The oldest haplogyne spider (Araneae: Plectreuridae), from the Middle Jurassic of China

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Abstract New fossil spiders (Arachnida: Araneae) from Middle Jurassic (ca. 165 Ma) strata of Daohugou, Inner Mongolia, China are described as *Eoplectreurys gertschi* gen. et sp. nov. and referred to the modern haplogyne family Plectreuridae. This small family is restricted to southwestern USA, Mexico, and the adjacent Caribbean area today and hitherto has only a sparse Cenozoic fossil record. The morphology of *Eoplectreurys* is remarkably similar to modern forms and thus demonstrates great evolutionary conservatism. This new discovery not only extends the fossil record of the family by at least 120 Ma to the Middle Jurassic but also supports the hypothesis of a different distribution of the family in the past than today and subsequent extinction over much of its former range.

Keywords Mesozoic · Daohugou · Fossil · Inner Mongolia · Palaeobiogeography

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Introduction

The fossil record of spiders broadly reflects the pattern suggested by their phylogeny: The primitive suborder Mesothelae is recorded first in late Palaeozoic strata, then both infraorders of Opisthothelae, Mygalomorphae and Araneomorphae, appear close together in the Triassic (Selden and Penney 2009). Within Araneomorphae, however, the Triassic forms, though poorly preserved, resemble the relatively advanced araneoid entelegynes. Jurassic spiders are also members of the Entelegynae, and a number of families of orb weavers (Orbiculariae) were present in that period. Until now, the earliest fossils of the Haplogynae, which show many plesiomorphies with respect to the Entelegynae, came from Early Cretaceous ambers of Lebanon and Jordan (Wunderlich 2008). Thus, haplogynes would be expected in earlier strata, and in this paper, we report on not only the earliest hitherto discovered but also an unmistakable member of the modern family Plectreuridae.

Plectreuridae is a small family (two extant genera with 30 species) of eight-eyed, ecribellate, haplogyne spiders known only from southwest USA, Mexico, Cuba, and Costa Rica (Ramírez 2000; Ubick 2005; Jocqué and Dippenaar-Schoeman 2007; Platnick 2009). Hitherto, only two fossil plectreurids have been described: *Palaeoplectreurys baltica* Wunderlich 2004, from late Eocene Baltic amber (ca. 44–49 Ma) and *Plectreurys pittfieldi* Penney 2009 from Miocene Dominican amber (Penney 2009), so the discovery of a plectreurid from Middle Jurassic strata (ca. 165 Ma based on radiometric dating of overlying tuff: Chen et al. 2004; Liu et al. 2004) extends the fossil record of the family nearly fourfold, by 120 Ma. The new species described here, as *Eoplectreurys gertschi* gen. et sp. nov., is of particular interest because it preserves nearly all of the characteristics of this small family; there is little doubt about its placement

in Plectreuridae, within which it is closest to the *tristis* group (Gertsch 1958) of the genus *Plectreurys*. The present-day distribution of plectreurids is restricted to the southern part of the North American continent, yet they occurred in northern Europe in the Eocene and China (specifically the North China plate) in the Middle Jurassic. It is probable that the plectreurids had a wider distribution across the northern continental area during the Mesozoic and early Cenozoic eras, but they became extinct in Eurasia during either the severe cooling of the Eocene–Oligocene transition or the Pleistocene glaciations.

Materials and methods

The specimens come from a finely laminated, pale gray tuff near Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19.532′ N, 119° 14.589′ E). The Daohugou deposits (see Ren et al. 2002 for details) consist of gray tuff, tuffaceous siltstones and mudstones, indicative of lacustrine conditions in a volcanic region, and have also yielded plants, insects, conchostracans, anostracans, arachnids (Selden et al. 2008; Huang et al. 2009), salamanders, theropod dinosaurs, pterosaurs, and mammals. A Middle Jurassic age for the Daohugou assemblage has been proposed based on the composition of the insect fauna (e.g., Ren et al. 2002; Huang et al. 2006), conchostracans (Shen et al. 2003), and isotopic dating (Chen et al. 2004; Liu et al. 2004). The types are deposited in the Nanjing Institute of Geology and Palaeontology. Recent comparative material studied (from the California Academy of Sciences): PLECTREURIDAE: *Kibramoa yuma* Gertsch 1958, California, Tulare County, Ash Mountain, Kaweah Power Station #3 (40 miles northeast of Visalia); coll. 2 July 1995 D. J. Burdick; det. 15 November 2008 P. A. Selden. SEGESTRIIDAE: *Ariadna pilifera* O. Pickard-Cambridge 1898, Arizona, Cochise County, Chiricahua Mountains, Southwestern Research Station (4500′), 12 July 1976; coll. & det. V. Roth.

Preparation was carried out using a sharp knife. The specimens were studied, drawn, and photographed under 60% ethanol using Leica M205C, MZ16, and MZ APO stereomicroscopes. Drawings were scanned and traced in Adobe Illustrator. Photographs were taken with a Canon EOS 5D Mark II digital camera attached to the microscopes, captured with Canon EOS Utility software, and manipulated with Capture One Pro and Adobe Photoshop on an Apple MacBook Pro 17″ computer. In many cases, sharper focus was achieved by merging a stack of images using Photoshop, and sometimes, it was beneficial to view part and counterpart of the specimen superimposed using this software. An example of when this was useful is in revealing the fine, helical tip to the embolus in the holotype

of *Eoplectreurys* (Fig. 1c). All measurements are in millimeters and were made from the photographs using Photoshop's analysis tools.

Abbreviations Leg formula (e.g., 1423) indicates the length of each leg relative to the other legs from longest to shortest. Abbreviations: car carapace, ch chelicera, cx coxa, fe femur, lb labium, mt metatarsus, mx maxilla, op opisthosoma, pa patella, Pd pedipalp, sp spinnerets, st sternum, ta tarsus, ti tibia.

Morphological interpretation

The fossils are preserved as brown cuticle patches, setae, macrosetae, and other structures on, and to some extent within, the rock matrix. Even though part and counterpart are preserved in most cases, the split has not necessarily separated dorsal and ventral surfaces. So, for example, both part and counterpart may preserve fragments of dorsal carapace superimposed on ventral structures, such as sternum, labium, and coxae. In general, usually the part (as designated) preserves mostly dorsal structures and the counterpart mostly ventral. Because some structures are more robust than others, they exert a greater influence on the appearance of the fossil; moreover, the fossils are squashed flat yet were three-dimensional in life. Hence, a certain amount of distortion has occurred during fossilization, which needs to be understood. In spider fossils, the chelicerae generally move from a hanging position to project forward, as if porrect in life. Eyes are almost never distinguishable from among the mass of cuticle at the anterior of the carapace. In plectreurids, the pedipalp coxae (maxillae) and the labium are particularly robust and so disproportionately affect the appearance of the prosoma. Consequently, the shape of the carapace may be poorly defined, but the maxillae and labium are distinct. Where both part and counterpart exist, a fuller picture of the morphology may be gained, as in, for example, the number of bristles at the distal end of the metatarsi and the helical end of the embolus seen in Fig. 1c.

