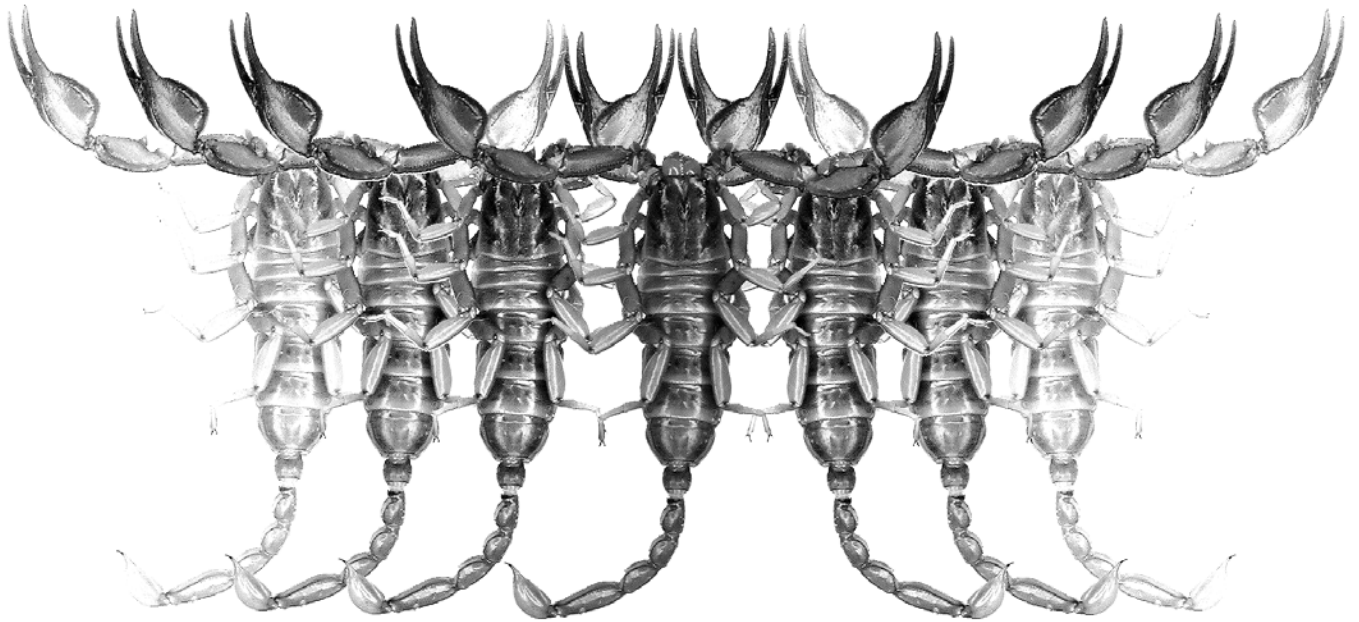# *Euscorpius*

Occasional Publications in Scorpiology

The Cretaceous Scorpion Genus, *Archaeobuthus,* Revisited
(Scorpiones: Archaeobuthidae)

Chris Baptista, Jorge A. Santiago-Blay, Michael E. Soleglad and Victor Fet

February 2006 — No. 35

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located on Website '**http://www.science.marshall.edu/fet/euscorpius/**' at Marshall University, Huntington, WV 25755-2510, USA.

The Cretaceous scorpion genus, *Archaeobuthus,* revisited (Scorpiones: Archaeobuthidae)

Chris Baptista [1], Jorge A. Santiago-Blay [2], Michael E. Soleglad [3] and Victor Fet [4]

[1] Arizona Department of Agriculture, State Agricultural Laboratory,
2422 West Holly Street, Phoenix, AZ 85009, USA; chrisb@sal.ah.state.az.us
[2] Department of Paleobiology, MRC-121 National Museum of Natural History, Smithsonian Institution,
P.O. Box 37012 Washington, DC 20013-7012, USA; blayj@si.edu
[3] P.O. Box 250, Borrego Springs, CA 92004, USA; soleglad@la.znet.com
[4] Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510, USA;
fet@marshall.edu

Summary

The monotypic family Archaeobuthidae Lourenço, 2001 is based on *Archaeobuthus* Lourenço, 2001 (type species, *A. estephani* Lourenço, 2001), described from Early Cretaceous amber from Lebanon. *Archaeobuthus estephani* is the oldest scorpion hitherto found in amber. We reanalyzed the unique type specimen of *Archaeobuthus* and clarified the observable trichobothrial pattern of the pedipalp as well as other morphological features. The full observed trichobothrial pattern includes 26 trichobothria: ten on the chela, Eb_1, Eb_2, Est, Et_1, V_1, db, dt, eb, est, and et; seven on the patella, d_1, d_3, i, eb_1, esb_1, est, and et_1; and nine on the femur, d_1, d_2, d_3, d_4, d_5, i_1, i_2, i_3, and e_3. The alignment of femoral trichobothria d_1, d_3, and d_4 is essentially parallel to the dorsoexternal carina; trichobothrium d_2 is located on the dorsal surface. Our analysis shows that *Archaeobuthus* cannot be assigned to any extant parvorder and superfamily of the infraorder Orthosterni. It clearly does not belong to parvorder Buthida (superfamily Buthoidea). This Cretaceous genus, along with two other, more fragmentarily known orthostern fossils (Triassic *Protobuthus* and Cretaceous *Palaeoburmesebuthus*) most likely represents other Mesozoic lineages, which probably did not survive the K-T extinction. These three taxa, therefore, occupy the position outside of four extant orthostern parvorders.

Introduction

While non-orthostern scorpions apparently were already extinct during the Mesozoic (last known from the Jurassic; Kjellesvig-Waering, 1986), several modern lineages of the scorpion infraorder Orthosterni survived the K-T extinction. Among the Cretaceous scorpion fossils, the oldest is the genus *Archaeobuthus*, described from Lebanese amber, ca. 135–120 Ma (Lourenço, 2001) and placed in an extinct monotypic family Archaeobuthidae. Although a few other existing Mesozoic orthosterns have been placed in modern taxonomic groups (parvorders; see Soleglad & Fet, 2003), *Archaeobuthus* has received two conflicting taxonomic placements: it has been either assigned to the superfamily Buthoidea (Lourenço, 2001, 2002, 2003; Lourenço & Gall, 2004) or to the parvorder *incertae sedis* (Soleglad & Fet, 2003). In this paper, we reanalyze the unique type specimen of this fossil. We find no synapomorphies justifying the placement of *Archaeobuthus* in any of the extant lineages (parvorders or superfami-

lies) of orthostern scorpions (see Soleglad & Fet, 2003, for the detailed survey of high-level systematics and phylogeny of the extant Orthosterni). Also, we reinterpret the position of *Archaeobuthus* in the context of scorpion phylogeny.

Paleobiological remarks

We follow the geological time scale of Gradstein & Ogg (2004) for nomenclature and age ranges. Fossilized plant resin, or amber, is unique in having exquisitely preserved organisms and some features of their biology as far back as the Early Cretaceous (Labandeira, 1994; Ross, 1999; Rasnitsyn & Quicke, 2002; Langenheim, 2003; Grimaldi & Engel, 2005). Resins are usually solid or semi-solid, complex mixtures of carbon-rich molecules based on the terpene building block, isoprene $[CH_2=CH-C(CH_3)=CH_2]$. They are soluble in many organic solvents (oils, hydrocarbons, alcohols), depending on the resin, and are generally insoluble in water.

Amber's botanical origin is taxonomically diverse. Plant exudates, including resins, gums, gum-resins, latexes, and others, have been found in over 600 genera and 160 vascular plant families (Santiago-Blay et al. 2002; Langenheim, 2003; Lambert et al., 2005; Santiago-Blay, unpublished compilation). However, it appears that only resins have survived deep geologic time, forming amber. Although the botanical source of many ancient resins remains unknown (Zherikhin & Eskov, 1998; Lambert & Poinar, 2002), amber from Lebanon has been attributed to the extinct conifer family Cheirolepidiaceae (Grimaldi et al., 2003).

While the most renowned amber deposits date from the Early Cretaceous and younger, "resin rodlets" were produced by the extinct *Myeloxylon* (Medullosales) as early as the Carboniferous (ca. 300 Ma; Taylor & Taylor, 1993; van Bergen et al., 1995). Other, lesser known, Triassic ambers have been described for Dolomites (northern Italy, Gianolla et al., 1998; Schmidt, pers. comm. to JASB 9 November 2005, fossiliferous) and for the Chinle formation (Colorado Plateau, Arizona and southwestern USA; Ash & Litwin, 1991; Litwin and Ash, 1991; Kay & Ash, 1999). Amber from Schliersee (southern Germany), originally considered to be Late Triassic (Carnian, 230–220 Ma), has been reinterpreted as Cenomanian (99–93 Ma, Schmidt et al., 2001). We cannot exclude the possibility that other pre-Cretaceous amber deposits containing macroscopic inclusions will be found. Amber production is not only ancient, but it is also geographically widespread, ranging from the Canadian Arctic (Anderson & LePage, 1995) to New Zealand (Poinar & Poinar, 1994).

The stratigraphy of Lebanese amber is discussed in Lourenço (2001). According to Grimaldi et al. (2003), "…all Lebanese amber is Lower Cretaceous, except for one outcrop [from Ghine: Upper Jurassic (which is not fossiliferous)] and the ages vary considerably among the Cretaceous outcrops." Early Cretaceous Lebanese amber has been considered Aptian (Grimaldi et al., 2003) to Hauterivan (Roth et al., 1996), ca. 135–120 Ma (Schlee & Dietrich, 1970; Schlee, 1972; Poinar & Milki, 2001), although most localities appear to be close to 120 Ma (Labandeira to JASB, pers. comm., October 2005).

Material and Methods

The piece of amber containing Archaeobuthus

The scorpion (Fig. 1) is preserved in a yellowish-reddish, fragile, fractured, irregularly shaped, and layered amber piece. According to Antoun Estephan, collector and owner of the specimen, the amber containing the scorpion was embedded in a relatively clear block of epoxy, under vacuum, by David Grimaldi (American Museum of Natural History, New York, NY, USA) in late July 2000 (Estephan to JASB, pers. comm., Nov. 8, 2005). Thereafter, Wilson Lourenço (Muséum national d'Histoire naturelle, Paris, France) split the block to better study the specimen for description. Currently, the block weighs 5.42 carats (1.08 g), is slightly irregular, and measures ca. 20 x 12 x 3–4 mm; the actual amber piece is ca. 16–17 x 7–8 x 1–2 mm (Estephan to JASB, Nov. 11, 2005).

The scorpion is generally concolorous, darkened or lightened by "artifacts," as Lourenço (2001) reported, from distortion or deterioration. As Lourenço (2001) indicates, the dorsal aspect of *A. estephani* is clearly visible but its ventral aspect is difficult to observe. In many places the scorpion is covered by a fine foam or froth of bubbles and dirt further complicating measurement. One of the fractures cuts through the right chela close to the base of palm. The ventral aspect of the chelicerae is obstructed by soil-like granular material. The scorpion lacks most of the left pedipalp patella; all left chela, metasomal segments II–V, and telson are missing.

Microscopy

Because the first few images taken of the fossil scorpion appeared sufficiently clear and the time the scorpion was available was limited, we decided to image the specimen without glycerin. An insect pinning stage (Bioquip microscope stage #6188; http:// www.bioquip.com) and a small piece of soft modeling clay was used to hold the block in place while being manipulated under the microscope, much like a pinned insect would have been. High-resolution digital images were obtained by author CB using an 'F'-mounted SPOT RT digital camera (Diagnostic Instruments) on a Nikon SMZ 1500 dissection microscope equipped with a double port image beamsplitter. A fiber optic illuminator (A. G. Heinze Dyna Lite 150 W) with two self-supporting bifurcated fiber optic light cables, each equipped with a focus lens, was used as the primary light source. Additional background lighting was provided by the microscope's diascopic stand. SPOT RT digital imaging software version 3.5 for Windows NT was used for initial image capture and measurements. The images were made available electronically to all authors, who provided quasi-instantaneous feedback to each other, communicating between Phoenix, Arizona (CB); Washington, DC (JASB); Winchester, California (MES); and Sofia, Bulgaria (VF). Selected images were minimally edited for brightness, contrast, color balance, and other factors to reveal additional details. In one case (Fig. 40), images were electronically composed using the extended depth of field (EDF) option in Image-Pro (Media Cybernetics, Inc., Silver Spring, Maryland, USA).
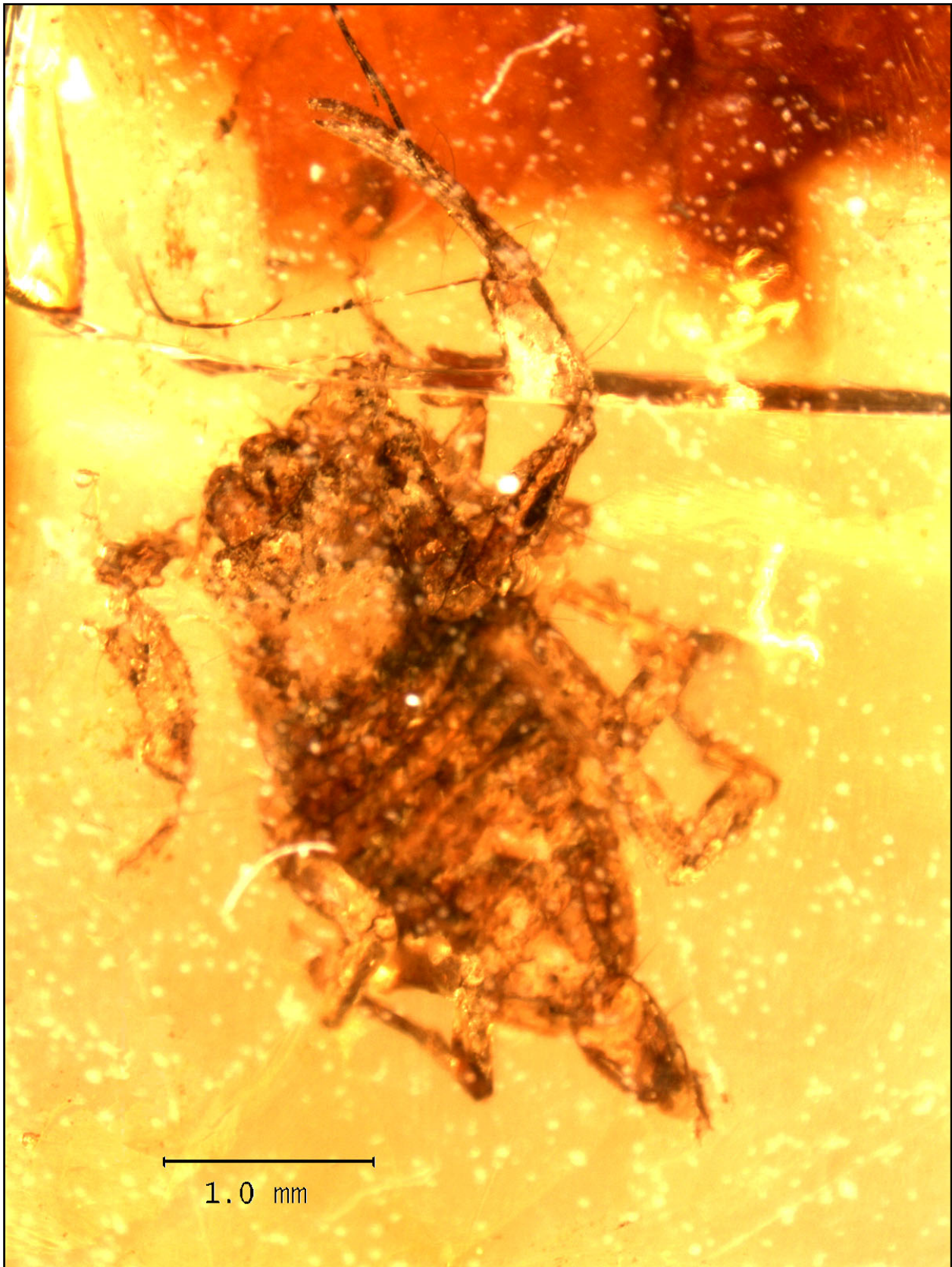
Figure 1: Dorsal view of *Archaeobuthus estephani*.

Nomenclature, mensuration, and illustrations

Nomenclature and mensuration of scorpion anatomical structures follow Sissom et al. (1990) and Soleglad & Fet (2001, 2003). Errors of mensuration caused by the optics of the microscope were corrected by using calibrated standards of magnification and were found to have an average error of only 3.4 %. We removed additional sources of measurement error, such as those caused by the curvature of the amber piece or the impossibility of always placing the structure of interest exactly perpendicular to axis of view. The scale bars that are automatically placed by the imaging system were corrected as needed.

All line drawings of *A. estephani* pedipalp segments and trichobothria (Figs. 2–5) were prepared by MES by carefully tracing over actual photographs (Figs. 6–9). In contrast, illustrations of Lourenço (2001, figs. 10–14) are non-scaled, non-proportional renderings.

Identification of trichobothria and evaluation of their homologies

We were especially interested in verification of trichobothrial homologies and patterns on all three segments of the pedipalp, since this unique character set is crucial for any high-level scorpion systematic study (Soleglad & Fet, 2001, 2003). Identification of a trichobothrium was based primarily on the presence of conspicuous long thin bristles protruding from the various surfaces of the pedipalp. In four cases (chela *dt* and V_1 as well as femur d_2 and d_5), trichobothria were identified only from their areolae. In general, identification based on long thin bristles is more reliable than that based on areola only because the irregular surface of the cuticle embedded in amber has more areola-like structures than in most extant scorpions. However, most trichobothrial areolae identified were clear and well formed. Furthermore, in many cases both the trichobothrial bristle and areola were visible providing further evidence of their identification. Once a bristle (or an areola) was recognized as a trichobothrium, the precise homologies were carefully evaluated by their relative position on images taken from different perspectives of the pedipalp segments, as evidenced by the photographs (Figs. 6–9, 36–47).

Repository

The holotype of *Archaeobuthus estephani* is deposited in a private collection. Although the International Code of Zoological Nomenclature (ICZN, 1999) contains Recommendation 16C on "Preservation and Deposition of Type Specimens," which states "…authors should deposit type specimens in an institution that maintains a research collection," this recommendation is not binding. Being in violation of a Recommendation of the Code does not make a name unpublished or unavailable, which may happen if an author is in violation of an Article. The only mandatory requirement stated by the Article 16.4.2 calls for the statement indicating the name and location of the collection where the type specimen is deposited. Occasionally, paleontologists describe unique type specimens from private collections, as was the case, for example, with another scorpion, *Electrochaerilus buckleyi* (Santiago-Blay et al., 2004a), drosophilids (Grimaldi, 1987), and halictid bees (Engel, 1997), all entombed in amber, as well as some Carboniferous hexapods (Kukalová-Peck, 1987). Mention of these authors does not imply that the practice of describing specimens from private collections is preferred by any of the authors herein listed. Furthermore, mention of these authors does not reflect our views about their professional or personal qualities. Also, the Code (ICZN, 1999) does not in any way regulate the ownership of specimens. Readers interested in examining the specimen may do so by contacting author JASB, who will then forward the request to A. Estephan.

Systematic Description

Order **SCORPIONES** C. L. Koch, 1850
Suborder Neoscorpiones Thorell & Lindström, 1885
Infraorder Orthosterni Pocock, 1911
Parvorder: *incertae sedis*
Superfamily: *incertae sedis*

Family ARCHAEOBUTHIDAE Lourenço, 2001

TYPE GENUS. *Archaeobuthus* Lourenço, 2001
DIAGNOSIS (after Lourenço, 2001, expanded and modified here). Conforms to orthobothriotaxic Type F1 (see Soleglad & Fet, 2001, as modified here, Figs. 2–5): ten trichobothria found on the chela, Eb_1, Eb_2, Est, Et_1, V_1, db, dt, eb, est, and et; seven trichobothria found on the patella, d_1, d_3, i, eb_1, esb_1, est and et_1; nine trichobothria found on the femur, d_1, d_2, d_3, d_4, d_5, i_1, i_2, i_3, and e_3. The alignment of femoral trichobothria d_1, d_3, and d_4 is essentially parallel to the dorsoexternal carina, and trichobothrium d_2 is located on the dorsal surface; leg tibial spurs are absent; ventral distal (*vd*) denticle of cheliceral movable finger extends beyond dorsal distal (*dd*) denticle; stigma small, oval to circular in shape. For additional secondary characters, see the description of *Archaeobuthus estephani* below.

