

ARTÍCULO:

A new fossil whip spider (Arachnida: Amblypygi) from the Crato Formation of Brazil

#### Jason A. Dunlop

Institut für Systematische Zoologie Museum für Naturkunde der Humboldt-Universität zu Berlin D-10115 Berlin Germany jason.dunlop@museum.hu-berlin.de

#### Victor Barov

Department of Biology Middle East Technical University 06531 Ankara Turkey e132025@metu.edu.tr

#### Revista Ibérica de Aracnología ISSN: 1576 - 9518. Dep. Legal: Z-2656-2000.

Vol. **12**, 31-XII-2005 Sección: Artículos y Notas. Pp: 53-62

#### Edita: **Grupo Ibérico de Aracnología (GIA)** Grupo de trabajo en Aracnología de la Sociedad Entomológica Aragonesa (SEA) Avda. Radio Juventud, 37 50012 Zaragoza (ESPAÑA) Tef. 976 324415 Fax. 976 535697

C-elect.: cribera@ub.edu Director: C. Ribera

Indice, resúmenes, abstracts vols. publicados:

http://entomologia.rediris.es/sea/ publicaciones/ria/index.htm

Página web GIA: http://entomologia.rediris.es/gia

Página web SEA: http://entomologia.rediris.es/sea

# A new fossil whip spider (Arachnida: Amblypygi) from the Crato Formation of Brazil

# Jason A. Dunlop & Victor Barov

## Abstract:

A new specimen of a fossil whip spider (Arachnida: Amblypygi) is described from the Early Cretaceous (Aptian: *ca.* 115 Ma) Crato Formation of southern Ceará, northeast Brazil. This is only the second formal description of Amblypygi from this important locality. It is tentatively assigned to the existing Crato species *Britopygus weygoldti* Dunlop & Martill, 2002; the diagnosis of which is emended based on our new material. Although much larger than the holotype – and with much longer pedipalps – these differences could be due to ontogeny and significantly both the holotype and our new fossil show evidence of a raised margin on the ventral pedipalpal trochanter which is similar to some extant members of the Central to South American family Phrynidae, and *Paraphrynus* Moreno, 1940 in particular. If these Crato fossils are phrynids, this represents the oldest record of the family.

Key words: Arthropoda, Arachnida, Amblypygi, Paleontology, Cretaceous, Brazil.

# Un nuevo amblipigio (Arachnida: Amblypygi) fósil procedente de la formación Crato de Brasil

#### Resumen:

Se describe un nuevo Amblipigio (Arachnida: Amblypygi) fósil del Cretácico temprano (Aptian: ca. 115Ma) procedente de la Formación de Crato, sur de Ceará, noreste de Brasil. Se trata de la segunda descripción de amblipigios de esta importante localidad. Provisionalmente se asigna a la especie ya conocida *Britopygus weygoldti* Dunlop & Martill, 2002, de la que se completa su diagnosis de acuerdo con el nuevo material estudiado. El nuevo material es mucho más grande que el holotyipo – y con los pedipalpos mucho más largos – aunque estas diferencias podrían ser debidas a su ontogenia. Tanto el Holotipo como el nuevo fósil presentan, en la parte ventral del trocanter, un margen alzado seme jante a algunas especies centro y sudamericanas pertenecientes a la familia Phrynidae, así como a *Paraphrynus* Moreno, 1940. Si estos fósiles de Crato son phrynidos, se trataría del registro fósil más antiguo de la familia.

Palabras clave: Arthropoda, Arachnida, Amblypygi, Paleontología, Cretácico, Brasil.

# Introduction

The Early Cretaceous Crato Formation in north-eastern Brazil is an important fossil locality, being one of the few Mesozoic sites to yield a rich and diverse fauna of arachnids. In addition to numerous plants, terrestrial and aquatic vertebrates, and many insects (e.g. Martill, 1993: appendix 1), the Crato Formation has also yielded well-preserved fossils of spiders (Araneae) (Selden *et al.*, in press), scorpions (Scorpiones) (Carvalho & Lourenço, 2001), camel spiders (Solifugae) (Dunlop & Martill, 2004), whip scorpions (Uropygi) and whip spiders (Amblypygi) (Dunlop & Martill, 2002). All of these closely resemble, or can even be referred to, living families. As an example of the significance of this locality, the single formally described Crato whip spider, *Britopygus weygoldti* Dunlop & Martill, 2002, is the only Mesozoic record of Amblypygi; a group whose fossil record in general is extremely sparse.

