SHELLS OF *PAPILLODERMA* WIKTOR, MARTÍN AND CASTILLEJO, 1990 (GASTROPODA, EUPULMONATA, PAPILLODERMATOIDEA) FOUND IN CAVES REVEAL AN UNKNOWN DWARF HYPOGEAN SPECIES

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Abstract The slug Papilloderma altonagai *Wiktor, Martín & Castillejo, 1990 was described from an adult from the Sanctuary of Covadonga (Asturias, Spain) and a juvenile from Puerto de Alisas (in neighbouring Cantabria), but it was never recorded again outside the first site, an anthropogenic environment. New data, based on limacellae recovered by sieving of gravitational sediments from fossil caves, provides the first records contributed after the initial description. The records confirm and expand the distribution in the eastern area (Cantabria, in the northern foothills of the Valnera massif) and validate the usage of* Papilloderma *shells as indicators of their presence. The morphological analysis of limacellae suggests that there are two closely related taxa in the eastern area, a large endogean species corresponding to* P. altonagai, *and a much smaller unknown species living in the epikarst environment. A recent new record for the Sierra de Cuera (Asturias) also expands the western range out from Picos de Europa.*

Key words Epikarst, dwarfed slug, sympatry, morphometry, limacellae

Introduction

A malacological tale

In the summer of 1987, the Malacological Team of the University of the Basque Country (K. Altonaga, R. Martín, C. Prieto, B. Gómez) received a visit from Dr. Andrej Wiktor, the world's leading specialist in slugs. On July 2, after two hours of sampling at the top of the Alisas Pass (Cantabria), Wiktor noticed a small slug in the Altonaga's catch and immediately perceived its uniqueness and relevance. The emotion that overwhelmed him spread to us and there was no choice but to resample the site; only the nightfall forced us to return. We no longer returned home, but ended up at the University until late at night, while Wiktor was drawing the first in vivo sketches. As the slug was immature, the Alisas Pass was repeatedly visited by the Team's slug-specialist R. Martín, but he never found it again. Although based on an immature specimen, Wiktor and Martín were preparing the publication when, luckily, the limacologist José Castillejo entrusted Wiktor with a completely unknown slug that his doctorate student Jesús Hermida had found on March 17, 1988 close to the Sanctuary of Covadonga (Picos de Europa, Asturias) in an anthropogenised habitat, far from the Alisas Pass. This, along with a large sample of 32 specimens collected by T. Rodriguez in Covadonga on November 12, enabled them to complete the study and describe both the juvenile and the adult of *Papilloderma altonagai,* and to erect a new genus and a new family (that they termed Papillodermidae) to accommodate it.

Current knowledge

P. altonagai is a fusiform slug up to 25mm long, with a yellowish-brown body covered by regular rows of conical papillae, and an undivided foot. The mantle is located at 1/3 of the way along the body and is annular, exposing the central part of the limacella. The genital apparatus is crossed by the right ommatophore retractor and has a clubbed penis (Wiktor *et al*. 1990).

Papilloderma altonagai was described in its own family (Wiktor *et al*. 1990), but the systematic position of Papillodermatidae is controversial. Initially, it was included in the superfamily Trigonochlamydoidea (Schileyko 2003), whose other family Trigonochlamydidae is distributed

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Figure 1 Adult specimen (paratype) of *Papilloderma altonagai* Wiktor, Martín & Castillejo, 1990 collected around the Sanctuary of Covadonga (Asturias) on November 12, 1988 (Photo by J. Castillejo, with permission) and (below) a juvenile specimen (not collected) in the same location on November 17, 2011 (Photo by A. Pérez-Ferrer, with permission), uploaded to the citizen science website Biodiversidad Virtual [https://www.biodiversidadvirtual.org/insectarium/Papilloderma-altonagai-img297509.html].

throughout the Caucasian region; although the slug *Selenochlamys ysbryda* Rowson & Symondson, 2008 was described from urban environments in Wales (Rowson and Symondson 2008) it would be an introduction originating in Crimea (Turbanov & Balashov 2015). The Trigonochlamydidae were transferred to the superfamily Parmacelloidea, and Papillodermatidae was placed in its own superfamily Papillodermatoidea by Bouchet *et al*. (2005). In the current classification of Gastropoda, Bouchet *et al*. (2017) places it among the "Taxa of Uncertain Position" within the Helicina suborder. There are no sequences for this species in GenBank.

The geographical distribution of *P. altonagai* is limited to the two sites cited in the description, but the unsuccessful searches in the Alisas Pass (mountain meadow on limestone pavement) and the anthropic environment in the Sanctuary of Covadonga with presence of nettle, alders, elms, ash and sycamore (Wiktor *et al*. 1990) suggest that the findings were made outside the species' natural habitat, with a calcareous substrate as the only shared characteristic. The last faunistic record was also provided from Covadonga, through a photo of a juvenile uploaded to a citizen science website (Fig. 1). According to Castillejo and Iglesias (2011), these slugs belong to a hypogean species, using earthworm galleries to bury themselves, and are possibly predators, feeding on terrestrial earthworms. The discovery of new localities, although based on shell remains of dead specimens, would be of great importance to more precisely define the habitat of this elusive species. In this paper, we describe the findings and significance of limacellae of *Papilloderma* in limestone caves from the Cantabrian mountains.

