THE SECOND CRETACEOUS SCORPION SPECIMEN FROM BURMESE AMBER (ARACHNIDA: SCORPIONES)

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SYNOPSIS A new specimen of *Palaeoburmesebuthus grimaldii* Lourenço, 2002, recently described from Cretaceous (Albian) Burmite, is reported. This is more complete than the holotype consisting of five scattered, unequal parts: a complete metasoma with an attached partial mesosoma bearing a visible stigma, a right pedipalp chela and three leg fragments. Comparisons to extinct and extant lineages of scorpions are made, although the partially observable trichobothrial pattern of the pedipalp chela precludes definitive family placement. The relative position of the fragments and the severe damage they have suffered imply that it was dismembered by a predator and provides the oldest evidence of scorpions being preyed upon by other animals.

KEY WORDS *Palaeoburmesebuthus*, scorpion, fossil, Cretaceous, metasoma, mesosoma, chela, trichobothria

INTRODUCTION

One scorpion fragment, the metasoma of a juvenile, was recently described from Cretaceous Burmese amber as *Palaeoburmesebuthus grimaldii* Lourenço, 2002; its type is deposited at the American Museum of Natural History (AMNH), New York. This taxon was not assigned to any family. We report the second Burmite scorpion, which appears to be a conspecific but older instar of *P. grimaldii*. This piece contains the only scorpion fossil among 1198 fossil specimens listed by Rasnitsyn & Ross (2000) from Burmese amber deposited in the collection of the Natural History Museum (NHM), London, UK. The scorpion inclusion consists of five scattered fragments: a complete metasoma with partial mesosoma; a pedipalp chela; and three leg fragments. Other arthropods, such as a cecidomyiid fly, a spider, two beetle larvae, an ichneumonid wasp, the abdomen of an orthopteroid insect, an aphid and part of an arthropod leg, are also present in the piece. The teardrop-shaped, dark yellowish brown amber piece (dimensions: 57 mm maximum length, 21 mm maximum width perpendicular to the maximum length, 16 mm maximum depth perpendicular to maximum length and maximum width; weight: 9.27 g) harbours the scorpion parts close to its surface (Fig. 1).

METHODS

Photography was performed using a dissecting microscope (Leica M420 with an apozoom 1:6 lens to which an additional 2 × objective extension was attached), equipped with a video digital camera (JVC KY-F70BU) and a 'cold' light source. The specimen was imaged while keeping the surface closest to the scorpion covered by a drop of glycerine under a cover slip. Further cutting and polishing was avoided as this unique piece appears fairly fragile. Photography was performed by electronically integrating images taken at slightly different focal planes using Auto-Montage (Synchroscopy, Frederick, MA, USA).

Nomenclature and morphological measurements follow the recommendations of Sissom *et al.* (1990). In the following description, left/right orientation is based on a dorsal view. In general, trichobothrial cup-like areolae (pits) are not visible (see exceptions stated in Description, under Pedipalps), only lateral views of trichobothrial setae are present. Consequently, we only considered setae that are long and evenly thin as possible trichobothria, ignoring other shorter setae.

Features of the AMNH holotype (metasoma) were extracted from Lourenço (2002) as neither the type nor additional specimens were available for study.
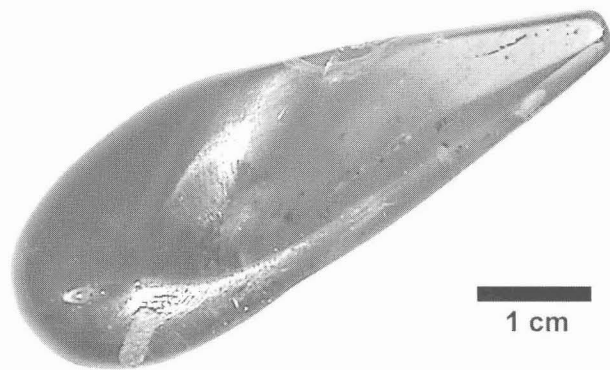
Figure 1   Overall view of amber piece containing *Palaeoburmesebuthus grimaldii* Lourenço: NHM ln. 20174.

SYSTEMATIC DESCRIPTION

Order **SCORPIONES** C. L. Koch, 1850
Superfamily: Incertae Sedis
Family: Incertae Sedis
Genus ***PALAEOBURMESEBUTHUS*** Lourenço, 2002

Palaeoburmesebuthus grimaldii Lourenço, 2002
(Fig. 2; see Pl. 4, figs 6–12)

1998 unidentified scorpion; Ross: 36, fig. 100.
2000 unidentified scorpion; Ross & York: 14.
2000 unidentified scorpion; Rasnitsyn & Ross: 24.
2002 unidentified scorpion; Grimaldi *et al.*: 10, 27–28, fig. 19b.
2002 *Palaeoburmesebuthus grimaldii* Lourenço: 97–101, figs 1–4.

