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WHEN SPIDERS FIRST WOVE WEBS

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Orb-web weaving spiders in the early Cretaceous

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THE use of a snare woven from spun silk as a means of capturing prey is the most outstanding achievement of spiders. Fossil spider spinnerets are known from the Devonian¹ and Carboniferous² periods. Presented here, however, is evidence of the antiquity of the use of woven silk in prey capture: spider fossils showing morphological adaptations for web weaving, from the Lower Cretaceous lithographic limestone of the Sierra de Montsech, north-east Spain. Reflected light microscopy reveals details of the pattern and structure of the tarsal claws, which were adapted for the handling of silk and locomotion on a web. As only two Mesozoic spiders, *Juraneus* and *Jurarchaea* from the Jurassic of the Soviet Union³, have been formally described, the four specimens reported here are an important addition to the fossil record. These belong to three new genera placed in the modern superfamilies Dinopoidea and Araneoidea. Members of both superfamilies weave orb webs or orb-web derivatives⁴. The Montsech spiders preyed on the abundant insect life which is also preserved in the Cretaceous lithographic limestone⁵.

The Lower Cretaceous lithographic limestone of the Sierra de Montsech, Lérida Province, north-east Spain, is renowned for its excellent preservation of land plants, crustaceans, insects, fish, amphibians, reptiles and birds^{5,6}. Four specimens of spiders are among the collections made in recent years at the quarries of La Cabrua (specimens LC 1150 IEI, LC 1753 AP, LC 1754 AP) and La Pedrera de Meia (LP 1755 AP). Locality details are given in ref. 7 and specimens are deposited in the Instituto de Estudios Ilerdenses, Lérida. The fifty-metre succession of limestone exposed in the quarries has been determined as late Berriasian to early Valanginian in age on the basis of microfossils^{6,8}. The fine-grained, thinly bedded limestones bearing the spider fossils represent a lagoonal or lacustrine environment between the Ebro continent to the south and marine conditions to the north⁶. The spiders are preserved as brittle, brown cuticle, and morphological details are seen best where the cuticle is covered by a thin layer of translucent matrix. Reflected light microscopy, using oil-immersion objectives, enables observation at high magnification. All three new genera belong to the suborder Araneomorphae; formal taxonomy of the new taxa will be published elsewhere⁹ and only brief descriptions follow here.

LC 1150 IEI (Fig. 1) is referred to the Araneoidea. This superfamily is inadequately defined at present¹⁰, but features include: lack of synapomorphies of other groups, serrate setae, paracymbium, few trichobothria, web-weaving and globose abdomen. Although none of these characters are unique to Araneoidea, their combined presence in LC 1150 IEI suggest its inclusion in this superfamily. The subelliptical carapace bears a raised cephalic area and no fovea. The abdomen (globular in life) bears a compact group of short spinnerets at the posterior. The sternum is subtriangular and there is a small, subtriangular labium. Serrate setae are present and no trichobothria can be seen on the specimen. The chelicerae are large (0.4 times the carapace length), forwardly directed and bear inner and outer rows of denticles and a mesal ridge. The specimen is an adult male, bearing a modified palp with a long embolus and what appears to be a small, proximal paracymbium. The legs are

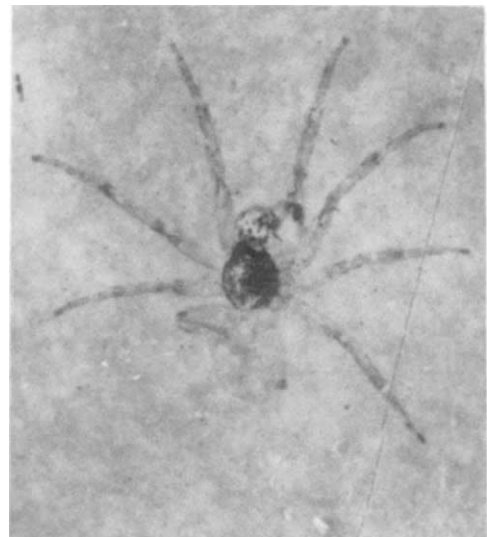


FIG. 1 Araneoid spider from the Lower Cretaceous of Montsech, Spain (LC 1150 IEI). Specimen compressed to the left; carapace offset to left, revealing right coxae; left male palp curved round anterior of left chelicera and showing long embolus, right palpal bulb lying on right leg 1; spinnerets appear as dark patch in lower right of abdomen (compressed to the left). Magnification, $\times 5.2$.



