

HEAD AND LEG MORPHOLOGY OF *ELONGATA* BRONGNIART, 1893: 433 (LATE CARBONIFEROUS, *ARCHAEORHTOPTERA*): PHYLOGENETIC AND PALAEOECOLOGICAL IMPLICATIONS

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Abstract.— The discovery of new specimens of the Late Carboniferous species *elongata* Brongniart, 1893: 433, belonging to the taxon *Archaeorthoptera* nom. Béthoux and Nel, 2002, dis.-typ. Béthoux, 2007c (i.e. is more closely related to the Linnaean order Orthoptera than to any other recent insect order) is reported. The head and leg morphology of the species could be investigated thanks to the good preservation of the specimens, and new preparation. The tarsus is 5-segmented, supporting the view that this state is plesiomorphic for orthopterans s. s. Morphology of mandibles indicates a carnivorous food-habit. Fore- and mid-leg femora and tibiae were provided with long and spaced out spines, most probably arranged in two rows. These spines might have assisted the entrapment of preys. The relative length of leg segments, and the length of antennae, are reminiscent of the condition exhibited by phasmidans, suggesting a similar locomotion behavior.



Key words.— Orthoptera, *Ctenoptilus elongatus*, Commentry, tarsus, cladotypic nomenclature.

INTRODUCTION

But for the wing venation, the morphology of Late Carboniferous insects is barely known with details. Although wing venation proved to be a valuable source of information for phylogenetic investigations, alternative source of data are important for testing phylogenetic hypotheses. In addition, the palaeoecology of Late Carboniferous winged insects, which lived in a complex environment, might be better assessed if additional information on their morphology is known. However this requires exceptionally well-preserved specimens and appropriate preparation.

Three specimens from the famous Late Carboniferous deposit of Commentry (France) were recently rediscovered. Two of them belong to a previously described species, namely *elongata* Brongniart, 1893: 433, currently assigned to the taxon *Archaeorthoptera* nom. Béthoux and Nel, 2002, dis.-typ. Béthoux, 2007c [in other words, this species is a stem-orthopteran, i.e. is more closely related to orthopterans than to any other recent winged insects; see Béthoux and Nel 2004, 2005; the species is named *Ctenoptilus elongatus* (Brongniart, 1893) under the Linnaean nomenclatural procedure, and is assigned to the taxon *Archaeorthoptera* Béthoux and Nel 2002]. Like most of

Commentary specimens, their preservation is remarkable. These specimens provide new information of the leg and head morphology of *Archaeorthoptera elongata*.

MATERIAL AND METHODS

The wing venation nomenclature elaborated by Béthoux and Nel (2002) for archaeorthopterans was utilized, and is repeated here for convenience: ScA, anterior Subcosta; RA, anterior Radius; RP, posterior Radius; M, Media; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA1, first anal. On figures, 'an' accounts for 'antenna', 'ar' for 'arolium', 'c' for 'tarsal claw', 'cl' for 'clypeus', 'e' for eye, 'm' for mandibule, 'p' for 'palp'.

I follow the cladotypic nomenclatural procedure (Béthoux 2007a, b). Hereafter the only implication of the application of this procedure regards the way species considered in this contribution are referred to, which follows propositions of Dayrat *et al.* (2004). In details, at their first mention, species are referred to as a uninomen followed by the author and year of publication (such as *elongata* Brongniart, 1893: 433; here the page has to be mentioned because there is another species named *elongata* in the same contribution). The uninomen can be preceded by the taxonomic address (e.g. *Archaeorthoptera*), which is a list of taxa to which the species can be attributed, following a decreasing order of inclusiveness. The taxonomic address can be limited to the least inclusive defined taxon to which the species can be assigned. If so, the combination takes the form of a Linnaean binomen (see Béthoux 2007c), such as *Archaeorthoptera elongata*. In the following, if a taxon is undefined under cladotypic taxonomy it will be referred to by a vernacular version of its name (i.e. orthopterans are members of the Linnaean taxon Orthoptera), or the Linnaean rank will be mentioned, so that to avoid confusion between cladotypic and Linnaean taxon names.

The cladotypic approach was preferred for two reasons. First, species mentioned in this contribution have been assigned to monotypic genera, the names of which carry no relevant information. They are redundant and better avoided. Second, the taxon *Archaeorthoptera* has the advantage of being associated with a definition, this allowing ambiguity inherent in the Linnaean approach to be avoided. Because no new nomenclatural act is performed in this contribution, its dissident aspect is actually limited.