DIAGNOSIS. A possible member of the Archaeobuthidae based on its trichobothrial pattern. A detailed comparison of *P. grimaldii* with the Archaeobuthidae and fossil genera of the Buthidae is provided in the section 'Comparison with other fossils' and in the Discussion, below.

HOLOTYPE. AMNH Bu-710 in Burmese amber; Tanai Village (on Ledo Rd. 105 km north-west of Myitkyna), Hukawng Valley, Kachin, Myanmar (Burma), coll. Leeward Capitol Corp., 2000.

ADDITIONAL MATERIAL. NHM In. 20174, in Burmese amber (specimen described herein); same locality as holotype.

RANGE. Various estimates of the age of Burmese amber have been proposed. Zherikhin & Ross (2000) and Grimaldi *et al.* (2002) considered the age to be probably Turonian-Cenomanian, (90–100 million years ago (Mya)) while Lourenço (2002: 97) gives the age as ±90 Mya. We follow the most recent age estimates for Burmese amber deposits (Cruickshank & Ko 2003), which date these materials as being from the Lower Cretaceous (Upper Albian), based on ammonites and palynomorphs for one amber locality. Although the exact localities that the NHM specimens came from are not known, it can be assumed that they are probably of this age (A. Ross, pers. comm., July 2003). The approximate duration of the Albian is 112.2–98.9 Mya (Gradstein *et al.* 1995; Harland *et al.* 1990; Poling 1997).

OTHER REFRENCES TO BURMESE AMBER SCORPIONS. A 'dorsal sclerite of the telson' (metasoma?) (AMNH Bu215c) mentioned by Grimaldi *et al.* (2002: 10); apparently, it was not studied by Lourenço (2002).

DESCRIPTION

General appearance. Amber inclusion containing five detached fragments of a single scorpion: metasoma with three mesosomal segments (one of them complete); right pedipalp chela to which the distal portion of the right patella is attached; and three leg fragments. Carapace, most of mesosoma and most of appendages are absent.

Basic colour. Pale yellow, with no patterning.

Carapace, chelicerae, sternum, pectines, genital operculum. Unknown.

Mesosoma (see Pl. 4, fig. 7). Tergites: present but not visible due to positioning of the specimen. Sternites. Sternites III (small portion), IV (4/5 posterior-left portion) and V (complete) are visible. Sternite III: two setae and one stigma (= spiracle) are visible on this small portion. Sternite IV: two circular stigmata are visible on this segment; three setae are situated on anterior edge. Sternite V: two pairs of delicately crenulate carinae are present, the left pair clearly visible; two small setae visible on posterior aspect of outer carinae; lateral edges equipped with small serrations.

Metasoma (see Pl. 4, figs 6, 8 & 9). Seen in dorsal and right lateral views. Segments I–IV. Carinae: dorsal pair on I–IV, delicate crenulation visible on segments I–II; dorsolateral pair on I–II (right aspect better seen than left on III–IV); delicate crenulation on segments I–II; lateral carina on I (right aspect only); inferior lateral of segments I–II (right aspect only); inferior median on segments II (right aspect only). Setation: two lateral pairs (one pair per side) on segment IV; three ventral pairs on II–IV (only two visible on III but placement implies three pairs). Segment V. Carinae: one dorsolateral pair; one inferior lateral (right aspect only); one inferior median. Setation: five pairs of lateral setae (one seta per side) visible; five pairs of conspicuously long (as depth of metasoma V) and thick ventrals emanating from somewhat protruding tubercles. Metasoma V ventral aspect not visible but lateral view of segment V implies that inferior median carina is singular because setal pairs are closely set, presumably straddling a single carina. Similarly, inferior median carinal pairs assumed to be present on segments I–IV (although only visible on segment II). In summary, ten carinae are found on segment I, eight on segments II–IV and five on segment V.

Telson (see Pl. 4, figs 8 & 9). Extremely elongated, relatively flat, lacking a subacular tooth; aculeus as long or longer than vesicle; vesicle–aculeus juncture not distinct, base of aculeus relatively thick, slightly thinner than vesicle at that point. Carinae: vesicle equipped dorsolaterally with two carinal pairs. Setation: two long setae at aculeus–vesicle juncture; four setae at midpoint of vesicle; two or three setae on base of vesicle.