FIG. 2 Araneoid spider from the Lower Cretaceous of Montsech, Spain (LC 1753 AP). Note subcircular carapace, right male palp with planospirally coiled embolus, elongate legs 1 and 2, abdomen absent in this specimen. Magnification, $\times 3.2$.

subequal in length (formula, shortest to longest, 1243) and are about 3 times the length of the carapace. The tarsi bear pectinate paired claws, a small, non-pectinate median claw and numerous serrate bristles (Fig. 4a). It is impossible to assign the specimen to a family on these characters, but a small, sheet-web weaving araneoid (such as linyphiid or theridiid) is suggested.

LC 1753 AP (Fig. 2) and LC 1754 AP belong to the same species, which is referred to the Araneoidea. The foveate carapace is slightly wider than long and the oval abdomen bears a subterminal group of short spinnerets. Serrate setae occur and trichobothria are present on the superior prolateral surface of femora 3 (double row) and 4 (single row). The sternum is circular. Both specimens are adult males bearing modified palps with a planospirally coiled embolus. The leg formula is 1243, leg 1 being 6 times the length of the carapace and more than twice the length of leg 3. The paired tarsal claws bear six teeth, the median claw is long, curved and not pectinate and accessory claws are present (Fig. 4b). The pattern of elongated anterior legs, short third legs and femoral trichobothria occurs as a convergent phenomenon in two extant spider families: the Uloboridae (Dinopoidea) and the Araneidae (Araneoidea). Both groups are wrap-attack orb-web weavers, the former using cribellum and calamistrum to produce non-viscid 'cribellate' silk in contrast to the viscid silk of araneids. LC 1753 AP and LC 1754 AP lack characters that would refer them to the Dinopoidea (see below) and appear to be closest to the Argiopinae within the family Araneidae.

The carapace of LP 1755 AP (Fig. 3) is oval, has no well-defined fovea and just posterior to the midline is a break of slope which accommodated the forwardly extended abdomen in life. A compact group of six spinnerets and a cribellum is present subterminally on the abdomen. The leg formula is 1243; leg 1 is more than 5 times the length of the carapace and more than twice the length of leg 3. Plumose setae are present and there are many trichobothria on what appears to be the retrolateral surface of femur 2 and possibly the prolateral surfaces of femora 3 and 4. The paired tarsal claws are small and lack teeth, the median claw is long and probably lacks teeth (if



FIG. 3 Dinopoid spider from the Lower Cretaceous of Montsech, Spain (LP 1755 AP). Specimen is dorsoventrally compressed, dorsal and ventral surfaces superimposed. Note elongate legs 1 and 2, dark line on superior (posterior in specimen) side of metatarsus 4 indicates calamistrum; abdomen (wrinkled posteriorly) with ventral group of small spinnerets, transverse line immediately anterior marks cribellum. Magnification, $\times 7.4$.

present, they are minute). A pair of large accessory claws is present on the tarsi. The superior surface of metatarsus 4 is curved and bears a calamistrum. The palps are unmodified, so this is a female or immature specimen. LP 1755 AP belongs in the superfamily Dinopoidea, possessing calamistrum and cribellum, plumose setae and a characteristic tarsal claw pattern; it lacks the tarsal macrosetae and feathery setae of uloborids¹¹, and is therefore not placed in that family.

All three Montsech spider genera possess three tarsal claws with the characteristic serrate accessory claws adapted for web-weaving¹². The combination of elongated anterior legs, short third legs and femoral trichobothria in LC 1753 AP, LC 1754 AP and LP 1755 AP occurs in only two groups of living spiders, Uloboridae and Araneidae, both of which are weavers of orb webs. These spiders rest in characteristic positions¹³, generally with the anterior legs outstretched, and the short third legs gripping a twig. The function of the femoral trichobothria is not understood, but the organs occur, as in the fossil spiders, on the retrolateral surface of forwardly directed femora and prolateral surfaces of backwardly directed femora. Thus, at rest, the trichobothria point to the lateral sides of the animal.

