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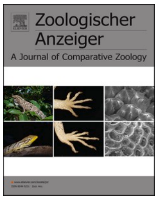

Description of the first continental European species of the huntsman spider *Cebrennus* (Araneae, Sparassidae), confirming the presence of the genus in the region

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ABSTRACT

Because of its wide variety of climates and habitats, the Iberian Peninsula harbors a rich and diverse arachnological fauna, including numerous endemisms. This is especially true for habitats like arid and semiarid areas. Many of them are threatened despite containing interesting –and sometimes uncharacterised– fauna, such as the huntsman spiders in the genus *Cebrennus*.

Previously known to occur from North Africa to the Middle East, new sightings of these spiders in Europe have drawn attention. Here, we use morphological and molecular data to describe a new species of *Cebrennus* from specimens collected in eastern Spain. Additionally, we use genetic data to place the new species, *Cebrennus herculis* sp. n., in a phylogenetic context and speculate on the biogeographic processes that lead to its presence in Europe.

Genetic distances among individuals of *C. herculis* sp. n. were low for the three molecular markers analysed (COI, 18S and 28S). Our phylogenetic tree recovered the monophyly of the Iberian *Cebrennus*, and placed them as sister to the only African representative with genetic data available, *Cebrennus rungsi*. Furthermore, divergence time analysis revealed a Palaeogene-Neogene split between the Iberian lineage and *C. rungsi,* compatible with an allopatric speciation following one of the ancient connections between Europe and Africa landmasses.

These findings show that habitats such as arid and semiarid areas still hide new and interesting diversity, underscoring the importance of preserving them.

1. Introduction

The Iberian Peninsula harbors a rich and diverse spider fauna, shaped by its varied climate, topography, and habitats. This diversity is supported by a wide range of landscapes, from forests and shrublands to high-altitude mountain ecosystems and arid areas. More than 1500 species have been recorded in the region (Nentwig et al., 2025), a number that continues to grow as new discoveries expand our understanding of its fauna (e.g. Méndez et al., 2024; Domènech et al., 2023). Notably, the Iberian Peninsula is home to nearly 300 endemic species (Branco et al., 2019) and is one of the most spider-rich regions in Europe (Nentwig et al., 2025). Importantly, recent research has shown that not only cryptic species remain undescribed, but also striking and easily recognizable ones (e.g. Azarkina et al., 2022). Ongoing studies continue

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to reveal new species and provide deeper insights into their distribution and ecological significance.

Among recent findings, observations of huntsman spiders of the genus *Cebrennus* Simon, 1880 (Sparassidae) have drawn particular attention. This genus comprises 20 species (World Spider Catalog, 2025), all adapted to arid environments where they build retreats under stones, on small plants, or in loose sand (Jäger, 2014). The genus is distributed from northern Africa to the Middle East, with some species living also on islands, namely *Cebrennus laurae* Jäger, 2014 in the Canary Islands and *Cebrennus wagae* (Simon et al., 1994) in Malta (World Spider Catalog, 2025). Recently, specimens of the genus *Cebrennus* were also reported in mainland Spain (Calatayud-Mascarell et al., 2024), although without an identification at the species level. Moreover, photographs of sparassids that can be assigned to the genus *Cebrennus* have been appearing in recent years in webpages and social networks such as iNaturalist (iNaturalist, 2025) and Facebook groups (Arácnidos Ibéricos, n. d.), suggesting the presence of these spiders in additional regions of Spain and in the island of Sardinia (Italy) (Fig. 1). However, it is difficult to tell whether these instances correspond to an actual range and population expansion of the genus outside their known distribution or to a bias due to an increasing number of people using these platforms.

Here, we use morphological and molecular data to describe a new species of *Cebrennus* collected in Spain, the first one of the genus to be recorded in continental Europe. Additionally, we use genetic data to place the new species in a phylogenetic context and speculate on the biogeographic processes that lead to its presence in Europe.

2. Material and methods

Female and juvenile specimens of *Cebrennus* were collected in 2021 in Valencia, Spain, as part of a project aiming at assembling a checklist of arachnids from coastal dunes (see more details in Calatayud-Mascarell et al., 2024). They were collected using pitfall traps, sweeping nets and active hand sampling in La Punta Ecological Reserve, a protected area that includes moving sand dunes (CORINE habitat code 2120) and fixed dunes, also known as gray dunes (CORINE habitat code 2210). An adult male individual was collected using pitfall traps in 2022 in Hoya de Baza, a semi-arid area dominated by low shrubland, located in Granada (Spain). An additional female specimen was collected by direct capture in a mediterranean shrubland in Nerpio, Albacete (Spain) in May 2022. Samples were stored in absolute ethanol, and the type material is stored at the Museu de Ciències Naturals de Barcelona. Some juvenile individuals sampled in Valencia were kept alive to obtain adult male specimens. Some of them moulted, but all died before reaching maturity. They were preserved in the same way as the adults.

Specimens were studied under a LeicaMZ16A stereoscopic microscope and a ZEISS Axio LAB.A1 microscope. Digital images were taken with a high-resolution digital camera LEICA DFC 450 and the software Leica Application Suite v4.4, as well as with a FLIR digital camera with a THORLABS C-mount CML15 lens attached to the microscope. Images were stacked with the Helicon Focus software (Helicon Soft, Ltd.). Epigynes were dissected and treated with potassium hydroxide to reveal internal details.

Measurements are in millimeters, and leg and palp measurements are given as: total (femur, patella, tibia, metatarsus, tarsus). The spination pattern given follows Davies (1994), listing the sums of all spines for palp and legs (prolateral, dorsal, retrolateral, ventral).

Abbreviations used: BL—body length (as sum of PL and OL), PL—length of dorsal shield of prosoma, PW—width of dorsal shield of prosoma, AW—anterior width of dorsal shield of prosoma, OL—opisthosoma length, OW—opisthosoma width, AME—anterior median eyes, ALE—anterior lateral eyes, PME—posterior median eyes, PLE—posterior lateral eyes, RTA—retrolateral tibial apophysis.

