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Lower Cretaceous spiders (Arthropoda: Arachnida: Araneae) from Spain

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With 5 figures

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Abstract: The first specimens of spiders in the early Cretaceous (Barremian) Konservat-Lagerstätte of Las Hoyas, Spain, are described. One is referred to *Macryphantes cowdeni* SELDEN, 1990, previously described from Montsech, another Spanish locality in early Cretaceous strata. The other is new, and is named as *Huergina diazromerali* n. g. n. sp. Both spiders are placed in the modern family Tetragnathidae. In a reassessment of the Montsech spiders, *Palaeouloborus lacasae* SELDEN, 1990 and *Cretaraneus vilaltae* SELDEN, 1990 are placed in Uloboridae and Tetragnathidae: Nephilinae, respectively.

Zusammenfassung: Aus der frühkretazischen (Barremian) Konservatlagerstätte Las Hoyas werden die ersten Spinnen beschrieben. Ein Exemplar wird *Macryphantes cowdeni* SELDEN, 1990 zugewiesen, einer Art, die bisher nur aus Montsech, einer anderen spanischen frühkretazischen Lagerstätte bekannt war. Das zweite Exemplar gehört zu einer neuen Art; sie wird *Huergina diazromerali* n. g. n. sp. genannt. Beide Spinnen gehören zu der, auch rezent vertretenen, Familie Tetragnathidae. Eine Neubewertung der Spinnen aus Montsech zeigt, daß *Palaeouloborus lacasae* SELDEN, 1990 zu den Uloboridae und *Cretaraneus vilaltae* SELDEN, 1990 zu den Tetragnathidae: Nephilinae gehören.

Introduction

Fossil spiders are relatively rare even in those Fossil Konservat-Lagerstätten which yield enormous numbers of insect fossils. At the Las Hoyas fossil site, Cuenca, Spain, the rocks of early Cretaceous (Barremian) age have produced

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only two spider specimens, among hundreds of insects, and these are described herein. There are few records of Cretaceous spiders: indeterminate Araneae from the ?Barremian-Aptian of Koonwarra, South Australia (JELL & DUNCAN 1986), mygalomorphs from the Lower Cretaceous of Transbaikalia and Mongolia (ESKOV & ZONSHTEIN 1990); orbicularian araneomorphs from the Berriasian-Valanginian of the Sierra de Montsech, Spain (SELDEN 1989, 1990, 1991); an unnamed lycosoid from Orapa, Botswana ('early Upper Cretaceous', RAYNER & DIPPENAAR-SCHOEMAN 1995), a poorly preserved specimen from the Albian of México (FELDMANN et al. 1998), and many new spider specimens reported from the Aptian Crato Formation of Brazil (but only one has so far been described by MESQUITA 1996). Spiders are known from Cretaceous amber from Canada (Campanian, MCALPINE & MARTIN 1969), Siberia (Albian-Santonian, ESKOV & WUNDERLICH 1994; ZHERIKHIN & ESKOV 1999), France (Cenomanian, SCHLÜTER 1978), Lebanon (Aptian, possibly reworked Hauterivian, SCHLEE & DIETRICH 1970; AZAR 1998; PENNEY & SELDEN 2002), Burma (reworked Cretaceous in Eocene sediments, COCKERELL 1920; RASNITSYN & ROSS 2000; ZHERIKHIN & ROSS 2000), Caucasus (Cenomanian, Coniacian, ESKOV & WUNDERLICH 1994), New Jersey (Turonian, GRIMALDI et al. 2000; PENNEY 2002), Álava, Spain (Albian-Aptian, ALONSO et al. 2000), Asturias, Spain (ARBIZU et al. 1999) and the Isle of Wight, England (SELDEN 2002). Few of these have been formally described and named.

The new specimens described here resemble most closely those from the Sierra de Montsech, Huesca, Spain, locality in slightly older (Berriasian-Valanginian) strata (MARTÍNEZ-DELCLÒS 1991a, b). Both sites have yielded a rich biota of terrestrial and freshwater organisms from lithographic limestones (Plattenkalk), including a few spiders (SELDEN 1989, 1990, 1991). Indeed, one of the new spiders described here is referred to a species from Montsech, *Macryphantes cowdeni* SELDEN 1990, family Tetragnathidae MENGE, 1866, whilst the other is a new genus and species in the same family. In the light of these new finds, previously described spiders from Lower Cretaceous strata of Montsech, Spain (SELDEN 1989, 1990), are re-evaluated. As a result, *Cretaraneus vilaltae* SELDEN, 1990 is placed in the modern subfamily Nephilinae SIMON, 1894 of Tetragnathidae, and *Palaeouloborus lacasae* SELDEN, 1990 in the modern family Uloboridae THORELL, 1869. *Palaeouloborus* was considered to be close to the Uloboridae by SELDEN (1990); PENNEY (2002) suggested placing it within that family, and it is formally assigned to the Uloboridae herein. Tetragnathine tetragnathids and uloborids construct similar, subhorizontal orb webs; uloborids use cribellate silk whereas the capture threads of tetragnathids have glue droplets. Many tetragnathids occur today near water where they weave their webs in the evening to catch nocturnal insects. These finds from Las Hoyas

add to the sparse record of Cretaceous Araneae and are further evidence that the orb-weaver families have a long history of diversity in the Mesozoic.