There is controversy over whether the orb web is a convergent phenomenon in Araneoidea and Dinopoidea, or whether it

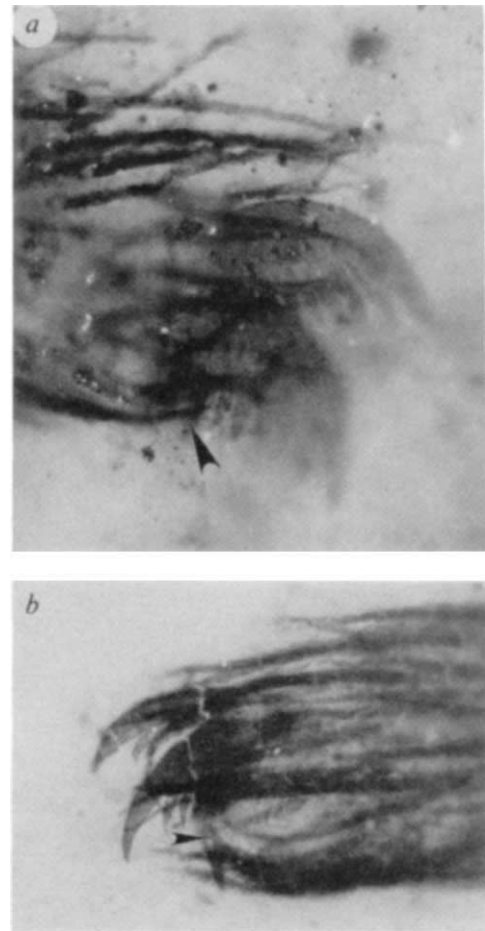


FIG. 4 a, Tarsal claws on left leg 2 of araneoid spider LC 1150 IEI. Note large, pectinate paired claws, small, uncinete median claw (arrowed), serrate accessory claws (bottom) and bristles. Magnification, $\times 290$. b, Tarsal claws on right leg 2 of araneid spider LC 1753 AP. Note pectinate paired claws, median claw (arrowed), and large, serrate accessory claws (bottom) and bristles. Magnification, $\times 250$. In web-weaving spiders, the silken thread is pulled by the median claw on to the serrations of the accessory claws; the median claws take no part in normal handling of silk¹⁵. Spiders which do not weave prey-capture webs do not possess accessory claws, and the median claw may be absent or greatly reduced.

evolved only once¹⁰. The Montsech spiders provide evidence that the two groups of orb-web weavers were already well defined by the early Cretaceous. No tarsal claw details are preserved in the Jurassic araneoid *Juraneus*¹⁴; nevertheless, it may have been an orb-web weaver. If the orb web evolved only once, in the common ancestor of Araneoidea and Dinopoidea⁴, its origin lies in the Jurassic or earlier. □

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Interspecific competition increases local extinction rate in a metapopulation system

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THE importance of interspecific competition for the distribution and abundance of organisms has been hotly debated during the last decade^{1–7}. Although many field experiments have shown effects of interspecific competition on abundance and reproduction^{1,3}, there is no unequivocal experimental evidence that interspecific competition can influence rates of local extinction in the field. Here I report that in a long-term field experiment with artificial rockpools, interspecific competition between three common rockpool zooplankton species led to increased local extinction rates. In addition, studies of the distributional dynamics of the species in natural rockpools also showed that interspecific competition increases extinction rates. These results imply that interspecific competition is likely to limit the regional richness of species in the rockpool metapopulation system. MacArthur and Wilson⁸ were the first to suggest that an increase in extinction rate per species with an increase in the number of species could influence species richness on islands. Moulton and Pimm⁹ found that this was so among birds introduced to the Hawaiian islands, but the present study is the first field experiment providing unequivocal evidence of the effect.

