

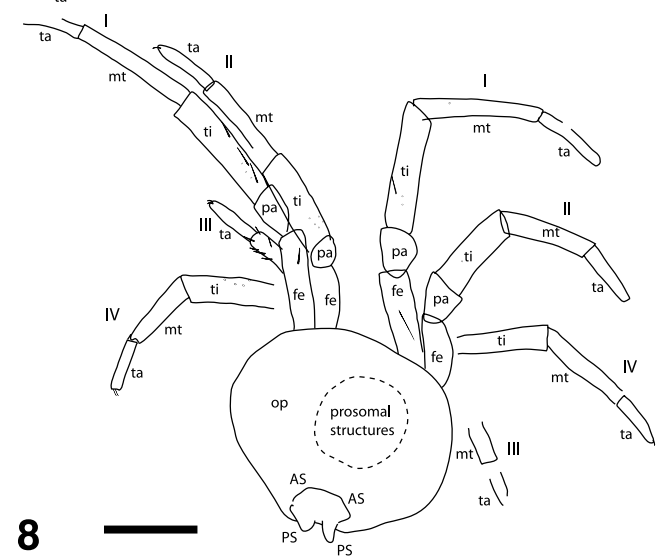
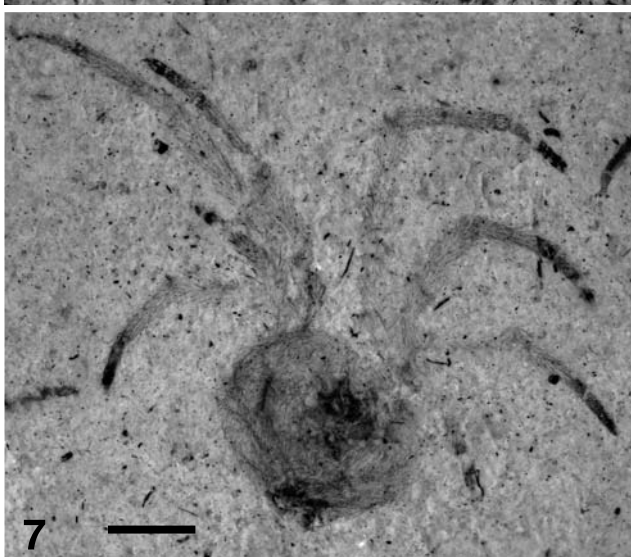
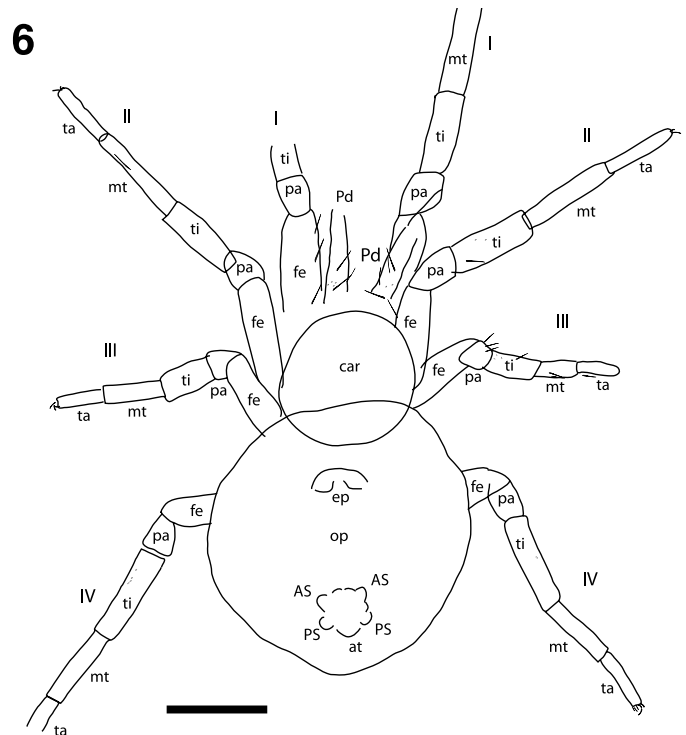
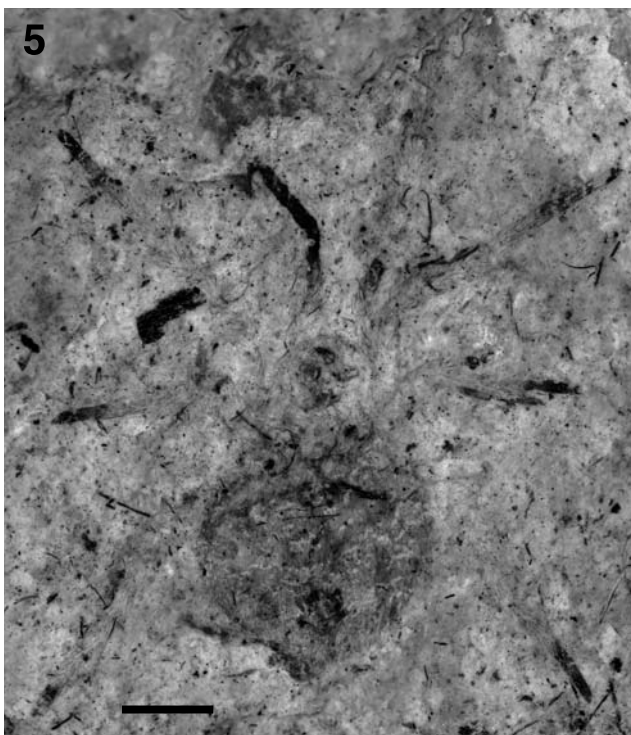
(1986) provided a review of the family and a cladogram for the genera. Theridiosomatidae are small to minute spiders (less than 3 mm body length) with short- to medium-length legs and relatively large male palpal bulbs. Synapomorphies for the family proposed by Coddington (1986) are a pair of pits on the anterior margin of the sternum near the base of the labium (absent from the Neotropical genus *Chthonos*), connate spermathecae (except in the Chinese *Coddingtonia*: Miller *et al.*, 2009), and elongate dorsal trichobothria on the tibia of the fourth leg.

Fossil theridiosomatids are known from Eocene Baltic, Oligocene Bitterfeld and Miocene Dominican Republic ambers (Wunderlich, 1988, 2004), of 44–49 million, 25.3–23.8 million and 16 million years old respectively (Dunlop & Mitov, 2009; Penney, 2008). The specimens described here, which are about 130–140

million years in age, thus extend the fossil record of the family threefold to the early Cretaceous.