Geological Setting

The lithographic limestones of Las Hoyas were laid down in a small, NW-SE elongated basin about 150 km² in area, one of many fault-bounded basins created during rotation of the Iberian plate adjacent to the Tethys ocean during early Cretaceous times (see FREGENAL-MARTÍNEZ & MELÉNDEZ 1995 for details). A maximum thickness of 300 m of limestones, the La Huérgina Formation, was laid down in Barremian times, of which two sections of rhythmically laminated limestones have yielded abundant insects. These laminated (lithographic) limestones show microscale (1-2 mm) laminations of alternating dark, organic-rich (3.73 %) and pale, relatively organic-poor (0.95 %) layers. The laminated limestones have been interpreted as a distal lacustrine facies.

Material and Methods

The specimens are deposited in the Museo del Instituto Tecnológico GeoMinero, Madrid. They are preserved as very flattened external moulds, with little relief, together with some adhering organic material such as cuticle and macrosetae on the appendages and well sclerotized parts of the body such as book-lung opercula and the pedicel plagula.

The fossils were studied with a Wild M7S stereomicroscope. Photographs were taken with a Minolta Dynax 9 camera attached to the Wild, onto Agfa ISO 100 color slide film which was then scanned using a Nikon LS-30 film scanner and VueScan software (HAMRICK 2002) at 2700 dpi before reprocessing in Adobe Photoshop. ADR-001-AR/A and ADR-001-AR/B are sufficiently flat that they were scanned directly into Photoshop from an Epson Perfection 1640SU (1600dpi) flatbed scanner. All image manipulation was carried out using Macintosh G3 and G4 computers. Drawings were made with a camera lucida attachment to the Wild.

All measurements are in millimetres (mm). ≥ denotes 'at least' with reference to lengths or numbers; e.g. macrosetae on a podomere. Standard leg formulae are used; e.g. 1423 indicates that walking leg 1 is the longest, 4 the next longest, and 3 the shortest. Setae are the normal, gradually tapering, socketed hairs; macrosetae (spines) are generally larger and thicker than setae, and can be distinguished from setae because they thicken distally before tapering towards the tip, whereas setae taper from the base. **Abbreviations:** 1, 2, 3, 4: walking legs 1-4; AS: anterior spinneret; b o: branchial operculum; car: carapace; ch: chelicera; cx: coxa; epg: epigyne; fe: femur, lab: labium; ms: macroseta; mt: metatarsus; op: opisthosoma; p: posterior; pa: patella; Pd: pedipalp; pl: plagula, ta: tarsus; ti: tibia; tr: trochanter.

Morphological Interpretation

Macryphantes

Specimens ADR-002-AR/A and ADR-002-AR/B (part and counterpart) (Figs. 2, 3e-f) can be referred to *Macryphantes cowdeni*. Fig. 1 shows a comparison of the podomere lengths of the Las Hoyas specimen with those of the described specimens of *M. cowdeni* (2 specimens) and *Palaeouloborus lacasae* from Montsech. It can be seen that the podomere lengths of the Las Hoyas and Montsech *Macryphantes* agree well whilst *Palaeouloborus* is clearly different. The Las Hoyas *M. cowdeni* also shows another feature consistent with its placement in this species: an abundance of spines on all podomeres except coxae and trochanters.

Huergina

The preservation of *Huergina* (Figs. 3a-e, 4, 5) is not good enough to identify the spider conclusively. Nevertheless, more information than is at first apparent can be extracted from the specimens by judicious use of alcohol and low-angle lighting. The only features still preserved in organic matter on ADR-001-AR/A, and their interpretations, are as follows. A trifoliate object situated in the anterior part of the prosoma (Fig. 2d) is interpreted as the labium and the endites of the pedipalp coxae ('maxillae'). Two parallel-sided, subrectangular plates which taper anteromedially to connect with a cross-shaped sclerite are interpreted as book-lung opercula and the pedicel plagula. Two-thirds of the way down the length of the opisthosoma is a mass of amorphous organic material which cannot be interpreted as any particular organ. A pair of faint sclerotized spots posterior to the book-lung opercula possibly represent the epigyne. There is also faint sclerotization near the trochanters of legs 1 and 4. Distal parts of the legs are preserved in darker (carbonized) material, and setae are visble in this darker material. Low-angle light reveals a cover of fine setae, but no macrosetae, over the whole of the specimen, in the form of fine striae in the rock matrix. Such illumination also helps to reveal the pattern of spinnerets.