Genus *ARCHAEOBUTHUS* Lourenço, 2001

TYPE SPECIES. *Archaeobuthus estephani* Lourenço, 2001
DIAGNOSIS. As for the family.

Archaeobuthus estephani **Lourenço, 2001**
(Figs. 1–10, 18, 26, 36–54)

DIAGNOSIS. As for the family.
Holotype. Gender and biological age of the specimen unclear.
Repository. Deposited in the private collection of Antoun Estephan (Frankfurt, Germany).
Range. Lebanese amber, 135–120 Ma.

Measurements (in mm). Carapace. Anterior width 1.06? (right lateral edge obscured). Width of carapace at lateral eyes 0.89; median length 0.98. Carapace + mesosoma length 2.82. Chelicerae. Width at the base 0.29. Right pedipalp. Femur length 1.06, width 0.27; patella length 1.21, width 0.37; chela length 2.10, width 0.34; chela palm length 0.82, width 0.34; movable finger length 1.28. Legs. Leg III tarsus length (dorsal 0.34, ventral 0.41), tarsus basal width 0.09. Metasoma I length/width (L/W) 0.53/0.44, 1.2. Total length: extrapolated to about 6.0 (after Lourenço, 2001).

Description. Yellowish brown, with reddish brown patches on pedipalp. Weakly to moderately granular. Anterior margin of carapace with a moderate median concavity. Anterior median superciliary carinae vestigial; other carinae obsolete. All furrows moderate to weak. Median ocular tubercle distinctly anterior to the center of carapace. Median eyes separated by almost twice their diameter**.** With two pairs of lateral eyes, the most distal pair (the third) appears to be missing. Pedipalps: right pedipalp well visible, see below for detailed discussion of trichobothria. Chelicerae: dentition was not fully visible but the ventral distal tine of movable finger is longer than the dorsal distal denticle**.** Sternum not observable. Pecten not available, only a few scattered teeth observable. Without tibial spurs on legs III–IV; with pedal spurs; tarsal armature reduced. Tergites weakly granular. Tergites I to VI with three longitudinal carinae, moderate to strong. Tergite VII pentacarinate. Sternites I–III not clearly visible, IV–VII rather smooth, with median longitudinal punctations; small oval to circular stigma visible on sternites V and VI. Metasomal segments II to V (and telson) missing. Metasomal segment I with 10 carinae; ventral carinae parallel; dorsolateral with spinoid granules.

Trichobothria

In the course of this study we were able to identify 26 trichobothria on various surfaces of the pedipalp. Figures 2–5 illustrate the 26 pedipalpal trichobothria identified in this study. These figures correspond directly to the amber photographs shown in Figs. 6–9.

Chela palm trichobothria (Figs. 2–3, 6–7): Five trichobothria are identified on the chelal palm: Eb_1, Eb_2, Est, Et_1, and V_1. Trichobothria Eb_1 and Eb_2 are readily visible in several photos, identified by their large bristles and areolae; they are positioned somewhat removed from the extreme proximal aspect of the palm. A third, much smaller bristle is also visible in the same vicinity in some photos but it is not consistent with the other longer bristles found on the specimen and is roughly the same length as similar shorter bristles found on the palm. Therefore, it has been excluded from consideration as a trichobothrium. On the exterodistal aspect of the palm we see two bristles identified in this study as trichobothria Est and Et_1. These two trichobothria are identified by their bristles only. Est is located at the juncture of an apparent fracture on the distal aspect of the palm (notice that the extreme distal aspect of the segment is partially severed from the palm, containing both the fixed and movable fingers). There are at least three non-trichobothrial bristles located between Eb_1, Eb_2, and Est. Et_1 is located at the fixed finger/movable finger juncture, adjacent to the external condyle. On the ventral surface of the palm the areola of V_1 is detectable, including its rim. This trichobothrium is located a little proximally from the external movable finger juncture, essentially in line with trichobothrium Est. There is no trace of a bristle.

Chela fixed finger trichobothria (Figs. 2 and 6): Five trichobothria are identified on the chelal fixed finger: *eb*, *est*, *et*, *db* and *dt*. The three trichobothria of the external series are all identified by conspicuous bristles, and for *eb* and *est*, by their areolae as well. All three external trichobothria are located close to the denticle edge of the fixed finger, *eb* quite close to the fixed finger/movable finger juncture, *est* roughly at midpoint of the fixed finger, and *et* is located on the distal one-third, closer to *est* than is *eb*. The two dorsal trichobothria are identified by areolae and one, *db*, also exhibits a conspicuous bristle. The areola of trichobothrium *dt* is well formed exhibiting a subtle rim circumscribing the areola. Trichobothria *db* and *dt* are located on dorsoexternal surface of the finger, *db* situated slightly beyond the midpoint between *eb* and *est*. Trichobothrium *dt* is located the most distally on the finger, roughly at the same distance from *et* as *et* is from *est*. The internal surface of the fixed finger is not visible so any indication of trichobothria is limited to profiled bristles. Several views of the distal dorsoexternal aspect of the fixed finger are available, and there is no apparent bristle protruding from the segment as seen in other fixed finger trichobothria. Based on this we must assume here that *Archaeobuthus* does not have internal trichobothria on the chela.
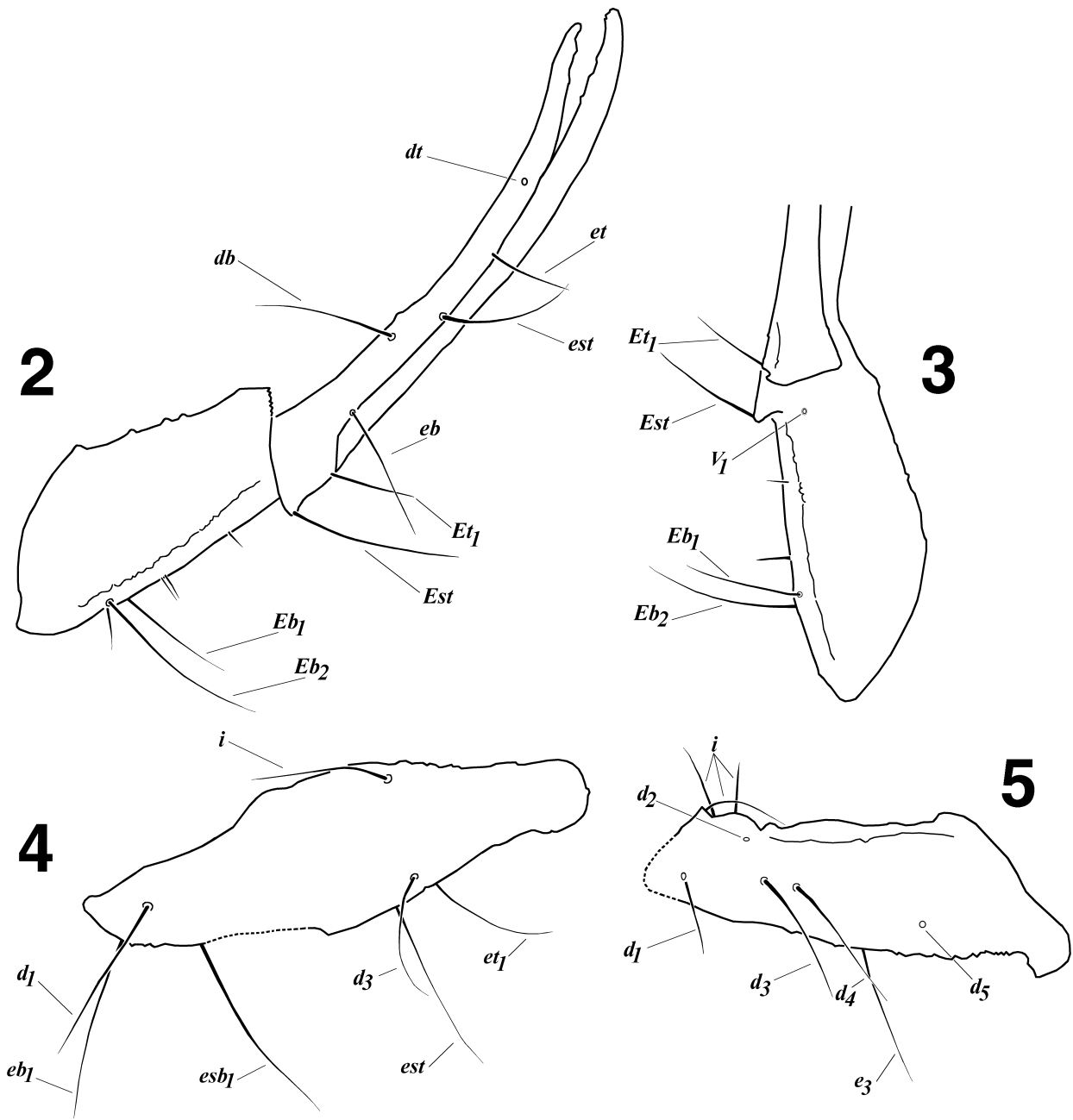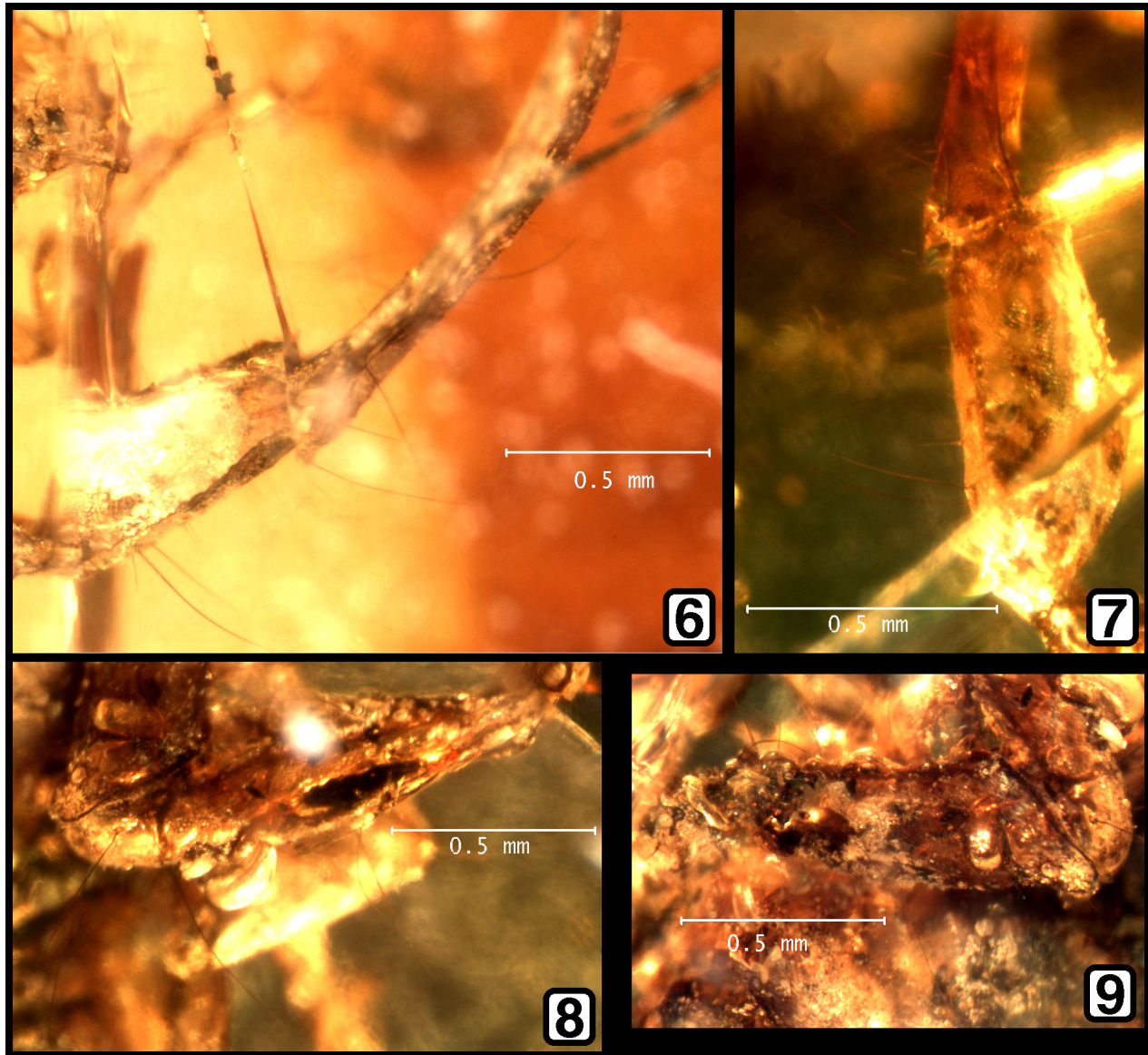
Figures 2–5: Pedipalp trichobothrial pattern of *Archaeobuthus estephani*. **2.** Dorsoexternal view of chela. **3.** Ventral view of chelal palm. **4.** Dorsal view of patella. **5.** Dorsal view of femur. Compare to Figs. 6–9.

Patella trichobothria (**Figs. 4 and 8**): Seven trichobothria were identified on the patella: d_1, d_3, i, eb_1, esb_1, est, and et_1. Two conspicuous dorsal trichobothria are visible based on bristles and areolae, herein designated as d_1 and d_3. Trichobothrium d_1 is located at the base of the segment, somewhat midpoint from the internal/external edges; d_3 is found on the distal one-third of the segment, considerably close to the external edge of the segment. A single internal trichobothrium, i, is located on the distal one-third of the segment, roughly in line with trichobothrium d_3. It is identified by an areola as well as a bristle that curves along the segment's internal edge. Four external trichobothria are visible based on protruding bristles only (no areolae): eb_1 is located at the extreme basal aspect of the segment, partially hidden by the bristle from trichobothrium d_1; esb_1 is located on the proximal one-quarter of the segment exhibiting a conspicuous bristle; est is found on the distal one-third of the segment, partially hidden by the bristle of d_3, and et_1 is located slightly more distal than est, exhibiting a curved bristle.

Figures 6–9: Pedipalp of *Archaeobuthus estephani* showing trichobothria; compare to Figs. 2–5. **6.** Dorsoexternal view of chela (also see Fig. 36). **7.** Ventral view of chelal palm (also see Fig. 37). **8.** Dorsal view of patella (also see Fig. 44). **9.** Dorsal view of femur (also see Fig. 45).

Femur trichobothria **(Figs. 5 and 9):** Nine trichobothria have been identified on the femur: d_1, d_2, d_3, d_4, d_5, i_1, i_2, i_3, and e_3. Five dorsal trichobothria are found on this segment, all with visible areolae, three of which also exhibit bristles, d_1, d_3 and d_4. The areola for trichobothrium d_5 is well defined; the areola for d_2 is less well defined. Trichobothria d_1, d_3, and d_4 are essentially aligned parallel to the external edge of the segment, d_5 situated slightly more externally. [Note that the parallel orientation of d_1, d_3, and d_4 is important phylogenetically, see discussion below.] Trichobothrium d_2 is situated on the basal fourth of the femur, close to the internal edge. We located three internal trichobothria, one of

which, i_1, is curved across the segment. All three trichobothria are located on the extreme basal aspect of the femur. One external trichobothrium, e_3, is identified by its bristle only and is located distally, slightly beyond the segment's midpoint.

***Comparison to Lourenço (2001)*:** In general, the trichobothria observed in this study are reasonably consistent with those originally reported by Lourenço (2001: 646). However, two out of 27 trichobothria reported by Lourenço were not located, and one new trichobothrium, i_1, was discovered. Based on our analysis, we have changed some of the designations of these trichobothria

compared to those originally reported by Lourenço (2001) and/or used by Soleglad & Fet (2001, 2003) in their analysis of the evolution of orthobothriotaxy (see below for the ramifications of these changes for the cladistic analysis). Finally, not all trichobothria reported by Lourenço in the text are shown in his figures (e.g. his reported two internal trichobothria of the femur are not shown). Table 1 specifies our hypothesized trichobothrial designations as contrasted to those stated by Lourenço and/or modified by Soleglad & Fet (2001).

Differences: Chela: we detected three, not four external trichobothria on the fixed finger as reported by Lourenço (2001): the trichobothrium *esb* was not detected. The designations and/or locations of the dorsal trichobothria are also different. What Lourenço (2001) declared as *esb* is designated by us as *db*, and Lourenço's *db* is our *dt*. These two trichobothria are found on the dorsoexternal aspect of the fixed finger and should both be designated as dorsal. Two distally positioned "bristles" depicted in Lourenço's fig. 12 (presumably *est* and *dt*) were not detected in this study.

Patella: We did not detect all dorsal patellar trichobothria reported by Lourenço (2001), and we also offer different designations of external trichobothria. Lourenço (2001) illustrated (fig. 13) and listed four trichobothria on the dorsal surface; we were only able to locate two dorsal trichobothria. Except for the position of our d_1, none of the positions depicted by Lourenço (2001) were verified in our study. In Lourenço (2001: fig. 13), we see four external trichobothria depicted, but in the text he only reports three. It appears that the two "bristles" depicted in close proximity in Lourenço's fig. 13 are our d_3 and *est*. The four external trichobothria (observed only as bristles since external surface is not visible) illustrated in our Fig. 4 are somewhat evenly distributed across the patella implying that these may be all the trichobothria found on this segment surface.

Femur: Here, we are essentially in agreement with Lourenço (2001) with respect to the identified trichobothria, except that we identified an **additional third internal trichobothrium. However, we differ significantly in interpreting the position of trichobothrium** d_5**, which in our observation (Fig. 5) is located on the distal one-third of the segment, and not in close proximity to trichobothrium** d_4 **as depicted by Lourenço.**

Discussion

Cladistic analysis of orthobothriotaxy

Table 1 depicts the differences in trichobothrial homologies for *Archaeobuthus* established in this study (gray shading) as compared to those stated by Lourenço (2001) and/or used by Soleglad & Fet (2001) in their cladistic analysis of scorpion orthobothriotaxy. Table 1 indicates the following changes:

Chela: the fixed finger trichobothrium *esb* is not present;

Patella: d_2 is not present, d_2 is reassigned to d_3, and em_1 is reassigned to esb_1;

Femur: an additional internal trichobothrium, i_3, is added.

We repeated the original cladistic analysis for the complete pedipalp by Soleglad & Fet (2001, fig. 8) incorporating these homology changes for *Archaeobuthus*; see Soleglad & Fet (2001) for details on the analytic methods.

The resulting topology differs from the original analysis of Soleglad & Fet (2001). Now, we obtain a completely ladderized topology of (P, (F1, (D, (A, (B, C))))) versus (P, (F1, (D, A), (B, C))) of the original study (the letters refer to orthobothriotaxic types as follows: P = Palaeopisthacanthidae, F1 = Archaeobuthidae, D = Pseudochactida, A = Buthida, B = Chaerilida, and C = Iurida; see also Fig. 35). It is also important to note here that this new topology is the same as that derived by Soleglad & Fet (2003) in their study of high-level systematics of Recent scorpions. The MP tree support of this study was also slightly better than that from the original orthobothriotaxy analysis of Soleglad & Fet (2001: Table 5): length/CI/RI/G-Fit = 95/0.6632/ 0.6522 /-25.957 vs. 98/0.6633/0.6333/-26.707, in particular three less steps and a slightly higher retention index (see Kitching et al., 1998, for definition of terms). Table 2 presents the bootstrap/jackknife support comparisons between the two interpretations of *Archaeobuthus* orthobothriotaxy. Clade A+B+C is significantly more supported in the new analysis (62/59 % vs. 9/9 %) and in contrast, the clade D+A is not well supported (only 11/12 % vs. 68/65 %). Based on this support, stated tree support improvement, and the demonstrated congruency of this current result with that of Soleglad & Fet (2003), which involved 62 trichobothria existence statements plus 105 other morphology-based characters, we can conclude that the homologies established in this study are more likely to be correct than those reported by Lourenço (2001) and/or used by Soleglad & Fet (2001). Finally, based on the overall consistency of bristle-based trichobothria identification, many observed via multiple perspectives (see Figs. 36–47), we can conclude that the 26 trichobothria reported for *Archaeobuthus* in this study are legitimate and *may* represent its *complete* configuration.