Whip spiders are an instantly recognisable order with, following Harvey (2003), 136 Recent species in seventeen genera and five families. As a group they occur today throughout the tropical and subtropical regions of the world. Whip spiders are characterised by long, slender legs – the first pair of which are essentially antenniform - and large, usually very spiny pedipalps. Unlike the similar-looking and closely-related whip scorpions, they have a more rounded prosoma and no terminal flagellum (telson) on the opisthosoma. In general whip spiders are more delicate-looking than whip scorpions and have a flattened body and legs orientated to move primarily in a horizontal plane, both features allowing them to crawl into narrow spaces. In fact whip spiders walk on only six legs and use the very slender first pair like antennae to probe in front of them. Prey thus detected are caught in a rapid movement using the sub-chelate, raptorial pedipalps and dragged up to the mouth where they are masticated by the chelicerae. These pedipalps can be quite long in some species with distinct patterns of spines forming a 'catching basket' or 'hand' in some groups. Whip spider biology was summarised by Weygoldt (2000).

With respect to fossils, the Devonian of the USA (ca. 380 Ma) has yielded cuticle fragments which might represent an early whip spider (Selden et al. 1991), but the group are first recorded in a recognisable form from the late Carboniferous (ca. 300-310 Ma) Coal Measures of Europe and North America (e.g. Petrunkevitch, 1955). The next oldest example is Dunlop & Martill's (2002) previously described Crato fossil (115 Ma), and there are further records of Amblypygi from the ca. 22-26 Ma, late Oligocene, Mexican (or Chiapas) amber (Petrunkevitch, 1971; Poinar & Brown, 2004) and from the probably Miocene (15-20 Ma) Dominican Republic amber (Schawaller, 1979, 1982); although some authors have suggested an older date for Dominican amber. There is also a highly doubtful record from the Tertiary of France (Gourret, 1887); see comments in Harvey (2003). Here, we describe a second Early Cretaceous whip spider from the Crato Formation. Much larger than the previously described example and with much longer pedipalps, it may nevertheless be an adult of Britopygus weygoldti; which we tentatively assign to the extant family Phrynidae based particularly on the structure of the pedipalpal trochanter. If this placement is correct, it makes it the oldest record of this clade to date and makes biogeographic sense as a Brazilian fossil in a family distributed widely across Central and South America today.

# Materials and methods

The fossil described here is held in the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS 66123). Due to its incomplete morphology it was originally speculated to be some sort of strange grasshopper or longicorn beetle, before being correctly identified as a whip spider, possibly related to the extant Brazilian genus *Trichodamon* Mello-Leitão, 1935 (G. Bechly, pers. comm. 2005). The fossil was largely prepared before purchase, but a fine needle was used to remove overlying pieces of matrix, particularly from parts of the body thought likely to be taxonomically significant (mouthparts, pedipalpal trochanter, spination, etc.). The fossil was compared to extant Amblypygi in the zoological collections of the Berlin museum as well as the literature. Morphological terminology is based on Shultz (1999) – particularly with respect to appendages – and Weygoldt (2000).

# **Geological setting**

The geological setting and associated biota of the Crato arachnid fossils has been reviewed by, e.g. Martill (1993) and Dunlop & Martill (2002, 2004). The fossilbearing Nova Olinda Member of the Crato Formation of southern Ceará, northeast Brazil is a finely-laminated limestone Konservat-Lagerstätte dated as Aptian (Early Cretaceous; *ca.* 115 Ma). The insect and arachnid fossils are typically preserved as reddish-brown geothitic pseudomorphs on a pale yellow limestone matrix in the weathered stone or as black, pyritic carbonised replicas on a dark blue/grey matrix in the fresh stone. Voids within the fossils are usually filled with clear calcite. Preservation is often excellent and slightly threedimensional and many fossils include details such as spines or features of the mouthparts; see also below.

## Morphological interpretation

The new fossil (Figs. 1-8) is a fairly large, partially complete whip spider in ventral view. The span across the extended pedipalps would have been around 15 cm in life. Legs 1-3 are missing and the opisthosoma is incomplete, but the pedipalps, mouthparts and fourth pair of legs are preserved quite well; at least proximally. The prosoma has slightly disarticulated from the opisthosoma such that the two parts of the body lie at an angle relative to one another (Figs. 1, 3). The opisthosoma is more-or-less rectangular in outline, but segmentation is indistinct anteriorly, thus preventing observation of any potential genital morphology. Parts of four distinct sternites in the posterior region of the opisthosoma are discernable. All have straight posterior margins, but lack ornament or further details. STERNAL AND MOUTHPART REGION

