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MYGALOMORPH SPIDERS (ARANEAE: DIPLURIDAE) FROM THE LOWER CRETACEOUS CRATO LAGERSTÄTTE, ARARIPE BASIN, NORTH-EAST BRAZIL

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Abstract: The first mygalomorph spiders from the Lower Cretaceous Crato Lagerstätte of Ceará Province, north-east Brazil, are described, from adult males and females, in two new genera and species: *Cretadiplura ceara* Selden, gen. et sp. nov. and *Dinodiplura ambulacra* Selden, gen. et sp. nov. They belong to the extant family Dipluridae, hitherto known as fossils only from Tertiary strata; thus this occurrence extends the family record by some 90 myr.

Key words: Arachnida, Arthropoda, Chelicerata, funnel-web.

THE Chapada do Araripe in north-east Brazil is renowned for having two world-class Fossil-Lagerstätten within the Lower Cretaceous sequence that crops out on its lower slopes. The younger Santana (Romualdo) nodules yield an extensive vertebrate fauna, including many fish and spectacular pterosaurs, whereas the older Crato Plattenkalks yield enormous numbers of invertebrates, mostly insects but also arachnids, and rarer vertebrates. The arachnid fauna of the Crato has received little attention hitherto (just one spider has been described: Mesquita 1996), yet many specimens are now available for study. In this paper, we describe two new genera and species of mygalomorph spiders from the Crato Lagerstätte.

Mygalomorphs include the well-known 'tarantula', funnel-web, trapdoor and bird-eating spiders. Mygalomorphae is sister to Araneomorphae ('true spiders') and the two infraorders form the suborder Opisthothelae, which is sister to the only other spider suborder, Mesothelae. The supposed Palaeozoic mygalomorph *Megarachne servinei* Hünicken, 1980 has been shown to be a eurypterid (Selden *et al.* 2005), so the oldest mygalomorph is the hexathelid *Rosamygale grauvogeli* Selden and Gall, 1992 from the Triassic of north-east France. A number of Cenozoic mygalomorphs are known (reviewed in Eskov and Zonshtein 1990; Dunlop 1993; Wunderlich 2004), including the hitherto oldest diplurid: *Clostes priscus* Menge, 1869, from Eocene Baltic amber.

Mesozoic mygalomorphs were first described by Eskov and Zonshtein (1990): three genera belonging to the families Antrodiaetidae and Atypidae from Lower Cretaceous strata of Mongolia, and one genus of Mecicobothriidae from the Lower Cretaceous of Transbaikalia. An additional Cretaceous form, belonging to Nemesiidae, was described from Isle of Wight amber (Selden 2001). No Jurassic mygalomorphs have yet been reported. Adult males and females of two species of mygalomorph from the Crato Lagerstätte are described here: a large species, *Dinodiplura ambulacra* gen. et sp. nov, and a smaller one, *Cretadiplura ceara* gen. et sp. nov. Both are referred to the family Dipluridae Simon, 1889. The occurrence of the smaller species was published in a conference report (Selden *et al.* 2002). They are the oldest diplurids, extending the record of the family by around 90 myr. The presence of Dipluridae in rocks of early Cretaceous age had already been predicted by the occurrence of its sister-group, the bipectinate family Nemesiidae Simon, 1889 (Selden 2001), in strata of this age. It is suggested that the Mygalomorphae had a worldwide distribution before the break-up of the Pangaean supercontinent. The occurrence of another Recent spider family in rocks of Mesozoic age is further evidence of the antiquity of modern spider families.

STRATIGRAPHY AND PALAEOECOLOGY

The specimens originate from the Nova Olinda Member of the Crato Formation (*sensu* Martill 1993), a sequence of laminated, organic-rich micrites (Plattenkalks), which crops out on the north side of the Chapada do Araripe, Ceará Province, north-east Brazil. Some authors (e.g. Maisey 1991) recognised a more inclusive Santana Formation with three members: a lower fossiliferous Plattenkalk (Crato Member), an upper Romualdo Member with the famous fish-bearing nodules, and an intervening gypsiferous Ipubi Member. The sedimentology, taphonomy and palaeoecology of the Crato and Santana (Romualdo) beds are quite distinct, and these Lagerstätten should not be confused. The fossiliferous Nova Olinda beds have been dated as Aptian in age (Maisey 1991; Martill 1993). The Crato lake or lagoon formed within the Araripe Basin, one of a number of fault-bounded Mesozoic basins which occupied the Atlantic rift zone between Africa and South America in early Cretaceous times. The fault lines in this part of Brazil align with the Benue Trough and other lineaments in West Africa, and it is suspected that these older faults were reactivated to become transforms at the onset of rifting (Berthou 1990). As far as the spiders are concerned, they could move freely over land at that time between what are now the African and American continents.