MATERIAL AND METHODS

The first limacellae of *Papilloderma* were unexpectedly found in samples of earthy- sandy ground substrate collected in karst caves while searching for shells of *Zospeum* spp. These samples were processed by drying, and then sequentially sieved (3, 1 and 0.35mm) to remove gravel and fine sand, and subsequently each fraction was immersed in water to collect the flotsam. This process only allows the recovery of intact floating shells; since the limacellae do not have an inner hollow space allowing them to retain an air bubble, they were only detected by chance when examining the non-floating subfractions in search of submerged shells of other species. Once the presence of *Papilloderma* limacellae was noted, a larger amount of substrate (15 kg) was subsequently collected in Cueva de Covallarco by CP to obtain a larger sample of shells. The site 1 (Fig. 2) is located in the middle of a passage, and 5 kg of soil substrate was collected along the passage wall; it is a sediment formed by fine to very fine clayish fractions, with few clasts of endogenous origin (travertines, crystals of spastic calcite and goethite and iron hydroxide nodules). The deeper site 2 is closer to the surface because there is an impenetrable fissure reaching the surface (daylight being visible) which favours the fall of vegetation and other epigean debris as land shells. Some amounts of soil substrate totaling 10 kg were collected in several locations, avoiding the area under the window. The resulting sediment consisted of clayey silts mixed with clasts, both limestone eboulis and endogenous concretions. It was enriched by humic contributions from outside and included bones of small mammals and gastropod shells. The sampled cave passages, belonging to the upper part of the cave, are fossil and the only assumed taphonomic processes are a displacement downwards by gravity and infiltration water and burial by clay deposition. Each sample was disaggregated in water, sieved/washed sequentially (3, 1 and 0.35mm) and each fraction was air-dried; afterwards it was examined under stereomicroscope and shells were removed (fragments were routinely discarded), and identified when possible.

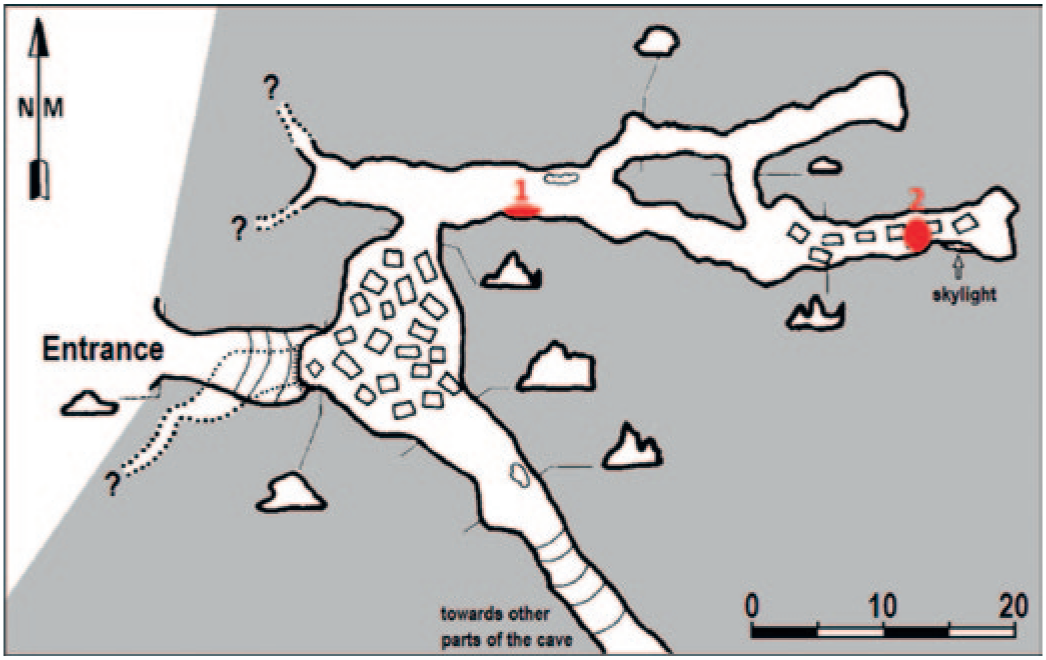

Figure 2 Topographic plan (partial) of the Cueva de Covallarco (Merilla, San Roque de Riomiera, Cantabria). Modified from Zubieta-Hyllenius and Noriega-Suárez (1975). Sampling sites (1, 2) and the location of the skylight are indicated. Scale in meters.

After that, SQS and AA collected another sample of 6kg of cave soil in the deeper site of Cueva de Covallarco. It was processed by SQS in a similar way and also provided shells of *Papilloderma* and many other species.

Shell figures are combined images produced through the Heliconfocus v.6.7.1 software from series of photographs taken with a Nikon DS5M camera on a Nikon SMZ- 1500 stereomicroscope. Shell measurements (precision, 0.001mm) were made using the Nikon DS-L1 analysis image system software of the Nikon DS5M camera. The projected area of the shells (= profile in apertural view) was measured in photographs with the free software @GIMP2.8, where the Histogram option was used for pixel count of selected areas; the measured area is considered a proxy of the real area of the shell in the face of the impossibility of measuring the entire surface. The shells (once they were carefully cleaned of the visible residues of clay and sand) were weighed using a @Sartorius balance (precision, 0.1 µg). The analyses and graphs were performed with @ Excel and the PAST free software (Hammer 2018) and the distribution map using the DMAPW software (Morton 2004).

Repositories, Institutional acronyms or Institutional abbreviations:

ZUPV: Collection of Cave Fauna of the Departamento de Zoología y Biología Celular Animal, Universidad del País Vasco (UPV/ EHU), Leioa, Bizkaia (Spain).