STERNAL AND MOUTHPART REGION The pedipalpal coxae are large and subtriangular

(Figs. 2, 4). The cuticle is broken in places, but they are ornamented with a series of denticles and, as in many modern taxa, these occur as a distinct mesal row (i.e. close to the midline), plus some more randomly distributed denticles in the distal region of each coxa. Compared to extant material, these denticles would have borne setae in life. Between the chelicerae we can resolve an area of cuticle close to the midline with closely-packed, oblique lines. Compared to dissections of extant material we identify this as part of the inside wall of the pedipalpal coxa. Like spiders, whip spiders are liquid-feeders that digest their food pre-orally. In living whip spiders this inner coxal wall is modified into a hairy, pre-oral filtering region surrounding a so-called 'pseudotrachea'; which is in fact a gutter in the coxal cuticle leading to the mouth and not a respiratory organ (see eg. Weygoldt, 2000, figs. 108-109) We cannot resolve a psuedotrachea in the fossil, but to our knowledge this modified cuticle around the mouth is the first record of the preoral filtering region in the whip spider fossil record. Leg coxae are not preserved. Extant species typically preserve three sclerites in the pliable sternal region between the coxae. The anteriormost of these is the tritosternum. It is probably homologous with the labium of spiders and other arachnids (e.g. Shultz, 1999), and is particularly well preserved in this fossil (Figs. 2, 4). In life a number of tritosternal setae would be expected. From a broad proximal base, which seems to articulate against another quadrate (but fragmentary) element, it narrows rapidly to form a blunt tube and thrusts forwards above the space between the pedipalpal coxae for some distance. Originating behind these coxae it extends about half way along their length and is thus similar in proportion to the larger tritosterna of extant species (see e.g. Weygoldt, 2000, figs. 2-4). Behind the tritosternum are the outlines of the two succeeding sclerotised sternal elements seen in living taxa. Interestingly, the shape of these elements is reminiscent of modern damonids or phrynichids (both Phrynichidae) (Peter Weygoldt, pers. comm. 2005).

Whip spider chelicerae consist of a basal article (or basipodite) and claw (or apotele). The fossil preserves both elements, but in ventral view only the fang-like apotele can be clearly seen and the taxonomically important dentition on the basal article cannot be resolved. Typically a number of teeth on the basal article oppose the movable claw to form the subchelate biting mouthparts used to masticate prey.

## PEDIPALPS

Of considerable taxonomic significance, and fortunately quite well preserved, is the trochanter of the pedipalp on the right side (Figs. 6, 8–10). This is a somewhat bellshaped limb article, narrower proximally and turning almost through a right angle to present a wider, curving distal margin. This orientation directs the pedipalpal femur laterally in the horizontal plane. A strong foldlike region between the trochanter and femur is almost certainly an impression of the arthrodial membrane between these adjacent articles, and also of note is the trochanter–femur articulation. In ventral view the articulation point lies relatively posterior, while in some extant taxa it characteristically sits more medially (see below).

The second feature of note is a quite stronglyexpressed, distinct, raised area which lies along the posterior-distal margin of the trochanter (Figs. 6, 8). It is wider and slightly bulbous anteriorly, and in this region there is a circular gap probably indicating the presence of a prominent spine in life which has broken off during preservation. A sketch reconstruction with the spine is shown in Fig. 10. The raised area becomes narrower posteriorly and closely follows the curvature of the distal trochanter margin. Indeed, this region, and projections from it, can be taxonomically significant in extant phrynid species (see below) and in this fossil it does not extend beyond the margins of the trochanter and terminates bluntly close to the putative trochanter–femur articulation point. There is no obvious break here whereby it might continue as a projecting apophysis more posteriorly beyond the margins of the trochanter. It is important to clarify that the structure in the fossil is not a ventral *anterior* apophysis (see e.g. Weygoldt, 2000, fig. 23 for *Charinus*, Simon 1892) which is a raised projection from the pedipalp trochanter, directed forwards like a large spine or flange.

Overall the pedipalps in the new fossil are long and rather gracile with relatively little evidence of strong spination. The left pedipalp is almost complete, the right one is missing the distal articles. When examined in detail the proximal region of the femur, close to the trochanter, shows two circular areas which were probably the bases of ventral spines in life (reconstructed in Fig. 10). Other femoral spines are equivocal and care must be taken not to misinterpret spots or detritus near the pedipalp as evidence of spination. The patella sensu Shultz - the pedipalpal tibia in Weygoldt's (2002, figs. 7–8) scheme – is likewise devoid of obvious spines along most of its length, except towards the end where there is evidence for at least three prominent spines in the distal 2.5 mm. The most proximal of these is preserved only in outline as a faint impression (Figs. 5, 7); the two distal ones are much clearer. Between them there is at least one - and maybe two - shorter spines, the problem being that one of these shorter elements is not demonstrably attached to the rest of the patella.