Material and methods

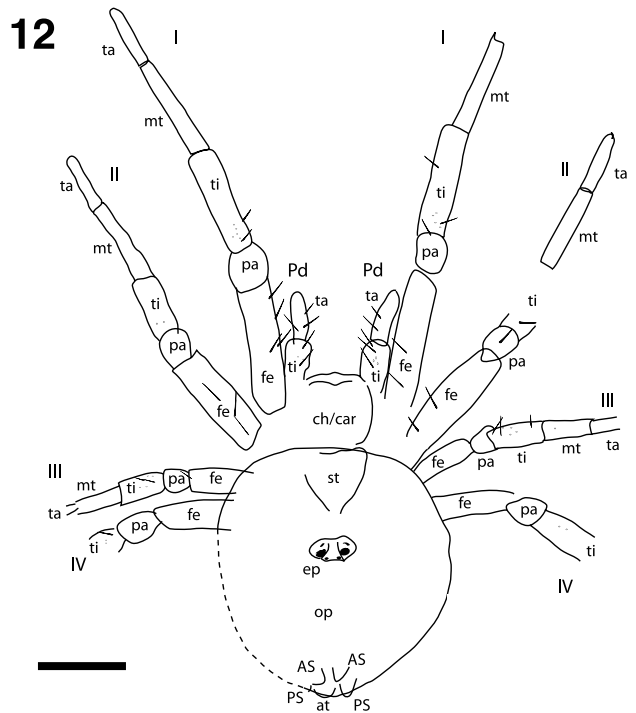
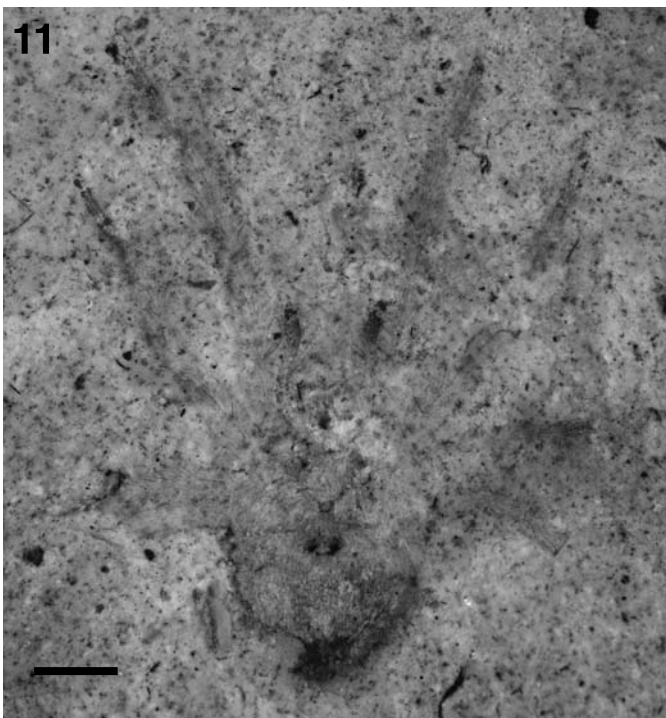
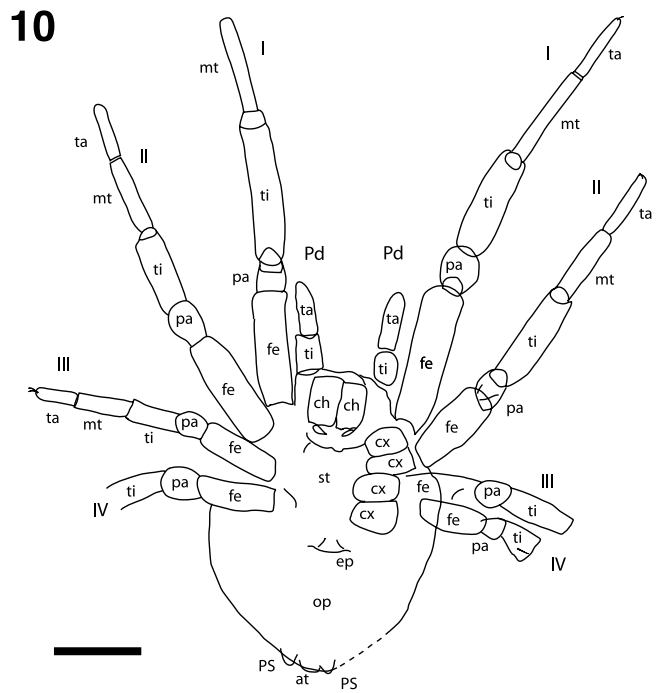
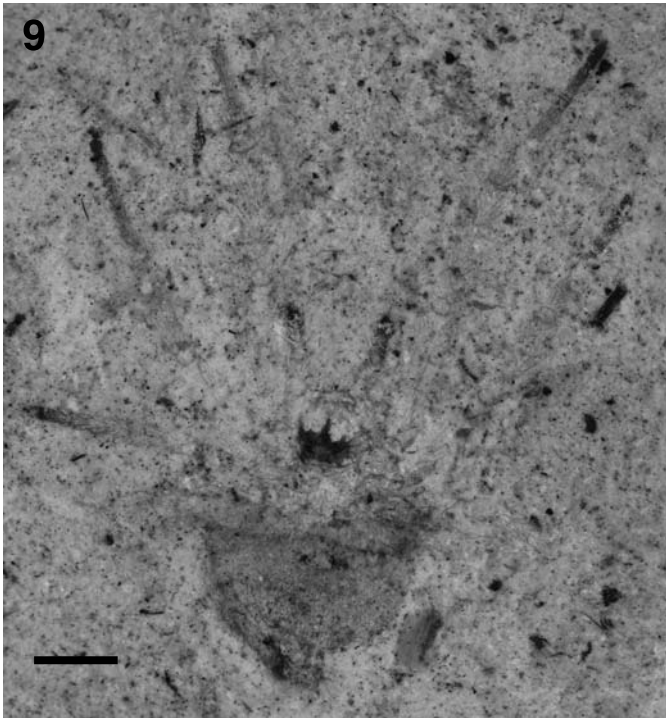
The specimens described here came from the famous Baissa fossil insect locality of the Buryat Autonomous Republic, western Transbaikalia, Russia (Zherikhin *et al.*, 1999). The main locality lies on the left bank of the Vitim river, 8 km below the mouth of the Baissa river, about 60 km from the village of Romanovka in the Eravnsky District. Stratigraphy is the Zazinskaya Formation, which is dated as Lower Cretaceous, Berriasian–Valanginian (130–140 Ma) (Vršanský *et al.*, 2002). Fossil insects occur throughout the section in the finer grained rocks; they are especially well preserved in the marls, which represent lacustrine deposits. More