Whereas the adult males of this species are easily recognizable by their distinctive pedipalps, females are more difficult to assign since, being haplogyne, they lack external genitalia. Among a number of apparently haplogyne females present in the Daohugou araneofauna, one form seems most likely to belong with the males of *E. gertschi* on account of the near-circular carapace; the others have elongated carapaces and greatly enlarged, porrect chelicerae.

Commonly in fossil spiders, the chelicerae splay apart during compression (e.g., in the palpimanoids from Daohugou: Selden et al. 2008); this phenomenon is not seen in these plectreurids which show a distinct overlap of the basal two

Fig. 1 *E. gertschi* gen. et sp. nov. a Holotype part (NIGP151720a), whole specimen showing mainly ventral structures. b Holotype counterpart (NIGP151720b), whole specimen showing mainly dorsal structures. c Composite of holotype part and counterpart (NIGP151720a,b), detail of tibia 1 and embolus of male pedipalp; *arrow* points to helical distal part of embolus. d Explanatory drawing to accompany a. e Paratype part (NIGP151719a), whole specimen showing mainly dorsal structures. f Paratype counterpart (NIGP151719b), whole specimen showing mainly ventral structures
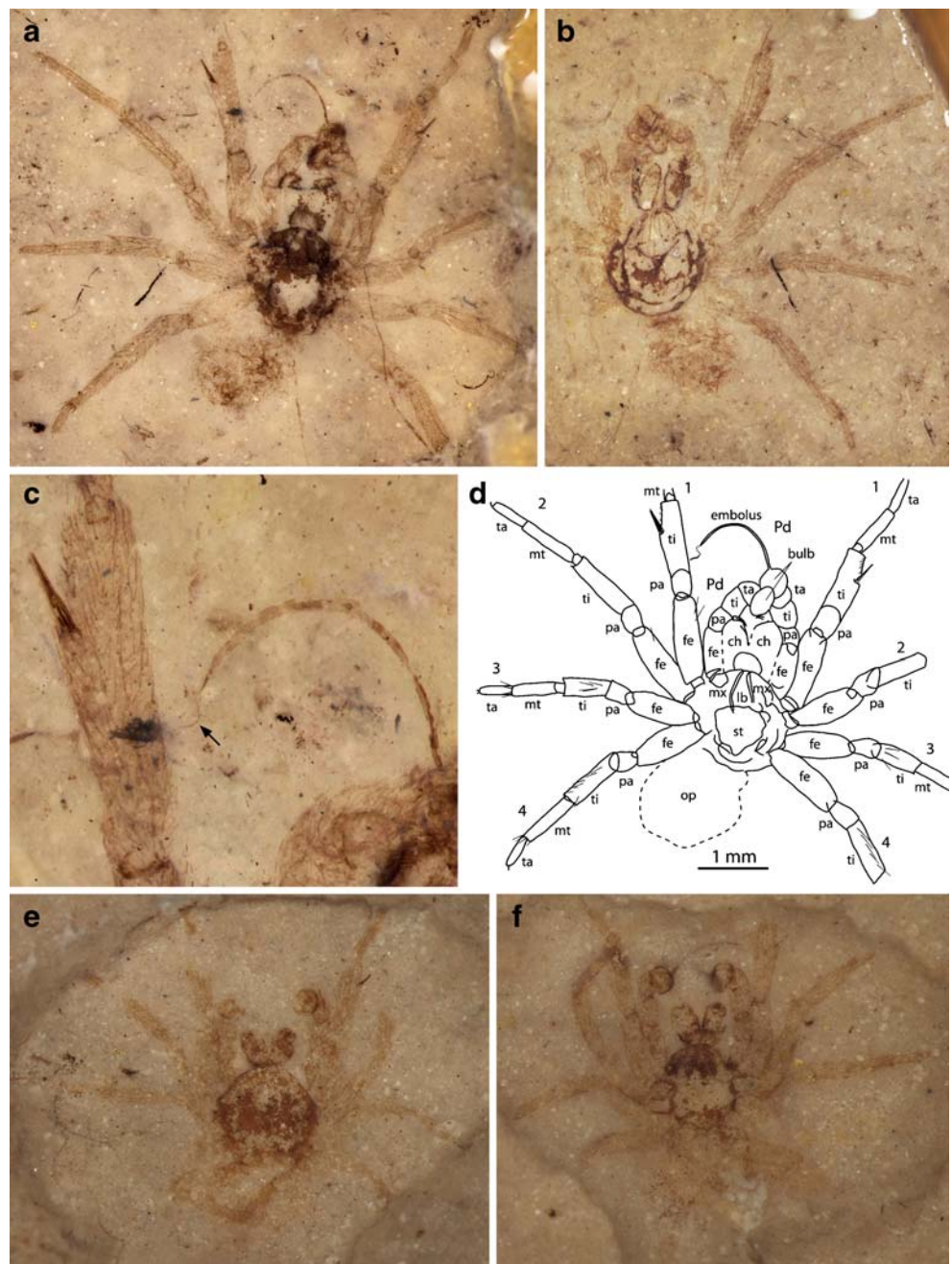
thirds of their length. This is evidence of cheliceral fusion which is common among haplogyne spiders.

Systematic paleontology

Order Araneae Clerck, 1757
    Family Plectreuridae Simon, 1893

Remarks Plectreuridae are defined as haplogyne spiders with eight eyes and differ from other haplogynes with eight eyes by being ecribellate (Filistatidae are cribellate), having

fused chelicerae (free in some Caponiidae) and relatively short legs (very long in Pholcidae). While the number of eyes cannot be seen in *Eoplectreurys*, the fossil is referred to Plectreuridae because it is a short-legged, ecribellate haplogyne with fused chelicerae and close similarities to modern plectreurid genera. The fossil appears to lack the stridulating file on the chelicerae which is normally present in plectreurids (Gertsch 1958), but the plectreurid file consists of extremely fine striations (it was described as "indistinct" by Ubick 2005) so, if present in the fossil genus, it is unlikely to be preserved. Additional features comparable with Plectreuridae are: tubercles with setae on

chelicera, denticles on cheliceral margin, male with strong leg 1 femur and tibia, tibia 1 with large macrosetae (spines) on basal tubercles in distal retrolateral position (clasping spur), macrosetae around distal joint of metatarsus, three-clawed tarsus, and simple palpal bulb with very long embolus sharply set off from bulb. The only other spider family which *Eoplectreurys* might be referred to would be Segestriidae in which *Ariadna*, for example, has a simple male pedipalp with a long embolus which is well set off from the bulb in some species (Beatty 1970). However, in many, but not all, species, the male metatarsus 1 is strongly modified with apophyses, but in all species, including those without apophyses, there are many more large macrosetae (spines) on the podomeres of the first legs, the overall body shape (e.g., carapace, sternum) is more elongated, and the maxillae, while long, do not meet in front of the labium.

