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A new cave-dwelling endemic *Ischyropsalis* C.L. Koch, 1839 (Opiliones: Dyspnoi: Ischyropsalididae) from the karstic region of Cantabria (Spain)

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Abstract

Ischyropsalis cantabrica **sp. n.** is described from coastal limestone caves in the municipal districts of Alfoz de Lloredo, Ruiloba, Udías and Cabezón de la Sal, in northeastern Cantabria, northern Spain. Its systematic position is discussed as are the differences to morphologically similar and geographically proximal species. *Ischyropsalis cantabrica* **sp. n.** is a strictly troglobitic species, adapted to deep cave environment. Discrimination of males is possible by genital morphological characters and especially by the unique shape of the cheliceral apophyses.

Key words: *Ischyropsalis cantabrica*, new species, taxonomy, SEM ultra-structure, cave-dwelling fauna, Basque-Cantabrian Mountains, North Spain

Introduction

Opiliones, commonly known as harvestmen, comprise an order of arachnids with 45 families, approximately 1500 genera, and more than 6400 described species (summarized in Kury 2011). One of its major clades, the Dyspnoi, include the monogeneric family Ischyropsalididae Simon, 1879 (*sensu* Shear 1986). Its sole genus *Ischyropsalis* C.L. Koch, 1839 is restricted to Europe, with species concentrated in the major mountain systems of the Alps and the northern Iberian Peninsula (Gruber 2007). The genus is unmistakable within the European fauna for animals showing enlarged chelicerae of more than body-size in length. *Ischyropsalis* has therefore traditionally received considerable attention in terms of species descriptions and taxonomy (e.g. Roewer 1950, Dresco 1968a, 1968b, 1969, 1972a, 1972b; Martens 1969, 1978). *Ischyropsalis* currently includes 11 accepted species from the Iberian Peninsula (>50 % of the total 21 species). Of these, 4 species have adapted a strictly troglobitic life-style in cave habitats. These troglobiont species show a very narrow distribution within the karstic area of central-northern Spain, specifically the Basque-Cantabrian Mountains.

The first troglobitic harvestman endemic reported from this area was *Ischyropsalis dispar* Simon, 1872 described from Albia Cave, Burgos, in northern Spain (discovered by Charles Piochard de La Brûlerie). Since then, 5 additional troglobitic taxa of the genus *Ischyropsalis* have been described or redefined: *I. magdalenae* Simon, 1881, *I. navarrensis* Roewer, 1950, *I. gigantea* Dresco, 1968, *I. espagnoli* Dresco, 1968 and *I. noltei* Dresco, 1972 (Simon 1881; Roewer 1950; Dresco 1968a, 1968b, 1972a; see also Dresco 1969, 1972b; Martens 1969; Prieto 1990; Luque 1991).

Prieto (1990) studied a series of *Ischyropsalis* from the Basque Country and Navarra key areas in northern Spain, and found that Martens (1969), based on morphological similarities, erroneously synonymized *I. navarrensis* with *I. magdalenae*. Prieto (1990) recognized both species as valid, but synonymized *I. espagnoli* Dresco, 1968 with *I. navarrensis*, a troglobitic endemic of the Sierra de Aralar Massif, in Navarra. Also, Prieto (1990) synonymized *I. noltei* with *I. dispar*, both species being recognized as valid by Dresco (1972a, 1972b). According to the revision conducted by Prieto (1990), the final number of strictly troglobitic *Ischyropsalis* from the Basque-Cantabrian Mountains was four. A further cave-dwelling species (*I. galani* nomen nudum) restricted to the

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Sierra de Arno-Izarraitz Massif, in Olatz (Mutriku), Guipúzcoa, the Basque Country, northern Spain: e.g. Kobetako Leizea Cave, will be added to this list. It was presented at the 8th Conference of the Iberian Group of Arachnology, Valencia, Spain 25–28 October 2007 and is in the process of description (Prieto 2007, see also Galán 2008).

In Cantabria, strictly troglobitic *Ischyropsalis* were represented by two species (Luque 1991): *I. gigantea* and *I.* sp. aff. *dispar* (the material originally collected by Luque from Rejuyo and Lastrilla Caves, incorrectly identified as *I. magdalenae*, is here reassigned to the *I. dispar*-group). These species are restricted to two discrete regions (see below): the southeast coastal region of Cantabria (inhabited by *I.* sp. aff. *dispar*) and the mountainous area of the upper Asón and Miera (inhabited by *I. gigantea*).

In this work, we describe a novel species of a troglobitic harvestman (*Ischyropsalis cantabrica* **sp. n.**) to be added to the list of previously reported species from the Basque-Cantabrian Mountains. A series of *Ischyropsalis* were captured by Menéndez (1973) in Cueva del Calero or Rogeria Cave (Figs 1–2) during caving exploration in the western part of Cantabria (at that time Santander province). These were erroneously identified as *I. espagnoli*. During a second visit of this cave, and others in the area between the towns of Alfoz de Lloredo, Ruiloba, Udías and Cabezón de la Sal, in 1994–1995 and 2001–2004, further sixteen specimens of the same species were captured (Labrada & Luque 2004). This new material enabled a detailed morphological study, revealing a suspected new cave species, which is described below (Fig. 3). It is the sixth known troglobitic species of the genus *Ischyropsalis* from the Basque-Cantabrian Mountains and is to date the first to be found isolated in western Cantabrian Spain (Figs 4–5). The study area is situated within a latitudinal belt (ca 42º to 46º N in Europe) of high terrestrial cave fauna biodiversity ('mid-latitude biodiversity ridge'), resulting from historical (mostly climatic) conditions (Culver et al. 2006).

All mentioned troglobitic *Ischyropsalis* are related species in the *kollari* group (*sensu* Martens 1969) and are almost completely restricted to the deep cave zone which provides a stable, humid environment. The second major group inhabiting the Basque-Cantabrian Mountains includes *I. nodifera* Simon, 1879, *I. petiginosa* Simon, 1913 and *I. hispanica* Roewer, 1953 of the *dentipalpis* group (*sensu* Martens 1969). In contrast, these species are predominantly epigeic and have no troglomorphic adaptations. Their occurrence in the caves is limited to the entrance zone (<30 m) where the environment is comparable to their epigeic habitat.

Material and methods

Adult specimens were collected manually (or by direct sampling) from cave walls and preserved in ethanol 70% and absolute. The morphological study was carried out with a Carl Zeiss IV stereoscopic microscope and micrographs obtained with a Philips XL-20 SEM. The specimens were mounted on an aluminium stub, metallized with gold (16 nm of deposit) in an Argon atmosphere with bio-rad SC-515 by the "Sputter coating" method and with acceleration velocities of 15 kv. Initially, some of the specimens were dehydrated in an ethanol series reaching 100 %, in order to be dried by CO_2 critical point in a pressure chamber. Line drawings were made using the same equipment (prepared with a Carl Zeiss IV stereoscopic microscope) with a light chamber included in the stative. The final versions of drawings were prepared using Adobe Photoshop software, version 7.0. All measurements are in millimetres with a precision in the measurement of 0.01 mm and were taken by means of a micrometer disc and by using the same optical devices. We give the mean value followed by minimum and maximum range in brackets. For measurements and terminology, in general we followed Martens (1969).

We used the following acronyms for the institutions or particular collections where material for this study is deposited:

AXLS	Collection of Dr A.L. Schönhofer, Institute of Zoology, University of Mainz, Germany.
CGL	Carlos G. Luque private collection, Santander, Spain.
MNCN	Museo Nacional de Ciencias Naturales de Madrid, Spain; J. Sánchez, Dr M. Villena (died in 2008).
NHMW	Naturhistorisches Museum Wien, Vienna, Austria; Mag. C. Hörweg, Dr J. Gruber (retired since 2002).

All data was collected with a GPS device and is given in UTM format (European Time Zone 30 North Datum 1950), followed by altitude above sea level. Data were checked with the GIS of the Ministry of Agriculture (SIGPAC) of the Government of Spain. Data on the geology was provided by the Continuous Geological Mapping Information System (SIGECO), according to the Geological Survey of Spain (IGME).

Taxonomy

Ischyropsalididae Simon, 1879

***Ischyropsalis* C.L. Koch, 1839**
Type species: *Ischyropsalis kollari* C.L. Koch, 1839 (by designation of Thorell 1876, see also Martens 1969).

***Ischyropsalis cantabrica* sp. n.**
(Figs 1–24)

FIGURES 1–3. Type locality and habitus of *Ischyropsalis cantabrica* **sp. n.** 1: Entrance to 'Rogeria Cave' in Spain, Prov. Cantabria. 2: 'Rogeria Cave' Digital Orthophoto with UTM grid, Zone 30, ED50; 3: Life female specimen from 'Rogeria Cave' (CGL 369).