Figs. 5–8: *Eocoddingtonia eskovi* gen. & sp. n., paratype females. **5** PIN 3064–8591, composite photograph of part and counterpart; **6** Explanatory drawing of PIN 3064–8591; **7** PIN 4210–5461, composite photograph of part and counterpart; **8** Explanatory drawing of PIN 4210–5461.

than 10,000 fossil insects, often of excellent preservation state, have been collected at Baissa (Zherikhin *et al.*, 1999), but only 22 spiders to date. One feature of the locality is the climatic change, from humid to dry then back to humid again, as reflected in changes in the composition of the fossil insect assemblages (Vršanský *et al.*, 2002). The spiders described here all came from layer number 31, which has also yielded abundant insects, ostracodes, plants, gastropods, and tetrapods, including feathers, and is among the layers with a humid climate (Zherikhin *et al.*, 1999; Vršanský *et al.*, 2002).

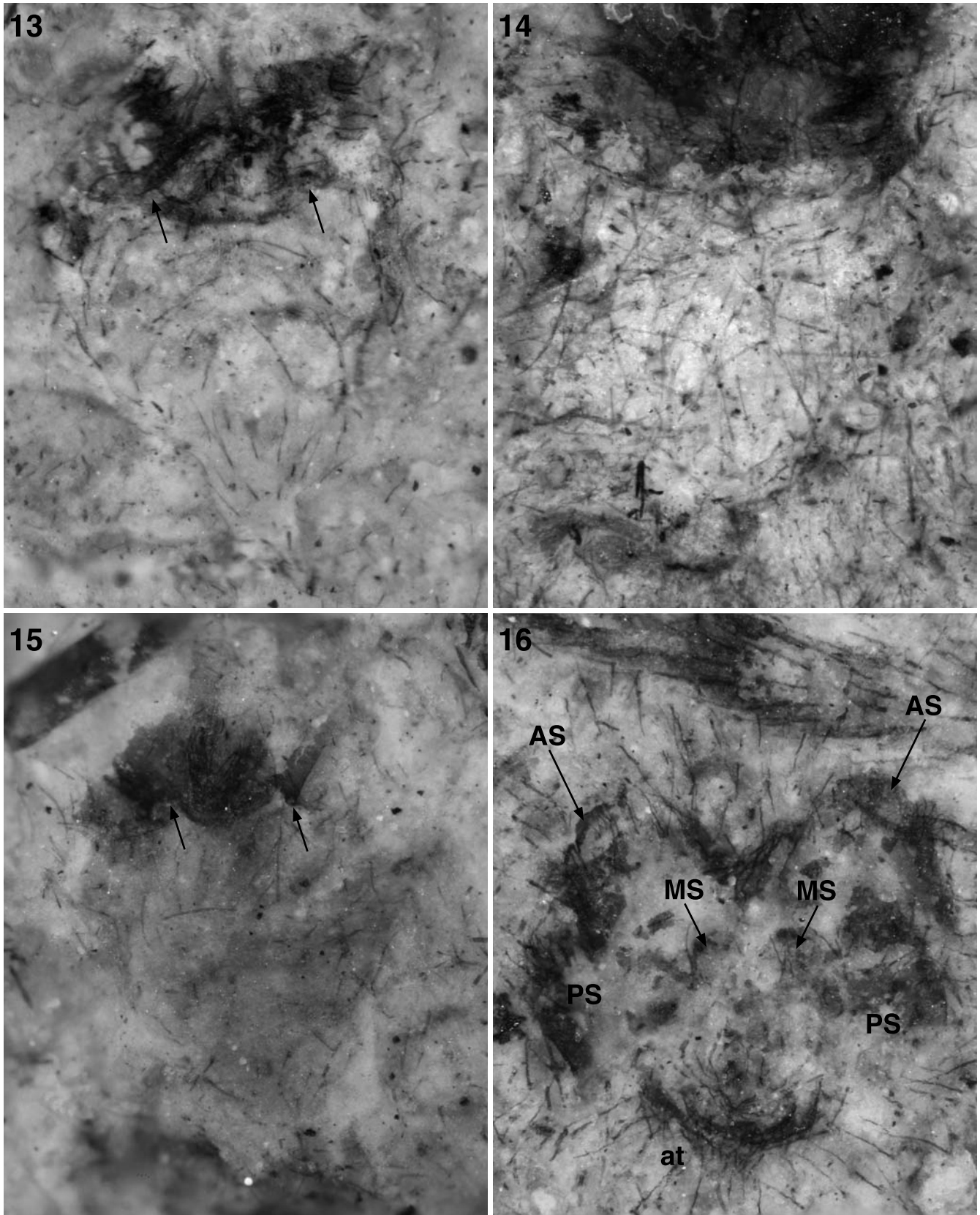
The spider specimens are preserved as organic material in fine clayrock, together with abundant comminuted carbonised plant fragments. The fossils were studied using a Wild MZ16 stereomicroscope, drawn using a camera lucida attachment, and photographed with a Canon 5D Mk II digital camera attached to the microscope. Photographs were taken with the specimens under ethanol to enhance contrast. High resolution composite photographs were prepared using Adobe Photoshop CS4 Professional. Drawings and photographs were prepared for publication using Adobe Illustrator CS4 and Adobe InDesign CS4 on an Apple



Figs. 9–12: *Eocoddingtonia eskovi* gen. & sp. n., paratype female, PIN 4210–5462. **9** Photograph of part, PIN 4210–5462a; **10** Explanatory drawing of part; **11** Photograph of counterpart, PIN 4210–5462b; **12** Explanatory drawing of counterpart.

