LOWER CRETACEOUS SPIDERS FROM THE SIERRA DE MONTSECH, NORTH-EAST SPAIN

by PAUL A. SELDEN

ABSTRACT. Four new specimens of spiders (Chelicerata: Araneae), from Lower Cretaceous (Berriasian–Valanginian) lithographic limestones of the Sierra de Montsech, Lérida Province, north-east Spain, are described, as *Cretaraneus vilaltae* gen. et sp. nov., *Macryphantes cowdeni* gen. et sp. nov. (two specimens), and *Palaeouloborus lacasae* gen. et sp. nov. All belong to the infraorder Araneomorphae. *Palaeouloborus* is the oldest representative of the superfamily Deinopoidea, *Cretaraneus* is referred to the superfamily Araneoidea, and *Macryphantes* is the oldest record of the superfamily Araneoidea, family Tetragnathidae (metine–tetragnathine–nephiline group). All three spiders were web weavers; *Macryphantes* and *Palaeouloborus* wove orb webs, and may have used a wrap attack to prey on the abundant contemporaneous insect life preserved in the Montsech deposit.

SPIDERS are rare in rocks of Mesozoic age. Only two specimens, *Juraraneus rasnitsyni* Eskov, 1984, and *Jurarchaea zherikhini* Eskov, 1987, from the Jurassic of the USSR, have been adequately described. Three specimens from the Lower Cretaceous of New South Wales (Jell and Duncan 1986) and twelve from the Trias of France (Gall 1971) were not identified to a taxonomic rank below that of order. Spiders reported from Canadian Cretaceous amber (McAlpine and Martin 1969), the Jurassic and Cretaceous of Siberia and Mongolia (reported in Eskov 1984), and the Cretaceous of Botswana (Waters 1989) await description. The four specimens described here are sufficiently well preserved for their taxonomic affinities to be determined with some precision, and thus they represent only the third find of Mesozoic spiders to be described and named. The fossil spiders described here are placed in extant superfamilies or families, but closer assignation is considered unwise pending the outcome of current studies on living and fossil members of these groups.

GEOLOGICAL SETTING

Locality. The Sierra de Montsech lies in the foothills of the eastern Pyrenees, between Balaguer and Tremp in Lérida Province, north-east Spain (see Schairer and Janicke (1970) for details and location map). Three quarries in the vicinity of the abandoned village of Rúbies, in the eastern part of the sierra, yield remarkable fossils. 'La Pedrera de Meià' and 'La Cabrúa' have been worked for many years, and 'El Reguer' is currently under investigation.

Stratigraphy. The 50 m succession of limestones exposed in the quarries, the 'Calcaires lithographiques à Plantes et Vertébrés de la Pedrera de Rúbies', is a facies development of the 100 m 'Calcaires à Charophytes du Montsech' (Peybernes 1976). The deposit has been determined as late Berriasian to early Valanginian in age on the evidence of ostracodes (Peybernes and Oertli 1972; Brenner, Goldmacher and Schroeder 1974; Whalley and Jarzembowski 1985), a conclusion consistent with evidence from palynology (Barale *et al.* 1984; R. Porter, personal communication 1988).

Sedimentology. The Calcaires à Charophytes du Montsech is a sequence of mostly pale, fine-grained, thinly-bedded limestones. Sedimentary structures include laminations, fine grading, minor deformation, and roll marks; trace fossils include arthropod trackways (Schairer and Janicke 1970). The environment of deposition deduced from the sedimentological and palaeontological evidence

(see below) is that of coastal lagoons within a large area of algal flats separating marine conditions to the north from the Ebro continent to the south (Barale *et al.* 1984). The spider-bearing sequence, the Lithographic Limestones, represents a particularly tranquil lacustrine depositional episode (Lacasa and Martinez 1986).

History of the fauna and flora. The exceptionally preserved biota of the Montsech lithographic limestone has received attention from palaeontologists since the beginning of this century. In the last few years, renewed interest in the deposit has brought new material to light, including the specimens described here, and avian fossils of phylogenetic importance from a locality of similar age and lithology in the neighbouring province of Cuenca (Sanz *et al.* 1988). Lists of the fauna and flora were given by Barale *et al.* (1984), with the most recent summary, especially of the insects, provided by Lacasa and Martinez (1986). All the indigenous microflora is of terrestrial or non-marine aquatic provenance; the macroflora includes a wide range of gymnosperms, progymnosperms, a few ferns and horsetails, and other, unclassified, plants. Animals include ostracodes, few decapod crustaceans, larval and mature insects belonging to eight extant orders, a wide variety of fish, a few frogs and reptiles, and some bird remains. The spiders were first mentioned by Lacasa (1985, p. 228), and a preliminary report of the results presented here was given by Selden (1989).

MATERIAL AND METHODS

Preservation. The spiders are preserved on thin slabs of pale buff-grey limestone. Grains are not visible in the rock, and the hackly fracture and vitreous appearance under high-power microscopy suggest crystallization from a lime mud. Calcite-filled cracks cross some specimens. The spiders are preserved as pieces of cuticle on the bedding surface. The cuticle is brittle and brown: thicker parts are deep brown and the thinnest cuticle pale buff. The cuticle has not been chemically analysed; it is presumed still to be organic, but probably not of the original composition. The best-preserved parts are visible through a thin layer of translucent limestone, but their morphological details are hazy due to the presence of the overlying matrix. In such instances, 2–4% hydrochloric acid was used, sparingly and with care, to remove the matrix and thus to reveal fine structural details. The spiders are in varying states of original decay: for example in LC 1753 AP the podomeres, of leg 1 in particular, are crowded with subcircular objects along the central parts of the shaft. These objects are interpreted as the decayed remnants of muscles. LC 1754 AP is very poorly preserved: mainly a mould remains, and this is interpreted as a specimen in which decay has progressed further.

Both part and counterpart of specimens LC 1753 AP and LC 1754 AP are preserved, but only the part of specimens LC 1150 IEI and LP 1755 AP was collected. Specimens LC 1753 AP B, LC 1754 AP A, LC 1150 IEI, and LP 1755 AP represent lower slabs preserving mainly ventral features of the specimens; LC 1753 AP A and LC 1754 AP B are upper slabs with dorsal features. However, splitting of the rock has not resulted in perfect separation of dorsal and ventral, and due to the mode of preservation within the limestone (described above), most of both dorsal and ventral parts are preserved on LC 1753 AP B, and LC 1150 IEI. LC 1754 AP is mainly an external mould with little cuticle remaining, but on LP 1755 AP ventral parts of the body and both dorsal and ventral sides of the distal parts of the legs are preserved. On all specimens, the legs and abdomen (when present) are crushed flat. The carapace has sufficient convexity to produce relief in the fossils, so that on LP 1755 AP, for example, the carapace shape can be determined by the relief of the fossil, and the shapes of the sternum and coxae are outlined by setae and cuticle. The male palps of LC 1753 AP, LC 1754 AP, and LC 1150 IEI appear to occupy depressions in the matrix. This is probably because they were bulbous structures in life and therefore created a concavity in the sediment into which the palp collapsed during burial.

The spiders were studied under a Wild M7S stereomicroscope, with the specimens immersed in ethanol or glycerine to enhance their contrast against the pale rock background. Camera lucida drawings were made and photographs were taken under the same conditions. In addition, a Zeiss photautomat microscope was used, in reflected light mode with oil immersion objectives, to view

and photograph details at higher magnifications. The computer program MacClade, version 2.1 (Maddison and Maddison 1987) proved very useful for exploring relationships.

Terminology. Setal terminology is somewhat problematical, since different authors have used the same terms in different ways. Furthermore, there is a complete gradation in size between setae (small, and may be short or long, thick or thin), bristles, and spines (large). Macroseta is a term used, for example by Opell (1979), to describe a large seta which could equally be called a small spine or bristle. The common hair-covering of *Cretaraneus* is the serrate seta, which is smooth apart from a few minute accessory spines which are no longer than the mean thickness of the seta (see Lehtinen 1967, fig. 10a; Kullmann 1972, fig. 7). Two fairly distinct setal types are commonly called plumose (e.g. by Forster and Wilton 1973; Forster and Blest 1979). The first, which is here called plumose, is generally thicker than the serrate seta, and has helical ridges bearing small accessory spines which are much shorter than the width of the seta (see Lehtinen 1967, fig. 8; Kullmann 1972, fig. 8). The second, which is here called feathery, is fine, smooth, and has long accessory branches which are much longer than the width of the seta (see Lehtinen 1967, fig. 9). Many other types of seta and spine exist; there may be complete gradations between them, and the extent of their phylogenetic importance is unknown.

Terminology of the sclerites of male palps differs between workers in different groups of spiders due to a lack of understanding of the homologies between the sclerites. Thus the task of recognizing palpal sclerites in fossil spiders is problematical. Useful descriptions of the constituent parts of male palpal organs are found in Comstock (1948), Levi (1961), Merrett (1963), and Millidge (1977).

In leg formulae (e.g. 1243), the leg lengths are ranked in order longest (first) to shortest (last). Abbreviations used in the text and text-figures are as follows:

ab	abdomen	l	labium	s	serrula
bo	book-lung operculum	lp	left palp	st	sternum
ca	cephalic area	m	maxilla	t	tegulum
cal	calamistrum	ma	median apophysis	ta	tarsus
ch	chelicera	mt	metatarsus	ti	tibia
cx	coxa	pa	patella	tia	tibial apophysis
e	embolus	pc	paracymbium	tr	trochanter
f	fovea	pe	pedicel		
fe	femur	rp	right palp		

Provenance and depository. Three of the fossil specimens, LC 1150 IEI, LC 1753 AP, and LC 1754 AP, come from the quarry of La Cabrúa, the fourth, LP 1755 AP, is from the locality of La Pedrera de Meià. Exact stratigraphical provenance is not known, but both of these localities are in the same 50 m sequence of lithographic limestones, the Calcaires lithographiques à Plantes et Vertébrés de la Pedrera de Rúbies, described above. The specimens are deposited in the Institut d'Estudis Ilerdencs, Lérida.

Preserved specimens of extant spiders were studied for comparative purposes, and in addition to those in the author's collection of mainly British species, the following specimens were examined. Uloboridae: *Hyptiotes flavidus*, female, Funchal, Madeira, M. J. Jones Collection No. 119, Manchester Museum; *Uloborus walckenaerius*, male and female, Chobham, Surrey, D. W. Mackie Collection No. G4999, Manchester Museum; *Philoponella* sp., male and female, Lake Naivasha, mature and immature males, Nairobi, Kenya, J. Murphy Collection Nos 1302, 1363. Deinopidae: *Deinopis guianensis*, female, British Guiana, British Museum (Natural History) (BM(NH)) No. 1939.3.24.228; *Deinopis stauntoni*, female, Durban, South Africa, BM(NH) No. 1903.8.20.1; *Deinopis* sp., female and immature, Kilifi, Kenya, J. Murphy Collection; *Menneus camelus*, females (types), Durban, South Africa, BM(NH) No. 1903.7.10.22; *Menneus* sp., male, Kitale, and female, Nairobi, Kenya, J. Murphy Collection; *Avella angulata*, female, Gayndah, Australia, BM(NH) No. 1919.9.18.5732; *Avella despiciens*, female, Sydney, Australia, BM(NH) No. 1919.9.18.5733.

Dictynidae: *Aebutina binotata*, immatures, Aguas Negras, near Tarapuy, Napo, Ecuador, British Museum (Natural History) Arachnid Collection.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder ARANEOMORPHAE Smith, 1902

Remarks. The phylogenetic scheme for the higher classification of spiders which is currently widely accepted originated with Pocock (1892). In this scheme, the Liphistiomorphae (Mesothelae) is the sister group to the Opisthothelae (Mygalomorphae + Araneomorphae). The morphology of liphistiomorphs is distinctive (Platnick and Gertsch 1976, fig. 5). The fossil spiders described here differ markedly from this pattern, lacking one or more of the following liphistiomorph synapomorphies: posteromedian invaginations of the fourth coxae, seven or eight forwardly situated spinnerets, sclerite of the first abdominal segment (Platnick and Gertsch 1976), and labium as wide as or wider than the sternum (Raven 1985). Thus they are referred to the Opisthothelae.

Mygalomorph synapomorphies include the following external morphological features: cheliceral fang which operates in the sagittal plane (orthognathous), complete loss of expression of the anterior median spinnerets, three or four articles in the posterior lateral spinnerets (Platnick and Gertsch 1976), labial and maxillary cuspules, and reduced male palpal sclerites (Raven 1985). The alternative character states typify the Araneomorphae, and it is to this latter group that the Montsech spiders are referred. In particular, the chelicerae of *Cretaraneus* gen. nov. are labidognathous (i.e. they operate transversely); the male palp of *Macryphantes* gen. nov. is more complex than the mygalomorph palp; and *Palaeouloborus* gen. nov. possesses a calamistrum and a cribellum; the latter is a homologue of the anterior median spinnerets. Neither labial or maxillary cuspules nor three- or four-segmented posterior lateral spinnerets are known in any of the Montsech spiders, and each of them shows greater affinity to araneomorph families than to mygalomorphs.

Assignment of the Cretaceous spiders to lower taxonomic categories presents greater difficulty. A competent araneologist can place most living spiders seen in the field into a family with a high degree of certainty. Even in the absence of field characters, such as web type and habitat, spider familial keys are relatively straightforward, only requiring the use of a binocular microscope and normally no dissection. Spider families are diagnosed on unique combinations of morphological characters such as number and position of eyes, spinneret pattern, and number of tarsal claws. However, research has shown that many of the characters on which the families are based are plesiomorphic at higher taxonomic levels, convergent with other groups, or are 'loss' characters (Lehtinen 1978). A classic example of this is the recognition of the cribellum as a synapomorphy for Araneomorphae: its presence in lower categories is merely the expression of the plesiomorphic state, and its absence illustrates convergence of the apomorphy in many araneomorph families. Whilst unique combinations of plesiomorphies may work as familial descriptions in practice, they cannot reflect true relationships between families. Of necessity, therefore, recent cladistic analyses have sought new or previously overlooked characters as apomorphies. These characters are commonly behavioural or anatomical, and may be poorly known in groups outside those under particular study. More important in the present work, such characters are most unlikely to be preserved in the fossil record.

An additional concern encountered when working with rare fossils which have Recent relatives arises from the possibility that the fossils may be ancestors of Recent species. Should the fossils be classified in the same scheme as their Recent relatives, or in a separate scheme? Such problems have been discussed by Crowson (1970), Farris (1976), Wiley (1981) and others. A useful device for classifying fossils with their Recent relatives is the plesion (Patterson and Rosen 1977); this presupposes, however, that the Recent classification is soundly based on shared derived characters.