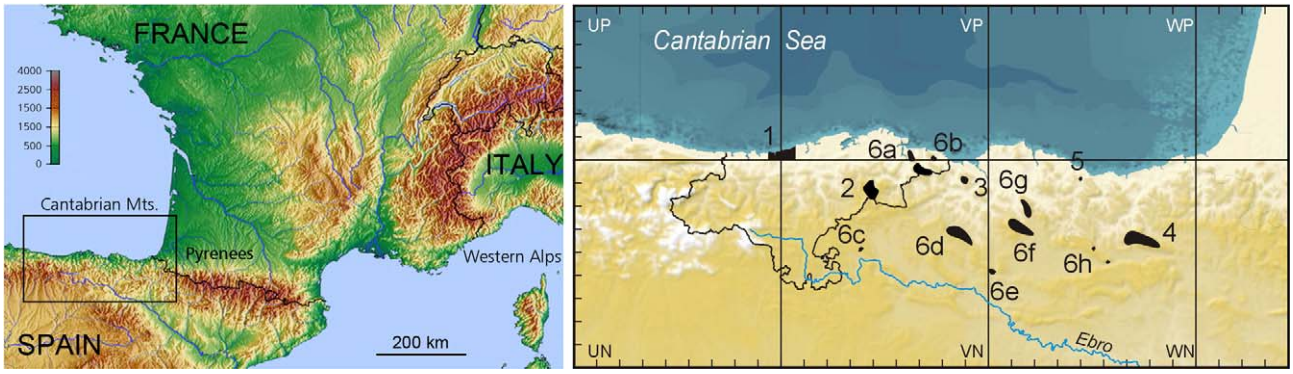


FIGURE 4. Geographical map of central to northern Spain and surroundings of the sampling area (left). *Ischyropsalis* collection sites, with new sampling in original localities (right). Numbers refer to the following regions and species (Provinces are indicated in parentheses): **1**, Western Coastal Cantabria inhabited by *I. cantabrica* **sp. n.**; **2**, Upper Asón and Miera Mountains (Cantabria) inhabited by *I. gigantea* Dresco, 1968; **3**, Triano-Galdames Mountains (Vizcaya) inhabited by *I. magdalenae* Simon, 1881; **4**, Sierra de Aralar Massif (Guipúzcoa-Navarra) inhabited by *I. navarrensis* Roewer, 1950; **5**, Sierra de Arno–Izarraitz Massif (Guipúzcoa) inhabited by *I. galani* nomen nudum; **6**, Eastern part of the Basque-Cantabrian Mountains (inhabited by the complex of *I. dispar* Simon, 1872), including the localities of **6a**, Laredo–Limpias–Rasines–Guriezo Mountains (Cantabria), **6b**, Castro Urdiales (Cantabria), **6c**, Soncillo (Burgos), **6d**, Sierra Salvada Massif (Burgos–Álava), **6e**, Sierra de Arkamo Massif (Álava), **6f**–**g**, Gorbea Massif (Vizcaya), and **6h**, Sierra de Aizkorri Massif (Guipúzcoa). For cave names, coordinates and altitudes see Appendix 1.

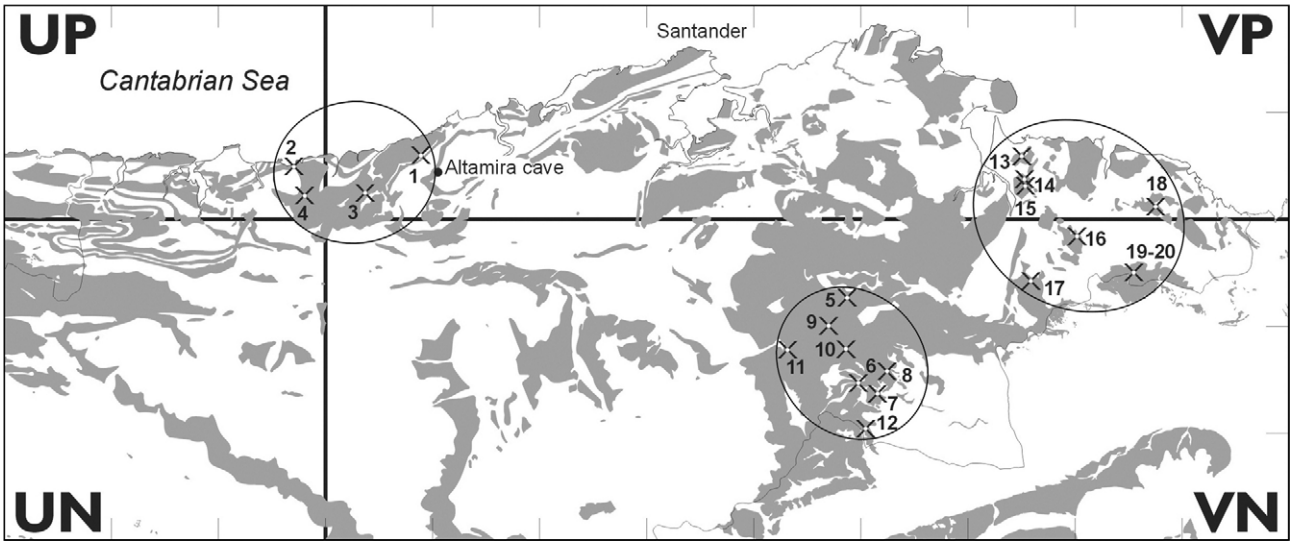
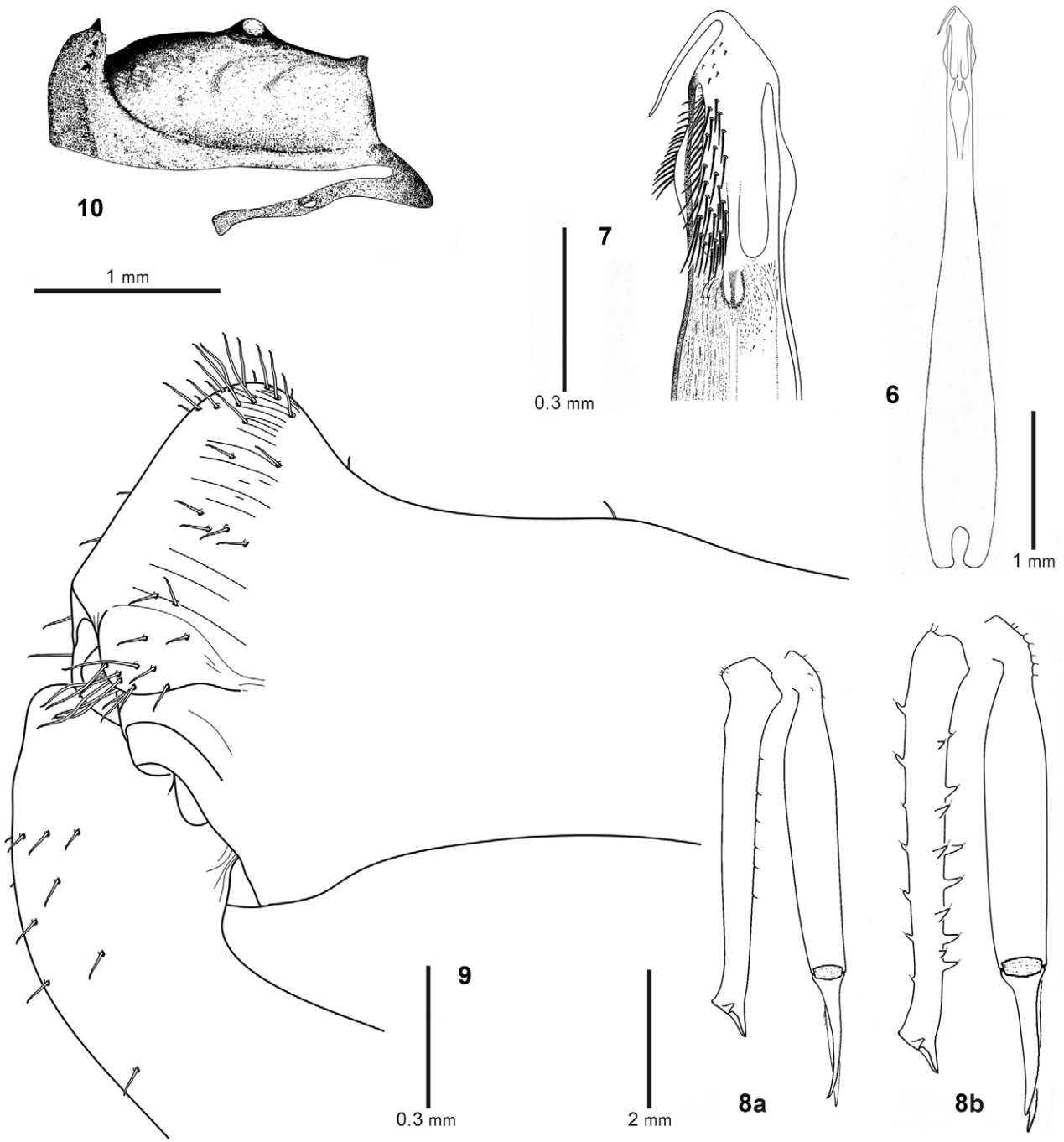


FIGURE 5. Map of the central region of the Cantabrian Mountain (northern Spain) to show the outcrops of the rock systems (in gray) which contain limestone and geographical situation of the study area with the distribution of the troglobitic species according to Luque (1991) and sampling of new localities (all species are allopatric): *Ischyropsalis cantabrica* sp. n.: Locus typicus 'Rogeria Cave' (1), Portillo Cave (2), Cerviz Cave (3), Cáscaras Cave (4); *Ischyropsalis gigantea* (see Appendix 2 for explanation of numbers 5–12): Cayuela or Cañuela Cave (5), Currutuerta or Posadía Cave (6), Becerral Cave (7), Mortero Pit (8), Calleja Lavalle Pit (9), Los Moros del Río Munio Cave (10), Recuistro Cave (11), and Canal de la Torca nº 3 Pit, The Peña del Trillo Cave karst system (12); and *Ischyropsalis* sp. aff. *dispar*: La Baja Cave (13), Hoyo Molino Cave (14), Perelada Cave (15), Rejuyo or 'S.E.I.I.-8' Cave (16), Tornillos or RN-30 Cave (17), La Lastrilla Cave (18), La Pasada Caves (19–20). Source: Geologic maps of Spain 1:50,000-scale corresponding to the Province of Cantabria (IGME).

