X-ray micro-CT reconstruction reveals eight antennomeres in a new fossil taxon that constitutes a sister clade to *Dundoxenos* and *Triozocera* (Strepsiptera: Corioxenidae)

Hans Henderickx, Jan Bosselaers, Elin Pauwels, Luc Van Hoorebeke, and Matthieu Boone

ABSTRACT

Eocenoxenos palintropos gen. nov. et sp.nov., a new fossil strepsipteran taxon from Baltic amber is described. The position of the new genus is based on cladistic analyses of morphological data sets. Most data of the fossil where retrieved with 3D micro-CT scan reconstructions. The new taxon is unambiguously situated as a sister group of the Dundoxenos-Triozocera clade within the Corioxenidae. The eocene taxon combines derived characteristics typical of Corioxenidae with the posession of eight antennomeres with five long flabella, a regained ancestral characteristic.

Hans Henderickx. Department of Biology, Universiteit Antwerpen, Groenenborgerlaan 171, 2020 Antwerpen, Belgium (Address for correspondence: Hemelrijkstraat 4, B-2400 Mol, cavexplorer@gmail.com

Jan Bosselaers. Section of invertebrates, Royal Museum for Central Africa, B-3080 Tervuren, Belgium dochterland@telenet.be

Elin Pauwels. Department of Physics and Astronomy, Gent University, Proeftuinstraat 86, B-9000 Gent, Belgium elin.pauwels@UGent.be

Luc Van Hoorebeke. Department of Physics and Astronomy, Gent University, Proeftuinstraat 86, B-9000 Gent, Belgium luc.vanhoorebeke@UGent.be

Matthieu Boone. Department of Physics and Astronomy, Gent University, Proeftuinstraat 86, B-9000 Gent, Belgium matthieu.boone@UGent.be

INTRODUCTION

Strepsiptera are regularly reported from Baltic amber. The fossil tree resin functioned in a way similar to a trunk eclector trap (Dubois and LaPolla, 1999) often capturing invertebrates that are seldom encountered in the field, for example because they are rare or have very short active adult live spans.

Most of these Strepsiptera fossils are closely related to representatives of extant genera or species (Pohl et al., 2005; Kathirithamby and Henderickx, 2008). However, Eocene Baltic amber also contains some typical ancestral forms: the extinct genus *Mengea* Grote, 1886 is only found in Baltic amber and in 2005 *Protoxenos janzeni* Pohl et al. was described, wich has a very basal position in the group.

The new Baltic amber fossil examined here was purchased on an auction on eBay from an amber dealer in Lithuania in March 2011. It showed a puzzling combination of characteristics and could not be placed in any of the recognized genera. Its phylogenetic position is evaluated cladistically, and a new species and new genus is described.

MATERIALS AND METHODS

Amber Fossil

The examined strepsipteran is fossilized in a 24.9 x 20.4 x 10.3 mm piece of Baltic amber (Figure 1.1). The specimen is mostly intact, and the left hind wing is spread. Larger parts of the body are covered with opaque whitish amber, 'Baltic mould' (Figures 1.1, 2.1), which obscures especially the ventral side. The inclusion reaches the surface of the amber matrix with a tip of the hind wing, some amber crazing (cracks and degeneration) and some brown discoloration appear near this tip, and before further manipulation the surface was stabilized with a coating of 0.5 mm ARALDITE 2020 epoxy, using the technique described in Henderickx et al., 2006, which allows further optical observation without repolishing. Optically visible details were observed and measured using reflected and translucent illumination on a Leitz microscope and a Canon MP-E objective in combination with Zerene stacker image processing software.

X-ray Scanning and Reconstruction

The amber sample was scanned at the 'Centre for X-ray Tomography' of the Gent University (UGCT; www.ugct.ugent.be) (Masschaele et al, 2007). UGCT develops its own micro- and nano-CT scanners which are characterized by a modular structure. In this way optimal scanning parameters, such as the detector, X-ray tube, and filter materials, can be selected for each sample. For this sample the transmission head of a dual head X-ray tube from Feinfocus (FXE 160) was chosen as a source and an a:Si flat panel (PerkinElmer XRD 1620 CN3 CS) with CsI scintillator was used as detector. The X-ray tube was operated at 100kV. The voxel size achieved for this sample was 3.0μm. Octopus (www.octopusreconstruction.com) (Vlassenbroeck et al, 2007), an in-house developed software package for parallel, fan, cone and helical cone beam geometry, was used for tomographic reconstruction. VGStudio MAX (www.volumegraphics.com) was used to render the 3D-volumes and to create an STL file. Based on this file, spatial 3D models could be created. Thomas Pilkington (Fablab, University Leuven) printed a white Acrylonitrile butadiene styrene (ABS) 3D model with fused depositioning modeling (10 cm large, layers of 0.254 mm) (Figure 2.2). Bart Grimonprez (Hogeschool West-Vlaanderen, Industrial Design Center) printed a black 3D model with polyjet modelling (5,5 cm large, layers of 0.028 mm, VeroBlack Plus). These prints appeared very useful in interpretation and observation of morphological details, such as the counting of the ommatidia and the observation of the flagellomeres.

Phylogenetic Analysis

Phylogenetic analyses were based on all 189 characters from the impressive data matrix of Pohl and Beutel (2005) and were performed using the computer programmes PAUP 4.0 beta 10 (Swofford, 2002), Winclada 1.00.08 (Nixon, 2002), TNT 1.1 (Goloboff et al., 2003, 2008b) and TreeRot v3 (Sorenson and Franzosa, 2007). Optimisation of character states and printing of the preferred tree was performed using Winclada, further layout modifications being executed in Adobe Photoshop Elements v8.0. All four cladistic programmes were run on a dual-core Intel iMac under a Windows XP virtual machine (VMware Fusion 2, VMware, Inc., 3401 Hillview Avenue, Palo Alto, California 94304, USA; Bugnion et al., 2000).

Abbreviations: ACCTRAN, accelerated transformation; ci, consistency index; ci-ex, consistency index excluding parsimony-uninformative characters; DELTRAN, delayed transformation; hi, homoplasy index; hi-ex, homoplasy index excluding parsimony-uninformative characters; rc, rescaled consistency index; ri, retention index; UNAMB, unambiguous optimisation.