Wunderlich (2004) described a fossil spider, *P. baltica*, from Eocene Baltic amber which he referred to Plectreuridae: Plectreurinae (note that Wunderlich considered this family to include Diguetidae and thus to include two subfamilies: Plectreurinae and Diguetinae). Characters which Wunderlich used to place *Palaeoplectreurys* in Plectreuridae were: eight eyes (most other haplogynes, including Diguetidae, have six), chelicerae fused for the first quarter of their length (although Gertsch's (1958) diagnosis has plectreurid chelicerae fused for half their length), stridulatory pick on pedipalp femur (and therefore stridulatory file presumed to be present on the chelicera), free labium, and converging maxillae. Stridulatory files occur in a few segestriids such as *Ariadna fidicina* (Beatty 1970). The pedipalp bulb of *Palaeoplectreurys* is certainly of the haplogyne type, but the embolus is not as sharply demarcated as in *Eoplectreurys* and most modern plectreurids (i.e., it is more similar to the *castanea* Group within the plectreurids and, indeed, Segestriidae). Moreover, the clasping spur of *Palaeoplectreurys* is on the metatarsus, not the tibia (where it occurs in *Plectreurys* and *Eoplectreurys*; it is absent in *Kibramoa*). The clasping spur occurs on the metatarsus of the segestriid *Ariadna*, which has a similar pedipalp bulb to *Palaeoplectreurys*, but only six eyes. So, there is substantial evidence which could argue for *Palaeoplectreurys* being referred to Segestriidae rather than Plectreuridae.

Distribution Recent species are found in southwestern USA, Mexico, Cuba, and Costa Rica (Gertsch 1958; Alayón 1993, 2003). Fossils are known from Hispaniola (Miocene Dominican amber; Penney 2009), possibly northern Europe (Eocene Baltic amber; Wunderlich 2004), and the Jurassic of China (this paper).

E. gertschi gen. et sp. nov. (Figs. 1, 2, and 3)

Diagnosis Small plectreurid (body length excluding chelicerae approximately 3 mm) with subcircular carapace, heart-shaped sternum, first leg femur shorter than carapace but not curved, male tibial clasper formed from numerous large macrosetae (4, cf. one or two in living *Plectreurys*), and a cluster of short, curved macrosetae distal to the clasper on tibia 1 in males.

Etymology Greek *eos*, dawn, and *Plectreurys*, the modern genus which the fossil closely resembles. The specific epithet honors Willis J. Gertsch for his revisionary work on the family Plectreuridae.

Type material, locality, and horizon Holotype: adult male, part and counterpart, NIGP151720a,b; allotype: adult? female, part and counterpart, NIGP151716a,b; paratypes: adult male, part and counterpart, NIGP151717a,b; adult male, part only, NIGP151718; adult male, part and counterpart, NIGP151719a,b; adult male, part and counterpart, NIGP151721a,b; adult male, part only NIGP151722; deposited in the Nanjing Institute of Geology and Palaeontology, from Middle Jurassic Jiulongshan Formation, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Description of male See Table 1 for measurements. Carapace very slightly longer than wide (length/width ratio approximately 1.03); subcircular with slight lateral salient; no fovea; carapace cuticle with reticulate ornament (Figs. 1a, b, 2f, and 4a, b); tubercles (Figs. 1a and 4a) with long, forwardly pointing setae (Figs. 2a, c, 3f, and 4b, c) in anterior (cephalic) region; eyes not visible. Sternum very slightly longer than wide (length/width ratio approximately 1.03); subcordate with straight anterior margin and extensions at each coxa (Figs. 2b, d and 4a, d). Labium nearly twice as long as wide (length/width ratio approximately 1.83; Figs. 1a, d and 4a, d). Maxillae large, converging to front of labium (Figs. 1a, d, f, 2a, c, and 4a, d). Chelicera length (including closed fang) approximately 0.66, paturon width approximately 0.34 (chelicera length/width ratio approximately 1.93); chelicerae fused for more than half of length from base (Figs. 1, 2, 3, and 4a–d); numerous (approximately five) acute denticles along cheliceral promargin, ending in cluster at distal end where fang tip occludes (Fig. 4a); paturon bearing setae on exposed surfaces (Figs. 4a–d); fang curved, length approximately 0.22, bearing serrate ridge (Fig. 4c). Pedipalp of simple, haplogyne form; femur length approximately 0.6, patella length approximately 0.31, tibia length approximately 0.38, tarsus length (including bulb) approximately 0.51, bulb length approximately 0.32, width approximately 0.43; all podomeres clothed in long, fine setae; bulb obovoid, without setae, with sharply demarcated, elongate embolus more than four times length of bulb (length of embolus