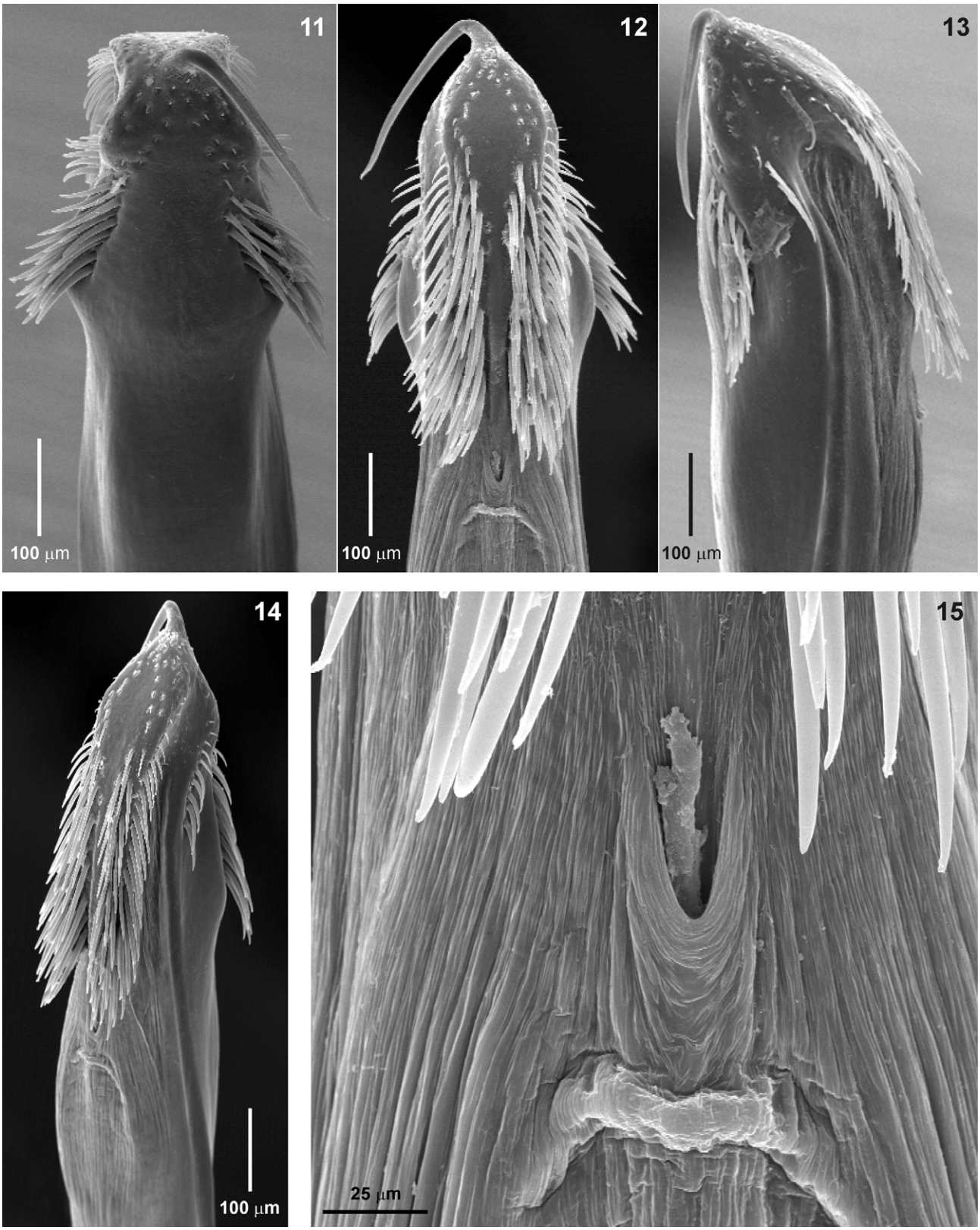
Type material: Holotype ♂ (MNCN 20.02/12828) and **Allotype** ♀ (MNCN 20.02/12829): **SPAIN, Cantabria:** Alfoz de Lloredo, Oreña: Rogeria Cave (30TVP0867005271, 90 m), 2-IV-1994, leg. C.G. Luque. **Paratypes: SPAIN, Cantabria:** Alfoz de Lloredo: 5 ♂♂, 4 ♀♀, same data as the holotype (1 ♂, 1 ♀ MNCN; 1 ♂, 1 ♀ NHMW, 1 ♂, 1 ♀ AXLS, the rest CGL); Ruiloba, Casasola: 1 ♂, 1 ♀, Portillo Cave (30TVP9639204775, 20 m), 25-III-1995, leg. C.G. Luque & E. Muñoz (CGL); Cabezón de la Sal, Bustablado: 1 ♂ mounted on SEM stubs (MNCN 20.02/12857), Cerviz Cave (30TVP0286800238, 365 m), 1-IV-1995, leg. C.G. Luque & J. Ruiz; Alfoz de Lloredo, Oreña: 2 ♂♂, Calero Cave, 12-VIII-2003, leg. L. Labrada & C.G. Luque (CGL).

Additional material studied: SPAIN, Cantabria: Udías, Canales: 1 ♀ (MNCN 20.02/12863), Cáscaras Cave (30TVP9894201878, 130 m), 2-IX-1915, leg. C. Bolívar (see Bolívar 1916, p. 319).

Diagnosis: A species of the *kollari* group (*sensu* Martens 1969) with long and slender chelicerae (spines completely absent in males); cheliceral apophysis high, not projected forwards, with rounded conical shape and the piliferous apex, with a series of deep parallel grooves, medial and characterized by an additional small piliferous and pocket-forming apophysis; dorsal region of the glans penis with a dense mass of very long bristles at its end; glans short and conical shaped at its apex; upper part of glans rounded-quadrangular shaped in cross-section; sclerite of glans long and narrow, almost parallel-sided, basal end tapering, median keel developed, bristle cover dense, widely separated into two lateral areas; body depigmented but scutum parvum uniformly dark colored (dorsal abdominal sclerites fused).



FIGURES 6–10. *Ischyropsalis cantabrica* **sp. n.**, male holotype from Rogeria Cave (MNCN 20.02/12828). Cephalothorax, lateral view (10). Male cheliceral apophysis on distal basal segment, medial view (8a, 9), female chelicerae (8b). Total view of ventral penis (6); distal part of penis with glans and stylus, ventral view (7).



FIGURES 11–15. *Ischyropsalis cantabrica* **sp. n.**, male paratype from Cerviz Cave (MNCN 20.02/12857). Distal part of penis with glans and stylus: dorsal view (11), ventral view (12), lateral view (13), dorsolateral view (14), detail of the funnel-like sclerite (15).

Description:

Measurements were taken for the holotype, allotype and paratypes (9 ♂♂ and 6 ♀♀). Body length (with distended abdomen): holotype 5.01, ♂♂ paratypes 5.01–5.45, allotype 5.58, ♀♀ paratypes 5.56–5.81; length of basal cheliceral segment (in parentheses, with length/width of distal cheliceral segment): holotype 5.20 (6.50/0.80),

♂♂ paratypes 5.20–5.54 (6.50–6.88/0.80), allotype 5.53 (7.25/0.84), ♀♀ paratypes 5.53–5.85 (7.25–7.68/0.84). Female show a wider range in body length due to different stages of gravidity but their chelicerae are less variable in size than in male. Total length of leg II of male holotype (paratypes in parentheses) and female allotype (paratypes in parentheses): 42.49 (42.49–44.82), 42.57 (42.57–43.78). Length of the II segments (in parentheses as before): femur: 8.82 (8.82–8.98), 9.32 (9.32–9.66); patella: 1.36 (1.36–1.41), 1.49 (1.49–1.56); tibia: 8.38 (8.38–8.94), 8.41 (8.41–8.78); metatarsus: 13.52 (13.52–13.89), 13.40 (13.40–13.81); tarsus: 10.41 (10.41–10.82), 9.95 (9.95–10.21). The measurements of the male (holotype) and female (in parentheses) femurs from the first to the fourth pair of legs are 6.45 (6.84), 8.82 (9.32), 5.34 (5.56), 7.08 (7.35).

Genital morphology (Figs 6–7, 11–15). **Penis**: Symmetrical, with robust truncus and the base long and split (Fig. 6); the truncus is of medium length (L: 4.0). The coloration is dark, from the truncus to the base, the ventral side is depigmented; the glans in contrast is blackish in colour. The glans at its apex is short conical shaped, with a long stylus (Figs 7, 13). On the dorsal side (Fig 11), the glans has a dense mass of very long bristles at its ends (the bristles become shorter nearer the apex of the glans). In the upper part of glans, the outline of the cross section is rounded-quadrangular shaped (Fig 11) and does not narrow gradually to acquire a triangular shape in lateral view. In contrast, the ventral side displays a sclerite of glans long and narrow, almost parallel-sided, basal end tapering, ventral median keel developed, bristle cover dense, widely separated into two lateral areas (Fig 12), and a large depigmented mouth indicating the attached muscular tendon (Fig 15). The glans is clearly inflated in lateral view, appearing swollen in mid-section. This spaces the ventro-lateral bristle areas wide apart from each other. The mid-area has a thin longitudinal row of short bristles (Figs 13–14). **Ovipositor**: bilobulate, with the ventral apex covered with few hairs; the seminal receptacle has four short tubes. In this respect not differentiated from other *Ischyropsalis* species (Martens 1969; Dresco 1968a, p. 313, fig. 19; Dresco 1968b, p. 966, fig. 20; Dresco 1972b, p. 356, fig. 25; see also Gruber 2007, p. 147, fig. 4.15i).

Chelicerae (Figs 8–9, 16–17): Sexually dimorph. In general, long and slender, black or dark brown. In males basal segment with a longitudinal row of small and flat spines with bristles ventrally and with 4 or 5 piliferous tubercles dorsally (Figs 8a, 9). Basal segment narrow at the base, widens distally to a pronounced triangular apophysis (lateral view; Figs 8a, 9, 16–17). The apophysis does not project proximal but dorsal, and has a rounded conical shape with the piliferous apex, with a piliferous pocket-forming apophysis and a series of deep parallel grooves on the inner side (Figs 9, 17). The distal segment is completely smooth, only few short hairs present at the base (Figs 8, 16–17). They are generally bristle-like and are set into a basal socket (Fig 34). The chelicerae of females are larger, with basal segment more robust and armed with long spines of different size over its whole length (six shorter spines on dorsal surface, ventro-medially with six, and ventro-laterally with five spines; Fig 8b). The distal segment is covered with small rounded piliferous tubercles at the dorsal knee, and also with some short hairs towards the base of the pincer.

Prosoma**:** Cephalothorax flat (Fig 10), black or dark brown, moderately ascending from border of second thoracic tergite, and ornamented with a transversal row of bristles with six denticles of different sizes; eye mound weakly developed, eyes widely separated, with small lenses in comparison to *I. gigantea* (Fig 27).