The Nova Olinda limestones are rich in insects (e.g. Grimaldi 1990), the small freshwater fish *Dastilbe*, land plants, other arachnids, frogs, birds and pterosaurs (Martill 1993). Most of the biota is allochthonous, having been blown or washed into the lake from the land or tributary streams, and there is evidence of mass mortality of fishes (Maisey 1991; Martill 1993), which may be related to increasing saline episodes which culminated in the gypsum-rich beds above.

MATERIAL AND METHODS

Material. No chemical analyses were carried out on the specimens, but in comparison with the insects preserved in the Crato (Grimaldi 1990), we presume that the spider fossils from the more weathered horizons are preserved in goethite (hydrated iron oxide) in a matrix of nearly pure calcite mud with clots of pyrolusite. The goethite is a tan colour which is darker where thicker and thus reflects the depth of coloration seen in the original cuticle. (Some fossils in the Crato are found in relatively unweathered matrix, so an unhydrated iron compound may be involved.) The mineralization has replaced the original organic material in great detail, so that spines, bristles and setae can be accurately traced in the matrix. Where absent, the former presence of spines and trichobothria is shown by the presence of spine bases and bothria on the cuticle surface. The opisthosoma of the allotype of *Dinodiplura* was filled with a soft, white mineral (kaolinite?), which has now been removed for this study.

The holotype of *Cretadiplura ceara* is a single slab with the specimen preserved a little dorsoventrally compressed, and with its dorsal side uppermost. Nearly all of the specimen is present, except for the right-hand side where most of the distal podomeres are absent (Text-fig. 1); at some point after its discovery, the missing leg parts were pencilled in using brown wax crayon, which is still visible in Plate 1, figure 2. In this specimen, and in the holotype and allotype of *Dinodiplura*, the internal surface of the opisthosoma is preserved, and the anal tubercle appears very large and obvious; this prominence is most likely because of internal sclerotization surrounding the tubercle, which would not be so visible externally in life. The allotype of *Cretadiplura* is compressed laterally, so that although both chelicerae and pedipalps are visible, only the right walking legs can be seen. The allotype preserves a great detail of setation whereas in the holotype, setae and macrosetae are evidenced mainly by their sockets; the differences may be due to different methods of preparation before the specimens were deposited in museums.

The holotype of *Dinodiplura* is a single slab with the specimen compressed dorsoventrally, dorsal side uppermost. The ocular tubercle is broken away, but its position and size can be estimated from its subcircular broken edge. The allotype of *Dinodiplura*, like the holotype of *Cretadiplura*, has been crudely prepared and some podomeres, e.g. the distal parts of right leg 4 and the distal half of right leg 2 metatarsus (Pl. 2, fig. 2) have been drawn in with wax crayon. Of the walking legs on this specimen, only left 1, right 2 and 3, and left 4 are preserved (Pl. 2, fig. 2). On both specimens of *Dinodiplura*, setation is evidenced almost entirely by sockets; on the allotype, crude preparation has lost many of the original podomere surfaces. On the allotype, the opisthosoma was preserved as an internal mould, which has now been removed to expose the ventral structures. On this specimen, book-lung lamellae can be seen preserved in buff-coloured calcite (Pl. 2, fig. 4), similar to the preservation of book-lungs in an Eocene spider from the Insect Limestone, Isle of Wight (Selden 2001).

Methods. The holotype female and additional specimens of *Cretadiplura*, and the allotype male of *Dinodiplura*, were studied, drawn and photographed using a Wild M7S stereomicroscope with a camera lucida tube for drawing and a Minolta Dynax 9 camera attached by means of a phototube for photomicrography. The allotype male of *Cretadiplura* and the holotype female of *Dinodiplura* were

studied in São Paulo and Portsmouth, respectively. Some preparation was carried out on the holotype of *Cretadiplura* and the allotype of *Dinodiplura* using an aeroneedle (Selden 2003); the opisthosoma of *Dinodiplura* was filled with a soft, white mineral which was removed to expose the wrinkled cuticle, the anal tubercle and the posterior book-lungs. The allotype of *Dinodiplura* was scanned directly onto an Epson Perfection 3200 scanner. Scanned slides, specimens and digital photographs were manipulated using Adobe Photoshop CS. Drawings were prepared using Adobe Illustrator CS. All computer manipulation was done on a Macintosh PowerBook G4 running OS X. Measurements were made using Carnoy 2.1 (http://www.kuleuven.ac.be/bio/sys/carnoy/). Description of the fossils is by PAS, who is responsible for the systematic palaeontology. Note that because of the lack of diagnostic characters in the fossils comparable with those in living diplurines (especially autapomorphies), the diagnoses are, of necessity, descriptive rather than comparative.