The chelicerae are not especially large; the pedipalps have somewhat thickened podomeres. However, there is no trace of modified pedipalp tarsi, so the spider cannot be a mature male. It is possibly a female, as evidenced by the paired sclerotization in the epigynal region, and female spiders commonly show slightly thicker pedipalp podomeres than leg podomeres. The book-lung opercula are thick and show very distinct longitudinal striations. These are clearly part of the structure of the operculum, but low-angle light suggests that these striations were also visible on the surface; there are no traces of transverse ridges or grooves.

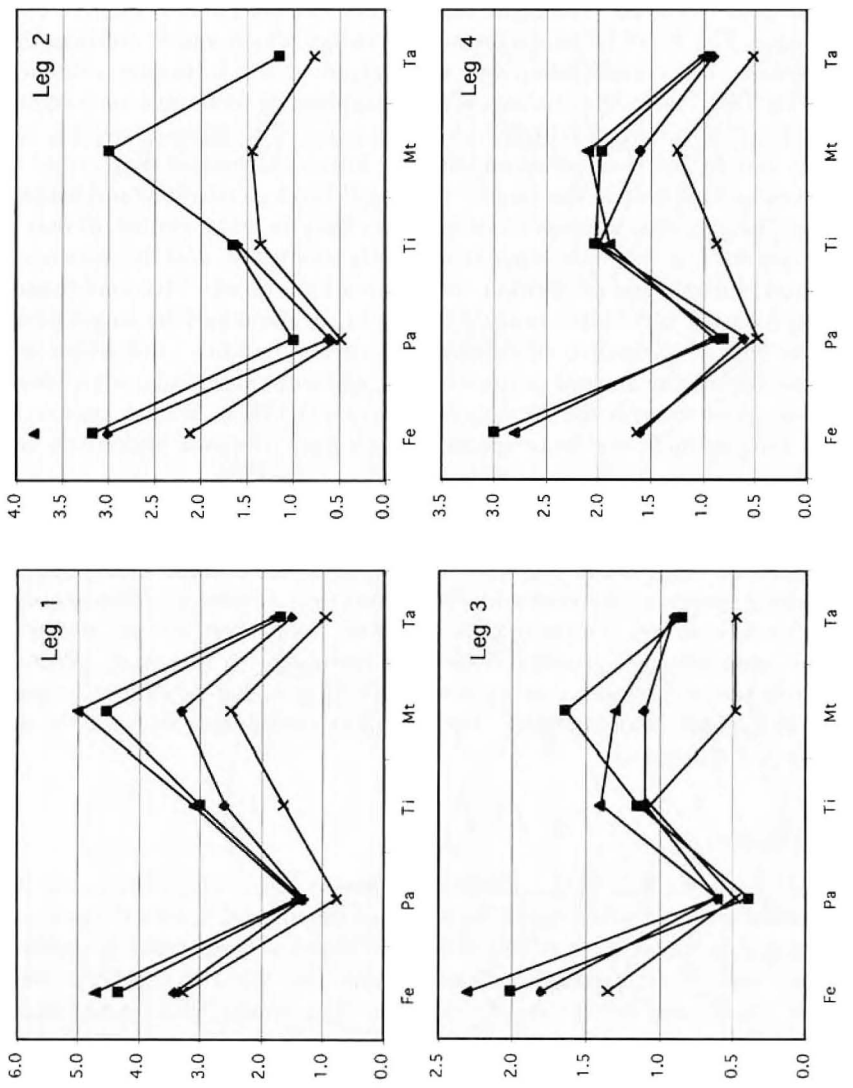

Fig. 1. Graphs comparing podomere lengths of walking legs 1-4 of *Macryphantes cowdeni* SELDEN, 1990, from Las Hoyas and Montsech, and *Palaeouloborus lacasae* SELDEN, 1990, from Montsech. Legend: ♦, *M. cowdeni*, Las Hoyas; ■ and ▲, *M. cowdeni*, Montsech; ×, *P. lacasae*, Montsech.

Huergina is placed, with some reservation, into the modern family Tetragnathidae. The fossil lacks diagnostic characters which would confirm this assignation, but consideration has been given to the following evidence. First, the fossil lacks the obvious synapomorphies of most ground-dwelling spiders and specialized families of Haplogynae. The tarsal claws are not clearly visible, but if scopulae and/or claw tufts were present they would be preserved and visible in the fossils. The fossil lacks a cribellum and calamistrum. The carapace appears to be about as long as wide, similar to that in *Macryphantes*; the opisthosoma is distinctly elongated, and the spinnerets are short, subterminal in position, and form a tight group. The combination of long legs 1, 2 and 4 with a very short leg 3 (i.e. about half the length of the longest leg) is distinctive of orb-weavers of the families Uloboridae and Tetragnathidae, the araneid genus *Argiope*, and some theridiids. All of these features point towards the Araneoidea Latreille, 1806. Within araneoids, many tetragnathids are large spiders which have elongate abdomens and weakly sclerotized epigynes. Theridiids are generally smaller. Arguing against this identification as a tetragnathid, many (but not all) members of this family have enlarged chelicerae, which the fossil does not. Some tetragnathids (e.g. *Meta, Nephila, Nephilengys*) have transversely ridged book-lung opercula, like araneoids, but others (e.g. *Leucauge, Glenognatha, Tetragnatha*) do not (Griswold et al. 1998). None that we are aware of shows longitudinally grooved book-lung opercula. To conclude, positive evidence places *Huergina* in Araneoidea, within which superfamily, most features suggest Tetragnathidae. The possibility exists that *Huergina* is the female of *Cretaraneus*.