MacBook Pro computer operating under Mac OS X. One advantage of computer manipulation is that better depth of focus can be achieved by stacking images taken at different levels of focus. Moreover, part and counter-

part of fossils can be superimposed to reveal more complete morphological information, which would otherwise be separated on two different slabs; see, for example, Figs. 5, 6 17, 23, 32–35. All measurements are



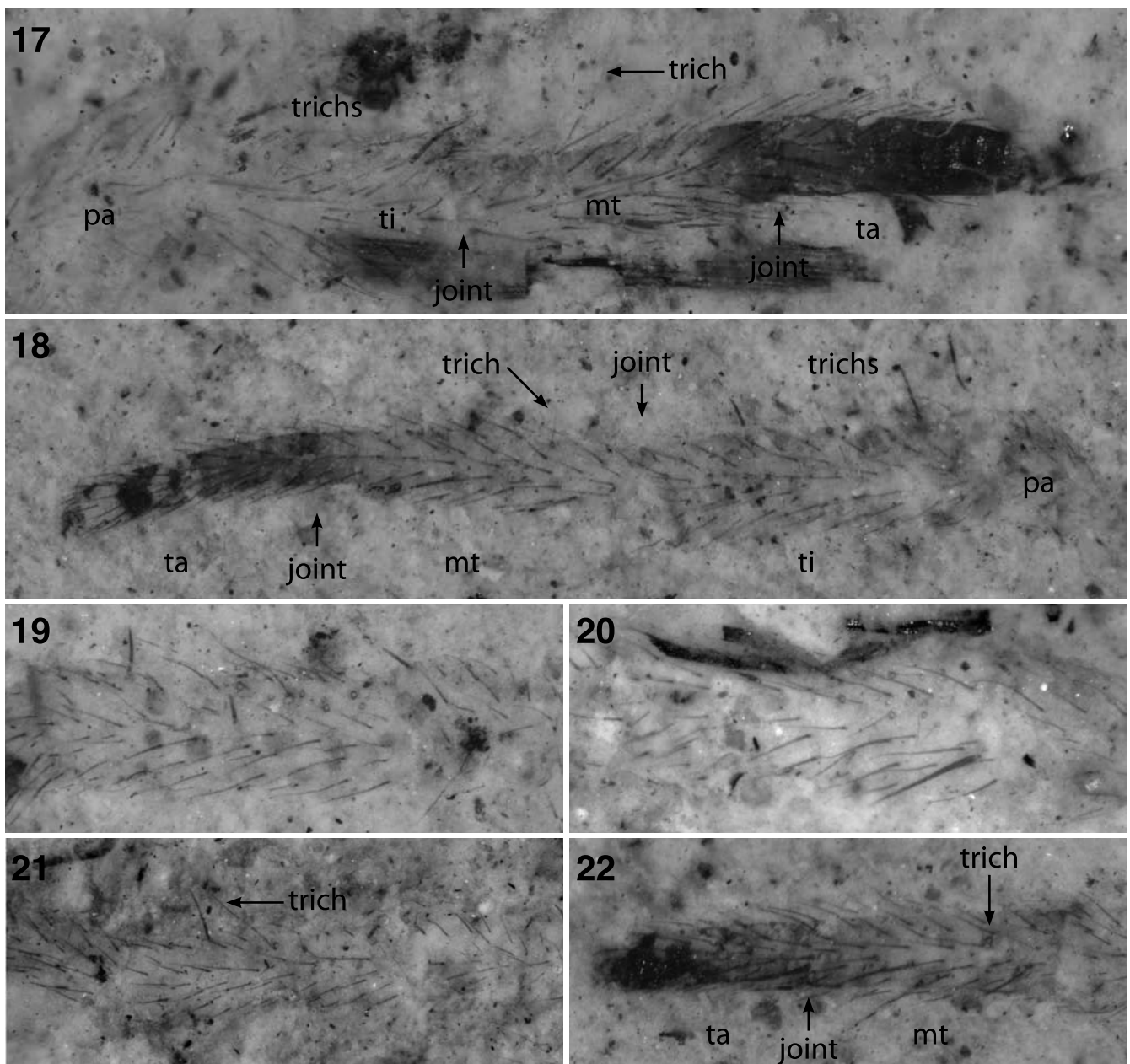
Figs. 13–16: *Eocoddingtonia eskovi* gen. & sp. n., sterna and spinnerets. **13** Holotype female part, PIN 3064–8593a, sternum, arrows show possible positions of gland openings; **14** Composite photograph of paratype female, PIN 4210–5462, sternum; **15** Allotype male part, PIN 4210–5463a, sternum, arrows show possible positions of gland openings; **16** Holotype female part, PIN 3064–8593a, spinnerets, note spinning field with notch and spigots on left AS.

in mm; scale lines in figures are 1 mm. Abbreviations: I, II, III, IV=leg numbers, AS=anterior spinneret, at=anal tubercle, car=carapace, ch=chelicera, cx=coxa, ep=epigyne, fe=femur, lb=labium, MS=median spinneret, mt=metatarsus, mx=maxilla, op=opisthosoma, pa=patella, Pd=pedipalp, PS=posterior spinneret, st=sternum, ta=tarsus, ti=tibia, trich=trichobothrium. Joint refers to the articulation between leg articles.

Morphological interpretation

The type series consists of four adult females and two adult males. Eyes are rarely preserved in compression fossil spiders, and these specimens are no exception; suggestions of eyes cannot be confirmed. The opisthosoma is interpreted to have been globose in life, and in

one specimen (PIN 4210–5461) it wholly, and in another partly (PIN 4210–5462), covers the carapace. In many compression fossils of spiders the chelicerae extend forwards and appear to be correct; in these theridiosomatids, however, the chelicerae are compressed in a vertical orientation (PIN 3064–8593) or are folded backwards and point towards the sternum (PIN 4210–5462a). Many features occur on both part and counterpart, and it is not possible to define part and counterpart as dorsal and ventral. For example, epigynes (Figs. 28–31) are preserved on both slabs, and the setal orientation on the opisthosoma shows both anterior–posterior (dorsal) and lateral (ventral) directions. The preservation is of sufficiently high quality that even such fine structures as trichobothrial hairs (Figs. 17–22) and epigynal internal structures (Fig. 30) can be seen. The interpretation of the



Figs. 17–22: *Eocoddingtonia eskovi* gen. & sp. n., legs of females. **17** Composite photograph of paratype female, PIN 3064–8591, leg III patella to tarsus; **18** Holotype female part, PIN 3064–8593a, leg I patella to tarsus; **19** Holotype female part, PIN 3064–8593a, leg IV tibia; **20** Paratype female counterpart, PIN 3064–8591b, leg II tibia; **21** Paratype female counterpart, PIN 3064–8591b, leg IV tibia; **22** Holotype female part, PIN 3064–8593a, leg III metatarsus and tarsus.