Pedipalps (Fig. 2; see Pl. 4, fig. 10). Right chela and extreme distal aspect of its attached patella are present. For the chela,
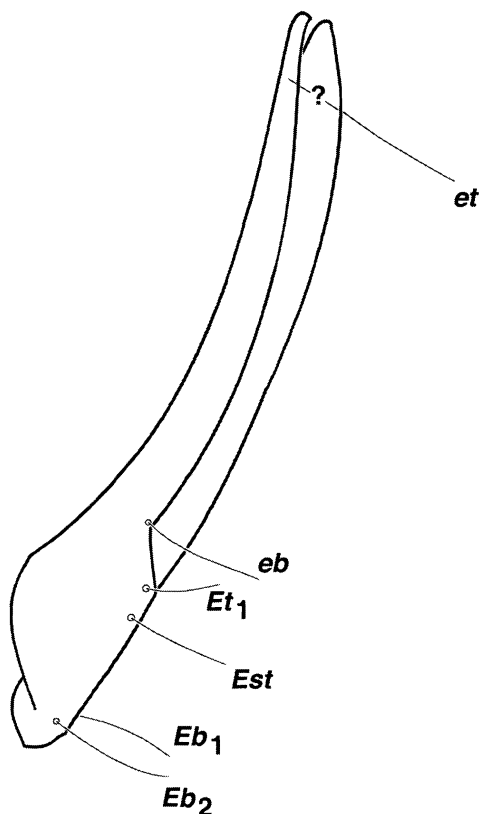
Figure 2 *Palaeoburmesebuthus grimaldii* Lourenço: NHM In. 20174. Diagrammatic outline of dorso-external view of right pedipalp chela showing hypothesised trichobothria (partial) for *P. grimaldii*. Trichobothrial abbreviations on chela manus: *Eb*, external basal; *Est*, external subterminal; *Et*, external terminal. Trichobothrial abbreviations on fixed finger: *eb*, external basal; *et*, external terminal.

dorso-external and ventro-external views are available. Chela very slender with short palm; fingers long and thin, distal denticles forming subtle hooks as typical of Recent scorpions with slender fingers; except for distal denticles, finger dentition not visible. Carinal structures of chelal palm not visible; internal aspect conspicuously protrudes forming a somewhat wide palm at that point. Trichobothria (Fig. 2). Only six external trichobothria are visible under stated criteria (see Methods, above): two basal trichobothria located on external aspect of palm, tentatively identified as Eb_1 and Eb_2; one trichobothrium on external distal half aspect of palm with areola, tentatively identified as *Est*; one trichobothrium on extreme distal aspect of palm with areola is tentatively designated as Et_1; one trichobothrium on base of fixed finger with areola, tentatively identified as *eb*; and one long seta on distal aspect of fixed finger, pointing in an external direction, tentatively identified as *et*. Shorter setae present may represent additional trichobothria but are excluded here from consideration based on the criteria stated in Methods, above. Other setation. There is a distinct seta protruding from the extreme internal aspect of the palm; numerous short setae are evident on the extreme finger tips; additional various sized setae are found on exterior aspect of movable finger.

Legs (see Pl. 4, figs 11 & 12). Three leg fragments are present. Fragment 1 (see Pl. 4, fig. 12): a terminal leg portion which

includes the epitarsus, unguicular spine, tarsus (= telotarsus), two pedal spurs, and a partial protarsus (= basitarsus); epitarsus (the ungues), long and thin, splayed in position with possible evidence of an unguicular spine at their base; tarsus exhibits two delicate rows of ventral spinules (areolae were not visible so we are assuming here that these are spinules, not setae); two pedal spurs are evident between tarsus and partial protarsus. Leg pair designation of Fragment 1 is unknown. Fragment 2 (see Pl. 4, fig 11): a leg portion which includes a tibia, possible tibial spur (arrow), and a partial patella; the tibia is somewhat short and thick, well developed tibial spur protrudes from tibial distal edge; patella portion is quite rounded (as all patellae seen in Recent scorpions). We conclude that Fragment 2 is either from legs III or IV since tibial spurs are only known from these two leg pairs, leg III is our best guess due to thickness and stockiness of tibia (i.e. leg IV usually much longer and thinner than leg III). Fragment 3 (unfigured): Found disjointed from the Fragment 2 patella–tibia leg portion, appears to be a partial femur and connecting trochanter. The trochanter is quite robust. Fragment 3 could belong to the same leg as Fragment 2.

MEASUREMENTS (in mm):

Metasoma and telson. Segment I: length/width/depth (L/W/D) = 1.55/1.08/0.73; segment II: L/W/D = 1.55/1.13/0.68; segment III: L/W/D = 1.75/0.85/0.83; segment IV: L/W/D = 2.00/0.75/0.73; segment V: L/W/D = 2.85/0.73/0.75; telson length = 2.83; vesicle depth = 0.63.

Pedipalp. Movable finger length = 2.05; chela palm length = 0.85.

REMARKS

Comparison with the holotype. The NHM specimen described here is consistent with the description provided by Lourenço (2002) for the holotype of *P. grimaldii*, both having the very distinctive telson with its elongated aculeus and flat vesicle, lacking a subaculear tooth.