In spider systematics this is not yet true. In this paper, the new taxa are classified as close as possible to their presumed position in the Recent classification. Inevitably this entails placement within taxa yet to be defined by synapomorphies or defined on shared derived characters which cannot be seen easily in fossils. Because these are among the first Mesozoic spiders to be described, and because of the paucity of diagnostic features in the fossils, and the present lack of knowledge of synapomorphies in living families, the fossil spiders are assigned to superfamilies, and in one case to a family, but to no extant lower taxa. (Note that among Cretaceous insects, classification to modern genera is not unusual.) More specimens of Mesozoic spiders which are becoming available for study may help to elucidate further the taxonomic positions of the specimens described here, and assist in unravelling the complexities of spider phylogeny and evolution. The 'consensus' spider classification scheme given in Shear (1986b) is followed here in general, but with discussion concerning the status of groups assigned to the Araneidae following recent work by Coddington (1989a, b, 1990).

Superfamily DEINOPOIDEA Koch, 1851

Remarks. This superfamily consists of the two cribellate families Uloboridae and Deinopidae, which weave orb webs (most Uloboridae) or spin modified orb webs which are then thrown, *retiarius*-like, at their prey (Deinopidae). Much more is known about uloborids than deinopids, though work on the latter is currently in progress. Although these two families have been considered closely related for nearly a century (Simon 1892), Coddington (1986, p. 359), with reference to his cladogram (p. 358), remarked that: 'the monophyly of the uloborid–deinopid lineage is based on only three characters, primarily because so little is known about deinopids.' The three characters Coddington accepted as deinopoid synapomorphies are: puffed cribellate silk, pseudoserrate plumose hairs, and fourth-tarsal macrosetae; however, he qualified this by suggesting that the first two characters may actually be synapomorphies for all orb-web weavers (Deinopoidea and Araneoidea) (Coddington 1986, pp. 327, 359). Recent work by Coddington (1989a, b, 1990) has resolved the apparent trichotomy between Araneoidea, Uloboridae, and Deinopidae (reported in Platnick 1986); Deinopoidea and Araneoidea being seen as sister groups in a monophyletic group of orb-web weavers: the Orbiculariae Walckenaer, 1802.

Palaeouloborus gen. nov., described below, possesses three tarsal claws with accessory claws typical of web weavers and lacks the tarsal adaptations of the superfamilies Thomisoidea, Philodromoidea, Lycosoidea, Clubionoidea, Salticoidea, and Pholcoidea. The fossil genus also lacks the synapomorphies of Scytodoidea (Lehtinen 1986), Dysderoidea (Forster and Platnick 1985), Palpimanoidea (Forster and Platnick 1984), Hersilioidea, Hypochiloidea (Platnick 1977), Eresoidea, and Agelenoidea. Dictynoidea are cribellates, and the deinopoid families have, at one time or another, been referred to this superfamily, and to the family Dictynidae in particular. However, dictynids are generally small spiders, with short legs of approximately equal length, and lack femoral trichobothria (see below); thus they are quite unlike *Palaeouloborus*.

The characters which are most useful in placing *Palaeouloborus* are: femoral trichobothria on legs 2, 3, and 4, leg 1 more than five times the length of the carapace and more than twice the length of leg 3, all leg tarsi with large accessory claws and apparently non-pectinate paired claws, presence of calamistrum and cribellum, and presence of plumose hairs.

Femoral trichobothria occur in only two groups of araneomorph spiders: the metine–tetragnathine lineage of the superfamily Araneoidea, and the family Uloboridae (Opell 1979; Lehtinen 1980; Levi 1980, 1981). In both of these groups there is great disparity in length between the elongate anterior legs (1 and 2) and the short third pair (Pl. 2, fig. 9), a feature also found in some other Araneoidea (Argiopinae, Levi 1983). *Palaeouloborus* is cribellate, and since only the Deinopoidea, but not the Araneoidea, are cribellate, this genus must be referred to the former superfamily. The calamistrum of *Palaeouloborus* is situated in a curved depression on the superior surface of the fourth metatarsus. Such a curvature occurs in uloborids (Pl. 2, fig. 10), to a much lesser degree in deinopids (Shear 1986a), and also in *Aebutina*, a poorly known genus tentatively referred to the Dictynidae (only females and immatures of this genus are known). Additionally,

Palaeouloborus bears plumose setae, which are found in Deinopoidea but not Araneoidea. The characteristic tarsal macrosetae of deinopoids (see below) appear to be absent from *Palaeouloborus*.

Palaeouloborus is referred to the superfamily Deinopoidea, on the evidence given above. The fossil clearly resembles members of the family Uloboridae more closely than the Deinopidae; the latter family has many autapomorphies (e.g. forwardly directed, enlarged, posterior median eyes, elongate legs all of a similar length, web-throwing) and lacks the femoral trichobothria typical of the Uloboridae and the fossil genus.

The position of *Palaeouloborus* within the Deinopoidea is now discussed. In a recent revision of the Uloboridae, Opell (1979) gave the following characters as diagnostic of the family: (1) lack of poison glands, (2) cribellate orb-web weavers, (3) femoral trichobothria, and (4) row of macrosetae (short spines) on metatarsus and tarsus of leg 4. The tarsal spines cannot be a synapomorphy for the Uloboridae since they also occur in Deinopidae (see below). Coddington (1986) added characters of the silk-glands described by Kovoor (1977), and some behavioural traits, to the list of uloborid synapomorphies, but omitted femoral trichobothria. Coddington's cladograms (1986, p. 358; 1989*b*, fig. 108) show the metine–tetragnathines, which also have femoral trichobothria, far from the dichotomy of Araneoidea with Deinopoidea, which presumes that femoral trichobothria are a convergent phenomenon in uloborids and metines–tetragnathines. The alternative hypothesis (that they are a synapomorphy for all orb-web weavers) would require their loss in many separate lines.

The row of tarsal and metatarsal macrosetae of uloborids was considered to be a synapomorphy of the family by Opell (1979), but in a later paper, Opell (1982) mentioned finding a poorly developed row on leg 4 of deinopids as well. My own observations confirm that macrosetae are present on the inferior surfaces of the distal half of the metatarsus and the tarsus of leg 4, and to a lesser extent on leg 3, in the deinopids *Deinopis*, *Menneus*, and *Avella*. These macrosetae are rather similar to the comb of serrate bristles seen in the Theridiidae in a similar position on the legs. However, they differ from theridiid bristles in being plumose, not serrate. As in the theridiids, they may need to be searched for, since they blend into the general hirsuteness of the tarsus. The macrosetae are not greatly different from the curved bristles normally present on the inferior surface of the distal end of the tarsus. Also, as in theridiids, they are not strictly confined to mt4 and ta4, also being present on leg 3, and they vary from species to species. In all the deinopids I studied they were quite unlike the comb of short, upstanding spines of the uloborid *Zosis geniculatus* illustrated by Opell (1979, pl. 1, figs. A and C). Rather, they resemble the row of macrosetae of the uloborid *Hyptiotes cavatus* figured by Opell (1982, pl. 1, fig. C). The similarity between theridiids and deinopids in this feature is presumably due to convergence in their prey-wrapping strategies rather than synapomorphy. Clearly, a comb of macrosetae on the fourth leg is a derived character of uloborids and deinopids which is not present in *Palaeouloborus*.

The legs of uloborids bear fine feathery setae amongst the normal setae; neither deinopids nor *Palaeouloborus* bear them.

Palaeouloborus cannot be included in the family Uloboridae because it has neither feathery setae nor fourth tarsal macrosetae. The fossil lacks the many specializations of the deinopids, and in addition the fourth tarsal macrosetal comb is absent. Rather than redefining the family Uloboridae to accommodate the fossil genus, it is left here within the superfamily Deinopoidea, closer to the Uloboridae than the Deinopidae, but not placed in either family. This placement indicates that the loss of a fourth tarsal macrosetal comb is autapomorphic for the fossil genus.

Genus PALAEOULOBORUS gen. nov.

Derivation of name. Greek, *palaios*, old, and the living genus, *Uloborus*, which the fossil genus resembles.

Type and only known species. Palaeouloborus lacasae sp. nov.

Diagnosis. Deinopoid with ovate carapace bearing marked break of slope separating anterior of carapace from sloping posterior area; leg 1 more than five times length of carapace and more than twice length of leg 3; many trichobothria on superior ?retrolateral surface of femur of leg 2 and superior ?prolateral surfaces of femora of legs 3 and 4; paired tarsal claws small, without teeth, median claw long, without teeth, pair of large accessory claws; superior surface of metatarsus of leg 4 in gentle S-shape, proximally convex and then concave, straightening out about half-way along podomere, bearing calamistrum which becomes row of curved bristles towards distal end of podomere; plumose setae present. Row of macrosetae absent from fourth tarsus.

Palaeouloborus lacasae sp. nov.

Plate 1; Plate 2, figs. 1–5, 7, 8, 10; text-fig. 1

Derivation of name. After Antonio Lacasa-Ruiz, palaeontologist at the Institut d'Estudis Ilerdencs, Lérida, Spain.

Type specimen. Holotype LP 1755 AP, from the quarry of La Pedrera de Meià, Sierra de Montsech, north-east Spain, and held in the collections of the Institut d'Estudis Ilerdencs, Lérida, Spain.

Diagnosis. As for the genus.

Description. The carapace shape is determined from fragments of cuticle and from the relief of the matrix. The scraps of cuticle preserved in the carapace region mainly represent coxae and sternum. However, on the left side between legs 2 and 3, cuticle of the carapace edge can be seen lying in a depression caused by pressure of the edge into the matrix. Faint traces of cuticle from the posterior edge of the carapace can also be discerned between the tarsi of legs 3. These cuticle remnants and the faint depression formed by the carapace margin suggests an ovate carapace with a truncated anterior margin. The carapace is 1·73 mm long, and 1·50 mm wide. It is widest just posterior to its midpoint. There does not appear to be a well defined cephalic area, nor an obvious fovea. There is a marked transverse break of slope just posterior to the widest part of the carapace and separating the raised foveal region from the backwardly sloping posterior part of the carapace. This slope is found in some living spiders (e.g. the uloborid *Philoponella*, Pl. 2, fig. 8), and accommodates an abdomen which extends forwards beyond the pedicel. Eyes not seen, no obvious tubercles.

The chelicerae are large, 0·67 mm long, and 0·33 mm wide, and somewhat forwardly directed, with parallel sides. The fangs cannot be seen, since the anterior edges of the chelicerae are obscured by overlying matrix.

The palps are clothed with setae, and short spines occur on the superior surface of the tarsus. The tarsus is oval, indicating that it was tumid in life. The distal end is not seen, so the presence of a claw cannot be confirmed. The specimen is therefore not a mature male, and could be an immature or a female. Very little of the basal parts of the palp can be seen, but superimposed on the anterior part of the carapace area is a dark line which, under high magnification, is seen to be serrate (Pl. 2, fig. 1). This is interpreted as the serrula of the left maxilla; cuticle is absent where the serrula of the right maxilla would have been preserved.

The leg formula is 1243. The coxae measure approximately 0·58 mm long, and the trochanters 0·18 mm. Lengths of the more distal podomeres, in mm, are as follows: leg 1: fe 3·27, pa 0·77, ti 1·64, mt 2·50, ta 0·96, total 9·14; leg 2: fe 2·11, pa 0·48, ti 1·35, mt 1·44, ta 0·77, total 6·15; leg 3: fe 1·35, pa 0·48, ti 1·06, mt 0·48, ta 0·48, total 3·85; leg 4: fe 1·64, pa 0·48, ti 0·87, mt 1·25, ta 0·52, total 4·76.

The legs are clothed with setae of the plumose type. Under high magnification, they are seen to bear a sculpture of striations arranged in a helical pattern, with abundant, minute serrae (Pl. 2, fig. 7). No feathery setae can be seen on the legs. The femora are only sparsely setose, setae and bristles becoming more abundant on distal parts of the legs. Groups of trichobothria are certainly present on the femora of legs 2–4, and on the tibia of leg 4. These trichobothria are not feathered (Pl. 2, fig. 2). Isolated trichobothria are more difficult to see, and their presence elsewhere on the legs cannot be confirmed. The leg spines are not large, and because only part of the specimen is preserved, the numbers of spines given below are not the maximum number which may be present on the legs. All tarsi are spineless, and bear two small, non-pectinate paired claws, a large median claw which appears to be non-pectinate or if pectinate then with only minute teeth, and two large accessory claws (Pl. 2, fig. 3). Fe1 bears few setae, mainly on the inferior surface (where they are curved) and on the superior surface, especially proximally and distally. Trichobothria may be present on fe1 (two possible trichobothrial bases can be seen on fe1 on the right side) but cannot be confirmed. Fe1 and pa1 are spineless.
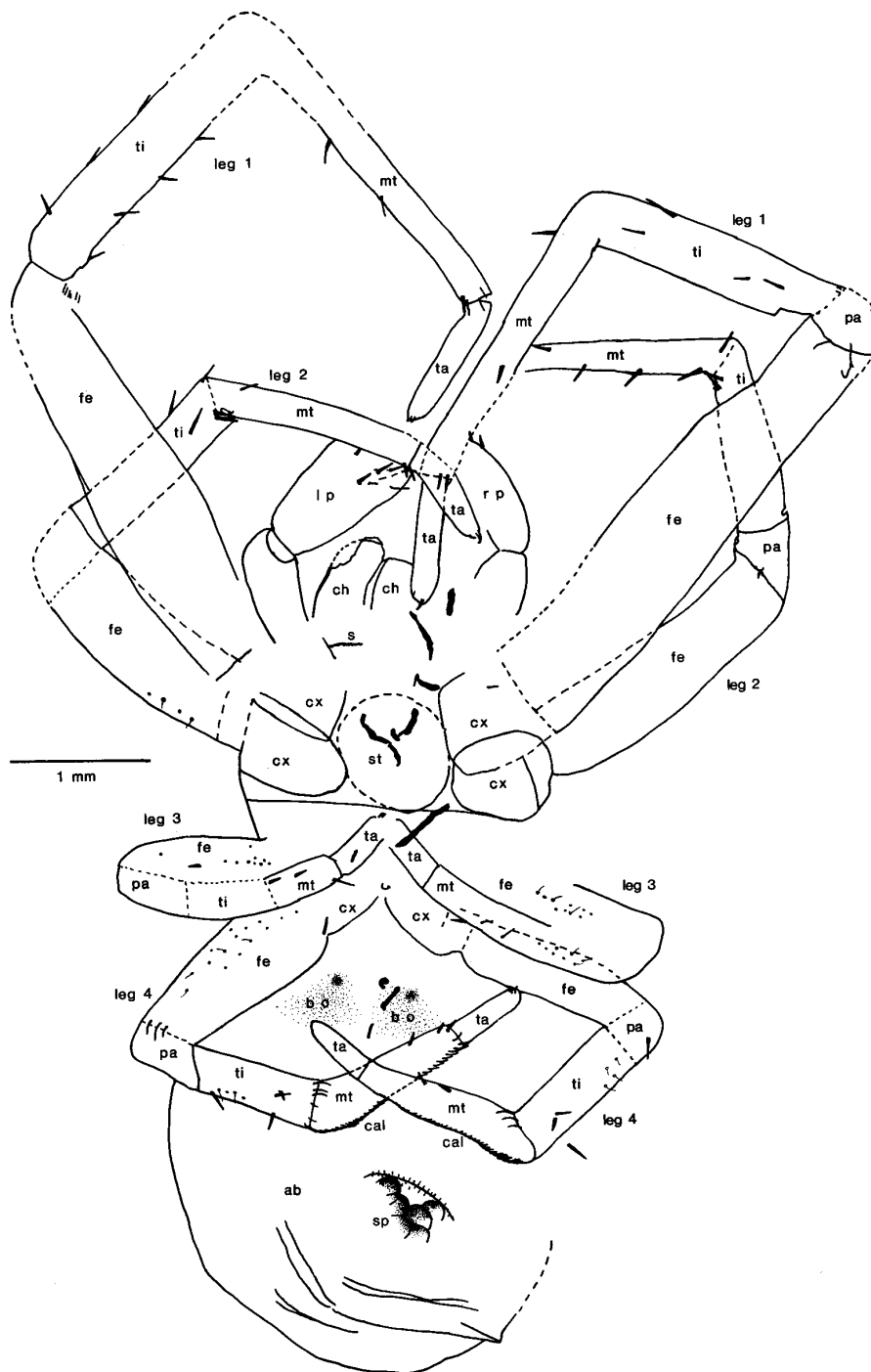
TEXT-FIG. 1. *Palaeouloborus lacasae* gen. et sp. nov., holotype, LP 1755 AP. Explanatory drawing for Pl. 1. See *Terminology* for explanation of abbreviations.