Three DNA markers were sequenced for our specimens to investigate their conspecificity, namely the Cytochrome *c* oxidase I (COI, ∼658 bp), the large subunit 28S rRNA (28S, ∼790 bp) and the small subunit 18S rRNA (18S, ∼685 bp). DNA was extracted with a Speedtools Tissue DNA Extraction kit (BioTools) following the manufacturer's default instructions. The pairs of primers used were LCOI1490-HCOI2198 (Folmer et al., 1994) for COI, as well as MT6-NANCY when amplification with the former pair was unsuccessful (Simon et al., 1994); 28SFw-28SRv for 28S (Platania et al., 2020); and 18S.1Fw (TACCTGGTTGATCCTGCCAGTAG) and 18S.5Rv (CTTGGCAAATGCTTTCGC) for 18S. PCR conditions were as follows: for COI, initial denaturing step at 95 °C for 5 min, 35 amplification cycles (94 °C for 30 s, 48 °C for 35 s, 72 °C for 45 s) and a final step at 72 °C for 5 min; for 28S, initial denaturing step at 95 °C for 5 min, 40 amplification cycles (94 °C for 30 s, 45 °C for 35 s, 72 °C for 45 s) and a final step at 72 °C for 5 min; for 18S, initial denaturing step at 95 °C for 5 min, 40 amplification cycles (94 °C for 30 s, 48 °C for 35 s, 72 °C for 45 s) and a final step at 72 °C for 5 min. PCR products were sent to the Scientific and Technological Centers of the University of Barcelona (CCiTUB) for sequencing. DNA sequences were cleaned and edited in Geneious Prime 2025.0.3 (Biomatters, 2025). For the male specimen (Ceb1), we found 10 instances of double peaks of nucleotides in the chromatogram of the COI sequence. We unsuccessfully tried cloning it and ended up resolving the consensus sequence with the nucleotides with the highest peak. Additional sequences belonging to Sparassidae and an extra one belonging to the marronoid family Stiphidiidae were downloaded from GenBank (Table 1). All sequences were then aligned using Mafft v7.520 (Katoh & Standley, 2013). We also initially included two available COI sequences of *Cebrennus* sp., one from Sudan (MT506051) and one from Algeria (KJ408724), but

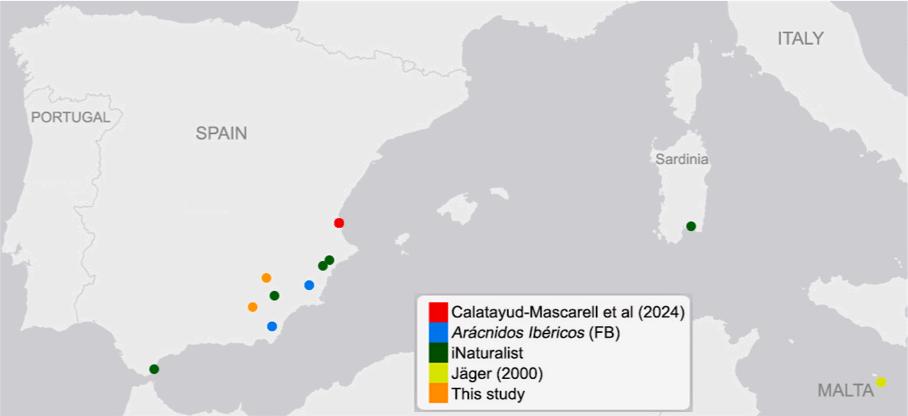

Fig. 1. Known European records of specimens attributable to the genus *Cebrennus*, recovered from different sources: the citizen science webpage iNaturalist, the Facebook (FB) group "Arácnidos Ibéricos" (two records per locality), the study of Jäger (2000) (corresponding to *Cebrennus wagae*), the samplings from Calatayud-Mascarell et al. (2024), and two new specimens from this study.

Table 1
List of all the DNA sequences used in this study (in bold those newly sequenced by us), including sex and locality of the Iberian *Cebrennus* (Gra: Granada, Val: Valencia, Alb: Albacete).

Species	COI	18S	28S
Sparassidae			
Cebrennus herculis (Ceb1, ♂ Gra)	**PV639489**	**PV640225**	**PV640229**
Cebrennus herculis (Ceb2, ♀ Val)	**PV639491**	**PV640226**	**PV640230**
Cebrennus herculis (Ceb3, ♀ Val)	**PV639492**	**PV640227**	**PV640232**
Cebrennus herculis (Ceb4, ♀ Val)	**PV639494**	**PV640228**	**PV640231**
Cebrennus herculis (Ceb5, ♀ Val)	**PV639493**		
Cebrennus sp. (Ceb6, ♀ Alb)	**PV639490**		
Cebrennus rungsi Jäger, 2000			KJ408624
Cerbalus sp.	KJ408725		KJ408625
Eusparassus sp.		KY016704	KY017360
Olios sp.	OK646538		OK545592
Carparachne alba Lawrence, 1962	KJ408722		KJ408622
Heteropoda tetrica Thorell, 1897	OK646520		OK545576
Thelcticopis severa (L. Koch, 1875)	KJ408779		KJ408677
Spariolenus sp.	KJ408777		JX137224
Polybetes pythagoricus (Holmberg, 1875)	KY017924	KY016709	KY017365
Palystes superciliosus L. Koch, 1875	OK646539		OK545593
Neostasina sp.	KY017923	KY016708	KY017364
Micrommata aljibica Urones, 2004	MT607817		MT651999
Isopeda parnabyi Hirst, 1992	KY017921	KY016706	KY017362
Stiphidiidae			
Neoramia setosa (Bryant, 1935)	KY017936	KY016719	KY017378

they were discarded after a BLAST search revealed high similarity with species of the family Lycosidae −99 % *Hogna ferox* (Lucas, 1838) and >96 % *Hippasa pisaurina* Pocock, 1900, respectively.