Specimens investigated in this contribution are housed at the Palaeontology Department, Muséum National d'Histoire Naturelle (Paris, France). They were rediscovered recently by J.-M. Pacaud (MNHN, Paris,

France) in the palaeontological collections of the University Claude Bernard (Lyon, France), and belong to a set of specimens studied by F. Meunier. Specimens bear evidence of earlier preparation. I carried out additional preparation with customized needles. Photographs were taken using a Canon EOS 400D digital camera coupled with a 50 mm Canon macro lens and an elongation tube, or a MP-E 65 mm Canon macro lens, as appropriate, and driven by corresponding Canon software. Original photographs were processed using Adobe Photoshop 7.0. In some cases more detail can be shown by combining photographs of a specimen dry and immersed in ethanol; such illustrations are referred to as dry-ethanol composites. Photographs were taken under polarized light.

SYSTEMATIC PALAEONTOLOGY

Archaeorthoptera nom. Béthoux and Nel, 2002,
dis.-typ. Béthoux, 2007c
Species *elongata* Brongniart, 1893: 433.
(Figs 1–2)

Descriptions. **Specimen MNHN A26167** (Fig. 1). Dorsal view of an incomplete individual; location of the negative imprint unknown; head, thorax, forelegs, mid-legs, and part of forewings and right hind wing preserved and visible. Head (Fig. 1B): 6.5 mm long, 4.8 mm wide; mandibles occluded, 2.0 mm long (apex to middle of the base), 1.2 mm wide at their base, with prominent teeth at their apex; two symmetrical, semi-circular, strongly sclerotized structures (?) visible in the middle of the head; eyes distinguishable, long and broad (about 1.7 mm long); antennae preserved for a short distance (12.3 mm for the left one), base indistinguishable.

Thorax (Fig. 1A): prothorax quadrate (about 5.0 mm long, 4.4 mm wide), no evidence of prothoracic winglets. Forelegs (Figs 1A, E): femur about 4.4 mm long, tibia 5.0 mm long, tarsus poorly preserved; spines present on the tibia, with several longitudinal ridges; mid-legs (Figs 1C, D): spines present on the femur and tibia; tarsus poorly preserved, with a pair of claws and an arolium; forewings (Figs 1A, F): overall poorly preserved and incomplete; ScA distinct from the anterior wing margin; RA and RP parallel and close to each other for a long distance; CuA + CuPa with numerous branches; AA1 strong, simple (as preserved); other AA branches diverging posteriorly from a unique stem; area along RA / RP, the anterior-most branch of CuA + CuPa, and along some basal posterior branches of CuA + CuPa with dark coloration.

Specimen MNHN A26168 (Fig. 2). Dorsal view of an incomplete specimen; location of the negative