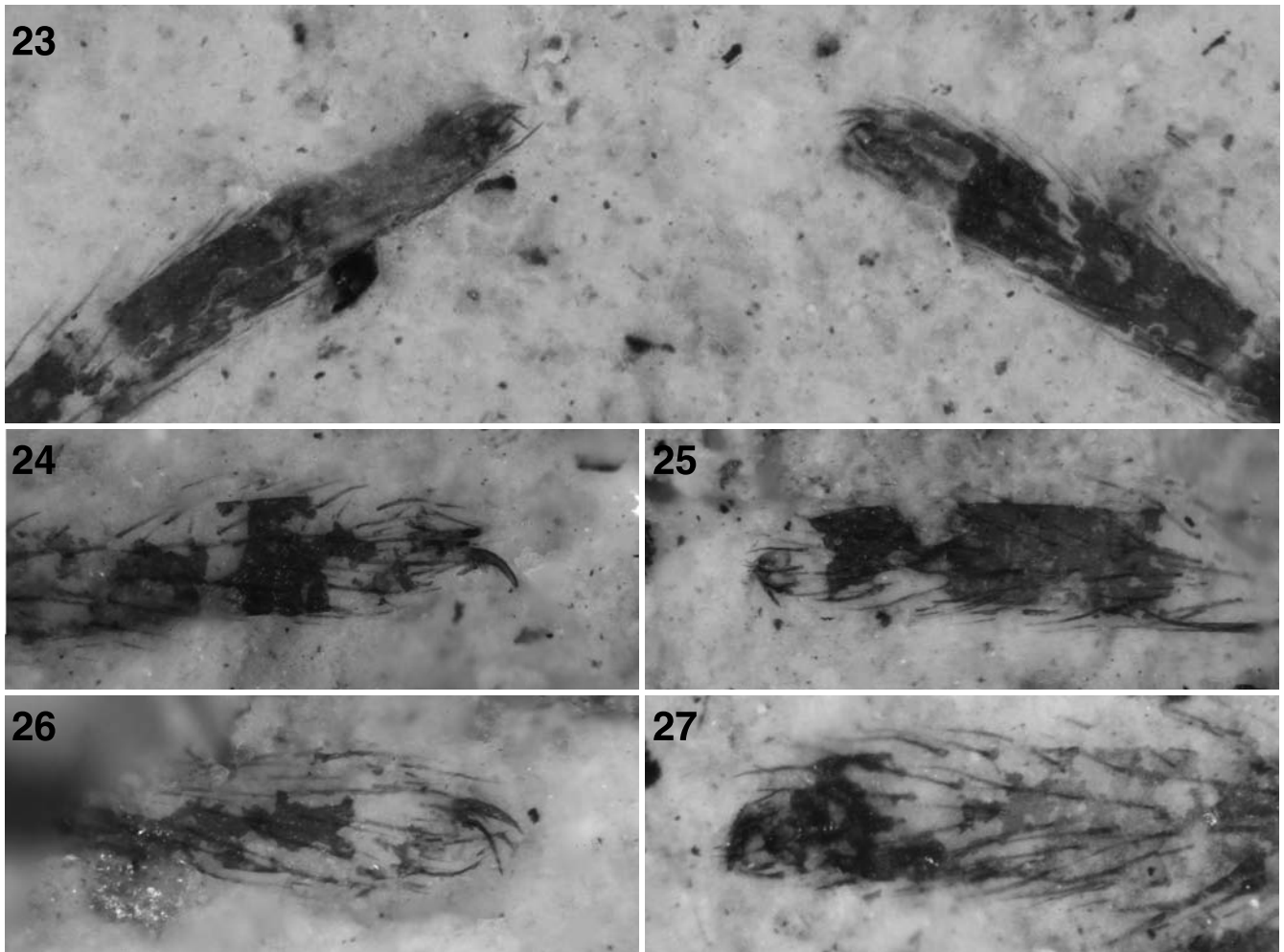
epigyne is difficult, but the excellent preservation means that more morphology can be inferred than is usually the case in matrix-preserved spider fossils. From comparison of Figs. 28 and 30, which are the best-preserved examples, it can be seen that a subtrapezoidal median lobe is flanked by dark areas. In Fig. 30, faint circular canals are shown in the postero-lateral corners of the median lobe, apparently originating from dark spots on the posterior border; these are interpreted as copulatory ducts coming from openings on the posterior border. The spermathecae are most likely in the region of the dark areas; indeed, circular structures can also be made out in these regions on Fig. 30 (see Fig. 32). Thus, the spermathecae are presumed to be separate rather than connate.

Identification of males is more problematic. Specimens PIN 4210–5463 and PIN 3064–8594 are adult males of similar size and habitus to the females, with globular opisthosomas, similar sternal shape (in PIN 4210–5463, designated here as the allotype), tibial trichobothria, and tarsal claw pattern. The large size and compact, globular shape of the cymbial parts of the male is typical of Theridiosomatidae. It is not possible to assign names accurately to the palpal sclerites, but the

morphology of the two large sclerites (Figs. 33–36) resembles that of the tegulum and/or conductor typical of theridiosomatid males (e.g. Miller *et al.*, 2009: fig. 2). Hence, these specimens are considered to be conspecific with the females.

Family Theridiosomatidae Simon, 1881

Remarks: The spiders are referred to this family on the following lines of evidence. The habitus is that of a small araneoid: globular opisthosoma with epigyne close to spinnerets, i.e. spinnerets ventral rather than terminal on opisthosoma, and opisthosoma held well forward over the prosoma, as evidenced by it wholly or mostly covering the carapace; lack of claw on female pedipalp tarsus (Figs. 10–12); numerous trichobothria on all tibiae; single trichobothrium in proximal position on metatarsus (Figs. 18, 22); the conformation of the sternum and labium is as that seen in other theridiosomatids, though the presence of sternal pits, while suggested in some specimens (Figs. 13–15) cannot be confirmed. The distal (cymbial) parts of the male pedipalp are large, compact and globose.



Figs. 23–27: *Eocoddingtonia eskovi* gen. & sp. n., tarsi. **23** Composite photograph of allotype male, PIN 4210–5463, legs IV tarsi; **24** Paratype female part, PIN 4210–5461a, leg II tarsus; **25** Paratype female part, PIN 3064–8591a, leg III tarsus; **26** Allotype male counterpart, PIN 4210–5463b, leg III tarsus; **27** Holotype female part, PIN 3064–8593a, leg I tarsus.

