interpretation and Puente (1994) stated that the species lives at low altitude. Elejalde (2008) selected two specimens from Urdón (Desfiladero de la Hermida), erroneously identified as *schaufussi*, for his molecular analysis of *schaufussi*. On the other hand, two of the samples used by Elejalde erroneously identified as *oberthuri* (*'P. oberthueri-05'*, *'P. oberthueri-06'*), can be identified as *schaufussi*. We refer to the specimens collected at 'Peña Santa Ana' (UTM 30TUN5282) at the border between Asturias and Cantabria. This peak is located at only 1 km from the southern slopes of Peña Vieja, the type locality of *schaufussi*. Assuming that Elejalde collected his samples at the easiest accessible part (the sw side at about 2100 m altitude, between La Vueltona and the Cabaña Verónica refuge) these can be considered as representative for *schaufussi* sensu Kobelt. Whereas the *schaufussi* sensu Prieto (1986) and Elejalde (2008) is clearly a form of *cantabrica*, this alpine taxon is very different and its status remains to be determined.

The first photographs of shells (Figs 8, 9) and a live specimen (Fig. 37) of *P. schaufussi* from the type locality are presented.

Pyrenaearia oberthuri (Ancey, 1884)

Figs 1, 12-13, 21, 27, 38

Helix oberthuri Ancey, 1884: 159-160. "aux Picos de Europa, à Engotable, dans las Asturias (Espagne), à une altitude de 2.000 mètres."

Type series. — Leg. Ch. & R. Oberthür. Syntypes: RBINS collection Dautzenberg, MT.1889 (2 sp).

According to the original description, it has a discoid shell of about 9 mm diameter, bluish white, with brown veins on the upper side. The aperture is oval, reddish, with a strong interior callus. The surface has oblique, irregular lines and the umbilicus is well marked, covering 1/5th of the diameter. The type locality, until now not located, is 'Engotable' (sic). Although the taxon was dedicated to Mr. René Oberthür, Ancey described it as *HELIX OBERTHURI* (in capitals). Therefore, the widespread spelling *oberthueri* (Puente & Prieto, 1991; Puente, 1994; Elejalde, 2008; Elejalde et al., 2009; Bank & Neubert, 2017; Caro et al., 2019) is wrong. Although this taxon was considered a synonym of *P. cantabrica* (Elejalde, 2008; Elejalde et al. 2009), it is still considered a valid species by some authors (Cadevall & Orozco, 2016; Bank & Neubert, 2017), albeit without presenting any arguments.

Ancey (1884) indicated that this taxon was collected in the Picos de Europa, at Engotable, in Asturias (Spain) at an altitude of 2000 m. Although 'Engotable' has not been located for over a century, a careful revision of the cartography led the authors to the conclusion that the name of type locality has been abbreviated and wrongly spelled in the original description, corresponding to the 'Rasa de la Inagotable' (UTM 30TUN6184; Fig. 27) in the eastern massif of the Picos de Europa, which is at an altitude of 2000 m (Instituto Geográfico Nacional (2002a; MTN25-56; Adrados 1993), and has a highest point called Pico Inagotable at 2285 m (Instituto Geográfico Nacional, 2002b; MTN50-56). The name derives from one of the mines of Ándara, with the same name ('Inagotable' meaning inexhaustible), exploited from 1850 to 1940 and, because of road building for its exploitation, was one of the most accessible points in the alpine zones of the Picos de Europa. Albeit actually located in Cantabria, until 1833 the locality belonged to the 'Asturias de Santillana' and was included in the 'Principado de Asturias' on contemporary maps (e.g. Dufour, 1837: Map 2: Reino de León y Principado de Asturias). It is concluded that, for the time being, the name *oberthuri* should be restricted to alpine specimens of *Pyrenaearia* from the eastern massif of the Picos de Europa, with a thick shell and edentate aperture. The first photographs of a topotype (Fig. 13) and a live specimen (Fig. 38) of *P. oberthuri* are here presented, matching the original description by Ancey and the syntypes in RBINS. There are two syntypes, a juvenile and young adult, from which specimen RBINS MT.1889 (Figs 12, 21) is designated as lectotype, which makes MT.1889/1 paralectotype. Notably, the surface of both specimens is clearly marked with fine hair pits, which demonstrates that even the lectotype is not fully grown. The topotypes range between 10.3 and 11.8 mm and in all those only on the first 1-3 whorls very fine hair pits are visible.