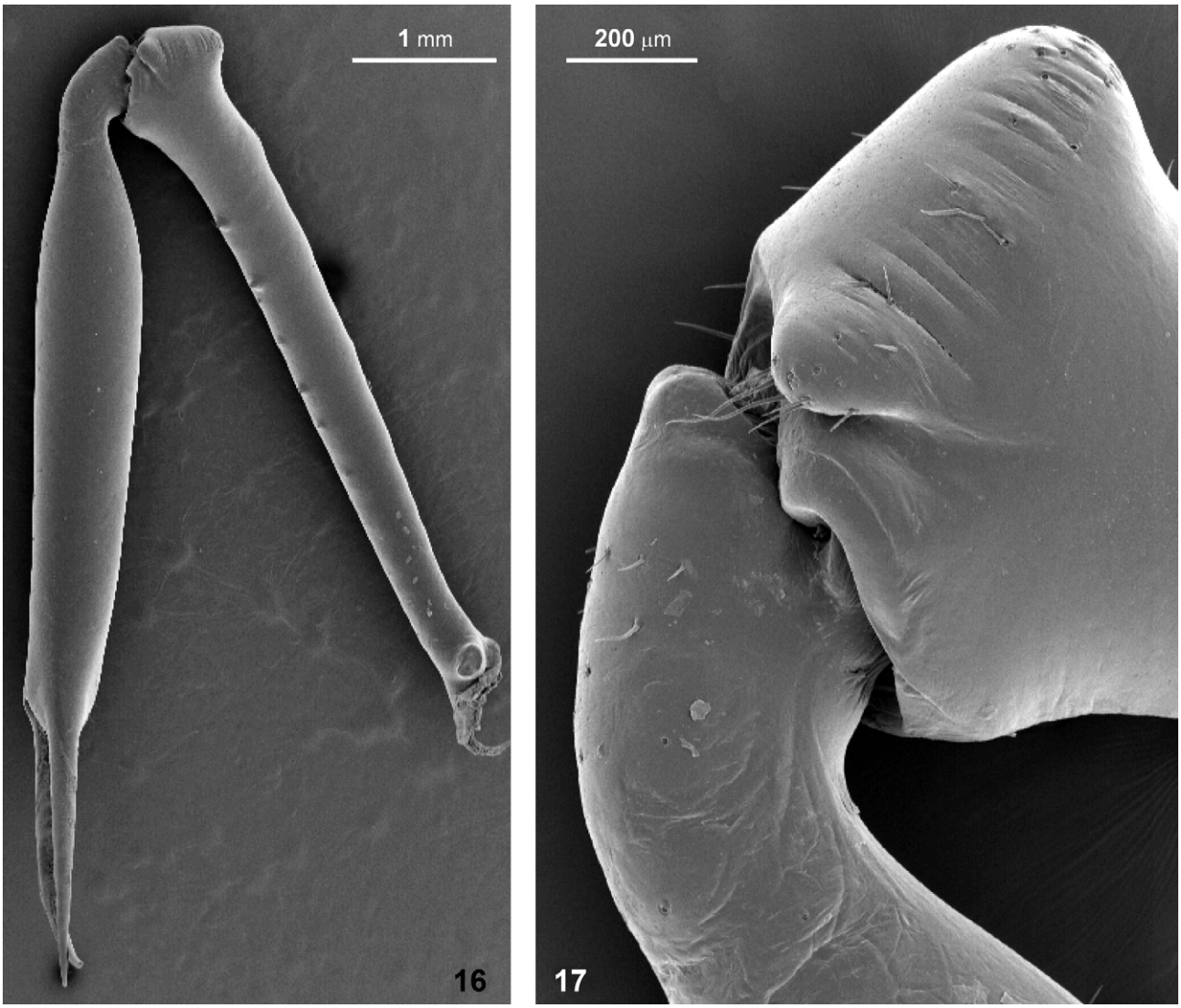
Opisthosoma**:** Males and females with scutum parvum, the last three tergites always free. Sclerotised area finely grained, surrounded by slight grooves, each with a transversal line of bristles (Fig 3).

Legs**:** Slender, of medium length, all segments rounded, light brown, metatarsus and tarsus of lighter colour, base of femora whitish to yellowish; femora without sculpture elements (spines or tubercles), only with microtrichia cover and setae; surface of basal segments (trochanter and coxa) with several types of sculpture elements (e.g. granules, tubercles and cones), with long macrotrichia, which arise from a basal socket (Figs 18–24).

Variability: There seems to be no extraordinary variation despite the general differences in *Ischyropsalis* species, e.g. in case of females spination is slightly more pronounced in larger specimens (see Martens 1969, pp. 160–165). The structure of the glans penis is relatively constant. This is also the case for the other species of the Iberian *kollari* group (*sensu* Martens 1969), except for the heterogeneous *I. dispar* group as shown in Figs 38–41 and 50–57 (see discussion).

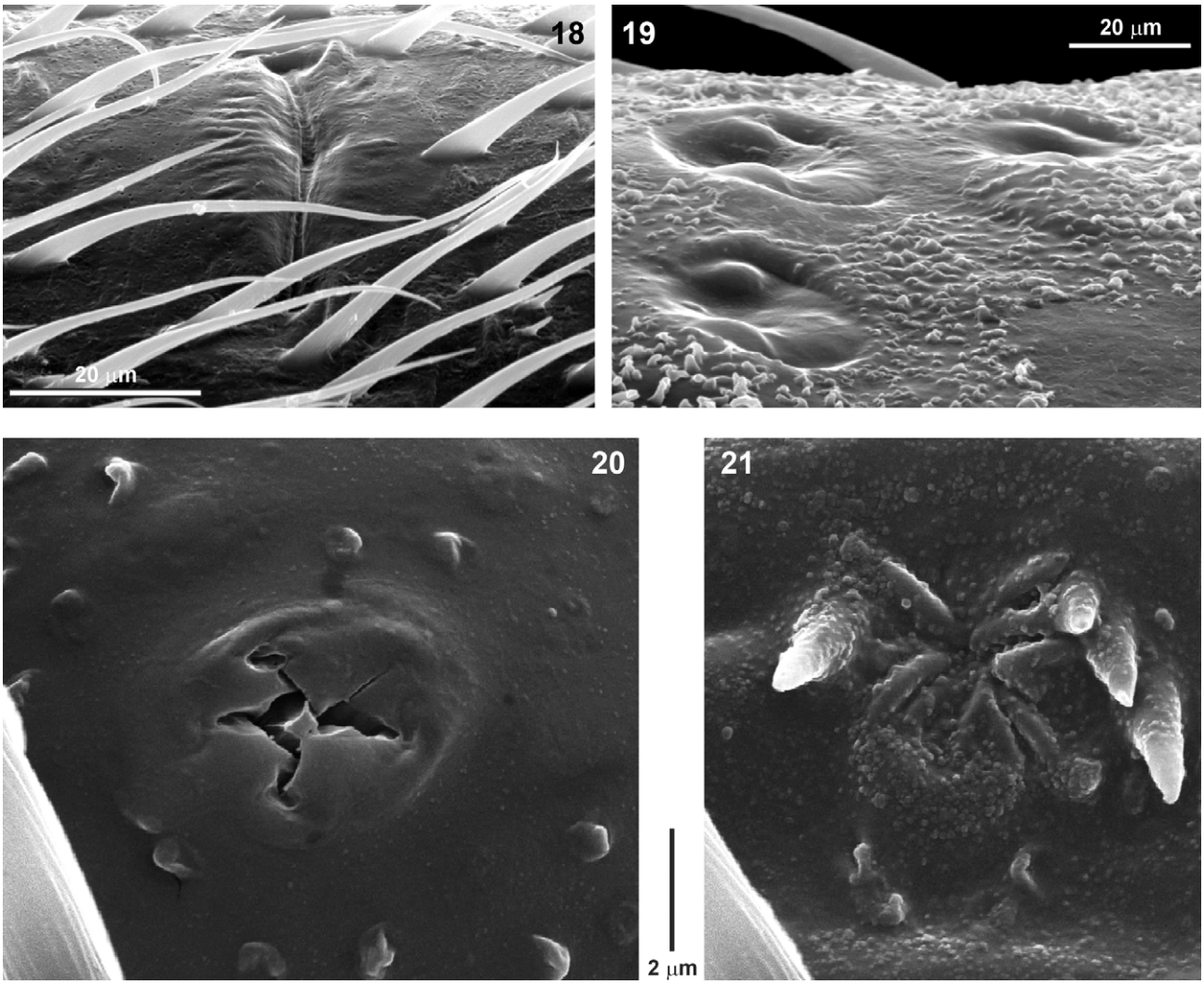
Etymology: The species is named for the Cantabria Region, for which it is endemic.

Distribution (Figs 4–5): Endemic to the northwestern Cantabrian coastal region in Spain, and restricted to a narrow band of karst systems along the coast within the municipal districts of Alfoz de Lloredo, Ruiloba, Udías and Cabezón de la Sal. Epigean species, like *I. nodifera* and *I. petiginosa*, occur in all caves visited along the Cantabria coast (see, e.g., Luque 1991), while restricted to the shallower zone (<30 m) and not interacting with *I. cantabrica* **sp. n.**