Distally the pedipalp bends sharply. The tibia sensu Shultz is a short, slightly bulbous article. It is not especially well preserved and any spination from life is equivocal. The distalmost region (the tarsus and apotele) is also not particularly well preserved and ends rather bluntly - a structure tapering to a sharp spine would be expected. Of interest are a row of four regular pits which seem to have some parallels with a region close to the so-called cleaning organ seen in some living taxa (see e.g. Weygoldt, 2000, figs. 14-22). The cleaning organ in extant whip spiders takes the form of two rows of setae. Such setae are equivocal in the fossil, and a potential difficulty with homologising these regular structures on the tarsus is that the limb article here is broken such that we are looking down onto an internal view of raised structures on the dorsal surface, thus they are not necessarily the raised denticles on the ventral surface of the palp in those extant genera (cf. Weygoldt, 1996, figs. 45–46) where they are present.

#### LEGS

Only leg four is preserved (Figs. 1, 3), and the full length of the appendage is not present. The trochanter is not so well preserved, while the femur is a flat-looking article which is wider at the proximal and distal ends, but curves noticeably, particularly on its inner margin, to become thinner along its length. As is typical for whip spiders, the patella is very short. The tibia in the fossil is long and cylindrical. In whip spiders the tibia is divided into a basi- and distitibia (e.g. Weygoldt, 2000). This basitibia can be further subdivided and the total number of tibial elements is taxonomically significant. Unfortunately only a single basitibial element is preserved. While it is followed by further fragmentary (?basitibial) elements, the total number of basitibial articles remains



**Fig. 1–2.** New specimen of *Britopygus weygoldti* Dunlop & Martill, 2002, SMNS 66123. **1.** Overview of body in ventral view. Scale bar: 10 mm. **2.** Detail of the mouth region showing particularly the chelicerae, palpal coxae and tritosternum. Scale bar: 2 mm.



Fig. 3–4. Camera lucida drawings of the specimen shown in Figs. 1–2. Scale bars: 10 mm (for 3) and 2 mm (for 4).

equivocal. In general the more complete right leg is clearly preserved lying on its side with the prolateral face uppermost. This is probably close to its life position where in Recent taxa the legs are usually rotated into approximately this orientation.

# Order AMBLYPYGI Thorell, 1883 Infraorder Neoamblypygi Weygoldt, 1996 Family ?Phrynidae Blanchard, 1852

**REMARKS:** The most comprehensive recent account of whip spider higher systematics is that of Weygoldt (1996), whose cladogram translated into a scheme of five families: (Paracharontidae (Charinidae (Charontidae (Phyrynidae + Phrynichidae)))). Weygoldt (2000) also offered a valuable general survey of the characteristic features of living whip spider genera. Although not all of Weygoldt's characters can be scored for the fossil, the large and horizontally-articulating pedipalps clearly exclude the monotypic, basal family Paracharonitidae from Africa in which the short pedipalps articulate in a more vertical plane. Our fossil is at least 22 mm long which makes it inconsistent with the circumtropical Charinidae; most of which fall into the 5-15 mm body length range and again typically have fairly short, robust pedipalps.

Our fossil can thus be referred with some confidence to the more derived infraorder Neoamblypygi i.e. charontids, phrynids and phrynichids - some of which can be quite large animals. Initially thought to be close to the one Brazilian phrynichid genus, Trichodamon (see above), we are also aware of a preliminary report of a further Crato whip spider (Giupponi & Baptista, 2003), which these authors also referred to Phrynichidae; again making direct comparisons with Trichodamon. Noted as a large specimen with long pedipalps ending in a distinctive 'hand', it is conceivable that Giupponi & Baptista's specimen is conspecific with ours, but without a formal description this cannot be assessed further. Nevertheless, this specimen is reportedly in excellent condition and is now provisionally thought to be a phrynid (Alessandro Giupponi, pers. comm. 2005). It is also worth noting that the two extant Trichodamon species in Brazil are highland taxa which also occur in caves (Weygoldt, 2000) and animals with this sort of ecology might not be expected to end up in the Crato lake environment so easily.