Fig. 2 *E. gertschi* gen. et sp. nov. a Paratype part (NIGP151717a), whole specimen showing mainly dorsal structures. b Holotype counterpart (NIGP151717b), whole specimen showing mainly ventral structures. c explanatory drawing to accompany a. d Explanatory drawing to accompany b. e Paratype (NIGP151718), whole specimen; arrow points to canals within pedipalp bulb. f Paratype (NIGP151722), whole specimen showing mainly dorsal structures
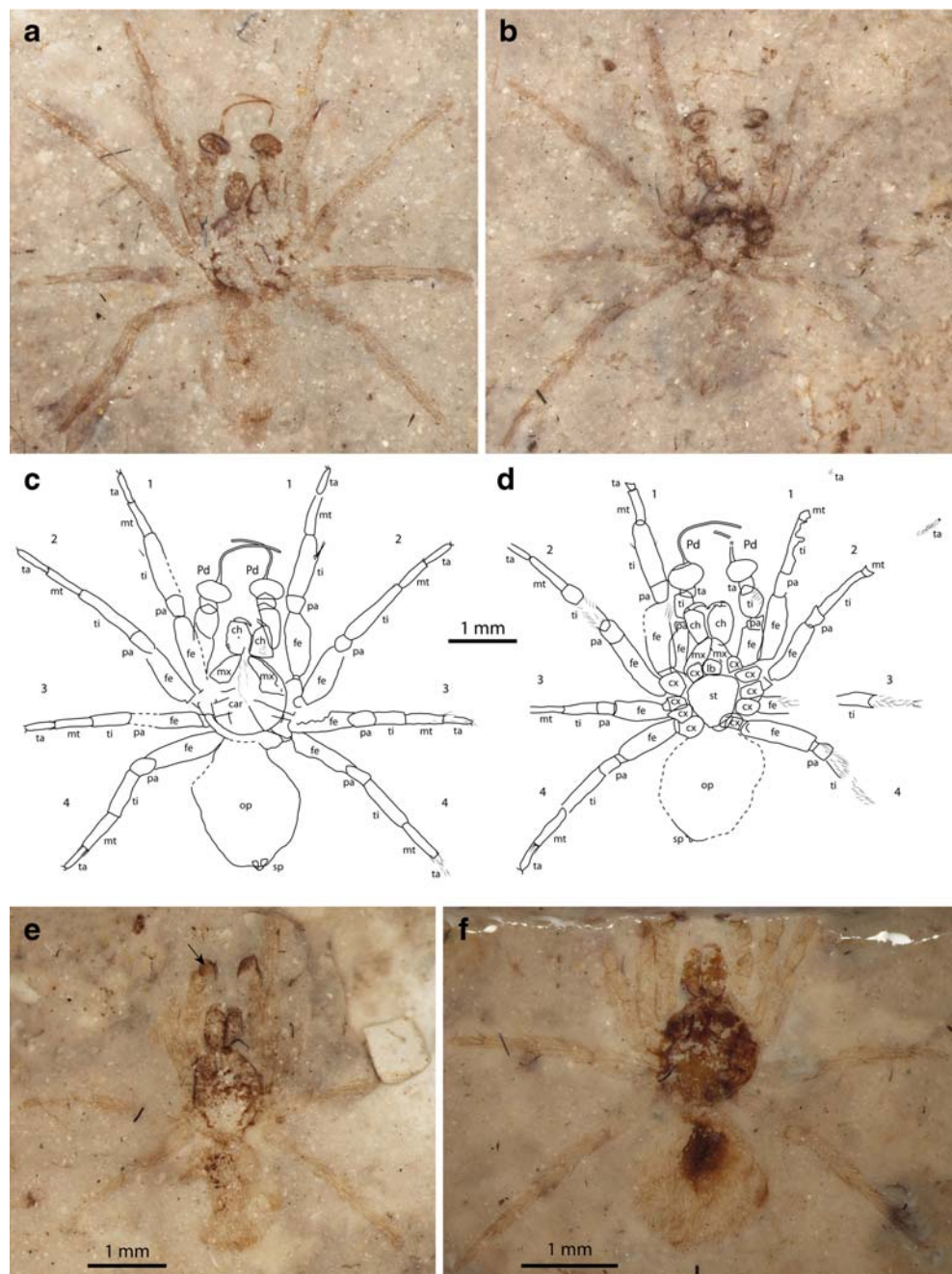

approximately 1.23 excluding terminal helical part); embolus curved, parallel-sided, scimitar-shaped except for thin, terminal, helical section (Fig. 1c). Canals can be seen inside bulb (Fig. 2e).

Walking legs not elongated, leg formula 1243; see Table 1 for measurements. All femora, and tibia of leg 1, rather stout; leg 1 metatarsus slightly curved; leg 1 femur with rugose cuticle. Legs clothed in curved setae, in numerous longitudinal rows on long podomeres, one or two rows of thin, erect macrosetae on long podomeres, becoming more numerous on distal podomeres; metatarsi 2, 3, and 4 bear four or more distinctive macrosetae on ventral side of distal joint (Fig. 4f);

tibia of leg 1 with clasper formed of four large macrosetae on retrolateral surface three quarters of length of podomere from proximal (clasper spine length approximately 0.31); row of at least six short, stout setae between clasper and distal end of podomere. Three tarsal claws, paired claws with teeth, unpaired claw small (Fig. 4e). Tarsus of leg 1 not obviously curved or with false jointing.