SQS: Private Malacological collection of Sergio Quiñonero Salgado, Hospitalet de Llobregat, Barcelona (Spain)

Results

The first findings came from two caves, San Juan de Socueva and Covallarco (see New records), which provided limacellae of two very different sizes: ten shells of less than 1.6mm and three larger than 3.0mm (Fig. 3). Subsequent sampling

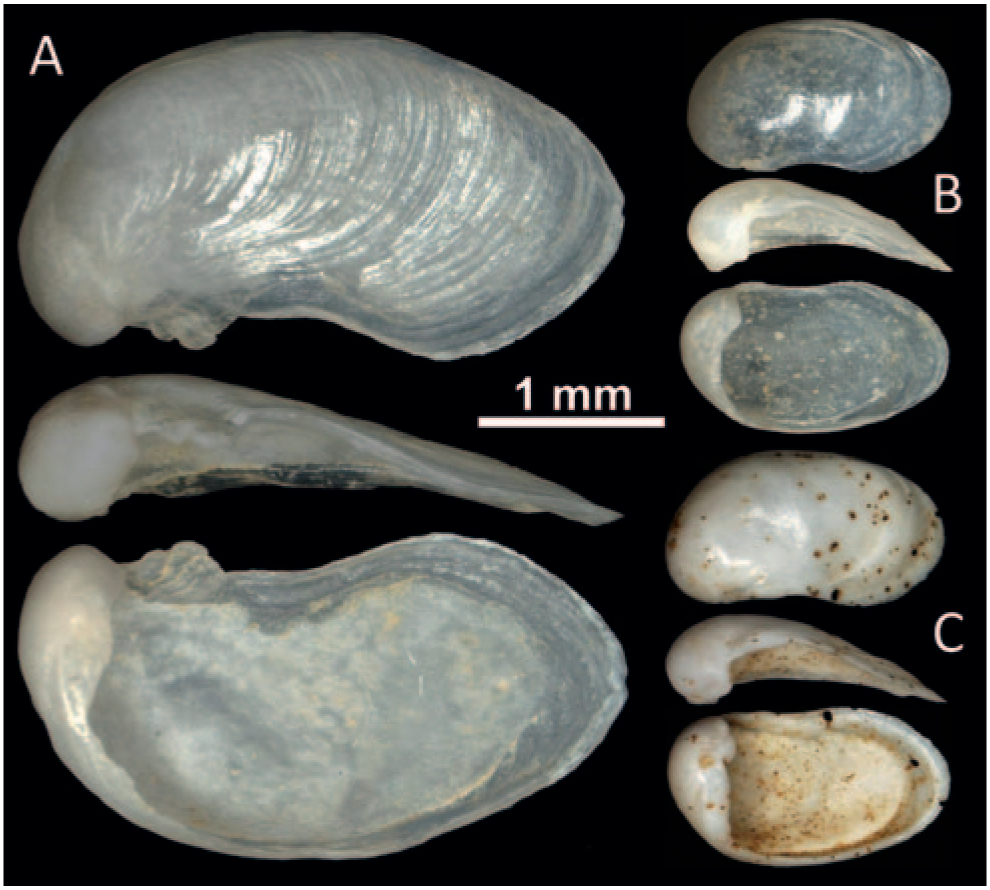

Figure 3 Shells of *Papilloderma* spp. A, *Papilloderma altonagai* Wiktor, Martín & Castillejo, 1990 (large morph), 3.25mm. B–C, small morph (= *Papilloderma* sp.), 1.42 and 1.47mm (shell of an older slug). A–B, Cueva de Covallarco. C, Cueva de San Juan de Socueva.

to enlarge the sample yielded 34 measurable limacellae and confirmed the previous observation, although differences in size between the smaller and larger shells decreased.

New records

[LL: large limacellae; SL: small limacellae; AA, CEP, JRC, SQS: authors]

SPAIN • Cantabria, Arredondo, Socueva, Cueva de San Juan de Socueva; 43.26671ºN, 3.61339ºW, 430m a.s.l.; 12 IV 2017, CEP, SQS, JRC and AA leg (Coll. ZUPV-4727: 6SL) • Cantabria, San Roque de Riomiera, Merilla, Cueva de Covallarco; 43.25654ºN, 3.73412ºW, 402m a.s.l.; 12 IV 2017, SQS and AA leg (Coll. SQS: 3 LL and 4 SL) • same collection data as for preceeding; 9 III 2018, CEP leg (Coll. ZUPV-5121: 7 LL and 5 SL) same collection data as for preceeding; 29 III 2018, SQS and AA (Coll. SQS: 7 LL and 18 SL) • Asturias, Llanes, Porrúa, Cueva El Mazu (La Verde); 43.4017ºN, 4.8213ºW ,140m a.s.l.; 30 V 2019, SQS leg (Coll. SQS: 1 LL).

Shell size

The measured limacellae (n=47) of Papilloderma ranged between 1.22 and 3.51 (mean=1.844), but the normality test (Jarque-Vera, p=0.018) indicates that the sample does not belong to a single population, as does the sample plot (Fig. 4), which shows a strong bimodal distribution. The mixture analysis, a maximum likelihood method for estimating the mean and standard deviation of two or more univariate normal distributions based on a pooled sample (Hammer 2018), shows that there are two distinct populations of slugs based on the greater dimension of the shell (Fig. 4). The t test (p< 0.001) confirms that the small morph and the large morph have different means.