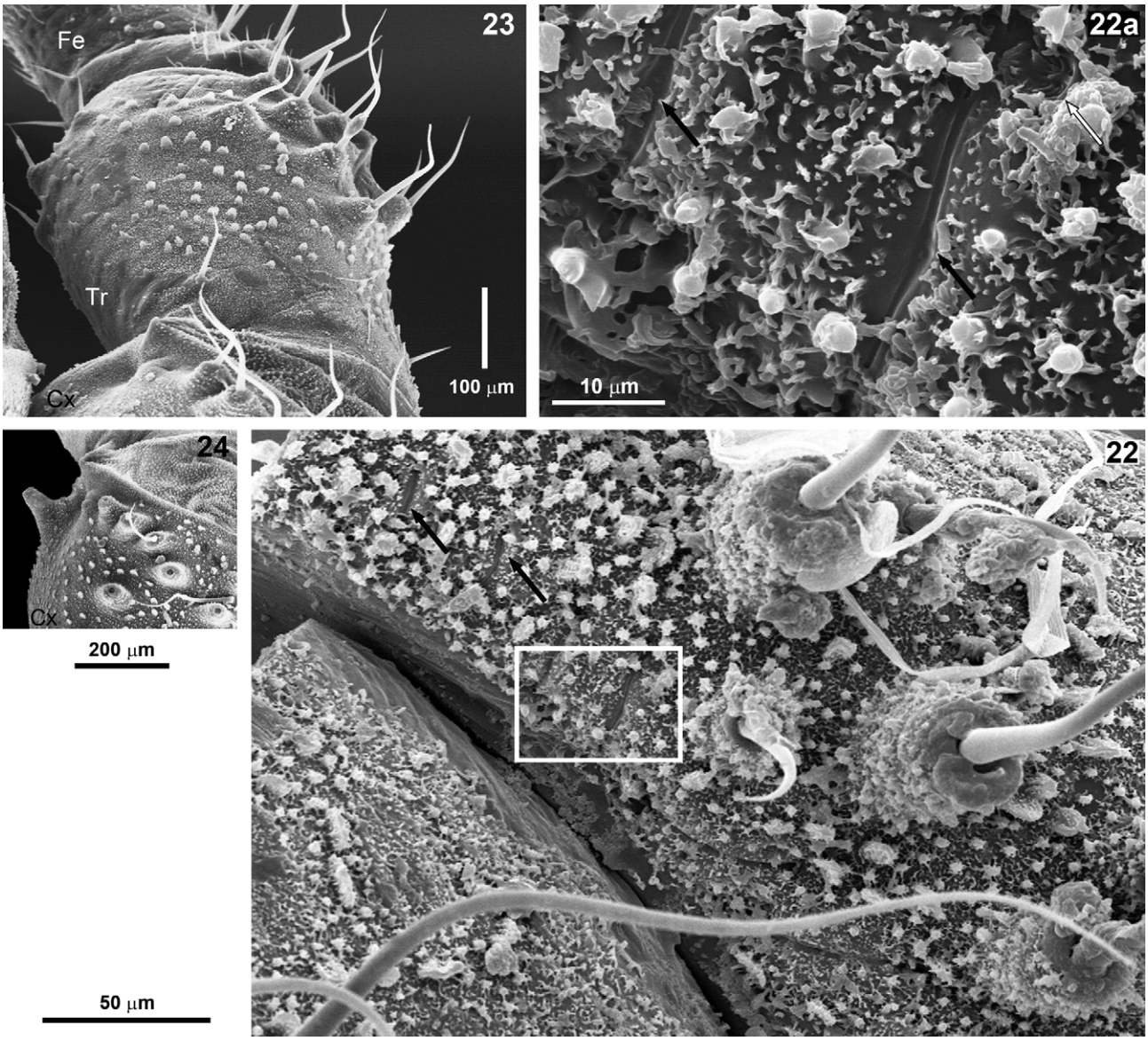
FIGURES 16–17. *Ischyropsalis cantabrica* **sp. n.**, male paratype from Cerviz Cave (MNCN 20.02/12857). Male cheliceral apophysis on distal basal segment, medial view.

Ecology: The caves inhabited by *I. cantabrica* **sp. n.** developed in the Lower Cretaceous (urgonian-type facies) limestones (Aptian age). All specimens were collected in the lightless zones of caves (especially in "deep cave" sites), about 300 m from the entrance of Rogeria Cave (Fig. 1), and about 150 m from the entrances of both Portillo and Cerviz Caves. The specimens were usually found close to water, on cave walls with abundant speleothems or mud-cover, and between 0.5 to 2 m above water level. In the Calero Cave *I. cantabrica* **sp. n.** was observed to prey on the small aquatic gastropod *Ancylus* sp. aff. *fluviatilis* (in spring of late to mid-1970s; Menéndez 1973). Although they are mainly active predators, in some cases they do not disdain carrion. Sixteen other invertebrates were recorded from the deep cave zone of all the caves inhabited by *I. cantabrica* **sp. n.** (Menéndez 1973; Labrada & Luque 2004): *Trichoniscoides cavernicola* (class Crustacea, order Isopoda); *Lithobius validus* and *L. tricuspis* (both class Chilopoda, order Lithobiomorpha); *Polydesmus coriaceus*, *Trachysphaera rousseti* and *Blaniulus dollfusi* (all three class Diplopoda, orders Polydesmida, Glomerida and Iulida); *Litocampa espanoli* (class Insecta, order Diplura); *Pseudosinella superoculata* and *Arrhopalites* sp. aff. *elegans* (both class Insecta, order Collembola); *Neobisium (Neobisium)* sp. aff. *cavernarum* (class Arachnida, order Pseudoscorpionida); *Nemastoma (s. lat.) sexmucronatum* (class Arachnida, order Opiliones); *Troglohyphantes cantabricus* and *Nesticus luquei* (both class Arachnida, order Araneae); *Quaestus (Quaestus) arcanus* and *Laemostenus (Antisphodrus) pelaeus* (both class Insect, order Coleoptera).



FIGURES 18–21. *Ischyropsalis cantabrica* **sp. n.**, male paratype from Cerviz Cave (MNCN 20.02/12857). Detail of the femoral plate with cuticular structures on legs II, showing the typical microtrichia and isolated slit sense organ (18), a group of deep-circular pits on the cuticle (19), the 'holes' of unknown function and identity (20) and an unidentified deep funnel-shaped depression surrounded by four spines (21).

Conservation: Although *I. cantabrica* **sp. n.** seems frequent in suitable habitats, which are numerous throughout its area, it is an extremely narrow endemic species and therefore requires particular conservational attention. So far, the species is not listed as 'vulnerable' under the Threatened Species Act of 2008 (enacted under Decree No. 120/2008, and regionally known as 'Catalogue of Threatened Species from Cantabria') or the Nature Conservation Act of 2006 (under the Cantabria Regional Government legislation; Labrada et al. 2010). These legislations cover the protection of a wide range of species (e.g. cave-dwelling bats and invertebrates such as cave-dwelling beetles *Quaestus arcanus*) and habitats (e.g., in the case of Rogeria Cave). This cave is further acknowledged as 'important bat underground habitat' (Menéndez 1973; Labrada & Luque 2004, unpublished results). Access to the cave is currently restricted, and occasionally prohibited, to protect threatened cave-dwelling bats —e.g. *Rhinolophus euryale*, *Miniopterus schreibersii* and *Myotis myotis*— particularly during their breeding season (from June to August-September). For this reason, Rogeria Cave is included in the list of Areas or Sites of Community Importance for the Atlantic biogeographical region as SCI ES-1300017 (Commission Decision 2010/43/EU of 22 December 2009 adopting, pursuant to Council Directive 92/43/EEC).



FIGURES 22–24. *Ischyropsalis cantabrica* **sp. n.**, male paratype from Cerviz Cave (MNCN 20.02/12857). Detail of cuticular structures on the coxal plate of the legs II (22a), showing the slit sense organ (black arrows), an unidentified deep funnel-shaped depression surrounded by four spines (white arrow), several long hairs (macrotrichia), which arise from a basal socket (22), and other types of sculptural elements (Figs 23–24): e.g. granules, tubercles and cones with long macrotrichia on the apex, which arise from a basal socket.

Discussion

As proposed by Martens (1969, 1978) and Gruber (2007), we found species delineating characters as male genital morphology (Figs 6–7, 11–15) and the structure of the male cheliceral apophyses and glandular secretion areas (Figs 9, 16–17) to clearly differentiate *I. cantabrica* **sp. n.** from other *Ischyropsalis*. Definite differences compared to all other species and forms mentioned in this work comprise the bristles on the apex of the penial glans. For example, in comparison with *I. magdalenae*, *I. navarrensis* and the complex of *I. dispar* (Figs 25, 26), the dorsal bristle areas of the penial glandes of *I. cantabrica* **sp. n.** and *I. gigantea* (both species of the *kollari* group; see Figs 6–7, 30–31) have a dense mass of very long bristles at their ends (Figs 11, 35). On the other hand, the cone-shaped tips of the penes of *I. cantabrica* **sp. n.** (Figs 12–13) and *I. gigantea* (Figs 36–37) are much shorter in comparison to other species: *I. magdalenae* (Figs 43–45), *I. navarrensis* (Figs 48–49) and the complex of *I. dispar* (see, e.g., Figs 40–41, 56–57). In the upper part of the glandes of these two species, the outline of the cross section is quadrangular-shaped (Figs 11, 35) and does not narrow gradually to acquire a triangular shape in lateral view, like in *I. magdalenae, I. navarrensis* and the complex of *I. dispar* (Figs 39, 43, 47, 51, 55).

Discrimination of *I. cantabrica* **sp. n.** from other *Ischyropsalis* males is also possible by the particular shape of the cheliceral apophyses, specifically by a small pocket-forming apophysis disto-medial on basal cheliceral segment (Figs 9, 17). There are also differences between the form and extent of the hair field. For example, in comparison with *I. gigantea* (Figs 28a, 29, 32–33), *I. magdalenae* (Fig 42) and the complex of *I. dispar* (Figs 38, 50, 54), the hair fields of *I. cantabrica* **sp. n.** are concentrated on the disto-dorsal tip of the cheliceral apophyses and the pocket-forming medial apophyses. The series of deep parallel grooves are seen in *I. navarrensis* (Figs 17, 46) as well, though much fainter.