Our new fossil preserves one character which is inconsistent with Phrynichidae. In this (mostly) African family the trochanter and femur of the pedipalp diagnostically articulate such that in ventral view the articulation point is more medial along the antero-posterior axis (Fig. 15); see also Weygoldt (1996, character 6). In other whip spiders, including our fossil, the trochanterfemur articulation point is more posterior (Fig. 9–14, 16). We must concede the possibility that the trochanter has twisted during compression, and shifted the position of the articulation point, but in overall appearance the palpal trochanter in our fossil does not resemble that of phrynichids. That said, the sternal area of the fossil *does* show some similarities with some modern phrynichids, as noted above. The southeast Asian to Australasian Charontidae are diagnosed by a setal pattern on the palpal cleaning organ which is, unfortunately, equivocal in this fossil. From a biogeographical perspective our Brazilian fossil fits better with Phrynidae which are distributed today across Central and South America, however the family is currently diagnosed on the shape of the female genitalia which is of course not visible in the fossil here.

Intuitively, we might expect our Brazilian fossil to be a phrynid (as opposed to a charontid or phrynichid) and there is some further morphological support for this hypothesis. The raised region on the pedipalpal trochanter in the fossil is remarkably similar to that seen in at least some Paraphrynus Moreno, 1940 material (compare Figs. 9-10, 12); although admittedly we only had a limited number of extant specimens available in which the species identity was unclear. There is a temptation to assign our fossil to Paraphrynus among the Phrynidae based on the raised margin and associated spination of the trochanter and femur (Figs. 9-10, 12), although in the revision of Mullinex (1975) none of the extant species have such long pedipalps as those in the new Crato specimen. In fact in further detail our fossil differs in numerous aspects from Mullinex's diagnosis of Paraphrynus; in particular there should be spines along the length of the pedipalpal patella and not clustered towards the distal end as preserved in our new fossil (Figs. 5, 7).

In overall size and appearance the new fossil is also reminiscent in overview of some large, longpedipalped *Heterophrynus* Pocock, 1894 species (also Phrynidae). In particular adult males of taxa such as *H. cheiracanthus* (Gervais, 1842) (see Pocock, 1902, pl. 12, fig. 1) or *H. batesii* (Butler, 1873) (see e.g. Butler, 1873, pl. 4, fig. 9; Weygoldt, 1974, fig. 10) resemble our material. However, *Heterophrynus* is defined by a distinct, backward-pointing apophysis (Fig. 14) on the ventral surface of the pedipalpal trochanter (see e.g. Weygoldt, 1996, 2000), and we can thus exclude our fossil from this extant genus as it is currently defined. In general, the character combination preserved in this fossil seems to be unique with respect to living genera.

To our knowledge such a distinctly raised trochanter margin is atypical for charontids and phrynichids (see e.g. Figs. 15–16). Although the taxonomic significance of this structure in phrynids other than Heterophrynus has not been investigated in detail, we suggest that the raised margin is most consistent with the new fossil being a member of the Phrynidae - possibly even related to Paraphrynus. We would caution, though, that this development is not so strong in e.g. Phrynus Lamarck, 1801 (Fig. 13) and that the sternal morphology in the fossil points instead more towards a phrynichid. Nevertheless, if our assignment to Phrynidae is correct it makes our Crato material the oldest example of this family; the only other unequivocal examples coming from Neotropical Tertiary ambers (Petrunkevitch, 1971; Schawaller, 1982; Poinar & Brown, 2004).



**Fig. 5–6.** New specimen of *Britopygus weygoldti* Dunlop & Martill, 2002, SMNS 66123. **5.** Detail of the distal end of the pedipalp and the spines on the patella (tibia in some nomenclatures). Scale bar: 2 mm. **6.** Detail of the pedipalpal trochanter showing a prominent ventral raised area close to the distal margin and the position of rounded spine bases. Scale bar: 1 mm.



**Fig. 7–8.** *Camera lucida* drawings of the specimen shown in Figs. 5–6. Scale bars: 2 mm (for 7) and 1 mm (for 8).

# Genus Britopygus Dunlop & Martill, 2002

**EMENDED DIAGNOSIS:** Cretaceous whip spider with a raised development bearing an anterior spine (or spine base) along the ventral, distal margin of the pedipalpal trochanter.