A Maximum Likelihood (ML) tree was built from the concatenation of the three markers using IQ-TREE 2.2.0.3 (Minh et al., 2020). The data was partitioned by gene, and the ModelFinder (Kalyaanamoorthy et al., 2017) option was used to select the best evolutionary model for each partition. The stiphidiid *Neoramia* sp. was placed as the outgroup (Wheeler et al., 2016). Support values were estimated using the Ultrafast Bootstrap method (UFB) (Hoang et al., 2018). Pairwise genetic p-distances were calculated with MEGA11 (Tamura et al., 2021).

Molecular clock analyses were run in PAML 4.7 (Yang, 2007). Branch lengths were estimated under the HKY85+G4 model on the topology found by the ML analysis and an independent rate relaxed-clock model was used to estimate divergence times. We obtained 20000 trees with a sampling frequency of 2 and discarded 2000 as burn-in. Parameters were set as follows: 'RootAge <1.7' (based on Fernández et al., 2018; indicating a maximum age for the root of 170 My), 'cleandata = 0', 'BDparas = 1 1 0.1', 'kappa_gamma = 6 2', 'alpha_gamma = 1 1', 'rgene_gamma = 2 20 1', 'sigma2_gamma = 1 10 1' and 'finetune = 1: 0.1 0.1 0.1 0.01 0.5'. Convergence was assessed through Tracer v.1.7 (Rambaut et al., 2018) as customary.

Two fossils were used to calibrate the tree, following best practices (Parham et al., 2012): *Eusparassus crassipes*, to calibrate the split between *Eusparassus* sp. and *Isopeda parnabyi* (minimum age = 33.9 Mya), and *Heteropoda robusta* to calibrate the split between *Heteropoda tetrica* and *Spariolenus* sp. (minimum age = 15.97 Mya) (Dunlop et al., 2013). We applied a non-uniform truncated Cauchy distribution (p = 0.1, c = 0.2) between minimum and maximum node age constraints. This interval was augmented by soft bounds with minimum tail probabilities of 2.5 %.

3. Results

3.1. Molecular results and phylogenetic analyses

Samplings in Valencia yielded 6 adult females, as well as 11 juveniles of *Cebrennus* putatively belonging to the same species (Calatayud-Mascarell et al., 2024). Sampling in Granada yielded 1 single male, while 1 female was collected in Albacete. Sequencing was successful for most of the individuals and molecular markers (see Table 1).

Overall, pairwise genetic distances were low for the three markers. For 18S, the divergences between the male individual and the three sequenced females from Valencia were 0 %, 0.54 % and 0 % (mean 0.18 %), with an average distance between those females of 0.36 %, and a general average distance in the Iberian *Cebrennus* of 0.27 %. For 28S, the divergences between the male individual and the same three sequenced females were 0 %, 0.44 % and 0.55 % (mean 0.33 %), with an average distance between those females of 0.24 % and a general average distance in the Iberian *Cebrennus* of 0.29 %. For COI, the average p-distance among the four females from Valencia was 0.08 %. The average distance between the male and those same females was 1,96 % (1.88 %, 1.92 %, 1.91 %, 2.12 %), while the distance between the female from Albacete and those from Valencia was 5.29 % (5.18 %, 5.27 %, 5.25 %, 5.46 %), notably higher. Finally, the COI divergence between the male from Granada and the female from Albacete was 3.85 %. The average 28S interspecific distance between the specimens sampled in this study and *Cebrennus rungsi*, the only species of the genus *Cebrennus* with previously available genetic data, was 1.86 %.

The ML tree recovered the monophyly of the four female specimens from Valencia, as well as the six specimens from Spain, albeit with low support (Fig. 2). The monophyly of the genus *Cebrennus* was also recovered (UFB = 93). *Cebrennus* appeared as the sister to *Cerbalus* (UFB = 100), and these two to *Olios* (UFB = 99) with high support. The split between *C. rungsi* and the Iberian *Cebrennus* was estimated to have occurred in an interval between 29.58 Mya and 7.15 Mya (spanning across the Palaeogene and Neogene periods).

3.2. Taxonomy

3.2.1. Cebrennus herculis sp. n. Domènech, Pérez-Gómez & Calatayud-Mascarell

Figs. 3 and 4.

Type material. SPAIN: Holotype male (Ceb1, MZB 2025–4347), Barranco de Mazarra, Hoya de Baza, Granada, 37.535051, −2.656986, 836 m a.s.l., pitfall trap in semi-arid shrubland, A. Iglesias leg. 9 April 2022. **Paratypes:** 1 female (Ceb2, P1D1F8, MZB 2025–4348), La Punta Reserve, Valencia, 39.312055, −0.296658, 2 m a.s.l., nocturnal hand collection in coastal sand dunes, E. Ribera and A. Calatayud-Mascarell leg. 3 October 2021. 1 female (Ceb3, P3SN4F8, MZB 2025–4349), La Punta Reserve, Valencia, 39.312055, −0.296658, 2 m a.s.l., nocturnal collection by sweeping net in coastal sand dunes, C. Navarro and A. Calatayud-Mascarell leg. 30 May 2021. 1 female (Ceb4, P3D3F3, MZB 2025–4350), La Punta Reserve, Valencia, 39.312055, −0.296658, 2 m a.s.l., nocturnal hand collection in coastal sand dunes, A. Calatayud-Mascarell leg. 3 October 2021. 1 female (Ceb5, PPI2-1-F3, MZB 2025–4351), La Punta Reserve, Valencia, 39.312055, −0.296658, 2 m a.s.l., pitfall trap in coastal sand dunes, A. Calatayud-Mascarell leg. 30 May 2021.