SYSTEMATICS

Systematic Paleontology

Family Corioxenidae Kinzelbach, 1970

The new species belongs in the Corioxenidae based on the absence of mandibles, the reduced posterior part of the labium, the elongated abdominal segment IX, and the long penis (formerly called aedeagus, but see Hünefeld et al. (2011: 299) and
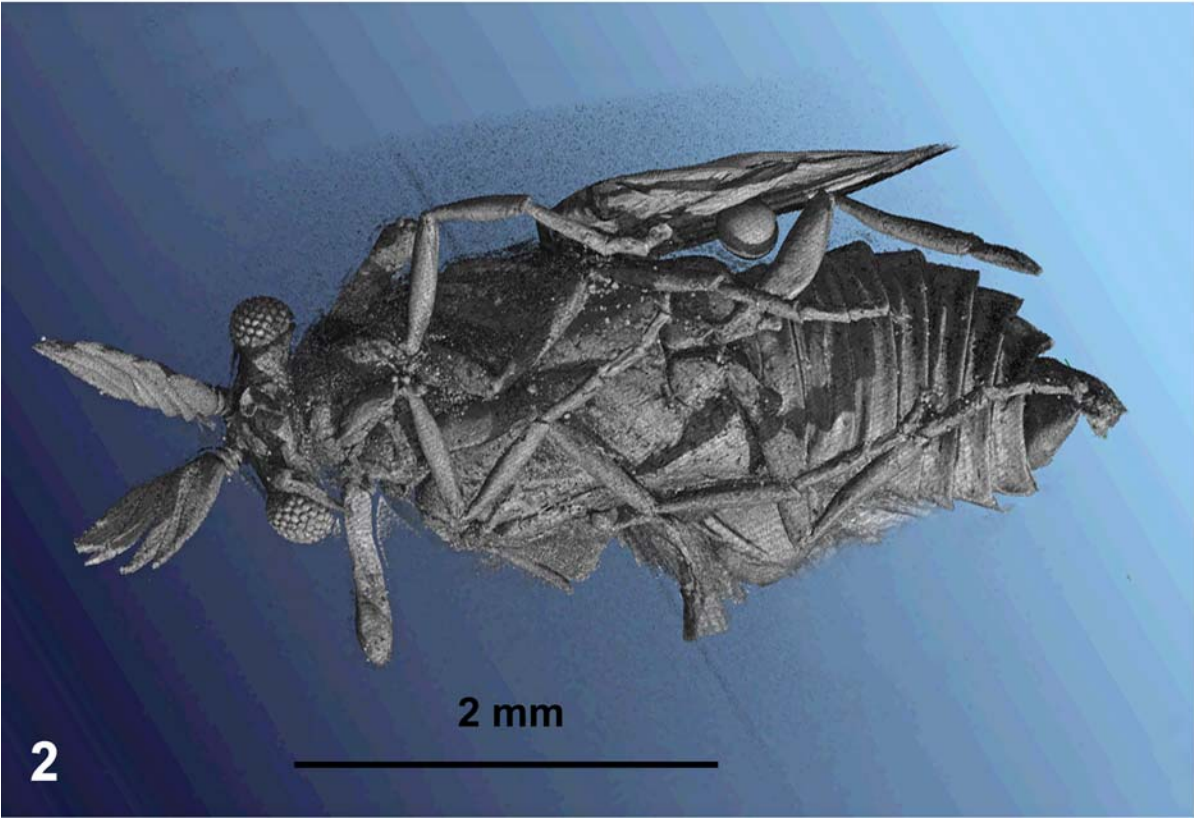
FIGURE 1. *Eocenoxenos palintropos* gen. nov. et sp.nov. 1.1: inclusion in amber, left lateral view, 1.2: micro-CT scan, reconstruction in VGL, ventral view.
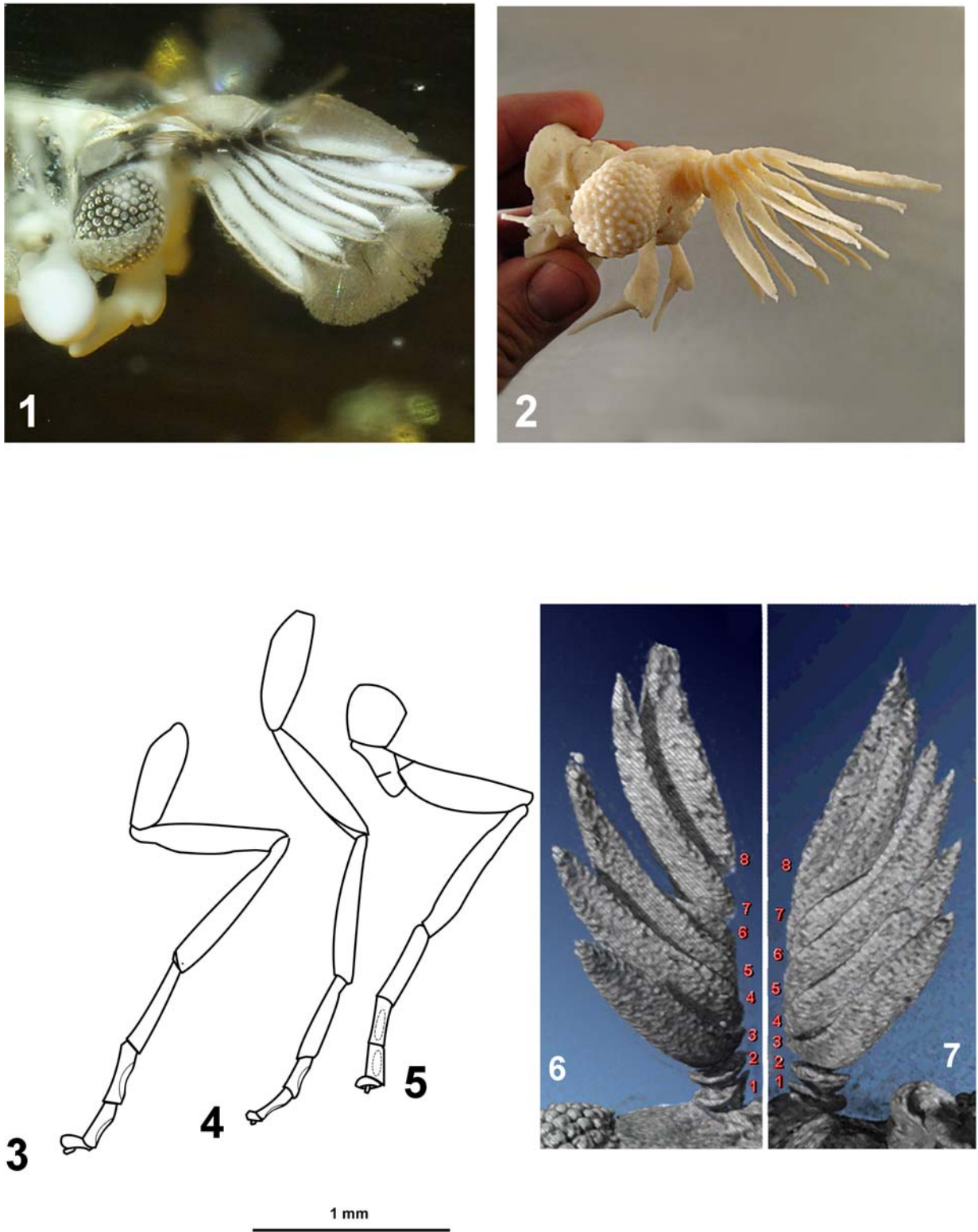
FIGURE 2. *Eocenoxenos palintropos* gen. nov. et sp.nov. 2.1: head with antenna, right lateral view. 2.2: Acrylonitrile butadiene styrene (ABS) 3D model with fused depositioning modeling (10 cm large, layers of 0.254mm). 2.3: prothoracic leg. 2.4: mesothoracic leg. 2.5: metathoracic leg. 2.6: micro-CT scan reconstruction of right antenna, ventral view, with numbered antennomeres. 2.7: micro-CT scan reconstruction of left antenna, ventral view, with numbered antennomeres.