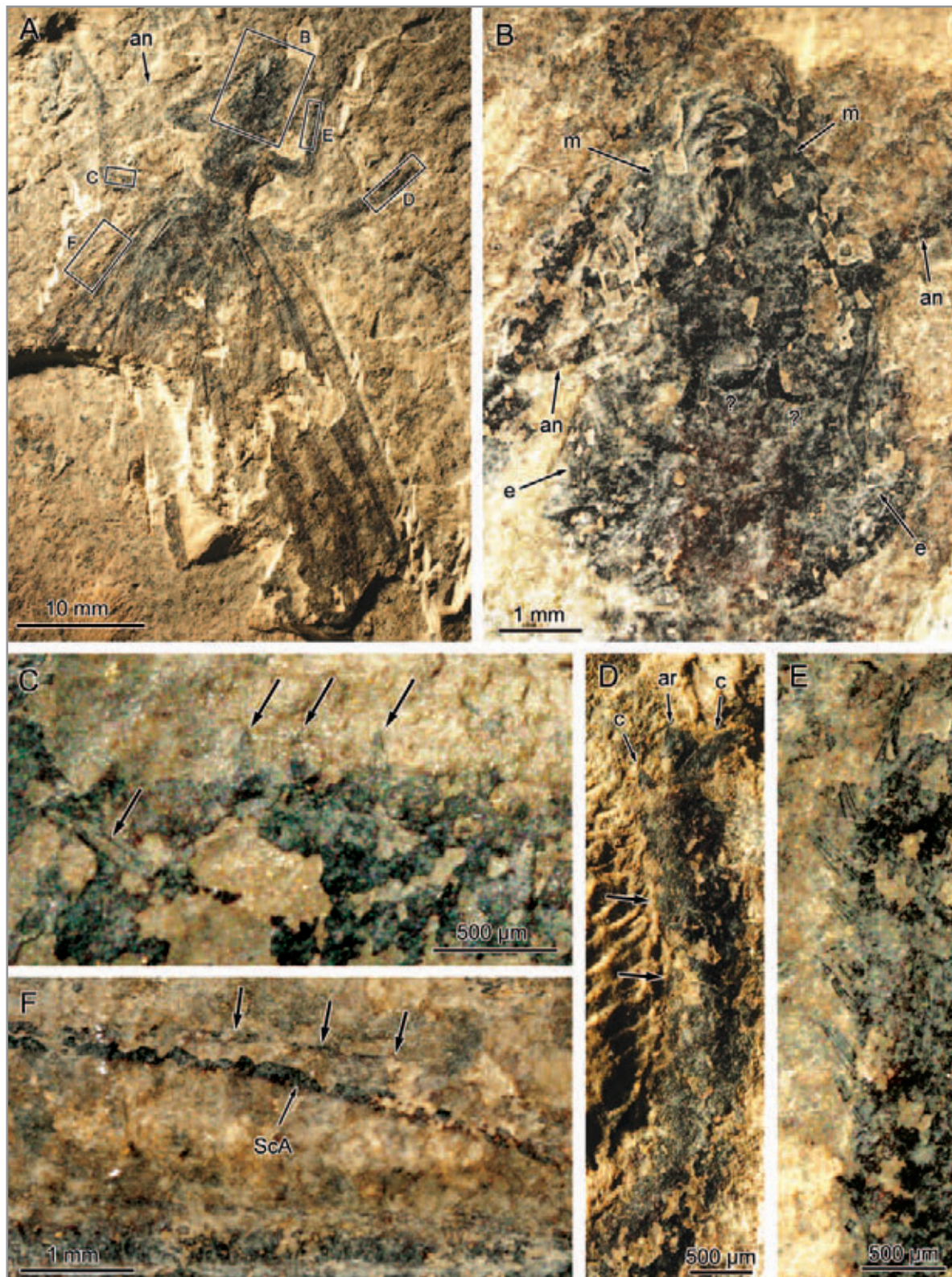


Figure 1. *Archaeorthoptera elongata* Brongniart, 1893: 433 (specimen MNHN A26167; see text for abbreviations; all photographs taken under polarized light; (A, B, D) dry-ethanol composites; (C, E, F) ethanol; (B–E): details as located on (A). (A) Habitus; (B) head; (C; arrows indicate spines) left mid-leg femur; (D; wide arrows indicate edges of the 2nd tarsomere) right mid-leg tarsus; (E) right foreleg tibia; (F; wide arrows indicate the anterior wing margin) area between the anterior wing margin and RA, left forewing base.