Discussion

The presence of a new tetragnathid spider species at Las Hoyas increases the number of spiders for this family known from the Spanish Lower Cretaceous. Tetragnathids are weavers of orb webs, and many of them make their webs sub-horizontally in vegetation close to water, so that the web can catch insects flying over water, usually at night. This habitat puts tetragnathids

Fig. 2. *Macryphantes cowdeni* Selden, 1990, Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain. Camera lucida drawing of part (ADR-002-AR/A, left) and counterpart (ADR-002-AR/B, right); explanatory drawings for Figs. 3f and 3g, respectively. Scale bar: 1 mm.

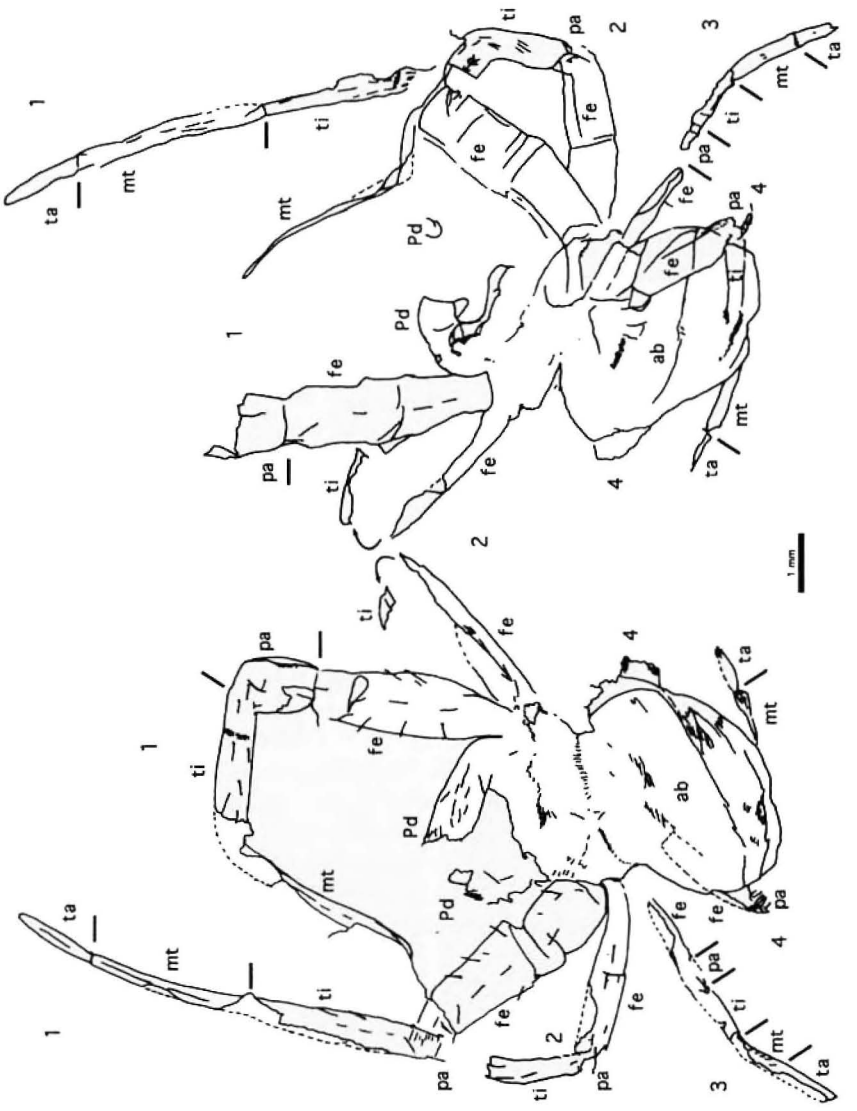

Fig. 2 (Legend see p. 180)

close to sites of sediment deposition in the lacustrine environment and a flood, for example, would be more likely to trap tetragnathids than other web weavers. Tetragnathids are very similar in many respects to the cribellate Uloboridae (superfamily Deinopoidea C. L. KOCH, 1850, sister-group to Araneoidea), which also commonly construct sub-horizontal orb webs and share many morphological features with tetragnathids.