Terminology. Macrosetae refer to large setae which thicken just distal to the base before tapering, unlike ordinary setae which do not; bristles resemble ordinary setae in shape but are as large as macrosetae. All three types occur on the legs of the fossil described here. Trichobothria are very long (more than the width of the podomere) hair-like structures which do not taper. They are recognisable in the fossils not only by their great length and consistent width but also because they are commonly bent (so were presumably less stiff than setae).

Abbreviations used in the figures. 1, 2, 3, 4, walking leg numbers; bl1, bl2, book-lung covers 1 and 2; car, carapace; ch, chelicera; cx, coxa; f, fovea; fe, femur; mt, metatarsus; op, opisthosoma; ot, ocular tubercle; pa, patella; pa or, palpal organ of male; Pd, pedipalp; PLS, posterior lateral spinneret; sp, spinnerets; ta, tarsus; ti, tibia; tr, trochanter. All measurements are in millimetres; mean of left and right if available.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder MYGALOMORPHAE Pocock, 1892
BIPECTINA Goloboff, 1993
Family DIPLURIDAE Simon, 1889

Remarks. *Cretadiplura* and *Dinodiplura* are referred to this family on the basis of their elongated posterior spinnerets.

Subfamily DIPLURINAE Simon, 1889

Remarks. *Cretadiplura* and *Dinodiplura* are referred to this subfamily on the basis of the unsegmented distal article of the posterior spinnerets and the recurved fovea. Raven (1985) and Coyle (1995) discussed the synapomorphies of the four diplurid subfamilies and, whilst not all of their diagnostic characters can be seen in the fossils, the two mentioned above clearly indicate the Diplurinae. The allotype males of *Cretadiplura* and *Dinodiplura* both have a rather short pedipalp tarsus (cymbium), which is elongated in Ischnothelinae (Coyle 1995).

Genus CRETADIPLURA Selden, gen. nov.

Derivation of name. Latin, *creta*, chalk, and basis for the Cretaceous Period; and *Diplura*, the type genus of the family Dipluridae, to which the fossil spider belongs.

Type and only known species. *Cretadiplura ceara* Selden, sp. nov.

Diagnosis. Diplurine of medium size; carapace widest behind midpoint, at level of recurved fovea, and midway between rear edge of ocular tubercle and posterior carapace margin; ocular tubercle two eye diameters behind anterior carapace margin; segments of posterior lateral spinnerets increase in length distally; legs robust in female, with many macrosetae; legs in male with femur to tibia robust, metatarsus and tarsus slender, at least tarsus 2 scopulate, strong macrosetae especially on anterior legs but no mating apophyses.

Cretadiplura ceara Selden, sp. nov.
Plate 1; Text-figures 1–2.

2002 Adult male of Dipluridae; Selden *et al.*, p. 89, fig. 2A–B.

Derivation of name. After Ceará province, where the fossils were found.

Type specimens. Holotype MB.A.979, single slab in the Museum für Naturkunde der Humboldt-Universität Berlin. Allotype A11, single slab in collections of the Laboratório de Geociências, Universidade Guarulhos, São Paulo, Brazil.

Additional material. Specimens of this species have been identified in collections belonging to the Department of Earth Sciences, University of Portsmouth, the research collections of the School of Earth, Atmospheric and Environmental Sciences, University of Manchester, and the collection of Jörg Wunderlich, Hirschberg, Germany.

Diagnosis. As for genus.

Description of holotype. Adult female. Carapace length 4·95, width 4·67; ocular tubercle length 0·74, width, 0·81, about two