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Rockpools, small bedrock depressions containing fresh or brackish water, are common in coastal areas around Scandinavia. The most abundant small crustaceans in rockpools are three waterflea species, *Daphnia magna*, *D. pulex* and *D. longispina* (Cladocera)^{10–15}, which coexist regionally along the coasts of Sweden¹¹ and Finland^{12–15}. The smallest rockpools containing *Daphnia* have a volume of ~20 litres, and the largest ~10⁵ litres. The niches of the species widely overlap along several habitat niche dimensions^{11,12}, as well as the food axis¹¹. Hanski and Ranta¹⁴ proposed that the distributions of *Daphnia* in rockpools could be explained in terms of a colonization–extinction model, in which interspecific competition was assumed to influence extinction- and colonization rates. Such metapopulation models, where a metapopulation is defined as a regional population consisting of a number of patchily distributed local populations, have begun to play an important part in basic as well as applied ecology^{16,17}, but there is little experimental or field evidence to support them.

The field experiment used the three *Daphnia* species mentioned^{10,11}. It was conducted during 1983–86 and 1984–87 in artificial rockpools of four different sizes, namely 4-, 12-, 50- and 300-litre plastic bowls, placed outdoors and filled with freshwater. Experiments were run with the three-species combination, the three two-species combinations, and several one-species controls (Tables 1 and 2). Probably about sixteen, but at the very least eight, *Daphnia* generations occurred during the four-year experimental period¹¹. In addition, species occurrences and environmental conditions were studied in more than 400 natural rockpools in three areas along the Swedish coast for five years (ref. 11; Tables 3 and 4).

Extinction rates (population⁻¹. yr⁻¹) were always higher in the three-species- than in the two-species experiments, and no extinctions occurred in the one-species controls (Table 1). Extinction rates were also greater the smaller the artificial pools (Table 1). Analysis of the results of all the 4-litre experiments, and those experiments that persisted until the end of the fourth

TABLE 1. Probabilities of extinction, average mean densities and average coefficients of variation in density of *Daphnia* populations in artificial rockpools

Volume (litres)	Extinction probability (per population per year) ± s.d.			Average mean population density (individuals per litre) ± s.d.		Average coefficient of variation in density ± s.d.	
	one-species experiments	two-species experiments	three-species experiments	Persisting populations	Extinct populations	Persisting populations	Extinct populations
4	0 (—) (n=6)	0.21 (±0.078) (n=28)	0.28 (±0.11) (n=18)	—	—	—	—
12	0 (—) (n=3)	0.028 (±0.019) (n=22)	0.20 (±0.10) (n=12)	125* (±97.9) (n=22)	5.4* (±3.66) (n=5)	131 (±38.3) (n=22)	122 (±40.8) (n=5)
50	0 (—) (n=4)	0 (—) (n=26)	0.10 (±0.047) (n=15)	54.1* (±30.9) (n=26)	10.6* (±10.4) (n=4)	143 (±37.1) (n=26)	188 (±64.7) (n=4)
300	—	0 (—) (n=2)	0.030 (±0.029) (n=9)	32.3 (±16.6) (n=10)	5.6 (—) (n=1)	159 (±38.5) (n=10)	137 (—) (n=1)

Experiments were performed during 1983–86 or 1984–87, except 4-l experiments, which lasted for one summer (1983 or 1984). Four (±1) replicates of each two-species combination and the three-species combination were run, except for 4-l pools where six three-species experiments were run, and for 300-l pools where only one two-species experiment was run. One-species controls, with at least one for each species, were run in 4-, 12- and 50-l pools. The experiments were inoculated with a natural pond phytoplankton assemblage in the middle of May the year of starting, and about two weeks later *Daphnia* from natural rockpools were introduced¹¹. *Daphnia* survived winters as resting eggs. The results are based on samples from three to four sampling dates per year spaced evenly from May to autumn. Only established populations were used when calculating extinction probabilities. An extinction was judged to have occurred if an established species present in one year was absent in the following years. The 4-l pools were sampled and analysed in their entirety (including counts of resting eggs) at the end of the summer. Extinction probabilities were calculated on a population basis, regardless of species. The mean population densities and coefficients of variation in density for each population in each two- and three-species experiment were used for calculating averages in persisting and extinct populations. Some vessels broke during winters, and those present in only the first year were excluded from these analyses. For extinct populations, only values of population densities before extinction had occurred were used. Coefficients of variation were corrected for unequal sample sizes. See ref. 11 for further information and data. n, Initial number of populations; asterisk indicates significant difference between persisting and extinct populations (Mann-Whitney U Test, P < 0.01).