

THE FIRST FOSSIL PROSCOPIIDAE (INSECTA, ORTHOPTERA, EUMASTACOIDEA) WITH COMMENTS ON THE HISTORICAL BIOGEOGRAPHY AND EVOLUTION OF THE FAMILY

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Abstract: *Eoproscopia martilli* gen. et sp. nov. is described from the Early Cretaceous (Aptian) Crato Formation Lagerstätte of Ceará State, north-east Brazil. The new taxon is assigned to the extant family Proscopiidae and represents the first occurrence of the group in the fossil record. *Eoproscopia* is similar to crown group proscopiids in its stick-like habitus, elongate prothorax and absence of the cryptopleuron, but differs in the presence of well-developed wings, the short head with a small, simple fastigium, the prothoracic legs

being inserted near the posterior margin of the prothorax, and the absence of spines on the metathoracic tibiae. The discovery of *Eoproscopia* extends the geological range of the family by approximately 110 myr and confirms the presence of stem-group proscopiids in the Atlantic rift zone of South America during the Early Cretaceous.

Key words: Insecta, Orthoptera, Eumastacoidea, Proscopiidae, Brazil, Cretaceous.

PROSCOPIIDAE are a group of highly cryptic eumastacoid grasshoppers characterised by their stick-like habitus, appendiculate ventral lobes on the apices of the metathoracic femora, loss of the auditory tympanal organ, and absence of the cryptopleuron. The family comprises some 215 species in 30 genera distributed throughout Central and South America and was subdivided by Liana (1980) into three subfamilies: Hybusinae comprising five species in the nominate genus *Hybusa*; Xeninae with 16 species in three genera; and Proscopiinae constituting the most speciose subfamily, with 182 species in 19 genera. In addition, there are a further 12 species in seven genera that remain unassigned to any subfamily (Eades 2002). Proscopiidae are entirely flightless and primarily wingless, though some genera retain vestigial wing rudiments (Mello-Leitão 1939; Jago 1989). Most species show marked sexual dimorphism, with males being much smaller than females, which are generally more robust and often have longer, more elaborate fastigia. Despite their extreme morphological crypsis, proscopiids are ecological generalists, occupying a number of different habitats and feeding on a variety of host plants. Indeed, a single species may feed on several different plant families and some are considered sporadic pests, especially in more arid regions such as the caatinga of north-east Brazil (Lima and Andrade

2002). Proscopiidae have been monographed by Brunner (1890) and Mello-Leitão (1939) and catalogued by Carbonell (1977), though the most recent comprehensive review was presented by Jago (1989) whose detailed studies of the unusual male genitalia of this group form the basis of their taxonomy. Although Jago (1989) developed a useful system for describing male genital morphology, he was unable to homologise any of the aedeagal sclerites of proscopiids with those of other acridomorphs, a feat that still evades workers on this group (Amedegnato 1985; Bentos-Pereira 2003b).

Proscopiidae were allied with the southern and central African Pneumoridae by Sharov (1968), and this relationship was also tentatively supported by Jago (1989) based on superficial similarities in the structure of the male genitalia. However, most authors support a relationship with the Eumastacidae and group the two families together in the superfamily Eumastacoidea (Uvarov 1966; Descamps 1973a, b; Dirsh 1975; Kevan 1977; Amedegnato 1993; Bentos-Pereira 2003b; Grimaldi and Engel 2005). Although Eumastacidae are known as fossils from the Early Jurassic onwards (Zeuner 1944; Sharov 1968; Lewis 1974, 1976; Carpenter 1992; Perez-Gelabert 2002), Proscopiidae have hitherto been known only from the extant fauna. Here, I describe the first fossil proscopiid, *Eoproscopia martilli* gen. et sp. nov., from the

Early Cretaceous Crato Formation Lagerstätte of Brazil, and discuss the phylogeny and historical biogeography of these enigmatic orthopterans.

MATERIAL AND METHODS

The new specimens originate from the Nova Olinda Member of the Crato Formation Lagerstätte (*sensu* Martill 1993); a suite of Early Cretaceous lacustrine–lagoonal micrites and argillaceous sediments that crop out around the flanks of the Chapada do Araripe in Ceará State, north-east Brazil. The Nova Olinda Member is the basal unit of the Crato Formation and comprises a sequence of millimetre-laminated, organic-rich micritic muds (Plattenkalks) which yield a diverse and exceptionally well-preserved biota (see Grimaldi 1990; Martill 1993; Heads *et al.* 2005; Martill *et al.* 2007).