Phylogenetic ramifications of orthobothriotaxy

Based on our observations, *Archaeobuthus* does not exhibit any of the petite trichobothria (Vachon, 1974; Soleglad & Fet, 2001, 2003) of the chelal palm that are found in most buthoids (i.e., Type A), Eb_3, Esb, and *esb*. These trichobothria are also absent in the fossil genera *Palaeopisthacanthus* (Carboniferous orthostern family

Type A (extant Buthida)	Chela (15)															Patella (13)													Femur (11)											
	i	db	dt	eb	esb	est	et	Eb1	Eb2	Eb3	Est	Et1	Et4	v1	v2	i	d1	d2	d3	d4	d5	eb1	eb2	esb	em1	est	et1	et2	i1	i2	i3	i4	d1	d2	d3	d4	d5	e1	e2	e3*
Palaeolychas	?	X	X	X	?	?	?	X	X	X	X	X	X	?	?	X	X	X	X	X	?	X	?	?	?	?	?	?	X	X	X	?	X	?	X	X	X	X	X	-
Palaeoprotobuthus	?	?	?	?	?	?	?	?	?	?	?	?	?	X	X	?	X	?	X	?	?	X	X	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	X	-
Palaeotityobuthus	X	X	X	?	?	X	X	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-
Palaeoakentrobuthus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	X	X	X	X	X	X	?	?	?	?	?	?	?	X	?	?	?	X	X	X	X	X	X	X	-
Palaeoananteris	?	X	X	?	?	?	?	X	X	X	X	?	X	?	?	X	X	X	X	X	X	?	?	?	?	?	?	?	?	?	?	?	X	?	X	X	X	X	X	-
Eocene buthids	X	X	X	X	?	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	?	?	?	?	?	X	X	X	?	X	X	X	X	X	X	X	-
Protobuthus	?	X	X	X	?	?	?	X	X	?	X	X	?	?	?	?	X	X	X	?	X	?	?	?	?	?	?	?	X	X	?	?	?	?	X	?	?	X	X	-
Archaeobuthus[1]	-	X	X	X	X	X	X	X	X	-	X	X	-	X	-	X	X	X	X	-	-	X	-	-	X	X	-	-	X	X	-	-	X	X	X	X	X	X	-	X
Archaeobuthus	-	X	X	X	-	X	X	X	X	-	X	X	X	X	-	X	X	-	X	-	-	X	-	X	-	X	X	-	X	X	X	-	X	X	X	X	X	X	-	X

Table 1 (after Soleglad & Fet, 2001 (in part), as Table 2): Partial trichobothria patterns reported for five Eocene "palaeo–buthid" genera (Lourenço & Weitschat, 1996, 2000, 2001), Triassic genus *Protobuthus* (Lourenço & Gall, 2004) and the pattern for Cretaceous *Archaeobuthus*, as verified in this study (*shaded* row), contrasted with standard Type A designations. "Eocene buthids" designates a consensus of all trichobothria reported for the five "palaeo-buthid" genera. * e_3 is reported for *Archaeobuthus* only, not occurring in standard Type A pattern. [1] as reported by Lourenço. Note: the designations for patellar dorsal series, d_1–d_5, follow that established by Vachon (1974) and therefore do not reflect homology-based designations used by Soleglad & Fet (2001).

	Bootstrap/Jackknife (New Analysis)	Bootstrap/Jackknife (Original Analysis)	Plus/Minus Differences (%)
F1+D+A+B+C	100/100	100/100	0 %/0 %
D+A+B+C	87/86	92/91	-5.4 %/-5.5 %
A+B+C	62/59	9/9	589 %/556 %
B+C	93/92	88/86	5.7 %/7.0 %
D+A	11/12	68/65	-83.8 %/-81.5 %

Table 2: Bootstrap/jackknife support (%) comparisons of the results of this analysis and that of Soleglad & Fet (2001) for relevant clades as defined by the basic orthobothriotaxic types. Original analysis based on the mean of eleven separate analyses, 1000 pseudorepilicates per sequence; new analysis based on the mean of five separate analyses, 10000 pseudoreplicates per sequence. *Shaded* rows depict significant differences between the resulting fundamental topologies of the new analysis, F1+(D+(A+(B+C))), and the original analysis, F1+((D+A)+(B+C)): Ladderization of A+(B+C) support *increases* well over 500 %; support for clade D+A *decreases* over 80 %. F1 = Type F1 (*Archaeobuthus*); D = Type D (Pseudochactida); A = Type A (Buthida); B = Type B (Chaerilida); C = Type C (Iurida).

Palaeopisthacanthidae) and *Palaeoburmesebuthus* (Fig. 34; note that *esb* is not determinable), as well as in the relict extant scorpion *Pseudochactas*. The apparent transformation of trichobothria Eb_3 and *esb* is quite interesting; they are missing in three fossil orthosterns and *Pseudochactas* (parvorder Pseudochactida), petite or sometimes missing in the buthoids (Type A), and present as full trichobothria in two other Recent scorpion groups, parvorders Chaerilida (Type B) and Iurida (Type C). This hypothesized transformation is in complete congruency with the upper-level phylogeny of Recent scorpions presented by Soleglad & Fet (2003). Soleglad & Fet (2001: 3, App. A) and Fet et al. (2004: 21, figs. 59–64) hypothesized that petite trichobothria are an intermediate state between a full and a non-existent trichobothrium. Based on the present phylogenetic position of parvorder Buthida (see Soleglad & Fet, 2003: fig. 114), we can suggest here that these trichobothria, as they exist in the buthoids, are remnants of early stages of their development, having later become fully developed trichobothria in the other groups.

Evolutionary significance of femoral trichobothria d_1, d_3, and d_4

We have confirmed the essentially parallel alignment of femoral trichobothria d_1, d_3, and d_4 to the dorso-external carina and, the dorsal placement of trichobothrium d_2. As discussed in detail in Soleglad & Fet (2003: 79, fig. 115) and Fet et al. (2005: fig. 2), we consider the parallel alignment of d_1–d_3 and d_3–d_4 with this carina and the dorsal placement of d_2 to be plesiomorphic states of the *alpha*/*beta* pattern originally defined by Vachon (1975), thus providing polarity information for the evolution of these patterns. In addition, the designated patellar trichobothrium d_3 is located quite external of the segment midpoint, as it is also in genus *Pseudochactas* (Figs. 18–19). Although neither genus exhibits a dorsomedian (DM_c) carina, seeing this d_3 location in both genera, as well as in the Triassic fossil *Pro-*tobuthus (Lourenço & Gall, 2004: fig. 12), provides strong evidence for suggesting the polarity of the DM_c-d_3 alignment character, with external location of d_3 being plesiomorphic (the subject of the detailed analysis by Fet et al., 2005). Note that Soleglad & Fet (2003) assumed that *Archaeobuthus* exhibited the DM_c carina, based entirely on the figure provided by Lourenço (2001: fig. 13). However, after the reanalysis of the type specimen we conclude that the existence of this carina in *Archaeobuthus* cannot be confirmed.

Original diagnosis of **Archaeobuthidae**

Lourenço (2001: 643) diagnoses the Archaeobuthidae using four characters with one divided into two sub-characters. We discuss each character below as to its applicability, in our opinion, to family-level diagnoses in orthostern scorpions.

Pectines small and bulky: Although we had difficulty locating the pectines discussed and described by Lourenço (2001, fig. 8), and certainly finding much of the details depicted in his figure, we will discuss this character based on Lourenço's original description. We do not believe the size, shape, or the presence or absence of fulcra of the pectines is germane to familial diagnoses. There are small pectines in small species of buthoids and there are unrelated buthoids that lack fulcra (e.g. *Ananteris*, *Microcharmus*, etc.). This is not a distinct diagnostic character that could separate Archaeobuthidae from the Recent families of Buthoidea.

Spiracles very small and rounded: Although *Archaeobuthus* stigmata are consistent with fossil orthosterns, this character alone would not necessarily imply a separate family of buthoids. In addition, the degree of difference between "circular" vs. "sub-oval" vs. "short and oval" is subtle.

Sculpture of dentition of pedipalp chela fingers: The "blade-like" outer denticles illustrated on the distal third of the fingers of *Archaeobuthus* are unusual, albeit in our analysis we could not detect denticles as large as

those shown by Lourenço (2001, figs. 10 and 15). In our opinion, the important observation of chelal finger dentition in *Archaeobuthus* is "… the distal third of the finger with three short series of small granules, separated by two …", implying the oblique orientation of denticle groups, a plesiomorphic character found in the Carboniferous Palaeopisthacanthidae as well as in the plesiomorphic Recent scorpion group parvorders Pseudochactida, Buthida, and Chaerilida. The "blade-like" outer denticles described by Lourenço (2001) would qualify, in our opinion, as only a genus or species-level character, certainly not family. What *A. estephani* has are enlarged denticles as seen in, for example, the serrated "blade-like" denticles in the vaejovid genus *Serradigitus* (Vaejovidae) or the sharp "hook-like" denticles of the euscorpiid genus *Chactopsis* (Euscorpiidae).

Femoral trichobothria, d_1, d_3, and d_4 parallel alignment to the dorsoexternal carina: This is an important observation of Lourenço (2001, also verified in this study) and certainly qualifies as a family-level character. Based on Soleglad & Fet (2003) and Fet et al. (2005), this parallel alignment can be considered plesiomorphic, a precursor to the *beta* pattern found in relatively primitive buthoids (i.e., the *Buthus*, *Ananteris*, and *Isometrus* groups).

Trichobothria, neobothriotaxy "minorante": Based on the analysis conducted in this study, we believe that the trichobothrial pattern is by far the most significant for the diagnosis of Archaeobuthidae. Soleglad & Fet (2001), assuming the pattern as specified by Lourenço (2001) was complete, assigned *Archaeobuthus* its own orthobothriotaxic type, F1. The trichobothrial pattern exhibited by *Archaeobuthus* (Figs. 2–5) is distinct from that of any Recent scorpion parvorder. We disagree with Lourenço's designation of "neobothriotaxy minorante", which was defined and used by Vachon (1974) as "based on Type A with the loss of trichobothria". This is not true for *Archaeobuthus* as the observed pattern is not based on (i.e. derived from) Type A. Therefore, it is more likely that the "missing" trichobothria alluded to by Lourenço (2001) never existed in *Archaeobuthus* because they evolved later in the lineage leading to the Recent scorpions.

Systematic position of Archaeobuthidae

Lourenço (2001: 646) contrasted *Archaeobuthus* with two extant **"buthoid"** families, Buthidae and Microcharmidae, listing characters it shares with one or both families. Although Lourenço states: "… trichobothrial pattern, and especially granulation of pedipalp fingers – place the new family in an isolated position in relation to both the Microcharmidae and the Buthidae …", he appears to imply that the buthoids are its closest relatives since he does not contrast *Archaeobuthus* with other Recent scorpion groups, in particular, *Pseudochactas*, which is never mentioned. Based on their cladistic analysis of orthobothriotaxy, Soleglad & Fet (2001) suggested that *Archaeobuthus* was the plesiomorphic sister group to all Recent scorpions (including *Pseudochactas*), thus challenging the notion that *Archaeobuthus* was a primitive member of Buthoidea. This current study further supports the hypothesized plesiomorphic position of *Archaeobuthus*. We can list four character groups that set *Archaeobuthus* apart from the buthoids: (1) trichobothrial patterns; (2) leg tarsus armature; (3) cheliceral dentition (in part); and (4) shape of the stigmata.

***Trichobothrial patterns*:** As described in detail elsewhere in this paper, we believe we have probably detected most, if not all, of the trichobothria in the single specimen known of *Archaeobuthus* (Figs. 2–5). Figures 10–17, 18–25, and 26–33 illustrate an idealized trichobothrial pattern of *Archaeobuthus*, patterns of *Pseudochactas*, and representatives of the six buthoid groups suggested by Fet et al. (2005). An examination of these figures, pedipalp segment by segment, reveals that *Pseudochactas* (Type D) generally represents an intermediate condition between *Archaeobuthus* (Type F1) and buthoids (Type A).

Chela (Figs. 10–17): *Archaeobuthus* and *Pseudochactas* have the same fundamental trichobothria except *Pseudochactas* exhibits two basally positioned internal trichobothria, which are absent in *Archaeobuthus*. In the buthoids we see three petite trichobothria, Eb_3, Esb, and esb, plus a second ventral trichobothrium. These are absent in both *Archaeobuthus* and *Pseudochactas*. The buthoids exhibit a distally placed internal trichobothrium which is absent in *Archaeobuthus* and potentially present in *Pseudochactas* if one chooses to accept it as homologous in this genus, again demonstrating the intermediate position of *Pseudochactas*.

Patella (Figs. 18–25): The number of dorsal trichobothria increases from *Archaeobuthus* (two) to *Pseudochactas* (three) to the buthoids (five). In the same fashion, the number of external trichobothria increases from *Archaeobuthus* (four) to *Pseudochactas* (six) to the buthoids (seven). It is interesting to note that in both *Archaeobuthus* and *Pseudochactas* the external trichobothria are located on the basal two-thirds of the segment, while in the buthoids, the *et* series is found more distally. All three assemblages have a single internal trichobothrium.