eye diameters behind anterior carapace margin; opisthosomal length (excl. spinnerets) 5·86, width, 4·24; foveal width 0·26; posterior lateral spinneret length 4·10 (basal segment 1·24, middle segment 1·35, distal segment 1·48). Podomere lengths: pedipalp femur 1·98; Leg 1: femur 3·05, patella 2·92, tibia 3·24, metatarsus 2·84, tarsus 1·92; Leg 2: trochanter 0·67, femur 3·05, patella 2·14, tibia 2·86, metatarsus 2·73, tarsus 2·24; Leg 3: trochanter 0·63, femur 3·88, patella 1·73, tibia 3·04, metatarsus 3·74, tarsus 2·35; Leg 4: trochanter 0·61, femur 3·21, patella 2·46, tibia 3·17, metatarsus 3·34, tarsus 3·07. Carapace slightly longer than wide, suboval, with straight posterior margin; subcircular ocular tubercle bearing eight eyes anterolaterally (not all preserved); small, recurved fovea situated midway between rear of ocular tubercle and posterior carapace margin. Opisthosoma suboval, slightly longer than carapace, with wrinkled cuticle, prominent internal basal ring to anal tubercle; two book-lung opercula in anterior half of ventral surface. Long posterior lateral spinneret of three segments, bearing spigots increasing in density from second to last segment. No other spinnerets visible in the fossil. Femora to tibiae robust, metatarsi and tarsi somewhat more slender on legs 3 and 4. Leg spination (maximum number of macrosetal follicles visible on fossil, principally superior/posterior podomere surfaces visible): Leg 1: femur 3, tibia 2, tarsus 4; Leg 2: femur 5, tibia 2, metatarsus 3; Leg 3: femur 5, tibia 4, metatarsus 6, tarsus 6; Leg 4: femur 2, tibia 4, metatarsus 3, tarsus 3.

Description of allotype. Adult male. Carapace length 4·01, width 2·28; opisthosomal length (excl. spinnerets) 3·24, width 2·53; posterior lateral spinneret length 2·36 (basal segment 0·78, middle segment 0·60, distal segment 1·06). Podomere lengths: chelicera 0·63; pedipalp femur 2·65, patella 1·70, tibia 2·90, tarsus 0·83; Leg 1: trochanter 0·68, femur 3·78, patella 1·15, tibia 2·86, metatarsus 3·05, tarsus ≥ 0·68; Leg 2: trochanter 0·66, femur 3·32, patella 1·18, tibia 3·40, metatarsus 3·16, tarsus 1·87; Leg 3: femur ≥ 2·95, patella 1·58, tibia 3·05, metatarsus 3·56, tarsus *c.* 1·74; Leg 4: femur ≥ 2·99, patella 1·48, tibia 4·98, metatarsus 4·24, tarsus 2·27. Carapace (laterally compressed) with prominent thoracic region (ocular tubercle not preserved); recurved fovea situated midway between rear of ocular tubercle and posterior carapace margin. Opisthosoma suboval, shorter than carapace, hirsute, two book-lung opercula in anterior half of ventral surface. Long posterior lateral spinneret of three segments, bearing spigots increasing in density from second to last segment. No other spinnerets visible in the fossil. Femora to tibiae robust, metatarsi and tarsi more slender. Leg spination (maximum number of macrosetal follicles visible on fossil, principally superior/posterior podomere surfaces visible): Leg 1: femur 3, tibia 2, tarsus 4; Leg 2: femur 5, tibia 2, metatarsus 3; Leg 3: femur 5, tibia 4, metatarsus 6, tarsus 6; Leg 4: femur 2, tibia 4, metatarsus 3, tarsus 3.

Genus DINODIPLURA Selden, gen. nov.

Derivation of name. After *deinos*, Greek for terrible, and Eberhard 'Dino' Frey, Karlsruhe Museum; and *Diplura*, the type genus of the family Dipluridae, to which the fossil spider belongs.

Type and only known species. Dinodiplura ambulacra Selden, sp. nov.

Diagnosis. Diplurine of large size; subhexagonal carapace outline, about as wide as long, widest at level of large, recurved fovea; ocular tubercle touching anterior carapace margin; prominent pattern of large setal follicles radiating laterally and anteriorly from fovea on female carapace, segments of posterior lateral spinnerets increase in length distally; legs robust in female; legs in male with femur to tibia robust, metatarsus and tarsus slender, tarsi (at least of legs 2 and 4) curved and fully scopulate on ventral surface, macrosetae present but no mating apophyses.

Dinodiplura ambulacra Selden, sp. nov.
Plate 2; Text-figures 3–4

Derivation of name. Ambulacra refers to the paired rows of setal follicles radiating from the fovea which resemble the ambulacra of echinoids.