Pohl et al. (2012: 81)), scored as character states 33:1, 49:3, 76:1, and 79:1 in the cladistic analysis discussed in the next part of the manuscript.

New genus: type species

Eocenoxenos Henderickx and Bosselaers, gen. nov.

http://zoobank.org/28E3CEDC-86D9-4EEB-B5CE-FD4094C48AAD

Type specimen: *Eocenoxenos palintropos* Henderickx and Bosselaers sp. nov.

Diagnosis

The males of the new genus can be recognized by the following unique combination of characters: Eight antennomeres (Figure 2.6-7) (character state 19:1), antennomeres III-VII being flabellate, mandibles absent, five tarsomeres with no claws and a shortened, triangular tarsomere IV (67:2), abdominal segment IX ventrally elongated for reception of the elongated penis.

Eocenoxenos shares the posession of five tarsomeres (62:0) and a slender tarsomere V (68:1) with the corioxenid genera *Dundoxenos* and *Triozocera* (Triozocerinae as defined by Kathirithamby (1989)) and *Proceroxenos* and *Uniclavus* (here considered the Uniclavinae of Kathirithamby (1989)). *Eocenoxenos* also differs from the genera in Triozocerinae and Uniclavinae by the absence of claws (63:3, a character state shared with all other Stylopidia) and by short antennomeres V, similar in length to antennomeres III (28:0), a character state also found in the corioxenid genera *Blissoxenos* and *Floridoxenos*, considered here subfamily Blissoxeninae as described by Miyamoto and Kifune (1984).

Etymology

The new genus-group name refers to the era in which Baltic amber was formed, the Eocene. The Appendix refers to the Greek 'ξενος', guest, stranger, commonly used in generic names of Strepsiptera.

New species

Eocenoxenos palintropos Henderickx and Bosselaers sp. nov.
(Figures 1, 2, 3, 4, 5)

http://zoobank.org/60F99337-16CE-440C-9E26-8318F5308EAD

Specimen provenance and deposition

The male holotype in Baltic amber was purchased in an auction on eBay in March 2011 by the first author and consecutively loaned to the RBIN (Royal Belgian Instistute of Natural Sciences – Entomology, Brussels) where it is available for study under registration number IG. 32.287 with the enlarged 3D prints, the microtomographic data, and the original and segmented slices.

Diagnosis

As for the genus (see above).

Description

Male holotype. Habitus Figure 5.1, body length 4.00 mm (all further measurements in mm), body with antenna 4.90; width of head 1.19; approximate length of antenna 1.00; length of hindwing 2.88; wingspan 6.64; forewing 0.88 x 0.16; length of metathorax 2.16. Colour very dark where not covered with whitish amber, antenna with white points (possibly chemoreceptors), ocelli bright with black interspace, however the color might be an effect of the fossilisation in amber. Head transverse, wide (Figure 5.2). Compound eye distinct, slightly oval in lateral view, right eye with 119, left eye with 122 ommatidia. Antenna 0.8 times as long as maximum width of head. Antennomeres 3-7 short, decreasing in width, Eight antennomeres, 5 flabellate antennomeres (flagellomeres I-V on antennomeres III-VII). Flabella long, flattened, widened medially, pointed. Flabella I-V all 4.3 times as long as maximum width, the flattened antennomere VIII slightly wider, 3.5 times as long as maximum width.

All 5 flabella approximately the same length, 0.40 mm.

Maxilla 2.1 times as long as wide, widening distally, palp1.3 times longer than maxilla, widening medially, pointed (Figure 5.2). Mandibles absent.

Venation hind wing (Figure 5.1) with vein R2 not present, R3 and R5 detached, R3 strongly developed. R5 long and running parallel to R4. CuA1 slightly shorter than CuA2.

Abdominal ninth segment (genital capsule) slender, segment X folded inwards on both sides, holding the tip of the long straight penis (Figure 5.3).

Legs (Figures 2.3-5, 4.1-6). Pro- and mesothoracic legs with trochanter and femur fused. Distal margin of tibiae straight. 5 tarsomeres without claws. Tarsomere 2 and 3 of all legs with an oval latero-ventral sensory spot that is dented in lateral view (compared with Pohl and Beutel, 2004). Basitarsus of prothoracic legs cylindrical, tarsomere 4 short-
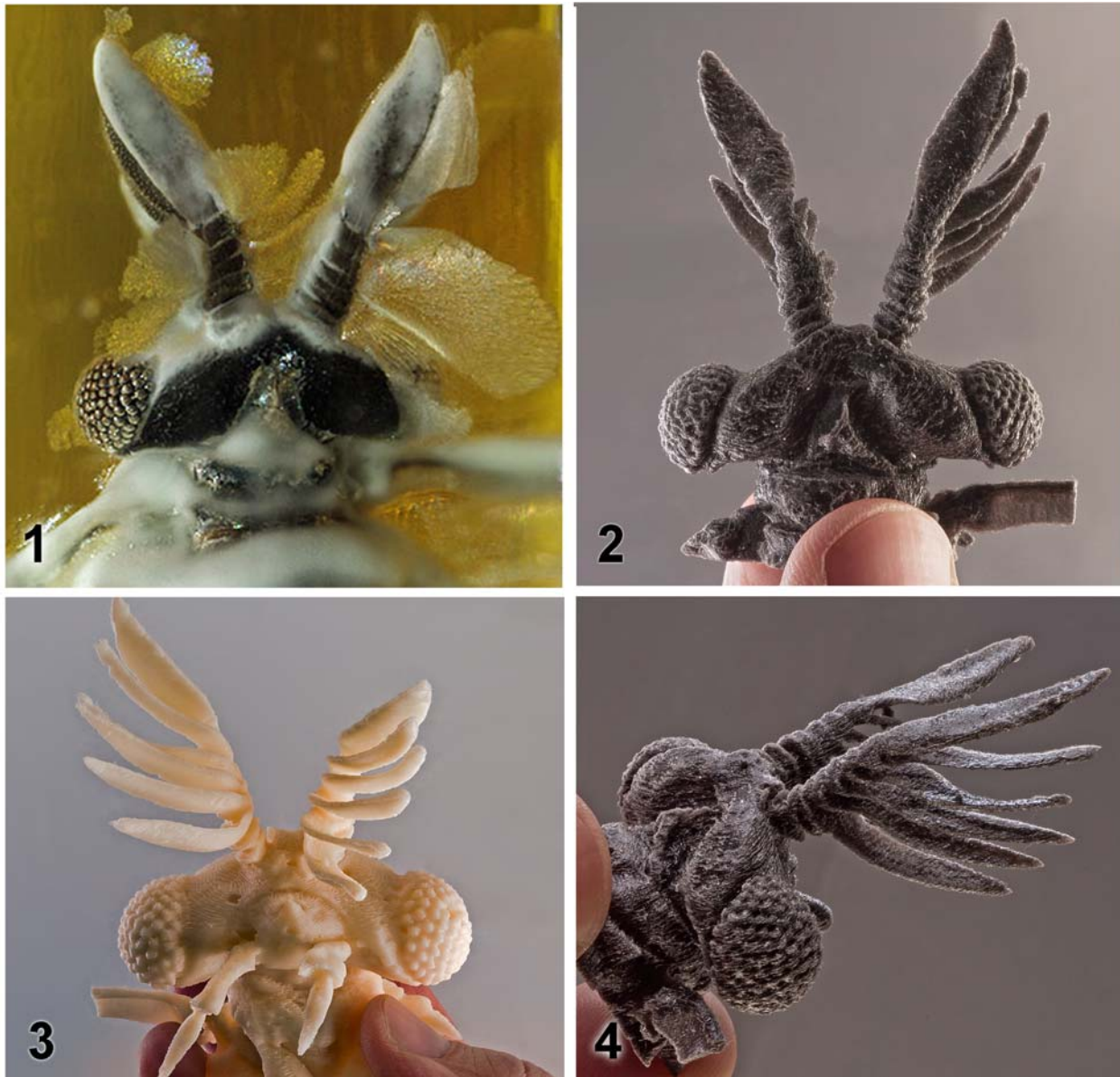
FIGURE 3. *Eocenoxenos palintropos* gen. nov. et sp.nov. (holotype). 3.1: head with antenna, dorsal view, in amber. 3.2: black 3D model with polyjet modelling (5,5 cm large, layers of 0.028 mm, VeroBlack Plus), dorsal view. 3.3: Acrylonitrile butadiene styrene (ABS) 3D model with fused depositioning modeling (10 cm large, layers of 0.254 mm), ventral view. 3.4: as 3.2, dorso-lateral view.