EXPLANATION OF PLATE 1

Palaeouloborus lacasae gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain. LP 1755 AP, whole specimen, lower slab, under ethanol, × 21. See text-fig. 1 for explanation.

PLATE 1

SELDEN, *Palaeouloborus*

Ti1 bears four inferior spines and three superior spines along the shaft of the podomere, one proximal lateral spine, one lateral subdistal spine, and one superior subdistal spine. Mt1 bears three inferior and two lateral spines down the shaft of the podomere. Proximally, mt1 bears one superior, one lateral, and one inferior spine, and two inferior distal spines are present. Fe2 is spineless and bears few setae, principally on the inferior and superior surfaces. Both second femora are poorly preserved, but a few trichobothrial bases can be seen proximally, apparently on the retrolateral surface. Pa2 is spineless. Ti2 bears bristles proximally and along the inferior surface. Ti2 bears two inferior distal spines, one lateral subdistal spine, one superior subdistal spine, and one superior distal spine. More spines are probably present on ti2 but on both sides of the specimen this podomere is crossed by the large femur of leg 1, which obscures the mid-sections of ti2. Mt2 is very setose, and bears bristles, especially along the inferior surface. Mt2 bears superior and inferior proximal spines, two median inferior spines, and one lateral and two inferior distal spines. Fe3 bears few setae, one tiny spine laterally, and many trichobothria (probably 20–40 in life) over a large area of the ?prolateral surface. Pa3 is spineless. Ti3 is poorly preserved on both sides of the specimen, but bears many bristles. Mt3 bears two short inferior spines and one lateral distal spine. Fe4 is spineless, bears strong, curved bristles distally, and many trichobothria (as many as on fe3) over a large area of the superior, ?prolateral surface. Pa4 bears large bristles laterally. Ti4 bears one superior proximal spine, and prolateral, retrolateral and superior spines subdistally. Ti4 bears about four trichobothria on the proximal superior surface, and long, curved bristles distally. The superior surface of mt4 follows a gentle S-shape, proximally convex and then concave, before straightening out about half-way along the podomere. The superior surface of mt4 bears a calamistrum composed of curved setae, apparently in one row, running from the proximal end of the podomere for about two-thirds of its length, where it passes indistinctly into a row of curved bristles which continues to the distal end of the podomere (Pl. 2, figs. 5 and 8). Mt4 bears two short inferior median spines, at least two very short spines inferodistally, and large bristles distally.

The abdomen measures 3·67 mm long, and 2·89 mm wide. It is ovate, wrinkled posteriorly, and compressed to the right, indicating that it was globose in life. The abdomen is sparsely setose, the setae becoming thicker, but not longer, posteriorly, where they show their plumose structure under high magnification (Pl. 2, fig. 7). A pair of subtriangular areas of darker cuticle, each with a small dark patch anteriorly, is situated at the anterior end of the abdomen. These are interpreted as book-lung opercula. Three pairs of spinnerets are visible in the posterior half of the abdomen. They are compressed to the right. Their position indicates that they were not terminal, but ventral, in position in life. A recurved line immediately anterior to the anterior pair of spinnerets represents the cribellum. Little detail can be discerned because the cribellar plate is not preserved (this is presumably on the counterpart), only the fold of cuticle anterior to the plate. (In living spiders the cribellum is commonly invaginated into a fold in front of the spinnerets when not in use, see Pl. 2, fig. 6.) Along this fold there are numerous short, blunt setae of a type not seen elsewhere on the spider (Pl. 2, fig. 4).

Superfamily ARANEOIDEA Latreille, 1806

Remarks. *Cretaraneus* gen. nov. and *Macryphantes* gen. nov., described below, are assigned to this superfamily. Both genera lack a calamistrum and cribellum. This does not, by itself, exclude them


Figs. 1–5, 7, 8. *Palaeouloborus lacasae* gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain, LP 1755 AP, oil immersion. 1, Serrula of left maxilla, bristle at left end, × 240. 2, Femoral trichobothria, × 150. 3, Claws on distal end of tarsus of left leg 4; note long median claw and accessory claws, × 100. 4, Spinnerets: anterior pair (at top), median pair, and posterior pair (part); recurved line of short setae (seen at left) in front of anterior spinnerets mark approximate position of cribellum; compare with fig. 6, × 85. 5, Proximal part of metatarsus of right leg 4, showing curvature of superior surface with calamistrum; note long, curved bristles at distal end of tibia (bottom left); compare with fig. 10, × 60. 7, Plumose seta, × 625. 8, Distal end of metatarsus of left leg 4, showing calamistrum (overlying tarsus of right leg 4, on right) terminating in row of curved bristles to left, × 85.

Figs. 6, 9, 10. *Philoponella* sp., Lake Naivasha, Kenya; J. Murphy Coll. No. 1363, under ethanol. 6, Ventral view of posterior end of abdomen of immature male, showing spinnerets and cribellum in front, × 36. 9, Left lateral view of immature male, × 13. 10, Metatarsus of right leg 4 of mature female, showing curvature of superior surface with calamistrum, × 50.
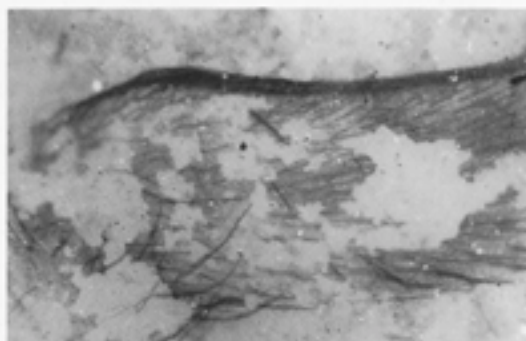
PLATE 2

SELDEN, *Palaeouloborus, Philoponella*
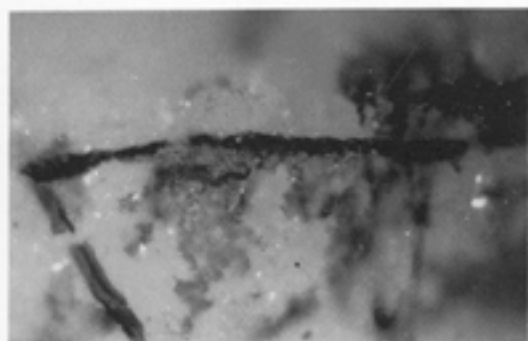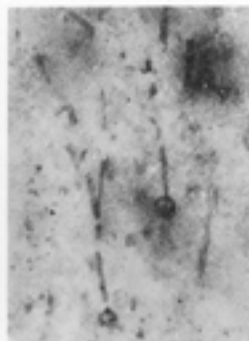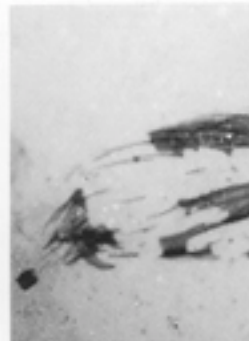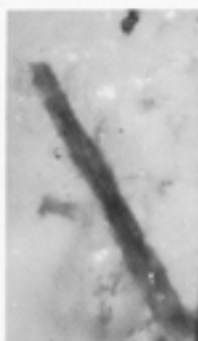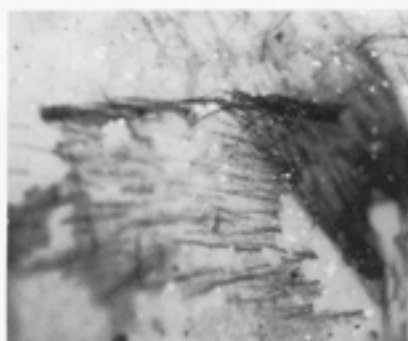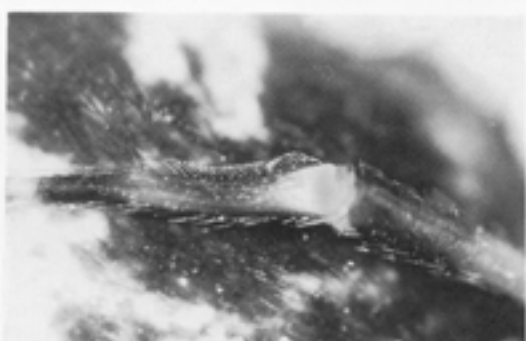
from a cribellate superfamily because mature males of many living cribellate genera commonly abandon web weaving with the concomitant degeneration of the cribellum and calamistrum, and the preserved specimens of both genera are mature males. However, evidence is presented below that *Cretaraneus* and *Macryphantes* show greater resemblance to araneoids than to any cribellate group. Tarsal adaptations (two claws, scopulae, tarsomeres, etc.) for cursorial, saltatorial, and other specialized locomotory habits, as found in the superfamilies Lycosoidea, Clubionoidea, Philodromoidea, Salticoidea, Thomisoidea, and Pholcoidea, are not found in *Cretaraneus* or *Macryphantes*, so referral of the fossil genera to any of these superfamilies is rejected. *Cretaraneus* and *Macryphantes* also lack the synapomorphies of Scytodoidea (Lehtinen 1986), Dysderoidea (Forster and Platnick 1985), Palpimanoidea (Forster and Platnick 1984; but see Archaeidae, below), and the superfamilies Hersilioidea, Dictynoidea, Hypochiloidea, and Agelenoidea.

Until recently, few strong synapomorphies could be mustered to support the monophyly of the superfamily Araneoidea (Coddington 1986). Those characters suggested by Coddington (1986) as araneoid synapomorphies (aggregate and flagelliform glands, paracymbium, serrate hairs, web construction technique) are not only difficult or impossible to see in fossils but also have yet to be thoroughly checked in many extant spiders both within and outside the superfamily. The problem of defining the Araneoidea was highlighted by Millidge (1988), in a discussion of the position of the Linyphiidae. He pointed out that the term 'paracymbium' covers a number of different morphological features on male palps in araneoid and some non-araneoid families, so this character should not be treated as a synapomorphy for the Araneoidea. He also argued that the sticky microdroplets present on the webs of some linyphiids are not produced by the same type of gland (aggregate glands) as in other araneoids, but may be more closely related to the sticky microdroplets found on agelenid webs. Millidge (1988) concluded (on the basis of other evidence as well as that reported here) that the Linyphiidae should be removed from the Araneoidea, and that the superfamily itself may be an unnatural grouping of families which merely share a lack of synapomorphies of other superfamilies. Millidge's arguments have not been accepted by Coddington (1990). Recent work by Coddington (1989a, b, 1990) has amassed a great deal more evidence supporting the monophyly of Araneoidea, including characters of the labium and the spinnerets.

Cretaraneus and *Macryphantes* are assigned to the superfamily Araneoidea. Cladistic analyses of the families within the Araneoidea were attempted by Heimer and Nentwig (1982) and Coddington (1986, 1989b, 1990). Shear (1986b) included the following major families in the Araneoidea: Theridiidae, Nesticidae, Linyphiidae, Araneidae (including Nephilinae, Metinae and Tetragnathinae), Theridiosomatidae, Symphytognathidae, Mysmenidae, and Anapidae. The latter four have synapomorphies (Forster and Platnick 1977; Platnick and Shadab 1978a, b; Coddington 1986) which are seen in neither *Cretaraneus* nor *Macryphantes*, so these families can be discounted. The familial status of Tetragnathidae is discussed below, under that family. The placement of *Cretaraneus* will be discussed first, followed by that of *Macryphantes*.

The following characters of *Cretaraneus* suggest the superfamily Araneoidea: broad, pyriform carapace lacking a distinct fovea, presence of a raised cephalic area, globose abdomen, three foot-claws with associated serrate bristles, serrate hairs, lack or paucity of trichobothria, paracymbium on the male palp, labium wider than long, and spinnerets in a compact group.