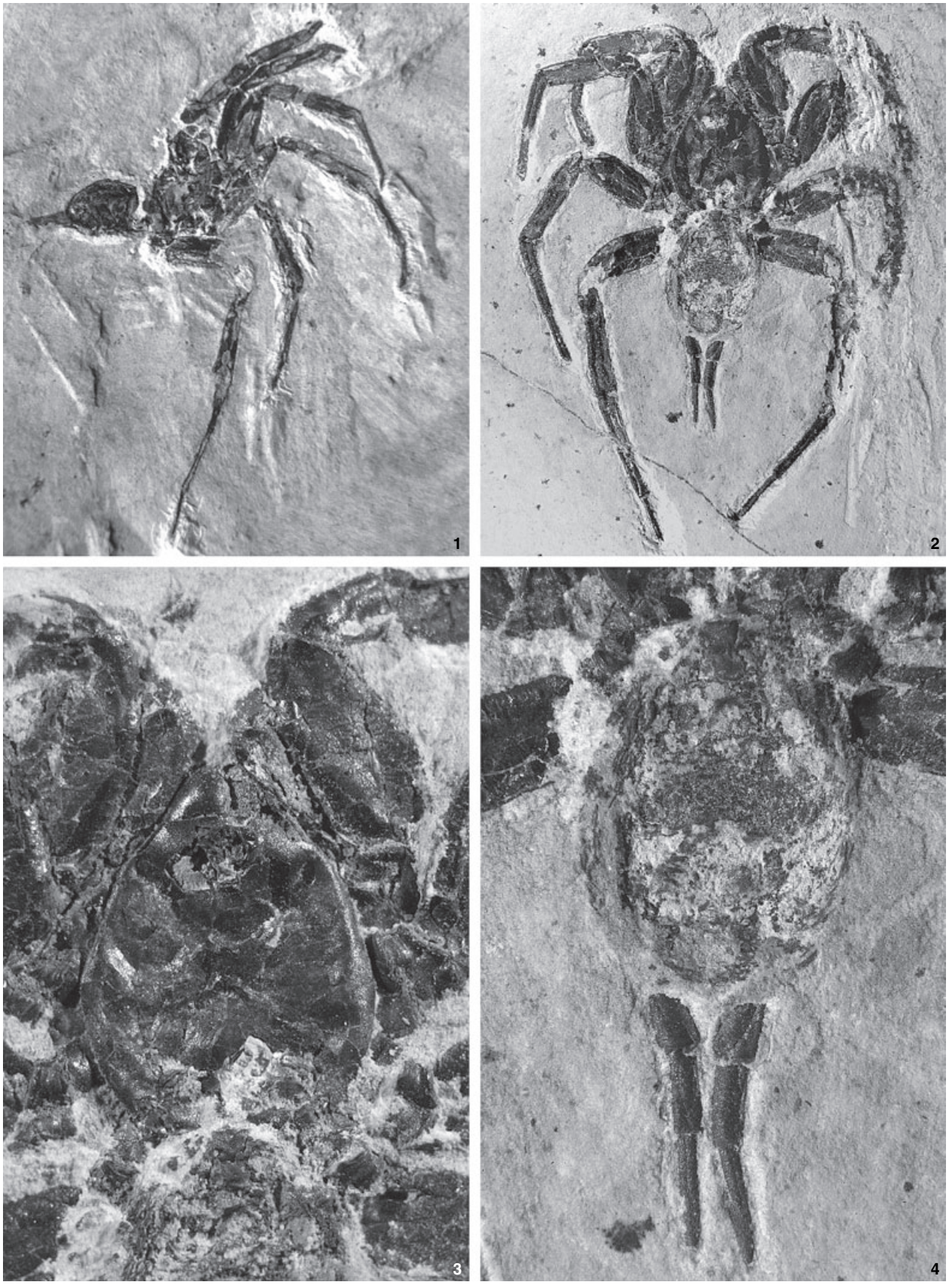
Type specimens. Holotype SMNK-PAL.3995, single slab (part) in the Staatliches Museum für Naturkunde, Karlsruhe, Germany (the counterpart is on display in the Museo do Santana do Cariri, Ceará, Brazil, numbered MPSC A883). Allotype F1417/SAN/AR/DIP/CJW, single slab in the collection of Jörg Wunderlich, Hirschberg, Germany.

Diagnosis. As for genus.