ened and triangular, diameter of tarsomere 5 less than 50% of tarsomere 4. Metacoxa immobilised and integrated into metathorax.

Etymology

The specific epithet is derived from the classical Greek παλίντροπος, returning, reverting. It refers to the fact that the present species seems to have regained eight antennomeres, a characteristic that normally belongs only in the more basal Strepsiptera.

CLADISTIC ANALYSIS

The phylogeny of Strepsiptera has been extensively studied by Pohl and Beutel (2005). Moreover, the same data matrix was re-analysed by Bravo et al. (2009) in order to elucidate the relationships of *Bahiaxenos* Bravo et al., 2009. Nevertheless, a cladistic analysis has to be re-run entirely when another taxon is added. Adding a single taxon to a data matrix thoroughly influences the accuracy, robustness, and node support of the
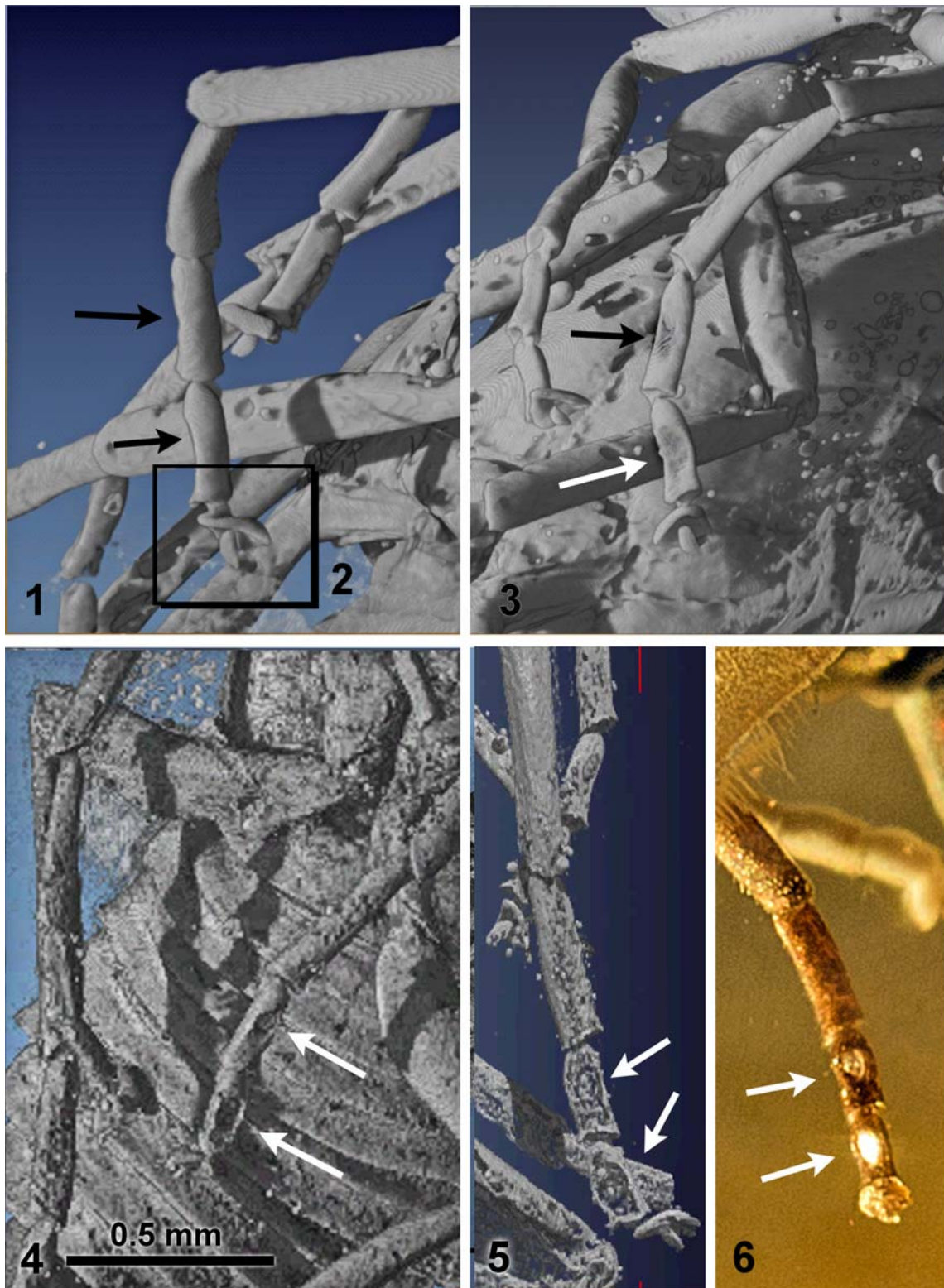
FIGURE 4. *Eocenoxenos palintropos* gen. nov. et sp.nov. male holotypus. (Figure 4.1- 4.5: micro-CT scan reconstruction). 4.1: tarsi of left prothoracic leg, position of sensorial spots indicated, latero-dorsal view. 4.2: left prothoracic leg, terminal tarsal segments. 4.3: left prothoracic leg, latero-ventral view, sensorial spots indicated. 