Diagnosis. Males of *C. herculis* sp. n. differ greatly in the shape of the palp from all other species for which males have been described by the elongated and subrectangular tegulum covering the alveolus almost entirely, together with a distally-pointing RTA emerging from a median-dorsal position. Only *Cebrennus cultrifer* from Algeria (Jäger, 2000: Figs. 1–2; Fage, 1922: Fig. 2), to which it may be related, bears some similarities with *C. herculis* sp. n. The distal part of the embolus is gently curved retrolaterally and sinuous in *C. herculis* sp. n (Fig. 3G and H), straight in *C. cultrifer*. The distal end of the tegulum is straight and reaching almost the end of the alveolus in *C. herculis* sp. n (Fig. 3G), while in *C. cultrifer* the distal part of the tegulum is clearly oblique, only the retrolateral side almost reaching the end of the alveolus. In retrolateral view, the RTA is aligned with the palp emerging from a median-dorsal position and points distally in *C. herculis* sp. n (Fig. 3C–K), while it emerges more ventrally in *C. cultrifer*. Females can be distinguished from all other species for which the females are known by the

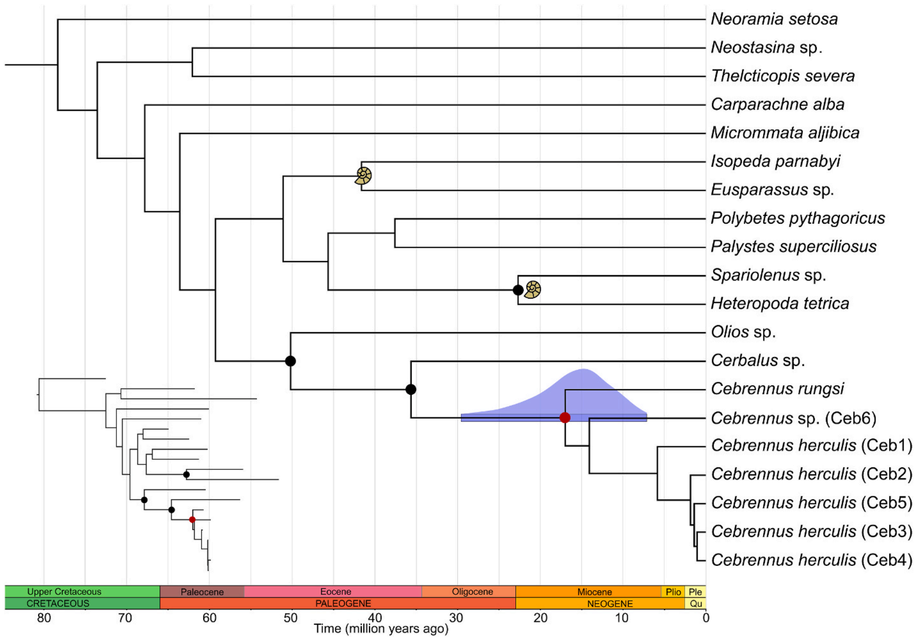

Fig. 2. Time-calibrated Maximum Likelihood tree of Sparassidae including all the specimens collected in this study. Black dots indicate UFB support above 95 %, red dot indicates UFB support between 90 % and 95 %. Only the 95 % interval distribution for the split between the African *Cebrennus rungsi* and the Iberian *Cebrennus* clade is shown (full time-calibrated tree in Supplementary Fig. S1). Calibrated nodes are represented with fossil icons. Bottom left, the phylogenetic tree with branch lengths (complete ML tree in Supplementary Fig. S2). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

unique shape of the genitalia: a median septum twice as wide as long, widely separated fertilization ducts, and an epigyne and internal duct system roughly as wide as long. However, it bears some similarities to *Cebrennus powelli* (Jäger, 2000: Figs. 28–29) and *Cebrennus atlas* (Jäger, 2014: Figs. 7–9). The median septum is longer in *C. herculis* sp. n (Fig. 4E). than in *C. atlas*, and the distance between fertilization ducts is clearly larger (Fig. 4F). Both the epigyne in ventral view and the sclerotised part of the internal duct system in dorsal view are approximately square in shape, roughly as long as wide (Fig. 4E and F), while they are wider than long in *C. powelli*.

Etymology. The latin specific epithet “herculis” refers to the Greco-Roman hero Hercules. According to classical mythology, Hercules created the Strait of Gibraltar by parting the mountains that connected Africa and Iberia, placing what became known as the Pillars of Hercules on either side. The name honors this mythological act of continental separation, which symbolically mirrors the split of the Iberian lineage from its African relatives.

Description of male holotype. BL 10.61, PL 5.22, PW 4.36, AW 3.06, OL 5.39, OW 4.31, AME 0.34, ALE 0.2, PME 0.23, PLE 0.23, AME–AME 0.23, AME-ALE 0.24, PME–PME 0.43, PME-PLE 0.64, AME-PME 0.33, ALE-PLE 0.54, clypeus-AME 0.17, clypeus-ALE 0.19. Spination: Palp: femur (1,3,0,0), patella (0,0,0,0), tibia (1,0,0,0), cymbium (1,0,0,0). Legs I, II and III: femur (3,2,3,0), patella (0,0,0,0), tibia (2,0,2,4), metatarsus (2,0,2,4). Leg IV: femur (3,2,2,0), patella (0,0,0,0), tibia (2,0,2,4), metatarsus (3,0,3,6). Ventral metatarsi I–IV with sparse scopula, without spines or bristles distally. Legs with claw tufts. Leg formula: 2413. Measurements of palp and legs: palp 6,6 (2.14, 0.8, 1.21, 2.45), leg I 24.26 (7.09, 2.52, 5.77, 6.8, 2.08), leg II 26.3 (7.86, 2.51, 6.63, 7.46, 1.91), leg III 20.26 (6.54, 2.17, 4.79, 5.35, 1.43), leg IV 24.27 (7.68, 2.3, 5.61, 6.83, 1.85). Trilobate membrane present on the distal part of the metatarsus, but only the median hook is recognizable, the lateral projections are reduced (Fig. 3F). Cheliceral furrow with 2 anterior and 5 posterior teeth (Fig. 3E). Numerous long setae on the internal surface of the distal third of the chelicerae, anterior to the fang. Longer setae arising near the base of the fang, 4 on the posterior side and numerous on the anterior side.