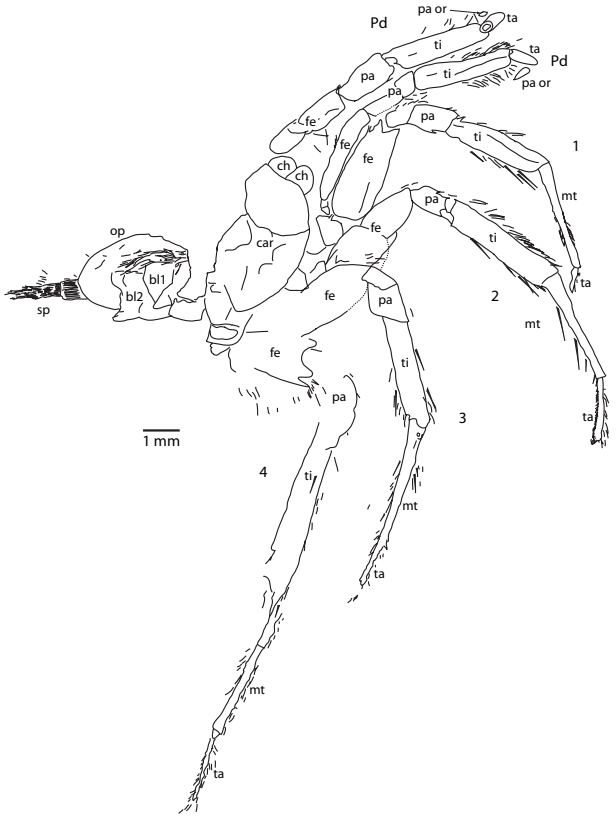
Description of holotype. Adult female. Carapace length 12·80, width 12·53, ocular tubercle width 1·80; opisthosomal length (excl. spinnerets) 13·35, width, 9·12; fovea width 1·97; posterior lateral spinneret length 7·27 (basal segment 6 > 1·4, middle segment 1·98, distal segment 3·82). Podomere lengths: chelicera > 3·27; pedipalp femur 7·05; Leg 1: femur 8·11; Leg 2: trochanter 1·73, femur 9·92, patella 2·14, tibia 12·17, metatarsus 9·42, tarsus > 2·64; Leg 3: trochanter 1·51, femur 10·81, patella 4·67, tibia 9·04; Leg 4: femur 11·84, patella 5·07, tibia 13·07. Carapace

EXPLANATION OF PLATE 1

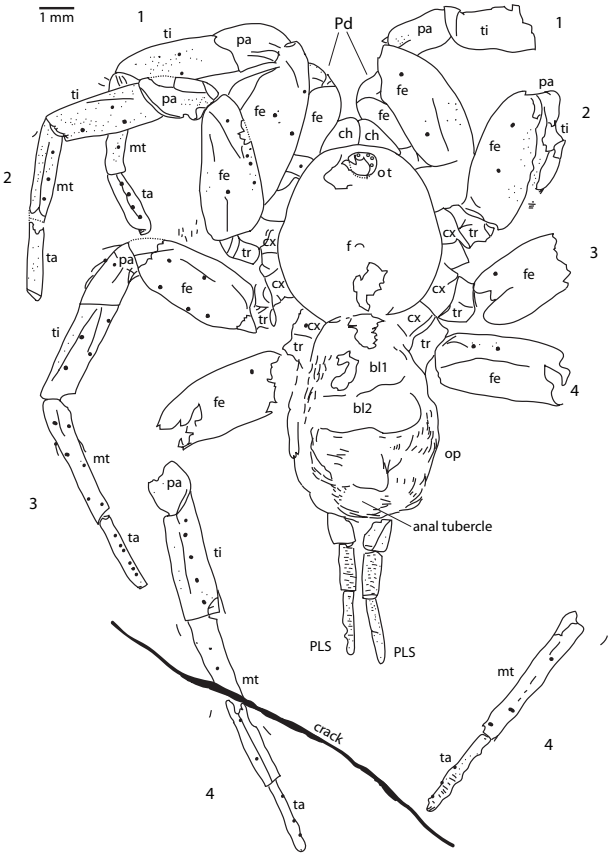
Figs 1–4. *Cretadiplura ceara* Selden gen. et sp. nov., Nova Olinda, Ceará, Brazil; Crato Formation. 1, allotype, adult male, A11; 2–4, holotype, adult female, MB.A.979. 1, complete, right-lateral view of laterally compressed specimen; × 8; for explanatory drawing see Text-figure 1. 2, complete, dorsal view; × 4; for explanatory drawing see Text-figure 2. 3, detail of carapace region; × 11. 4, detail of opisthosoma, including spinnerets; × 11.



SELDEN *et al.*, *Cretadiplura*



TEXT-FIG. 1. Camera lucida drawing of *Cretadiplura ceara* Selden gen. et sp. nov., allotype, adult male (A11); explanatory drawing for Plate 1, figure 1. See 'Material and methods' for explanation of abbreviations.



TEXT-FIG. 2. Camera lucida drawing of *Cretadiplura ceara* Selden gen. et sp. nov., holotype, adult female (MB.A.979); explanatory drawing for Plate 1, figures 2–4. See 'Material and methods' for explanation of abbreviations.