Along with shell length, the projected area and shell weight were also measured. As expected, the projected area for the shells belonging to the so-called small morph (Fig. 6, left) is strongly correlated with the shell length, but the correlation decreases notably when considering the

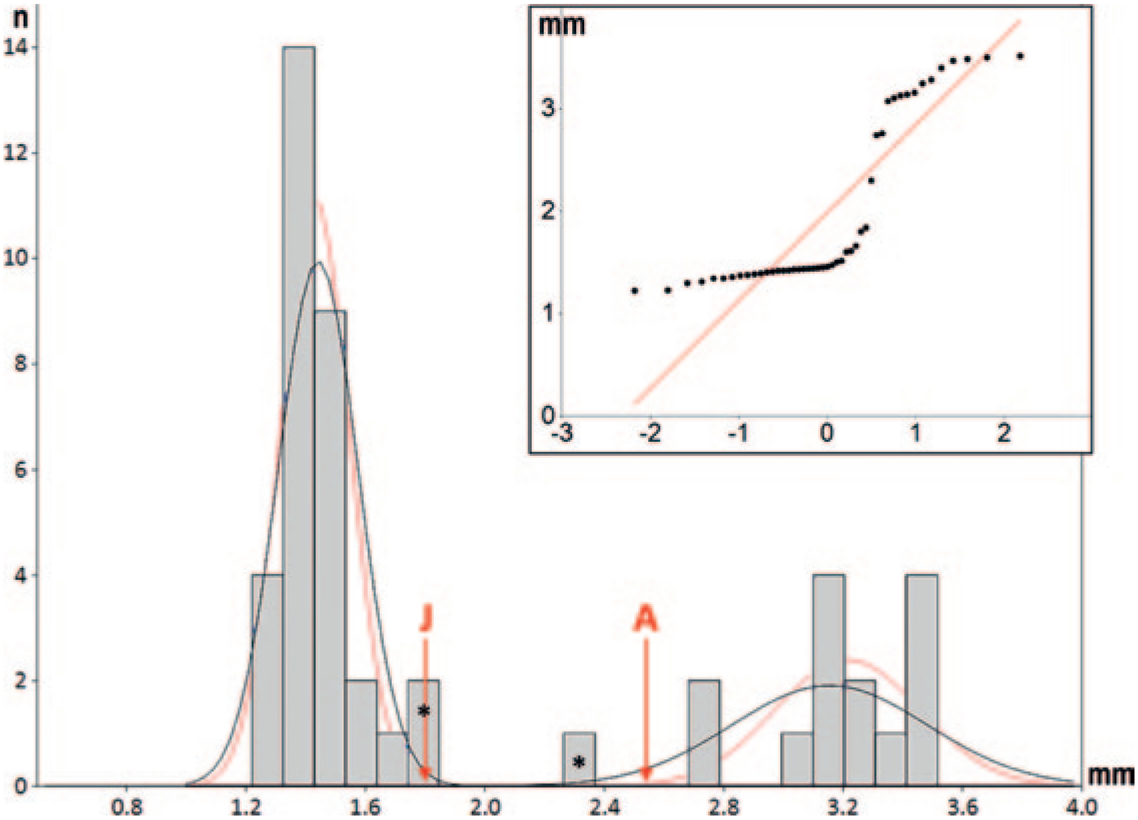

Figure 4 Mixture analysis of *Papilloderma* shells. Size classes (grey bars) and the 'two- population solution' (grey curve; back red curve is for the same data without two supposed juvenile shells of the large morph of 1.84 and 2.30mm). Shell sizes for the juvenile (J) paratype from Alisas Pass and the adult (A) holotype from Covadonga (Wiktor *et al*. 1990) are also added. The normal probability plot (inset) also shows that there are two different size classes.

shell weight, suggesting the concurrence of, at least, another factor of variation. When a proxy of the shell thickness is considered (as estimated by considering the shell weight per its projected area), the correlation is virtually zero; this indicates that there are significantly heavier shells (up to twice) and, hence, thicker than others of similar or larger size. This circumstance has also been observed for the large morph (Fig. 6, right), where a shell of 3.5mm in length three times heavier than the closest shell weight (3760 µg vs. 1380 µg) was noteworthy and excluded from the analysis. The extreme, irregular thickness (Fig. 5) of the nacreous layer, with an invasive peripheral outgrowth, suggest a teratological condition.

Limacellae description

Large morph (Fig. 3A, 5): Dimensions: 2.74–3.51mm (n=14,×= 3.205, sd=0.252). Shell dextrogyre, hyaline (older shells of milky white colour) and dorsoventrally planate with spire formed by about two whorls. The shell aperture is more than 4/5 parts of the total length (shell width), spoon-shaped, with the palatal edge remarkably concave and more arched (in side view) than the basal edge that is convex, giving a kidney-shaped outline to the limacella. The palatal edge has a corrugated excrescency protruding between the spire and the shallow groove arising from the shell nucleus (Fig. 5A). The columellar border curves toward the basal edge and is strongly thickened by the presence of a callus. The outer surface has distinct growth lines; the inner surface showing a pearlescent luster along the peristome and a matt central zone, which can be quite thickened by nacreous layers (Fig. 5B), and delimited by a narrower groove in the palatal and external zones.

Small morph (Fig. 3B–C): Dimensions: 1.22–1.80mm (n=31,×= 1.426, sd=0.117). Shell dextrogyre and hyaline (agged shells of milky white colour) with spire formed by less than two whorls. The shell aperture is more than ¾ parts of the length, spoon-shaped, with the palatal edge barely concave and more arched than the basal edge (in side view) that is convex, giving a kidney-shaped outline to the limacella. The columellar edge is almost perpendicular to the basal edge and is strongly thickened by the presence of a callus. The outer surface is mostly smooth, but with indistinct growth lines on the right side; the inner surface showing a broad band with pearlescent luster along the peristome and the matt central area, which can be quite thickened by nacreous layers (Fig. 1C), and delimited by a narrower groove in the palatal and external zones.