From Montsech, *Palaeouloborus lacasae* was described as a deinopoid close to the modern family Uloboridae by SELDEN (1990). It was not included in Uloboridae because it lacks two synapomorphies (feathery setae and fourth tarsal macrosetae) of that family. *Macryphantes cowdeni* was described as a tetragnathid, and an additional specimen of this species is described herein. The third spider species found at Montsech, *Cretaraneus vilaltae*, was unassigned within Araneoidea. These were only the third to fifth Mesozoic spiders ever to be described, so SELDEN (1990) was cautious about referring them to modern families and genera because of the possibility that they were plesiomorphic stem groups or ancestors to modern families. Now, with our greater knowledge that many modern spider families, especially araneoids, extend far back into the Mesozoic (SELDEN & PENNEY 2001), this caution is less justified, and the phylogenetic positions of the Montsech spiders are discussed below.

The single specimen of *Cretaraneus vilaltae* is an adult male exhibiting a very distinctive pedipalp with a long, slightly twisted, embolus (SELDEN 1990, Text-fig. 4c, d, f, g). As was mentioned by SELDEN (1990), this form of male pedipalp is characteristic of the genus *Nephila*, a tetragnathid (see, for example, CANARD & DRESCO 1975, figs. 8, 9; DAVIES 1988, fig. 19; LEVI & VON EICKSTEDT 1989, figs. 1, 2, 5, 6, HORMIGA et al. 1995, fig. 10). Consequently, we assign *Cretaraneus vilaltae* to the Tetragnathidae: Nephilinae on the basis of its distinctive pedipalp. Generally, the pedipalps of *Nephila* are quite distinct from those of other nephilines, such as *Nephilengys*, and *Herennia* (e.g. LEVI & VON EICKSTEDT 1989, figs. 16-19, HORMIGA et al. 1995, figs. 11, 12), although the pedipalp of *Cretaraneus* is quite close in

Fig. 3. *Huergina diazromerali* n. g. n. sp. (**a-e**) and *Macryphantes cowdeni* SELDEN, 1990 (**f-g**), Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain. **a:** ADR-001-AR/A x 1.25; **b:** ADR-001-AR/B x 1.25, **c:** ADR-001-AR/A, body, x 6.4; **d:** ADR-001AR/B, body, x 6.4; **e:** ADR-001-AR/A, close-up of trifoliate structure (labium and pedipalp coxal endites), plagula and book-lung opercula, x 18; **f:** ADR-002-AR/A x 5.7; **g:** ADR-002-AR/B x 5.7.

