Campanian terrestrial arthropods from the Cerro del Pueblo Formation, Difunta Group in northeastern Mexico

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Abstract: The Campanian assemblage of arthropods from the Cerro del Pueblo Formation in northeastern Mexico display some primitive characteristics. It consists of a small spider, a dragonfly assigned to the Libelluloidea, and cockroach Xonopeptla rinconensis Cifuentes-Ruiz et Vršanský, gen. et sp. nov. — the latest record of the family Blattulidae and appears to be derived from the Aptian or Albian Cretaceous cockroaches of the genus Elisiana Giebel, 1856 from the Crato Formation, Brazil.

Key words: Cretaceous, Campanian, NE Mexico, Insecta, Odonata, Blattaria (=Blattodea), new genus, new species, Aranea.

Introduction

The fossil record of terrestrial arthropods in Mexico is scarce. A preliminary report on Cretaceous and Oligocene insects from northeastern and central Mexico was presented by Cifuentes-Ruiz et al. (2002). Most of the few arachnid reports from Mexico come from the Miocene Simojovel amber in Chiapas (Petrunkevitch 1963, 1971; Perrilliat 1989; Poinar 1992; Santiago-Blay & Poinar 1993; García-Villafuerte & Vega 2002), where insects are well known and diverse (Poinar & Doyen 1992; Poinar & Brown 2002; Engel 2004 etc.). A Cretaceous spider has been reported from the Albian Tlayúa Formation in Tepexi de Rodríguez, Puebla. Another odonate larva (Feldmann et al. 1998) and a pair of tipulid wings (Pantoja-Alor 1992) were described from the Lower Cretaceous Tlayúa Formation of Tepexi de Rodríguez, Puebla. Another odonate larva has been reported from the Lower Cretaceous Sierra Madre Formation in Chiapas (Vega et al. 2003b). An Upper Permian insect was described by Carpenter & Miller (1937) from Valle Las Delicias in Coahuila. More recently, Epicauta sp. was described from Trias beds of Jalisco (Zaragoza-Caballero & Vela-Sánchez-de León 2003).

The Cerro del Pueblo Formation is the oldest unit of the Difunta Group (Figs. 1–2). It was deposited in sedimentary basins Parras and La Popa with a total thickness of more than 4000 m (McBride et al. 1974). Since its original description (Murray et al. 1962), the Cerro del Pueblo Formation has attracted the attention of diverse investigators due to its diversity of fossils including pollen, leaves, fruits, coprolites, corals, gastropods, bivalves, ammonites, crustaceans, anelids, echinoids, reptile tracks and dinosaur bones (Wolleben 1977; Rodríguez de La Rosa & Cevallos-Ferriz 1994, 1998; Rodríguez de La Rosa et al. 1998, 2002; Hernández et al. 1995; De León-Dávila et al. 1999; Kirkland et al. 2000; Brinkman et al. 2002; Kirkland & Aguillón-Martínez 2002; Eberth et al. 2003; Perrilliat et al. 2003; Vega et al. 2003a, 2004). Ammonites include sphenodiscid forms (unpublished observation). Eberth et al. (2004) reported Inoceramus vanuxemi from Rincón Colorado and La Escondida sections of the Cerro del Pueblo Formation, and based on reports of this species in localities with baculitids (Kauffman et al. 1993), they suggested I. vanuxemi can be considered as a Middle–Late Campanian index fossil.

The Campanian age has been recently suggested for the Cerro del Pueblo Formation based on magnetostratigraphic data (Eberth et al. 2004). These authors measured a total thickness of 449 m for the formation at the study localities here reported, deposited between magnetozones 32n.3r–32n.2n, an interval that corresponds to the Western Interior biozones of Baculites reesidei and B. jenseni, and suggest a maximum age of 72.5 Ma for the Cerro del Pueblo Formation. Eberth et al. (2004) also reported that these sediments were deposited in an embayment where sediments prograded to the east and northwest, and formed a thick uppermost Cretaceous to Lower Tertiary Difunta Group sequence in the Parras Basin (Figs. 2–3). The assemblage appear to be the only Campanian one known worldwide.