**REMARKS:** The previous Crato whip spider (Dunlop & Martill, 2002) and the new specimen described here appear quite different, both in terms of overall body size and in the proportions and spination of the pedipalp. Neither specimen is complete and both are only known from ventral features. The temptation would be to treat them as two species, defined principally on the pedipalp which is proportionately longer and thinner in the new fossil, with the principal spines closer to the distal end of the patella. However, detailed studies of whip spider ontogeny, e.g. Weygoldt (1974) for phrynids and Weygoldt (1977a, 1995) for phrynichids, indicate that the juvenile instars of taxa with long pedipalps as adults can start with relatively short, spine-rich appendages. These pedipalps grow allometrically, becoming progressively longer with each moult and reducing their spination to approach the final adult morphology. This is especially clear in Weygoldt's (1974, fig. 11) growth graph for Heterophrynus batesii - which in overview resembles our new fossil (see above) - or in Weygoldt's (1977a, figs. 1-2) study of Trichodamon. The fact that pedipalps can be sexually dimorphic, typically with noticeably longer appendages in mature males (cf. Weygoldt, 1974, fig. 10), must also be taken into consideration. We must, therefore, entertain the possibility that the two described Crato whip spiders are extremes (the first free-living stage or protonymph and an adult male?) along a single ontogenetic sequence. Although different species of living whip spider *can* occur sympatrically, they are usually allopatric (Weygoldt, 1977b) and we do not wish to fall into the common trap of naming each fossil example of a rare animal group as a new species.

Further fossil material (*cf.* Giupponi & Baptista, 2003) would undoubtedly help to clarify this situation by potentially offering intermediate growth stages and/or additional character sets. Although Dunlop & Martill (2002) originally left the familial position of *Britopygus weygoldti* open, they commented that it could be either a charinid or a (small) phrynid and ten-



**Fig. 9–16.** Comparative outline sketches of the pedipalpal trochanter in various fossil and Recent whip spiders. Important is the fact that both the small holotype and new larger fossil show the raised region distally, with a large spine base, on the distal margin (mg) of the trochanter. This most closely matches the Phrynidae condition, most notably *Paraphrynus* (compare 10 and 12). Note also the position of the articulation points (A), particularly in Phrynichidae (15) which differs from that in our fossils and can perhaps be used to exclude their referral to Phrynichidae. All drawn directly from the fossils or from alcohol-preserved material in Berlin; not to scale. **9.** New fossil assigned to *Britopygus weygoldti* Dunlop & Martill, 2002 (SMNS 66123). **10.** Reconstruction of the same, but with spines added. **11.** Holotype of *B. weygoldti* (SMNS 64332) – image inverted to match orientation of other sketches and with spination tentatively reconstructed. **12.** *Paraphrynus* sp. (P. Weygoldt, det.) (Phrynidae). **13.** *Phrynus marginemaculatus* CL Koch, 1841 (Phrynidae). **14.** *Heterophrynus* sp. (P. Weygoldt, det.) (Phrynidae) with ventral posterior apophysis (vpa). **15.** *Euphrynichus bacillifer* (Gerstaecker, 1873) (Phrynichidae). **16.** *Charon grayi* (Gervais, 1842) (Charontidae).

ded to favour charinid affinities; whereas the large fossil described here is certainly not a member of Charinidae (see above). However, we can offer one explicit character shared by both Crato fossils which could support the hypothesis that the new large specimen is conspecific with Britopygus weygoldti. We re-examined the small holotype (SMNS 64332) and noted that the coxatrochanter articulation was rather poorly figured in the original description where the two articles seem to appear as a single structure. The holotype trochanter in fact seems to have a development along its distal margin with the base of a spine – like our new fossil (compare Figs. 9–11) – and again similar to certain phrynids (Fig. 12) as discussed above. We do not have any data about whether this raised development is seen in juvenile phrynids too, but its presence in both fossils is a potential character linking these specimens and is used in an emended diagnosis of the genus (see above).

# Britopygus weygoldti Dunlop & Martill, 2002 Figs. 1–11.

Britopygus weygoldti Dunlop & Martill, 2002: pp. 330–331, figs. 1a, 2a. Britopygus weygoldti Dunlop & Martill; Giupponi & Baptista, 2003: p. 104.

**MATERIAL:** SMNS 64332 (holotype) and SMNS 66123 (new specimen). Both from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian).

DIAGNOSIS: As for the genus.

**DESCRIPTION:** SMNS 66123. Measurements (in mm) – Prosoma and opisthosoma slightly disarticulated, but total preserved body length *ca*. 22. Opisthosoma length *ca*. 14, width, *ca*. 6; two fully preserved sternites with length *ca*. 1.7. Mouthparts include tritosternum, length 2.9, basal width 1.3 and pedipalpal coxae, length 4.1. Length of cheliceral fang *ca*. 2. Total preserved length of pedipalp *ca*. 78, article lengths: femur, 32.4; patella, 39.4; tibia 3.2; tarsus at least 1.2. Leg 4 with article lengths: femur, 14.6; patella, 2.2 and (?first) element of basitibia *ca*. 10.