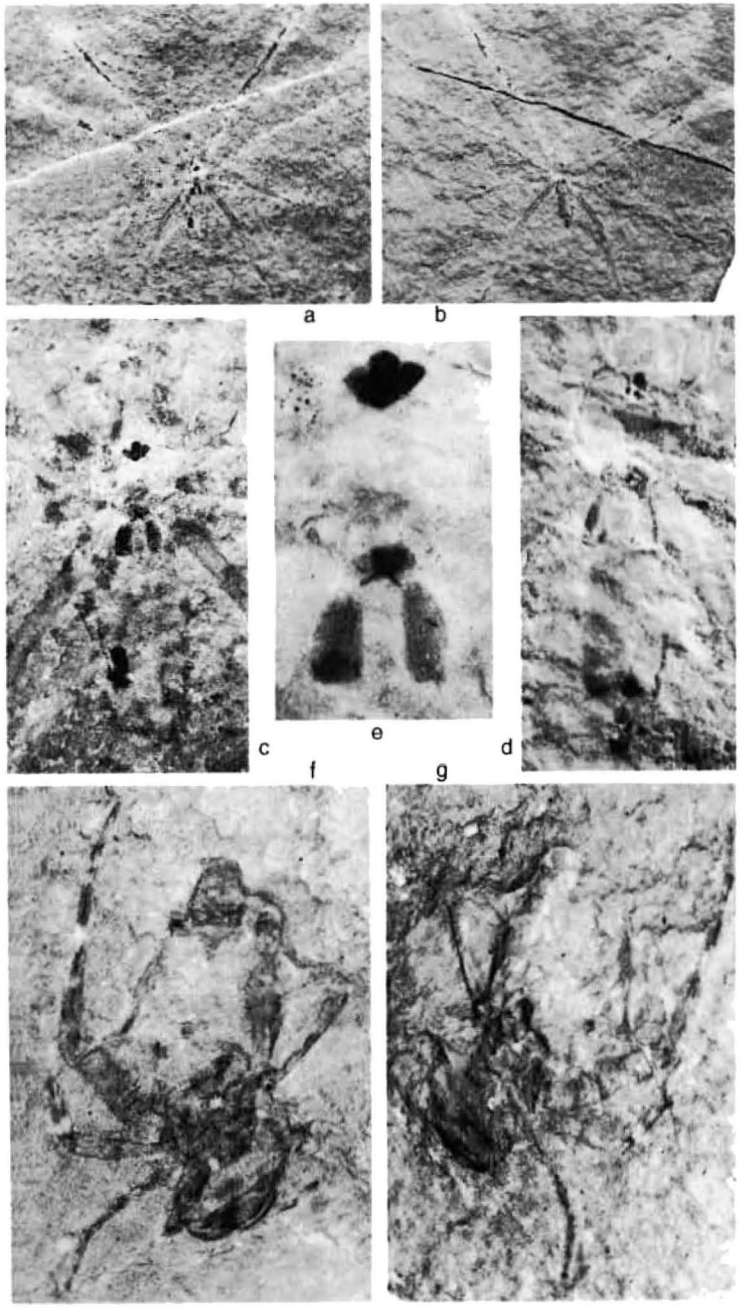

Fig. 3 (Legend see p. 182)

general morphology to that of *Nephilengys malabarensis* (DAVIES 1988, fig. 20). Modern nephilines exhibit quite extreme sexual size dimorphism, the males being considerably smaller than the females. *C. vilaltae* has a body length of less than 4 mm, excluding chelicerae, which is about the same size as the males of many nephilines (e.g. LEVI & VON EICKSTEDT 1989, figs. 8, 20). Another species of *Cretaraneus*, *C. martinsnetoi* MESQUITA, 1996, was described from the Lower Cretaceous Crato Formation of the Chapada do Araripe, north-east Brazil. The holotype of this species lacks identifiable characteristics; it was referred to *Cretaraneus* because there were few other described Cretaceous spiders known at that time, and its habitus matched that of the Spanish specimen. Of the diagnostic characters of *C. martinsnetoi* ('chelicerae turned upon the abdomen', 'absence of a claw', and 'presence of spines on the patella', MESQUITA 1996 p. 24), the first two are artefacts due to preservation and incorrect interpretation, whilst the last appears to be a real difference between the species. There are no features of *C. martinsnetoi* which would suggest its inclusion in Nephilinae, but at present there seems no reason to exclude it from the genus. Many specimens of spiders are now available for study from the Brazilian Crato Formation, so it is likely that future work (planned by SELDEN and MESQUITA) will reveal the true identity of these spiders.

Palaeouloborus was referred to Deinopoidea on the basis of the distinctive calamistrum set in a curved depression on the superior surface of leg 4 metatarsus; femoral trichobothria on legs 2, 3 and 4; elongate leg 1 and short leg 3; plumose hairs; and accessory claws on the tarsi. SELDEN (1990) suggested that, of the two deinopoid families *Palaeouloborus* was closer to Uloboridae than Deinopidae C. L. KOCH, 1850. Deinopids show significant modifications for prey capture: enormous, forwardly directed, anterior median eyes (one of their common names is 'ogre-faced spiders'), and specialized predatory behaviour involving capturing prey with a miniature orb-like web held between legs 1 and 2 (hence another common name of 'net-casting spiders'). Many are stick-like with long legs and elongate bodies. Whilst some uloborids have an elongate prosoma and/or opisthosoma, many are shaped like *Palaeouloborus*, which shows none of the synapomorphies of Deinopidae. The key question is how to deal with a stem-group 'uloborid'. There is much discussion among systematists concerning whether to define taxa to include or exclude the clade stem. This is not the place for continuing this debate. The present problem can be solved in one of two ways: include *Palaeouloborus* in Uloboridae, in spite of the fact that it appears to lack tarsal macrosetae and feathery setae (it is possible that these have simply not been preserved in the only known specimen), or to restrict Uloboridae to the crown group. In the latter case, a new name would

be required for the clade (*Palaeouloborus* + Uloboridae). The former option seems preferable and, indeed, would be the obvious solution were *Palaeouloborus* a Recent spider.

Systematic Descriptions

Order Araneae CLERCK, 1757
Suborder Opisthothelae POCOCK, 1892

Infraorder Araneomorphae SMITH, 1902

Remarks: The new genus *Huergina* belongs in this infraorder because of its single pair of book lungs; two pairs of book lungs occur in suborder Mesothelae POCOCK, 1892, infraorder Mygalomorphae POCOCK, 1892 and primitive araneomorphs.

Superfamily Deinopoidea C. L. KOCH, 1850
Family Uloboridae THORELL, 1869

Palaeouloborus lacasae SELDEN, 1990

1990 *Palaeouloborus lacasae*. – SELDEN, p. 263, text-fig. 1, pl. 1, pl. 2 figs. 1-5, 7, 8.
1991 *Palaeouloborus lacasae*. – SELDEN, p. 83, fig. 1.

Remarks: *P. lacasae* is placed in this family on the basis of its general shape like that of uloborids and lack of the distinctive synapomorphies (e.g. stick-like form, extremely large anterior median eyes) of Deinopidae, the only other family in this superfamily.