Concurrent fauna

Samples from Cueva de Covallarco provided the taxa indicated in Table 1. The sample from Cueva de San Juan de Socueva also provided *Hydrocena*? sp.n. (under study) (Cycloneritimorpha),

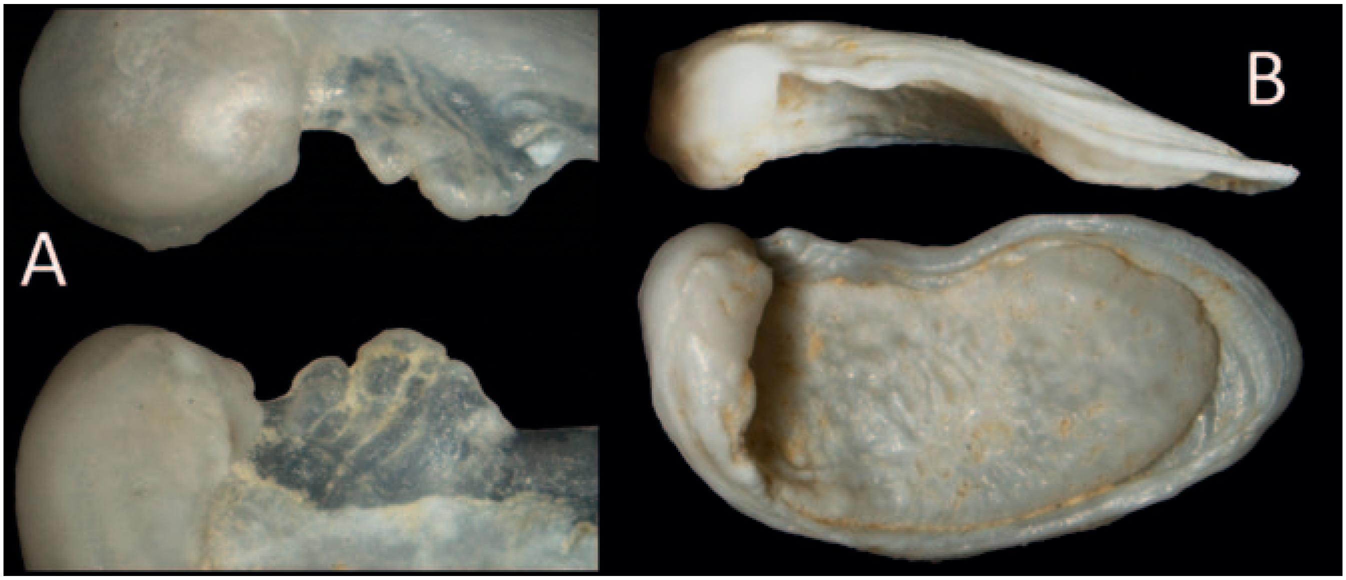

Figure 5 *Papilloderma altonagai* Wiktor, Martín & Castillejo, 1990. A. Upper and aperture views of the excrescence in the upper palatal area. B. A thick shell (L=3.5mm) three times heavier than the next heaviest shell. Note a possibly teratological thickening of the inner nacreous layer.