Palp: distal third of cymbium with dorsal scopula (Fig. 3I). RTA curved distally, thick at its base in ventral view but ending in a pointy tip (Fig. 3B–L). Tegulum long, almost reaching the distal part of the alveolus (Fig. 3G). Comparing with Jäger (2000), the hyaline part at the top of the tegulum which is slightly visible in ventral-prolateral view may correspond to the membranous remnant of the conductor. Distal part of the tegulum and conductor slightly covering the embolus. Embolus straight except at its terminal part, which is gently curved retrolaterally and sinuous (Fig. 3G).

Colouration: Prosoma pale yellow to light orange (Fig. 3A). Distinct longitudinal fovea. Anterolateral margin of dorsal shield of prosoma and distal chelicerae darker. Irregular black patches between the eyes and around the clypeus below AME. Sternum, labium, gnathocoxae and ventral coxae yellow. Palp and legs also yellow to light orange, with cymbium slightly darker. Opisthosoma yellowish brown. Spinnerets appearing in ventral view dark by dark setae, otherwise body and legs with white setae.

Description of female paratype (Ceb2). BL 10.05, PL 4.05, PW 3.97, AW 3.29, OL 5.41, OW 3.64, AME 0.3, ALE 0.22, PME 0.22, PLE 0.22, AME–AME 0.25, AME-ALE0.33, PME–PME 0.51, PME-PLE 0.81, AME-PME 0.38, ALE-PLE0.64, clypeus-AME 0.15, clypeus-ALE 0.16. Spination: Palp: femur (0,2,0,0), patella (0,0,0,0), tibia (1,0,0,0), tarsus (1,0,0,0). Leg I: femur (2,2,3,0), patella (0,0,0,0), tibia (2,0,2,4), metatarsus (2,0,2,4). Leg II: femur (1,2,2,0), patella (0,0,0,0), tibia (2,0,2,4), metatarsus (2,0,2,4). Leg III: femur (0,2,1,0), patella (0,0,0,0), tibia (2,0,2,4), metatarsus (2,0,2,4). Leg IV: femur (0,2,1,0), patella (0,0,0,0), tibia (2,0,2,3), metatarsus (4,0,3,4). Ventral metatarsi I–IV with short sparse scopula only in distal-most part. Legs with claw tufts. Palp ending in a palpal claw. Leg formula: 2143. Measurements of palp and legs: palp 6,02 (1.99, 0.96, 1.23, 1.85), leg I 17.48 (5.2, 2.07, 4.23, 4.57, 1.41), leg II 19.01 (5.74, 2.14, 4.67, 5.05, 1.42), leg III 13.76 (4.25, 1.7, 3.18, 3.45, 1.19), leg IV 17.26 (5.48, 1.93, 3.98, 4.59, 1.29). Trilobate membrane present on the distal part of the metatarsus, but only the median hook is recognizable, the lateral projections are reduced (Fig. 4D). Cheliceral furrow with 2 anterior and 5 posterior teeth in the left chelicera, and 2 anterior and 4 posterior teeth on the right chelicera (the one closest to