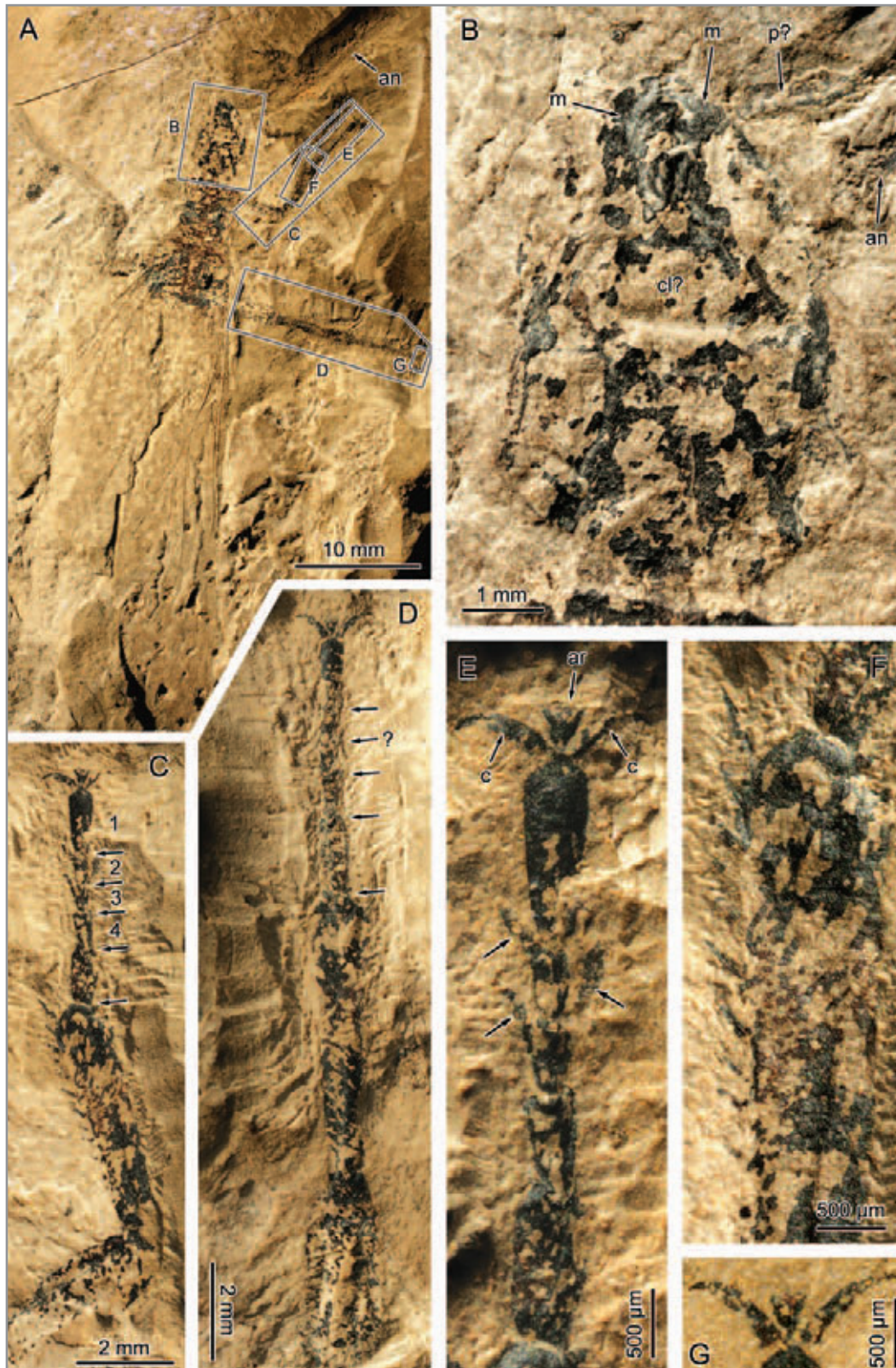


Figure 2. *Archaeorthoptera elongata* Brongniart, 1893: 433 (specimen MNHN A26168; see text for abbreviations; all photographs taken under polarized light; (A–D, F) dry-ethanol composites; (E, G) ethanol; (B–G) details as located on A). (A) Habitus; (B) head; (C; arrows indicate edges of tarsomeres) right foreleg; (D; arrows indicate edges of tarsomeres) right mid-leg; (E; arrows indicate lateral extensions of 2nd and 3rd tarsomere) right foreleg tarsus; (F) detail of the right foreleg tibia; (G) right mid-leg tarsal claws and arolium.

imprint unknown; head, right antenna, right fore- and mid-legs, base of the left mid-leg, thorax, and part of forewings preserved and visible.

Head (Fig. 2B): 6.3 mm long, 4.6 mm wide, poorly preserved; imprint of a groove might delimit the frons from the clypeus; labrum apparently not preserved; remain of right palp (?), poorly preserved; mandibles 2.0 mm long (apex to middle of the base), about 1.0 mm wide at their base; eyes not distinguishable; right antenna about 15.6 mm long.