Fairly large whip spider. Opisthosomal sternites quadrate with straight anterior and posterior margins. Chelicerae of the 'clasp-knife' type, ending in tapering fang. Pedipalpal coxae large, subtriangular, ornamented with denticles which form, in part, a mesal row. Inner wall of palpal coxae in the preoral area with fine pattern of striations; presumably part of a filtering device. Tritosternum elongate, with wide base tapering rapidly into a slender rod-shape extending across about half the length of the palpal coxae. Tritosternum articulates with remainder of sternal region, including incomplete parts of two further sternal elements. Pedipalpal trochanter globose, articulating posteriorly with the femur and anterior of this with a wide arthrodial membrane region between the trochanter and femur. Trochanter with raised development towards the distal margin. Anterior region of this globose with base of one large spine. More posterior region of this raised area tapers towards the ventral trochanter-femur articulation point where it ends bluntly. Pedipalpal femur elongate, slender and with little or no curvature. Proximal ventral region close to trochanter with the bases of at least two large, ventral spines. Other femoral spines equivocal. Pedipalpal patella also elongate, approximately the same length as femur. Proximal spines equivocal or absent, but distally with three prominent spines (one only preserved in outline) and one or two minor spines between the two distal spines. Tibia and tarsus region of patella short, but details lacking. Leg 4 with broad, flat femur, lying with the prolateral surface uppermost and wider proximally and distally than in the middle. Patella short, basitibia longer and cylindrical; further tibial elements unknown.

# Acknowledgements

We thank Günter Bechly (Stuttgart) for making this specimen available for study, Carsten Kamenz (Berlin) for access to live whip spiders and their exuviae for comparative purposes, Ricardo Pinto da Rocha (São Paulo) and Alessandro Ponce de Leão Giupponi (Rio de Janeiro) for helpful comments and hints about further Crato material and Olli Coleman (Berlin) for help with photography. Peter Weygoldt and David Penney are thanked for valuable reviews of this manuscript.

#### References

- BLANCHARD, E. 1852. Arachnides in L'Organisation du Règne Animal 2<sup>nd</sup> edition, vol. 2. E. Blanchard, Paris, 232 pp.
- BUTLER, A. G. 1873. A monographic revision of the genus *Phrynus*, with descriptions of four remarkable new species. *Ann. Mag. Nat. Hist. Ser.* 4, **12**: 117–125.
- CARVALHO, M. DA G. P. DE & W. LOURENÇO 2001. A new family of fossil scorpions from the early Cretaceous of

Brazil. C. R. Acad. Sci. Paris, Sciences de la Terre et de planètes, **332:** 711–716.

DUNLOP, J. A. & D. M. MARTILL 2002. The first whipspider (Arachnida: Amblypygi) and three new whipscorpions (Arachnida: Thelyphonida) from the Lower Cretaceous Crato Formation of Brazil. *Trans. R. Soc. Edinburgh: Earth Sci.*, **92:** 325–334.