4.4.: left mesothoracic leg, latero-ventral view, sensorial spots indicated. 4.5: left metathoracic leg, latero-ventral view, sensorial spots indicated. 4.6: left metathoracic leg, optical view in amber, ventral, sensorial spots indicated.
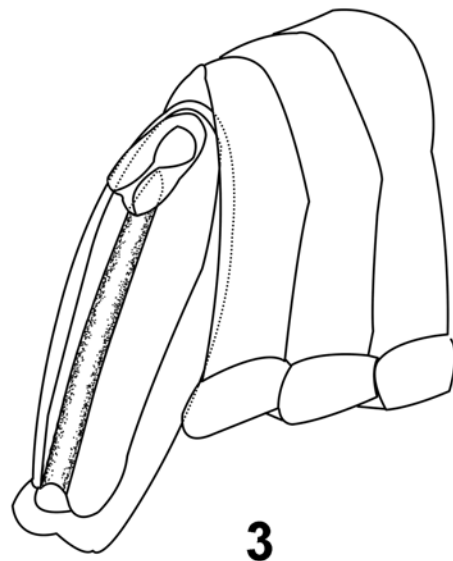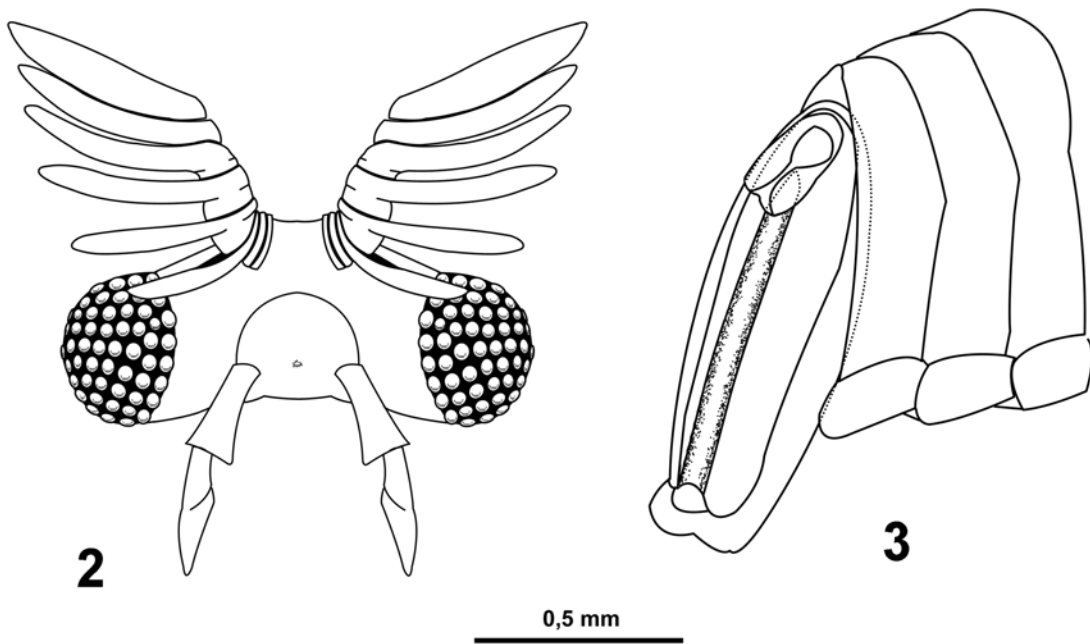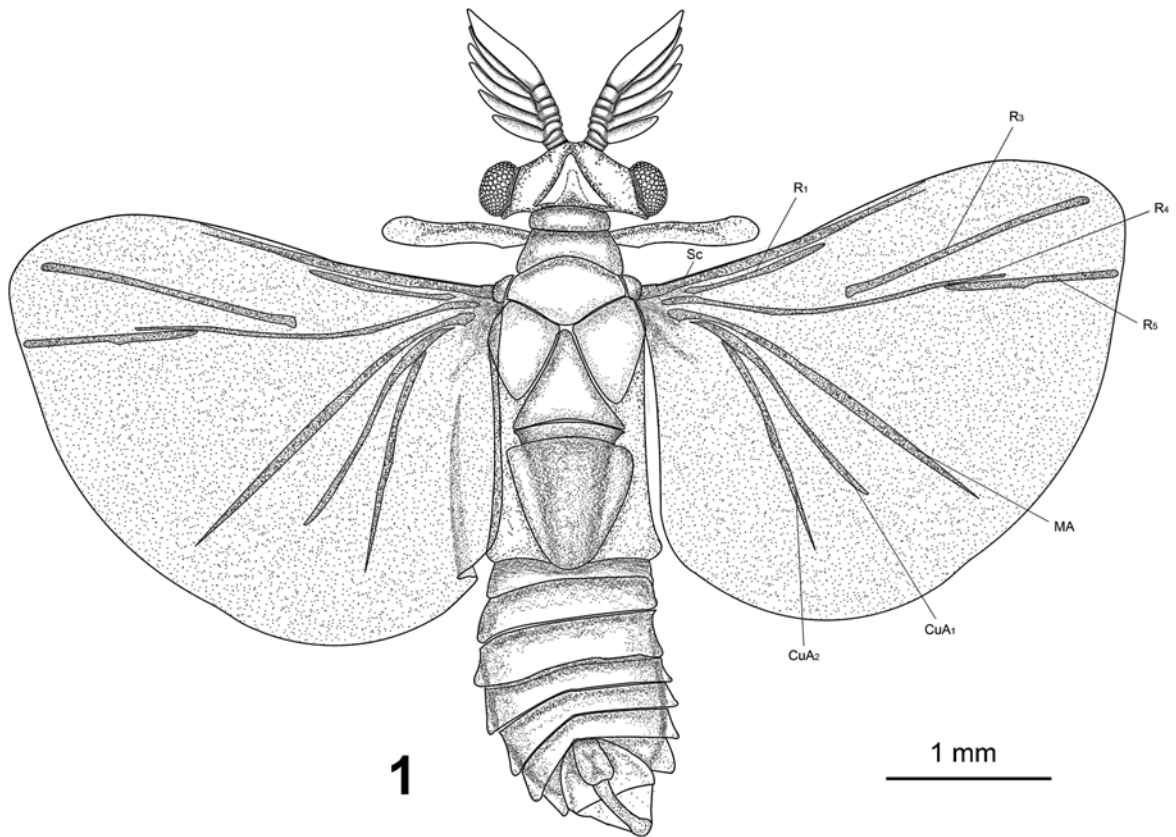
FIGURE 5. *Eocenoxenos palintropos* gen. nov. et sp.nov. male holotypus. 5.1: habitus, reconstruction; 5.2: head, frontal view, 5.3: abdominal segments with penis.

results obtained, as discussed by Kim (1998: 55-56), Bremer et al. (1999), and Poe and Swofford (1999). Indeed, modifying even a single entry in a data matrix can result in a totally different outcome of the analysis (Hovenkamp, 1999). In addition to that, repeating a cladistic analysis with a slightly modified data matrix and using a somewhat different algorithm gives a much better idea of the support and the stability of the results obtained (Hovenkamp, 2009). In view of all this, it was decided to repeat the entire analysis, using different software and settings, such as running all characters unordered and using implied weighting (Goloboff, 1993).