Vein nomenclature for the dragonfly wing (Rieck & Kukalová-Peck 1984): RA = radius anterior; RP = radius posterior (RP1, RP2); IR = interradial (IR1, IR2); MA = me-
Fig. 1. Location of study area in northeastern Mexico, and placement of localities IGM 3500 (A) and IGM 3501 (B).

Localities and paleoenvironment

Material was collected in two localities from the basal portion of the Cerro del Pueblo Formation. The first one (A Locality; Rincón Colorado 2; IGM 3500) is found next to the dirtroad that leads to Rincón Colorado town, approximately 40 km west of Saltillo (Fig. 1), 25°45' 20" N, 101°10' 21" W. Lithology is represented by olive-grey mudstone, in which scarce palm and other angiosperm leaves were found. The second (B Locality; Presa San Antonio; IGM 3501) is in Ejido Presa San Antonio, approximately 70 km west of Saltillo (Fig. 1), at 25° 28' 05" N, 101° 42' 48" W. Fine olive sandstone crops out here, and relevant dinosaur remains have been recovered from the same locality. Both lateral and vertical facies changes can be detected in relatively short distances. The formation consists of cyclic alternations of marine, estuarine and freshwater environments. The described specimens were deposited in lakes or small ponds, associated with the deltaic system that prevailed in northeastern Mexico during Campanian times (Fig. 3). The organisms here described formed part of a dynamic environment.
where aquatic systems supporting subaquatic vegetation changed rapidly both geographically and temporarily on the ancient east coast of northeastern Mexico. However, insects were able to live in humid areas with high mean temperature and were able to interact with plants, as suggested by galleries with insect coprolites reported in several fruit types of this formation (Rodríguez de la Rosa & Cevallos-Ferríz 1994). Further studies on plant-animal interactions are promising.

This is the first report of terrestrial arthropods from this unit and contributes to the understanding of the paleoecology of this interesting formation.

The specimens are deposited in the Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, under acronyms IGM.

Systematic paleontology

Order Araneida Clerck, 1757

Infraorder incertae sedis (Fig. 4)

Material: IGM 8825; part and counterpart of complete specimen; Cerro del Pueblo Formation, Coahuila, Mexico. Campanian.

Description: Body small (Table 1). Two halves of the type preserved ventrally, ovate form. Prosoma suboval, coxosternal region with wide, low sternum, unsegmented, subcircular opisthosoma: sternum oval, longer than wide, length about four-tenths length of body, width half of its length. Left pedipalp coxa and first three left leg coxae subcircular, almost as wide as long. Fourth left leg coxa small, half the length of third left leg coxa, three-quarters its width. Impressions of the second left leg femur, and of the right leg femur present; articulation between left pedipalp trochanter and its femur preserved. Trochanter rectangular, broader than long, length seven-tenths its width. Portion of pedipalp femur much longer than wide, length four times its width. Portion of first leg femur longer than wide, length about twice its half. Portion of second left leg femur, more or less complete, much longer than wide, length more than three times its width.

Impression of the right pedipalp femur is observed at the front of the most anterior region of the prosoma, as a result of deformation during fossilization. Right pedipalp femur stout, longer than wide, length about twice its width.

Opisthosoma subcircular, almost as long as wide, length about half of total length of body. Its width eight-tenths maximum width (prosoma width).

Abdominal segments difficult to distinguish. Pedicel partially visible between the fourth coxae.