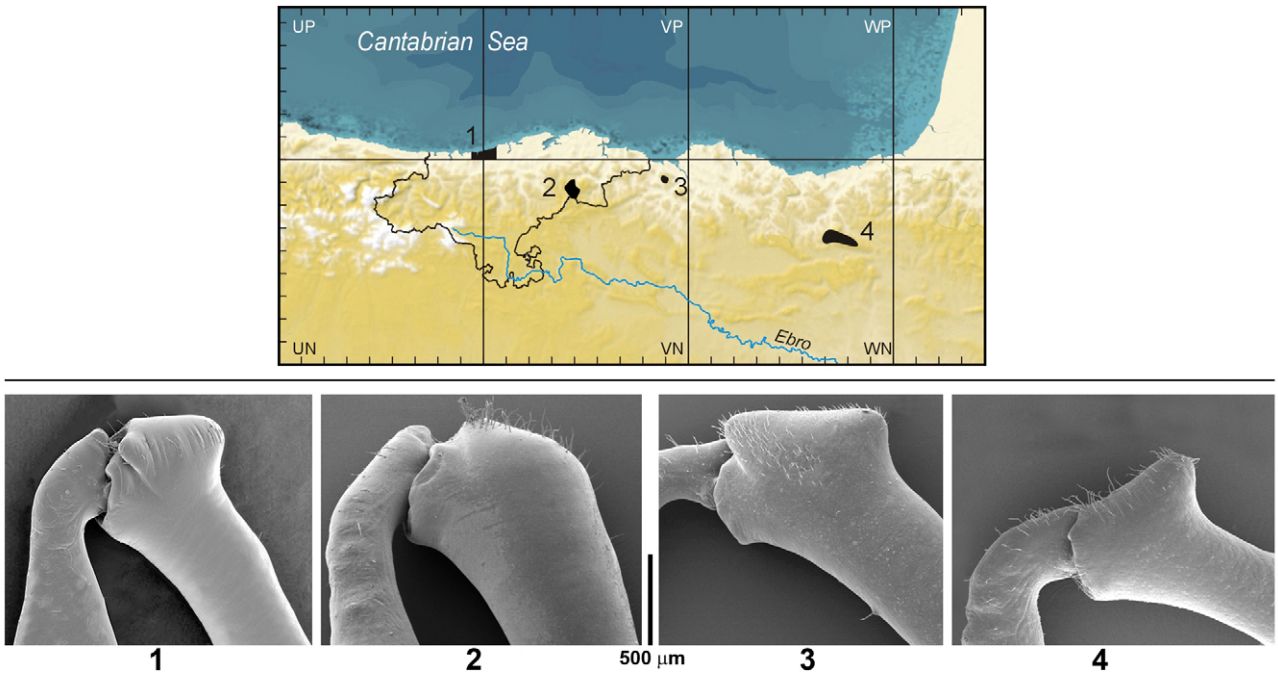


FIGURE 25. Distribution of described strictly troglobitic *Ischyropsalis* other than *I. dispar*, showing male cheliceral apophysis on distal basal segment (medial view): *Ischyropsalis cantabrica* **sp. n.** (1), *I. gigantea* (2), *I. magdalenae* (3) and *I. navarrensis* (4).

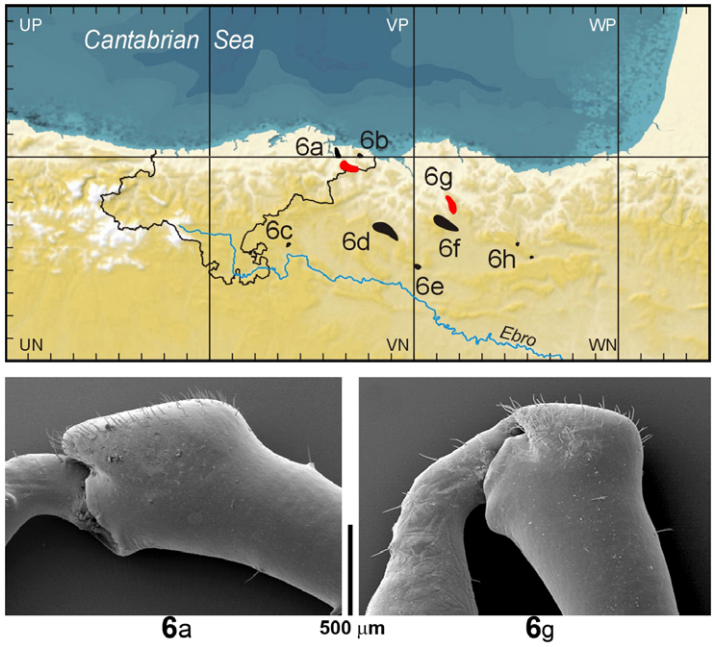
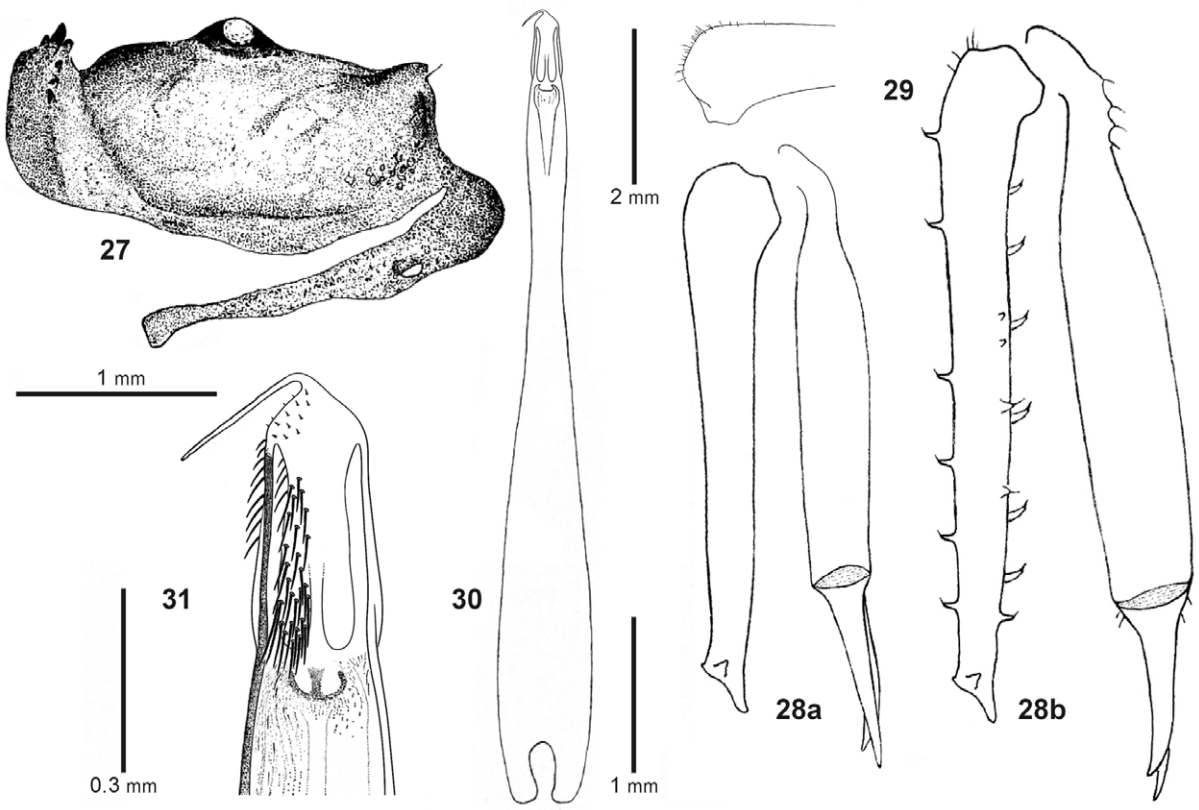


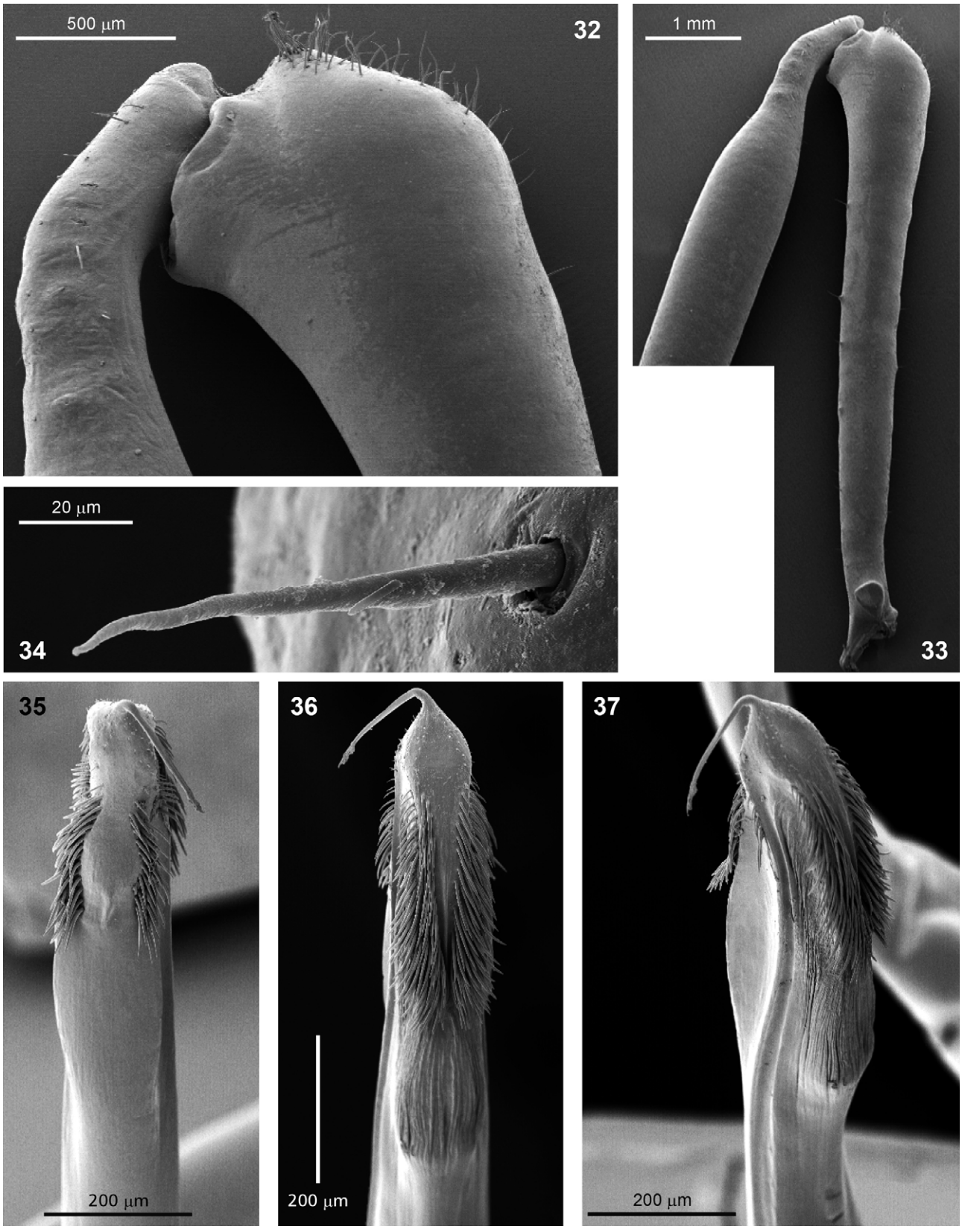
FIGURE 26. Distribution of the *Ischyropsalis dispar* complex, showing male cheliceral apophysis on distal basal segment (medial view): *Ischyropsalis* sp. aff. *dispar* (area 6a) and *Ischyropsalis* cf. *noltei* (or *Ischyropsalis* sp. aff. *dispar*) (area 6g).