The fossils described here are exceptionally preserved as goethite replacements (after pyrite) in a matrix of millimetre-laminated limestone. The holotype (SMNS 66000-135; Pl. 1, fig. 1) is preserved in left lateral aspect on a single slab 184 × 165 mm. The specimen is nearly complete except for the distal parts of the legs. The meso- and metathoraces and the apex of the abdomen are poorly preserved and fragmentary. The paratype (MB.I. 2077; Pl. 1, fig. 2) is preserved in right lateral aspect on a single rounded slab 135 × 123 mm. The specimen is less well-preserved than the holotype with most of the body highly oxidised. The head and thorax are largely missing and preserved only in outline, having presumably been retained on the counterpart. The abdomen is a little dorsolaterally compressed and some of the tergites are very well preserved. The terminalia are also preserved but appear to have been damaged during preparation. Like the holotype, most of the legs are missing the distal portion. However, the apical part of the tibia and the tarsus of the left prothoracic leg and the basitarsus of the right metathoracic leg are preserved.

The specimens were studied and drawn using Olympus SZH and Zeiss stereomicroscopes with camera lucida drawing tubes. No mechanical preparation was necessary as both specimens were adequately prepared prior to their study. Photographs were taken with a Nikon D1X digital SLR and manipulated using Adobe Photoshop CS. Drawings were prepared using Adobe Illustrator CS. All computer manipulation was conducted on an Apple iBook G4

running Mac OS X. Measurements are given in millimetres.

Terminology and abbreviations. The terminology used here follows Uvarov (1966). Abbreviations used in figures are as follows: an, antenna; bt, basitarsus; cr, carina; cx, coxa; e, eye; fa, fastigium; fm, femur; mp, maxillary palp; pn, pronotum; ps, prosternum; ptx, prothorax; s, abdominal sternites (numbered); tb, tibia; t, abdominal tergites (numbered); vv, valvulae of ovipositor.

SYSTEMATIC PALAEOLOGY

Order ORTHOPTERA Olivier, 1789

Suborder CAELIFERA Ander, 1936

Superfamily EUMASTACOIDEA Burr, 1899

Family PROSCOPIIDAE Audinet-Serville, 1839

Genus EOPROSCOPIA gen. nov.

Type species. *Eoproscopia martilli* sp. nov. by monotypy.

Derivation of name. Greek prefix *eo-*, dawn (indirectly a reference to ‘early in the day’ and thereby ‘early’), and *Proscopia*, the type genus of the family.

Diagnosis. Proscopiidae with wings present and well developed; head short with small, simple fastigium; antennae as long as prothorax; terminal two antennomeres expanded distally; pronotum and prosternum with distinct longitudinal carinae; prothoracic leg inserted near posterior margin of prothorax; metathoracic tibiae without spines.

Eoproscopia martilli sp. nov.

Plate 1; Text-figures 1–2

v 2007 Proscopiidae gen. et sp. nov. Heads and Martins-Neto in Martill *et al.* p. 277, pl. 11a.

Type material. Holotype, SMNS 66000–135, near complete adult female preserved in left lateral aspect on a single slab in the Staatliches Museum für Naturkunde, Stuttgart, Germany. Paratype, MB.I. 2077, near complete adult specimen preserved in right lateral aspect on a single slab in the Museum für Naturkunde der Humboldt-Universität Berlin (ex coll. Schwickert no. 68).

EXPLANATION OF PLATE 1

Figs 1–2. *Eoproscopia martilli* gen. et sp. nov., Nova Olinda Member, Crato Formation; Chapada do Araripe, Ceará State, north-east Brazil. 1, holotype, adult female, SMNS 66000-135; for explanatory drawing see Text-figure 1. 2, paratype, adult (sex indeterminate), MB.I. 2077; for explanatory drawing see Text-figure 2. Scale bars represent 10 mm.



HEADS, *Eoproscopia*

Type horizon and locality. Nova Olinda Member, Crato Formation (Aptian, Early Cretaceous); the exact provenance of the type material is unknown but the specimens are likely to have originated from quarries in the region between Nova Olinda and Santana do Cariri in Ceará, north-east Brazil (see Heads *et al.* 2005 for map).