Table 1: Measurements of the specimen IGM 8825.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
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</thead>
<tbody>
<tr>
<td>Total length</td>
<td>2.05</td>
<td>1.15</td>
</tr>
<tr>
<td>Prosoma</td>
<td>1.07</td>
<td>1.07</td>
</tr>
<tr>
<td>Sternum</td>
<td>0.88</td>
<td>0.48</td>
</tr>
<tr>
<td>Right pedipalp femur</td>
<td>0.70</td>
<td>0.28</td>
</tr>
<tr>
<td>Right leg femur</td>
<td>0.65</td>
<td>0.21</td>
</tr>
<tr>
<td>First left pedipalp coxa</td>
<td>0.28</td>
<td>0.35</td>
</tr>
<tr>
<td>First left leg coxa</td>
<td>0.26</td>
<td>0.27</td>
</tr>
<tr>
<td>Second left leg coxa</td>
<td>0.27</td>
<td>0.27</td>
</tr>
<tr>
<td>Third left leg coxa</td>
<td>0.23</td>
<td>0.29</td>
</tr>
<tr>
<td>Fourth left leg coxa</td>
<td>0.12</td>
<td>0.22</td>
</tr>
<tr>
<td>Left pedipalp trochanter</td>
<td>0.25</td>
<td>0.18</td>
</tr>
<tr>
<td>Left pedipalp femur</td>
<td>0.58</td>
<td>0.17</td>
</tr>
<tr>
<td>First left leg femur</td>
<td>0.56</td>
<td>0.21</td>
</tr>
<tr>
<td>Second left leg femur</td>
<td>0.80</td>
<td>0.23</td>
</tr>
<tr>
<td>Opisthosoma</td>
<td>0.94</td>
<td>0.93</td>
</tr>
<tr>
<td>Pedicel</td>
<td>0.25</td>
<td>0.21</td>
</tr>
</tbody>
</table>
Remarks: The specimen could not be a mesothelae, because of a wide sternum (instead of a narrow one — Raven 1985), it lacks the sternite of the first abdominal segment, and the fourth coxae are not invaginated at their postero-median corners (Platnick & Gertsch 1976).

Other diagnostic characters like the spinnerets or the chelicerae are not visible, preventing taxonomic placement at the infraorder level. However, mygalomorph characteristics (Selden 2002), such as relatively robust podomeres are visible in the specimen. Nevertheless, this placement also appears questionable (K. Eskov, pers. comm.), since pedipalp is clearly shorter than legs, while mygalomorph pedipalp is long and leg-like. Also pedipalp coxae are subcircular, while in mygalomorphs they are more or less rectangular.

Order Odonata Fabricius, 1793
Suborder Anisoptera Selys, 1854 in Selys & Hagen 1854 gen. et sp. incertae sedis (Fig. 5)

Material: IGM 8826; single fragment of fore wing.
Cerro del Pueblo Formation, Coahuila, Mexico. Campanian.

Description: The convexity and concavity of the wing veins, as well as the intercalary veins apparent. Postnodal crossoveins present; pterostigma well developed, length four times its width, about two-tenths total fragment length, width one-tenth maximum width, parallel ending; four crossoveins beneath.
RA, RP1, IR1, RP2, IR2, RP3–4, MA present. RA, RP1 parallel. RP2 and IR2 nearly parallel with two rows of cells beginning halfway along pterostigma. RP2 arching anteriorly just before level of pterostigma, then abruptly bent; close and parallel to IR1. IR2 and RP3–4 strongly divergent with many rows of cells between them distally. RP 3–4 and MA sigmoidally curved with one row of cells between them.

Measurements: Fragment length/width 13.7/6.8 mm.
Pterostigma length/width: 2.4/0.6 mm.

Remarks: Systematics of fossil Odonata is based on the structure of adult wings. From the six odonate suborders, there are only three which have Cretaceous representatives: Anisozygoptera, Anisoptera and Zygoptera (Carpenter 1992).

The following features in the wing fragment are diagnostic of the Odonata: distinctive complex venation, a conspicuous pterostigma on the anterior margin of the wing distally; convexity and concavity of the main wing veins.

Although additional taxonomically relevant venational characters are absent, a well developed pterostigma is present, as well as the typical venational pattern of Anisoptera i.e., RP with three main branches (Rieck & Kukalová-Peck 1984; Carpenter 1992). Nevertheless, according to D. Vasilenko (pers. comm.), a similar venation of wing apex can be found in some Anisozygoptera, e.g., in the Late Jurassic Turanothermes (Turanothermidae) described by Pritykina (1968).

Order Blattaria Latreille, 1810
Suborder Polyphagoidea Walker, 1868
Family Blattulidae Vishniakova, 1982
Xonpepetla Cifuentes-Ruiz et Vršanský, gen. nov.