Femur (Figs. 26–33): In the important dorsal series all three assemblages have five trichobothria. However, the parallel alignment of trichobothria d_1, d_3, and d_4 and the dorsal placement of d_2 in *Archaeobuthus* is hypothesized as primitive. The arrangement found in *Pseudochactas* agrees, in part, with this alignment and d_2 position, thus exhibiting a partial *beta* pattern as originally defined by Vachon (1975). Three of the buthoid groups of genera, *Buthus*, *Ananteris* and *Isometrus*, exhibit a
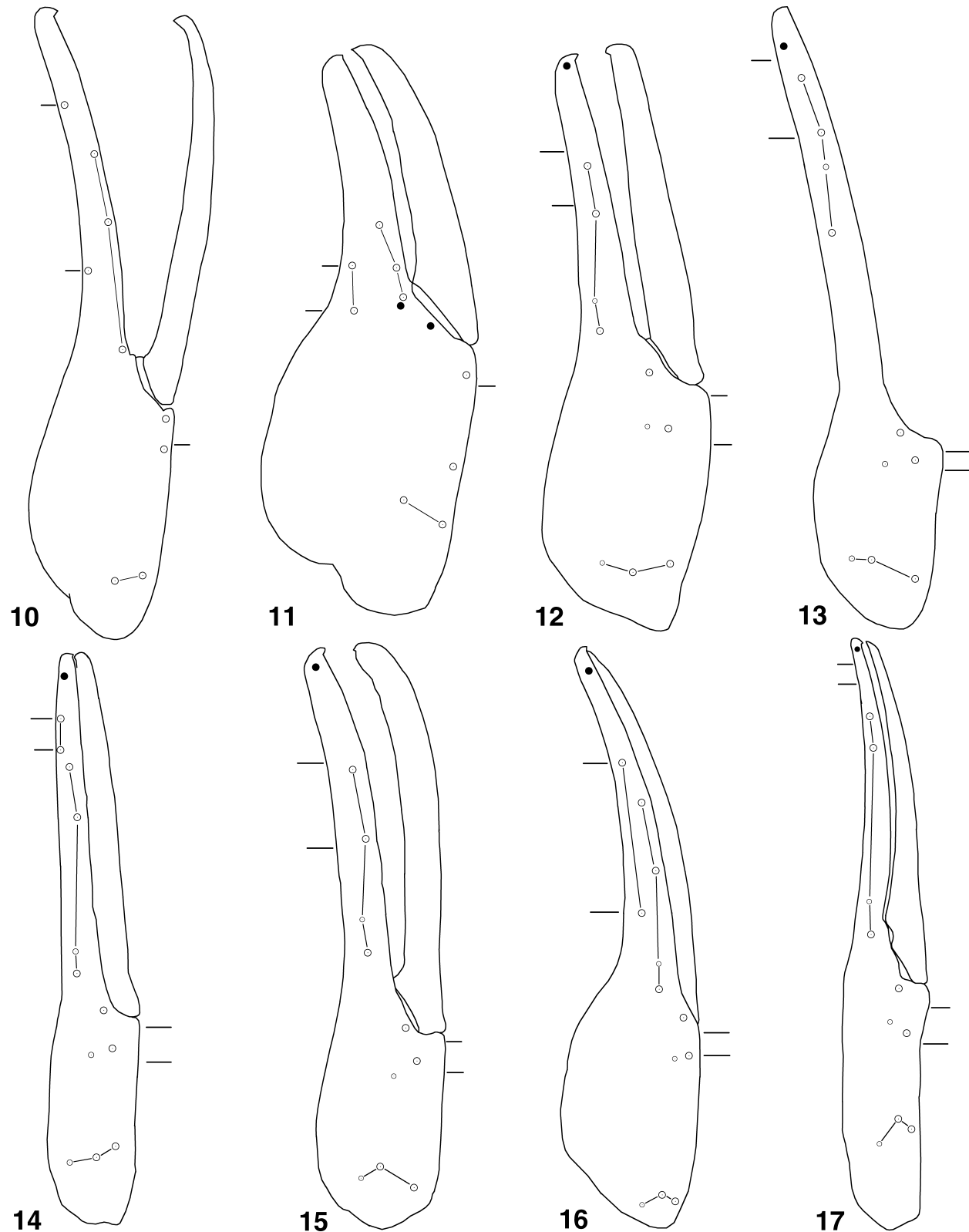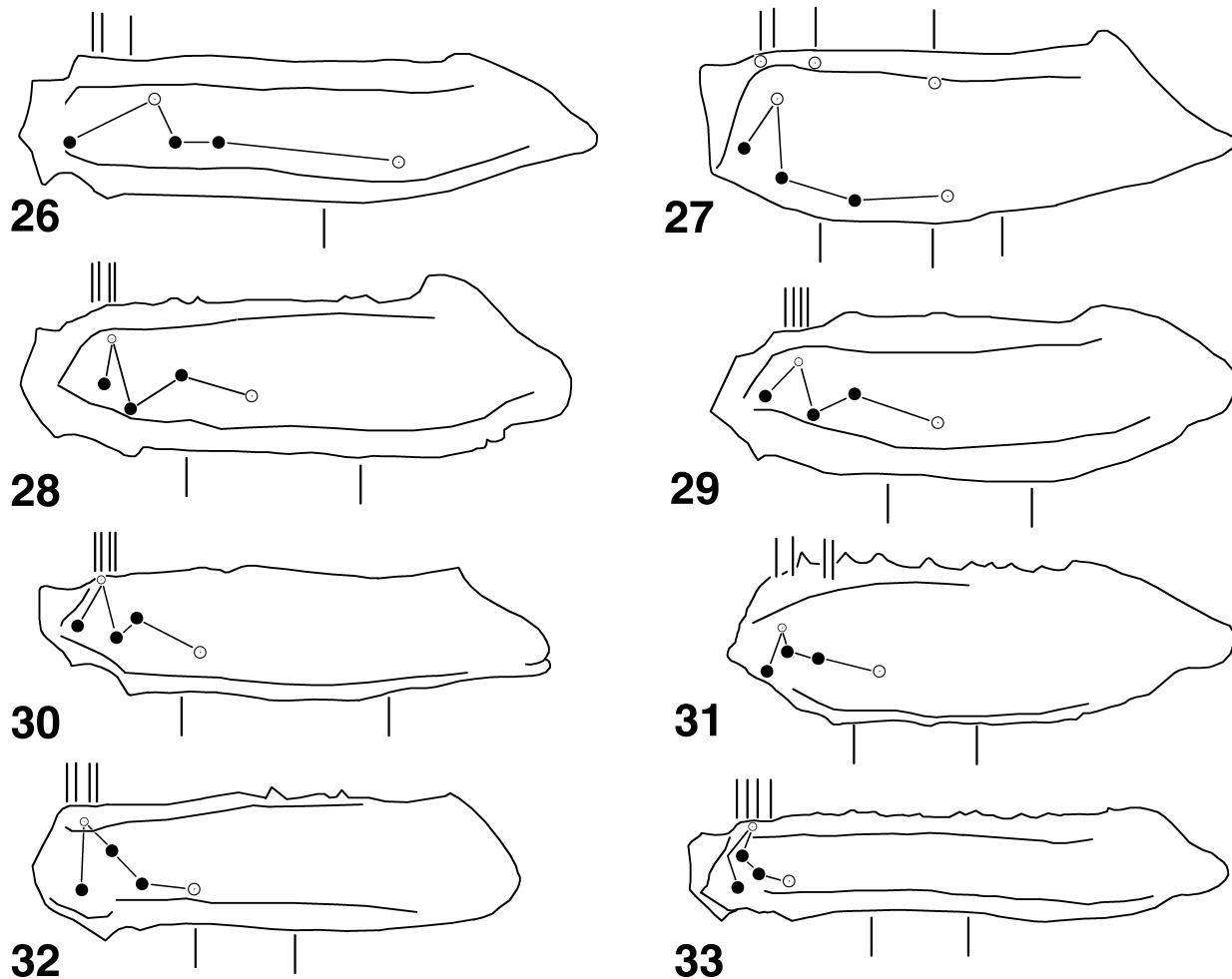
Figures 10–17: Diagrammatic trichobothrial patterns of pedipalpal chela for *Archaeobuthus*, *Pseudochactas*, and representatives of the six buthoid groups suggested by Fet et al. (2005). **10.** *Archaeobuthus estephani* (idealized). **11.** *Pseudochactas ovchinnikovi* (after Soleglad & Fet, 2001, in part). **12.** *Buthus bonito* (after Lourenço & Geniez, 2005, in part). **13.** *Ananteris luciae* (after Lourenço, 1984, in part). **14.** *Isometrus sankeriensis* (after Tikader & Bastawade, 1983, in part). **15.** *Charmus indicus* (after Lourenço, 2000b, in part, and Tikader & Bastawade, 1983, in part). **16.** *Uroplectes occidentalis* (after Vachon, 1950, in part). **17.** *Tityus shiriana* (after González-Sponga, 1991, in part). Closed circles depict location of internal trichobothria; horizontal bars depict location of V_1–V_2 and *db*–*dt* series.
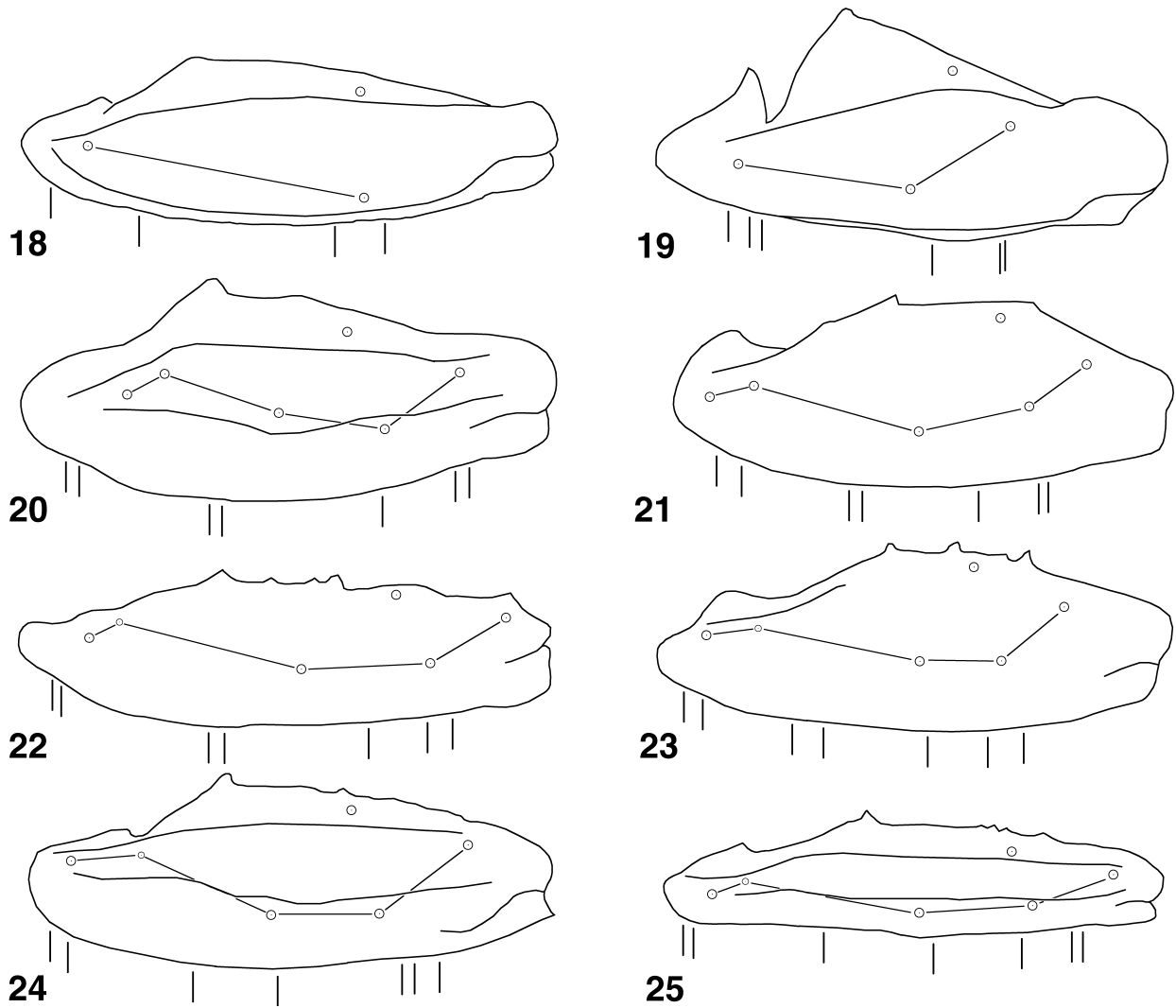
Figures 18–25: Diagrammatic trichobothrial patterns of pedipalpal patella for *Archaeobuthus*, *Pseudochactas*, and representatives of the six buthoid groups suggested by Fet et al. (2005). **18.** *Archaeobuthus estephani* (idealized). **19.** *Pseudochactas ovchinnikovi* (after Soleglad & Fet, 2001, in part). **20.** *Buthus bonito* (after Lourenço & Geniez, 2005, in part). **21.** *Ananteris luciae* (after Lourenço, 1984, in part). **22.** *Isometrus sankeriensis* (after Tikader & Bastawade, 1983, in part). **23.** *Charmus indicus* (after Lourenço, 2000b, in part, and Tikader & Bastawade, 1983, in part). **24.** *Uroplectes occidentalis* (after Vachon, 1950, in part). **25.** *Tityus shiriana* (after González-Sponga, 1991, in part). Vertical bars depict location of external trichobothria.

completely defined *beta* pattern, whereas the *Charmus*, *Uroplectes* and *Tityus* groups exhibit the derived *alpha* pattern. Again, we see that *Pseudochactas* is intermediate between *Archaeobuthus* and the presumably primitive *Buthus*, *Ananteris*, and *Isometrus* buthoid groups. The number of internal trichobothria in *Archaeobuthus* (three) increases to four in *Pseudochactas* and the buthoids. For external trichobothria, again *Archaeobuthus* has the lowest number (one), the buthoids have two, and *Pseudochactas* has three ― in this one case *Pseudochactas* is not intermediate.

    Leg tarsus armature: Although we cannot see details of the ventral surface of the leg tarsus in *A. estephani*, it is clear (see Figs. 53–54) that its armature is

reduced and *does not* exhibit the multiple rows of long, well developed setae typically present in the buthoids (see Soleglad & Fet, 2003: figs. 15–18). In *Pseudochactas* (Soleglad & Fet, 2003: figs. 11–12), there is a delicate median double row of short spinules, unique among Recent scorpions. Santiago-Blay et al. (2004a: 149) also reported a pair of delicate spinule rows on the ventral surface of the tarsus in the Cretaceous scorpion *Palaeoburmesebuthus grimaldii*, which is currently not placed in any family or parvorder. Jeram (1994a: 536, Text-fig. 5J and 1994b: 293) reported a single ventral row of "fixed thorns" for fossil scorpions *Compsoscorpius elegans* Petrunkevitch, 1949 (suborder Neoscorpionina) and non-orthostern *Pulmonoscorpius kirktonensis*

Figures 26–33: Diagrammatic trichobothrial patterns of pedipalpal femur for *Archaeobuthus*, *Pseudochactas*, and representatives of the six buthoid groups suggested by Fet et al. (2005). **26.** *Archaeobuthus estephani* (idealized). **27.** *Pseudochactas ovchinnikovi* (after Soleglad & Fet, 2001, in part). **28.** *Buthus bonito* (after Lourenço & Geniez, 2005, in part). **29.** *Ananteris luciae* (after Lourenço, 1984, in part). **30.** *Isometrus sankeriensis* (after Tikader & Bastawade, 1983, in part). **31.** *Charmus indicus* (after Lourenço, 2000b, in part). **32.** *Uroplectes occidentalis* (after Vachon, 1950, in part). **33.** *Tityus shiriana* (after González-Sponga, 1991, in part). Vertical bars depict location of *internal* and *external* trichobothria; closed circles depict trichobothria d_1, d_3, and d_4, emphasizing the *alpha*/*beta* pattern.

Jeram, 1994 (suborder Mesoscorpionina), respectively. From this sparse information, one may assume that the presence of spinules, not setae, represents the inferred basal state of this structure.

Cheliceral dentition: Lourenço (2001: 644–645, fig. 6) reports, "…dentition reduced; external distal tooth in movable finger longer than internal distal; median reduced; median and basal fused in a single tooth on the fixed finger …". Interestingly, Lourenço reports that the ventral distal tine of the movable finger is longer than its dorsal counterpart, but his fig. 6 shows only one denticle, presumably from the dorsal side since the chelicerae are not readily visible ventrally, which would imply that the dorsal distal denticle is the largest, hence blocking the ventral denticle from view. Although the dentition of the chelicerae was not fully visible for our analysis, we

were able to confirm that the ventral distal tine is longer than the dorsal distal denticle, as reported in the text of Lourenço (2001). This condition is considered plesiomorphic (e.g. the ventral distal denticle of the palaeopisthacanthids is considerably longer than the dorsal denticle). In *Pseudochactas*, they are subequal, the ventral slightly longer, and in the Buthida (see Soleglad & Fet, 2003: figs. 40, 41, 43) the dorsal distal tine is, in many genera, longer than the ventral counterpart, a feature not present in any other Recent scorpions.

Stigmata: The stigmata, as reported by Lourenço (2001, fig. 7) and verified in this study (see Fig. 52), are quite small and oval to round. This condition is hypothesized as plesiomorphic since stigmata are also circular in the Carboniferous Palaeopisthacanthidae and the Cretaceous scorpion *Palaeoburmesebuthus* (Santiago-Blay et
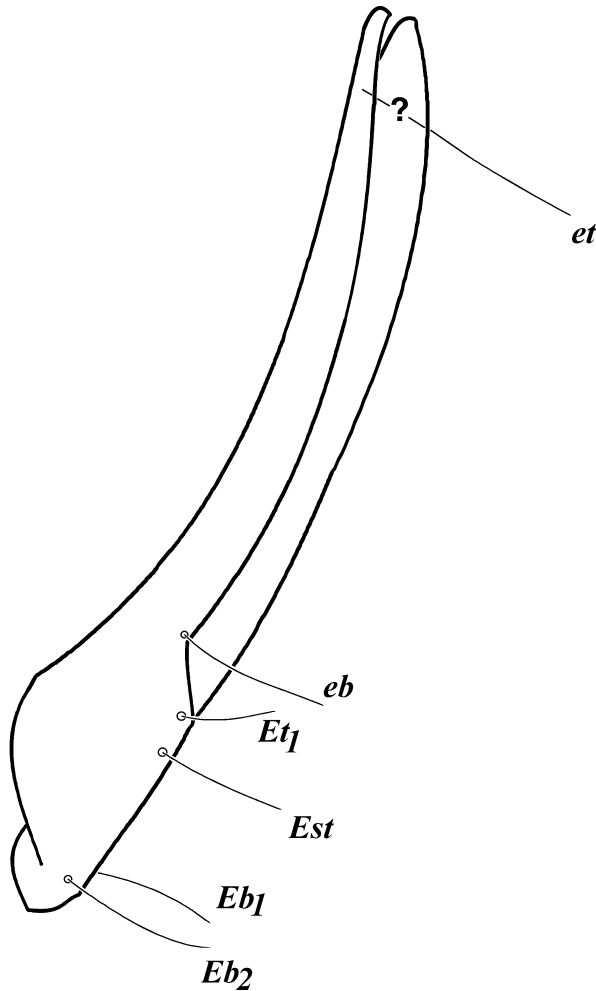
Figure 34: Partial trichobothrial pattern of pedipalpal chela of fossil *Palaeoburmesebuthus grimaldii* Lourenço, 2002 (after Santiago-Blay et al., 2004a: fig. 2, in part); compare with that of *Archaeobuthus estephani* in Fig. 2.

al., 2004b: 150, fig. 7). Generally in the Buthidae, the stigmata are well developed and slit-like in shape. In the family Microcharmidae they are variable, from small and oval to slit-like in shape, and in the relict genus *Pseudochactas* (parvorder Pseudochactida) the stigmata are small and oval in shape.

Phylogenetic perspective

Soleglad & Fet (2003) provided a brief systematic account of all known Mesozoic orthostern scorpions. Two of these fossils remained unassigned to any of the extant parvorders or superfamilies: one of these is *Archaeobuthus* (Archaeobuthidae); another is *Palaeoburmesebuthus* from Burmese amber (ca. 100 Ma), which has not been assigned to any family (Lourenço, 2002; Santiago-Blay et al., 2004b). Among other Mesozoic records, four genera belong to two modern parvorders (Chaerilida and Iurida). The only extant scorpion family

so far found in the Mesozoic, Chaerilidae (parvorder Chaerilida) is represented in Burmese amber, ca. 100 Ma, by the genus *Electrochaerilus* (Santiago-Blay et al., 2004a). Two extinct orthostern families from the Early Cretaceous have been placed in the modern parvorder Iurida (Soleglad & Fet, 2003): the monotypic family Palaeoeuscorpiidae (*Palaeoeuscorpius*, French amber, ca. 100 Ma; Lourenço, 2003) and Protoischnuridae (Crato Formation, Brazil, ca. 110 Ma; Carvalho & Lourenço, 2001). The family Protoischnuridae includes two genera, of which *Protoischnurus* seems to have affinities to modern Hemiscorpiidae (=Liochelidae) (superfamily Scorpionoidea), while *Araripescorpius* appears to be closer to modern Chactidae (superfamily Chactoidea) (F. Menon, pers. comm. to VF and MES, 2004); see Selden & Nudds (2004) for a general review of Crato Formation fossils.

Recently, Lourenço & Gall (2004) described the earliest Mesozoic orthostern, *Protobuthus* (placed in a new monotypic family, Protobuthidae) from the Early Triassic (ca. 240 Ma, France); see Selden & Nudds (2004) for a general overview of Grés à Voltzia Formation fossils of the northern Vosges. *Protobuthus* is a very important discovery, because it bridges an enormous gap in the fossil record of orthostern scorpions, between the Carboniferous Palaeopisthacanthidae (ca. 300 Ma) and Cretaceous *Archaeobuthus* (ca. 135–120 Ma). The description of *Protobuthus* by Lourenço & Gall (2004) is based on the holotype male (total length 32.5 mm). Important taxonomic structures visible include the pedipalps, showing a partial trichobothrial pattern, and the metasoma with telson. Important structures *not* visible include the chelicerae, all sternites (thus no information on sternum, stigmata, and pectines), and the leg armature. Notable metasomal structures indicated are the number of carinae exhibited, 10-8-8-8-5 for segments I–V, respectively; and the telson lacking a subaclear tooth. Also of interest, the measurements provided (Lourenço & Gall, 2004, table 1) do not show a significant increase in length from metasomal segment II to segment V, as that found in all Recent scorpions (see Soleglad & Fet, 2003: 9–10, for a discussion of this issue). On the pedipalp, only two weak dorsal carinae are reported for the patella, thus apparently lacking a dorsomedian (DM_c) carina (Lourenço & Gall, 2004, fig. 12). Trichobothria (partial pattern) reported for the holotype include the following [original designations of Lourenço & Gall (2004) unless modified here, in which case the original designations are parenthesized]: chela: Eb_1 (Eb_2), Eb_2 (Eb_3), $Et?$, Est (Esb), db, dt, and eb; patella: d_1, d_2, d_3, and d_5 (d_4); femur: i (d_1), i (d_2), d_3, e_1, and $e_2?$. Trichobothria indicated with a "?" are only possible detections; our changes in designations are based on the sketch-like figure provided by Lourenço & Gall (2004: fig. 12).
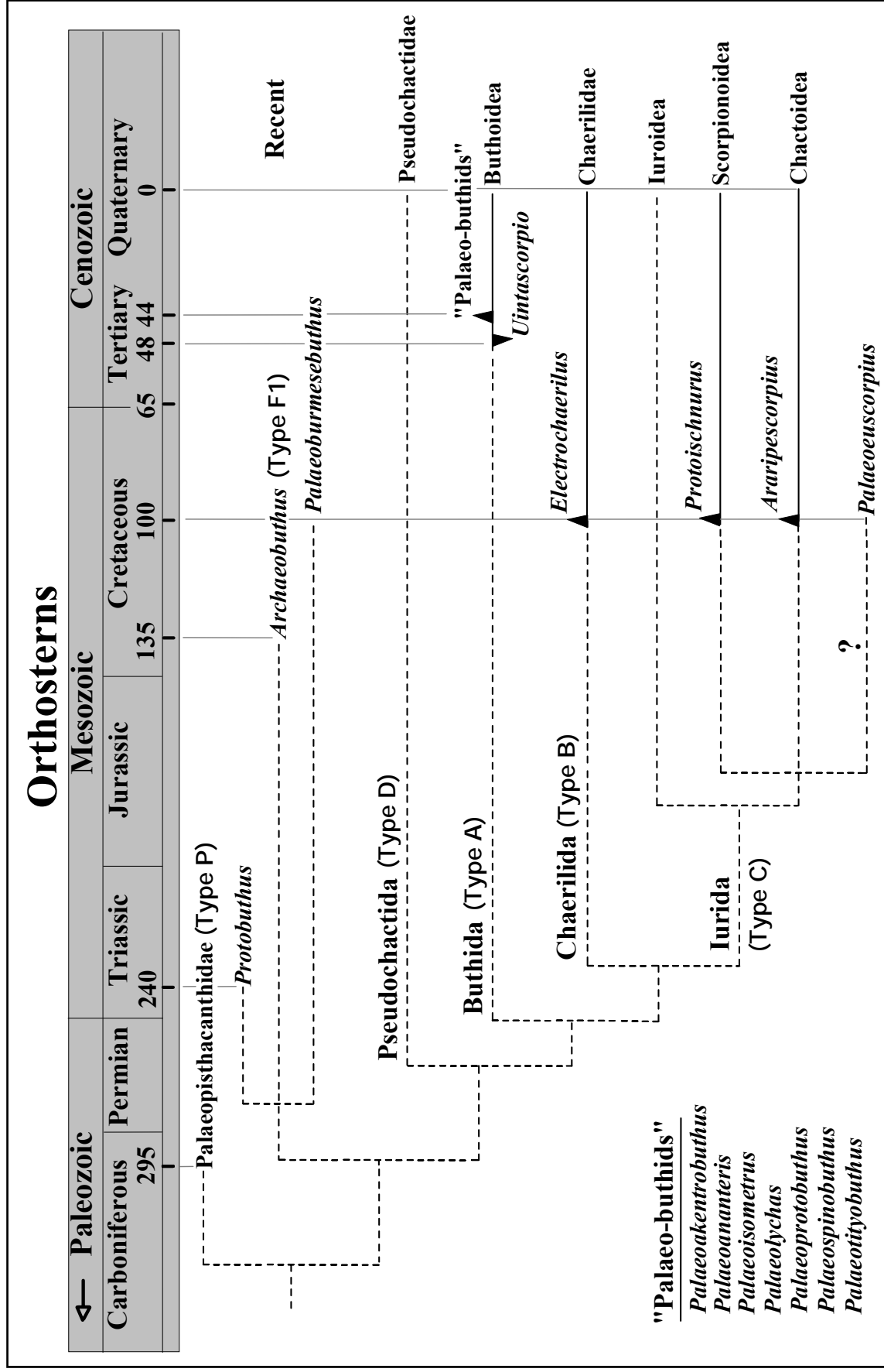
Orthosterns

Figure 35: High-level cladogram of scorpion infraorder Orthosterni showing timeline (in Ma) of major fossil scorpions as they relate to Recent scorpion parvorders. Note that fossil scorpion *Palaeoeuscorpius* is assigned to parvorder Iurida but superfamily placement is uncertain. Type designations refer to orthobothriotaxic types as established by Vachon (1974) and Soleglad & Fet (2001).