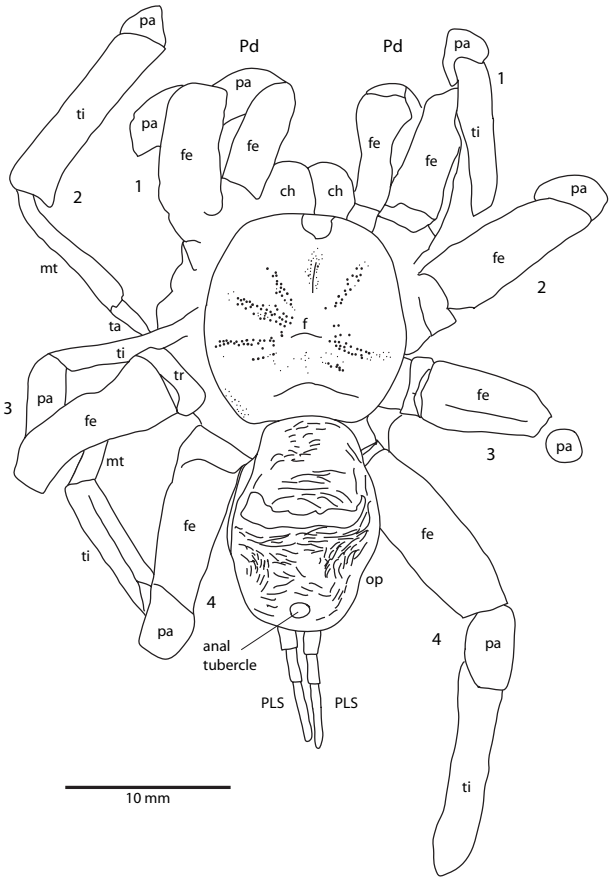
slightly wider than long, subhexagonal in outline, with slightly recurved anterior and posterior margins, and more strongly ouwardly curved lateral margins; subcircular ocular tubercle at anterior carapace margin; small, recurved fovea situated midway between rear of ocular tubercle and posterior carapace margin. Opisthosoma suboval, slightly longer than carapace, with wrinkled cuticle, prominent internal basal ring to anal tubercle. Long posterior lateral spinneret of three segments, bearing spigots increasing in density from second to last segment. No other spinnerets visible in the fossil.

Description of allotype. Adult male. Carapace length 9·06, width 10·04; opisthosomal length (excl. spinnerets, from rear of carapace) 13·50, width 6·70; fovea width 1·29; posterior lateral spinneret length 4·50 (basal segment 0·98, middle segment 1·69, distal segment 1·83). Podomere lengths: chelicera > 2·95; pedipalp femur 6·28, patella 3·06, tibia 4·90; Leg 1: femur 9·54, patella 4·94, tibia 10·12, metatarsus 7·63; Leg 2: femur 8·76, patella 4·79, tibia 9·15, metatarsus 8·89, tarsus 5·50; Leg 3: trochanter 1·99, femur 9·76, patella 4·27, tibia 6·43; Leg 4: trochanter 1·68, femur 10·91, patella 3·98, tibia 10·35, metatarsus 12·07, tarsus 6·27. Carapace subhexagonal in outline, slightly wider than long; recurved fovea situated approximately centrally. Opisthosoma elongate, longer than carapace, ventral cuticle prominently wrinkled, two book-lungs in anterior half, prominent internal basal ring to anal tubercle. Long posterior lateral spinneret of three segments. No other spinnerets visible in the fossil. Femora to tibiae robust, metatarsi and tarsi becoming more slender; tarsi curved, at least tarsus of leg 4 with dense scopula on ventral sur-