Taxon Choice

The data matrix from Pohl and Beutel (2005) was used, with scores for the males of *Bahiaxenos* (as specified in Bravo et al., 2009: appendix) and *Eocenoxenos* gen. n. added. As a result, a matrix with 43 taxa is obtained, encompassing 40 genera of Strepsiptera and three outgroup taxa (Maddison et al., 1984, Watrous and Wheeler, 1981): *Priacma* LeConte, 1874 (Coleoptera), *Sialis* Latreille, 1802 (Megaloptera), and *Tipula* Linnaeus, 1758 (Diptera). Five strepsipteran genera in the matrix are only known from fossils and presumed extinct (indicated by † in Figure 6): *Cretostylops* Grimaldi and Kathirithamby, 2005 (Cretaceous), *Eocenoxenos* gen. n. (Eocene), *Mengea* Grote, 1886 (Eocene), *Protelencholax* Kinzelbach, 1979 (Miocene), *Protoxenos* Pohl et al., 2005 (Eocene). *Stichotrema* Hofeneder, 1910 was originally considered to encompass both Miocene and Eocene fossils (Pohl et al., 2005: table 1), and recent species. The fossil species were transferred to *Palaeomyrmecolax* Kulicka, 2001 by Pohl and Beutel (2005: 366) and both groups are scored in the matrix, as explained in Pohl and Beutel (2005: 370).

Characters

A series of 189 characters (144 binary and 45 multistate) was coded for the 3 outgroup taxa and 40 ingroup taxa. Fourteen characters (16, 32, 46, 73, 78, 91, 96, 141, 147, 148, 155, 164, 174, and 178) are parsimony-uninformative, but have been included for the sake of completeness. Character 51 (mouthfield sclerite) is scored as binary, as character state 2 does not occur in the matrix of Pohl and Beutel (2005: table 1).

ANALYSIS AND RESULTS

The matrix of character states, as well as the character parameters and properties on the implied weighting consensus tree, can be found in Appendix. All multistate characters were run unordered in the analyses performed, contra Pohl and Beutel (2005) and Platnick (2012). Running multistate characters as ordered, or splitting them into characters with hierarchically related character states, as advocated by Hawkins et al. (1997), did not improve the resolution or the consistency of the results obtained.

An equally weighted analysis of the data matrix was performed in PAUP with **hsearch addseq = random nreps = 5000** (heuristic search with tree bisection and reconnection swapping and 5000 random addition sequences). In order to avoid spurious resolution due to unsupported (Coddington and Scharff, 1994; Wilkinson, 1995) or ambiguously supported (Nixon and Carpenter, 1996) branches, those with a minimum length of zero were collapsed with **pset collapse = minbrlen**. Multistate character states were coded as polymorphic with **pset mstaxa = polymorph**. In total, 15 shortest trees (length = 356) were found 4989 times, with a strict consensus of length 367, $ci = 0.7166$, ci-ex = 0.7045, hi = 0.3188, hi-ex = 0.2955, rc = 0.6219, and ri = 0.8679. The equally weighted consensus tree is identical to the tree found by Pohl and Beutel (2005, figure 28), but with *Bahiaxenos* branching off between *Mengea* and Mengenillidae, as found by Bravo et al. (2009, figure 6), and *Eocenoxenos* added to the unresolved clade of *Dundoxenos*, *Triozocera*, *Proceroxenos,* and *Uniclavus.*

Because cladograms obtained by attributing *a posteriori* weights to characters based on their relative degrees of homoplasy on a set of heuristic trees, explain the data better (Bosselaers and Jocqué, 2002; Goloboff et al., 2008a), a weighted analysis was also performed.

Implied weighting (Goloboff, 1993) was preferred for this purpose. When applying implied weighting in PAUP with pset goloboff = yes, pset collapse = minbrlen, pset mstaxa = polymorph, and hsearch addseq = random nreps = 1000, using a relatively mild concavity constant = 4, two fittest trees with fit = -160.33718 (PAUP attributes a negative sign to fit values) were found 218 times. The two fittest trees only differ in the position of *Protoxenos* and *Cretostylops*, which are interchanged. An additional implied weighting search run in TNT using Settings / implied weighting and Analyze / Traditional search (TBR or SPR, 1000 replications) as well as New Technology search (Collapse trees after search; Driven search, 500 init. addseqs, find min. length 100 times, 1 random seed; Sectorial
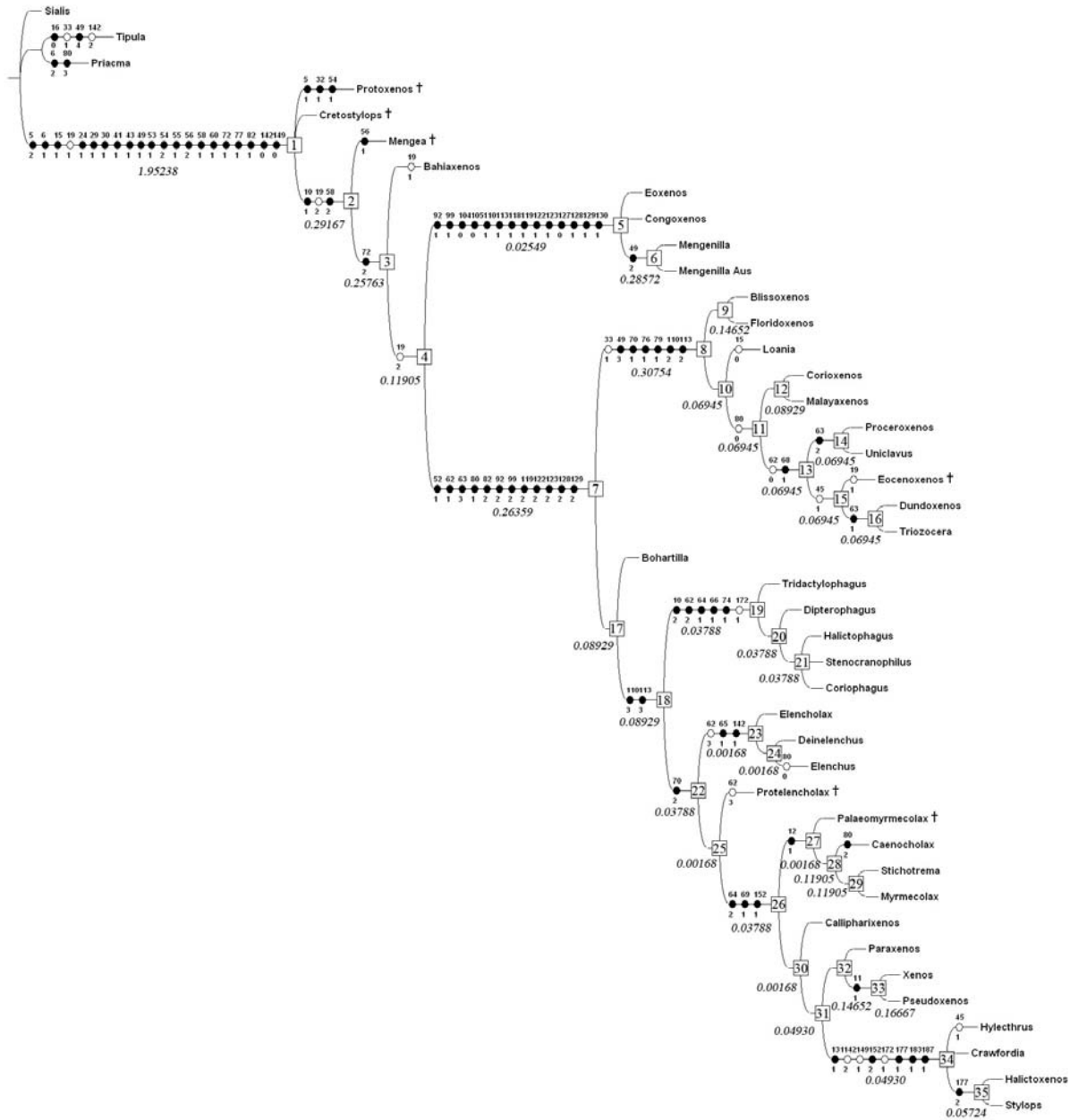
FIGURE 6. Strict consensus tree of the 12 fittest trees obtained under implied weighting. State changes are indicated on the tree for 44 characters (see Appendix 1). Non-homoplasious character state changes are in black, homoplasious state changes in white. Nodes are numbered on the tree and Goloboff fit Bremer support values, as calculated in both TNT and PAUP/TreeRot, are indicated in italics below branches.