Superfamily Araneoidea LATREILLE, 1806

Remarks: Characters placing *Macryphantes* in this superfamily were discussed by SELDEN (1990). *Huergina* is placed here because of its long, slender legs, lack of tarsal scopulae, elongate abdomen, tightly grouped, short, subterminal spinnerets, and lack of distinctive synapomorphies of other superfamilies.

Family Tetragnathidae MENGE, 1866

Remarks: Characters placing *Macryphantes* in this family were discussed by SELDEN (1990). *Huergina* is placed here because of its large size, elongate abdomen, and leg 3 about half the length of the longest leg (1).

Huergina n. g.

Type and only species: *Huergina diazromerali* n. sp.

Etymology: After the La Huérgina Formation, the stratum in which the specimen was discovered.

Diagnosis: Tetragnathid spider with longitudinal striations on book-lung operculum.

Huergina diazromerali n. sp. (Figs. 3a-e, 4, 5)

Holotype and only specimen: ADR-001-AR/A (part) and ADR-001-AR/B (counterpart), from the Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain, held in the Museo del Instituto Tecnológico GeoMinero, Madrid. Adult female?

Etymology: In honour of Sr ARMANDO DIAZ-ROMERAL of Cuenca, who discovered the specimen.

Diagnosis: As for the genus.

Description: Carapace as wide as long; length 1.9, width 1.9. Chelicera length 1.1. Pedipalp length 2.0. Walking leg formula 1243; podomere lengths: fel 5.5, pal 1.0, til 5.8, mtl 4.5, tal 2.0, fe2 5.5, pa2 1.0, ti2 4.8, mt2 3.8, ta2 1.8; fe3 2.8, pa3 0.8, ti3 2.2, mt3 1.6, ta3 1.1; fe4 4.7, pa4 1.1, ti4 4.0, mt4 2.5, ta4 1.5. Opisthosoma length 6.4, width 2.6, parallel-sided, pedicel with bifid plagula, its lateral branches diverging posteriorly and each touching anterior edge of branchial operculum, branchial operculum with longitudinal striations; possible epigyne with paired pockets; AS short, conical, 2-segmented, subterminal.

Macryphantes cowdeni SELDEN, 1990 (Figs. 2, 3f-g)

1990 *Macryphantes cowdeni*. – SELDEN, p. 275, text-figs. 5-6, pls. 3-4.
1991 *Macryphantes cowdeni*. – SELDEN, p. 84, fig. 3.
1991 *Macryphantes cowdeni*. – MARTÍNEZ-DELCLÓS et al., p. 161, photo 4.

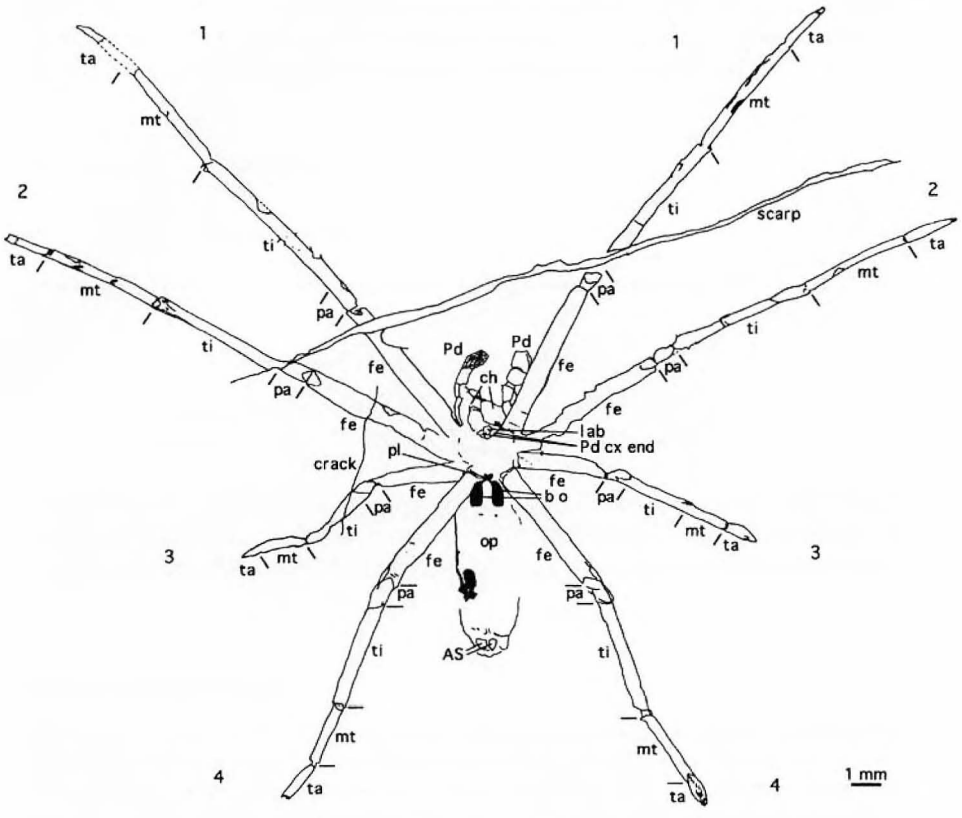

Fig. 4. *Huergina diazromerali* n. g. n. sp., Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain. Camera lucida drawing of ADR-001-AR/A; explanatory drawing for Figs. 3a, e, d.