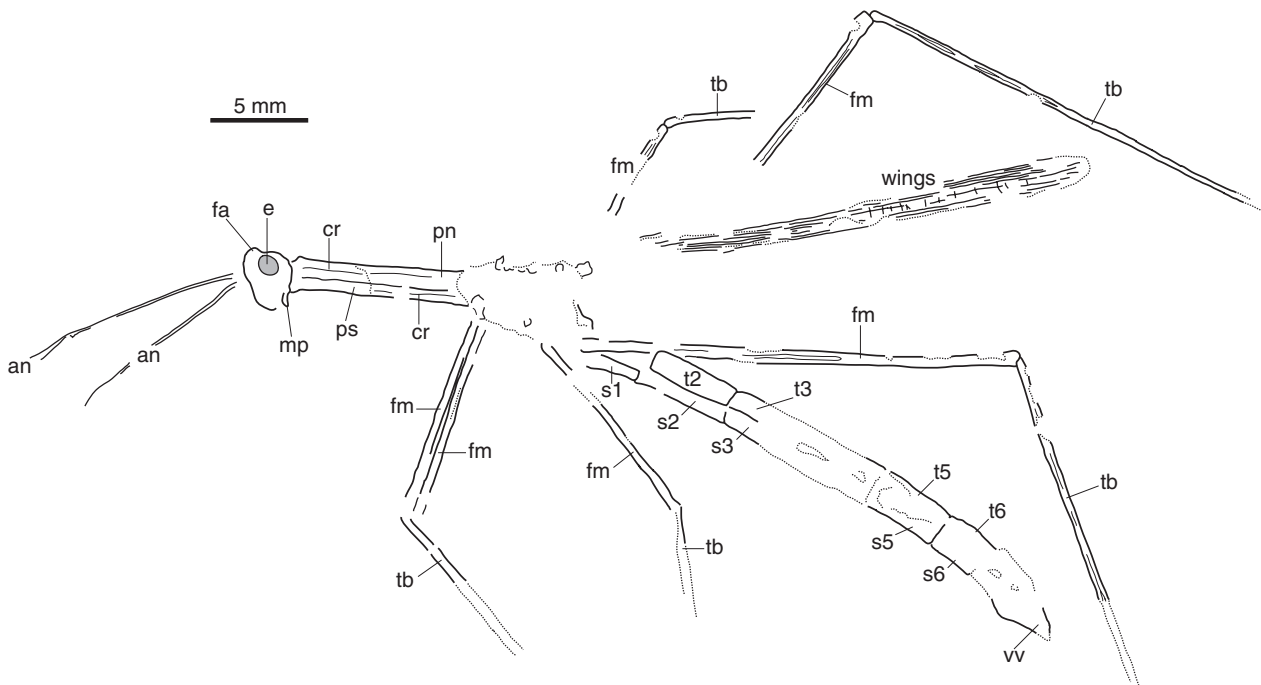
Derivation of name. After Dr David Martill (University of Portsmouth, UK) for his friendship and guidance over the years, and in recognition of his important contribution to the geology and palaeontology of the Crato Formation Lagerstätte.

Diagnosis. As for the genus.

Description of holotype. Adult female (Pl. 1, fig. 1; Text-fig. 1). Head length 4.0 (measured from distal end of labrum to the apex of the fastigium), antero-posterior width 3.5 at widest point; fastigium length 1.25; eye length 1.25; length of antennae 12.5; maxillary palp length *c.* 1.5. Length of prothorax *c.* 11.0; combined length of meso- and metathoraces *c.* 6.0. Abdominal metamere lengths: metameres 1–4 of uniform length, 5.0; metamere 5, 3.75; metamere 6, 3.25; metamere 7, 3.0. Wing length 31.0. Prothoracic leg: femur 13.0; tibia ≥ 14.0 ; tarsus not preserved. Mesothoracic leg: femur *c.* 11.0; tibia > 7.0 (only proximal part preserved); tarsus not preserved. Metathoracic leg: femur 23.5; tibia ≥ 23.0 ; tarsus not preserved. Head hypognathous with small, apically rounded fastigium. Eye subovate, situated near the top of the head directly beneath the fastigium. Antennae filiform, inserted to the anterior of the eye, with last two antennomeres expanded distally. Anterior margin of labrum slightly curved. Maxillary palp poorly preserved. Prothorax elon-