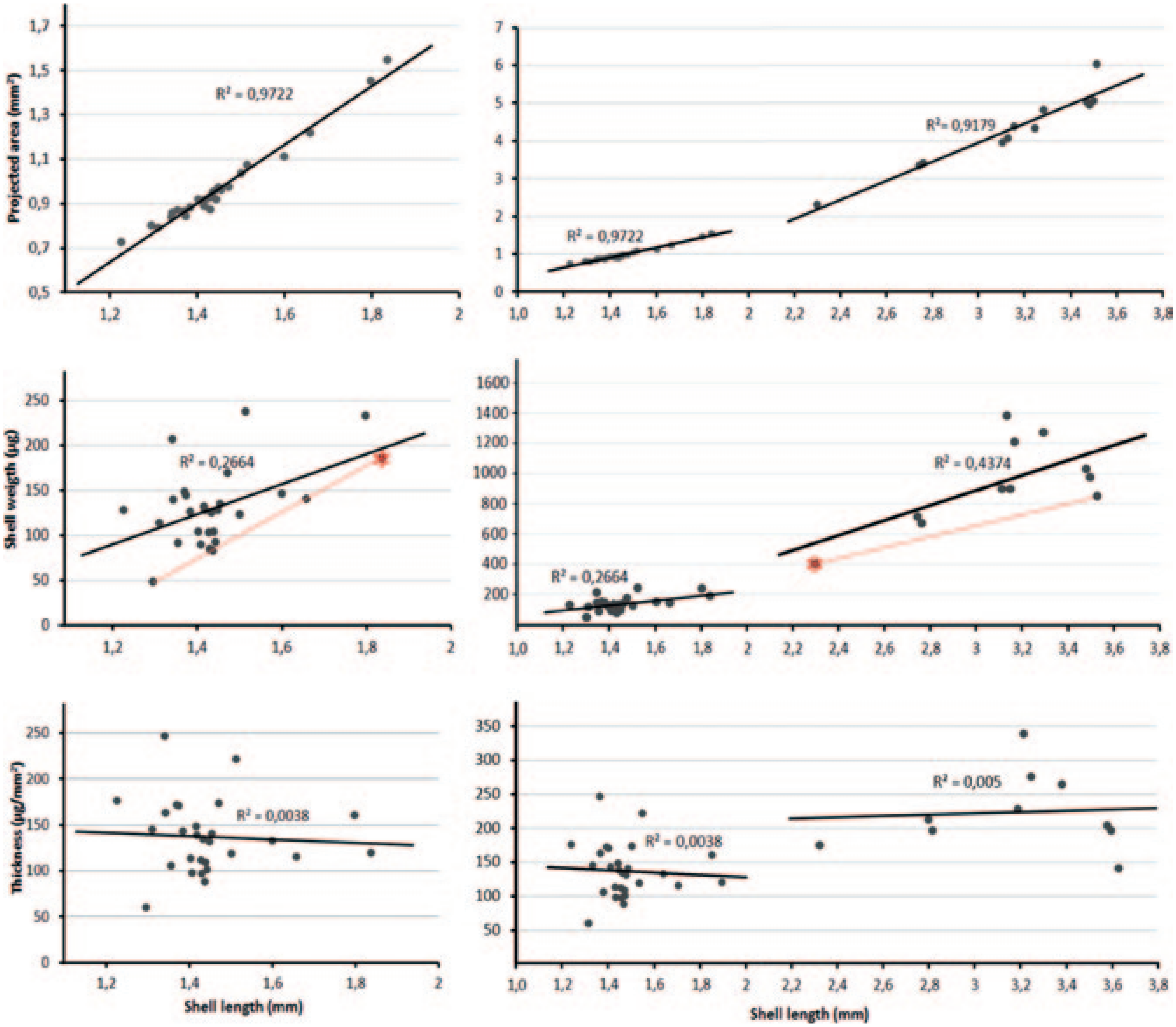

Figure 6 Correlation of shell parameters in *Papilloderma* spp. Shell length vs. Projected area (above), Shell weight (middle) and Shell thickness (below). Left: the small morph (= *Papilloderma* sp.). Right: both, small and large (= *Papilloderma altonagai*) morphs. Note that left plots are the rescaled left part of plots on the right. Asterisks in middle plots denote two possibly juvenile shells of 1.84 and 2.3mm belonging to the *P. altonagai*). The red line in the middle graphs along lighter shells depicts the minimum recorded weight for different shell sizes; the vertical span between the red line and each dot is interpreted as the increased weight of the corresponding shells after the slug maturity time, and indicates the aged condition of the heavier shells.

Alzoniella montana (Rolán 1993) (Littorinimorpha), *Zospeum* spp (Archeopulmonata), all with depigmented shells.

Geographical distribution (Fig. 7)

The new data provided confirms the validity of the easternmost area of *P. altonagai* and slightly extends its distribution to the South, constituting a chorological nucleus around the northern foothills of the Sierra de Valnera Massif (Fig. 7B), which is the highest mountain massif (up to 1717m in the Castro Valnera) of the Eastern Cantabrian Mountains. As mentioned earlier, the western (Covadonga in Picos de Europa) and the eastern (Alisas Pass and new localities) areas are widely separated by a distance of more than 100km; plausibly, both areas are not connected. The small morph described herein has been found only in the eastern region. A last minute new record is the first finding of *Papilloderma*

Table 1 Shelled species (and living snails: s) found in samples from Cueva de Covallarco. See sampling sites in Fig. 2. Ecological characteristics of each species, if not epigean, are indicated as Endogean or Hypogean.

Family	Species	Site 1	Site	2	Ecology
Hydrocenidae	*Hydrocena*? sp. n. (under study)	10	720 +9s	110	Hypogean
Pomatiasidae	*Pomatias elegans* (Müller, 1774)	-	4	-	-
Cochlostomatidae	*Obscurella crassilabra* (Dupuy, 1849)	-	2	-	-
	Obscurella hidalgoi (Crosse, 1864)		4	9	-
	Obscurella oscitans (Gofas, 1989)	-	44	4	-
Aciculidae	*Acicula fusca* (Montagu, 1803)	-	-	2	Endogean
	Platyla callostoma (Clessin, 1911)	-	3	-	Endogean
	Platyla merillaensis Quiñonero-S. et al. 2017	2	6	2	Hypogean
Carychiidae	*Carychium tridentatum* (Risso, 1826)	-	32	-	-
	Zospeum schaufussi von Frauenfeld, 1862	80	-	2	Hypogean
Clausiliidae	*Clausilia bidentata bidentata* (Strøm, 1765)	-	-	4	-
Chondrinidae	*Abida bigerrensis* (Moquin-Tandon, 1856)	-	3	-	-
Ferussaciidae	*Cecilioides acicula* (Müller, 1774)	-	1	-	Endogean
Azecidae	*Azeca goodalli* (Férussac, 1821)	-	1	2	-
	Cryptazeca vasconica (Kobelt, 1894)[1]	5	290 +2s	64	Hypogean
Papillodermatidae	*Papilloderma altonagai* Wiktor et al., 1990	2	5	7	Endogean
	Papilloderma sp. (SMALL form)	3	2	18	Hypogean?
Discidae	*Discus rotundatus* (Müller, 1774)	-	20	4	-
Oxychilidae	*Oxychilus navarricus* (Bourguignat, 1870)	-	25	-	-
Punctidae	*Punctum pygmaeum* (Draparnaud, 1801)	-	3	-	-
Pristilomatidae	*Vitrea contracta* (Westerlund, 1871)	-	2	3	-
	Vitrea subrimata (Reinhardt, 1871)	-	-	8	-
Euconulidae	*Euconulus trochiformis* (Montagu, 1803)	-	16	-	-
Trissexodontidae	*Oestophorella buvinieri* (Michaud, 1841)	-	12	3	-
Elonidae	*Elona quimperiana* (Férussac, 1821)	-	65	3	-

[1] A synonym of *Cryptazeca subcylindrica* Folin and Bérillon, 1877 according to Holyoak and Holyoak (2012).

altonagai from Cueva El Mazu (Llanes, Asturias) out of previously known areas (Fig. 7A); it is based also in sieved soil from the entrance of the cave.