Members of the families Theridiidae and Nesticidae possess a comb of serrate setae on the inferior side of the fourth tarsus. Such a feature cannot be seen on *Cretaraneus*, but since the serrate setae are not always present, or not obviously serrate, in smaller species of living theridiids, the lack of this feature in the fossil genera does not necessarily exclude them from the Theridiidae. Levi and Levi (1962) gave as a diagnostic character for the Theridiidae, chelicerae with up to three teeth on the outer margin and rarely one to three teeth or denticles on the inner margin; *Cretaraneus* has more cheliceral teeth than this. One feature of *Cretaraneus* which suggests a link with the Theridiidae (but not the Nesticidae) is the labium which appears not to be rebordered. Palpal characters in *Cretaraneus* are not sufficiently distinct to suggest any particular araneoid family; although the simplest palps in the Araneoidea occur in the Theridiidae (Levi 1961), and the

Cretaraneus palp appears to be relatively simple for an araneoid, palps are variable within spider families. Therefore *Cretaraneus*, though apparently lacking a comb of serrate setae on the fourth tarsus, cannot be excluded with confidence form the Theridiidae.

Stridulatory ridges are commonly present on the chelicerae of male linyphiids, but may be obscure in some species, and the labium is usually rebordered. Neither stridulatory ridges nor a rebordered labium is seen in *Cretaraneus*. A link between *Cretaraneus* and linyphiids is provided by the raised cephalic area, a feature common in linyphiid males. However, a presumed lateral condyle on the chelicera and accessory tarsal claws (serrate bristles) are features not found in the Linyphiidae, but characteristic of the Araneidae.

The rotation of the male palpal sclerites in some Araneidae mentioned by Levi (1983) cannot be confirmed in *Cretaraneus* because of the rotation produced during fossilization, although the general appearance of the palp in the fossil genus is not reminiscent of the araneid palp. The apparent presence of a median apophysis in the palp of the fossil may provide information on its placement, but at present this character is unresolved (Coddington 1989b). The wide labium, presumed cheliceral condyle, and accessory tarsal claws of *Cretaraneus* are characteristic of most araneoids (Levi 1980). The rather large, forwardly directed chelicerae, and relatively simple palp of *Cretaraneus*, suggest the metine–tetragnathine lineage, but the fossil lacks other characteristics of this group, and mature males of some linyphiids also possess enlarged chelicerae. Male palps with a superficially simple appearance are characteristic of the genus *Nephila* (Schult 1983), but *Cretaraneus* bears few other similarities to the genus.

The Jurassic spider *Juraraneus rasnitsyni* Eskov, 1984 was placed in a monospecific family, the Juraraneidae Eskov, 1984. Eskov (1984) defined the family on a unique combination of araneoid characters and could find no apomorphies for the family. *Cretaraneus* resembles *Juraraneus* in many ways, including: overall size and shape; leg (but not tarsal) lengths; approximate shapes of sternum, labium, and maxillae; general shape of chelicerae. *Cretaraneus* differs from *Juraraneus* in lacking the irregular group of denticles on the inner margin of the chelicera, and the palpal characters interpreted by Eskov (1984) as a large, hook-like paracymbium, a large, pointed median apophysis, and a long, straight conductor (= embolus?).

The family Archaeidae is included in the Araneoidea by many arachnologists but, in a radical revision of archaeids and some other small families (for example Mimetidae, previously always placed in Araneoidea), Forster and Platnick (1984) removed them to the Palpimanoidea. They also created the monogeneric families Pararchaeidae and Holarchaeidae for genera previously included in the Archaeidae. Forster and Platnick (1984, p. 99) proposed two synapomorphies for the superfamily Palpimanoidea: cheliceral peg-teeth (modified setae as opposed to cuticular teeth), and an elevated cheliceral gland mound. They also mentioned that peg-teeth are found in some unrelated thomisoid and scytodoid genera, as convergent phenomena, and have been secondarily lost in members of six families assigned by them to the palpimanoids. *Cretaraneus* possesses true teeth on the chelicerae, but is mentioned here because of some similarities with the Pararchaeidae. The Pararchaeidae differ from the other palpimanoids in having serrate, rather than plumose, hairs, and show similarity with *Cretaraneus* in the enlarged chelicerae with a prominent keel and large bristles, the pectinate paired foot-claws, uncinate median claw, serrate bristles and lack of an onychium on the tarsus. A cheliceral keel is also found in other groups, for example the Leptonetidae (Gertsch 1974). The male palp of pararchaeids has a strongly developed embolus and a large tegular plate (Forster and Platnick 1984, p. 70), features also apparent in the palp of *Cretaraneus*. It is possible, therefore, that some relationship exists between *Cretaraneus* and the Pararchaeidae, which may or may not be an araneoid family. An archaeid spider has been described from the Jurassic (Eskov 1987).

Since it seems impossible to refer *Cretaraneus* to an araneoid family, there are two available options. First, a new, monospecific family could be defined to accommodate *Cretaraneus*. This course of action would be difficult, given the lack of specialized features displayed by the fossil, and would not provide any additional phylogenetic information. The second option, and the one chosen here, is to leave the genus unplaced within the superfamily Araneoidea. It is possible that future

discoveries will reveal that *Juraraneus* and *Cretaraneus* belong to the same group of Mesozoic araneoids.

Genus CRETARANEUS gen. nov.

Derivation of name. Latin *creta*, chalk, and *araneus*, a spider.

Type and only known species. Cretaraneus vilaltae sp. nov.

Diagnosis. Araneoid spider with subelliptical carapace bearing raised cephalic area and no fovea; subtriangular sternum; small, subtriangular labium; serrate setae covering all parts of body. Chelicerae relatively large (0·4 × length of carapace), forwardly directed (at least in adult male), with inner and outer row of denticles (not peg-teeth), and mesal ridge; male palp with long embolus, and small, proximal ?paracymbium; legs relatively equal in length, about three times the length of carapace; femora, tibiae and metatarsi with spines; tarsi with pectinate paired claws, small median claw, and associated serrate bristles; no true trichobothria; globose abdomen.

Cretaraneus vilaltae sp. nov.

Text-figs. 2–4

1986 Araneae: Lacasa and Martinez, p. 218; pl. 2, fig. 1.
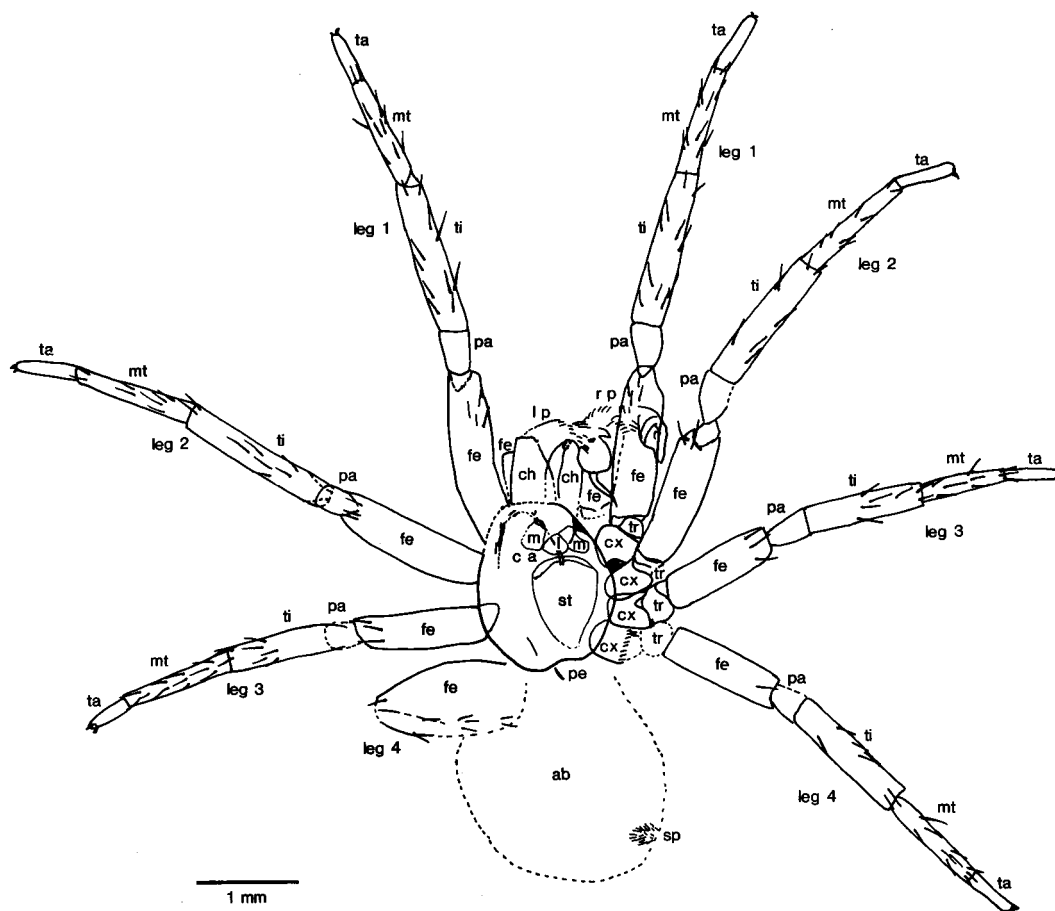
TEXT-FIG. 2. *Cretaraneus vilaltae* gen. et sp. nov., holotype, LC 1150 IEI. Explanatory drawing for text-fig. 3. See *Terminology* for explanation of abbreviations.

*Derivation of name.* After Sr Ramón Vilalta-Oliva, President of the Institut d'Estudis Ilerdencs, Lérida.

Type specimen. Holotype and only known specimen, LC 1150 IEI, complete specimen on single piece of limestone from quarry of La Cabrúa, Sierra de Montsech, north-east Spain; held in collections of Institut d'Estudis Ilerdencs, Lérida, Spain.

Diagnosis. As for the genus.

Description. A well-preserved spider, and the smallest of the specimens known from Montsech. The carapace cuticle is preserved and is golden brown in colour. The carapace is 1·73 mm long and 1·37 mm wide, and pyriform; its greatest width occurs at four-fifths of the length behind the anterior margin. From greatest width
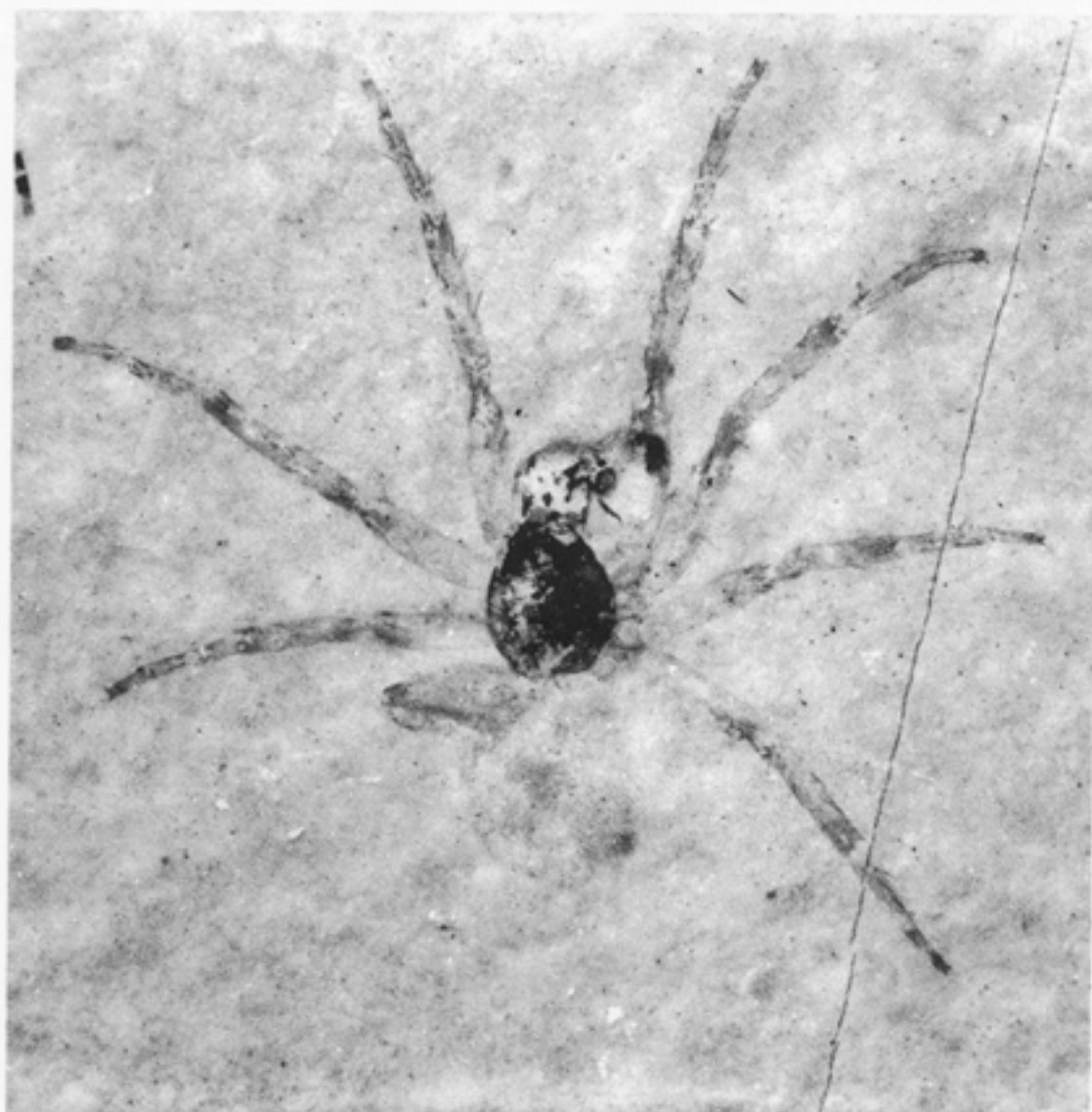
TEXT-FIG. 3. *Cretaraneus vilaltae* gen. et sp. nov., holotype. Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain, LC 1150 IEI. See text-fig. 2 for explanation, × 13.
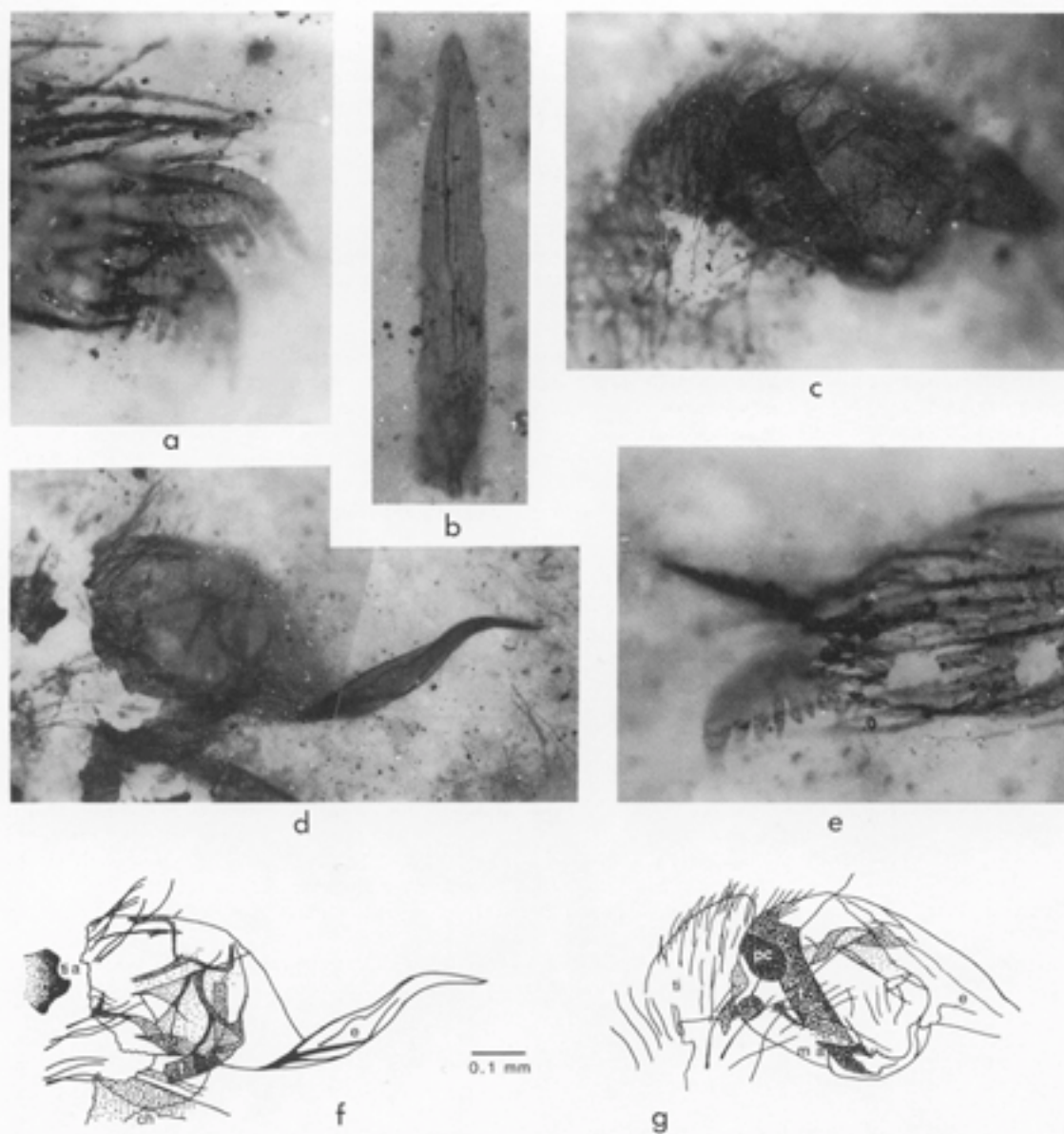
TEXT-FIG. 4. *Cretaraneus vilaltae* gen. et sp. nov., holotype. Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain, LC 1150 IEI. *a*, tarsal claws on left leg 2; note large, pectinate, paired claws, small, uncinate, median claw (bottom centre), and curved, serrate bristles, especially inferiorly, × 220. *b*, typical spine, on tibia of left leg 1, showing striations × 400. *c*, right palpal tibia and tarsus; see *g* for explanation, × 88. *d*, left palpal tarsus; see *f* for explanation, × 88. *e*, tarsal claws on right leg 4, × 220. *f*, explanatory drawing of *d*. *g*, explanatory drawing of *e*. See *Terminology* for explanation of abbreviations.