Because only the telson and metasomal segments III–V are known in the holotype, the discovery of a second specimen of *P. grimaldii* is noteworthy since it provides additional information on the entire metasoma with the telson, metasomal sternites IV–V with a stigma, three leg segment portions representing, in part, all tarsal segments, tibia, a tibial spur, patella, femur and trochanter, and a complete pedipalp chela, exhibiting six trichobothria. In addition, the exceptional setation of the metasoma and telson, which is fully visible on the NHM fossil, is obscured in the illustrations given of the holotype by Lourenço (2002).

Lourenço's measurements (2002: 100) of the same structures in the holotype as listed above are as follows (in mm): segments I–II: not available due to positioning; segment III: L/W/D = 1.000/0.452/0.435; segment IV: L/W/D = 1.161/0.420/0.420; segment V: L/W/D = 1.774/0.387/0.322; telson length = 1.450; vesicle depth = 0.258. These show that the holotype of *P. grimaldii* is considerably smaller than the NHM specimen (segment V length in holotype = 1.77 mm, in the NMH specimen = 2.85 mm). This indicates that the NHM specimen represents an older instar, possibly an adult.

Evidence of predation. The relative position and preservation of the inclusion parts, containing severe organismic damage

(Labandeira 2002), including a ragged edge on the mesosoma (see Pl.4, fig.7), suggest that the scorpion was dismembered by a predator, which is the oldest (and first) evidence of scorpions being prey to other animals. While there are no studies addressing remnants of extant scorpions, it is anecdotally known that many invertebrate and vertebrate predators readily consume scorpions (Polis *et al.* 1981). In fact, scorpions themselves are often the most important predator group, being highly cannibalistic (McCormick & Polis, 1990).

COMPARISON WITH OTHER FOSSIL SCORPIONS

Archaeobuthus estephani Lourenço, 2001 (Archaeobuthidae).

Lourenço (2001) described a new genus and family from the Lebanese amber of Early Cretaceous [Barremian – Aptian (127–112.2Mya)]. This is the oldest known Cretaceous scorpion. Significantly, the complete trichobothrial patterns were visible on this specimen. The detailed comparison between *A. estephani* and *P. grimaldii* is as follows.

Chela fingers: exaggerated 'knife-like' spines (or denticles?) on distal two-thirds of finger in *Archaeobuthus*. Dentition in the NHM specimen of *P. grimaldii* is not visible. However, due to the large size of its chela, one would assume that, if 'knife-like' spines were present as illustrated for *Archaeobuthus*, they also would be visible in the NHM specimen of *P. grimaldii*).

Chela finger/palm proportions: both species have slender fingers, but much more so in the NHM specimen of *P. grimaldii*.

Trichobothria of chela: *Archaeobuthus* has 11 trichobothria, six of which match those identified for the NHM specimen of *P. grimaldii*. Also, trichobothria Eb_3 and i are absent on *Archaeobuthus*, which presumably is also the case for the NHM specimen of *P. grimaldii*.

Legs: No tibial spur reported for *Archaeobuthus*, whereas it is present on the NHM specimen of *P. grimaldii*. Note that the English translation of the legend for figure 9 in Lourenço (2001) incorrectly identifies pedal spur ('l'éperon tarsal' in French) as a 'tibial spur'.

Mesosoma: All tergites are present; sternites reported with small, 'almost round' stigmata, four crenulate carinae are illustrated for sternite V. The NHM specimen of *P. grimaldii* exhibits the same structure of stigmata and sternite V.

Metasomal segments: Segment I: ten carinae; segments II-V and telson missing in *Archaeobuthus*. The NHM specimen of *P. grimaldii* exhibits the same structure of segment I.

In general, the NHM specimen of *P. grimaldii* is consistent with *Archaeobuthus*. If we hypothesise that chelal trichobothria Eb_3 and i are absent in *P. grimaldii*, then we can conclude a close relationship between *Palaeoburmesebuthus* and *Archaeobuthus*. The only primary character in which they disagree is the presence of a tibial spur on the NHM specimen of *P. grimaldii*. However, this would, at most, be a genus-level difference (see inconsistency in the same structure for the five 'palaeo-buthids' discussed below).

'Palaeo-buthids' (*five genera, Buthidae*). The five extinct 'palaeo-buthid' genera described by Lourenço & Weitschat

(1996, 2000, 2001) were all discovered in Baltic amber in a deposit dated to the Eocene (55 Mya), although the amber itself may be 5–10 million years older. All other known amber Buthidae belong to the extant genera *Tityus, Microtityus* and *Centruroides* (Schawaller 1979, 1981, 1984; Santiago-Blay & Poinar 1988, 1993; Santiago-Blay 1990; Santiago-Blay *et al.* 1990; Fet *et al.* 2000), and were found in Dominican and Mexican amber of Oligocene to Miocene age (26–15 Mya). A brief description of each is given below.