Type species: Xonpepetla rinconensis described below.

Composition: Type species only.

Diagnosis: Robust cockroach with short and very wide forewings (autapomorphies). Venation regular, with the exception of area between CuA and CuP; subcostal area narrow and short (autapomorphy); radial field wide (plesiomorphy) with most veins simple (apomorphy); CuA reduced to several veins (apomorphy). Clavus narrow and long (apomorphy), reaching almost half of the wing.

Description: Forewing without coloration, short and very wide, venation simplified with rather thick veins. Subcosta simple, costal area narrow and short; most of R simple; M rich (plesiomorphy), CuA with few branches. Clavus narrow and long with sharply curved CuP. A simple.

Remarks: The new genus is highly advanced as shown by numerous autapomorphies. This make its phylogenetic position rather unclear. On the other hand, plesiomorphies exclude the relationship of the genus to other advanced blattulids such as Tarakanula Vršanský, 2003 or Laurasian representatives of the genus Elisama.

Therefore the most probable ancestor of the new genus is close to the Gondwanian representatives of Elisama such as E. americana Vršanský, 2002 which share the wide R, simplified venation (synamopomorphy) and rather thick veins. Thus, the absence of a dark macula near the CuA basis may be considered for an apomorphy (unless absent in E. americana).

Etymology: After xonpepetl (Aztec for cockroach).
Xonpepetla rinconensis Cifuentes-Ruiz et Vršanský, gen. et sp. nov. (Figs. 6—7)

Holotype: IGM 8827. both forewings. Cerro del Pueblo Formation, Coahuila, Mexico. Campanian.

Additional material: IGM 8828. Hindleg. The same locality and horizon as the type.

Description: Forewing wide, length/width: 9.3/3.6 mm. Total number of veins at the margin about 40, with intercalaries present between all branches including A. Costal space short and narrow taking up less than a third of the wing length. Sc short, simple and straight (slight asymmetry is present in the only known pair of tegmina); R with 18 mostly simple veins; M9; CuA7, A5. CuP sharply curved, running close to CuA. Without coloration.

Additional material is represented by an adult hindleg, part and counterpart, with preserved coxa, trochanter, femur and tibia; tarsus incomplete. Femur robust but not elongated, with a spine on anterior margin of distal portion. Tibia and tarsus with numerous spines. Coxa two-tenths total leg length. Trochanter quadrangular, shorter than coxa, its length one-twentieth total length. Its width half maximum width (femur width).

Femur longer than coxa and trochanter, shorter than tibia and tarsus, about three-tenths total length, widest toward the middle; curved spine on the apex. Spine length same as trochanter length, two-tenths its width.

Tibia and tarsus fragment length half of total length, their width one-tenth maximum width. Short slender erect spines along the lateral margins. Their length, half of femur spine length. Coxa length 4.2 mm, trochanter 1 mm, width 1.0 mm, femur length/width 5.7/2.0 mm. Femur spine length/width 1.0/0.2 mm. Tibia-tarsus fragment length/width 9.3/0.6 mm.

Remarks: Long coxae and short, wide femora of the leg are characteristic for the Blattulidae. This determination is supported by its size. According to the relict character of the family in the Campanian, and a similar size of the leg, it is most likely that the extremity fragment belongs to the same taxon. The presence of the two sister species in the advanced Campanian cenoses seems unlikely. Two finds representing the same taxon may be caused by stochastical reasons but also it may indicate a comparative abundance of the species and thus its near-water occurrence, and/or destabilized cenosis.

Only slight asymmetry of the wing indicate the individual was a good flier.

Etymology: The specific name is based on Rincón Colorado, a regionally famous dinosaur-bearing locality in Coahuila.