Thorax (Fig. 2A): prothorax quadrate (5.0 mm long, 4.8 mm wide; no evidence of prothoracic winglets; mesothorax at least 7.6 mm wide. Right foreleg (Figs 2A, C, E, F): well preserved; femur about 4 mm long, 1.5 mm wide; tibia 4.8 mm long, 1.0 mm wide, with a single row of 10 distinct spines, the base of which being hidden by the tibia; tibial spines progressively longer from the base to the apex of the tibia; tarsus 4.4 mm long, with 5 distinct tarsomeres, respectively 1.10 mm long (basitarsus), 0.77 mm long (4th tarsomere), 0.55 mm long (3rd tarsomere), 0.56 mm long (2nd tarsomere), and 1.46 mm long (1st tarsomere); 3rd and 2nd tarsomeres provided with lateral extensions, partly damaged by preparation; tarsus provided with paired claws and arolium. Right mid-leg (Figs 2A, D, G): well-preserved, stretched out; femur about 5 mm long and 1.4 mm wide, tibia 6.1 mm long, about 0.9 mm wide, without evidence of spines; tarsus 5.5 mm long, with 4 or 5 tarsomeres; basitarsus and 1st tarsomere 1.56 mm long each; tarsus provided with a pair of long and slender claws and an arolium. Forewings (Fig. 2A): right forewing with area between anterior wing margin and RA mostly missing; apex incomplete, 34.6 mm long (as preserved); left forewing with distal half missing, anterior wing margin poorly preserved, 9.4 mm wide; no evidence of coloration; for both forewings, RA and RP diverging basally, parallel and close to each other for about half of their course; M barely visible, except at its origin from M + CuA; CuA + CuPa strong, posteriorly pectinate, with several posterior branches being branched; CuPb not discernible; AA1 strong, simple as preserved; other anal veins diverging posteriorly from a unique pectinate stem; in right forewing, RP with at least 8 branches; cross-veins preserved in the apical half, not reticulated.

Remarks. The two specimens can be assigned to the species *elongata* Brongniart, 1893: 433 based on their forewing venation pattern and shape (see Béthoux and Nel 2004, 2005). In details, the length and number of branches of CuA + CuPa, the proximal branching of R (into RA and RP), the narrowness of the area between RA and RP in the first half of the forewing, and the occurrence of a ScA distinct from the anterior wing margin, are all diagnostic features of *elongata*. Alike in *elongata* and unlike in *mazonus* Béthoux, 2005, the putatively closest known relative of

elongata (known from a single isolated forewing), the right forewing of the specimen MNHN A26168 is provided with cross-veins that do not reticulate in the distal half. Whether the specimen MNHN A26167 belong to *elongata* or *mazonus* Béthoux, 2005 is difficult to determine unambiguously because the wing venation is very poorly preserved in this specimen. The forewing coloration pattern is similar to that of the holotype of *elongata* (Béthoux and Nel 2004: fig. 8). However, it must be noted that forewings of the specimen MNHN A26168 exhibit no coloration pattern, such as some other specimens assigned to *elongata* by Béthoux and Nel (2004). This difference could be due to taphonomic bias (Béthoux and Nel 2004), or to a sexual dimorphism (MNHN A26167, which exhibit colored wings, is slightly larger than MNHN A26168, without wing coloration), and does not allow a possible assignment of the specimen MNHN A26167 to *mazonus* to be discarded. The estimated forewing length of the specimen MNHN A26167 is about 45–50 mm, which is more consistent with an assignment to *elongata* (*mazonus* has an estimated forewing length of about 60 mm). In addition, the specimen MNHN A26167 was discovered in the type-locality of *elongata*, from which there is no evidence of the occurrence of *mazonus*.

The location of tibial spines as observed in the two new specimens indicates that forelegs were provided with two rows of spines. A single row can be observed on the right foreleg of the specimen MNHN A26168 (Figs 2C, F), while two rows are arguably visible on the right foreleg of the specimen MNHN A26167 (Fig. 1E). It is hypothesized that the former specimen exhibit a dorso-lateral view of the foreleg tibia, while a lateral view is visible on the latter specimen. Similar tibial spines were observed on mid-legs of both specimens, but their orientation is conjectural. Femoral spines were observed on the left mid-leg of the specimen MNHN A26167 only (Fig. 1C). It is probable that such spines were present on forelegs as well but are not visible, due to the orientation of the forelegs, as preserved.

DISCUSSION

Phylogenetic implications

Based on characters of the forewing venation, Béthoux and Nel (2004) assigned the species *elongata* to the taxon *Archaeorhoptera* (see also Béthoux 2005). In other words, *elongata* is more closely related to the Linnaean order Orthoptera than to any other recent insect order. The comparison of the condition exhibited by various polyneopteran orders and by *elongata* allows relevant characters to be polarized for orthopterans, and discussed for some other taxa.