Genus *Eocoddingtonia* gen. n.

Type species: Eocoddingtonia eskovi sp. n.

Etymology: The name *Eocoddingtonia* is derived from the Greek *eos*, dawn, and *Coddingtonia*, a genus of Theridiosomatidae which the fossil genus resembles.

Diagnosis: *Eocoddingtonia* differs from all other theridiosomatids except *Coddingtonia* by having separate spermathecae in the female epigyne. The new genus differs from *Coddingtonia* by its globose abdomen. With a body length of around 4 mm, *Eocoddingtonia* is the largest known theridiosomatid.

***Eocoddingtonia eskovi* sp. n.** (Figs. 1–36)

Etymology: After Dr Kirill Eskov, PIN, Moscow.

Diagnosis: As for the genus.

Material: Holotype: adult female, PIN 3064–8593, part and counterpart; allotype: adult male, PIN 4210–5463, part and counterpart. Paratypes: adult female PIN

3064–8591, part and counterpart; adult female, PIN 4210–5461, part and counterpart; adult female, PIN 4210–5462, part and counterpart; adult male PIN 3064–8594, part and counterpart. All specimens are held in the Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), and came from the Baissa locality on the left bank of the Vitim river, c. 60 km from the village of Romanovka, Buryat Autonomous Republic, Transbaikalia, Russia; Zazinskaya Formation, Lower Cretaceous (Berriasian–Valanginian).

Description: Female: See Table 1 for measurements. Carapace slightly longer than wide, elliptical in outline. Chelicera (inc. fang) about twice as long as wide; fang short (Figs. 9–10). Pedipalp short; tibia and tarsus with numerous curved macrosetae; tibia with cluster of trichobothria (Figs. 11–12); tarsus without a claw. Leg formula I, II, IV, III, all legs with numerous curved macrosetae: dorsal row on femur, one on patella, proximal one on tibia. All tibiae with cluster of trichobothria

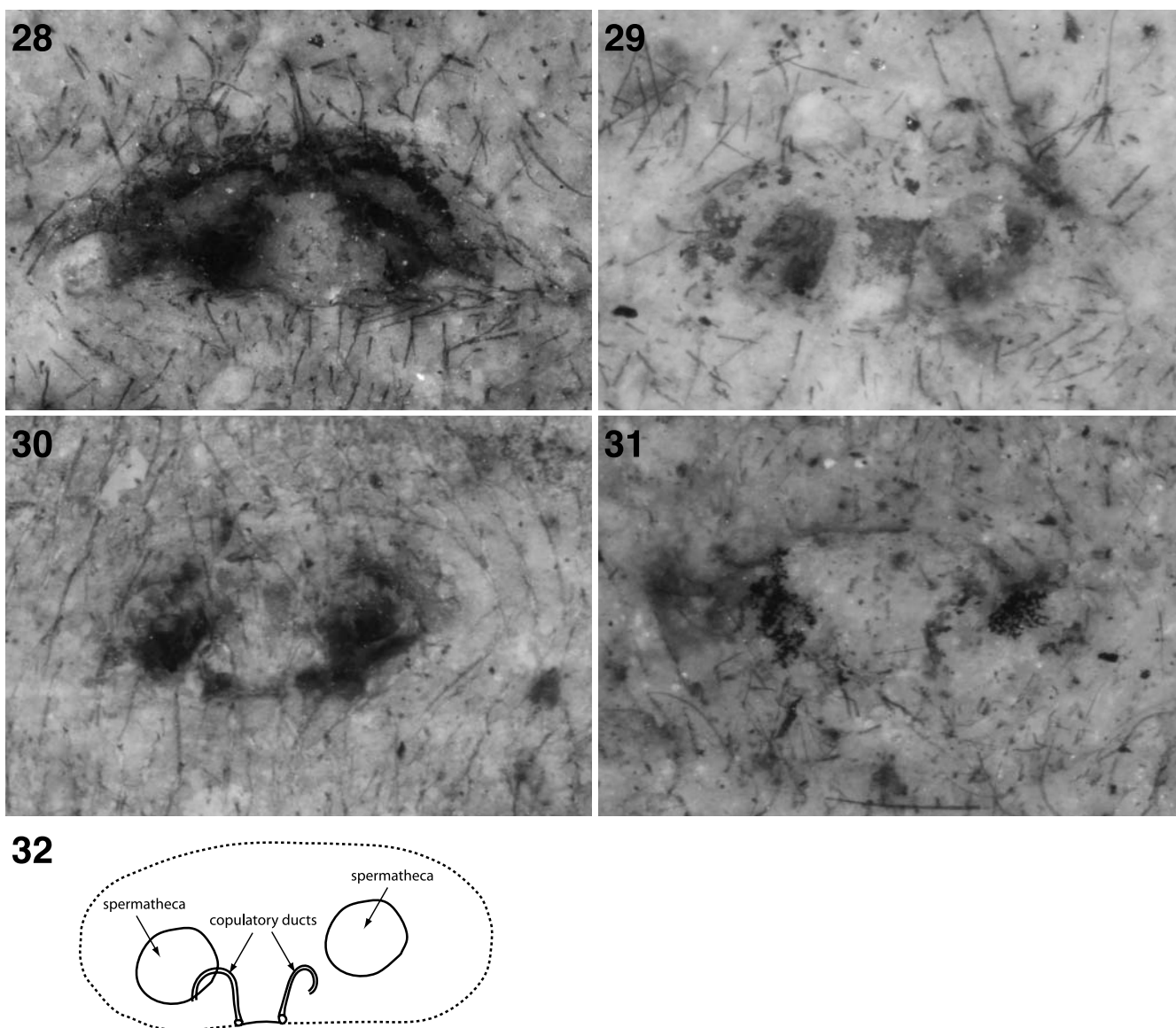
	♀ 8593	♀ 8591	♀ 5461	♀ 5462	♂ 8594	♂ 5463
Body length	4.52	3.76		3.80		
Carapace length	1.64	1.38				
Carapace width	1.53	1.26				
Length/width ratio	1.07	1.10				
Sternum length	0.71			0.71		
Sternum width	0.63			0.65		
Length/width ratio	1.13			1.09		
Labium length	0.23					
Labium width	0.32					
Labium length/width ratio	0.72					
Chelicera length				0.65		
Chelicera width				0.32		
Length/width ratio				2.03		
Labium length	0.30					
Pedipalp tibia	0.54			0.51		
Pedipalp tarsus	0.59			0.60		
Leg I femur–tarsus	5.74		4.86	5.25	>3.15	
Leg I femur	1.64			1.56		
Leg I patella	0.60		0.43	0.45		
Leg I tibia	1.52		1.40	1.50	1.04	1.41
Leg I metatarsus	1.38		1.38	1.23	1.00	
Leg I tarsus (inc. claw)	0.84		0.80	0.81	0.62	
Leg II femur–tarsus	4.65		3.86	4.36	4.00	
Leg II femur	1.70			1.50		
Leg II patella	0.70	0.50	0.51	0.40	0.34	0.40
Leg II tibia	1.15	0.95	1.06	0.98	0.94	1.02
Leg II metatarsus	1.04	1.00	1.05	0.95	0.81	1.08
Leg II tarsus (inc. claw)	0.72	0.73	0.75	0.75	0.52	0.70
Leg III femur–tarsus	3.30			3.14	>2.56	
Leg III femur	1.30			0.95	0.84	0.97
Leg III patella	0.40	0.38		0.40	0.32	0.35
Leg III tibia	0.68	0.60		0.65	0.48	0.50
Leg III metatarsus	0.66	0.60		0.55	0.53	0.59
Leg III tarsus (inc. claw)	0.50	0.50		0.53	0.48	0.44
Leg IV femur–tarsus	4.36		3.34			
Leg IV femur	1.50			1.28		1.30
Leg IV patella	0.52	0.52				0.37
Leg IV tibia	0.94	0.94	0.95			0.82
Leg IV metatarsus	0.90	0.86	0.90			0.84
Leg IV tarsus (inc. claw)	0.60	0.56	0.60			0.60
Opisthosoma length	3.10	2.78	2.27	2.81		1.77
Opisthosoma width	2.90	2.65	2.54	2.70		1.78
Opisthosoma length/width ratio	1.07	1.05	0.89	1.04		0.99