the carapace edges converge in very gentle convex curves to the rounded anterior margin, and in similar shaped curves which converge more rapidly to the posterior margin. The posterior margin is broad and has a distinct median embayment. There is no prominent foveal depression, from which it can be concluded that a fovea was probably absent. About one-quarter of the way back from the anterior margin of the carapace, on each lateral margin, is a slight embayment and a dark patch of cuticle which forms a linear feature extending radially

inwards. This is interpreted as a shallow sulcus which reflects a condyle for articulation of the chelicera on the inner surface of the carapace. A radial crack in the posterior right-hand quadrant indicates some crushing of the carapace. Dark areas in the anterior half form a V-shape pointing forwards. The V-shape is asymmetrical with respect to the midline, the left limb being more parallel to the midline than the right, and the whole shape is left of the midline. Some folding is associated with the limbs of the V-shape. This shape is interpreted as a sulcus or break in slope separating the peripheral parts of the carapace from a raised cephalic area in the anterior half of the carapace. The asymmetry of the V-shape, in contrast to the symmetry of the rest of the carapace, indicates left-lateral compression of the cephalic area during compaction of the sediment. A small, semicircular, dark area of cuticle approximately centrally placed near the anterior border of the carapace is interpreted as the posterior border of a right eye, the anterior half of which is missing. Other eyes, if similar in size, are most likely to be obscured by the dark lines of crumpled cuticle around the anterior edge of the cephalic lobe. The whole carapace is separated from the ventral prosoma and moved slightly to the left, exposing the right coxae.

A pair of dark lines in the posterior half of the carapace, subparallel to the midline but diverging towards the anterior, are interpreted as left and right edges of the sternum. The anterior border of the sternum is seen as a transverse, recurved line just anterior to the midpoint of the carapace. Due to the left-lateral movement of the carapace, the sternum appears mainly to the right of the midline. The sternum is widest anteriorly, and narrows gradually to a blunt point situated between the coxae of the fourth pair of legs. In front of the anterior margin of the sternum are some rounded dark areas. The somewhat triangular dark area anterior to the midline of the sternum is interpreted as the labium. The labium is widest posteriorly, where it is distinctly separate from the sternum. The lateral edges converge to a rounded anterior margin. The two areas to the right of the sternum represent the right maxilla with the anterolateral carapace sulcus superimposed. The posterior part of the left maxilla can be seen to the left of the labium, but its anterior part is obscured by the right limb of the V-shape surrounding the carapace cephalic area. No serrulae can be seen on the maxillae; there are many setae visible in the intermaxillary area.

The chelicerae are about 0·69 mm long, and project forwards in front of the carapace. Their lateral sides are straight and parallel to each other, their inner sides are convex and partly overlap in the fossil. Their dorsal (superior) surfaces bear numerous short, stiff setae; laterally, curved bristles are present. Each chelicera bears two rows of denticles extending from the mesal side of the anterior border to about half-way down the inner edge, the outermost row bearing at least three and probably five denticles, the inner row with at least two denticles. The fangs are not preserved, and were presumably on the counterpart which was not collected. A prominent ridge, or keel, runs from the end of the tooth row (which is ralatively short, about one quarter the length of the chelicera) along the mesal surface. No stridulatory ridges can be seen. The presence of a thickened sulcus on the anterolateral side of the carapace (see above), which probably reflects an internal apophysis for articulation of the chelicera, suggests the presence of a condyle on the chelicera; the condyle itself is not preserved on the specimen. From the morphology of the preserved cheliceral parts, it is apparent that the fangs worked transversely (labidognathous).

This specimen is a mature male because the palps are modified for the transmission of sperm (text-fig. 4c, d, f, g). Both palps are bent over to the right due to the left oblique compression of the specimen. The tarsus of the left palp now appears to the right of the right chelicera, and the right palpal tarsus lies beneath the femur of right leg 1. The appearances of the sclerites on each palp differ because the palps are compressed in different ways. The left palp presents a mesal view, and the right an ectal view. The total length of the palp, from the maxilla to the tip of the bulb (i.e. excluding the embolus, see below) is approximately 2·20 mm. The palpal femur is about equal in length to the adjacent chelicera. The patella and tibia are covered with long setae. The tibia is a distally expanded, triangular podomere, bearing long bristles which radiate distally to partly cover the tarsus. Distal to the tibia is an ovoid body with numerous sclerites superimposed on it. The ovoid body is interpreted as the superimposed bulb and cymbium (modified tarsus). The cymbium is not separately recognizable from the bulb, and is therefore presumed to be no longer than the bulb and related parts. The right palp seems to present an approximately ectal view, and the left palp an approximately superomesal view. Immediately distal to the tibia, an elliptical dark area may represent a small, separate paracymbium. On the right bulb, a curved, lath-like sclerite extends from the superoproximal edge to the inferior side of the bulb. This may be the tegulum. On the left palp, the different direction of compression has caused this structure to appear curving from the apparent inferior edge towards the superodistal direction. On the right palp below the supposed tegulum is a rather complex, hooked structure, also visible on the left palp. This may represent a median apophysis. The interpretations of both tegulum and median apophysis are uncertain. The gently helical, acuminate structure, as long as the bulb itself, extending distally from the distal end of the bulb is interpreted as the embolus. It is easily seen on the left palp, but on the right palp only its basal part is visible, the remainder

disappearing into the matrix beneath. It is possible that this structure represents the conductor (see, for example, the helical conductors of some tetragnathines, Levi 1981) in which case the embolus cannot be seen.

The legs are short and nearly equal in length. The leg length formula is 1243. The coxae are visible on the right side. Each is about 0·39 mm long, and slightly longer than broad. The trochanters are very short (about half as long as broad), and each is about 0·19 mm in length. Approximate lengths of more distal podomeres and total leg lengths, in mm, are as follows. Leg 1: fe 1·73, pa 0·46, ti 1·64, mt 1·08, ta 0·58; total 6·07. Leg 2: fe 1·54, pa 0·46, ti 1·50, mt 1·17, ta 0·69; total 5·94. Leg 3: fe 1·25, pa 0·46, ti 1·04, mt 0·87, ta 0·52; total 4·72. Leg 4: fe 1·31, pa 0·46, ti 1·25, mt 0·92, ta 0·52; total 5·04.

All legs are thickly clothed in long, fine setae, and the femora, tibiae, and metatarsi bear spines. The setae are not plumose, under high magnification, but some appear to be sparsely serrate, and on the larger ones a rectilinear pattern, as observed on the spines, can be seen. Among the leg setae, especially on the distal podomeres, there are a few short and thin, gently S-shaped, rather crumpled, setae which extend outwards from the podomeres at high angles, and are set in follicles which appear rather too large for the thickness of the seta. Some of these hairs are interpreted as chemosensory setae, as described by Foelix (1970b). Others may have had a function akin to that of trichobothria; no undoubted trichobothria can be seen. The spines have a rectilinear sculpture (text-fig. 4b). The numbers of leg spines given here are the maximum number which can be seen on the specimen. This must be considered to be either the actual or the minimum number present in life, since in this specimen the counterpart was not collected, and some spines may be preserved on the counterpart only. However, since by far the greater part of both dorsal and ventral sides of the animal is preserved on the slab, it is considered likely that few spines are unaccounted for. The femora bear stout, curved spines and some curved bristles in the distal area. Four spines are present on fe1, all apparently on the superior side of the podomere, of which two are subdistal and two distal in position; there are three on fe2 and fe3, superior in position; there is at least one on the posterior side of fe4. No other spines are present on the femora. The patellae are spineless. The tibiae and metatarsi bear spines in three areas: proximal, median, and distal. The distal spines are stout, curved, and inferoanterior and inferoposterior in position; the others are longer, straighter, and occur on all sides of the podomeres. In addition, stiff bristles occur in the median and distal areas of these podomeres. Ti1 bears five spines in a whorl on the proximal area, four (supero- and inferoanterior and supero- and inferoposterior) in the median area, and two distally. Ti2 bears four spines (one superior and three inferior) in the proximal area, two superior median, and two in the distal area. Ti3 has no proximal spines, five in a whorl in the median area, and two distally. Ti4 bears at least five spines in various positions in the proximal and median areas, and two distal spines. Mt1 bars five proximal spines, two pairs in the median area, and two distally. Mt2 has four proximal spines, two in the median area, and two distally. Mt3 has three spines in each of the three areas. Mt4 bears three proximal spines, probably four in the median area, and at least three distal spines (one superior in addition to the usual anterior and posterior). All tarsi are spineless. Distally, pectinate paired claws are present, each with one row of nine teeth, and a small, unciform median claw, but no onychium (text-fig. 4a, e). Surrounding the claws are a number of serrate bristles; these are gently S-shaped at the end with the serrations on one side. There is no comb of serrate bristles along the shaft of this podomere.

The abdomen is 2·17 mm long and elliptical to subcircular in outline. Very little cuticle is preserved, so it is presumed to have been thin in life, but the abdomen outline is clearly seen due to its covering of setae. Cuticle between the setae can only be seen in ill-defined areas mainly in the left half of the abdomen; these are interpreted as ?dorsal pigmented areas in life. Generally darker coloration and greater density of setae indicate position of spinnerets which, however, are not separately discernible. The spinneret region can be seen on the right side of the abdomen (due to the left oblique compression) and appears to have been subterminal in position. A longitudinal dark streak left of the midline between the carapace and abdomen is presumed to represent the remains of the pedicel.

Family TETRAGNATHIDAE Menge, 1866

The familial status of Tetragnathidae has been supported by many authors (for example, Kaston 1948, 1978; Locket and Millidge 1953), but resisted by others (Levi 1980; Roberts 1985, p. 198) in the past. The situation is further complicated by the position of the Metinae, placed by some in Tetragnathidae and by others in Araneidae. The most recent opinions of Levi (1986), Coddington (1989b), and Platnick (1989) are that tetragnathines, metines, and nephilines should be placed together in the family Tetragnathidae, separate from the Araneidae. In the past, these subfamilies

have been placed in the family Araneidae, but Coddington (1989b, fig. 108) considered the clade Nephilinae + (Tetragnathinae + Metinae) as the sister group to Araneidae + Linyphiidae.

First impressions of *Macryphantes* suggested the 'crab-spiders' (superfamilies Thomisoidea and Philodromoidea), on account of the subcircular carapace, prominent eyes, subcircular palp, and long, spinose anterior legs. However, these features are not confined to crab-spiders, and the characteristic features of crab-spiders (two claws, tarsal scopulae, clavate setae, etc.) are lacking in *Macryphantes*. Furthermore, in thomisoids and philodromoids the legs are laterigrade, not densely setose, and the spines on the legs are concentrated on the mesal surfaces of the tibiae and metatarsi of the anterior prey-capturing legs. This is not the case in *Macryphantes*.