While the tarsus of recent orthopterans is three- or four-segmented (see Beutel and Gorb 2001; Gorb 2001 for data on extant taxa), that of *elongata* is five-segmented. In addition, representatives of the taxon *Titanopterida* Béthoux, 2007c, an orthopteran taxon that could be excluded from the two extant orthopteran lineages (namely, the Linnaean infra-orders Ensifera and Caelifera), possessed a 5-segmented tarsus (Sharov 1968: fig. 50E). Therefore a 5-segmented tarsus is likely the plesiomorphic condition for orthopterans. Indeed, dictyopterans and phasmidans, among other putative adelphotaxa, exhibit a five-segmented tarsus (in the phasmidan genus *Timema*, the tarsus is 3-segmented, but five pulvilli can be observed on the ventral side, suggesting that the first three tarsomeres are fused; Kristensen 1975; Tilgner *et al.* 1999). These lines of evidence suggest that the character state 'tarsus 5-segmented' does not support the monophyly of a clade Grylloblattodea + Phasmatodea + Dictyoptera from which Orthoptera would be excluded (Linnaean taxon names; Beutel and Gorb 2006; contra Beutel and Gorb 2001: 196).

The pretarsus of *elongata* is provided with a pair of curved claws and an arolium of moderate size. A similar condition is exhibited by dictyopterans and phasmidans, among other putative adelphotaxa. This is likely the plesiomorphic condition in polyneopterans (Beutel and Gorb 2006), and the reduction of the arolium in ensiferans (Beutel and Gorb 2001) is likely a derived condition. Unlike *elongata*, mantophasmatodeans and phasmidans exhibit an enlarged pan-shaped arolium (Beutel and Gorb in press). Considering that putative successive adelphotaxa of phasmidans (or phasmidans + mantophasmatodeans) exhibit an arolium of moderate size (Beutel and Gorb in press), the morphology exhibited by *elongata* supports the view that the condition exhibited by phasmidans (or phasmidans + mantophasmatodeans) is derived.

Palaeoecological inferences

The morphology of *elongata*, as deduced from the study of the two new specimens, allows some inferences on the palaeoecological preferences of this species to be drawn. A particular aspect that *elongata* shares with some stick-insects is that tarsi are as long as tibiae (see Key 1991; see also Tilgner *et al.* 1999). In particular the basitarsus and the first tarsomeres are longer than other segments. In addition, as far as it could be determined from the foreleg morphology of the specimen FMNH A26168, the second and third tarsomeres are provided with latero-dorsal projections. Although friction with substrate is mainly restricted to euplantulae and pretarsus, the tarsus of *elongata* is long and has many points of flexion, in relation to its high number of segments (at least with

respect to extant orthopteran relatives). This morphology might have allowed individuals of *elongata* to attach to thin stems (see Gladun and Gorb 2007). Alike in some stick-insects (Blaesing and Cruse 2004; Dürr 2001), the long antennae might have been used as exploring tactile probes, allowing the insect to detect ground support and cross over large gaps. In summary, legs and antennae morphology indicate a lifestyle of *elongata* similar to that of extant stick-insects, moving about in an environment composed of thin stems and large gaps, such as bushy arborescent sphenopsids (Daviero and Lecoustre 2000), contemporaneous with *elongata*.

Although mandibles occlude on the specimen MNHN A26167 (Fig. 1B), prominent and sharp incisors are visible in their distal part. Coupled with the elongate triangular shape of the mandibles, the most likely food-habit of *elongata* is carnivorous, or omnivorous. Relevant comparison can be made with species of the Linnaean genera *Mantis* (praying mantid, carnivorous; see Yuasa 1919: figs 65–76), *Stenopelmatus* (omnivorous cricket; see Yuasa 1919: figs 83–84), *Ceuthophilus* (omnivorous cricket; see Gangwere 1965: figs 5–6), and *Orchelimum* (carnivorous-forbivorous katydid; see Gangwere 1965: figs 19–20). In addition, assuming a carnivorous food-habit, the entrapment of preys might have been assisted by spines present of the fore- and mid-legs tibiae and femora, and lateral extensions of some of the foreleg tarsomeres. In that respect, a relevant model-taxa-by-homoplasy is the Linnaean family Tettigoniidae, in which foreleg tibiae are armed with two rows of long and spaced out spines, which are used by some species for holding preys during consumption (Betz and Kölsch 2004; Kaltenbach 1990; Rentz 1995).

Nomenclatural approach

Béthoux (in press) suggested that alternative nomenclatural procedures should be experimented. This contribution demonstrates that names resulting from the application of different procedures can be used concurrently. Confusion is avoided if ranks of Linnaean-based names are mentioned, or if these names are vernacularized, and if names resulting from the application of the cladotypic approach are italicized. Contributions mixing different approaches are possible until an alternative nomenclature reaches a matured state, allowing it to be experimented independently from the Linnaean one.

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