Lourenço & Gall (2004) placed *Protobuthus* in the superfamily Buthoidea "*sensu* Lourenço" referring to Lourenço (2000a) where, however, only extant families Buthidae and Microcharmidae were included in Buthoidea, but no fossil families. Therefore, the circumscription of the superfamily Buthoidea "*sensu* Lourenço (2000a)" is identical to that of superfamily Buthoidea and parvorder Buthida "*sensu* Soleglad & Fet (2003)". (The parvorder Buthida is currently monotypic, including only the superfamily Buthoidea). Later, Lourenço (2001, 2002) added *Archaeobuthus* and *Palaeoburmesebuthus* (the latter from a metasomal fragment only) to Buthoidea, therefore expanding the scope of this superfamily to Cretaceous taxa. Soleglad & Fet (2001, 2003), however, did not agree with these placements, and instead demonstrated that *Archaeobuthus* is an outgroup to all extant scorpion lineages, including the relict genus *Pseudochactas*, recently discovered in Central Asia (Gromov, 1998). *Pseudochactas* was placed in the superfamily Chaeriloidea by Lourenço (2000a), without any justification or analysis. The detailed study by Soleglad & Fet (2001, 2003) led to the understanding of *Pseudochactas* as the most basal extant scorpion, a sole member of the parvorder Pseudochactida and superfamily Pseudochactoidea. Later, Santiago-Blay et al. (2004b) described another, more complete specimen of *Palaeoburmesebuthus*, demonstrating that it cannot be placed in Buthoidea. Most recently, Fet et al. (2005) further confirmed, through analysis of extant Buthoidea, that *Archaeobuthus* is an outgroup not only to parvorder Buthida but also to Pseudochactida.

The Triassic *Protobuthus*, in our opinion, also lacks diagnostic buthoid features (Table 1). Based on the lack of important taxonomic structures (i.e., chelicerae and leg tibia and tarsus armament, etc.) and only a partial trichobothrial pattern, as discussed above, we do not have enough information to reliably place *Protobuthus* into any extant parvorder, including Buthida. However, assuming information on the partial trichobothrial pattern is correct, as presented by Lourenço & Gall (2004), we note that the chelal palm trichobothrium Eb_3 is absent while the fundamental trichobothria Et and Est are present. The same pattern is observed in palaeopisthacanthids, *Archaeobuthus*, and *Palaeoburmesebuthus* (albeit information on the latter is based on a partial pattern). In addition, the patellar trichobothrium d_3 in *Protobuthus* is situated on the external aspect of the segment, as in *Archaeobuthus* (Fig. 4); this feature we hypothesize elsewhere in this paper as a primitive condition. Related to this, the DM_c carina of the pedipalp patella is apparently absent (its presence being a synapomorphy for parvorder Buthida; see Soleglad & Fet (2003) and Santiago-Blay et al., 2004c). Of less importance is the fact that all three fossil genera referenced above have quite slender chela with somewhat elongated fingers. Based on this limited data, it seems reasonable

to place *Protobuthus* close to *Archaeobuthus* and *Palaeoburmesebuthus*, likewise well removed from the Recent scorpions (Fig. 35).

It is an old but unfortunate tradition in fossil scorpion taxonomy to create generic names ending with "–*buthus*". Some of these were based on very superficial similarities such as a slender pedipalp chela. However, the superfamily Buthoidea (based on the generic name *Buthus*) is defined by its precise diagnostic features/synapomorphies. We strongly advise zoologists who describe new fossil scorpions to refrain from generic etymology based on modern names, unless they can justify true phylogenetic relationship. Then it would be possible to avoid misleading names such as, for example, *Eobuthus*, *Isobuthus*, or *Palaeobuthus* (none of which belong to Buthoidea, or even to the infraorder Orthosterni).

Our present reinvestigation of *Archaeobuthus* (Archaeobuthidae) supports the placement of this unique fossil by Soleglad & Fet (2001, 2003) well outside of parvorder Buthida and superfamily Buthoidea. This Cretaceous genus, along with two other, more fragmentarily known orthostern fossils (Triassic *Protobuthus* and Cretaceous *Palaeoburmesebuthus*) most likely represents other Mesozoic lineages, which probably did not survive the K-T extinction (Fig. 35). These three taxa, therefore, occupy the position outside of four extant orthostern parvorders, while the Carboniferous Palaeopisthacanthidae form a sister group to all other known Orthosterni (Fig. 35). Calibration of the high-level orthostern phylogeny (Soleglad & Fet, 2003) according to a few known Mesozoic fossils indicates that the major divergence into four extant parvorders (Pseudochactida, Buthida, Chaerilida, and Iurida) should have probably occurred in the Permian-Triassic (Fig. 35). We confirm that two extant parvorders, Chaerilida and Iurida, are represented in the Cretaceous fossils (Soleglad & Fet, 2003; Santiago-Blay et al., 2004a). However, in our opinion, the earliest representatives of parvorder Buthida in the fossil record are the extinct Eocene genera, mainly known from Baltic amber (ca. 40–55 Ma; Lourenço & Weitschat, 1996, 2000, 2001, 2005; Lourenço et al., 2005; Santiago-Blay et al., 2004b, 2004c) (see Selden & Nudds, 2004, for a general review of Baltic amber). This does not mean, of course, that Buthida did not exist in the Mesozoic — only that they have not been yet found among Mesozoic fossils.

Acknowledgments

mens available to qualified researchers. Special thanks are due to Dave Mills and Doug Marsh (State Agricultural Laboratory, Phoenix, Arizona) for authorizing the use of the S.A.L. digital imaging system. We are grateful to Paul Selden and Federica Menon (Manchester University, Manchester, UK) and Günter Bechly (Staatliches Museum für Naturkunde, Stuttgart, Germany) for sharing the unpublished information on Crato fossil scorpions of Brazil. We thank Alexander Schmidt (Museum für Naturkunde zu Berlin, Germany) for providing information on Triassic amber. Scott D. Whitaker (SEM Laboratory, Laboratories of Analytical Biology, Smithsonian Institution, Washington, DC) assisted with Image Pro (Fig. 40). We thank Jason Dunlop, Paul Selden and one anonymous reviewer for their valuable comments.

References

ANDERSON, K. B. & B. A. LePAGE. 1995. The nature and fate of natural resins in the geosphere. VI. Analysis of fossil resins from Axel Heiberg Island, Canadian Arctic. Geochemical and paleobotanical implications. Pp. 170–192 *In*, Anderson, K. B. & J. C. Crelling (eds). 1995. *Amber, Resinite, and Fossil Resins. Developed from a symposium sponsored by the Division of Geochemistry, Inc., at the 208th National Meeting of the American Chemical Society. Washington, D.C. August 21–24, 1994.* American Chemical Society: Washington, District of Columbia, USA, 296 pp.

ASH, S. R. & R. J. LITWIN. 1991. On the widespread occurrence of amber in the Upper Triassic Chinle Formation, Southwestern United States. *In*, *Geological Society of America, Rocky Mountain Section (Albuquerque, New Mexico, USA, April 22–24, 1991). Abstracts with programs*, 23(4): 3.

CARVALHO, M. G. P., DE & W. R. LOURENÇO. 2001. A new family of fossil scorpions from the Early Cretaceous of Brazil. *Comptes Rendus des Séances de l'Académie des Sciences, Paris*, 332: 711–716.

ENGEL, M. S. 1997 (1996). New augochlorine bees (Hymenoptera: Halictidae) in Dominican amber, with a brief review of fossil Halictidae. *Journal of the Kansas Entomological Society*, 69(4), Supplement: 334–345.

FET, V., M. E. SOLEGLAD & G. LOWE. 2005. A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthida). *Euscorpius*, 23: 1–40.

FET, V., M. E. SOLEGLAD, D. P. A. NEFF & I. STATHI. 2004. Tarsal armature in the superfamily Iuroidea (Scorpiones: Iurida). *Revista Ibérica de Aracnología,* 10: 17–40.

GIANOLLA, P., E. RAGAZZI & G. ROGHI. 1998. Upper Triassic amber from the Dolomites (Northern Italy). A paleoclimatic indicator? *Rivista Italiana di Paleontologia e Stratigrafia*, 104(3): 381–389.

GONZÁLEZ-SPONGA, M. A. 1991. Arácnidos de Venezuela. Escorpiones del tepui "La Neblina", Territorio Federal Amazonas, Venezuela (Scorpionida: Chactidae: Buthidae). *Boletín de la Academia de Ciencias Fisícas, Matemáticas y Naturales* (Venezuela), 51(163–164): 95–136.

GRADSTEIN, F. M. & J. C. OGG. 2004. Geologic Time Scale 2004 – why, how, and where next! *Lethaia*, 37: 175–181.

GRIMALDI, D. A. 1987. Amber fossil Drosophilidae with particular reference to the Hispaniolan taxa. *American Museum Novitates*, 2880: 1–23.

GRIMALDI, D., D. DE SOUZA AMORIM & V. BLAGODEROV. 2003. The Mesozoic family Archizelmiridae (Diptera: Insecta). *Journal of Paleontology*, 77 (2): 368–381.

GRIMALDI, D. & M. S. ENGEL. 2005. *Evolution of the Insects*. Cambridge University Press: New York, New York, USA, 755 pp.

GROMOV, A. V. 1998. A new family, genus and species of scorpions (Arachnida, Scorpiones) from southern Central Asia. *Zoologichesky Zhurnal*, 77(9): 1003–1008 (in Russian, English summary).

ICZN. 1999. *International Code of Zoological Nomenclature*. 4th Edition. The International Trust for Zoological Nomenclature: London, UK, 305 pp.

JERAM, A. J. 1994a. Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology*, 37(3): 513–550.

JERAM, A. J. 1994b. Scorpions from the Viséan of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 84: 283–299.

KAY, P. T. & S. R. ASH. 1999. Triassic ambers from the Chinle, USA, help provide preliminary biochemical links to the identity of contributor plants.

In, Geological Society of America. Annual Meeting (Denver, Colorado, USA, October 25–28, 1999). Abstracts with Programs, 31(7): 467.

KITCHING, I. J., P. L. FOREY, C. J. HUMPHRIES & D. WILLIAMS. 1998. *Cladistics – Theory and Practice of Parsimony Analysis*. 2nd ed. Oxford University Press: London, UK, 242 pp.

KJELLESVIG-WAERING, E. N. 1986. *A Restudy of the Fossil Scorpionida of the World*. Palaeontographica Americana. No. 55. Paleontological Research Institution: Ithaca, New York, USA, 287 pp.

KUKALOVÁ-PECK, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings. *Canadian Journal of Zoology*, 65: 2327–2345.

LABANDEIRA, C. C. 1994. A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology*, 88: 1–71.

LAMBERT, J. B. & G. O. POINAR, JR. 2002. Amber: The organic gemstone. *Accounts of Chemical Research*, 35: 628-636.

LAMBERT, J. B., Y. WU & J. A. SANTIAGO-BLAY. 2005. Taxonomic and chemical relationships revealed by nuclear magnetic resonance spectra of plant exudates. *Journal of Natural Products*, 68(5): 635–648.

LANGENHEIM, J. H. 2003. *Plant Resins: Chemistry, Evolution, Ecology, and Ethnobothany*. Timber Press: Portland, Oregon, USA, 612 pp.

LITWIN, R. J. & ASH, S. R. 1991. First early Mesozoic amber in the Western Hemisphere. *Geology* (Boulder, Colorado), 19(3): 273–276.

LOURENÇO, W. R. 1984. *Ananteris luciae*, nouvelle espèce de Scorpion de l'Amazonie brasilienne (Scorpiones, Buthidae). *Journal of Arachnology*, 12(3): 279–282.

LOURENÇO, W. R. 2000a. Panbiogeographie, les familles des scorpions et leur repartition geographique. *Biogeographica*, 76(1): 21–39.

LOURENÇO, W. R. 2000b. Taxonomic considerations about the genus *Charmus* Karsch, 1879 (Chelicerata, Scorpiones, Buthidae) with description of a new species to India. *Memorie della Società Entomologica Italiana*, 78(2): 295–303.

LOURENÇO, W. R. 2001. A remarkable fossil scorpion from the amber of Lebanon. Implications for the phylogeny of Buthoidea. *Comptes Rendus des Séances de l'Académie des Science*, 332: 641–646.

LOURENÇO, W. R. 2002. The first scorpion fossil from the Cretaceous amber of Myanmar (Burma). New implications for the phylogeny of Buthoidea. *Comptes Rendus Palevol*, 1: 97–101.

LOURENÇO, W. R. 2003. The first scorpion fossil from the Cretaceous amber of France. New implications for the phylogeny of Chactoidea. *Comptes Rendus Palevol*, 2(3): 213–219.

LOURENÇO, W. R. & J.-C. GALL. 2004. Fossil scorpions from the Buntsandstein (Early Triassic) of France. *Comptes Rendus Palevol*, 3(5): 369–378.

LOURENÇO, W. R. & P. GENIEZ. 2005. A new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Morocco. *Euscorpius*, 19: 1–6.

LOURENÇO, W. R., H. HENDERICKX & W. WEITSCHAT. 2005. A new genus and species of fossil scorpion from Baltic amber (Scorpiones, Buthidae). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg,* 89: 159–166.

LOURENÇO, W. R. & W. WEITSCHAT. 1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion "*Tityus eogenus*" Menge, 1869 can finally be clarified. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg,* 79: 189–193.

LOURENÇO, W. R. & W. WEITSCHAT. 2000. New fossil scorpions from the Baltic amber – implications for Cenozoic biodiversity. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 84: 247–260.

LOURENÇO, W. R. & W. WEITSCHAT. 2001. Description of another fossil scorpion from the Baltic amber, with considerations on the evolutionary levels of Cenozoic Buthoidea. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg,* 85: 277–283.

LOURENÇO, W. R. & W. WEITSCHAT. 2005. A new genus and species of fossil scorpion from a different kind of Baltic amber (Scorpiones, Buthidae). *Mitteilungen aus dem Geologisch-*

Paläontologischen Institut der Universität Hamburg, 89: 183–188.

POINAR, G. O. JR. & R. MILKI. 2001. *Lebanese Amber the Oldest Insect Ecosystem in Fossilized Resin*. Oregon State University Press: Corvallis, Oregon, USA, 96 pp.

POINAR, G. O. JR. & R. POINAR. 1994. *The Quest for Life in Amber*. Addison-Wesley: Wesley, Massachusetts, USA, 219 pp.

RASNITSYN, A. P. & D. L. J. QUICKE (eds). 2002. *History of Insects*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 517 pp.

ROSS, A. 1999. *Amber*. Harvard University Press. Cambridge, Massachusetts, USA, 74 pp.

ROTH, B., G. O. POINAR, JR., A. ACRA & F. ACRA. 1996. Probable pupillid land snail of Early Cretaceous (Hauterivian) age in amber from Lebanon. *Veliger*, 39(1): 87–88.

SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & S. R. ANDERSON. 2004a. A new genus and subfamily of scorpions from Cretaceous Burmese amber (Scorpiones: Chaerilidae). *Revista Ibérica de Aracnología*, 9: 3–14.

SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & P. R. CRAIG. 2004b. The second Cretaceous scorpion specimen from Burmese amber (Arachnida: Scorpiones). *Journal of Systematic Palaeontology*, 2(2): 147–152.

SANTIAGO-BLAY, J. A., M. E. SOLEGLAD & V. FET. 2004c. A redescription and family placement of *Uintascorpio* Perry, 1995 from the Parachute Creek Member of the Green River Formation (Middle Eocene) of Colorado, USA (Scorpiones: Buthidae). *Revista Ibérica de Aracnología*, 10: 7–16.

SANTIAGO-BLAY, J. A., J. B. LAMBERT & Y. WU. 2002. Chemical analyses of fossil and modern plant exudates using C-13 (solid state nuclear magnetic resonance spectroscopy). *In, Geological Society of America. Annual Meetings and Exposition Abstracts. Science at the highest level. October 27–30, 2002*. Denver, Colorado, USA, p. 428.

SCHLEE, D. 1972. Bernstein aus dem Lebanon. *Kosmos*, 68: 46–463.

SCHLEE, D. & H. G. DIETRICH. 1970. Insectenführender Bernstein aus der Unterkreide des Libanon. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Monatshefte*, 1970: 40–50.

SCHMIDT, A. R., H. VON EYNATTEN & M. WAGREICH. 2001. The Mesozoic amber of Schliersee (southern Germany) is Cretaceous in age. *Cretaceous Research*, 22(4): 423–428.

SELDEN, P. A. & J. R. NUDDS. 2004. *Evolution of Fossil Ecosystems*. Manson Publishing: London, England, UK, 160 pp.

SISSOM, W. D., G. A. POLIS & D. D. WATT. 1990. Field and laboratory methods. pp. 445–461. *In*, Polis, G. A. (ed.). *Biology of Scorpions*. Stanford University Press: Stanford, California, USA, 587 pp.

SOLEGLAD, M. E. & V. FET. 2001. Evolution of scorpion orthobotriotaxy: a cladistic approach. *Euscorpius*, 1: 1–38.

SOLEGLAD, M. E. & V. FET. 2003. High-level phylogeny and systematics of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11:1–175.

TAYLOR, T. N. & E. L. TAYLOR. 1993. *The Biology and Evolution of Fossil Plants*. Prentice Hall: Englewood Cliffs, New Jersey, USA, 982 pp.

TIKADER, B. K. & D. B. BASTAWADE. 1983. *The Fauna of India. Vol. 3. Scorpions (Scorpionida: Arachnida)*. Zoological Survey of India, Calcutta, 671 pp.

VACHON, M. 1950. Subsidios para o estudo da biologia na Lunda. Remarques sur les scorpions de l'Angola (Première note). *Publicacões Culturais da Companhia de Diamantes Angola* (Luanda), 1950: 5–18.

VACHON, M. 1974. Etude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 3 (140): 857–958.

VACHON, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. *Comptes Rendus des Séances de l'Académie des Science, Paris,* (D), 281 (21): 1597–1599.

VAN BERGEN, P. F., M. E. COLLINSON, A. C. SCOTT & J. W. DE LEEUW. 1995. Unusual resin chemistry from Upper Carboniferous pteridosperm resin rodlets. Pp. 149-169 *In*, Anderson, K. B. & J. C. Crelling (eds). 1995. *Amber, Resinite, and Fossil Resins. Developed from a symposium sponsored by the Division of Geochemistry, Inc., at the 208th National Meeting of the American Chemical Society. Washington, D.C. August 21–24, 1994.* American Chemical Society: Washington, District of Columbia, USA, 296 pp.