The presence of femoral trichobothria in *Macryphantes* points to the Deinopoidea or Araneoidea. As discussed above with regard to *Palaeouloborus*, only the Uloboridae (Deinopoidea) and the metines–tetragnathines in the Araneoidea bear femoral trichobothria. Since *Macryphantes* is an adult male, it could lack a calamistrum and cribellum, and correlated with the loss of cribellum and calamistrum in adult male uloborids appears to be the loss of the comb of macrosetae on the fourth tarsus (personal observation from *Uloborus walckenaerius*). Arguing against its inclusion in the Uloboridae are: the presence of serrate setae, the absence of plumose setae, and the absence of feathery setae. Serrate setae are characteristic of araneoids (Coddington 1986) and members of the superfamily lack plumose hairs which are found in deinopoids. Furthermore, the large, pectinate, paired tarsal claws of *Macryphantes* resemble those of araneoids more than the uloborid claw pattern of relatively small, sparsely toothed or non-pectinate paired claws.

The presence of femoral trichobothria in *Macryphantes* places it among the tetragnathines within the Araneoidea; this character has been used to distinguish tetragnathids in familial keys (Kaston 1948; 1972; Locket and Millidge 1953). As mentioned above, Coddington (1989b) has argued that the tetragnathines are closely related to the metines and nephilines. Whilst a number of other features, such as leg length and possible paracymbium, add weight to this assignation, some characters of *Macryphantes* are unusual for this group, including: subcircular or broadly pyriform carapace, planospiral embolus, and prominent, dorsally directed, posterior median eyes. Therefore, whilst the presence of femoral trichobothria appear to ally *Macryphantes* most closely with the tetragnathines, rather than the metines and nephilines which lack this feature, these other characters suggest that inclusion of the fossil in the Tetragnathinae is unwise.

Genus MACRYPHANTES gen. nov.

Derivation of name. Greek *makros*, long, large, and *yphantes*, a weaver.

Type and only known species. Macryphantes cowdeni sp. nov.

Diagnosis. Tetragnathid spider with subcircular, or broadly pyriform, foveate carapace; leg 1 six times the length of carapace and more than twice the length of leg 3; double row of prolateral trichobothria on femur of leg 3, single row of prolateral trichobothria on femur of leg 4; paired tarsal claws pectinate with six teeth, median claw long, curved, not pectinate, serrate bristles (accessory claws) present; male palp with planospirally coiled embolus; serrate, but not plumose, setae present.

Macryphantes cowdeni sp. nov.

Plates 3 and 4; text-figs. 5 and 6

Derivation of name. In remembrance of a friend and a fellow arachnologist, Dr Douglas Cowden of Worcester.

Type specimens. Holotype, LC 1753 AP A (part) and LC 1753 AP B (counterpart). Paratype, LC 1754 AP A (part) and LC 1754 AP B (counterpart). Both are from the quarry of La Cabrúa, Sierra de Montsech, north-east Spain, and are held in the collections of the Institut d'Estudis Ilerdencs, Lérida, Spain.

Diagnosis. As for the genus.

Description. This is the largest and one of the best preserved of the spiders from Montsech, with long, outstretched legs 1. The description is based on specimen LC 1753 AP (Pl. 3; text-fig. 5), which is better preserved (though slightly smaller) than LC 1754 AP (Pl. 4, figs. 2 and 4; text-fig. 6); the latter is referred to for confirmation of details. Both specimens are mature males.

The carapace is slightly wider (2·83 mm) than long (2·65 mm), and is widest at about midlength. The carapace outline is subcircular, but may be somewhat produced anteriorly where the edge is not preserved. The
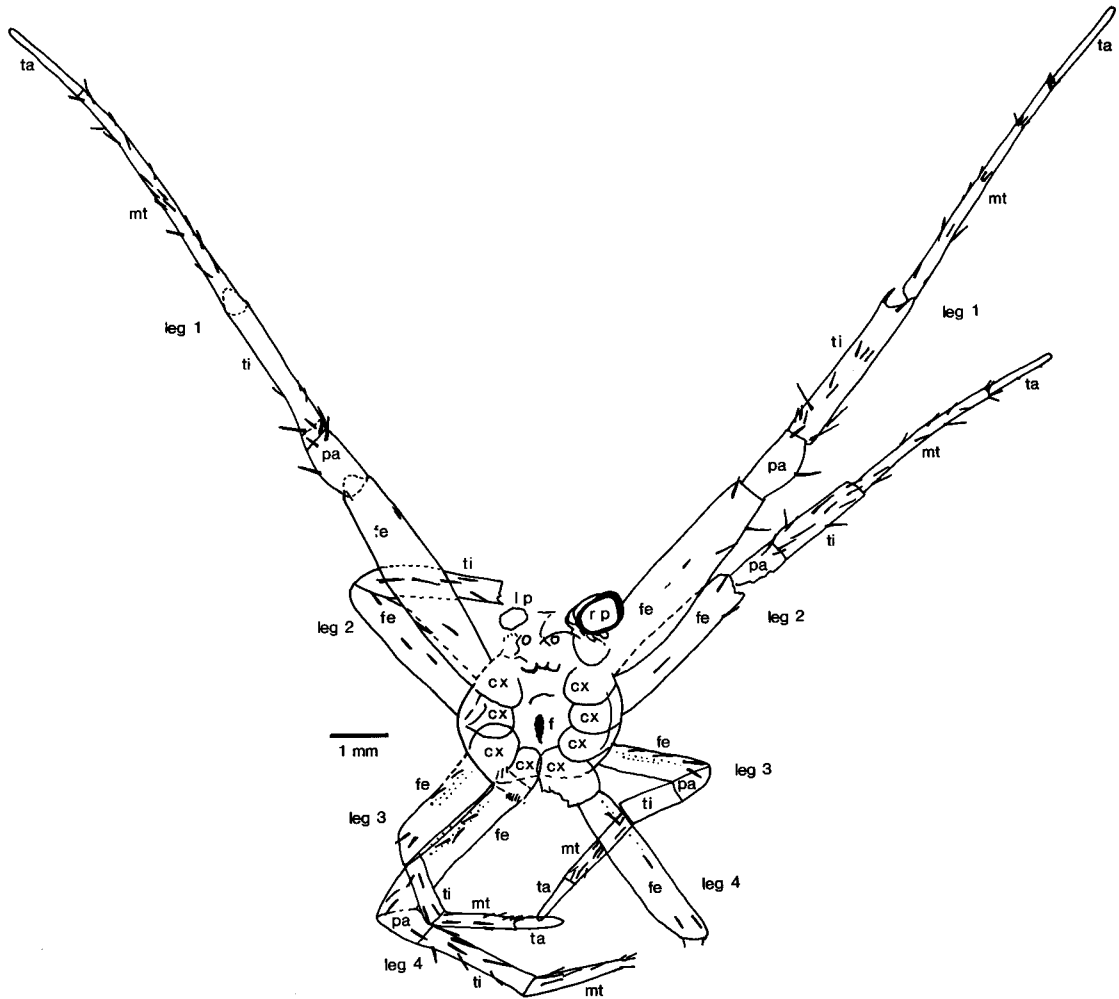
TEXT-FIG. 5. *Macryphantes cowdeni* gen. et sp. nov., holotype, LC 1753 AP B. Explanatory drawing for Pl. 3, fig. 1. See *Terminology* for explanation of abbreviations.

EXPLANATION OF PLATE 3

Figs. 1 and 2. *Macryphantes cowdeni* gen. et sp. nov., holotype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain; under ethanol. 1, LC 1753 AP B, lower slab, ×7; see text-fig. 5 for explanation. 2, LC 1753 AP A, upper slab, ×7.

PLATE 3
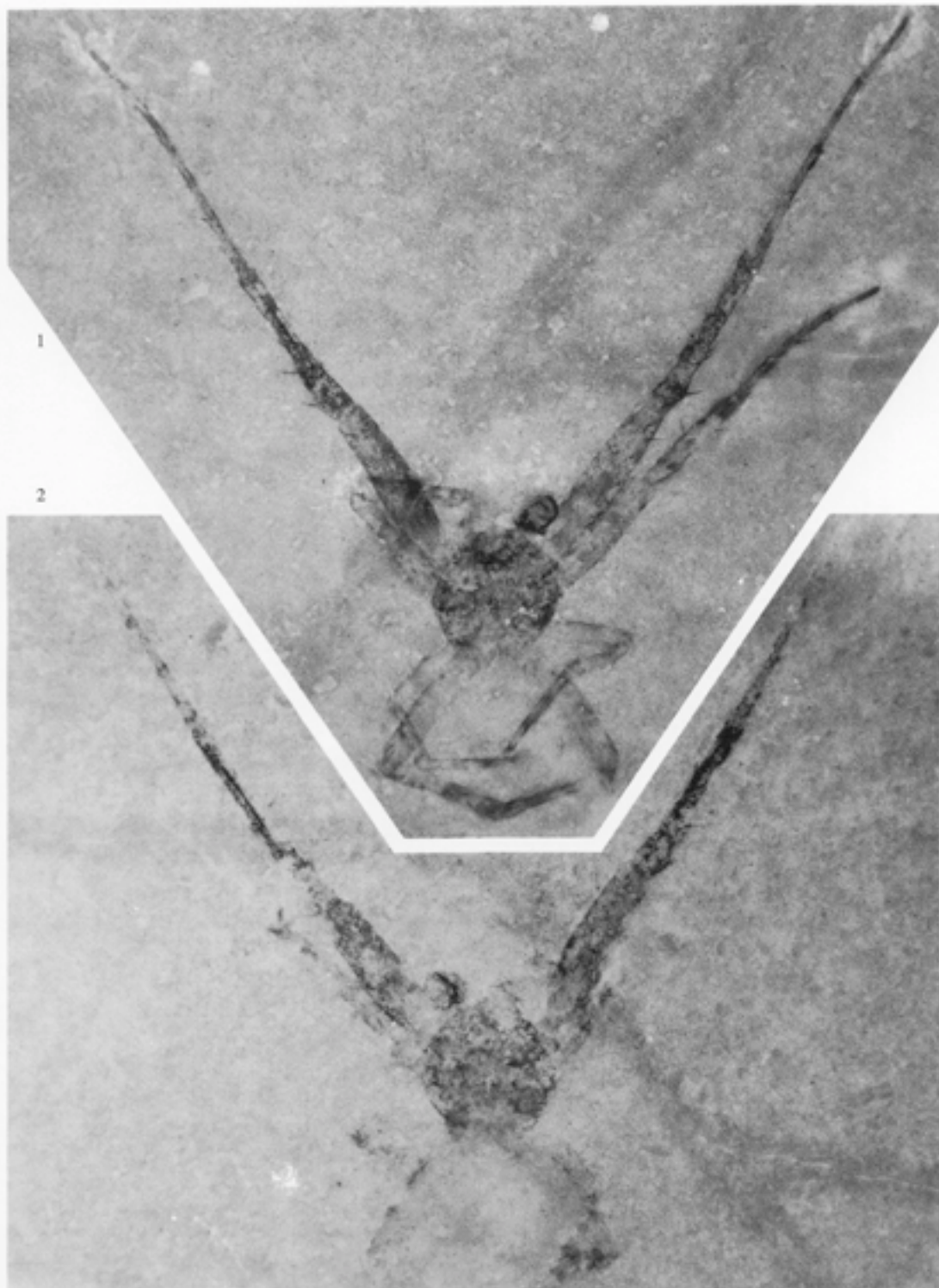
SELDEN, *Macryphantes*

TEXT-FIG. 6. *Macryphantes cowdeni* gen. et sp. nov., paratype, LC 1754 AP A. Explanatory drawing for Pl. 4, fig. 4. See *Terminology* for explanation of abbreviations.
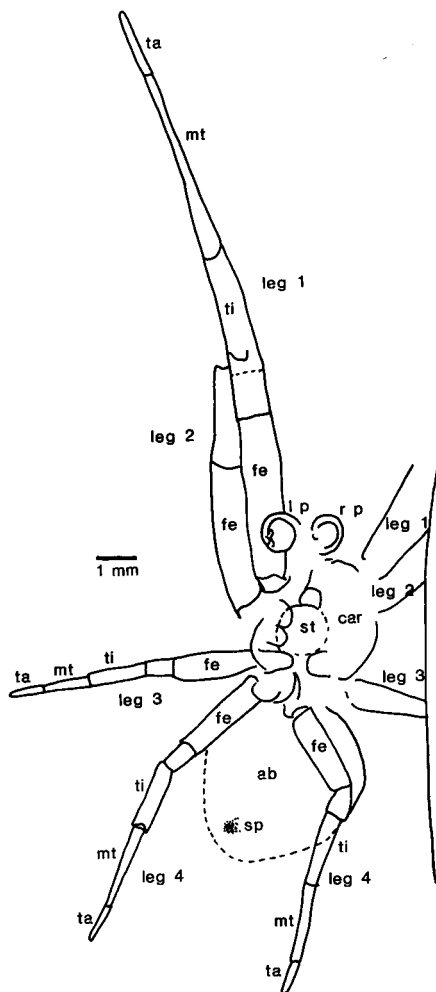
carapace is covered in setae. At the anterior side of the carapace, there are forwardly directed setae and long, curved bristles. At the anterior margin of the carapace two circular structures are interpreted as median eyes. Just posterior to the centre of the carapace, a deep, drop-shaped depression, with its blunt end anteriormost, marks the fovea. The carapace shape is confirmed by specimen LC 1754 AP, in which the carapace is 3·25 mm wide.