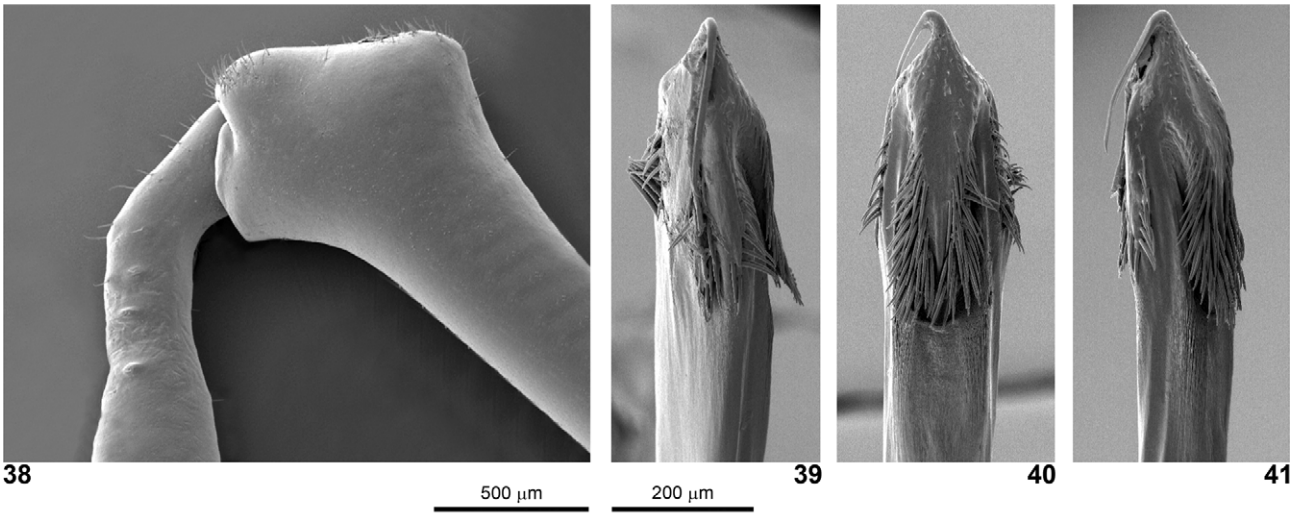
FIGURES 27–31. *Ischyropsalis gigantea*, male from Los Moros del Río Munio Cave (Upper Asón Mountain). Cephalothorax, lateral view (27). Male cheliceral apophysis on distal basal segment, medial view (Figs 28a–29, female 28b). Total penis, ventral view (30); distal part of penis with glans and stylus, ventral view (31).

Most *Ischyropsalis* species show special mating behaviour with males offering secretion from nuptual glands on the chelicerae (in the distal part of the proximal male cheliceral article; Martens & Schawaller 1977). The glans is associated with apophyses and bristle fields that are prone to sexual selection and, together with the form of male genitalia, enable species delineation in this genus. These hairs are similar to the sensilla chaetica, which are thick-walled bristles with a socket-like, circular structure surrounding the base – a characteristic feature of these sensorial structures. SEM micrographs suggest that the bristles shown in Fig 34 are sensilla chaetica, although histological studies are required to confirm this assumption. SEM micrographs also reveal that the distal tip of these bristles (see Fig 34) have whorled striae on the external surface and lack a discernable pore at the tip.

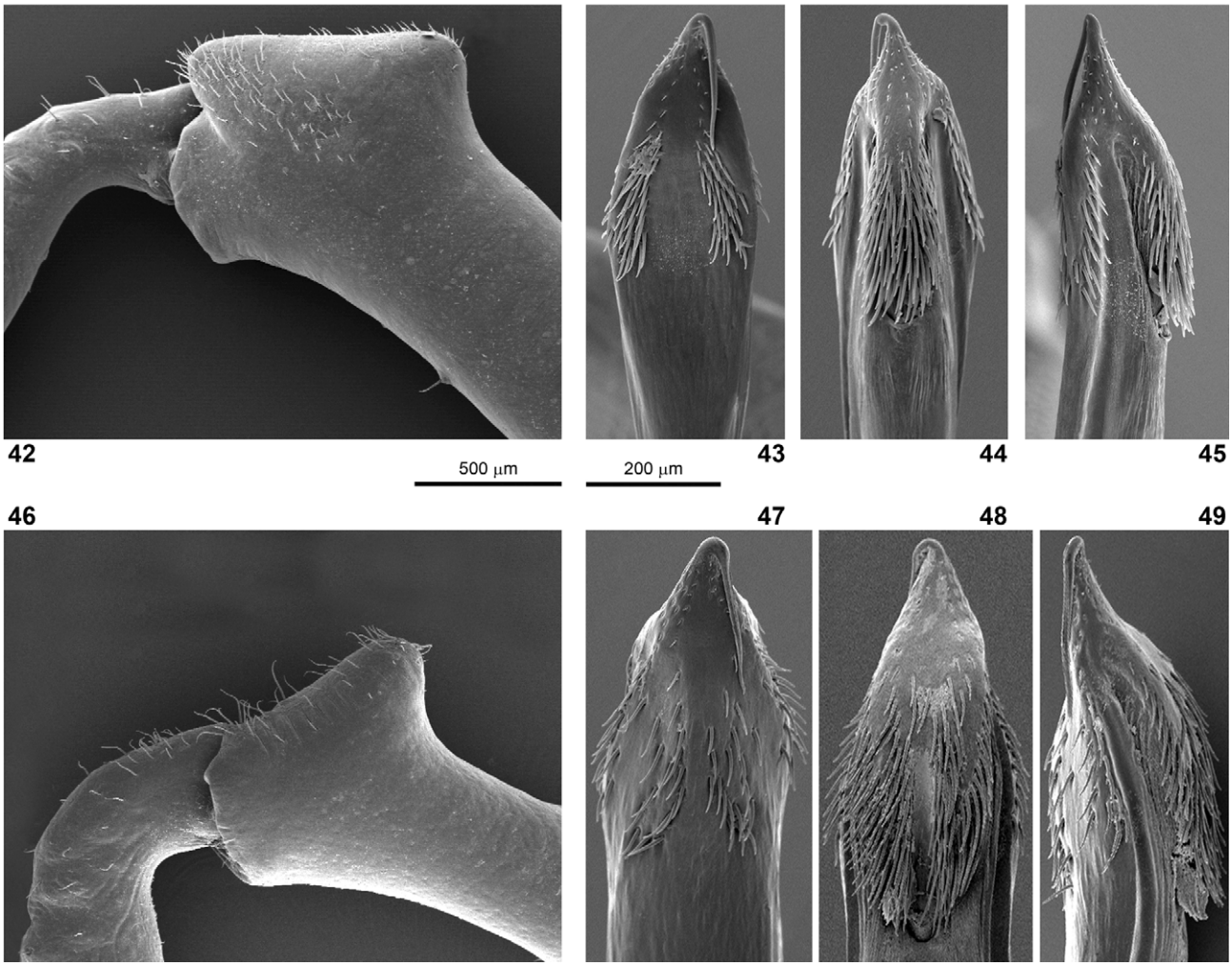
The description of *I. cantabrica* **sp. n.** does not resolve all questions concerning the Basque-Cantabrian *Ischyropsalis* fauna. *Ischyropsalis* species are characterized by low vagility, i.e. limited dispersal ability, especially in the troglobiont representatives. This leads to isolation and small scaled endemism, and may has been an important factor promoting divergence in the karstic areas of Northern Spain. Examining a few males of the complex *I. dispar* group (Fig 26) from all but three of the 8 areas (12 caves were explored) we found little differences between the form and extent of the hair field and shape of the cheliceral apophyses, but ample variation in the glans penis (Figs 51, 55, dorsal view), e.g., from areas 6a (La Pasada Caves, Cantabria) and 6g (Abaro Pit, Vizcaya) (both Fig 26). A more detailed investigation in La Pasada Caves suggests the occurrence of another species with unique characteristics (Figs 54–57). It seems neither related to *Ischyropsalis noltei* Dresco, 1972 (Figs 50–53, areas 6f and 6g) nor to *I. dispar* (C.G. Luque and L. Labrada, work in progress). Likewise, the population of La Baja Cave (Figs 38–41) seems distant from *I. dispar* (particularly the specimens of area 6a, see black shaded area in Fig. 26) (C.G. Luque and L. Labrada, work in progress). In fact, *Ischyropsalis noltei* Dresco, 1972 might not be synonymous with *Ischyropsalis dispar*, which would greatly decrease the range of the latter species. As the characters of all these forms can be placed within a morphological gradient, further research is needed to outline possible cryptic diversity and delineate species borders. A molecular phylogenetic analysis may be the appropriate method and could also to shed light on the evolutionary and biogeographic history of the genus and especially on the species set of the western sector of the Basque-Cantabrian area (northern slopes of the Upper Ebro River Basin).