Palaeolychas balticus Lourenço & Weitschat, 1996. Trichobothria of chela: with eight trichobothria but hypothesised to have all 15 Type A trichobothria. Trichobothrium Eb_3, which is reported for this species, is presumably missing in the NHM specimen of *P. grimaldii*. Legs with tibial spurs; short small stigmata present; 10 carinae on metasomal segment I, consistent with the NHM specimen of *P. grimaldii*. Telson with a strong subacular tooth, which is absent in the NHM specimen of *P. grimaldii*.

Palaeotityobuthus longiaculeus Lourenço & Weitschat, 2000. Trichobothria of chela: with five trichobothria but hypothesised to have all 15 Type A trichobothria. Note that trichobothrium i, which is reported for *Palaeotityobuthus*, is presumably absent in the NHM specimen of *P. grimaldii*. Legs lacking tibial spurs; long slit-like stigmata; 10 carinae reported on metasomal segments I–II, eight on segments III–IV, and five on V. The NHM specimen of *P. grimaldii* has 10 carinae on segment I, eight on segments II–IV and five on V. Telson with a strong subacular tooth.

Palaeoprotobuthus pusillus Lourenço & Weitschat, 2000. Trichobothria of chela: with only two trichobothria (i.e. V_1 and V_2) but hypothesised to have all 15 Type A trichobothria. Legs lacking tibial spurs; small oval to almost rounded stigmata; metasomal segment I with 10 carinae, segments II–III with eight, others unknown; telson unknown.

Palaeoakentrobuthus knodeli Lourenço & Weitschat, 2000. Trichobothria of chela: no trichobothria are visible but hypothesised to have all 15 Type A trichobothria. Legs with tibial spurs; small oval to slit-like stigmata; metasomal segment I with 10 carinae, segments II–IV with eight carinae and segment V with five. Telson with a strong subacular tooth.

Palaeoananteris ribnitiodamgartensis Lourenço & Weitschat, 2001. Trichobothria of chela: with five trichobothria, including Eb_3, but hypothesised to have all 15 Type A trichobothria. Legs with tibial spurs; small oval to almost round stigmata; metasomal segments I–II with 10 carinae, segments III–IV with eight carinae and segment V with five. Telson with a subacular tubercle.

By creating a composite depiction of these five genera from Baltic amber we can deduce that they are most probably members of Buthidae, as suggested by Lourenço & Weitschat (1996, 2000, 2001). With respect to trichobothria, 31 of them are accounted for out of the 39 defined for Type A scorpions. Of these 31 trichobothria, 18 are confirmed for at least two genera (see Soleglad & Fet 2001: table 2; Lourenço & Weitschat 2001). Three out of five of these genera are found with tibial spurs and four are equipped with a subacular tooth (for one genus the telson is unknown), characters typically associated with buthids.

DISCUSSION

Kjellesvig-Waering (1986), in his comprehensive review of fossil scorpions, did not list any Cretaceous taxa. Since then, four Cretaceous scorpion genera have been described: non-amber *Araripescorpius* Campos, 1986 (family placement unclear) and *Protoischnurus* Carvalho & Lourenço, 2001 (Protoischnuridae) (both from the 120–100 Mya Santana Formation of Brazil; Campos 1986; Carvalho & Lourenço 2001; Santiago-Blay *et al.* 2001), *Archaeobuthus* Lourenço, 2001 (Lebanese amber, 135–130 Mya; Lourenço 2001) (Archaeobuthidae), and *Palaeoburmesebuthus* Lourenço, 2002 (Burmese amber, now considered Upper Albian, see above) (family placement unclear). Note that Lourenço (2001, 2002) gives the Lebanese amber age as approximately 130–125 Mya, while it is estimated by Schlee (1990) and Poinar & Milki (2001) as approximately 135–130 Mya (late Valanginian or Hauterivian to Barremian). Therefore, the four Cretaceous scorpion fossil genera span the period from late Valanginian to the late Albian (approximately 135–100 Mya).

We believe that the fundamental orthobothriotaxic trichobothrial patterns discussed and described by Soleglad & Fet (2001) provide the most reliable and basic character set for differentiating major higher-level clades in scorpion systematics. Soleglad & Fet (2001) identified two fossil patterns, one for the Upper Carboniferous Palaeopisthacanthidae, Type P, and one for the Cretaceous Archaeobuthidae. The trichobothrial Type A pattern, identified for the Buthidae, has been established since the Palaeocene to Eocene, based on five genera described by Lourenço & Weitschat (1996, 2000, 2001) from Baltic amber. *Palaeoburmesebuthus*, at approximately 100 Mya, falls midway between the Archaeobuthidae and Buthidae.

It is also important to note that the Lebanese and Burmese amber biotas lay at approximately similar palaeolatitudes (Smith *et al.* 1994): the Lebanese locality had a palaeolatitude of 10–15°N while the Burmese locality was at a palaeolatitude of 12°N, corresponding to a distinct tropical biota (Grimaldi *et al.* 2002). Therefore, the general habitat conditions for *Archaeobuthus* and *Palaeoburmesebuthus* could have been similar.