search with RSS, CSS and XSS, fuse trees 10 times; Ratchet with 10 iterations; Tree drifting with 20 cycles; Tree fusing with 10 rounds), using the same concavity constant, which equals 5 instead of 4 in TNT (see Bosselaers and Jocqué, 2002: 16), produced the same two fittest trees. Because TNT calculates weighted homoplasy (a complement of fit) for implied weighting trees, another fit value, 13.33730 was reported for these same trees. The strict consensus of these two trees, which has length = 357 and fit -160.17051, PAUP value (13.50397 TNT value), is our preferred solution. It is illustrated in Figure 6. This tree has ci = 0.7367, ci-ex = 0.7251, hi = 0.2997, hi-ex = 0.2749, rc = 0.6487, and ri = 0.8806.

Bremer support (a statistic based on the number of extra steps needed on a tree in order to collapse a branch, Bremer, 1988, 1994), expressed as TNT fit values, was calculated in TNT, using Analyze / suboptimal, followed by Analyze / Traditional search / tree bisection reconnection (TBR)) and Trees / Bremer Supports, retaining trees suboptimal up to 10 units of fit and combining various numbers of replications (between 1 and 90000) with various numbers of trees saved per replication (between 1 and 90000, inversely related to the number of replications) until the solution stabilised. Bremer support was also assessed using PAUP in combination with TreeRot v3 (Sorenson and Franzosa, 2007), a programme calculating branch support using reverse constraints. For that purpose, a Nexus treefile of the implied weighting consensus tree was converted to a PAUP command file by TreeRot. This command file was subsequently run in PAUP to produce a ".results" file. Bremer support in PAUP fit values was calculated manually from the TreeRot ".results" file. Although PAUP and TNT assign different values and signs to the overall fit value of trees, Bremer support values obtained with both programmes were quite similar. In the case of small differences, the lowest (TreeRot) value was chosen.

DISCUSSION

The preferred strict consensus tree with node numbers, state changes for 60 characters and Goloboff fit Bremer support values (as reported in TNT and PAUP) in italics below branches is illustrated in Figure 6. Each ambiguity on the tree was optimized in isolation, in order to avoid scoring character states for absent structures, and also because only a combination of ACCTRAN ("fast") and DELTRAN ("slow"") optimisation can produce the most robust proposal for a supposed homology. Indeed, the use of ACCTRAN only, as is often preferred, does not always maximize parallel loss of complex traits over convergent gains (Agnarsson and Miller, 2008). Characters 19, 29, 49, 142, 149, 172, and 177 were optimised under ACCTRAN on the tree, characters 62, 80, 92, 99, 110, 113, 119, 122,123, 128,129, and 152 were optimised under DELTRAN, and only unambiguous state changes were plotted for character 68, in order to avoid scoring this character for an absent structure, as five tarsomeres are only present in clade 13 within Stylopidia (Figure 6, clade 7; Figure 7.3).

Homoplasy is rather low in the data matrix under study: 128 out of 189 characters are completely free of homoplasy on the consensus tree (Appendix). Sanderson and Donoghue (1989: 1785, Figure 1) performed a polynomial regression analysis on data from 60 cladistic analyses, and derived the following equation based on them: $c_i = 0.90 - 0.022*(\text{number of taxa}) + 0.000213*(\text{number of taxa})^2$. Applying this equation, 43 taxa would yield a ci value of 0.3478. The preferred tree has a significantly higher ci value of 0.7251, excluding parsimony-uninformative characters.

The consensus tree obtained (Figure 6) is almost identical to the tree of Pohl and Beutel (2005, figure 28), the only differences being *Bahiaxenos* branching off between *Mengea* and Mengellidae and Corioxenidae being fully resolved with the addition of *Eocenoxenos* to the *Dundoxenos - Triazocera - Proceroxenos - Uniclavus* clade. Monophyly of Mengenillidae (clade 5) is recovered, but, as already mentioned in Pohl and Beutel (2005, p. 367) and in Bravo et al. (2009: 620), it is not very well supported (Figure 6).

Stylopidae too are poorly supported in our preferred solution, as are Halictophagidae, Elenchidae and Myrmecolacidae. Nevertheless, Stylopidia (node 7) and Stylopiformia (node 17) are resolved exactly as in Pohl and Beutel (2005), although the relationships within Stylopiformia seem far from being settled, as McMahon et al. (2011) recently obtained yet another phylogeny, based on molecular evidence. Well supported nodes in the implied weighting consensus tree are node 1 (Strepsiptera), node 2, node 3, node 6 (*Mengenilla*), node 7 (Stylopidia), and node 8 (Corioxenidae). Within Corioxenidae, subfamily Corioxeninae as defined by Kathirithamby on the basis of four-segemented tarsi and the absence of claws (1989: 74) is paraphyletic in our cladogram and cannot be considered a natural taxon. A similar result was obtained by Pohl and Beutel (2005) and McMahon et al. (2011). On the other hand, Blissoxeninae, defined here as consisting of the genera *Blissoxenos* and *Floridoxenos*, is rather well supported on the preferred tree, confirming the findings of Pohl and Beutel (2005: 368).