Opisthosoma slightly longer than wide (length approximately 1.74, width approximately 1.47; length/width ratio 1.18), subovate, densely clothed in fine setae; dorsal anterior part with thicker cuticle (Fig. 2e, f). Spinnerets terminal (Fig. 2a–d).
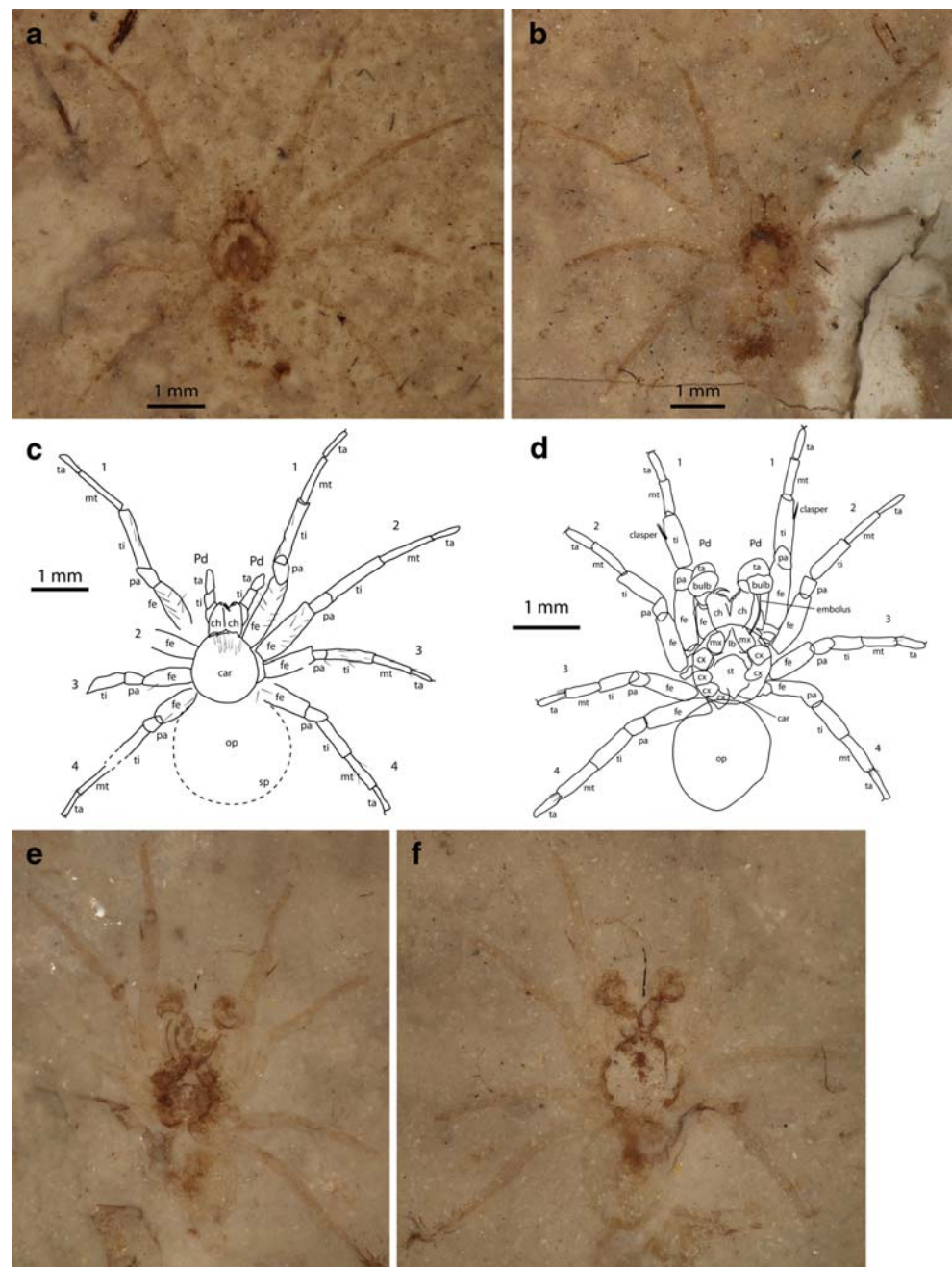
Description of female See Table 1 for measurements.
Carapace very slightly longer than wide (length/width ratio
approximately 1.02); subcircular with slight lateral salient;
no fovea; carapace cuticle with long, forwardly pointing
setae in anterior (cephalic) region; eyes not visible. Sternum
very slightly longer than wide (length/width ratio approxi-
mately 1.05); subcordate with straight anterior margin and
extensions at each coxa. Chelicera length (including closed
fang) approximately 0.67, paturon width approximately 0.35
(chelicera length/width ratio approximately 1.90); chelicerae
fused for more than half of length from base; numerous acute
denticles along cheliceral promargin; paturon bearing setae
on exposed surfaces; fang curved. Pedipalp patella length
approximately 0.23, tibia length approximately 0.23, tarsus
length approximately 0.44; all podomeres clothed in long,
fine setae; tarsus with few stout bristles but without a claw.

Walking legs not elongated, leg formula 1243; see
Table 1 for measurements. Legs clothed in curved setae,
in numerous longitudinal rows on long podomeres, one or
two rows of thin, erect macrosetae on long podomeres,
becoming more numerous on distal podomeres; metatarsi 2,
3, and 4 bear four distinctive macrosetae on ventral side of
distal joint. Three tarsal claws, paired claws with teeth,
unpaired claw small.

Table 1 Measurements (in mm) of type specimens of *E. gertschi* gen. et sp. nov. described herein

| Specimen no.	♂ NIGP 151720	♂ NIGP 151717	♂ NIGP 151719	♂ NIGP 151721	♂ NIGP 151718	♂ NIGP 151722	♂ Mean	♀ NIGP 151716
Body length (exc. chelicerae)		3.36			2.64		3.00	3.03
Carapace length	1.41		1.31	1.25	1.14	1.18	1.26	1.22
Carapace width	1.41		1.29	1.22	1.08	1.14	1.23	1.20
Carapace length/width ratio	1.00		1.02	1.02	1.06	1.04	1.03	1.02
Sternum length	0.71	0.76	0.67	0.70			0.71	0.61
Sternum width	0.63	0.77	0.67	0.70			0.69	0.58
Sternum length/width ratio	1.13	0.99	1.00	1.00			1.03	1.05
Labium length	0.51						0.51	
Labium width	0.28						0.28	
Labium length/width ratio	1.82						1.82	
Chelicera length (paturon + fang)	0.75	0.70	0.60	0.70	0.60	0.63	0.66	0.67
Chelicera paturon width	0.37	0.37	0.32	0.35	0.32	0.33	0.34	0.35
Chelicera length/width ratio	2.03	1.89	1.88	2.00	1.88	1.91	1.93	1.90
Fang length	0.21	0.24	0.23	0.23	0.22	0.21	0.22	
Pedipalp femur	0.65	0.69	0.56	c. 0.65	0.44	0.61	0.59	
Pedipalp patella	0.30	0.38	0.30	c. 0.3	0.28	0.29	0.31	0.23
Pedipalp tibia	0.40	0.47	0.30	c. 0.32	0.35	0.44	0.39	0.23
Pedipalp tarsus (inc. bulb if ♂)	0.55	0.52	0.52	0.53	0.43		0.51	0.44
Bulb length	0.35	0.35	0.30	0.34	0.24		0.32	
Bulb width	0.44	0.54	0.41	0.42	0.35		0.43	
Embolus length (exc. helical tip)	1.45	1.45	1.13	≥0.9			1.34	
Leg 1 femur-tarsus	3.70	3.50		3.06			3.42	4.18
Leg 1 trochanter length	0.14						0.14	
Leg 1 femur length	1.12	1.11	1.00	1.03	0.88	1.03	1.03	1.26
Leg 1 patella length	0.38	0.45	0.40	0.38	0.36	≥0.32	0.39	0.48
Leg 1 tibia length	1.20	1.05	0.80	1.00	≥0.67		1.01	1.19
Leg 1 metatarsus length	0.75	0.68	0.76	0.61			0.70	0.96
Leg 1 tarsus length (inc. claw)	0.60	0.52		0.55			0.56	0.56
Leg 2 femur-tarsus	3.90	3.68	2.67	3.10			3.34	4.13
Leg 2 femur length	1.18	1.15	0.90	0.95		0.94	1.02	1.18
Leg 2 patella length	0.45	0.45	0.36	0.44		0.37	0.41	0.48
Leg 2 tibia length	1.03	0.91	0.70	0.70			0.84	1.06
Leg 2 metatarsus length	0.99	0.79	≥0.6	0.65			0.81	0.96
Leg 2 tarsus length (inc. claw)	0.52	0.48		0.50			0.50	0.56
Leg 3 femur-tarsus	3.02	3.06	2.55	2.50		2.43	2.71	2.93
Leg 3 femur length	0.90	0.90	0.73	0.80		0.86	0.84	0.90
Leg 3 patella length	0.40	0.45	0.30	0.35		0.38	0.38	0.32
Leg 3 tibia length	0.61	0.70	0.60	0.53		0.56	0.60	0.70
Leg 3 metatarsus length	0.65	0.62	0.57	0.56		0.56	0.59	0.69
Leg 3 tarsus length (inc. claw)	0.48	0.50	0.48	0.50		0.41	0.47	0.45
Leg 4 femur-tarsus	3.42	3.38	3.05	2.95		2.92	3.14	3.29
Leg 4 femur length	1.10	1.04	1.00	0.93		0.88	0.99	1.04
Leg 4 patella length	0.40	0.40	0.38	0.37		0.38	0.39	0.38
Leg 4 tibia length	0.85	0.87	0.71	0.90		0.91	0.85	0.76
Leg 4 metatarsus length	0.83	0.70	0.60	0.65		0.66	0.69	0.78
Leg 4 tarsus length (inc. claw)	0.48	0.44	0.37	0.50		0.41	0.44	0.51
Opisthosoma length	1.60	2.14		1.69	1.55	1.70	1.74	2.11
Opisthosoma width	1.33	1.69		1.49	1.33	1.49	1.47	2.02