However, a definite family placement of *Palaeoburmesebuthus* cannot be determined with the minimal chelal trichobothria pattern visible in the NHM specimen of *P. grimaldii*. In addition, we have no data on the trichobothria of the patella or femur, which are also important in establishing family affinities. The six chelal trichobothria hypothesized for this specimen are consistent with both Archaeobuthidae and Buthidae, and, in fact, also for all other trichobothria-bearing scorpions – from the palaeopisthacanthids to all Recent scorpions. What is crucial in this new fossil specimen are the trichobothria that appear to be absent. If trichobothria Eb_3 and i are indeed missing on *P. grimaldii* (there is no trace of them on the NHM specimen), then it is clearly not a member of Buthidae, but shows a much closer affinity to Archaeobuthidae. For trichobothrial Type A scorpions (Buthidae), Eb_3 is either petite or rarely may be missing in some genera (i.e. *Karasbergia* and *Microbuthus*). Eb_3, hypothesised as a trichobothrium in the process of evolving, is proving to be a pivotal trichobothrium in the higher systematics of scorpions (Soleglad & Fet 2001: 34): it is absent in the palaeopisthacanthids, the archaeobuthids, and also in the 'relict' Recent scorpion from Central Asia, *Pseudochactas ovchinnikovi* Gromov, 1998 (Pseudochactidae, trichobothrial Type D). Evidently, Eb_3 is also missing in *Palaeoburmesebuthus*.

Palaeoburmesebuthus is equipped with a tibial spur, which is absent in *Archaeobuthus*. Jeram (1994, text-fig. 5D) illustrated a tibial spur for the palaeopisthacanthid *Compsoscorpius elegans* Petrunkevitch. Tibial spurs in 'palaeobuthids' are present on three out of five genera. Both *Archaeobuthus* and *Palaeoburmesebuthus* have circular stigmata, which are also reported for the palaeopisthacanthid *C. elegans* (Jeram, 1994), and for the 'palaeo-buthids', the stigmata are variable in size, from near oval to long slit-like. The circular stigmata associate *Palaeoburmesebuthus* with the Archaeobuthidae.

Although we cannot assign *Palaeoburmesebuthus* to a family, we suspect it is a member of Archaeobuthidae based on the observed chelal trichobothria pattern and circular stigmata. If this is correct, then the geological occurrence of the Archaeobuthidae will be expanded from 135–130 to *ca.* 100 Mya. This is consistent with the observation by Soleglad & Fet (2001) that time-line range 125–110 Mya may have witnessed significant trichobothria derivation.

Lourenço (2001, 2002) placed Archaeobuthidae in the superfamily Buthoidea. This statement, however, has not been confirmed by a cladistic analysis of scorpion orthobothriotaxy (Soleglad & Fet 2001), where the archaeobuthids are shown to be the plesiomorphic sister group to all Recent scorpions and thus with no close affinity to the Buthidae. Lourenço's (2002) statement that *Palaeoburmesebuthus* is undoubtedly a 'member of the Buthoidea' is also incorrect if it proves to be a member of Archaeobuthidae, which the preliminary data seem to imply. Lourenço (2002: 100) states that '. . . shape of the metasomal segments and telson, structure of carinae, and especially the presence of a simple anal arch with one lateral lobe – the specimen is unquestionably a member of the Buthoidea'. However, none of these characters are germane to superfamily (or family) placement. Soleglad & Fet (2003: 118–119), defining four parvorders and six superfamilies within the scorpion infraorder Orthosterni, listed both the genus *Palaeoburmesebuthus* and the family Archaeobuthidae under 'Parvorder incertae sedis' and did not assign these taxa to any superfamily.

Analysis of described Cretaceous scorpions is crucial for our understanding of the evolution of scorpions, an 'essentially fossil group' (Kjellesvig-Waering 1986). We know that several major scorpion clades survived the end-Cretaceous extinction. Dating the common ancestor of various lineages of modern scorpions is a challenging task, and fossils such as *Palaeoburmesebuthus* will add to this understanding.