Discussion

There are few records of Cretaceous spiders — five Mesozoic mygalomorphs have been described by Selden (2002), who highlights the records of Araneae from this period and includes fossils from the Barremian or Aptian strata of Koonwarra in South Australia (Jell & Duncan 1986), orbicularian araneomorphs from the Berriasian or Valanginian deposits of the Sierra del Montsec in Spain (Selden 1989, 1990, 1991); an unnamed lycosoid from Orapa in Botswana (Upper Cretaceous — Rayner & Dippensaer-Schoeman 1995), and many new specimens are reported from the Aptian or Albian Crato Formation of Brazil (Grimaldi 1991). After the description of Atocatle ranulfii Feldmann, Vega, Applegate et Bishop, 1998, a mesothelae species from the Albian Tlayúa Formation (Feldmann et al. 1998), the current find is the second oldest spider reported from Mexico.
Eskov & Zonshtein (1990) point out that orthognathous chelicerae (present in mygalomorphs and liphistiids) lying on the same plane as the carapace cannot avoid being in the same imprint during fossilization. So the imprint of a spider containing the palps but not chelicerae, must surely have belonged to a creature with labidognathous chelicerae (present in araneomorphs). Chelicerae are not visible in the specimen.

The infraorder Araneomorphae, sometimes referred to as "true" spiders, includes some 90 families, 2700 genera, and 32,000 species described (Coddington & Levi 1991). Habitats within this group are highly variable, and include vegetation, as well as soil-inhabiting, lapidicolous spiders (Lehtinen 1967).

Anisoptera consists of five families with Cretaceous representatives: Gomphidae, Aeshnidae, Aeschniidae, Peta luridae and Hemerocopiidae (Carpenter 1992). The absence of a brace vein, the large area between veins IR2 and RP3-4, and the general venational pattern (i.e., moderate wing reticulation, and longitudinal veins configuration), could point to a rather recent group within the Libelluloida (Jarzembowski & Nel 1996), although this lineage is present from the Middle Jurassic (Rasnitsyn & Pribykina 2002).

The occurrence of cockroaches in a new Campanian locality is not surprising. The cockroaches represent dominant elements of Cretaceous cenoses, including over 200 species in 8 families (Vršanský 1997, 1998a,b, 1999a,b, 2000, 2002, 2003a,b, 2004; Vršanský et al. 2002a). Localities from the American continent are characterized by low diversity. Several hundred Gondwanian cockroaches from the Aptian or Albian Santana Formation comprise only 4 species in 3 families (Vršanský 2004), and in the Turonian sediments of New Jersey, there are 4 species of 4 families (P. Vršanský, in preparation). Nevertheless, in both localities, modern families dominate.

The dominant occurrence (2/2) of the Jurassic-Creta ceous family Blattulidae in the Campanian assemblages of Mexico, which is the latest known record of the family, is more surprising. Additionally, the newly described genus and species possess many plesiomorphies within the family, indicating some degree of isolation of the assemblage.

The family Blattulidae has been designated by Vishniakova (1982) in order to separate distinct representatives formerly placed in Mesoblattinidae (currently Caloblattinidae Vršanský & Ansorge in Vršanský 2000). The family had evolved from predecessors of Lepidoblattinidae Vršanský, 2002 during the latest Triassic or earliest Jurassic, indicating some degree of isolation of the assemblage.

The derivation of the new genus and species from the American taxa such as *Clerck C.A. 1757: Svenska spindlar uti sina hufvud-slagter indelete *, is the case for *Xonpepetla rinconensis* sp. nov.

Other things being the same, it is an evidence for adaptability of the group (known from at least 100 species), which was able to compete even with modern taxa up to the Campanian. However, they did not pass through the K/T boundary.

**Conclusions**

— The latest record of the family Blattulidae is present ed from the Campanian strata of northeastern Mexico.

— *Xonpepetla rinconensis* Cifuentes et Vršanský sp. nov. (Blattulidae) possessed a combination of numerous autapomorphies and plesiomorphies, indicating that the progressive representatives of the family, known from much older deposits of Laurasia were possibly rare at the assemblage of the Cerro del Pueblo Formation.

— The second oldest spider record from Mexico is present in the Campanian strata of northeastern Mexico. It is likely to represent an opistothelae araneomorph (the oldest record from Mexico in such a case).

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tebrates (late Campanian, Cerro del Pueblo Formation) from southeast Coahuila, Mexico. VIII Congreso Nacional de Paleontología, Sociedad Mexicana de Paleontología, Resúmenes, 75–76 (in Spanish).