- Jason A. Dunlop & Victor Barov
- DUNLOP, J. A. & D. M. MARTILL 2004. Four additional specimens of the fossil camel spider *Cratosolpuga wunderlichi* Selden 1996 (Arachnida: Solifugae) from the lower Cretaceous Crato formation of Brazil. *Rev. Ibér. Aracnol.*, **9:** 143–156.
- GERSTAECKER, A. 1873. Glidertierfauna des Sansibargebietes. Arachnoidea. in C. C. von der Decken (ed). *Reisen in* Ost-afrika in den Jahren 1859-1865, **3:** 461–503.
- GERVAIS, P. 1842. *Histoire Naturelle des Insectes Aptéres, Vol. 3.* Libraire Encyclopédique de Roret, Paris, 476 pp.
- GIUPPONI, A. P. L. & R. L. C. BAPTISTA 2003. Primeiro registro fóssil de Phrynichidae (Amblypygi). P. 104. in: IV Encontro de Aracnólogos do Cone Sul, São Pedro. 7-12 Dezembro 2003, Programa & Resumos, G. Machado & A. D. Brescovit (eds).
- GOURRET, P. 1887. Recherches sur les Arachnides tertiaires d'Aix en Provence. *Rec. Zool. Suisse*, **4:** 431–496.
- HARVEY, M. S. 2003. *Catalogue of the Smaller Arachnid Orders of the World*. CSIRO Publishing, Collingwood, xi + 385 pp.
- KOCH, C. L. 1841. Die Arachniden. Getreu nach der Natur Abgebildet und Beschrieben. Vol. 8. C.H. Zeh'schen, Nürnberg, 131 pp.
- LAMARCK, J. B. P. A. de 1801. Système des animaux sans vertèbres. Lamarck and Deterville, Paris, 432 pp.
- MARTILL, D. M. 1993. Fossil of the Santana and Crato Formation, Brazil. The Paleontological Association, London, 159 pp.
- MELLO-LEITÃO, C. 1935. Novo Pedipalpo do Brasil. Ann. Acad. Brasil Sci., 7: 183–184.
- MORENO, A. 1940. Pedipalpida emmendata. *Mem. Soc. Cubana Hist. Nat. 'Felipe Poey'*, **14:** 167–168.
- MULLINEX, C. L. 1975. Revision of *Paraphrynus* Moreno (Amblypygi: Phrynidae) for North America and the Antilles. *Occ. Pap. Cali. Acad. Sci.*, **116**: 1–80.
- PETRUNKEVITCH, A. I. 1955. Arachnida. Pp. 42–162. in *Trea*tise on Invertebrate Paleontology, R. C. Moore (ed). Geological Society of America and University of Kansas Press, Lawrence, Kansas xvii + 181 pp.
- PETRUNKEVITCH, A. I. 1971. Chiapas amber spiders, II. Uni. California Pub. Entomol., 63: 1–44.
- POCOCK, R. I. 1894. Contributions to our knowledge of the arthropod fauna of the West Indies. III. Supplement on the Pedipalpi of the West Indies. *Zool. J. Linn. Soc. London*, **24**: 527–542.
- POCOCK, R. I. 1902. Arachnida: Scorpiones, Pedipalpi, and Solifugae. in F. D. Godman & O. Salvin (eds) *Biol. Centr. Am.*, **3:** 1–71.
- POINAR, G. O. Jr. & A. E. BROWN 2004. A new whip spider (Arachnida: Amblypygi), *Phrynus mexicana*, is described from Mexican Amber. in *Fossil Spiders in Amber* and Copal, J. Wunderlich (ed.), *Beitr. Araneol.*, **3B**: 1881–1885.

- SCHAWALLER, W. 1979. Erstnachweis der Ordnung Giesselspinnen in Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Amblypygi). *Stutt. Beit. Natkde.* (B), **50:** 1–12.
- SCHAWALLER, W. 1982. Neue Befunde an Geisselspinnen in Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Amblypygi). *Stutt. Beit. Natkde.* (B), 86: 1–12.
- SELDEN, P. A., F. C. CASADO & M. V. MESQUITA. In press. Mygalomorph spiders (Araneae: Dipluridae) from the Lower Cretaceous Lagerstätte, Araripe Basin, northeast Brazil. *Palaeontology*.
- SELDEN, P. A., W. A. SHEAR & P. M. BONAMO 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaeontology*, 34: 241–281.
- SHULTZ, J. W. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock) (Arachnida: Amblypygi), and its evolutionary significance. *Zool. J. Lin. Soc.*, **126**: 81–116.
- SIMON, E. 1892. Arachnides. in Etude sur les Arthropodes cavernicoles de île Luzon, Voyage de M. E. Simon aux îles Philippines (Mars et avril 1890), A. Raffray, I. Bolivar & E. Simon (eds). Ann. Soc. Entom. France, 61: 35–52.
- THORELL, T. 1883. Descrizione di alcuni Aracnidi inferiori dell' Arcipelago Malese. Ann. Mus. Civ. Stor. Nat. Genova, 18: 21–69.
- WEYGOLDT, P. 1974. Vergleichende Untersuchungen an zwei Heterophrynus (Admetus)-Arten, H. longicornis Butler und H. batesii Butler (Arachnida, Amblypygi, Tarantulidae). Zool. Anz., Jena, **192:** 175–191.
- WEYGOLDT, P. 1977a. Beobachtungen zum postembryonalen Wachstum von *Trichodamon froesi* Mello Leitao (Amblypygi, Arachnida). *Zoomorph.*, 86: 287–296.
- WEYGOLDT, P. 1977b. Coexistance of two species of whip spiders (Genus *Heterophrynus*) in the Neotropical rain forest (Arachnida, Amblypygi). *Oecologia (Berl.)*, 27: 363–370.
- WEYGOLDT, P. 1995. The development of the phrynichid "hand": notes on allometric growth and introduction of the new generic name *Euphrynichus* (Arachnida, Amblypygi). *Zool. Anz.*, 234: 75–84.
- WEYGOLDT, P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). J. Zoo. Syst. Evol. Research 34: 185–202.
- WEYGOLDT, P. 2000. Whip Spiders (Chelicerata: Amblypygi). Their Biology, Morphology and Systematics. Apollo Books, Stenstrup, 163 pp.

62