gate, widening slightly towards posterior; pronotum and prosternum with distinct longitudinal carinae. Meso- and metathorax (poorly preserved) bulging dorsally and apparently more robust than the prothorax. Abdomen of seven metameres, each with pleural margin of tergum overlapping that of the sternum laterally. Terminalia poorly preserved; ventral valves of ovipositor visible. Wings well developed, tightly folded, obscuring most of the venation. Legs elongate and slender with longitudinal sulci on femora and tibiae (more prominent in the metathoracic legs). Prothoracic leg inserted near posterior margin of prothorax. Metathoracic leg saltatorial, markedly longer than prothoracic and mesothoracic legs; tibiae without spines.

Description of paratype. Adult specimen, sex indeterminate (Pl. 1, fig. 2; Text-fig. 2). Head length 4.0, antero-posterior width 3.0 at widest point; fastigium length *c.* 1.0. Length of prothorax 11.25; combined length of meso- and metathoraces *c.* 7.5. Abdominal metamere lengths: combined length of metameres 1–3, *c.* 13.0; metamere 4, 5.0; metamere 5, 4.75; combined lengths of metameres 6 and 7, *c.* 12.5. Wing length 32.5. Prothoracic leg: femur 12.0; tibia *c.* 12.0; basitarsus 1.5; first tarsomere 1.0; second tarsomere 0.5. Mesothoracic leg: femur ≥ 10.0 ; tibia > 9.0 (only proximal part preserved); tarsus not preserved. Metathoracic leg: femur 24.5; tibia ≥ 24.0 ; basitarsus *c.* 2.0. Head and prothorax poorly preserved and slightly disarticulated from one another. Fastigium rounded. Antennae and eyes not preserved. Anterior margin of labrum much like that of holotype. Prothorax elongate, widening towards posterior; carinae not visible. Meso- and metathoraces poorly preserved with slight dorsal bulge. Abdomen slightly dorsolaterally compressed; metameres 4 and 5 well preserved with very fine tuberculate ornament on



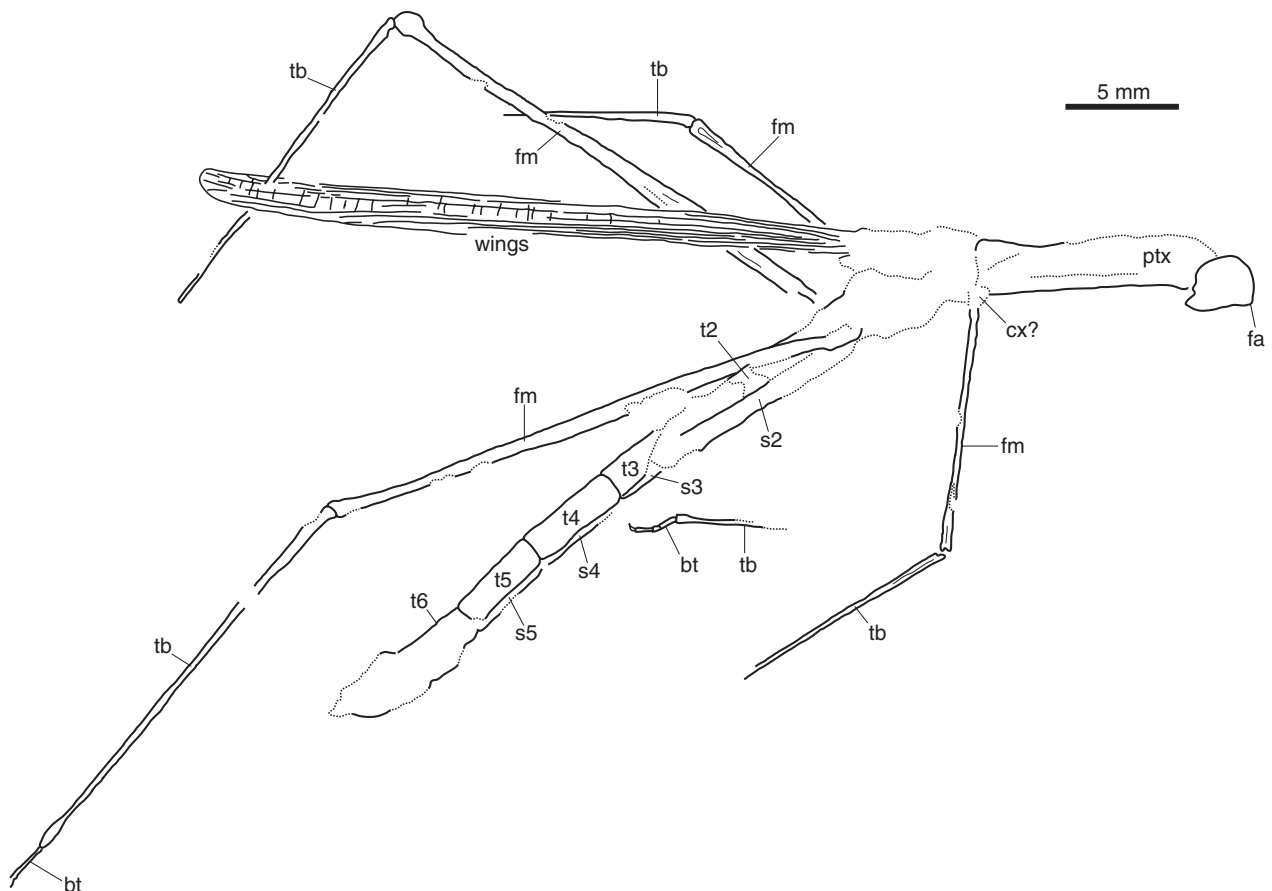
TEXT-FIG. 1. Camera lucida drawing of *Eoprosopia martilli* gen. et sp. nov., holotype, adult female, SMNS 66000-135; explanatory drawing for Plate 1, figure 1. For list of abbreviations, see text.