Table 1: Specimen measurements (in mm).

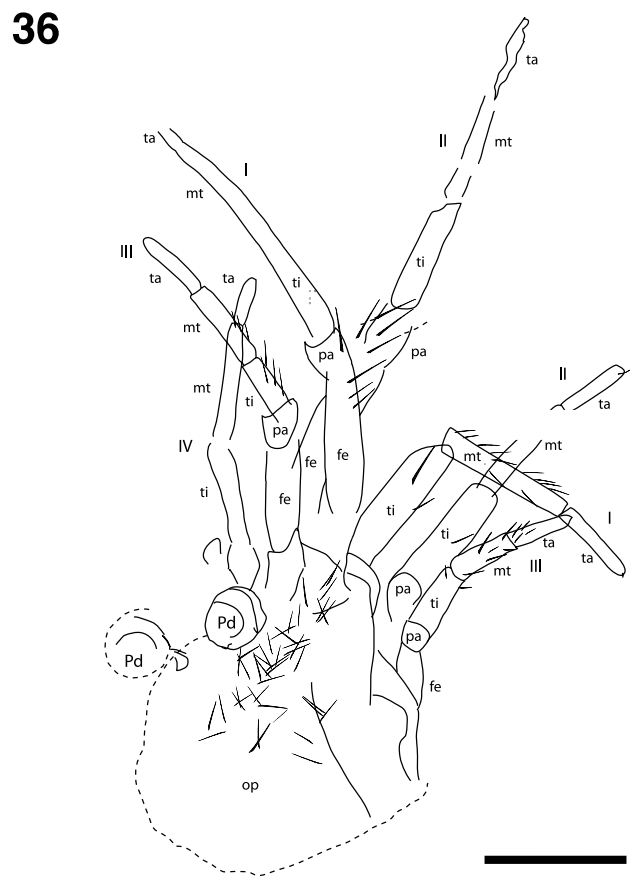
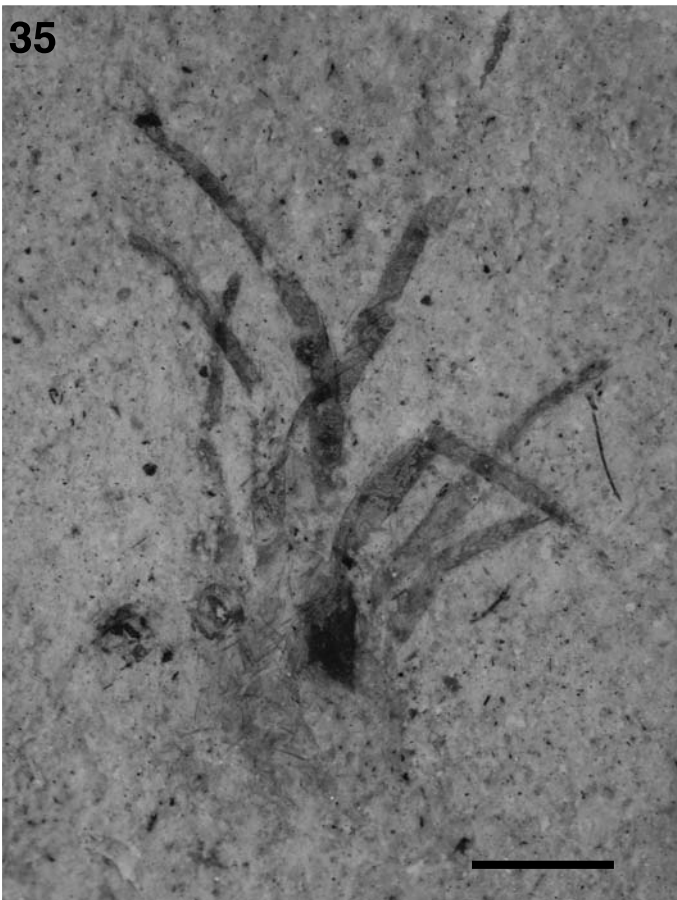
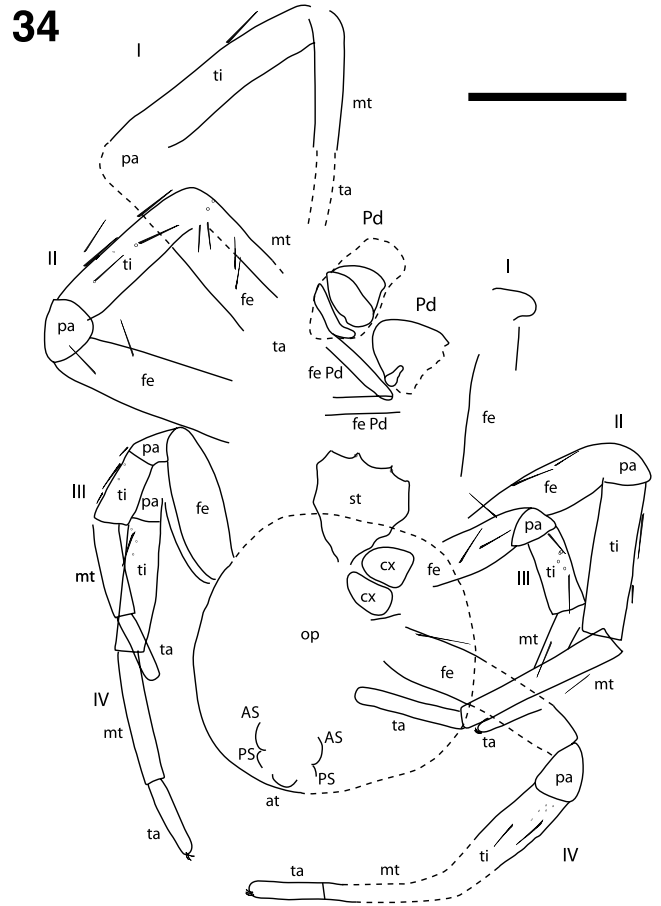
in approximately two rows dorsally; length of some trichobothrial hairs on tibia IV at least twice that of tibial width (Fig. 21). Metatarsi I–III with single trichobothrium in proximal half. Tarsi with three claws; paired claws with numerous blade-like teeth (Fig. 24); median claw as long as paired claws, strongly recurved (Fig. 25); few S-curved, serrate bristles distally on tarsi (Fig. 27). Sternum cordate, lateral borders slightly scalloped between coxae, posteriorly protruded between coxae IV into rectangular profile; possible sternal pit openings at base of labium (Figs. 13–14). Labium wider than long, with well-defined suture with sternum (Figs. 13–14). Opisthosoma slightly wider than long, globose, setose; epigyne and spinnerets close together ventrally on opisthosoma. Spinneret group (Fig. 16) with equal-sized anterior (AS) and posterior (PS) spinnerets, small median (MS) spinnerets. AS and PS conical with elliptical cross-section; AS shows very short distal segment with notch, bearing spigots (Fig. 16). Colulus may be present but not visible.