Discussion

The determination of limacellae as belonging to Papilloderma is straightforward since its morphology is in accordance with the drawings by Wiktor *et al*. (1990), although some details, such as the excrescence of the palatal edge and the groove along the aperture edge, were neither described nor figured. Moreover, no slug from the Iberian Peninsula has shells similar to the figured here (Castillejo and Iglesias 2016); *Testacella* spp also have shells with an evident spire, but the contour of the shell is ovate and the apex is sharp and pointed (Taylor 1902). The only relevant discrepancy for *Papilloderma* shells concerns their size. Wiktor *et al*. (1990) figured an adult shell (holotype) slightly larger than 2.5mm, which is smaller than all measured shells of the large morph. This difference could be because they come from isolated populations since they are separated by a wide non-limestone area, but it might simply reflect the intraspecific variability occurring within each of the populations. Since only a single measurement was known from Covadonga, we tried to measure the shells of three paratypes (Malacological Collection of the Universidad del País Vasco), but it was unsuccessful due to their excessive fragility (perhaps caused by the long-term corrosive action of ethanol) and were accidentally broken during the removal attempt. Despite the difference in size, we cannot doubt that the large morph belongs to *P. altonagai*.

The case of the smaller shells is distinct. Wiktor *et al*. (1990) also figured a shell of 1.8mm from the Alisas Pass, corresponding to a juvenile specimen of 17mm live length (14mm fixed), but we have from the same area a large number of shells of 1.22–1.8mm (small morph) which should correspond to juvenile specimens. If the ratio of live

Figure 7 Geographical distribution of *Papilloderma* spp. in the northwestern part of the Iberian Peninsula (rectangles correspond to enlarged areas, below): circle, known record of *P. altonagai*; cross, new record. A, the oriental third of the Asturian region (new record from northern foothills of Sierra de Cuera). B, detail of the oriental half of the Cantabrian region (new records for both large and small morphs). Colour contour lines every 300m. Scale line, 10km.

body length/shell length (≈9.5, based on data cited by Wiktor *et al*. 1990) is constant along the slug growth, the smaller shells described should belong to slugs between 11.5 and 15mm in length. It is possible that the smallest, and hence more fragile, shells could have been under recorded by being broken during the sieving process or be overlooked during the sorting procedure, but that does not seem arguable for shells larger than 1.8mm and smaller than 2.7mm. Therefore, we consider that the gap in shell size between the large morph and the small morph is real and not an artifact. Why are shells of intermediate size absent? Strictly, they are not absent because the immature slugs of the large morph must grow through those intermediate sizes before reaching the adult size, and we can expect that premature death in juveniles will leave lighter (thinner) shells of intermediate size, as did the juvenile paratype from Alisas Pass. In this sense, two shells of 1.84 and 2.30mm are noticeably lighter and both are considered belonging to juveniles.

A priori, we would expect the small morph to be conspecific with the large morph, thus being shells of prematurely dead juvenile slugs. Certainly, small shells present an ample smooth dorsal surface (>2/3 of total length), which suggest its formation during embryonic development, and a narrow fringe with indistinct growth lines on the right side, which suggest a high mortality rate before maturity, that is reached by the large morph and its much greater striated part. Usually, invertebrates have a Type III survivorship curve, with a high initial mortality rate decreasing during growth, and reaching maturity with only a small fraction of the progeny (Demetrius 1978; Wikipedia 2018); however, accurate information for terrestrial molluscs is scarce. Therefore, the most abundant shells should be smaller (from new-born slugs), decreasing in number as they increase in size, although this pattern can be altered by sampling bias (as indicated above, by overlooking or by breaking). Thus, we should expect to find shells of various sizes until maturity size (high dispersion), but the low dispersion of the sample (coefficient of variation 9.3%) would indicate the existence of a critical stage of high juvenile mortality having 11–15mm slug size, with very low mortality once that stage has been surpassed.

Heller (1990) revised the longevity in molluscs and stated that most slugs are short- lived, experimentally confirmed for five *Arion* species (Hutchinson *et al*. 2017), but the predatory (worm-eating) *Testacella* lives up to 6 years, with no information for other carnivorous slugs. Taylor (1902) indicated that *Testacella* spp reach maturity in 18 months, with a 3–4 times longer mature life and laying small clutches of large eggs (up to 6×4mm for *Testacella haliotidea*). Although its diet is unknown, Barker and Efford (2004) placed *Papilloderma* among the strict carnivorous molluscs, assuming they are predators of earthworms, due to the elongated buccal mass and large unicuspid radular teeth. Thus, as in other predatory molluscs, we could expect a long lifespan with iteroparity of small clutches of large eggs, which is related to K strategy of life in stable environments, e.g. hypogean environment (Heller 2001). A suggestion of a long lifespan is the thickness of the shell; as in other long-lived snails, with continuous deposition of nacreous layers until death, thicker shells indicate a longer life than thinner shells, at least for the same species and population. The shell shown in Fig. 3A was selected for its freshness and is a relatively thinner shell, but most shells of the large morph are thick- shelled, which is easily perceivable by the depth of the groove surrounding the central part of the shell (Fig. 5), suggesting a long lifespan of nacreous deposition. Thus, we can state that a shell is thin during the growth period and only gets thickened during adult life; then, if thin subadult shells are more fragile, then they should be less represented in soil samples.