cuticle. Terminalia poorly preserved, apparently damaged during preparation. Wings well developed, tightly folded as in holotype. Legs elongate and slender with longitudinal sulci on femora and tibiae. Prothoracic leg inserted near posterior margin of prothorax; basitarsus markedly longer than remaining tarsomeres. Metathoracic leg saltatorial; tibiae without spines.

DISCUSSION

Eoproscopia is typical of stem-group taxa in that it is defined by a novel combination of both plesiomorphic and derived character states. The short head with a small, simple fastigium and long antennae, and the well-developed wings are almost certainly plesiomorphic. Nevertheless, the elongate prothorax and absence of the cryptopleuron are characteristic of the family and clearly support assignment to Proscopiidae. In addition, the posterior insertion of the prothoracic leg and the absence of spines on the metathoracic tibiae are unique to *Eoproscopia* and probably apomorphic. Almost all extant Proscopiidae have the prothoracic leg inserted in the anterior half of the prothorax with only a few genera of the tribe Tetra-

norhynchini (Proscopiinae) having the leg inserted at the mid-point of the prothorax (Bentos-Pereira 2003b). Like other acridomorphs, all extant proscopiids have longitudinal rows of subapical spines on the metathoracic tibiae, but these are entirely absent in *Eoproscopia*. In addition, the head capsule is not as elongate as in most modern members of the family and the fastigium is also much shorter. However, fastigial morphology is highly variable in Proscopiidae and subject to not only interspecific variation but also intraspecific variation, with some species occurring in both brachyrostrate and nasute forms (Text-figs 3–4). In addition, marked sexual dimorphism is true of most proscopiids, with females often having longer and more elaborate fastigia than males of the same species (Text-figs 3A, 4E–F). The head capsule of *Eoproscopia* is most closely comparable to that of the extant *Bazylukia* Liana, 1972 from Sabanilla, Ecuador. Jago (1989) noted that *Bazylukia* is unlike any other extant proscopiid genus in that it has a short head and very small fastigium (Text-fig. 4A). In this respect, both *Bazylukia* and *Eoproscopia* resemble certain Eumastacidae rather than typical proscopiids (see Text-fig. 4B–F). Elongation of the head



TEXT-FIG. 2. Camera lucida drawing of *Eoproscopia martilli* gen. et sp. nov., paratype, adult (sex indeterminate), MB.I. 2077; explanatory drawing for Plate 1, figure 2. For list of abbreviations see text.