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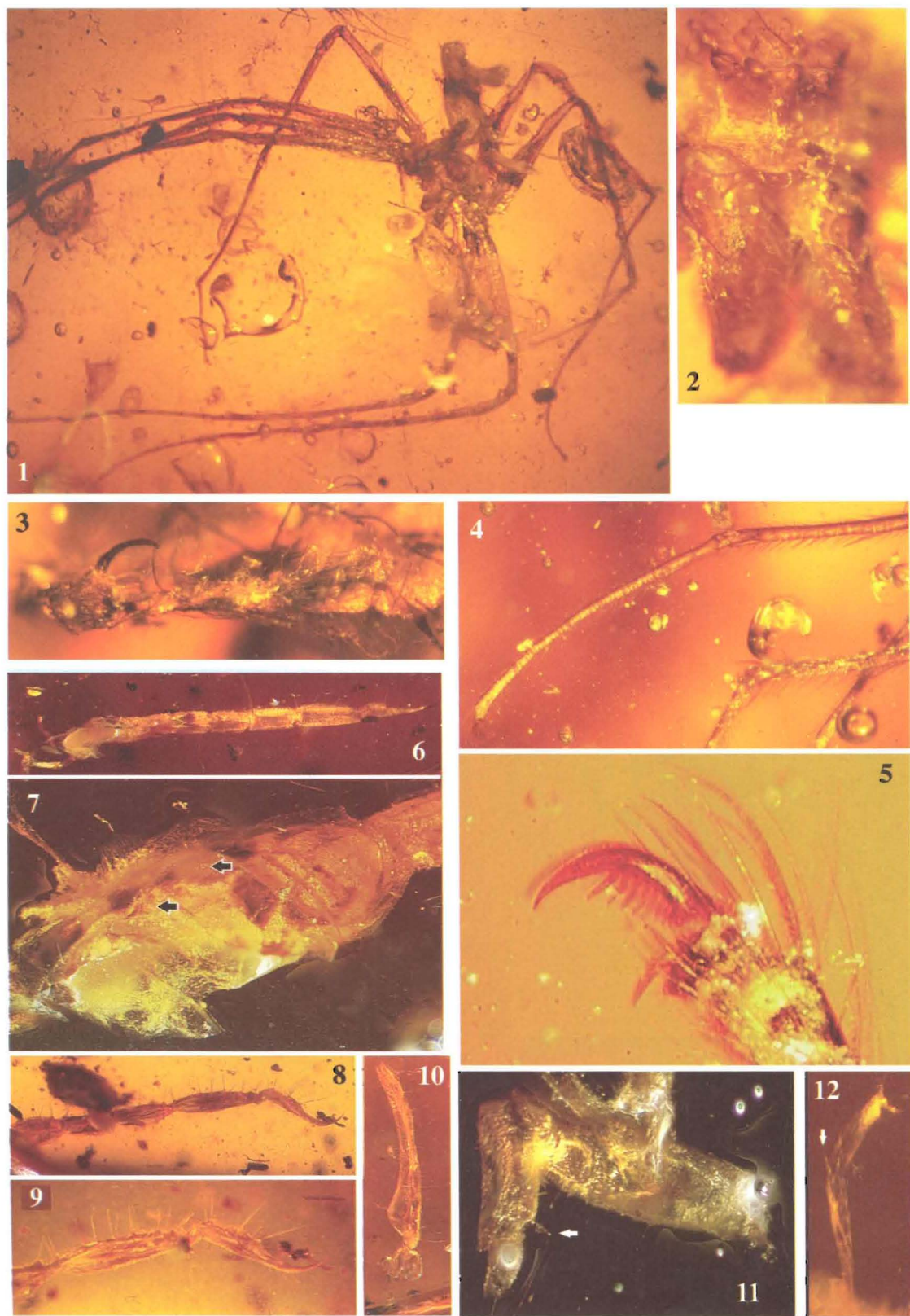
Plate 4 **Figs 1–5.** *Palaeohygropoda myanmarensis* gen. et sp. nov., Penney. Holotype BMNH In. 19132(1). (Araneae: Pisauridae). **1.** Dorsal view, whole specimen. **2.** Anterior view, showing eyes, clypeus and chelicerae. **3.** Pedipalp, showing diagnostic prolateral patellar clasping spur. **4.** Metatarsus and tarsus showing curvature and apparent pseudosegmentation. **5.** Superior and inferior tarsal claws. **Figs 6–12.** *Palaeoburmesebuthus grimaldii* Lourenço. BMNH In. 20174. (Scorpiones: incertae sedis). **6.** Metasoma and telson. **7.** Ventral aspect of mesosoma, showing sternite V, two pairs of carinae, sternite IV (almost complete) with two stigmata, and sternite III (in part) with one stigma. All stigmata are pointed to by arrows. **8.** Metasoma and telson, right lateral aspect. **9.** An enlargement of metasoma IV (distal end), metasoma V and the telson. **10.** Right pedipalp chela, with visible trichobothria, dorsoexternal aspect. **11.** Leg fragment, showing tibia with a possible tibial spur (arrow), and patella (partial and angled in view). **12.