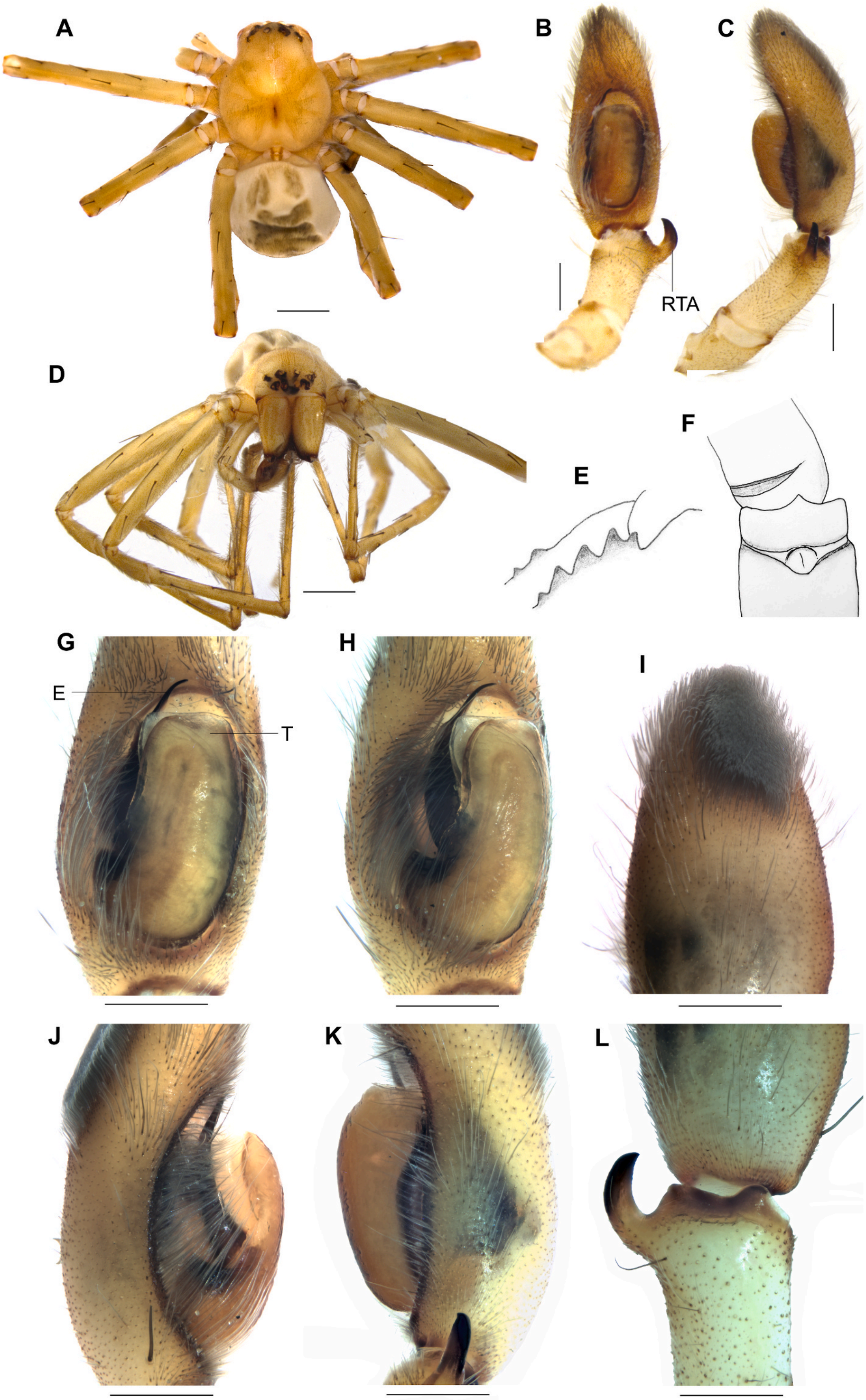

Fig. 3. *Cebrennus herculis* sp. n. male holotype (Ceb1, MZB 2025–4347), from Granada. A) Habitus, dorsal view. B) Pedipalp, ventral view. C) Pedipalp, retrolateral view. D) General frontal view. E) Cheliceral dentition, ventral view of left chelicera. F) Trilobate membrane (dorsal aspect). G) Copulatory bulb, ventral view. H) Copulatory bulb, ventral-prolateral view. I) Top part of cymbium, dorsal view. J) Copulatory bulb, prolateral view. K) Copulatory bulb, retrolateral view. L) Detail of the tibia and the base of the cymbium, dorsal view. RTA, retrolateral tibial apophysis; T, tegulum; E, embolus. Scale bar A,D: 2 mm; B-C, G–L: 0.5 mm.

the fang absent) (Fig. 4C). Numerous long setae on the internal surface of the distal third of the chelicerae, anterior to the fang. Longer setae arising near the base of the fang, 3 on the posterior side and numerous on the anterior side.

Copulatory organ: epigynal plate roughly as long as wide. Lateral ridges subparallel, slightly closer anteriorly (Fig. 4E). Median septum ovalish, wider than long. Anterior transversal rim of median septum located approximately at the median part of the epigyne (Fig. 4E). Vulva: sclerotised part of the internal duct system roughly square in shape, as long as wide (Fig. 4F). Sclerotised glandular appendages located medially, covered with well-visible gland pores (Fig. 4F). The distance between fertilization ducts is almost half the width of the vulva (0.43).

Colouration: Prosoma pale yellow to light orange. Anterolateral

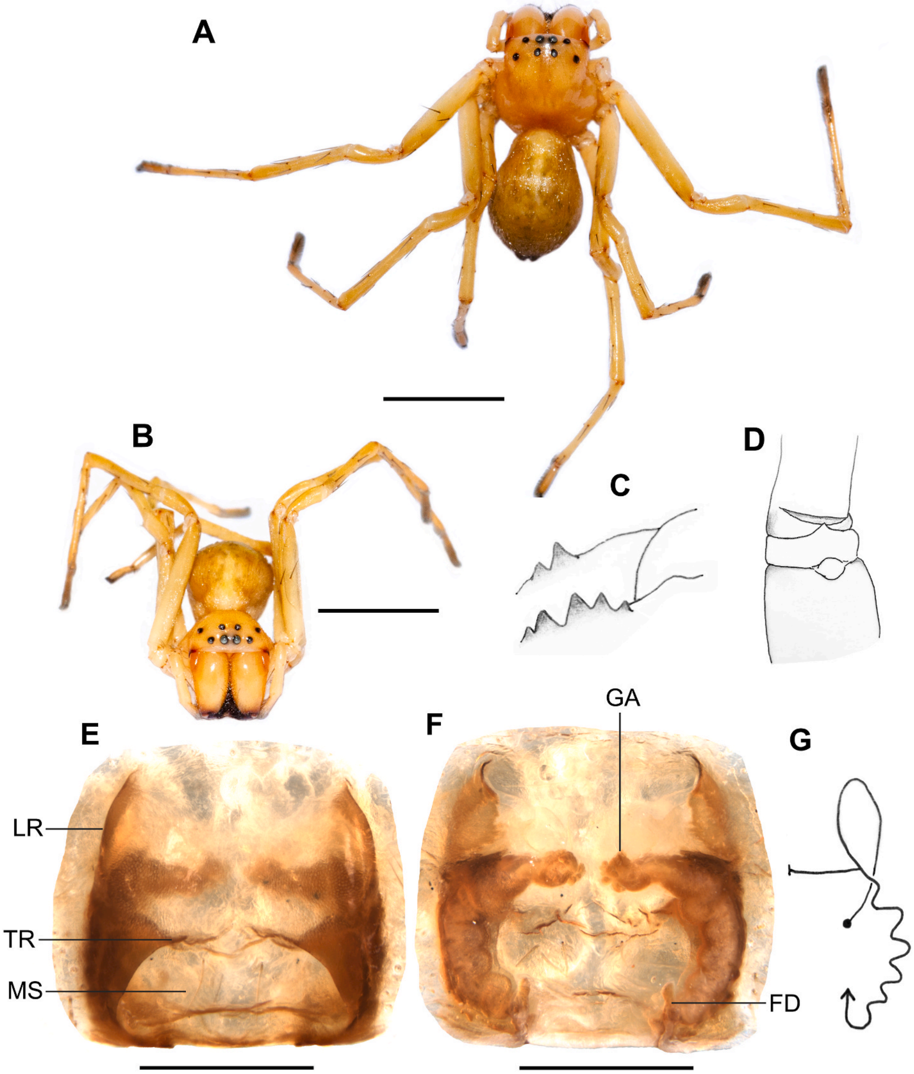

Fig. 4. *Cebrennus herculis* sp. n. described female paratype (Ceb2, MZB 2025–4348), from Valencia. A) Habitus, dorsal view. B) General frontal view (from Calatayud-Mascarell et al., 2024). C) Cheliceral dentition, ventral view of left chelicera. D) Trilobate membrane (dorsal aspect). E) Epigyne, ventral view. F) Vulva, dorsal view. G) Inferred schematic course of internal duct system, dorsal. LR, lateral ridges; MS, median septum; TR, transversal rim of median septum; FD, fertilization ducts; GA, glandular appendages. Scale bar A,B: 5 mm; E,F: 0.5 mm.