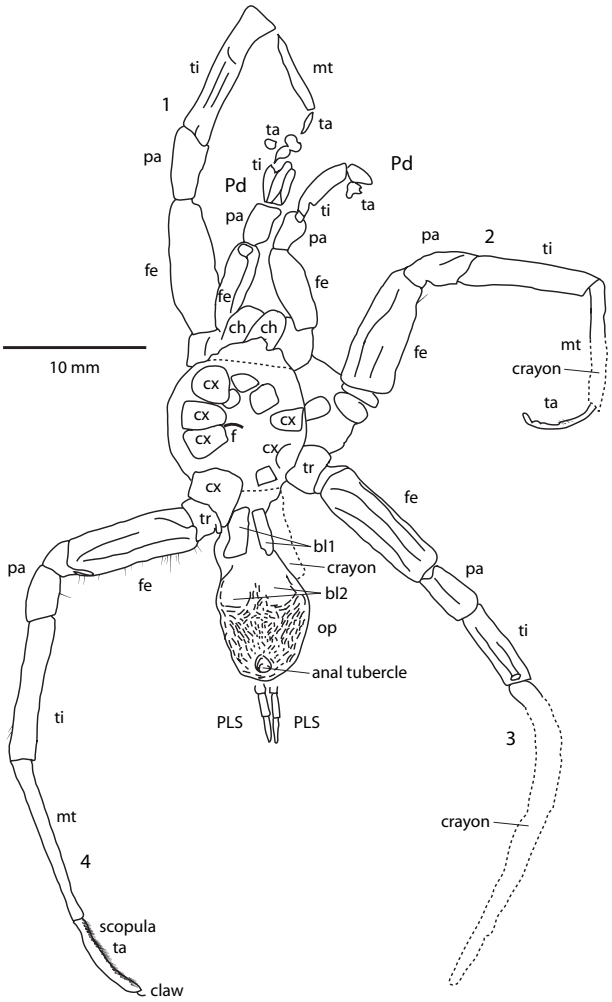
EXPLANATION OF PLATE 2

Figs 1–4. *Dinodiplura ambulacra* Selden gen. et sp. nov., Nova Olinda, Ceará, Brazil; Crato Formation. 1, 3, holotype, adult female, SMNK-PAL.3995. 2, 4, allotype, adult male, F1417/SAN/AR/DIP/CJW. 1, complete, dorsal view; × 2; for explanatory drawing see Text-figure 3. 2, complete, dorsal view; × 2; for explanatory drawing see Text-figure 4. 3, detail of body; × 3. 4, detail of opisthosoma; × 4.

SELDEN *et al.*, *Dinodiplura*



TEXT-FIG. 3. *Dinodiplura ambulacra* Selden gen. et sp. nov., holotype, adult female (SMNK-PAL.3995); explanatory drawing for Plate 2, figures 1, 3. See 'Material and methods' for explanation of abbreviations.



TEXT-FIG. 4. *Dinodiplura ambulacra* Selden gen. et sp. nov., allotype, adult male (F1417/SAN/AR/DIP/CJW); explanatory drawing for Plate 2, figures 2, 4. See 'Material and methods' for explanation of abbreviations.

face, tarsal claw visible on tarsus of leg 4. Some macrosetal follicles and dense setal follicles visible on femora to tibiae of walking legs.

DISCUSSION

The four specimens described here are considered to belong to two genera because they differ greatly in size, but the difference cannot be explained by ontogeny because the males show mature pedipalp structures. The males and females of each genus are comparable in size and morphological features (e.g. the subhexagonal carapace of *Dinodiplura*). The great difference in size between the genera suggests that they should be distinguished at this rank rather than at the specific level, in comparison with morphological differentiation among living diplurid genera.

The discovery of members of the Dipluridae in the early Cretaceous (Aptian, 112–125 Ma) pushes the age of this group back some 90 myr because the previously described earliest diplurid is *Clostes priscus*, and two indeterminate genera, from Eocene (*c.* 35 Ma) Baltic amber (Petrunkevitch 1946; Wunderlich 2004). Three genera (including two extant) of diplurids are known from Oligocene Dominican amber (Schawaller 1982; Wunderlich 1988, 2004). The presence of Dipluridae in the early Cretaceous had been predicted by the presence of its likely sister group (Nemesiidae: see Goloboff 1993) in strata of this age (Selden 2001).

The family Dipluridae is widespread in tropical to temperate regions, but the subfamily Diplurinae is restricted to Central and South America. Although a few genera are burrowers, diplurids are characteristically weavers of funnel-webs, their long, manoeuvrable posterior lateral spinnerets being adapted to this purpose (Coyle 1986). Indeed, one of the commonest spiders to be found in the quarries in Crato limestone around Nova Olinda, weaving

its funnel-webs beneath loose slabs of limestone, is the ischnotheline diplurid *Ischnothele annulata* Tullgren, 1905. Funnel-webs are designed to catch jumping prey, such as orthopteran insects. The long posterior lateral spinnerets of the fossil genera suggests they, too, would have woven funnel-webs and, because Orthoptera are abundant in the Crato limestone, there was plenty of food available for the spiders in the early Cretaceous. The suggested palaeoenvironment of the early Cretaceous of north-east Brazil is arid or semi-arid (Martill 1993), and both diplurids and their orthopteran prey are plentiful in semi-arid environments today (Main 1982; Hunter *et al.* 2001).

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