ZHERIKHIN, V. V. & K. Y. ESKOV. 1998. Mesozoic and Lower tertiary resins in former USSR. p. 51. *In, World Congress on Amber Inclusions. 20–23 October 1998. Vitoria-Gasteiz* [Alava, Basque Country (Spain)], 175 pp.
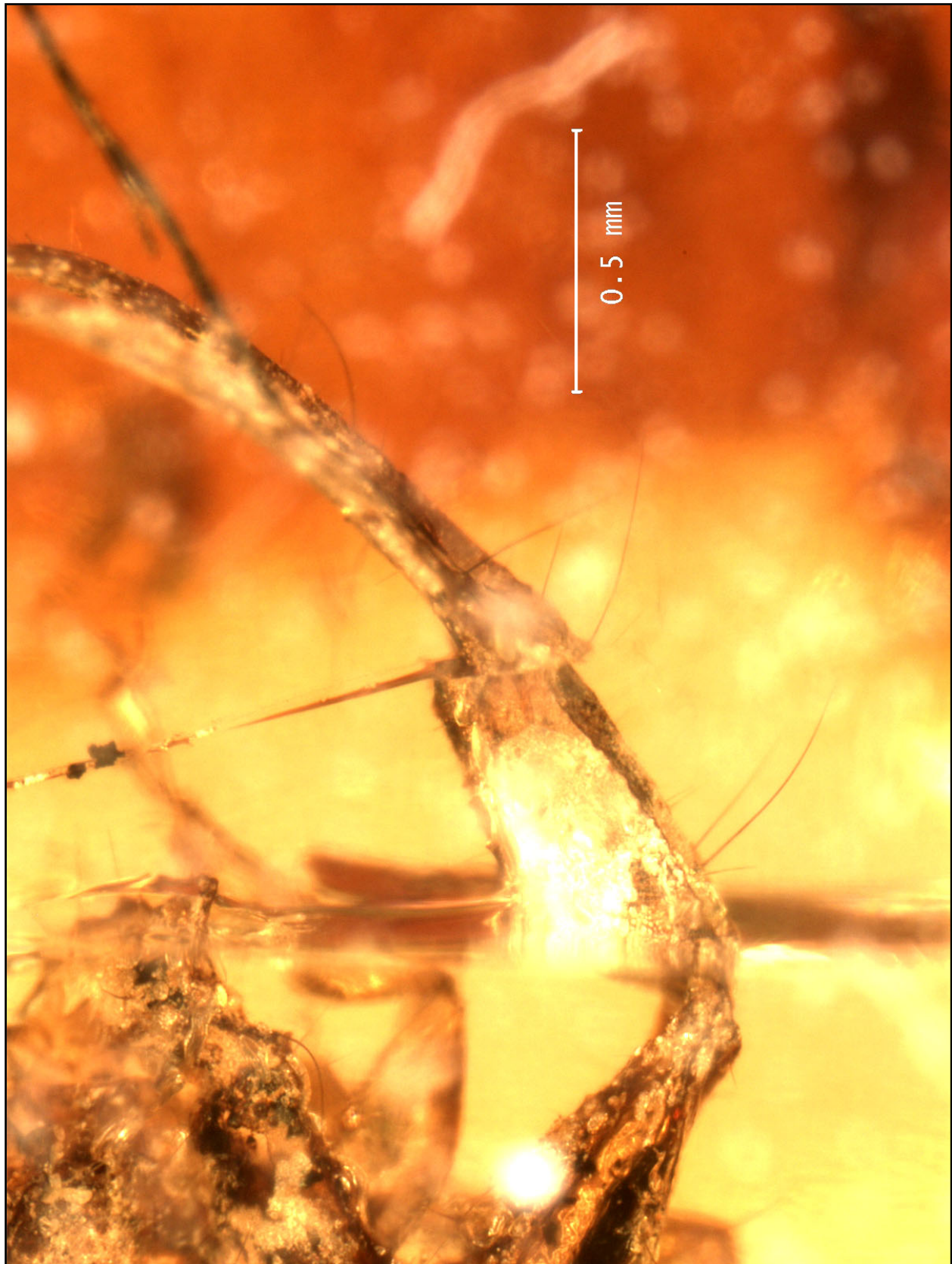
Figure 36: *Archaeobuthus estephani*. Dorsoexternal view of pedipalpal chela showing trichobothria *Eb$_1$*, *Eb$_2$*, *Est*, *Et$_1$*, *eb*, *est*, *et*, and *db*.

Figure 37: *Archaeobuthus estephani.* Ventral view of pedipalp chelal palm showing trichobothria Eb_1, Eb_2, V_1 (areola only), *Est*, and Et_1.

Figure 38: *Archaeobuthus estephani*. Dorsoexternal view of pedipalp chelal fixed finger showing trichobothria *eb*, *est*, *et*, *db*, and *dt* (areola only).
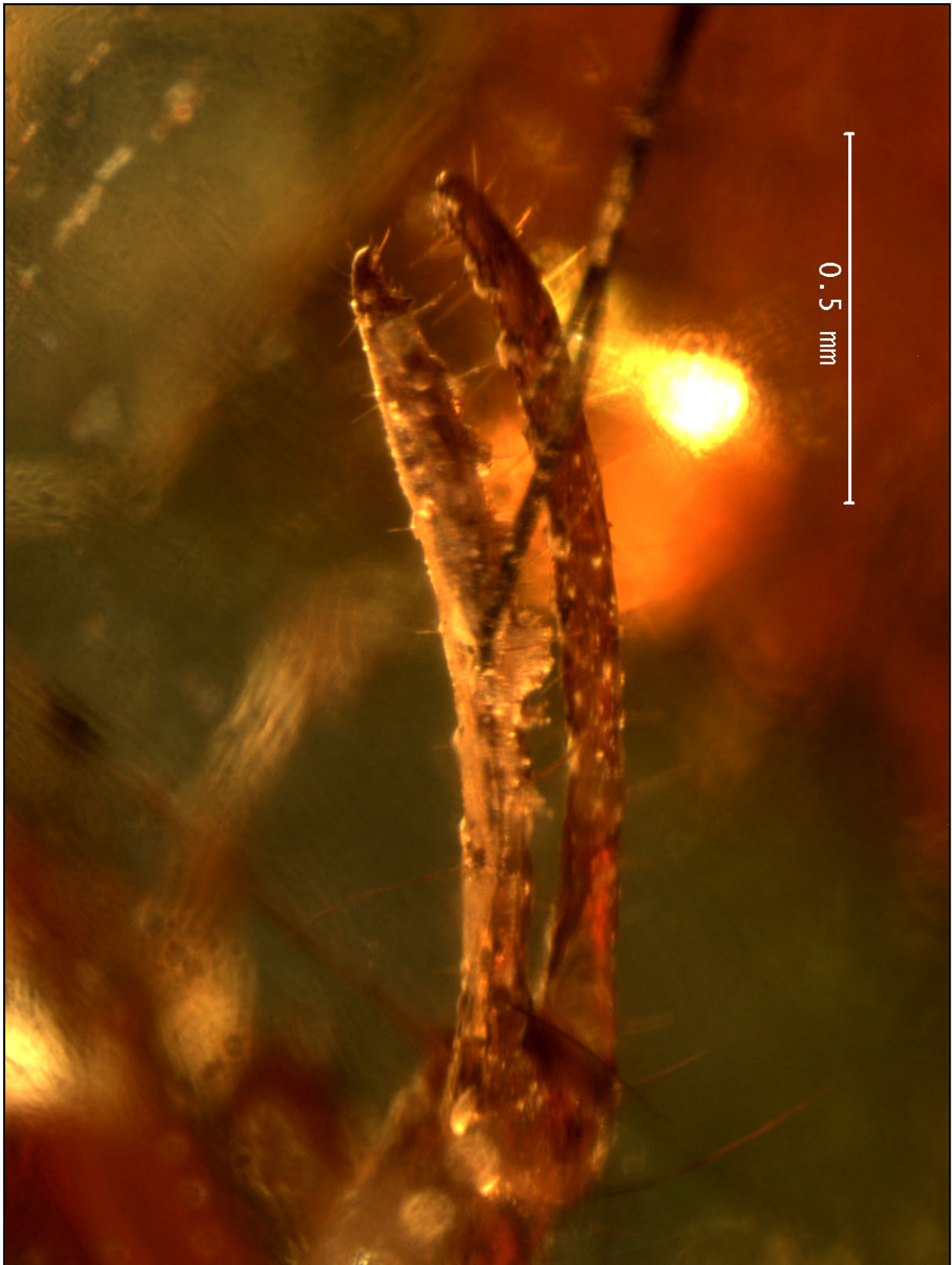
Figure 39: *Archaeobuthus estephani*. External view of pedipalp chelal fixed finger showing trichobothria *Est*, *Et₁*, *eb*, *est*, *et*, *db*, and *dt* (areola only).
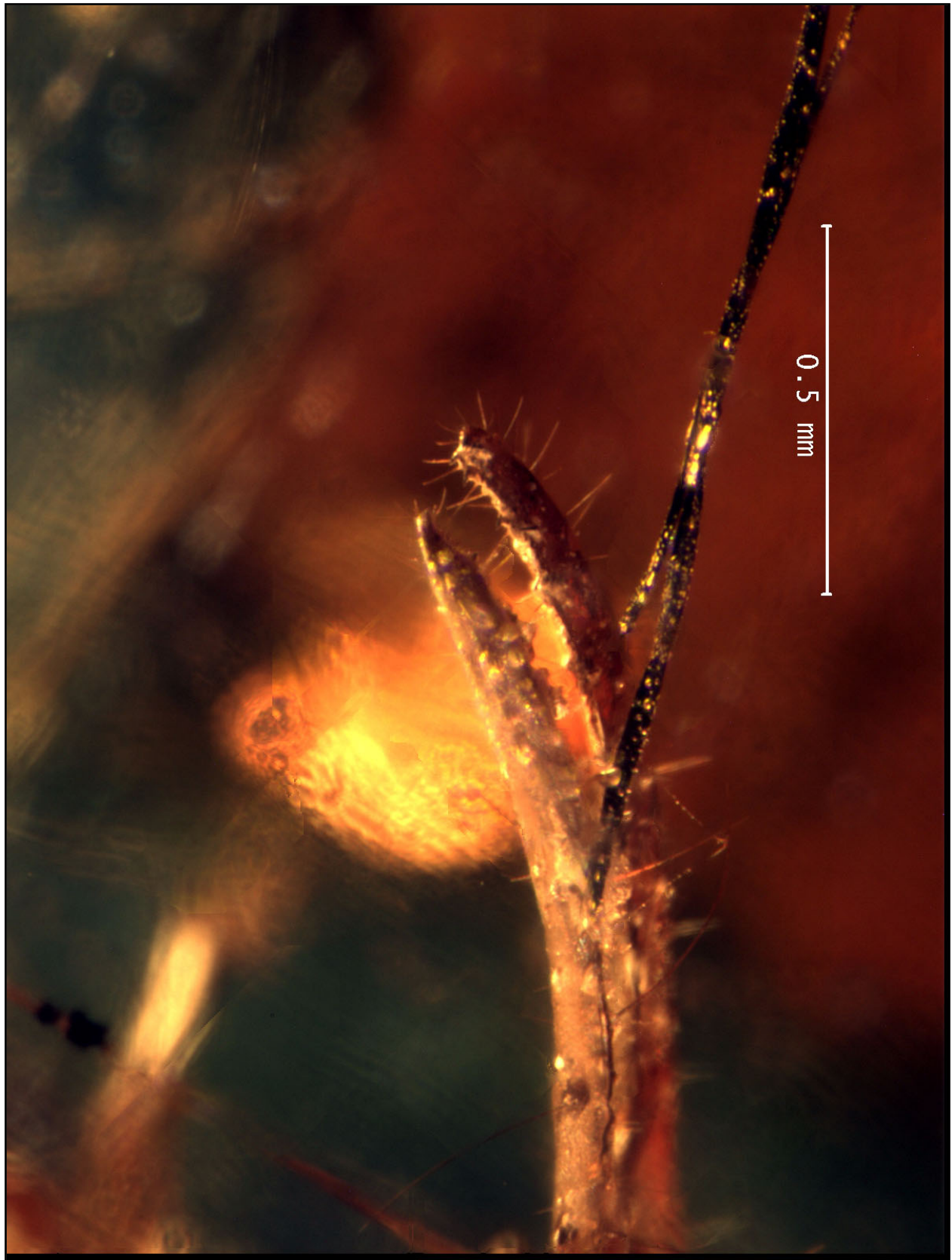
Figure 40: *Archaeobuthus estephani*. Pedipalp chelal fingers showing dentition on distal aspects.
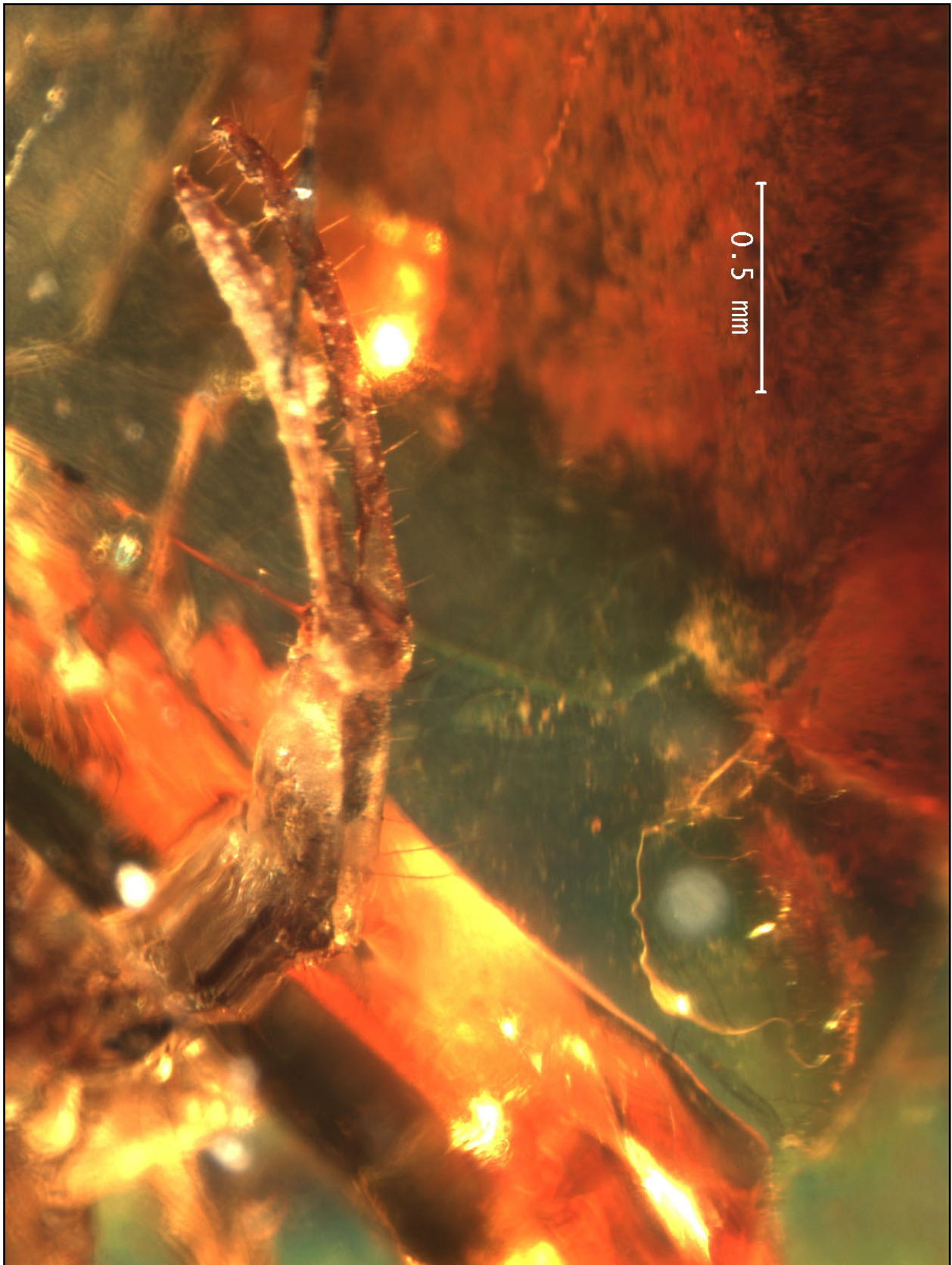
Figure 41: *Archaeobuthus estephani*. Dorsoexternal view of pedipalpal chela showing trichobothria Eb_1, Eb_2, Est, and *db*.
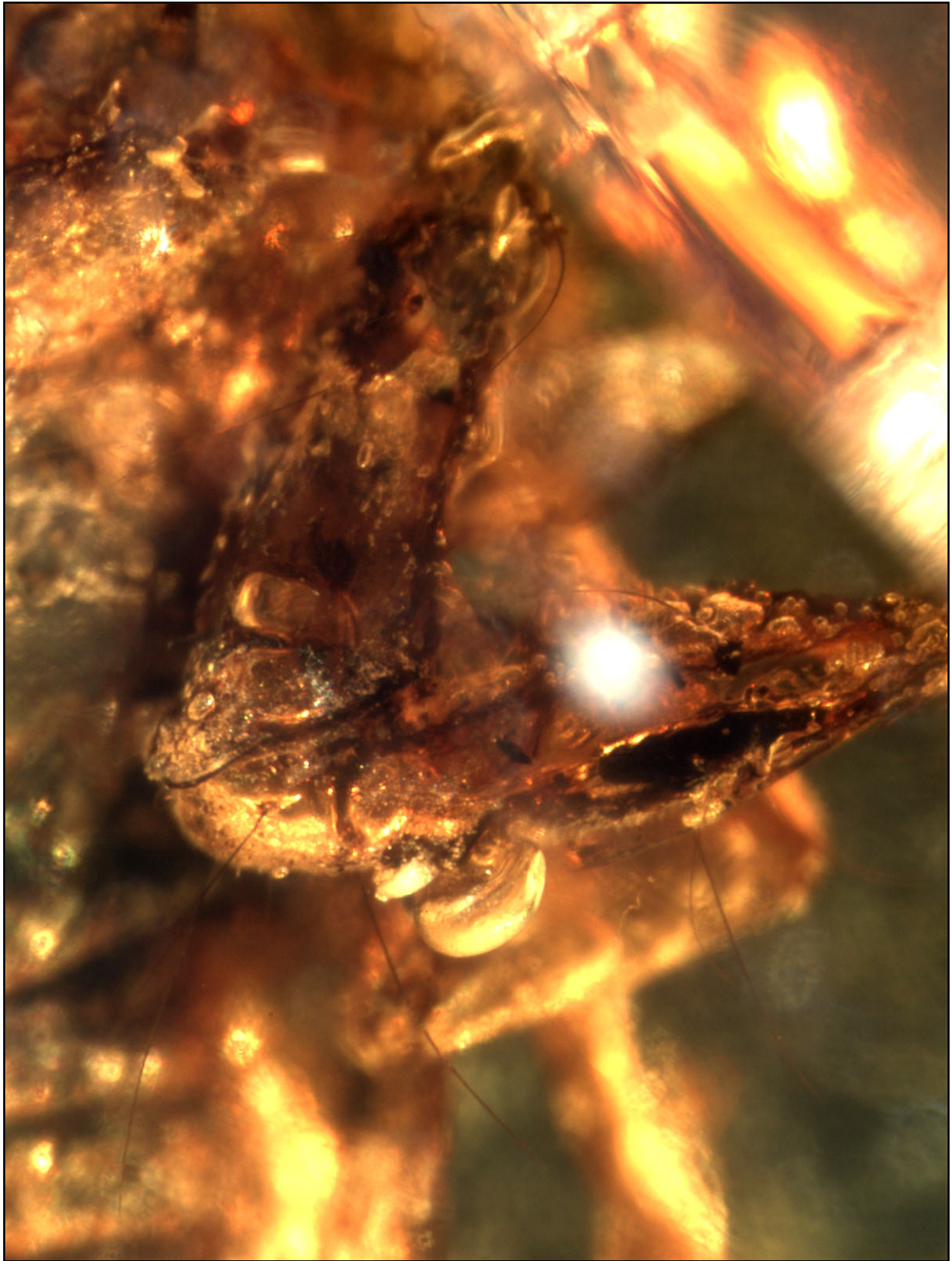
Figure 42: *Archaeobuthus estephani*. Dorsal view of pedipalpal femur and patella showing trichobothria. Patella: d_1, d_3, i, eb_1, esb_1, est, and et_1; femur: d_3 and i_1.
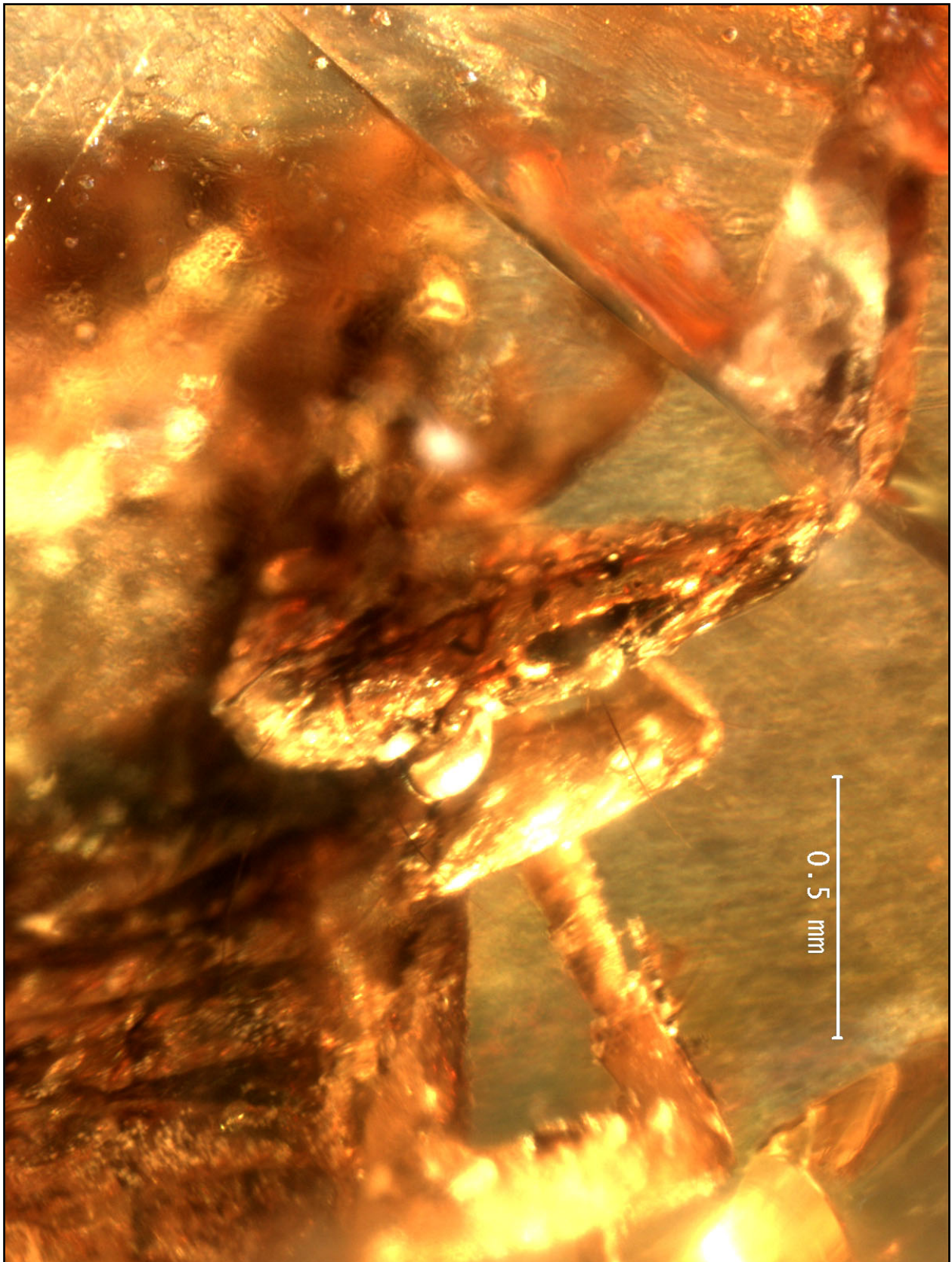
Figure 43: *Archaeobuthus estephani*. Pedipalpal patella showing four external trichobothria, *eb₁*, *esb₁*, *est*, and *et₁*.
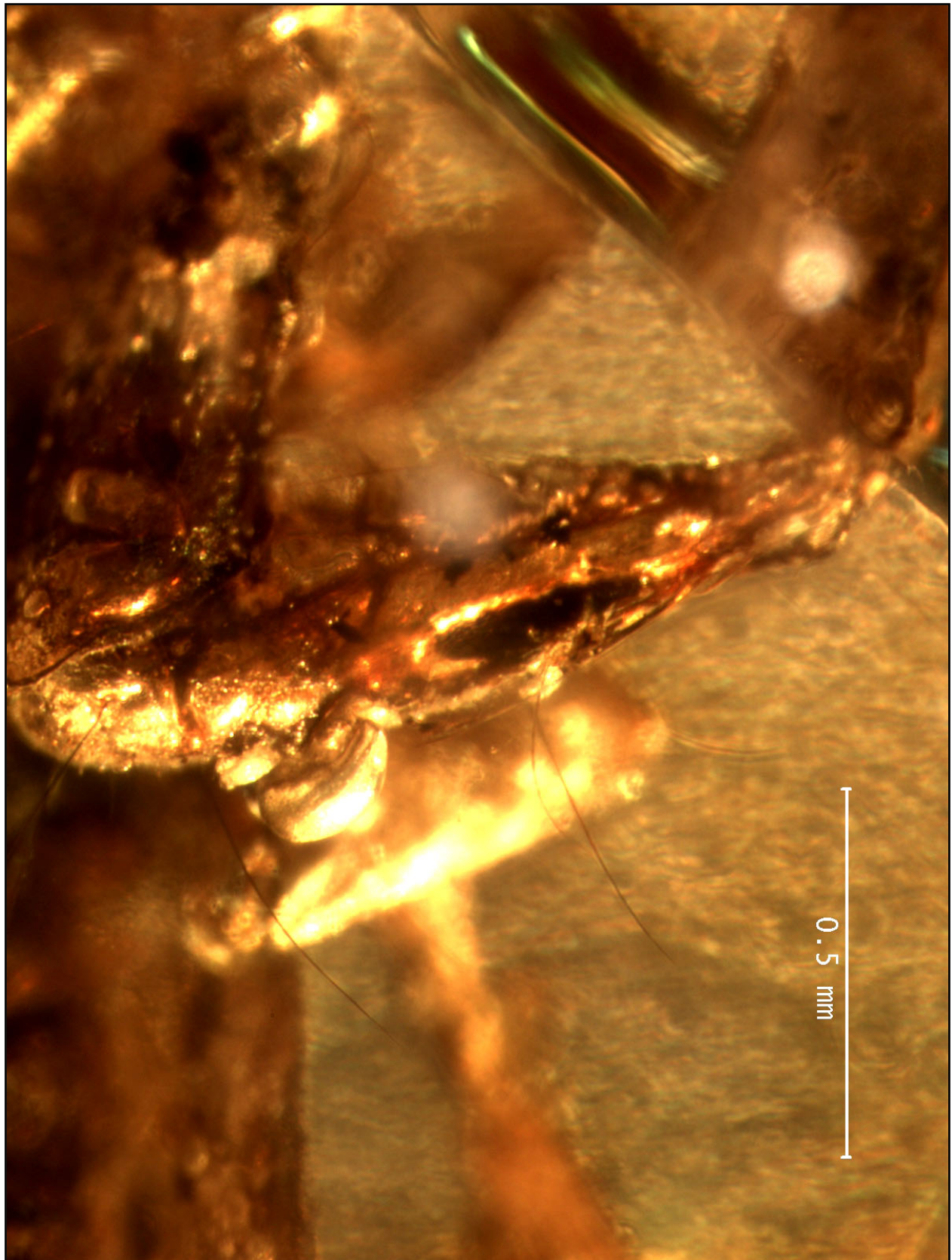
Figure 44: *Archaeobuthus estephani*. Pedipalpal patella showing trichobothria d_1, d_3, i, esb_1, est, and et_1.