In opposition to the conspecific hypothesis, the position advocated here is that both large and small morphs belong to different evolutionary entities. The supporting evidence is limited only to the thickness of the small shells, but a heavier (thickened) shell indicates a long period for deposition of nacreous layers, which is achieved only during its maturity. If it is admitted that the small form constitutes a separate evolutionary entity, we can make some insights about its habitat and biology.

Regarding the habitat, *P. altonagai* (represented by large shells) seems to belong to the endogean fauna, although the three times it was captured were on the surface. Due to its relatively large size, the space required for pairing and mating could not be found in the soil crevices, but in cool and moist surface environments (Castillejo, pers.comm.), linking it to epigean habitat. Buried dead shells would remain in situ or be dragged down and eventually fall into the galleries of the cave, being affected by taphonomic processes such as size/shape selection, mixing of different faunal assemblages and so on. On the contrary, we suggest that *Papilloderma* sp., i.e. the species represented by small shells, belongs to the hypogean realm and lives in the epikarst.

The epikarst was initially defined as perched aquifers in fissured limestone above the vadose zone (Bakalowicz 2012), with communities dominated by aquatic crustaceans, mainly copepods (Culver and Pipan 2009). There is consensus that the epikarst is not only formed by saturated narrow fissures, but also by "small cavities and crevices, some of which are water-filled, some of which are filled by organic material, humus and insoluble material, and some of which are air-filled" (Culver *et al*. 2012: p.288). The crevice net must have spaces ranging from a few μm wide to mesocavernous size, up to 20cm wide, allowing the existence of an immense surface to hold dissolution clay nourished by the organic matter that percolates from the surface and providing a niche for air-breathing invertebrates. Epikarst communities are poorly known due to difficulties in direct sampling methods, being explored by collecting percolating water from trickles or filtering dripping pools (Culver *et al*. 2012; Pipan 2017; Pipan *et al*. 2008, 2018), thus biasing the richness towards the aquatic fauna, especially crustaceans of reduced size. Nevertheless, there are few records of terrestrial fauna from the epikarst, but the snail *Zospeum* can be considered an epikarst specialist (Culver *et al.* 2012).

There has been a long-standing debate about the border between the epigean and hypogean domains (Gilgado 2016), but most authors concede that the MSS and the epikarst belong to the latter, together with the cave habitat. Land snails are most easily detected as empty dead shells because their persistence after death facilitates transport and accumulation in favourable sites such as cave entrances and vertical holes, thus taphonomic processes favouring the mixture of faunal assemblages. The collected shells (Table 1) belong to species from different communities, and its number is related to this: *Elona quimperiana* and *Oxychilus* spp. are common epigean species from upper passages (troglophiles) represented by many shells (including young shells), while *Obscurella* spp. and *Abida bigerrensis* are rupicolous species that accidentally fall from the walls of the upper entrance, together with other edaphic species such as *Oestophorella buvinieri, Discus rotundatus, Euconulus trochiformis, Punctum pygmaeum* or *Carychium tridentatum*. Endogean species such as *Platyla callostoma*, which feed on buried snail eggs, or *Cecilioides acicula* are poorly represented, but we gathered up many shells in all growing stages of *Hydrocena*? sp., *Platyla merillaensis, Cryptazeca vasconica* or *Zospeum schaufussi.* All these species show transparent, depigmented shells, being nearly confined to the hypogean environment, although scattered shells of *C. vasconica* are obtained by sieving soil from crevices in limestone rocks, but a sample from the damp bottom of a 5m depth doline provided 32 snails and shells (Holyoak and Holyoak 2012). The finding of 220 adult and 70 juvenile shells of *C. vasconica* in Covallarco (more than all previous records combined) strongly support its belonging to the hypogean realm. *P. merillaensis*, which Quiñonero-Salgado *et al*. (2017) recently described from Cueva de Covallarco, is the only Iberian species of the family Aciculidae with a completely transparent shell, which supports its status of hypogean species. Additionally, its short shell with fewer whorls than all the other Iberian congeneric species together with the absence of the characteristic cervical callus could suggest a pedomorphic origin. On the other hand, *Hydrocena*? sp. (an undescribed species with a completely colourless shell) and *Zospeum schaufussi* have been found in large numbers, but show different distributions; while *Hydrocena*? sp. seems to be an abundant species in the entry passages, and *Zospeum* spp. are deeper troglobionts (although shells can also sometimes be found in upper passages).

The calcareous massifs located in the northern foothills of Castro Valnera Massif are constituted by compact limestones of Urgonian rudists (Aptian-Lower Albian) that surround an extensive zone of limestone banks and alternating terrigenous formations that extend to the coast (Rat 1958). They form a karstic region of great magnitude, with cave systems of large extension and complexity (AER 2014; Degouve-de-Nuncques 2014; Martínez-Cedrún *et al.* 2014; Simmonot 2014; Sosa-Bravo *et al*. 2014). This region harbors highly significant relict elements, such as the isopod *Cantabroniscus primitivus* Vandel, 1965, diplopods as *Cantabrodesmus lorioli* Mauriès, 1971 and *Cantabrosoma rogeri* Mauriès, 1971, the chilopod *Lithobius drescoi* Demange, 1958 or the beetle *Speocharinus llosesi* (Español & Escolà, 1977) (Bellés 1987). On the other hand, this karstic massif would be linked biogeographically with the impressive Picos de Europa, as shown by the troglobiont diplurans of the primitive genus *Oncinocampa*, with two species from Picos de Europa and *Oncinocampa asonensis* Sendra and Condé, 1988 described from cavities of the headwater region of the Asón River (Sendra and Condé 1988).

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