Table 1 (continued)

Specimen no.	♂ NIGP 151720	♂ NIGP 151717	♂ NIGP 151719	♂ NIGP 151721	♂ NIGP 151718	♂ NIGP 151722	♂ Mean	♀ NIGP 151716
Opisthosoma length/width ratio	1.20	1.27		1.13	1.17	1.15	1.18	1.05
Clasper spine length	0.36	0.34	0.21	0.31			0.31	

Opisthosoma slightly longer than wide (length approximately 2.11, width approximately 2.02; length/width ratio 1.05), subovate, densely clothed in fine setae; dorsal anterior part with thicker cuticle. Spinnerets terminal.

Remarks Of the known genera of Plectreuridae, *Plectreurys*, *Kibramoa*, and *Palaeoplectreurys*, *Eoplectreurys* is closest to the type genus *Plectreurys*. The fossil *Palaeoplectreurys* differs from other plectreurids in that its clasping spur is on

Fig. 4 *E. gertschi* gen. et sp. nov. a Holotype part (NIGP151720a), prosoma excluding appendages, showing mainly ventral structures: chelicerae with denticles, labium, maxillae, sternum, coxae; carapace reticulate cuticle, and tubercles on left. b Holotype counterpart (NIGP151720b), prosoma excluding appendages, showing mainly dorsal structures: chelicerae, carapace with reticulate cuticle and long median setae. c Paratype part (NIGP151717a), anterior carapace with long median setae, chelicerae with ridged fang. d Holotype counterpart (NIGP151717b), prosoma excluding appendages, showing mainly ventral structures: chelicerae, labium, maxillae, sternum, coxae. e Holotype part (NIGP151720a) left leg 1 tarsus showing comb-like paired claws, small median claw, and curved serrated bristles. f Holotype part (NIGP151720a) left leg 4 metatarsus showing proximal joint articulations and tendon attachment (*right*) and distal macrosetae (*left*). See explanatory drawings for scale
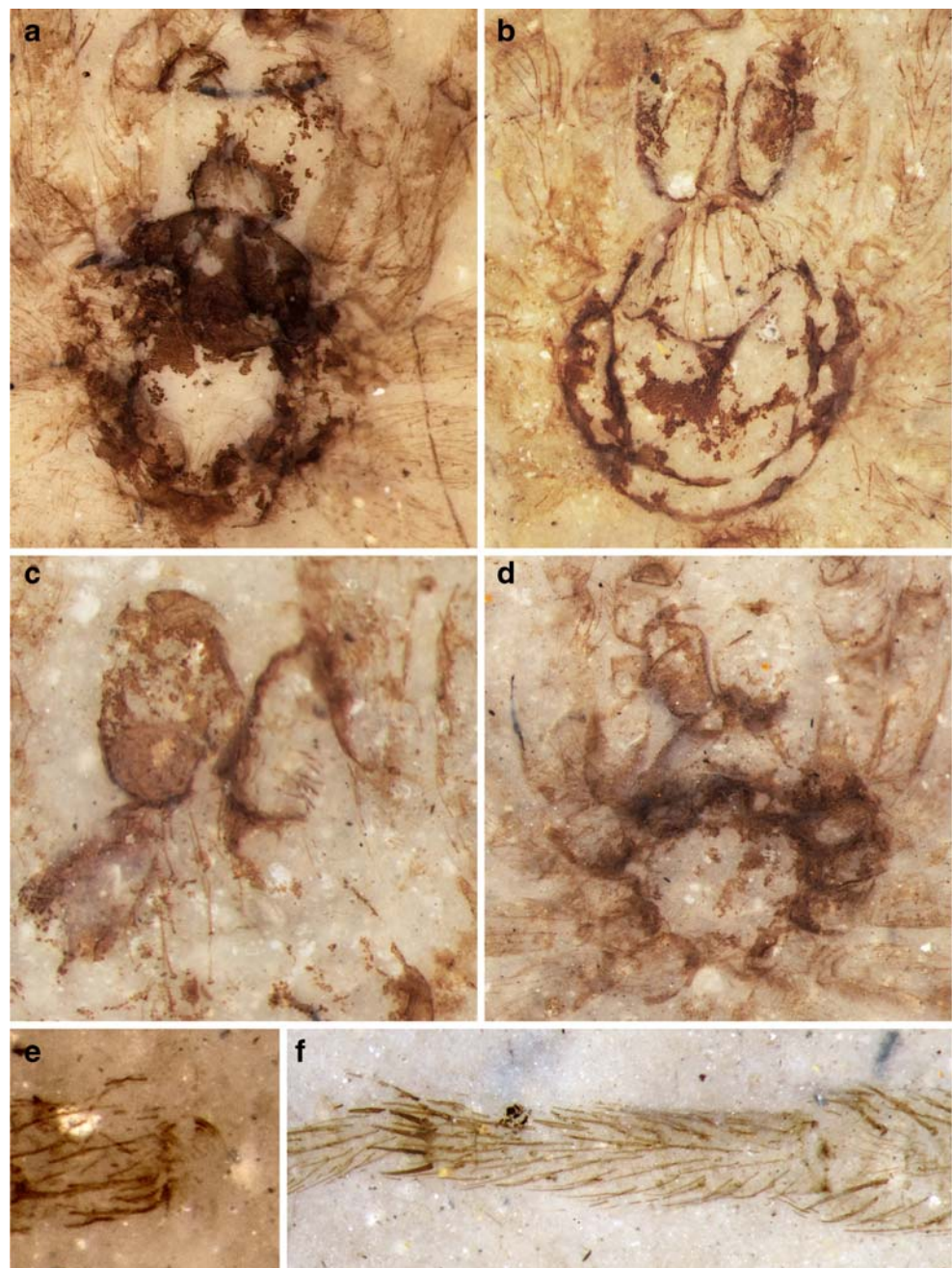
the metatarsus, not the tibia, and Wunderlich's conclusion that it nevertheless belongs in Plectreuridae is based on the eight eyes in the fossil. In *Kibramoa*, femur 1 is not robust and is longer than the carapace, the legs are generally longer than in *Plectreurys*, the first leg lacks a clasping spur in males (Gertsch 1958), and the legs generally have more and stouter macrosetae than in *Plectreurys*. Gertsch (1958) divided *Plectreurys* into two groups: the *castanea* group and the *tristis* group. In the *castanea* group, the male embolus is short, quite unlike that in other plectreurids, and the penultimate male pedipalp is not much modified. In the *tristis* group, the male pedipalp is quite distinct from the bulb and greatly elongated and that of the penultimate instar male can be quite distinctively modified in some species. Penney's (2009) species *P. pittfieldi* was placed in the *tristis* group. *Eoplectreurys* appears closer to the *tristis* group of *Plectreurys* than to any other plectreurid. With an adult male maximum body length of <3.5 mm, *Eoplectreurys* is the smallest known plectreurid.