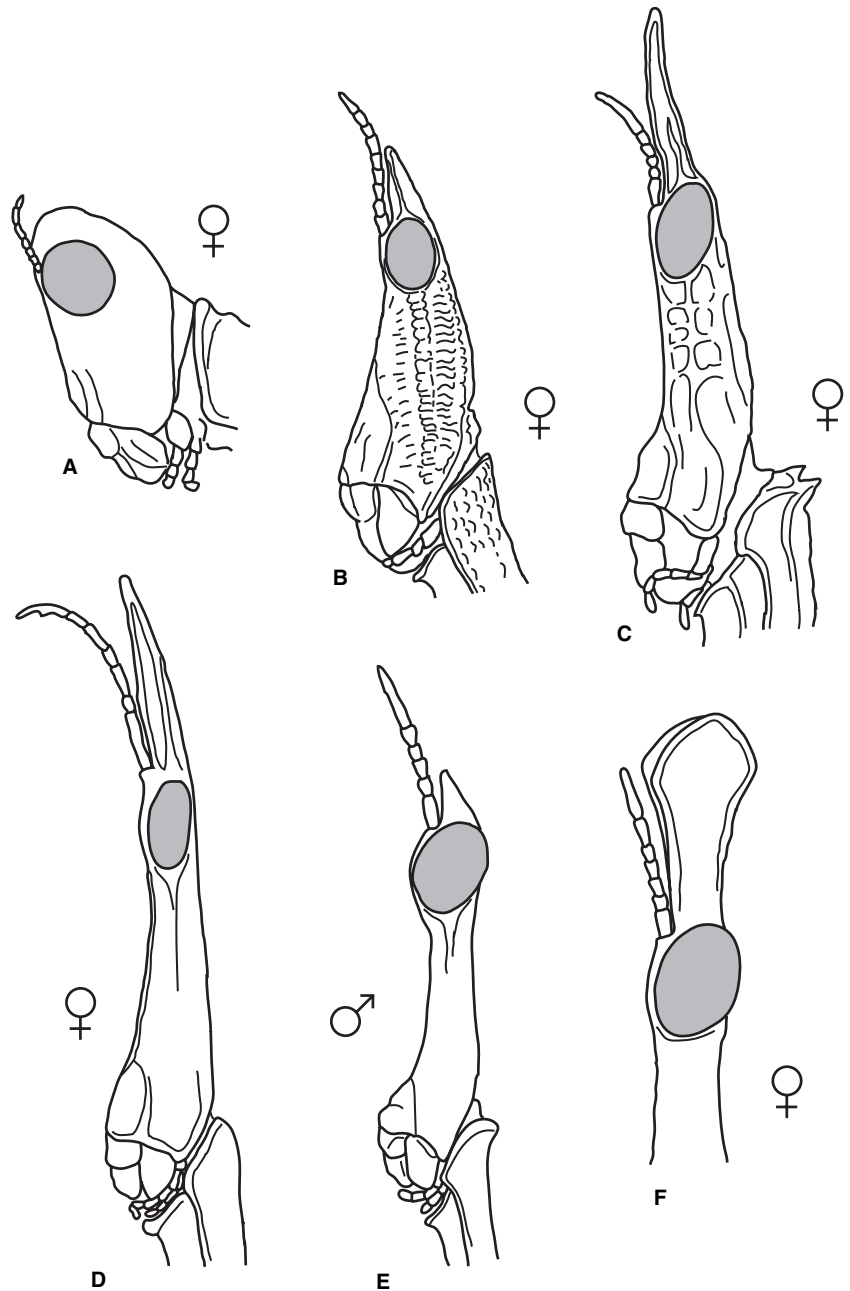
TEXT-FIG. 3. Extant Proscopiidae from Brazil. A, a mated pair of *Corynorhynchus* sp. (Proscopiinae) encountered in caatinga forest near the village of Boa Vista, c. 7 km west of Nova Olinda. Note the smaller size of the male and the sexual dimorphism in the size of the fastigium (markedly longer in female). B, brachyrostrate female *Stiphra robusta* Mello-Leitão, 1939 (Proscopiinae) found on a slab of Nova Olinda Member limestone in a disused quarry near Araporonga, north-west of Santana do Carriri. This species is abundant in the north-east of Brazil where it is considered a sporadic pest and is commonly encountered in and around the quarries near Nova Olinda and Santana do Carriri. Scale bar represents 20 mm. Photographs taken by David M. Martill, July 2006.

capsule and exaggeration of the fastigium are both closely related to the development of stick mimesis, and it is clear that *Eoproscopia* is less specialised than modern forms in this regard. Nonetheless, *Eoproscopia* does have the remarkable stick-like body typical of crown-group proscopiids, and it would appear that the family adopted their cryptic mode of life as stick mimics very early in their evolution, a situation somewhat analogous to that observed in phylline Phasmatodea (Wedmann *et al.* 2007), but clearly much older in proscopiids.