Eocenoxenos gen. n. fits well in Stylopidia (Figure 6, clade 7) by the presence of a membranous coronal suture (9:2), a wide mouthfield sclerite (52:1), and the absence of claws (63:3). *Eocenoxenos* also clearly belongs in Corioxenidae, sharing many autapomorphies of the family (Figure 6), as detailed in the description above. It is the sister genus of node 16, encompassing *Dundoxenos* Carvalho, 1956 and *Triozocera* Pierce, 1909, the Triozocerinae of Kathirithamby (1989: 71) and
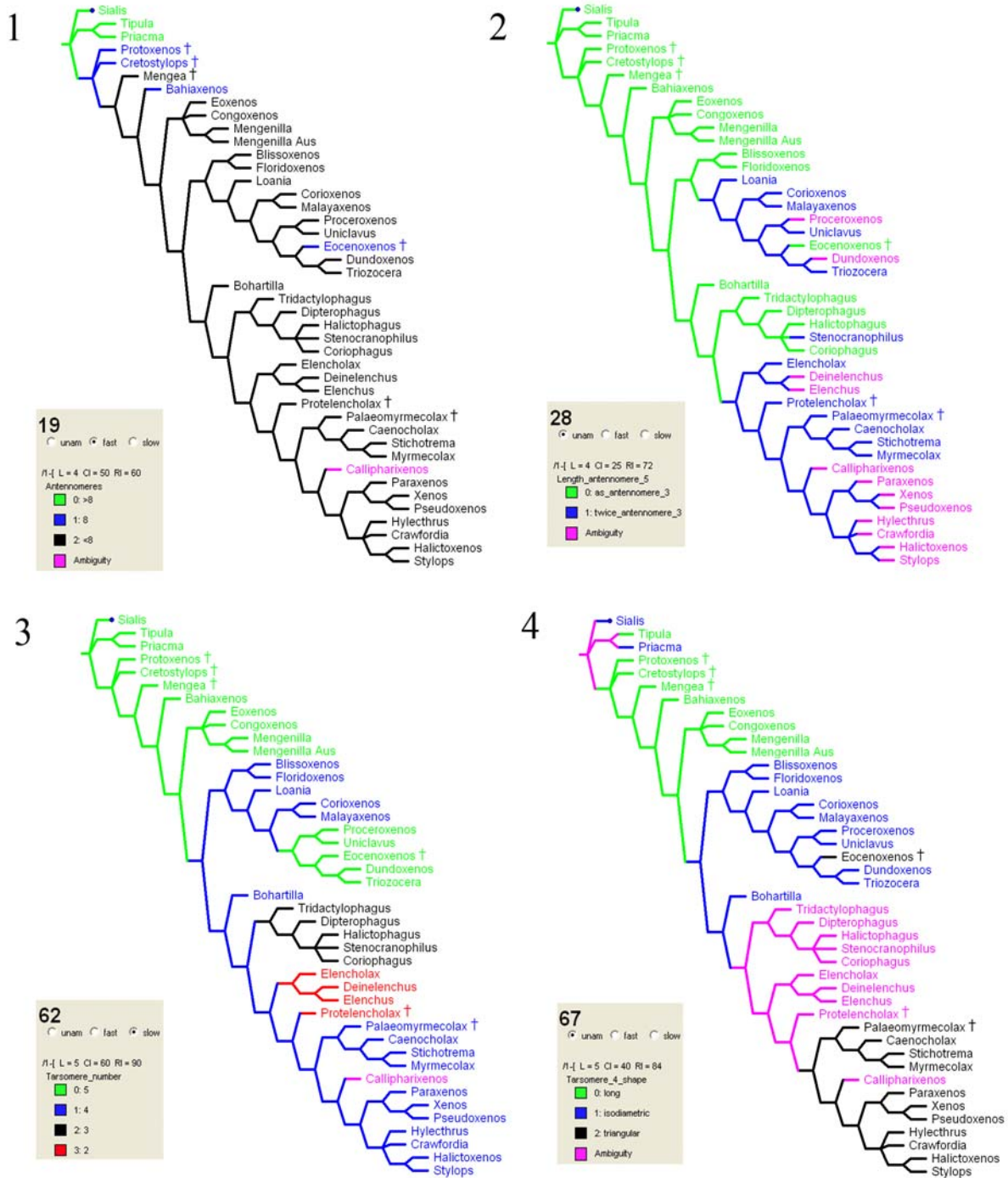
FIGURE 7. Character state distribution of four characters on the consensus tree. 7.1: Char. 19, ACCTRAN; 7.2: Char. 28, UNAMB; 7.3: Char. 62, DELTRAN; 7.4: Char. 67, UNAMB.

shares with them a palpus maxillaris inserted proximad of the apical stipital margin (45:1). *Eocenoxenos* also shares a straight aedeagus (80:0) with Triozocerinae, Uniclavinae and the genera *Corioxenos* and *Malayaxenos* within Corioxenidae.

Eocenoxenos also differs from the hypothetical common ancestor of clade 15 (Triozocerinae and *Eocenoxenos*) by the presence of eight antennomeres (19:1) instead of less than eight (Figure 7.1), antennomere 5 as long as antennomere 3 (28:0)

instead of twice as long (Figure 7.2), and a triangular (67:2) instead of isodiametric tarsomere 4 (Figure 7.4). A striking feature of *Eocenoxenos* is the combination of derived characteristics typical for Corioxenidae, as summarised in the description, with a character only known from Strepsiptera holding a basal position in the phylogeny: the presence of eight antennomeres (19:1), present in the fossil genera *Protoxenos* and *Cretostylops*, and regained independently in *Bahiaxenos* (Figure 7.1). The elaborate, extensively flabellated antennae, as well as the large compound eyes of *Eocenoxenos* can be considered an adaptation associated with the necessity to find females in a very short time span while being unable to feed, under environmental conditions that we are unable to reconstruct (Beutel and Pohl, 2005, p. 17).

Eocenoxenos will most probably have parasitized on Heteroptera, as is typical for Corioxenidae. Possibly, the hosts belonged to Cydnidae (Kathirithamby, 1989: 71), a family which has been described from the Tertiary (Schaefer and Crepet, 1986; Thomas, 1988) and even from the Secondary era (Yao et al., 2007). As most other Stylopidia, *Eocenoxenos* lacks tarsal claws, although they are still present in its close relatives in clades 14 and 16, Uniclavinae and Triozocerinae. However, the claws in clades 14 and 16 are reduced and differ significantly from the claws in more basal Strepsiptera. If these claws would have been regained in the course of evolution, instead of being plesiomorphic, this aberrant morphology would be in accordance with Dollo's principle (Dollo, 1893).

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APPENDIX

Character-taxon matrix. Abbreviations: * = non-homoplasious character, ? = unknown or unapplicable character state, a = 0 or 1, b=1 or 2, A = character optimization ambiguous, ci = consistency index, F = illustrated on tree in Figure 6, ri = retention index, U = parsimony uninformative character.
See PDF online.