It might appear, then, that *Eoplectreurys* could be accommodated in the recent genus *Plectreurys*. This seems unlikely, given that *Eoplectreurys* is Jurassic in age, but there are a few characters which can be used to separate the fossil genus from *Plectreurys*. Some characters which might be useful in diagnosis but are not observable in the fossil are: eye arrangement, flexibility of the first tarsus in males (this appears straight, but there is insufficient cuticle remaining on any of the specimens to tell whether false articulations existed or not), and the stridulating file on the chelicera. However, the carapace of *Eoplectreurys* is subcircular and the sternum heart-shaped, whereas in modern plectreurids, both of these sclerites are typically elongated. The differences could be related to the small size of *Eoplectreurys*. In *Eoplectreurys*, the first leg femur is shorter than the carapace and straight, whereas in *Plectreurys*, it is shorter than the carapace and curved, and in *Kibramoa*, it is longer than the carapace and straight (Gertsch 1958). In addition, in *Eoplectreurys*, the base upon which the clasping spines are situated is not as long, nor as close to the distal end of the tibia, as in *Plectreurys*, and there is a row of short, curved macrosetae distal to the clasper in *Eoplectreurys*.

General discussion

Evolution Eoplectreurys is remarkably similar to the living genus *Plectreurys*. Therefore, is Plectreuridae a unique relict from the distant past—a living fossil family—or just one of many modern spider families which date back to the Jurassic period with relatively little modification? It is noteworthy that Gertsch (1958, p. 1), in the opening sentence to his family revision, stated: "The primitive

hunters of the family Plectreuridae are among the most generalized of all the haplogyne ecribellate spiders." Among araneomorph spiders, the Haplogynae are considered more primitive than the Entelegynae, but within haplogynes, Plectreuridae are not considered particularly basal; however, in their study of karyotypy among basal spider clades, Král et al. (2006) showed that plectreurids exhibit the most plesiomorphic state. Eight eyes may be considered primitive, but their spinnerets are undoubtedly derived (Platnick et al. 1991), and the ecribellate state is also a derived condition within spiders.

The earliest known araneomorph spiders are Triassic and resemble araneoids (Selden et al. 1999), which are entelegynes. The Jurassic period has few described spiders: *Jurarchaea zherikhini* Eskov 1987 from Kazakhstan was described as an archaeid, pararchaeid, or holarchaeid (all of which are palpimanoid entelegynes), and *Juraraneus rasnitsyni* Eskov 1984 from Transbaikalia was placed in the entelegyne superfamily Araneoidea, in its own family Juraraneidae. Some specimens from the Daohugou locality were described as palpimanoid entelegynes, including one species placed in the modern family Archaeidae (Selden et al. 2008). Most other spiders from this locality belong to the modern entelegyne family Uloboridae and will be the subject of another publication. A specimen from the Jurassic of Grimmen, Germany has been figured (Ansorge 2003), but not yet formally described; preliminary investigation by PAS suggests it may also be a palpimanoid. So, by Jurassic times, the level of complexity of spiders had reached at least that of entelegynes, and all sufficiently well-preserved specimens can be placed within modern families or superfamilies. In the Cretaceous, spider families are diverse (Vollrath and Selden 2007), and it is likely that most modern families were established by then, with the notable exception of the most diverse and derived modern family, Salticidae. On this evidence, it is quite possible that most modern spider families extend back to the Jurassic period and that Plectreuridae is not unusual in this respect. Clearly, more data are required to test this hypothesis.

Biogeography The occurrence of a plectreurid in Middle Jurassic strata of the North China Block is remarkable considering their range today is restricted to southwestern USA and parts of the Caribbean region. Numerous hypotheses have been put forward for the position of the North China Block during the late Palaeozoic and early Mesozoic; according to the latest consensus (Metcalfe 2009), it probably separated from the North Australian part of Gondwana in the Devonian and docked fully with Pangaea in Middle Jurassic times. However, the presence of the Late Permian terrestrial vertebrate *Dicynodon* on the North China Block and the Indochina terrane indicates that dispersal of terrestrial faunas between Pangaea and terranes

north of Meso-Tethys was possible at that time, probably via the North China Block (Metcalfe 2009), and thus spiders could have dispersed between these areas as well.

The oldest, and most primitive, fossil spiders are known from the Carboniferous of Eurasia (Selden 1996), at a time when the North China Block was isolated from other landmasses, so it is very unlikely that Araneae originated on the North China Block or adjacent terranes. The earliest known opisthothele fossils are from the Triassic of Pangaea (present-day France, Virginia, and South Africa), and both mygalomorphs and araneomorphs were present at that time (Selden et al. 1999, 2009). The Triassic araneomorphs resemble higher Entelegynae, so it is likely that araneomorphs originated on Pangaea and dispersed to the North China Block before the Middle Jurassic.