Figs 34-39. Live specimens of *Pyrenaearia* from their respective type localities. **34.** *P. cantabrica*, Peña Avis (Oviedo, Asturias) (photo: Jairo Robla Suárez). **35.** *P. cantabrica* var. *covadongae*, Covadonga sanctuary (Onís, Asturias). **36.** *P. poncebensis*, La Infiesta near Poncebos (Cabres, Asturias). **37.** *P. schaufussi*, La Vueltona, south of Peña Vieja (Liébana, Cantabria). **38.** *P. oberthuri*, Rasa de la Inagotable (Liébana, Cantabria). **39.** *P. daanidentata*, Camino del Burro, Picos de Europa (Valdeón, León).

As the type locality was not identified previously, several mistakes and erroneous identifications have been made. In his monograph of the genus *Pyrenaearia*, Ortiz de Zárate López (1956), recognising explicitly that he had not read the original description, identified several forms from the western and central massifs of the Picos de Europa as *oberthuri*. He put generations of malacologists on the wrong foot with his description of a heterogeneous series of shells collected along the path from Arenas de Cabrales (270 m altitude) to Vega de Urriellu (2000 m altitude), which he jointly identifies as *oberthuri*, but his series clearly includes non-alpine specimens. Based on the records by Ortiz de Zárate López, Puente & Prieto (1991) assure the species is ‘endemic to the central and western massifs of the Picos de Europa’, an erroneous distribution which nevertheless is validated in all successive papers (e.g. Puente, 1994; Altonaga et al., 1994; Elejalde, 2008; Cadevall & Orozco, 2016). In various recent papers the taxon is still considered a valid species, but that opinion is largely based on specimens from the central massif of the Picos de Europa that correspond to *P. schaufussi*. Thus far the taxon is only known from its type locality and is very similar to *schaufussi* as defined above and therefore likely a junior synonym.

Pyrenaearia daanidentata Raven, 1988

Figs 1, 14–15, 30, 32–33, 39

Pyrenaearia daanidentata Raven, 1988: 121–123. “Hoyo del Burro, 2.5 km S of Peña Santa de Castilla, Picos del Cornión, Macizo Occidental, Picos de Europa, province of León, Spain, 2100 m alt.”

Type series. — Leg. Daan. Holotype: NBC RMNH.MOL.56016 (1 sp). Paratypes: NBC RMNH.MOL.296521 (4 sp).

This species has been described as having a discoid shell, with a callus in the aperture provided with two small teeth that are well separated (Fig. 14). The type locality ‘Hoyo del Burro’ was reported by Mr. Daan, who collected the specimens, and was located by Raven (1988) 2.5 km south of ‘Peña Santa de Castilla’, at 2100 m altitude in the UTM square 30TUN4182. The systemic sampling by the authors has revealed the existence of other alpine forms of *Pyrenaearia* that are edentate or have varying dentition in the southern half of the western massif of the Picos de Europa, each with a very limited distribution. Therefore, respecting the clarity and precision of the original description herein the name *daanidentata* is applied exclusively to forms with the dentition as described by Raven, excluding other forms with a single tooth or a palatal lamina.

The toponym ‘Hoyo del Burro’ (‘Donkey hole’) was located only after consulting an old map (Instituto Geográfico Nacional, 1944; MTN50-55), being a depression (Fig. 31)

that is named ‘Hoyo de Argüelles’ on recent maps (Instituto Geográfico Nacional, 2002a; MTN25-55C4; Adrados, 1990), placed some 500 m west of the path known as ‘Camino del Burro’. The reported UTM coordinates of the type locality (30TUN4182) do not match with the coordinates of ‘Hoyo del Burro’ (30TUN4083), that lies about 1 km west.

Fieldwork at the area soon showed that the type material of *daanidentata* was not collected at ‘Hoyo del Burro’, but along the quite similar named path ‘Camino del Burro’ (Figs 29–30), at 2100 m altitude (UTM 30TUN4182 and 30TUN4183), by far the only relatively easy trail in the area, surrounded by a complex karstic landscape, and which altitude and location (2.5 km south of Peña Santa de Castilla) match with the data recorded by Raven (1988). On the contrary, ‘Hoyo del Burro’ is a depression 130 m lower, difficult to access because of the precipitous terrain. This conclusion was inferred from the specimens sampled in the area, as only those collected along the first kilometre of ‘Camino del Burro’ match exactly in shape and dentition with the type of Raven (Fig. 15). On the contrary, those from the reported type locality ‘Hoyo del Burro’ (to the West, lower, carefully sampled at four different points), at ‘Torre de Cotalbín’ (north) or ‘Hoyos del Caballo Cimero’ (east, lower) are edentate (Fig. 16) or have quite different dentition (‘Canal del Perro’, Fig. 17; ‘Collado del Burro’, Fig. 18; both south and lower). Therefore the type locality is herein corrected to ‘Camino del Burro, between Collado del Burro and Torre de Cotalbín’. Caro et al. (2019) report the type locality of *P. daanidentata* as “Collado del Perro – Canal del Burro” (sic), mixing up the toponyms ‘Canal del Perro’ and ‘Collado del Burro’, neither of which was the type locality designated by Raven.