Figure 45: *Archaeobuthus estephani*. Pedipalpal femur and patella showing trichobothria. Patella: d_1, d_3, eb_1, esb_1, est and et_1; femur: d_2, d_3, d_4, d_5, e_3, i_1, i_2, and i_3.
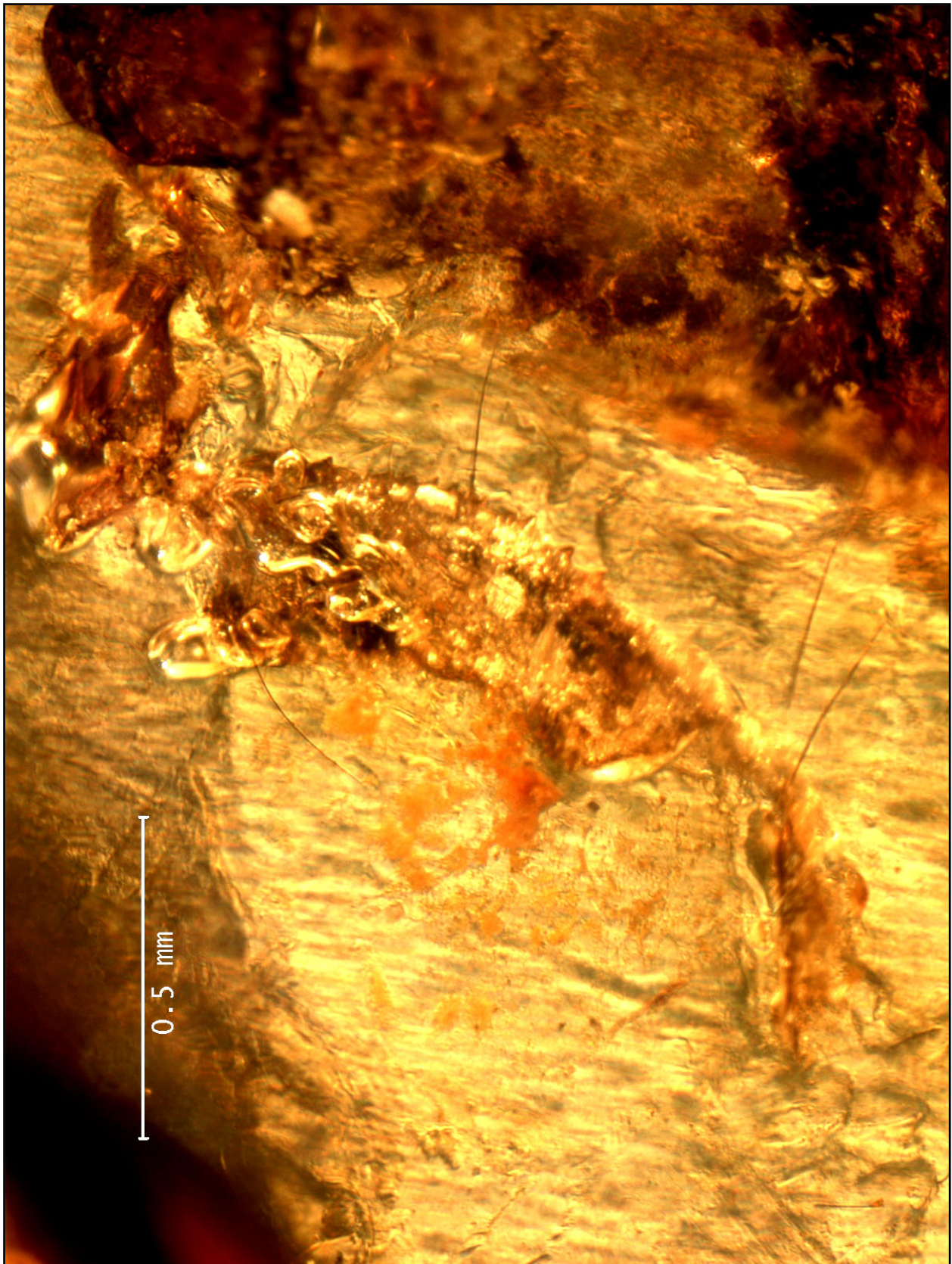
Figure 46: *Archaeobuthus estephani.* Dorsal view of left pedipalpal femur and patella (basal extremity only) showing trichobothria *i* and e_3 on femur and d_1 and eb_1 on patella.
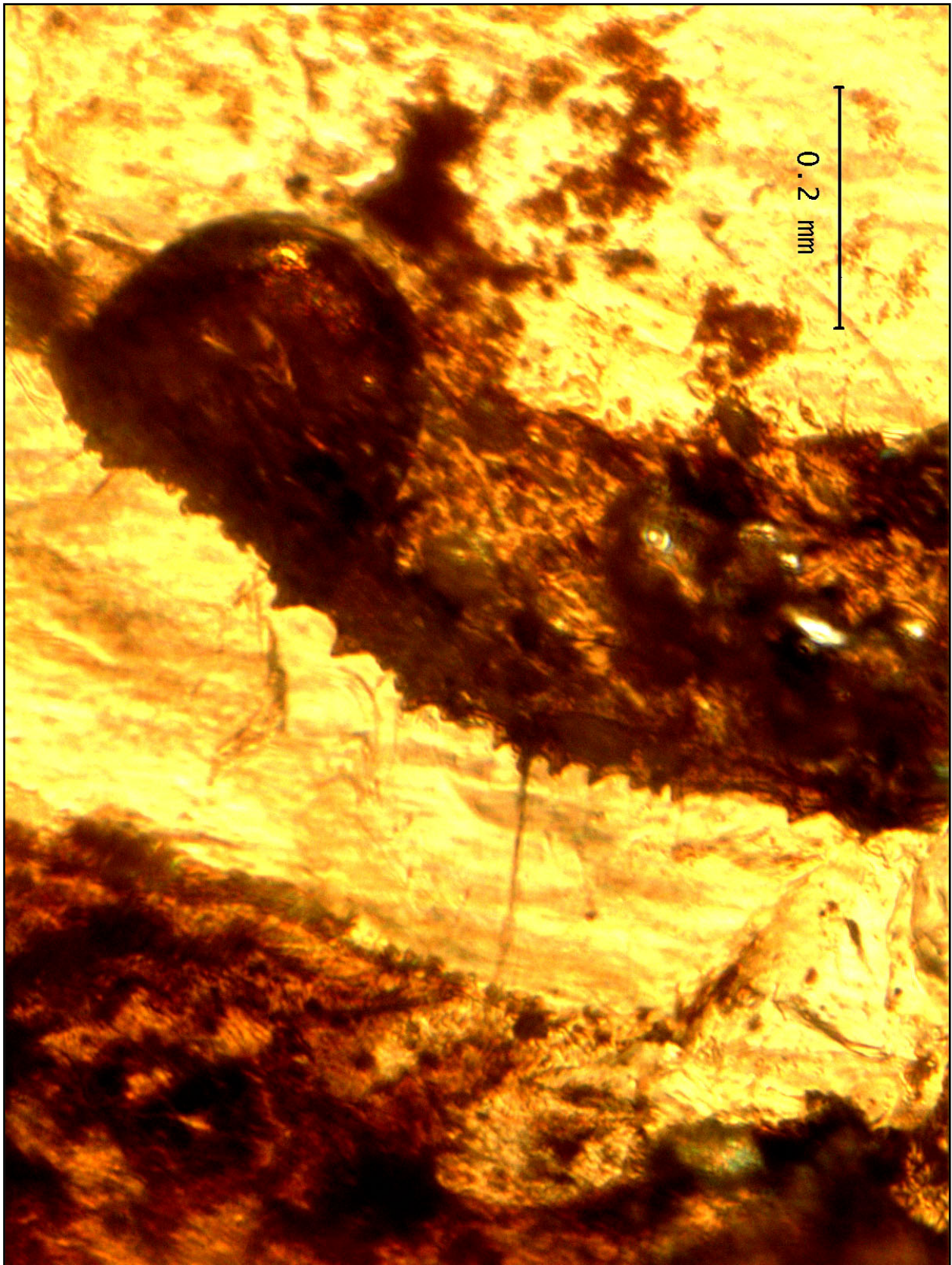
Figure 47: *Archaeobuthus estephani*. Left pedipalpal femur dorsal view showing trichobothria *i* and e_3, and the heavy serration of the ventroexternal carina.
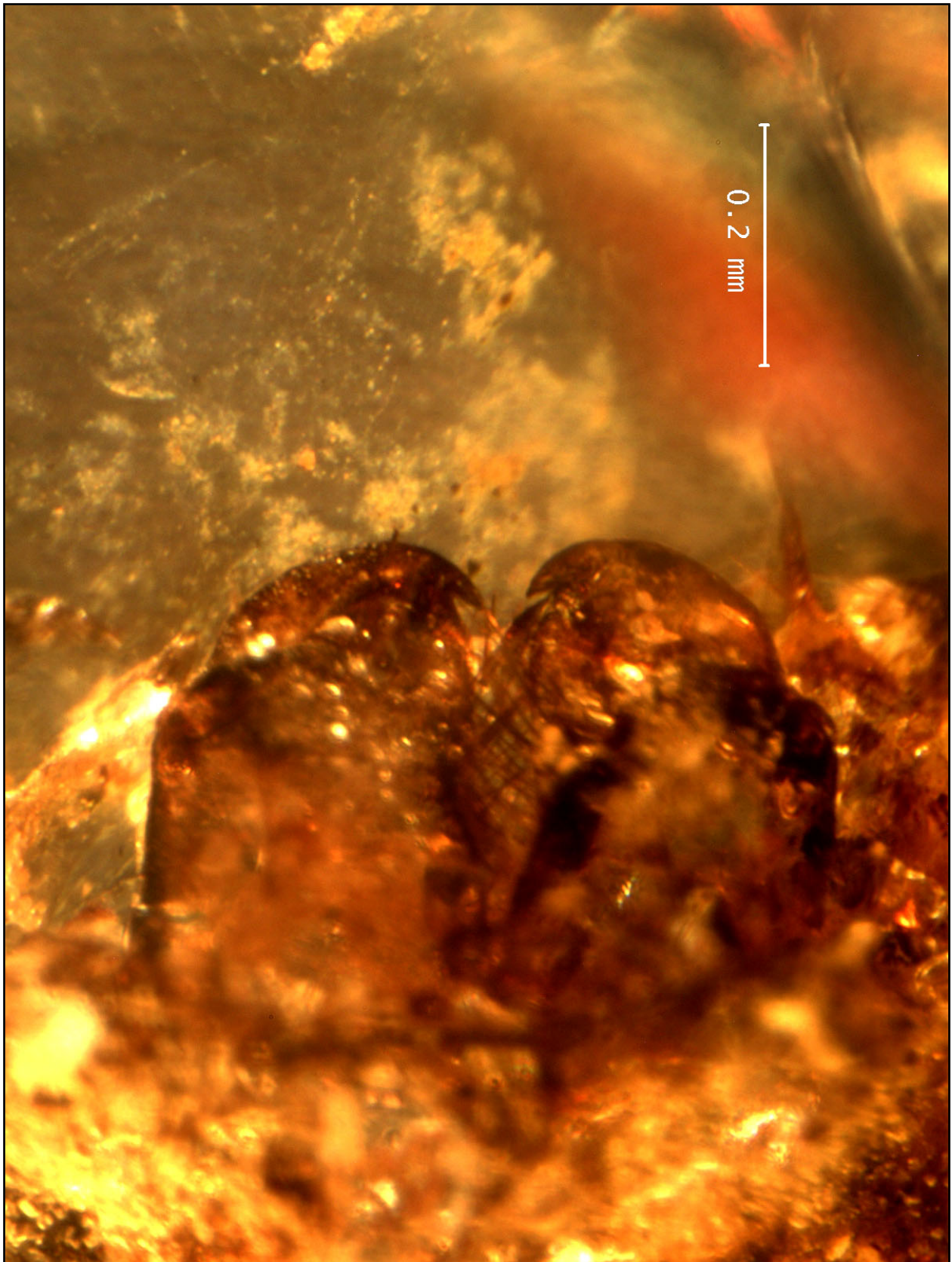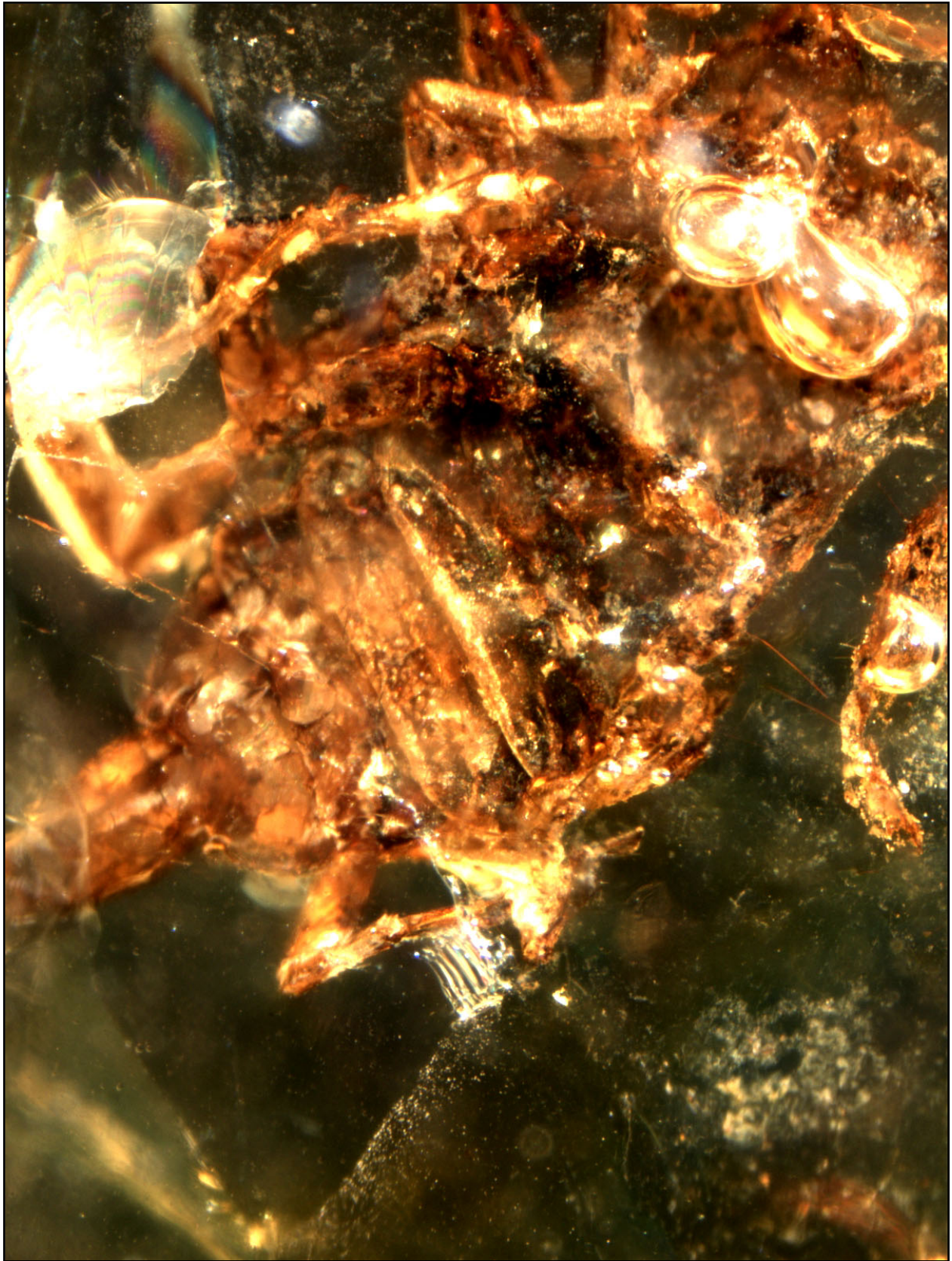
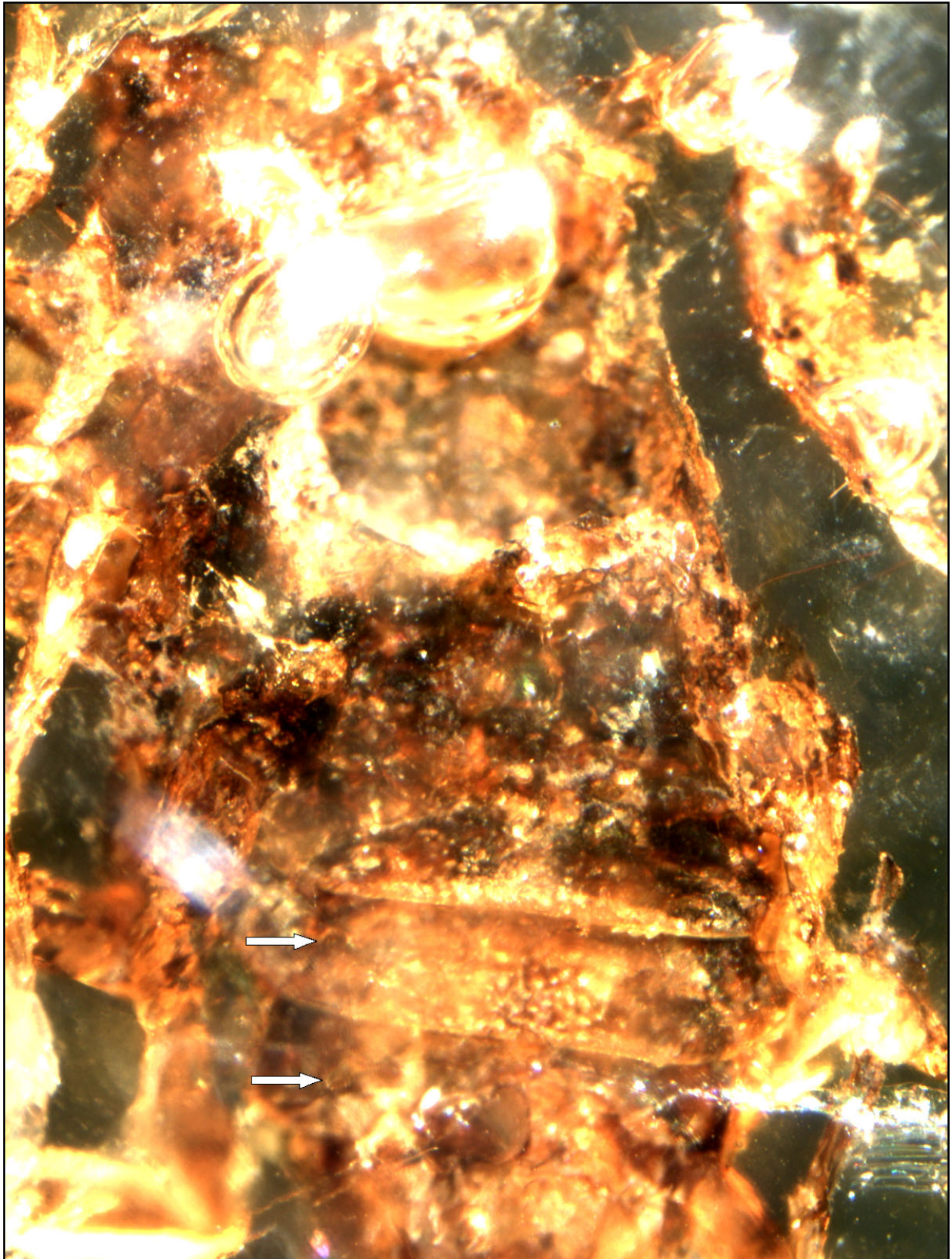**Figure 48:** *Archaeobuthus estephani*. Closeup dorsal view of chelicerae.