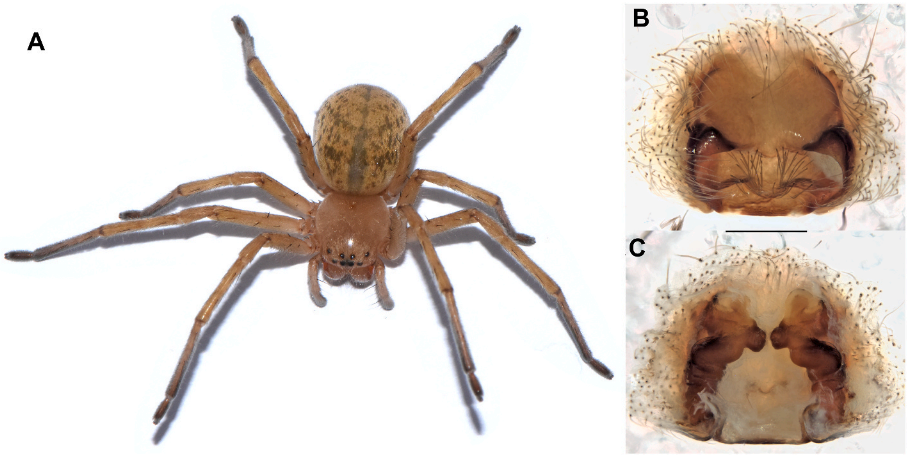

Fig. 5. Female of *Cebrennus* sp. (Ceb6), from Albacete (photo by Maite Mojica). A) Habitus of the specimen alive. B) Epigyne, ventral view. C) Vulva, dorsal view. Scale bar B,C: 0.5 mm.

margin of dorsal shield of prosoma and distal chelicerae darker (Fig. 4B). Proximolateral chelicerae orangish. Fovea not clearly visible. Palps and legs yellow, tarsus slightly darker. Opisthosoma yellowish brown, with slightly darker irregular spots on dorsal and lateral sides. Eyes with small black circle around them. Sternum, labium, gnathocoxae and ventral coxae yellow. Spinnerets appearing in ventral view dark by dark setae, otherwise body and legs with white setae.

Relationships and identification key. Fage (1922) distinguished two groups within the genus *Cebrennus*: one including *Cebrennus aethiopicus*, *Cebrennus castaneitarsis* and *C. wagae*, and another one containing *Cebrennus kochi*, *Cebrennus tunetanus* and *C. cultrifer*. Later, Jäger (2014) reclassified the known species in three groups (*kochi* group, *wagae* group and *villosus* group), while leaving *C. cultrifer*, *Cebrennus mayri* and *C. tunetanus* as unassigned. Due to the similar structure of the palp of *C. cultrifer* and the newly described *C. herculis* sp. n., both species could be grouped and form a fourth species group. In the case of the male specimen, following the identification key by Jäger (2014) would lead to *C. cultrifer* (1 > 5>10 > 13), although *C. herculis* sp. n. would differ in the shape of the embolus: "long spine-shaped" in the key for *C. cultrifer*, gently bent retrolaterally at its distal part in *C. herculis* sp. n.

Regarding the females, the key would lead to *C. atlas* (1 > 3>8 > 10) due to the internal duct system being as wide as long. However, the description mentions "two eyebrow-like anterior rims close to copulatory openings" in *C. atlas*, which are absent in *C. herculis* sp. n.

Biology and behaviour. Calatayud-Mascarell et al. (2024) list four females and five juveniles from Valencia that were collected in autumn, and two females and six juveniles that were collected in spring. The adult male from Granada was also collected in spring. This suggests that this species may have a prolonged breeding season or perhaps a semivoltine life cycle with overlapping generations. The presence of juveniles in both seasons indicates that reproduction could occur across a wider timeframe, potentially with multiple generations per year. However, further studies are necessary to fully understand the phenological patterns and reproductive cycles of the species. Additional juvenile individuals of *Cebrennus* sampled in the same location and similar dates as female paratypes, thus potentially belonging to *C. herculis* sp. n., were kept alive in small terrariums with sand as substrate and some sparse twigs. They were observed building small burrows under the sand, not very deep, with a lid covered by sand, making the entrance almost indistinguishable when closed. At night, they would wander around and return to the burrow. Six of the specimens in Calatayud-Mascarell et al. (2024) were collected in the low vegetation using a sweeping net, indicating that this species is not only a ground dweller but can also crawl around low plants.

3.2.2. *Other material*

A female *Cebrennus* sp. (Ceb6) was collected in the surroundings of Nerpio, Albacete (38.148601, −2.294640), at 1130 m a.s.l., by direct hand-capture at night in a Mediterranean shrubland, on 23 May 2022 (M. Mojica and J. J. Guerrero leg.). This specimen could not be unequivocally assigned to *C. herculis* sp. n. due to slight differences in the shape of the epigyne and vulva, and to a COI genetic distance above 5 % with Valencian females. Therefore, it remains undetermined until further samplings in the area yield more specimens.Fig. 5

4. Discussion

As stated in Calatayud-Mascarell and collaborators (2024), the *Cebrennus* specimens reported in this study represent the first record of the genus in continental Europe. In this study, thanks to the finding of an additional male individual, we have been able to confirm this population as a new species for science, *C. herculis* sp. n.