Material: ADR-002-AR/A (part) and ADR-002-AR/A (counterpart), from the Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain, held in the Museo del Instituto Tecnológico GeoMinero, Madrid.

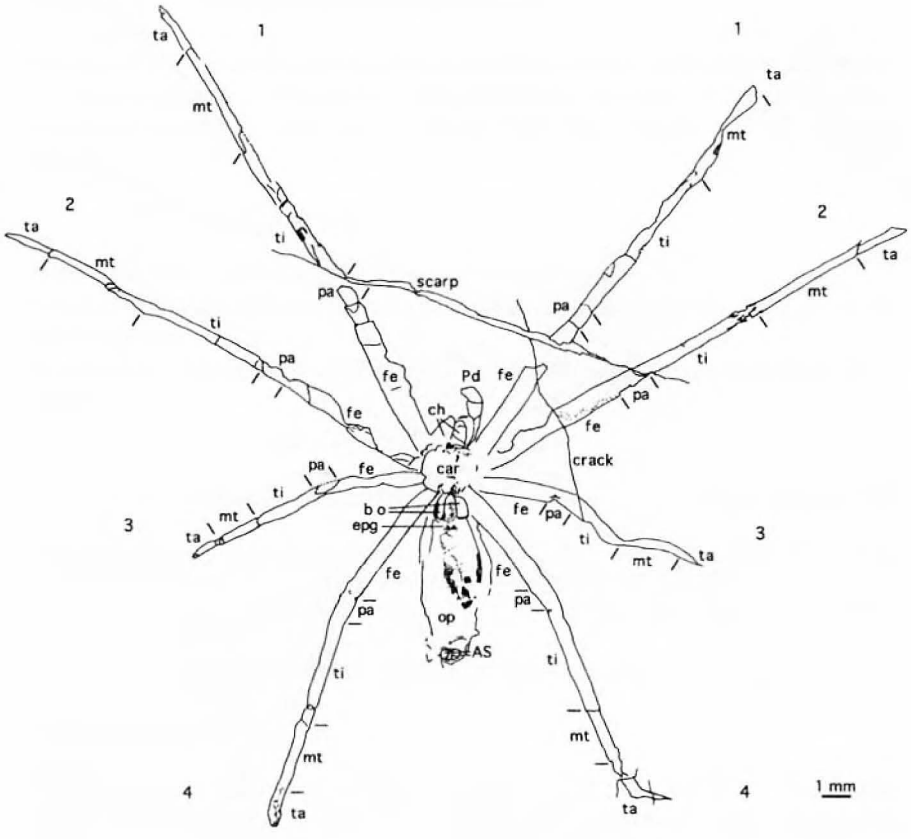

Fig. 5. *Huergina diazromerali* n. g. n. sp., Lower Cretaceous (Barremian) La Huérgina Formation of Las Hoyas, Cuenca, Spain. Camera lucida drawing of ADR-001-AR/B; explanatory drawing for Figs. 3b, e.

Description: Because of the poor preservation of this specimen, measurements are very approximate. Carapace, chelicerae and ventral prosomal elements poorly preserved. Pedipalp length ≥ 2.2. Walking leg formula 1243; podomere lengths: fel 3.4, pal 1.3, til 2.6, mtl 3.3, tal 1.5; fe2 3.0, pa2 0.6, ti2 1.6; fe3 1.8, pa3 0.6, ti3 1.1, mt3 1.1, ta3 0.9-, fe4 1.6, pa4 0.6, ti4 4.0,

mt4 1.6, ta4 0.9. Numerous macrosetae, arranged in whorls, on at least pedipalp and legs 1 & 2 (≥ 5 on Pd; ≥ 9 on fe1, ≥ 1 on pal, ≥ 6 on ti1; ≥ 4 on fe2, ≥ 2 on pa2, ≥ 2 on ti2). Opisthosoma length 3.0, width 3.8.

Subfamily Nephilinae SIMON, 1894

Cretaraneus SELDEN, 1990

Included species: *C. vilaltae* SELDEN, 1990 & *C. martinsnetoi* MESQUITA, 1996.

Cretaraneus vilaltae SELDEN, 1990

1990 *Cretaraneus vilaltae*. – SELDEN, p. 270, text-figs. 2-4.
1991 *Cretaraneus vilaltae*. – SELDEN, p. 83, fig. 2; p. 85, photo 1.

Remarks: *C. vilaltae* is referred to Nephilinae on the basis of the male pedipalp which has a distinctive, tapering, moderately helical embolus as long as the basal body of the pedipalp tarsus, characteristic of the subfamily.

Acknowledgements

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