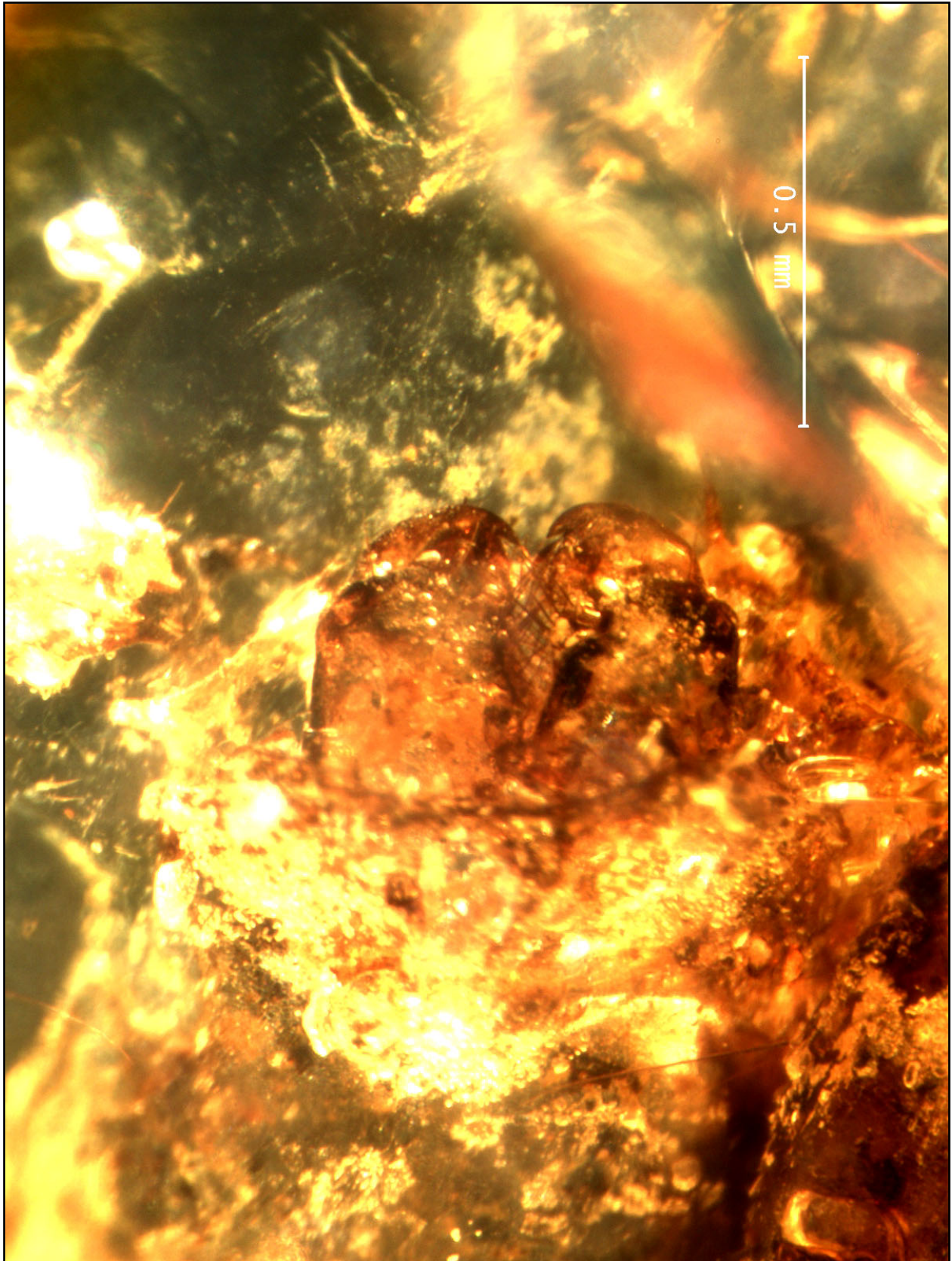
Figure 49: *Archaeobuthus estephani*. Dorsal view of carapace anterior edge and chelicerae.
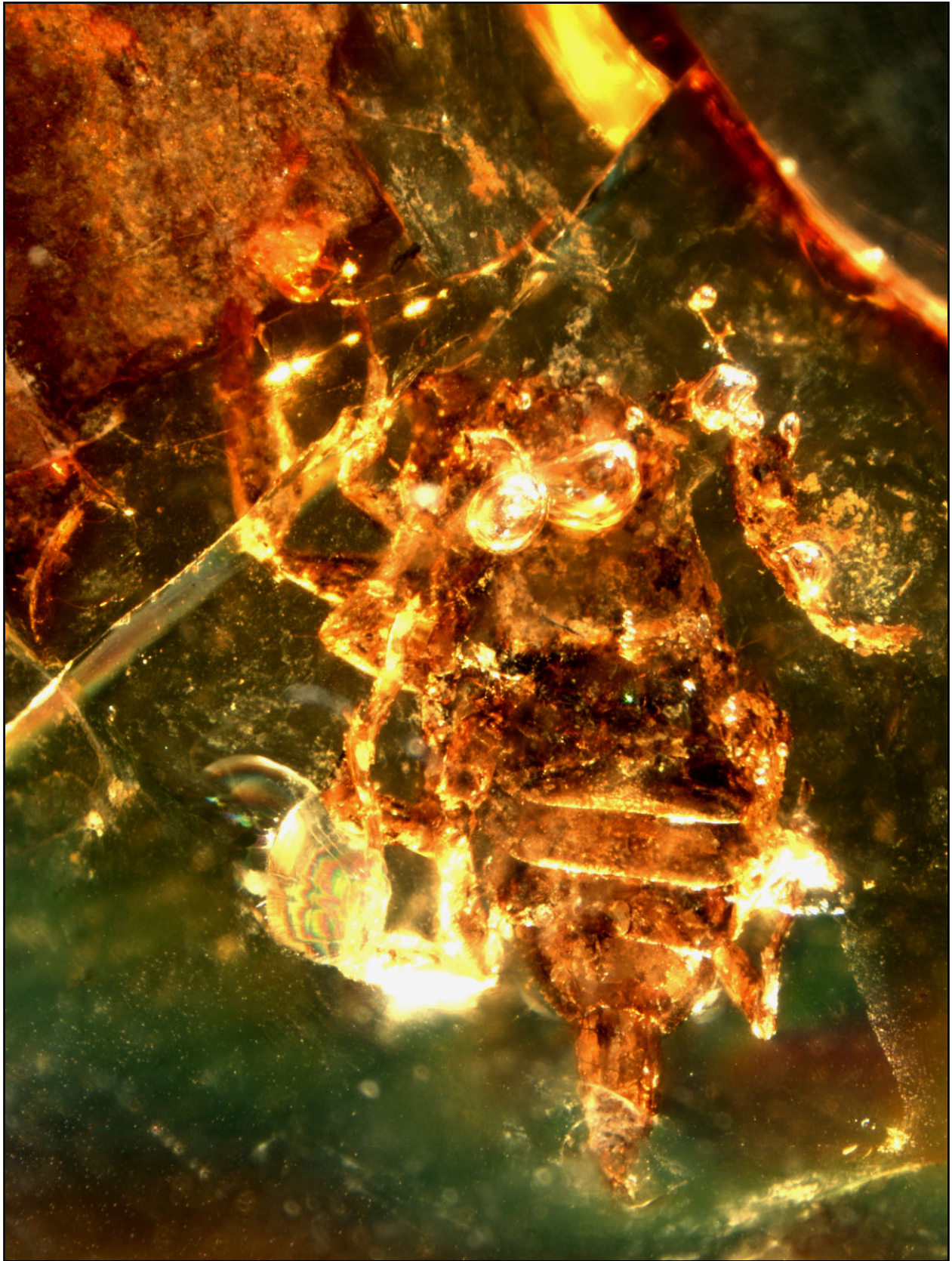
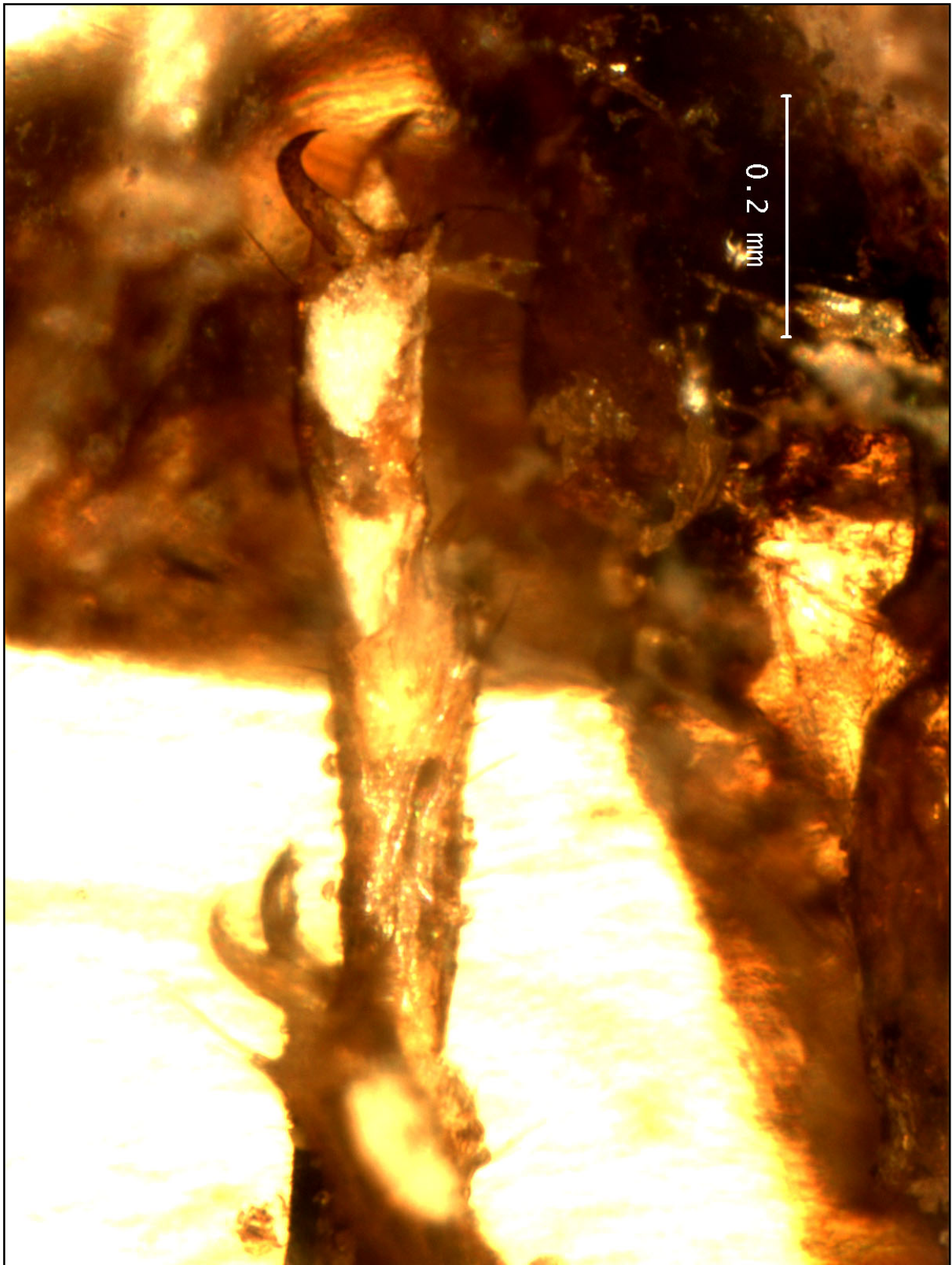**Figure 50:** *Archaeobuthus estephani*. Overall ventral view.

Figure 51: *Archaeobuthus estephani*. Ventral view showing sternal plates and metasomal segment I.

Figure 52: *Archaeobuthus estephani*. Ventral view showing right stigma (indicated by white arrows) on sternites III and IV.

Figure 53: *Archaeobuthus estephani*. Right leg III showing basitarsus, tarsus, epitarsus, and retrolateral pedal spur.

Figure 54: *Archaeobuthus estephani*. Right leg IV showing tibia (partial), basitarsus, tarsus, epitarsus, and pedal spurs.