Regarding the graphical representation, Elejalde (2008: 35), Gómez-Moliner et al. (2011: 908), and Cadevall & Orozco (2016: 362) figured as *daanidentata* specimens from ‘Canal del Perro’ and ‘Collado del Burro’, with different dentition, similar to those found in our samplings (Figs 17–18), none of which correspond to the holotype (Fig. 14). Samples employed by Elejalde (2008), Elejalde et al. (2009) and Caro et al. (2019) (*daanidentata*-01, *daanidentata*-02) for phylogenetic studies do not correspond to the type of *daanidentata*, but to single toothed specimens sampled from Canal del Perro (Gómez-Moliner, pers. comm.). The first photographs of the holotype (Fig. 14), the shell of a toptype (Fig. 15), a live specimen (Fig. 39) and the habitat (Fig. 30) of *P. daanidentata* are here presented.

CONCLUSIONS

This study identifies the correct type localities of *P. schaufussi*, *P. oberthuri* and *P. daanidentata*. This provides a solid basis for further study of this clade. It is here demonstrated

that the specimens used in the molecular studies by Elejalde (2008), Elejalde et al. (2009) and Caro et al. (2019) as representative of those taxa did not include specimens from the type localities and in the case of *P. schaufussi* and *P. daanidentata* specimens were used that do not correspond with the types. Despite these mistakes, the molecular studies are valid as long as the new data are taken into account, making the following corrections:

- the specimens identified as ‘*P. schaufussi*-01’ and ‘*P. schaufussi*-02’ should be treated as *P. cantabrica*;
- those identified as ‘*P. oberthueri*-05’ and ‘*P. oberthueri*-06’ should be treated as *P. schaufussi*;
- those identified as ‘*P. oberthueri*-01’, ‘*P. oberthueri*-02’, ‘*P. oberthueri*-03’ and ‘*P. oberthueri*-04’, should be treated as *Pyrenaearia* sp. 1;
- and the specimens ‘*daanidentata*-01’ and ‘*daanidentata*-02’, should be treated as *Pyrenaearia* sp. 2.

These corrections do not alter the fundamental results of the molecular analyses of Elejalde (2008) and Elejalde et al. (2009) which are based on a wide and representative set of samples, pointing towards the existence of two basic clades of *Pyrenaearia* in the Cantabrian and Basque mountains, which correspond to *P. velascoi* (or *P. carascalensis* (Michaud, 1831) s.l.) in the Basque area and the polymorph clade of *P. cantabrica* sensu lato (including all its forms).

Within *P. cantabrica* there are different forms or subspecies (*cantabrica*, *covadonga*, *poncebensis*). Based on their extensive sampling, the authors tried to find populations with a sympatric occurrence of two taxa of *Pyrenaearia*, but did not succeed. Throughout the Cantabrian mountains the populations show a high variability (including forms hitherto not described), making it impossible to allocate each population to a specific form. This supports the presence of a single species, *P. cantabrica*, in all but the alpine zones. Typically, the forms with thin and flat shells and with hairs in adult specimens are restricted to the lower parts of valleys, whereas the forms with more solid and smooth shells live in the higher parts of valleys and mountains. In the alpine zones very thick specimens with strong apertural callus appear. We agree with Elejalde et al. (2009) that during glaciations the valleys functioned as refuges, from where zones of higher elevation were repopulated during warmer periods like present-day.

Three alpine taxa were described from the Picos de Europa (*schaufussi*, *oberthuri* and *daanidentata*), and Elejalde (2008) analysed four specimens from the same area, two of them edentate (named ‘*oberthueri*-05’ and ‘*oberthueri*-06’, herein identified as *schaufussi*) and two with a single tooth (named ‘*daanidentata*-01’ and ‘*daanidentata*-02’, which do not match with *daanidentata*). Though the specific or subspecific status of the taxa *schaufussi*, *oberthuri* and *daanidentata* was not definitively addressed in the molecular

analyses, it showed that *schaufussi* and the toothed forms from ‘Canal del Perro’ belong to the clade of *P. cantabrica*, and it is likely that other forms from the Picos de Europa are closely related and also part of the same clade.

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