Genetic divergences for 18S and 28S between the female specimens from Valencia and the male from Granada were very low. These markers, though, are known to have low mutation rates (Brown et al., 1979; Hasegawa & Kazuya, 2006), and therefore, low divergence values are expected even among different species. Regarding the COI, while the genetic distances were low between the females from Valencia and the male (never exceeding 2.2 %), they were higher between those females and the one from Albacete (consistently above 5.1 %). Although it may vary among different taxa, it has been shown that a value around 3 % of COI p-distance can be an accurate threshold for species diagnosis (Hebert et al., 2003). Therefore, we consider the females from Valencia and the male from Granada to be conspecific, while the female specimen from Albacete is tentatively left as an unconfirmed putative different species, waiting for ongoing samplings in the area to yield male specimens.

The results of the ML tree confirm the new species as a member of the genus *Cebrennus* by placing it in a clade together with *C. rungsi*. At the same time, both of them are recovered as closely related to *Cerbalus*, a genus with a notably overlapping distribution with *Cebrennus*, as well as with similar appearance and adaptations. Unfortunately, the scarcity of genetic sequences for representatives of *Cebrennus* makes it impossible to investigate the molecular phylogenetic position of the new species within the genus. Moreover, a more comprehensive taxon sampling and gene completeness would be necessary to assess the relationships among sparassid genera with greater certainty.

Beyond systematics, the discovery sheds light on the ecological richness and understudied nature of arid and semi-arid environments. These habitats have traditionally received limited attention in both conservation policy and scientific research, despite harbouring high levels of biodiversity, often composed of species with specialised adaptations to extreme environmental conditions (Zhang et al., 2023; Lozano-Fernandez et al., 2024). The discovery of a striking and visually prominent spider species highlights the knowledge gaps that persist in these ecosystems. Such findings suggest that significant portions of their invertebrate fauna remain undocumented. The continued discovery of novel taxa in these habitats underscores their evolutionary relevance and the need for increased research and conservation efforts, particularly in light of ongoing anthropogenic pressures such as land-use change and climate-driven desertification (Timis-Gansac et al., 2025).

Due to the numerous species of *Cebrennus* present in North Africa in contrast to the single one in continental Europe, it could be assumed that the Iberian populations derive from an African lineage. However, the biogeographical processes that led to their presence in Southern Europe are unknown. The land masses of Europe and Africa have been in contact multiple times in the past. For example, the terrains north of the High Atlas, the Rif and the Kabyles were once connected to the Iberian Peninsula. During the early Burdigalian (21 Mya), the Kabyles split and drifted away, eventually colliding with Africa. Later, during the middle Miocene, the Rif-Betic block drifted westward (Rosenbaum et al., 2002). During the late Tortonian to early Messinian (9–7 Mya), marine passages, the Betic corridor to the north, and the Rif corridor to the south, separated the Rif-Betic block from Iberia and Africa, respectively (Abbassi et al., 2020). The two corridors closed during the Messinian Salinity Crisis (late Miocene, ~5.96–5.33 Mya), when the Mediterranean temporarily desiccated due to tectonic closure, creating a continuous land mass that connected Iberia and Africa. The modern Strait of Gibraltar formed afterwards (~5.33 Ma), reestablishing permanent marine exchange between the Atlantic and Mediterranean while definitively separating Iberia from northern Africa (Krijgsman et al., 1999).

If the estimated time for the divergence between the Iberian *Cebrennus* and the only African representative *C. rungsi* was significantly younger than the last reopening of the Strait of Gibraltar (<5.33 Mya), it would imply that the Iberian lineage had to reach Europe by crossing the sea. On the contrary, a divergence time older than 5.33 Mya also opens the possibility that the Iberian lineage diverged from an African one by allopatric speciation following former connections between the two landmasses, leaving *Cebrennus* populations on either side. We obtained a wide divergence-time estimation interval (29.6–7.2 Mya), a lack of precision likely due to the scarcity of available calibration points, necessary to get more precise time estimates in node dating analyses.

The younger limit of this interval is still older than 5.33, which would make both scenarios possible. It is worth noting that the African representative in our analyses is the only *Cebrennus* species with previously available genetic data (specifically with only a 28S sequence), and it most likely does not correspond to the sister species of *C. herculis* sp. n. In this regard, based on the similarity in the structure of the male copulatory bulb, we suggest that *C. cultrifer* might be the sister species of *C. herculis* sp. n., or at least very closely related to it. Therefore, it should be expected that the divergence time between the Iberian lineage and its closest African lineage happened more recently. A more complete representation of genetic data from other *Cebrennus* species will help obtain more precise time estimates and will yield a more accurate picture of the biogeographic processes that shaped the distribution of this remarkable genus.

5. Conclusions

The newly described *C. herculis* sp. n. represents the first species of the genus *Cebrennus* in continental Europe. It inhabits dry shrublands and sandy areas in the Mediterranean regions of Spain. An additional specimen of *Cebrennus* was collected but could not unequivocally be assigned to the new species, which indicates that further samplings and studies are needed to unravel all the diversity of the genus in the Iberian Peninsula. A time-calibrated phylogeny of the family Sparassidae, including individuals of the new species, suggests that the Iberian lineage could have diverged from an African one by allopatric speciation, following an ancient connection between the European and African landmasses.

These results highlight the importance of preserving arid and semi-arid areas, both in coastal regions and inland. These habitats harbor unique fauna and flora with high levels of endemicity, to the point that they can easily be overlooked for years, even in the case of relatively large and noticeable animals such as the *Cebrennus* spiders described in this study.

CRediT authorship contribution statement

Marc Domènech: Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Arnau Calatayud-Mascarell:** Writing – original draft, Resources, Investigation. **Álvaro Pérez-Gómez:** Writing – original draft, Resources, Investigation. **Mattia Giacomelli:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis. **Arturo Iglesias Baquero:** Writing – review & editing, Resources. **Maite Mojica:** Writing – review & editing, Resources, Investigation. **Juan José Guerrero:** Writing – review & editing, Resources. **Miquel A. Arnedo:** Writing – original draft, Validation, Supervision, Investigation. **Jesus Lozano-Fernandez:** Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2025.08.005.

Data availability

Genetic data has been uploaded to GenBank, and accession numbers are provided.

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