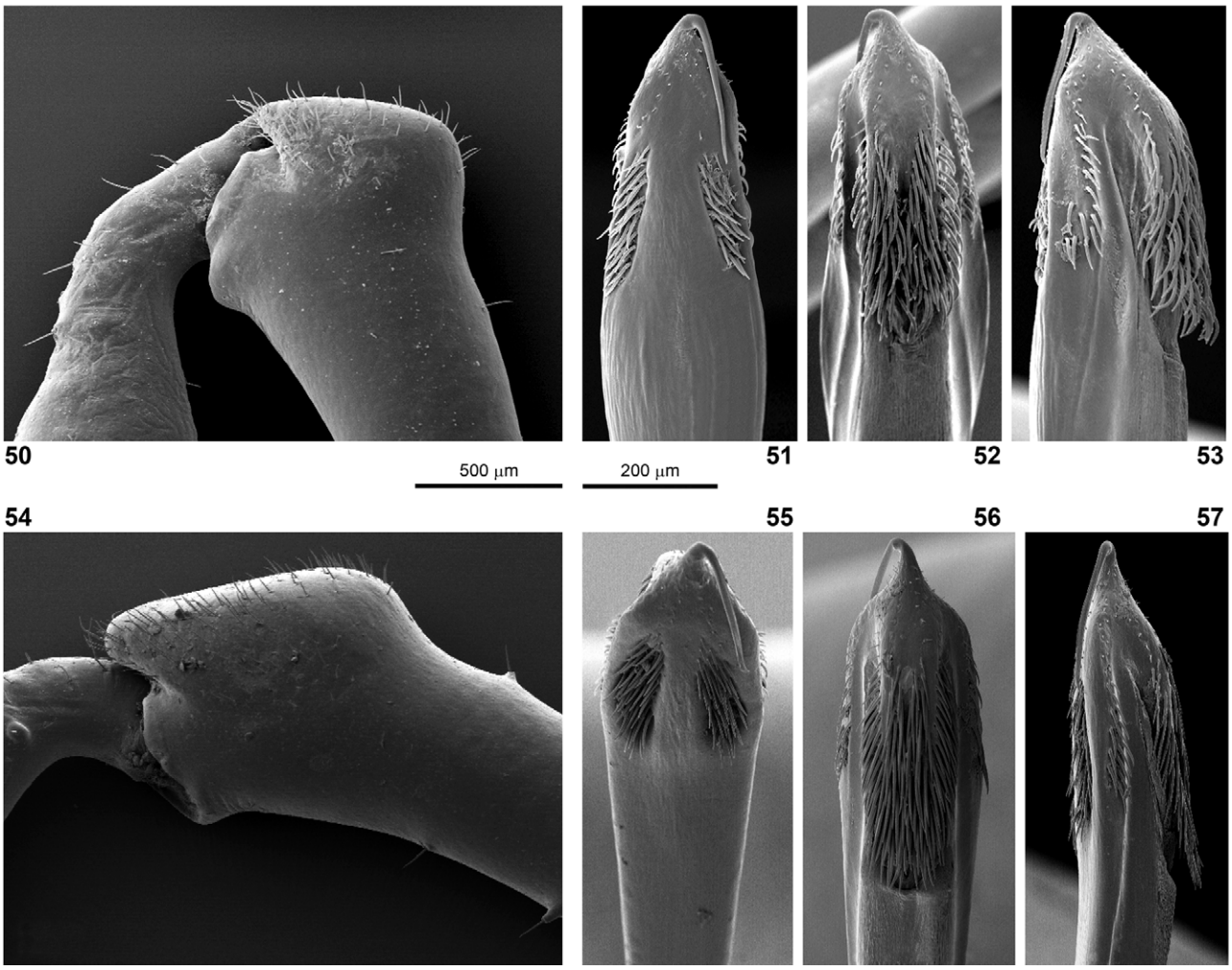
FIGURES 32–37. *Ischyropsalis gigantea*, male from Recuistro Cave (MNCN 20.02/9957, Upper Miera Mountains). Male cheliceral apophysis on distal basal segment, medial view (32–33). Detail of bristle with basal socket structure revealing the whorled striae on the external surface and the lack of a discernable pore at the tip (34). Distal part of penis with glans and stylus: dorsal view (35), ventral view (36) and lateral view (37).



FIGURES 38–41. *Ischyropsalis* sp. aff. *dispar* from La Baja Cave (MNCN 20.02/12858, Laredo, Hacha Mountain). Male cheliceral apophysis on distal basal segment, medial view (38). Distal part of penis with glans and stylus: dorsal view (39), ventral view (40) and lateral view (41).



FIGURES 42–49. *Ischyropsalis magdalenae* from Arenatza Cave (MNCN 20.02/12861, Galdames Mountain; 42–45); *Ischyropsalis navarrensis* from Putxerriko Cave (MNCN 20.02/12862, Sierra de Aralar Massif, 1-VIII-1929, leg. C. Bolívar; 46–49). Male cheliceral apophysis on distal basal segment, medial view (42, 46). Distal part of penis with glans and stylus: dorsal view (43, 47), ventral view (44, 48) and lateral view (45, 49).



FIGURES 50–57. *Ischyropsalis* cf. *noltei* (or *Ischyropsalis* sp. aff. *dispar*) from Abaro Pit (MNCN 20.02/12860, Indusi Mountain; 50–53); *Ischyropsalis* sp. aff. *dispar* from La Pasada Cave (MNCN 20.02/12859, Guriezo; 54–57). Male cheliceral apophysis on distal basal segment, medial view (50, 54). Distal part of penis with glans and stylus: dorsal view (51, 55), ventral view (52, 56) and lateral view (53, 57).

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APPENDIX 1. List of caves with UTM coordinates and altitude inhabited by six species: **1.** *I. cantabrica* **sp. n.** (restricted to the coastal limestone areas between Alfoz de Lloredo, Ruiloba, Udías and Cabezón de la Sal, Cantabria); **2.** *I. gigantea* Dresco, 1968 (restricted to the Upper Asón and Miera Mountains, Cantabria; see Fig 5, Appendix 2); **3.** *I. magdalenae* Simon, 1881 (restricted to the Triano Mountains, Galdames, Vizcaya: e.g. Arenatza Cave, 30TVN9200389842, 195 m, 1 ♂, 5-VII-1989, leg. C.G. Luque); **4.** *I. navarrensis* Roewer, 1950 (restricted to the Sierra de Aralar Massif, Guipúzcoa-Navarra: e.g. Lizurritzetako Leizea Pit, 30TWN7856561355, 1280 m, 2 ♂♂, 1 ♀, 10-VIII-1999, leg. C.G. Luque; and Putxerriko Cave, Putxerri Mountain, Alsasua, 30TWN7698058270, 1220 m, 8 ♂♂, 4 ♀♀, 8-VIII-1999, leg. C.G. Luque); **5.** *I. galani* nomen nudum (restricted to the Sierra de Arno–Izarraitz Massif, Olatz, Mutriku, Guipúzcoa: e.g. Kobetako Leizea Cave, 30TWN4835091900, 295 m, 2 ♂♂, 27-IX-1969, leg. C. Galán, coll. The Aranzadi Science Society); **6.** *I. dispar*-group Simon, 1872 distributed in Cantabria's more Eastern limestone regions, towards N-Burgos and W-Basque Country areas, at the present time existing eight known areas: **6a.** Laredo–Limpias–Rasines–Guriezo–Ranero Mountains (e.g. La Baja Cave, Laredo, Cantabria, 30TVP6605005430, 50 m, 4 ♂♂, 3 ♀♀, 22-VIII-2003, leg. L. Labrada & C.G. Luque; Hoyo Molino Cave, Seña, Limpias, Cantabria, 30TVP6657503290, 175 m, 1 ♂, 25-IV-1993, leg. C.G. Luque; La Pasada Caves, Llaguno, Guriezo, Cantabria, 30TVN7676094810, 460 m, 1 ♂, 25-IV-1993, leg. C.G. Luque; **6b.** La Lastrilla Cave (Castro Urdiales, Cantabria, 30TVP7935500970, 60 m, 1 ♂, 26-VI-1988, leg. C.G. Luque); **6c.** Covanegra Pit (Soncillo, Burgos, 30TVN4283555488, 1020 m); **6d.** Sierra Salvada Massif (e.g. Albia Cave, The Pozalagua Cave karst system, Villalba de Losa, Burgos, 30TVN9407557546, 810 m, 1 ♂, 19-VII-2008, leg. C.G. Luque & L. Labrada); **6e.** Sierra de Arkamo Massif (e.g. Solacueva de Lakozmonte Cave, Jócano, Kuartango, Álava, 30TWN0525845858, 940 m, 1 ♂, 16-VIII-1994, leg. C.G. Luque); **6f**–**g.** Gorbea Massif (population described as *I. noltei*; Dresco 1972a): **6f.** Itxina Mountain (e.g. Otxabide Pit, Urigoiti, Orozko, Vizcaya, 30TWN1542768792, 797 m, 1 ♂, 19-VIII-1994, leg. C.G. Luque); **6g.** Amboto–Aramotz Mountains (e.g. Abaro Pit, Indusi, Dima, Vizcaya, 30TWN2245074535, 375 m, 1 ♂, 19-III-1994, leg. C.G. Luque); **6h.** Sierra de Aizkorri Massif (e.g. Urdabide IV Cave, Oltza, Urbía, Guipúzcoa, 30TWN5375055680, 1120 m, 1 ♂, 10-VII-1965, leg. F. Leizaola, tube nº 795, coll. M. Rambla, The Aranzadi Science Society; and Basotxo Cave, Peña de Arbara–Eguino, Álava, 30TWN6156047745, 689 m, 12-VIII-2003, leg. C. Galán, coll. The Aranzadi Science Society)

APPENDIX 2. List of caves with UTM coordinates and altitude inhabited by *Ischyropsalis gigantea* Dresco, 1968: **5.** Cayuela or Cañuela Cave, Bustablado, Arredondo, 30TVN4966091720, 305 m, 1 ♂, 1 ♀, 6-IV-1996, leg. C.G. Luque; **6.** Currutuerta or Posadía Cave, Bustalveinte, Soba, 30TVN4987084434, 1010 m, 1 ♀, 2-IV-1990, leg. C.G. Luque; **7.** Becerral Cave, La Gándara, Soba, 30TVN5260282601, 695 m, 2 ♂♂, 2-VIII-1998, 21-VII-1990, leg. C.G. Luque; **8.** Mortero Pit, Astrana, Soba, 30TVN5384084375, 720 m, 1 ♀, 2-VIII-1998, leg. C.G. Luque; **9.** Calleja Lavalle Pit, Ajanedo, Alto del Tejuelo Cave karst system, San Roque de Riomiera, 30TVN4471590685, 650 m, 1 ♀, 22-VI-1992, leg. C.G. Luque; **10.** Los Moros del Río Munio Cave, Rolacía-Asón, Soba, 30TVN4809087295, 850 m, 1 ♂, 18-VIII-2001, leg. C.G. Luque; **11.** Recuistro Cave, Calseca, Ruesga-San Roque de Riomiera, 30TVN4611787730, 1300 m, 1 ♂, MNCN 20.02/9957, 2-VIII-1998, leg. C.G. Luque; **12.** La Canal de la Torca nº 3 Pit, The Peña del Trillo Cave karst system, Zucia, Soba, 30TVN5129079475, 1157 m, 2 ♂♂, 18-VIII-2008, leg. C.G. Luque.