Epigyne (Figs. 28–32) about twice as wide as long, with broadly recurved anterior border, slightly procurved posterior border. Long setae situated near centre of anterior edge of epigyne. Subelliptical lateral lobes of epigyne extend from lateral corners along anterior border towards midline, but separated by about one-sixth of width of epigyne; lateral lobes with darker pigmented areas anteriorly and, especially, posteriorly, where they presumably cover spermathecae. Subtrapezoidal median lobe of epigyne smooth, unpigmented and hairless, shorter, anterior border separates lateral lobes, posteriorly diverging lateral borders adjacent to posterior borders of lateral lobes, long posterior border forms anterior edge of epigynal furrow. Presumed copulatory openings seen as dark spots at posterior lateral corners of median lobe, leading to circular ducts beneath median lobe and adjacent to dark areas of lateral lobes (Fig. 30).

Male: See Table 1 for measurements. Carapace and chelicerae not visible in either specimen. Leg formula I, II, IV, III. Numerous macrosetae on femora to metatarsi



Figs. 28–31: *Eocoddingtonia eskovi* gen. & sp. n., female epigynes. **28** Holotype female part, PIN 3064–8593a; **29** Holotype female counterpart, PIN 3064–8593b; **30** Paratype female counterpart, PIN 4210–5462b; **31** Paratype female part, 4210–5462a; **32** Explanatory drawing of PIN 4210–5462b.



Figs. 33–36: *Eocoddingtonia eskovi* gen. & sp. n., males. **33** Composite photograph of allotype, PIN 4210–5463; **34** Explanatory drawing of PIN 4210–5463; **35** Composite photograph of paratype, PIN 3064–8594; **36** Explanatory drawing of PIN 3064–8594.

of all legs; tibiae of all legs with cluster of trichobothria (Figs. 33–36). Tarsi with three claws; median claw as long as paired claws, strongly recurved (Figs. 23, 26); few S-curved, serrate bristles distally on tarsi (Figs. 23, 26). Sternum (Fig. 15) cordate, lateral borders slightly scalloped between coxae, posteriorly protruded between coxae IV into rectangular profile; possible sternal pit openings at base of labium. Labium wider than long, with well-defined suture with sternum (Fig. 15). Opisthosoma with sparse, fine setae and long, thin macrosetae. Pedipalp with thin femur; cymbium and endites showing a compact, globose morphology.

Discussion

The genus *Coddingtonia* was erected by Miller *et al.* (2009) for a Chinese theridiosomatid with separate, rather than connate, spermathecae. Miller *et al.* (2009) gave no indication of how their new genus might be related to other theridiosomatids. Since all other extant theridiosomatids have connate spermathecae and other symphatognathoids and araneoids have separate spermathecae (Griswold *et al.*, 1998), the connate state is apomorphic within Theridiosomatidae and both *Coddingtonia* and the fossil *Eocoddingtonia* show the plesiomorphic state of this character. The globose opisthosoma, which serves to separate the fossil *Eocoddingtonia* from *Coddingtonia*, provides little phylogenetic information because the globose abdomen occurs commonly in other small araneoids and not in all theridiosomatids. Given the present knowledge of *Eocoddingtonia*, its position within the Theridiosomatidae would be on the stem of the family, either as sister to all other theridiosomatids or to all except *Coddingtonia*.

Griswold *et al.* (1998) placed Theridiosomatidae as sister to a clade including Mysmenidae, Symphytognathidae and Anapidae. The fossil records of these other symphatognathoid families extend no older than Eocene: Baltic amber for Mysmenidae and Anapidae (Wunderlich, 2004), and no record of Symphytognathidae (see Selden & Penney, 2010). Accordingly, the symphytognathoids as a clade would be expected to extend back at least to the Early Cretaceous. This was already predicted by the occurrence of Linyphiidae in the Early Cretaceous (Penney & Selden, 2002).

Acknowledgements

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