No phylogenetic analysis of Proscopiidae has ever been undertaken. Most of the classic accounts are synoptic

(e.g. Carbonell 1977) or phyletic (Mello-Leitão 1939; Liana 1972, 1980; Descamps 1973*a*), and more recent studies have been concerned primarily with species description (Jago 1989; Bentos-Pereira and Rowell 1999; Bentos-Pereira 2000, 2003*a, b*; Bentos-Pereira and Listre 2005). Liana (1980) presented a tree showing the relationships between her three subfamilies, although her hypothesis has never been tested phylogenetically. In addition, she did not include *Bazylukia* in her analysis, although she did discuss the problem of placing the genus. *Eoproscopia* almost certainly represents the stem-group to modern Proscopiidae, but the relationships between

TEXT-FIG. 4. Variation in head and fastigial morphology in extant Proscopiidae. A, head of female *Bazylukia sabanillensis* Liana (subfam. indet.); $\times 10$. B, head of female *Hybusa occidentalis* Westwood (Hybusinae); $\times 6$. C, head of female *Astroma plicatum* Liana (Xeniinae); $\times 8$. D, head of female *Cephalocoema multispinosa* Brunner (Proscopiinae); $\times 5$. E, head of male *Nodutus asymmetricus* (Mello-Leitão) (Proscopiinae); $\times 5$. F, apex of head, female *N. asymmetricus*; $\times 5$. Modified from Liana (1972, 1980).



Eoproscopia, *Bazylukia* and the more derived crown-group proscopiids remain enigmatic. A comprehensive phylogenetic analysis with character polarities based on outgroup comparison is required in order to resolve this problem. Moreover, the phylogenetic position of the family itself is still somewhat uncertain. Most workers support a relationship with Eumastacidae based on similarities of the male genitalia and other aspects of internal anatomy including details of the proventricular lining and structure of the gastric caeca (Bentos-Pereira and Lorier 1995). However, the molecular phylogenetic studies of Rowell and Flook (1998) and Flook *et al.* (1999) have failed to support a monophyletic Eumastacoidea, and it is possible that Eumastacidae are paraphyletic with respect to Proscopiidae. A sister group relationship between Proscopiidae and Morabinae (Eumastacidae) has been suggested by Blackith and Blackith (1968) and was supported recently by Baum *et al.* (2007) based on the similarly elongated head capsules of these two groups. However, such a relationship is unlikely given the plesiomorphic morphology of the head capsule in *Eoproscopia*. Again, a rigorous phylogenetic analysis of eumastacoid taxa is needed to resolve the relationships of these groups.

The discovery of stem-group Proscopiidae in the Crato Formation confirms the presence of the family in the Atlantic rift zone of South America during the Early Cretaceous. Presumably, they would have been able to move freely across Gondwana between what are now the African and American continents. Why then are modern proscopiids restricted entirely to the Neotropical region? Proscopiidae are generalist phytophages that occupy a broad spectrum of biotopes and feed on a variety of host angiosperms, and should have been able to disperse easily across the tropical belt of northern Gondwana. It is likely then, that proscopiids were widely distributed across northern Gondwana during the Cretaceous but became extinct in Africa following the break-up of the southern continents. The present distribution of Proscopiidae in Central and South America reflects their radiation in these regions following the isolation of South America during the Late Cretaceous. In the Cenozoic, the rise of the Andes, the closing of the Panamanian Isthmus and the development of temporarily isolated forest refugia during periods of glaciation almost certainly influenced the dispersal and speciation patterns of Proscopiidae, as for the entire Neotropical biota (Haffer 1967; Vanzolini and Williams 1970; Vuilleumier 1971; Carbonell 1978; Amedegnato 1993; Cox and Moore 2005).

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