The breakup of northern Pangaea began in Middle Jurassic times when rifting occurred along a line between present-day Greenland and Norway, forming a narrow, deep-water seaway by the Late Jurassic (Torsvik et al. 2002). However, it is likely that dispersal was still possible across Laurasia, especially via north polar regions during the Paleocene–Eocene Thermal Maximum (e.g., Smith et al. 2006) until about Miocene times. The discovery of a plectreurid in the Miocene of Hispaniola (Penney 2009) is unsurprising. It barely extends the present-day geographic range of the family and, indeed, living plectreurids may await discovery on the island, the modern araneofauna of which is not well sampled (Penney 2007). However, the presence of a possible plectreurid in Baltic amber (Wunderlich 2004) would indicate that the family may have had a different geographic range in the Eocene than today. Wunderlich (2004) suggested that a reduction in range occurred during the Eocene–Oligocene climatic cooling, but the disappearance of Plectreuridae from Eurasia may not have occurred until the Pleistocene northern hemisphere glaciations.

References

Alayón GG (1993) Redescripción de *Plectreurys globosus* Franganillo (Araneae: Plectreuridae). Poeyana 429:1–7

Alayón GG (2003) Nueva especie de *Plectreurys* Simon (Araneae: Plectreuridae) de Cuba. Rev Iber Aracnol 7:85–88

Ansorge J (2003) Insects from the Lower Toarcian of Middle Europe and England. Acta Zool Cracov 46(Supplement—fossil insects):291–310

Beatty JA (1970) The spider genus *Ariadna* in the Americas (Araneae, Dysderidae). Bull Mus Comp Zool 139:433–517

Chen W, Ji Q, Liu D-Y, Zhang Y, Song B, Liu X-Y (2004) Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. Geol Bull China 23:1165–1169 (in Chinese, English abstract)

Eskov K (1984) A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). N Jb Geol Paläont Mh 1984:645–653

Eskov K (1987) A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called "Gondwanan" ranges of recent taxa. N Jb Geol Paläont Abh 175:81–106

Gertsch WJ (1958) The spider family Plectreuridae. Am Mus Novit 1920:1–53

Huang D-Y, Nel A, Shen Y-B, Selden PA, Lin Q-B (2006) Discussions on the age of the Daohugou fauna—evidence from invertebrates. Prog Nat Sci Special Issue 16:308–312

Huang D-Y, Selden PA, Dunlop JA (2009) Harvestmen (Arachnida: Opiliones) from the Middle Jurassic of China. Naturwissenschaften 96:955–962

Jocqué R, Dippenaar-Schoeman AS (2007) Spider families of the world, 2nd edn. Koninklijk Museum voor Midden-Afrika, Tervuren

Král J, Musilová J, Šťáhlavský F, Řezáč M, Akan Z, Edwards RL, Coyle FA, Ribera C (2006) Evolution of the karyotype and sex chromosome systems in basal clades of araneomorph spiders (Araneae: Araneomorphae). Chromosome Res 14:859–880

Liu Y-Q, Liu Y-X, Li P-X, Zhang H, Zhang L-J, Li Y, Xia H-D (2004) Daohugou biota-bearing lithostratigraphic succession on the southeastern margin of the Ningcheng basin, Inner Mongolia, and its geochronology. Geol Bull China 23:1180–1185 (in Chinese, English abstract)

Metcalfe I (2009) Late Palaeozoic and Mesozoic tectonic and palaeogeographical evolution of SE Asia. In: Buffetaut E, Cuny G, Le Loeuff J, Suteethorn V (eds) Late Palaeozoic and Mesozoic ecosystems in SE Asia. Geol Soc Spec Publ 315:7–23

Penney D (2007) Hispaniolan spider biodiversity and the importance of combining neontological and palaeontological data in analyses of historical biogeography. In: Schwartz J (ed) Focus on biodiversity research. Nova Science Publishers, New York, pp 63–100

Penney D (2009) A new spider family record for Hispaniola—a new species of *Plectreurys* (Araneae: Plectreuridae) in Miocene Dominican amber. Zootaxa 2144:65–68

Pickard-Cambridge O (1898) Arachnida. Araneida. In: Biologia Centrali-Americana, Zoology. London 1:233–288

Platnick NI (2009) The world spider catalog, version 10.0. American Museum of Natural History. Online at http://research.amnh.org/entomology/spiders/catalog/index.html

Platnick NI, Coddington JA, Forster RR, Griswold CE (1991) Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Am Mus Novit 3016:1–73

Ramírez MJ (2000) Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). J Arachnol 28:149–157

Ren D, Gao K-Q, Guo Z-G, Ji S-A, Tan J-J, Song Z (2002) Stratigraphical division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. Geol Bull China 21:584–591 (in Chinese, English abstract)

Selden PA (1996) Fossil mesothele spiders. Nature 379:498–499

Selden PA, Penney D (2009) Fossil spiders. Biol Rev 85:171–206

Selden PA, Anderson HM, Anderson JM, Fraser NC (1999) The oldest araneomorph spiders, from the Triassic of South Africa and Virginia. J Arachnol 27:401–414

Selden PA, Huang D, Ren D (2008) Palpimanoid spiders from the Jurassic of China. J Arachnol 36:306–321

Selden PA, Anderson HM, Anderson JM (2009) A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South Africa. African Invertebrates 50:105–116

Shen Y-B, Chen P-J, Huang D-Y (2003) Age of the fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia. J Strat 27:311–313 (in Chinese, English abstract)

Smith T, Rose KD, Gingerich PD (2006) Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. Proc Natl Acad Sci USA 103:11223–11227

Torsvik TH, Carlos D, Mosar J, Cocks LRM, Malme T (2002) Global reconstructions and North Atlantic palaeogeography 400 Ma to recent. In: Eide EA (coord.) Batlas–Mid Norway plate reconstruc-tion atlas with global and Atlantic perspectives. Norg Geol Unders, Trondheim, pp 18–39

Ubick D (2005) Plectreuridae. In: Ubick D, Paquin P, Cushing PE, Roth V (eds) Spiders of North America: an identification manual. American Arachnological Society, College Park, MD, USA, pp 201–202

Vollrath F, Selden PA (2007) The role of behavior in the evolution of spiders, silks, and webs. Ann Rev Ecol Evol Syst 38:819–846

Wunderlich J (ed) (2004) Fossil spiders in amber and copal. Beitr Araneol 3:1–1908

Wunderlich J (ed) (2008) The dominance of ancient spider families of the Araneae: Haplogynae in the Cretaceous, and the late diversification of advanced ecribellate spiders of the Entelegynae after the Cretaceous–Tertiary boundary extinction events, with descriptions of new families. Beitr Araneol 5:524–675