A pair of deep depressions just posterior to the anterior median eyes are surrounded posteriorly by dark

EXPLANATION OF PLATE 4

Figs. 1–7. *Macryphantes cowdeni* gen. et sp. nov., holotype and paratype; Lithographic Limestone, Lower Cretaceous; Sierra de Montsech, Lérida Province, Spain. 1, 3, 5–7, LC 1753 AP B, holotype, oil immersion. 1, Trichobothria, setae, and spines on prolateral surface of femur of right leg 3, × 85. 3, Right palp, showing apophysis on right side, × 47. 5, Distal end of tarsus of right leg 2, showing paired pectinate claws, long median claw, and curved, serrate bristles (accessory claws), × 320. 6, Spines and setae on shaft of metatarsus of left leg 4, superior to top, × 85. 7, Distal half of tarsus of right leg 2, showing terminal claws and short spine on inferior surface of podomere, × 130. 2, LC 1754 AP B, paratype, upper slab, × 4·5. 4, LC 1754 AP A, paratype, lower slab, × 3·6; see text-fig. 6 for explanation. Both under ethanol.
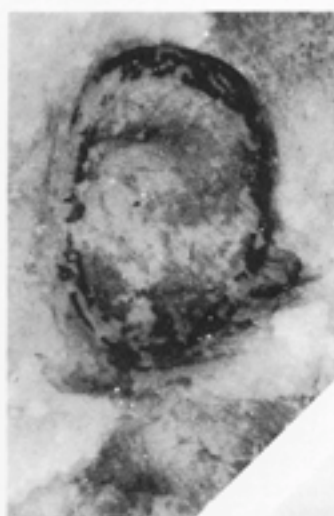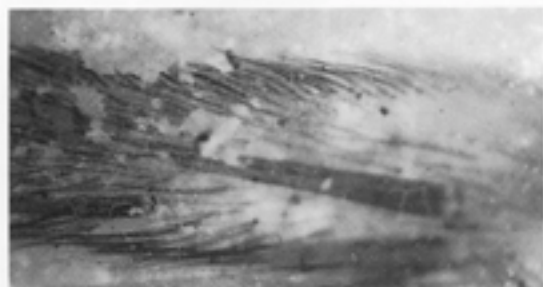
PLATE 4
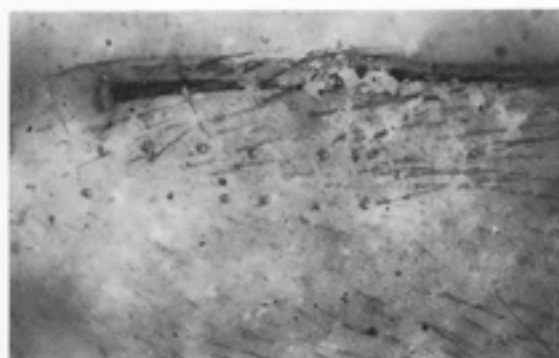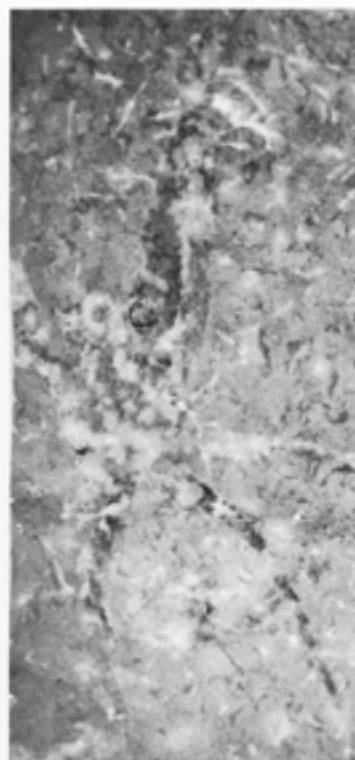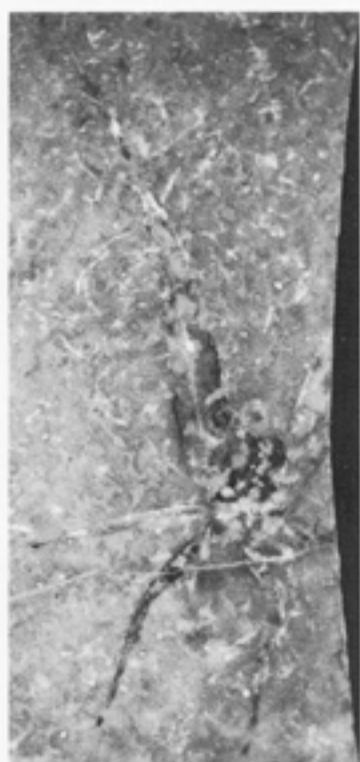
cuticle. These structures are interpreted as the proximal ends of the chelicerae which are directed ventrally; the chelicerae presumably disappear into the matrix beneath the specimen. The sternum appears to be circular; its shape is suggested by the arrangement of the coxae, as seen on both LC 1753 AP and LC 1754 AP. The coxae of legs 4 meet in the midline, and on both the holotype and paratype some remnants of the anterior edge of the sternum can be discerned.

The palp on the right side of LC 1753 AP B (the left side of LC 1753 AP A) is preserved (Pl. 4, fig. 3), and confirms that the specimen is an adult male. The palpal tarsus is subcircular in outline with a mesal bulge. This bulge represents either the mesal part of a circular cymbium or a mesally situated crescentic cymbium. The bulge extends beyond the oval dark band which is interpreted as the embolus (this structure could be the conductor or some other sclerite functioning as a guide for the embolus). The embolus is coiled in a horizontal planospiral, which in LC 1754 AP A can be seen to be sinistral on the left palp, and dextral on the right, as viewed from above. On the proximolateral side, a thick, reniform lobe is interpreted as a median apophysis. A dark area can be seen on the proximal edge of the cymbium within the coiled embolus; this is inferior in position; this dark area belongs to a sclerite of the palp. A smaller dark patch occurs just anterior to the midpoint of the palp, on the inferior surface; this represents part of another sclerite. Numerous long bristles run right laterally from the base of the tarsus, and some curved bristles are present on its superior surface. Larger, curved spines are present around the base of the tarsus; these appear to originate proximal to the tarsus, that is, on the tibia, which is otherwise poorly preserved.

The leg length formula is 1243. The legs are very unequal in length, leg 1 being more than twice the length of leg 3. The coxae are approximately equidimensional, each about 0·58 mm long and wide. The trochanters are not easily visible, but each measures about 0·25 mm in length. Lengths of the more distal podomeres and total leg lengths, in mm, are as follows: leg 1: fe 4·33, pa 1·35, ti 3·00, mt 4·55, ta 1·70, total 15·76; leg 2: fe 3·17, pa 1·00, ti 1·64, mt 3·00, ta 1·15, total 10·79; leg 3: fe 2·01, pa 0·39, ti 1·15, mt 1·64, ta 0·85, total 6·87; leg 4: fe 3·00, pa 0·81, ti 2·04, mt 1·98, ta not preserved (presumed to be c. 0·95 by comparison with ratio of mt4 to ta4 seen in LC 1754 AP, see below), total c. 9·61. LC 1754 AP is poorly preserved, and slightly larger than LC 1753 AP, and its leg measurements are as follows (in mm but with a lesser degree of certainty than in LC 1753 AP): coxae 0·9, trochanters 0·3; leg 1: fe 4·7, pa 1·4, ti 3·1, mt 5·0, ta 1·8, total 17·2; leg 2: fe 3·8; leg 3: fe 2·3, pa 0·6, ti 1·4, mt 1·3, ta 0·9, total 7·7; leg 4: fe 2·8, pa 0·9, ti 1·9, mt 2·1, ta 1·0, total 9·9.

All legs are thickly clothed with long setae. These setae appear smooth, but high magnification reveals minute accessory spines, especially distally; thus they are the serrate type. No plumose or feathery hairs can be seen. Spines are mostly large and numerous, occurring on all podomeres except the coxae and trochanters. Some spines show a helical pattern of longitudinal lines. Most spine are quite large (mean length 0·48 mm) and straight (Pl. 4, fig. 6), but spines at the distal end of podomeres are commonly curved and/or short. Fe1 bears five pairs of spines along the superior surface and an inferoanterior distal spine (this may be one of a pair). Fe1 also has many very short, fine hairs on the inferior surface of the distal half of the podomere. Pa1 bears a prominent posterior spine, and antero- and posteroinferior distal spines. Ti1 bears a whorl of about five spines proximally, two pairs of spines inferiorly and two single spines superiorly along the podomere, and postero- and anteroinferior distal spines. Mt1 bears eight pairs of spines along the inferior surface, including and distal pair. Fe2 bears four pairs of superior spines along the shaft, and postero- and anteroinferior distal spines. Pa2 bears one lateral and antero- and posteroinferior distal spines. Ti2 bears ten long spines along the shaft of the podomere, and two short distal spines. Mt2 bears a pair of spines proximally, a whorl of four spines and then five more along the shaft, with a whorl of five spines distally. Ta2 on the right side of LC 1753 AP B is particularly well preserved (Pl. 4, figs. 5 and 7), and shows curved paired claws each with six teeth, an equally long curved median claw, and numerous serrate accessory claws (i.e. hypertrophied bristles, as seen in living Araneidae, see Foelix 1970a). Ta2 bears two small spines on is inferior surface. Along the superior prolateral side of the proximal three-quarters of fe3 are about 24 trichobothria arranged mainly in two rows (Pl. 4, fig. 1). The trichobothrial hairs are not feathered. This podomere bears many fine, curved hairs inferiorly, two median superior spines, and two posterior distal spines. Pa3 appears to be spineless. Ti3 bears long, stiff setae, and one median and two subdistal spines. Mt3 has three inferior and one superior proximal spines, one superior, antero- and posterolateral, and two short inferior median spines, followed by one lateral and three curved inferior spines and a whorl of five distal spines. Ta3 bears two small spines on its inferior surface, like those which occur on Ta2. Fe4 bears at least one superior prolateral row of about sixteen trichobothria, fine, curved hairs inferiorly, three superior median spines, and three superior subdistal spines. Pa4 bears one lateral spine. Ti4 has three superior, two inferior, and two lateral spines along the shaft, and apparently no distal spines. Mt4 bears antero- and posteroinferior and posterolateral spines proximally, two inferior median spines, one small curved superior median spine, two small curved distal spines, and two small and one large inferior distal spines. The numerous setae on the superior surface of mt4 are gently curved, giving

the appearance of a weak calamistrum (Pl. 4, fig. 6). However, the high density of setae may be an artefact of compression, since a similar density of curved setae is observed on the opposite side of the podomere, and high magnification reveals that the setae are no different in structure from any others. Thus mt4 does not bear a calamistrum.

No trace of the abdomen is preserved on LC 1753 AP, but it is preserved on LC 1754 AP; it is oval, and measures 4·80 mm long and 4·20 mm wide. The greatest width is in the anterior half. The abdomen is compressed to the right in LC 1754 AP A, and was probably quite bulbous in life. The spinnerets are not elongated, and form a compact group in a subterminal position on the abdomen.

MODES OF LIFE

Palaeouloborus can be compared most closely with the Uloboridae. Uloborids are orb-web weavers which use a characteristic 'wrap attack' to subdue prey (Robinson 1975). In *Uloborus* and *Hyptiotes* (Nielsen 1932) the median tarsal claw is relatively large, the paired claws are fine and bear few (*Hyptiotes*) or no teeth (*Uloborus*), and in both genera there are large, serrate accessory claws. A similar pattern of tarsal claws occurs in *Palaeouloborus*, and it is unlike that found in araneoids, in which the paired claws are large and pectinate (see, for example, Levi 1978). Nielsen (1932, pp. 26–28) described the method of silk handling by *Hyptiotes* using this claw pattern. Whilst accessory claws are widespread among web-spinning spiders, and are used for silk handling, they are particularly well developed in orb-web weavers; the pattern in the living uloborids studied seems distinctive, and these genera are orb-web weavers.

Trichobothria occur on the femora of *Palaeouloborus* and uloborids. The function of these is not known, but it is interesting that among living araneomorph spiders they are found only in tetragnathines and uloborids, both of which are orb-web weavers. Femoral trichobothria are absent from some adult *Pachygnatha*, tetragnathines which make no web when adult (Levi 1980). Many orb-web weavers have no femoral trichobothria, but their presence in tetragnathines and uloborids appears to be linked with the habit. Another behavioural similarity between tetragnathines and uloborids is in resting postures (Levi 1980). Tetragnathines and many metines rest with their long legs 1 and 2 stretched out forwards, the fourth legs outstretched behind, and the short third legs pointing backwards and where necessary gripping the twig on which the spider is resting. Opell and Eberhard (1983) distinguished four types of resting posture in uloborids; in three, legs 1 and 2 are stretched forwards in some manner, whereas in the fourth, legs 1 and 2 are held folded with the femora projecting at right angles to the long axis of the body. Opell and Eberhard (1983) remarked on the close similarities of resting postures between uloborids and araneids. The femoral trichobothria are generally on the superior or retrolateral sides of femora 1 and 2, and on the prolateral sides of femora 3 and 4 (Opell 1979). Thus they point laterally when the animal is in the normal resting posture. It is likely that the presence of femoral trichobothria is linked with the uloborid and tetragnathine–metine resting postures. These behavioural characters may be due to convergence, but could conceivably be synapomorphies for all orb-web weavers (Shear 1986a). The great similarity in leg lengths, femoral trichobothrial pattern, and tarsal claws between *Palaeouloborus* and the Uloboridae suggests that the web-building and resting behaviour of the fossil genus resembled that of typical members of the living family.

The wrap-attack prey capture in uloborids was described by Opell (1979) and Lubin (1986). In it, the spider hangs by the first and second pairs of legs whilst throwing silk over the prey using the fourth leg-pair. After further entanglement of the prey in these threads, the spider approaches closer to the prey and, holding it now with the second and third leg-pairs, wraps it more tightly with silk combed by the row of macrosetae on the fourth legs. A wrap attack is found in a number of spider groups, such as the Theridiidae and Nesticidae (both of which have a comb of setae on the fourth legs), Metinae, Tetragnathinae, Araneidae, Oecobiidae, Hersiliidae, and Pholcidae (Coddington 1986). The wrap attack of uloborids differs from that of other spider families because uloborids lack poison glands and the prey is killed by digestive enzymes during feeding (Opell 1979). Since a wrap attack is found in families which do not have a comb of setae on the fourth legs, such a comb is

not essential for this method of prey capture. Wrap attack is therefore a possible method of prey capture in *Palaeouloborus*.

Macryphantes compares most closely in general appearance with large, long-legged araneoids such as the argiopine araneids, tetragnathines, and nephilines. Argiopines are similar in general appearance and habits to uloborids (both are orb-web weaving wrap-attack predators) but they lack femoral trichobothria. *Macryphantes* has an araneoid pattern of tarsal claws, and bears femoral trichobothria. Therefore, it is suggested that *Macryphantes* wove an orb web, rested in a posture like that of uloborids or metines–tetragnathines, and may have used a wrap-attack method of prey capture.

Cretaraneus has few positive features which would indicate its possible mode of life. The fossil genus is small, short-legged, and bears pectinate, paired claws and serrate accessory claws, which indicate that it is a web-weaving spider. Small, short-legged araneoids, such as *Cretaraneus* and most theridiids and linyphiids, are weavers of sheet webs in litter, undergrowth, or bushes; such webs catch pedestrian or small flying prey. It is likely that *Cretaraneus* occupied a similar ecological niche.

A great variety of orb webs are woven by uloborid and araneoid spiders, each designed to capture a specific type of prey. They are put up for short periods or longer, day or night, and in open or secluded situations (Riechert and Gillespie 1986; Stowe 1986; Lubin 1986). They vary from massive, collective structures to minimalist devices hardly recognizable as orb web derivatives. It is impossible to suggest what type of prey *Macryphantes* and *Palaeouloborus* captured with their orb webs. There was a wide diversity of insect life in the Montsech area during the early Cretaceous, which suggests that prey specialization may have been practised by orb-web weavers at that time.