** Leg showing epitarsus, tarsus with two delicate rows of ventral spinules, pedal spur (arrow) and protarsus (partial). All from Lower Cretaceous (Albian) Burmese amber of Myanmar. For measurements see the text. Photographs of Figs 1–5 by D. Penney, photographs of Figs 6–12 by J. Santiago-Blay and P. Craig.
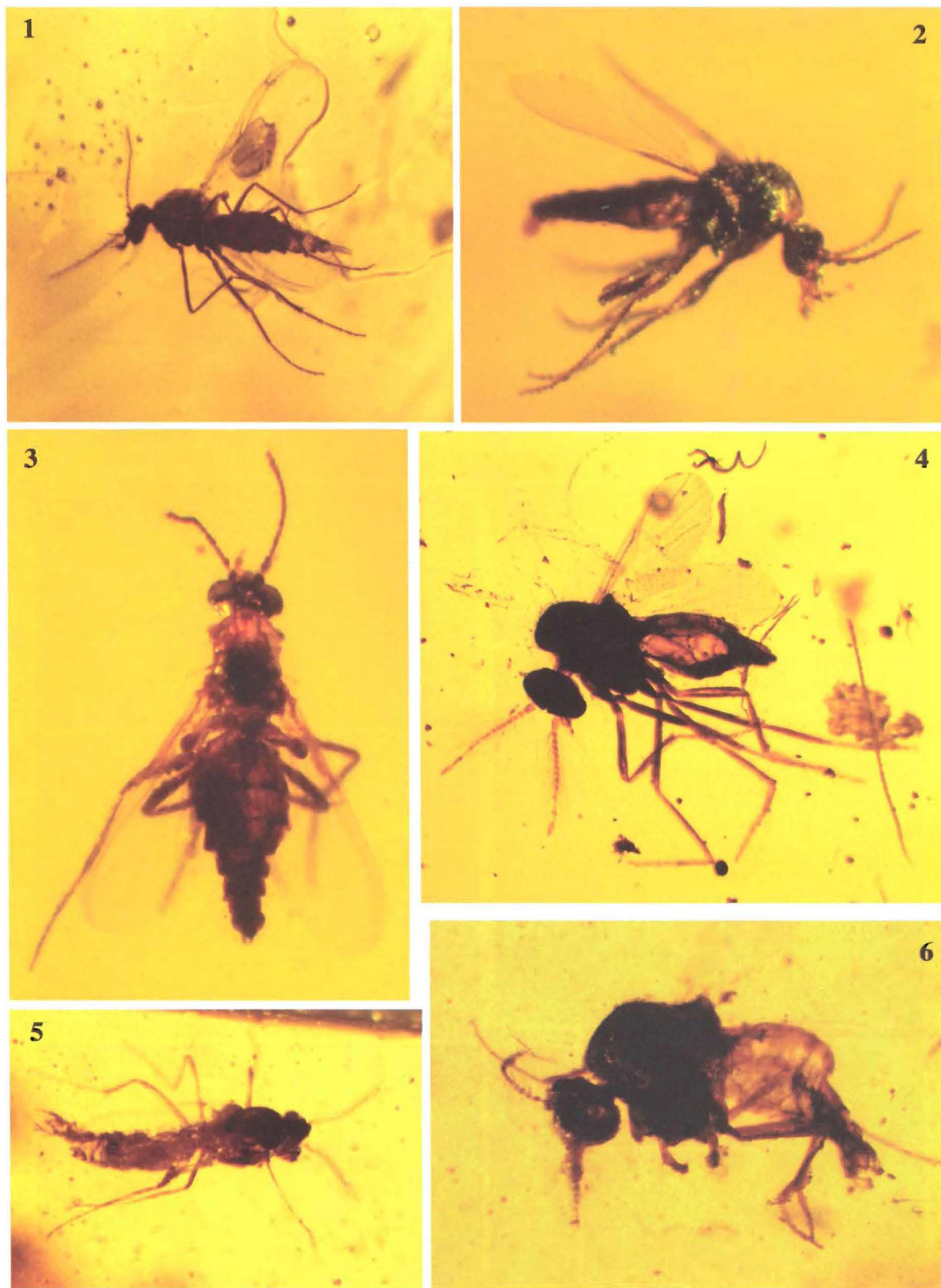
Plate 3   Fig. 1. *Leptoconops myanmaricus* sp. nov., Szadziewski. Holotype, BMNH In. 20168(6). (Diptera: Ceratopogonidae). **Figs 2–3.** *Leptoconops burmiticus* sp. nov., Szadziewski. Holotype, BMNH In. 20700. (Diptera: Ceratopogonidae). **2.** Lateral view. **3.** Dorsal view. **Fig. 4.** *Atriculicoides swinhoei* (Cockerell, 1919). Holotype BMNH In. 19133. (Diptera: Ceratopogonidae). **Fig. 5.** *Leptoconops rossi* sp. nov., Szadziewski. Holotype, BMNH In. 20173(1). (Diptera: Ceratopogonidae). **Fig. 6.** *Austroconops asiaticus* sp. nov., Szadziewski. Holotype, BMNH In. 20173(4). (Diptera: Ceratopogonidae). All from the Lower Cretaceous (Albian) Burmese amber of Myanmar. For measurements see the text. Photographs by P. York.