CONCLUSIONS

Described here are the oldest known representatives of the spider superfamily Deinopoidea, the family Tetragnathidae, and the second oldest record of the superfamily Araneoidea in the fossil record. The Deinopoidea and the Araneoidea both contain weavers of orb webs of remarkable similarity. Indeed, there is continuing debate about whether the orb web evolved only once, in the common ancestor of the Deinopoidea and Araneoidea, or is a convergent phenomenon in these two groups. Shear (1986*a*) comprehensively reviewed the evidence for and against these conflicting hypotheses, and further discussion is not attempted here. However, the presence of well-defined deinopoids and araneoids in the Lower Cretaceous indicates that, whichever hypothesis is favoured, both groups of orb-web weavers were in existence at that time, and suggests that the orb web originated earlier in the Mesozoic, if not before.

REFERENCES

BARALE, G., BLANC-LOUVEL, C., BUFFETAUT, E., COURTINAT, B., PEYBERNES, B., VIA BOADA, L. and WENZ, S. 1984. Les gisements de calcaires lithographiques du Crétacé inférieur du Montsech (Province de Lérida, Espagne). Considérations paléoécologiques. *Geobios*, Mémoires, no. spécial **8**, 275–283.

BRENNER, P., GOLDMACHER, W. and SCHROEDER, R. 1974. Ostrakoden und Alter der Plattenkalk von Rubies (Sierra de Montsech, Prov. Lérida, NE-Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1974**, 513–524.

CLERCK, C. 1757. *Svenska spindlar (Araneae suecici)*. L. Salvii, Stockholm, 154 pp. [In Swedish and Latin].

CODDINGTON, J. 1986. The monophyletic origin of the orb-web. 319–363. *In* SHEAR, W. A. (ed.), *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii+492 pp.

—— 1989a. Spinneret spigot morphology: evidence for the monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. *Journal of Arachnology*, **17**, 71–95.

—— 1989b. Ontogeny and homology in the male palpus of orb-weaving spiders and their potential outgroups, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology*, in press.

—— 1990. Cladistics and spider classification: araneomorph phylogeny and the monophyly of orb-weavers. *Annales Zoologici Fennici*, in press.

COMSTOCK, J. J. 1948. *The spider book*. Revised and edited by W. J. GERTSCH. Comstock Publishing Company, Ithaca, New York, xii+729 pp.

CROWSON, R. A. 1970. *Classification and biology*. Heinemann, London, x+350 pp.

ESKOV, K. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1984**, 645–653.

—— 1987. A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called 'Gondwanan' ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **175**, 81–106.

FARRIS, J. S. 1976. Phylogenetic classification of fossils with Recent species. *Systematic Zoology*, **25**, 271–282.

FOELIX, R. F. 1970a. Structure and function of tarsal sensilla in the spider *Araneus diadematus*. *Journal of Experimental Zoology*, **175**, 99–124.

—— 1970b. Chemosensitive hairs in spiders. *Journal of Morphology*, **132**, 313–334.

FORSTER, R. R. and BLEST, A. D. 1979. The spiders of New Zealand. Part V. *Otago Museum Bulletin*, **5**, 1–173.

—— and PLATNICK, N. I. 1977. A review of the spider family Symphytognathidae (Arachnida, Araneae). *American Museum Novitates*, **2619**, 1–29.

—— —— 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). *Bulletin of the American Museum of Natural History*, **178**, 1–106.

—— —— 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. *Bulletin of the American Museum of Natural History*, **181**, 1–229.

—— and WILTON, C. L. 1973. The spiders of New Zealand. Part IV. *Otago Museum Bulletin*, **4**, 1–309.

GALL, J.-C. 1971. Faunes et paysages du Grès à *Voltzia* du nord des Vosges. Essai paléoécologique sur le Buntsandstein supérieur. *Mémoires du Service de la Carte Géologique d'Alsace et de Lorraine*, **34**, 1–318.

GERTSCH, W. J. 1974. The spider family Leptonetidae in North America. *Journal of Arachnology*, **1**, 145–203.

HEIMER, S. and NENTWIG, W. 1982. Thoughts on the phylogeny of the Araneoidea Latreille, 1806 (Arachnida, Araneae). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **20**, 284–295.

JELL, P. A. and DUNCAN, P. M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists*, **3**, 111–205.

KASTON, B. J. 1948. Spiders of Connecticut. *Connecticut State Geological and Natural History Survey Bulletin*, **70**, 1–874.

—— 1978. *How to know the spiders*. 3rd edn. William C. Brown, Dubuque, Iowa, vii+272 pp.

KOCH, C. L. 1851. *Übersicht des Arachnidensystems* Heft 5. C. H. Zeh, Nürnberg, 104 pp.

KOVOOR, J. 1977. L'appareil séricigènes dans le genre *Uloborus* Latr. (Araneae: Uloboridae), I: Anatomie. *Revue Arachnologique*, **1**, 89–102.

KULLMAN, E. 1972. The convergent development of orb-webs in cribellate and ecribellate spiders. *American Zoologist*, **12**, 395–405.

LACASA, A. 1985. Nota sobre las plumas fosiles del yacimento eocretácico de 'La Pedrera – La Cabrúa' en la Sierra del Montsec (Prov. Lleida, España). *Ilerda*, **46**, 227–238.

LACASA, A. and MARTINEZ, X. 1986. Fauna y flora de los yacimentos Neocomienses del Montsec (Prov. Lérida). *Paleontologia i Evolución*, 20, 215–223.

LATREILLE, P.-A. 1806. *Genera crustaceorum et insectorum* (4 vols, 1806–9.) Aranéides. Vol. 1, 82–127. A. Koenig, Paris.

LEHTINEN, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici*, 4, 199–468.

—— 1978. Definition and limitation of supraspecific taxa in spiders. 255–271. *In* MERRETT, P. (ed.). *Arachnology*. (Proceedings of the 7th International Congress of Arachnology.) *Symposia of the Zoological Society of London*, 42, 1–530.

—— 1980. Trichobothrial patterns in high-level taxonomy of spiders. *Proceedings of the 8th International Arachnological Congress, Vienna, 1980*, 493–498.

—— 1986. Evolution of the Scytodoidea. 149–157. *In* EBERHARD, W. G., LUBIN, Y. D. and ROBINSON, B. C. (eds.). *Proceedings of the Ninth International Congress of Arachnology, Panama, 1983*. Smithsonian Institution Press, Washington DC and London, 333 pp.

LEVI, H. W. 1961. Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. *Journal of Morphology*, 108, 1–9.

—— 1968. The spider genera *Gea* and *Argiope* in America (Araneae, Araneidae). *Bulletin of the Museum of Comparative Zoology, Harvard University*, 136, 319–352.

—— 1978. Orb-webs and the phylogeny of orb-weavers. 1–15. *In* MERRETT, P. (ed.). *Arachnology*. (Proceedings of the 7th International Congress of Arachnology.) *Symposia of the Zoological Society of London*, 42, 1–530.

—— 1980. The orb-weaver genus *Mecynogea*, the subfamily Metinae, and the genera *Pachygnatha*, *Glenognatha*, and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology, Harvard University*, 149, 1–74.

—— 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). *Bulletin of the Museum of Comparative Zoology, Harvard University*, 149, 271–318.

—— 1983. The orb-weaver genera *Argiope, Gea,* and *Neogea* from the western Pacific region (Araneae: Araneidae: Argiopinae). *Bulletin of the Museum of Comparative Zoology, Harvard University*, 150, 247–338.

—— 1986. The neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). *Bulletin of the Museum of Comparative Zoology, Harvard University*, 151, 91–215.

—— and LEVI, L. R. 1962. The genera of the spider family Theridiidae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 127, 1–71.

LOCKET, G. H. and MILLIDGE, A. F. 1953. *British spiders*. Vol. II. The Ray Society, London, vii + 449 pp.

LUBIN, Y. D. 1986. Web building and prey capture in the Uloboridae. 132–171. *In* SHEAR, W. A. (ed.). *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii + 492 pp.

MCALPINE, J. F. and MARTIN, J. E. H. 1969. Canadian amber – a paleontological treasure-chest. *The Canadian Entomologist*, 101, 819–838.

MADDISON, W. P. and MADDISON, D. R. 1987. *MacClade*. Version 2.1. An interactive, graphic program for analyzing phylogenies and studying character evolution; for the Apple Macintosh™ computer. (Available from the authors at: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA).

MENGE, A. 1986. Preussischen Spinnen. *Schriften der Naturforschenden Gesellschaft in Danzig, N.F.*, 2, 1–152.

MERRETT, P. 1963. The palpus of male spiders of the family Linyphiidae. *Proceedings of the Zoological Society of London*, 140, 347–467.

MILLIDGE, A. F. 1977. The conformation of the male palpal organs of linyphiid spiders, and its application to the taxonomic and phylogenetic analysis of the family (Araneae: Linyphiidae). *Bulletin of the British Arachnological Society*, 4, 1–60.

—— 1988. The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). *Bulletin of the British Arachnological Society*, 7, 253–268.

NIELSEN, E. 1932. *The biology of spiders*. Vol. I [in English] 248 pp. + 32 pls. Vol. II [in Danish] 723 pp. + 5 pls. Levin and Munksgaard, Copenhagen.

OPELL, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 148, 443–549.

—— 1982. Cribellum, calamistrum, and ventral-comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *Bulletin of the British Arachnological Society*, 5, 338–343.

—— and EBERHARD, W. G. 1983. Resting postures of orb-weaving uloborid spiders. *Bulletin of the British Arachnological Society*, 11, 369–376.

PATTERSON, C. and ROSEN, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, **158**, 81–172.

PEYBERNES, B. 1976. Le Jurassique et le Crétacé inférieur des Pyrénées Franco-Espagnoles entre la Garonne et la Méditerranée. Thèse Doctoral Sci. Nat. No. 646, Université Paul-Sabatier, Toulouse.

—— and OERTLI, H. 1972. La série de passage du Jurassique au Crétacé dans le Bassin sud-pyrénéen (Espagne). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris, série D*, **274**, 3348–3351.

PLATNICK, N. I. 1977. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). *American Museum Novitates*, **2627**, 1–23.

—— 1986. Seminar: Establishment of phyletic seriations. 55–57. *In* BARRIENTOS, J. A. (ed.). *Actas X Congreso Internacional de Aracnología, Jaca (España), 1986*. Vol 2. Instituto Pirenaico de Ecología, Jaca, 73 pp.

—— 1989. Advances in spider taxonomy 1981–1987: a supplement to Brignoli's A catalogue of the Araneae described between 1940 and 1981. Manchester University Press, Manchester, vii + 673 pp.

—— and GERTSCH, W. J. 1976. The suborders of spiders: a cladistic analysis (Arachnida, Araneae). *American Museum Novitates*, **2607**, 1–15.

—— and SHADAB, M. U. 1978a. A review of the spider genus *Mysmenopsis* (Araneae, Mysmenidae). *American Museum Novitates*, **2661**, 1–22.

—— —— 1978b. A review of the spider genus *Anapis* (Araneae, Anapidae), with a dual cladistic analysis. *American Museum Novitates*, **2663**, 1–23.

POCOCK, R. I. 1892. *Liphistius* and its bearing upon the classification of spiders. *Annals and Magazine of Natural History*, (6), **10**, 306–314.

RAVEN, R. J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bulletin of the American Museum of Natural History*, **182**, 1–180.

RIECHERT, S. E. and GILLESPIE, R. G. 1986. Habitat choice and utilization in web-building spiders. 23–48. *In* SHEAR, W. A. (ed.). *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii + 492 pp.

ROBERTS, M. J. 1985. *The spiders of Great Britain and Ireland*. Vol. I. Harley Books, Colchester, 229 pp.

ROBINSON, M. H. 1975. The evolution of predatory behaviour in araneid spiders. 293–312. *In* BAERENDS, G., BEER, C. and MANNING, A. (eds.). *Function and evolution in behaviour*. Clarendon Press, Oxford, xxxi + 393 pp.

SANZ, J. L., BONAPARTE, J. F. and LACASA, A. 1988. Unusual Early Cretaceous birds from Spain. *Nature, London*, **331**, 433–435.

SCHAIRER, G. and JANICKE, V. 1970. Sedimentologisch-paläontologische Untersuchungen an den Plattenkalken der Sierra de Monsech (Prov. Lérida, NE-Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **135**, 171–189.

SCHULT, J. 1983. Simple bulbs in male spiders – simple or derived? (Arachnida: Araneae). *Verhandlung der Naturwissenschaftlichen Verein in Hamburg*, **26**, 155–160.

SELDEN, P. A. 1989. Orb-web weaving spiders in the early Cretaceous. *Nature, London*, **340**, 711–713.

SHEAR, W. A. 1986a. The evolution of web-building behavior in spiders: a third generation of hypotheses. 364–400. *In* SHEAR, W. A. (ed.). *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii + 492 pp.

—— 1986b. Taxonomic glossary. 401–432. *In* SHEAR, W. A. (ed.). *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii + 492 pp.

SIMON, E. 1892. *Histoire naturelle des araignées*, 2nd edn, vol. 1, part 1. Libraire Encyclopédique de Roret, Paris, viii + 256 pp.

SMITH, F. P. 1902. The spiders of Epping Forest. *Essex Naturalist*, **12**, 181–201.

STOWE, M. K. 1986. Prey specialization in the Araneidae. 101–131. *In* SHEAR, W. A. (ed.). *Spiders – webs, behavior, and evolution*. Stanford Press, Stanford, California, viii + 492 pp.

WALCKENAER, C. A. 1802. *Faune parisienne, insectes*. Dentu, Paris, 250 pp.

WATERS, S. B. 1989. A new hybotine dipteran from the Cretaceous of Botswana. *Palaeontology*, **32**, 657–667.

WHALLEY, P. E. S. and JARZEMBOWSKI, E. A. 1985. Fossil insects from the Lithographic Limestone of Montsech (late Jurassic–early Cretaceous), Lérida Province, Spain. *Bulletin of the British Museum (Natural History) (Geology)*, **38**, 381–412.

WILEY, E. O. 1981. *Phylogenetics*. Wiley, New York, Chichester, Brisbane, and Toronto, xvi + 439 pp.

PAUL A. SELDEN
Department of Extra-Mural Studies
University of Manchester
Manchester M13 9PL