

## Is *Crowsoniella relictata* really a cucujiform beetle?

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**Abstract.** *Crowsoniella relictata* Pace, one of the most obscure and cryptic beetle taxa, was recently transferred from Archostemata to the polyphagan series Cucujiformia. We discuss the arguments in favour of this hypothesis. The placement of the species is evaluated with a cladistic approach and two different morphological data sets: one aiming mainly to clarify the relationships of extinct and extant archostematans, and one aimed at resolving species-level phylogeny for the suborder. The results suggest clearly that a position of *Crowsoniella* within a polyphagan subgroup is very unlikely, and that a placement in Archostemata is justified and should be maintained. Due to the serious lack of anatomical information, non-destructive  $\mu$ -CT scanning of enigmatic taxa like *Crowsoniella* Pace and *Sikhotealinia* Lafer should have high priority.

### Introduction

Apart from *Sikhotealinia zhiltzovae* Lafer (Jurodidae) (Lafer, 1996; Kirejtshuk, 1999/2000), *Crowsoniella relictata* Pace is arguably the most obscure and cryptic species of beetles. Since the type series was collected by washing calcareous soil around the base of an old chestnut tree (*Castanea sativa* Miller) in central Italy (Pace, 1975), not a single additional specimen has been found. Recently a team of American and Italian coleopterists under the leadership of Prof. M.A. Ivie invested considerable effort to seek out *Crowsoniella* at the type locality. However, the intensive search remained unsuccessful. Therefore, only the dried and mounted type specimens are available, which are unsuitable for detailed anatomical or molecular investigations. The immature stages and the biology of the species remain unknown.

*Crowsoniella* was placed in the suborder Archostemata by Pace (1975) and Crowson (1975) as the only extant European species of this ‘ancestral’ coleopteran lineage (e.g. Beutel *et al.*, 2008). This was mainly based on characters of the male genital apparatus (Fig. 1). The adult morphology of the small and strongly flattened species is highly modified,

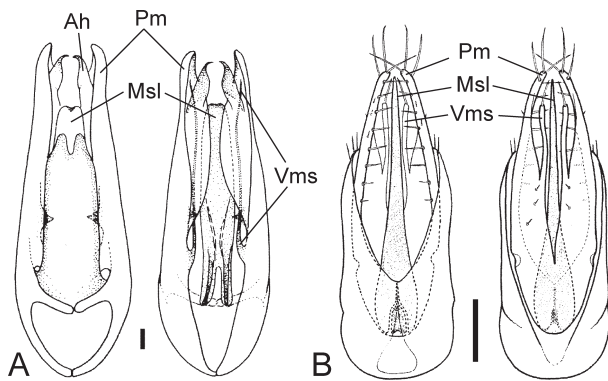
probably as a result of miniaturization and specialized life habits. The systematic position within Archostemata was later confirmed by cladistic analyses of several extensive, only partly overlapping, morphological data sets (Beutel *et al.*, 2008; Hörnschemeyer, 2009). However, Kirejtshuk *et al.* (2010) recently suggested that *Crowsoniella* should be transferred to Polyphaga–Cucujiformia. The main focus of their study was to describe some new fossil taxa; we do not take issue with this part of their paper. However, for reasons we outline below we find the placement of *Crowsoniella* suggested by Kirejtshuk *et al.* (2010) to be highly problematic and in need of a refutation.

### Material and methods

#### *Material and morphology*

Dried specimens of *C. relictata* were examined during visits to The Natural History Museum (London) and the Museo Civico di Storia Naturale (Verona) with light microscopes. PAUP v3.1 (Swofford, 1991) was used for the cladistic analyses of two separate data sets [see Tables S1 and S2 (Supporting Information); nexus files will be made available by the corresponding author upon request]. The analyses were conducted with and without enforced topology (heuristic search, 500 replicates).

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**Fig. 1.** Male genitalia. (A) Aedeagus of *Tenomergera cinerea* (Cupedidae), slightly schematized (after Neboiss, 1984): left, dorsal view; right, ventral view. Scale bar: 100 µm. (B) Aedeagus of *Crowsoniella relict* (after Pace, 1975): left, dorsal view; right, ventral view. Scale bar: 50 µm. Note the ventromarginal spines in both species. Ah, apical hook; Msl, mesal lobe; Pm, paramere; Vms, ventromarginal spine.

*Evaluation of phylogenetic arguments in Kirejtshuk et al. (2010)*

Kirejtshuk *et al.* (2010) did not base their phylogenetic hypothesis for the placement of *Crowsoniella* on a stringent cladistic analysis, restricting their justification to an informal discussion of selected morphological characters (see below). However, we stress that major (or minor) taxonomic shifts, in this case from one beetle suborder (Archostemata) to another (Polyphaga-Cucujiformia), should not be based on an informal and superficial character discussion, especially if thorough evaluations of extensive data sets are already available. Another point of criticism is the inadequate treatment of relevant literature. Three out of four recent comprehensive phylogenetic studies on Archostemata (Beutel & Hörnschemeyer, 2002; Beutel *et al.*, 2008; Friedrich *et al.*, 2009) were ignored by Kirejtshuk *et al.* (2010), as was Lawrence's (1999) study on Ommatidae, a group that formerly included *Crowsoniella* (e.g. Crowson, 1975; Lawrence, 1982; Lawrence & Newton, 1982, 1995). The species-level phylogeny of Archostemata by Hörnschemeyer (2009) is cited. However, its results, notably the very specific structural affinities of the male genitalia of *Crowsoniella* with those of other archostematans (especially Cupedidae), are not discussed properly.

The systematic position of *C. relict* in Polyphaga-Cucujiformia, stated as a fact and not as a hypothesis by Kirejtshuk *et al.* (2010), is not supported by relevant evidence, and the justification is far from convincing. The first argument presented is 'that this specimen has only one suture on the underside of prothorax' (Kirejtshuk *et al.*, 2010: 217). It is likely that the authors implicitly interpreted this as an internalization of the propleura, as it is characteristic for polyphagan beetles (e.g. Hlavac, 1972, 1975; Lawrence, 1982, not cited). However, it is unclear which parts are internalized or fused in *Crowsoniella*, and all prothoracic sutures are missing in the small archostematans species *Micromalthus debilis* LeConte

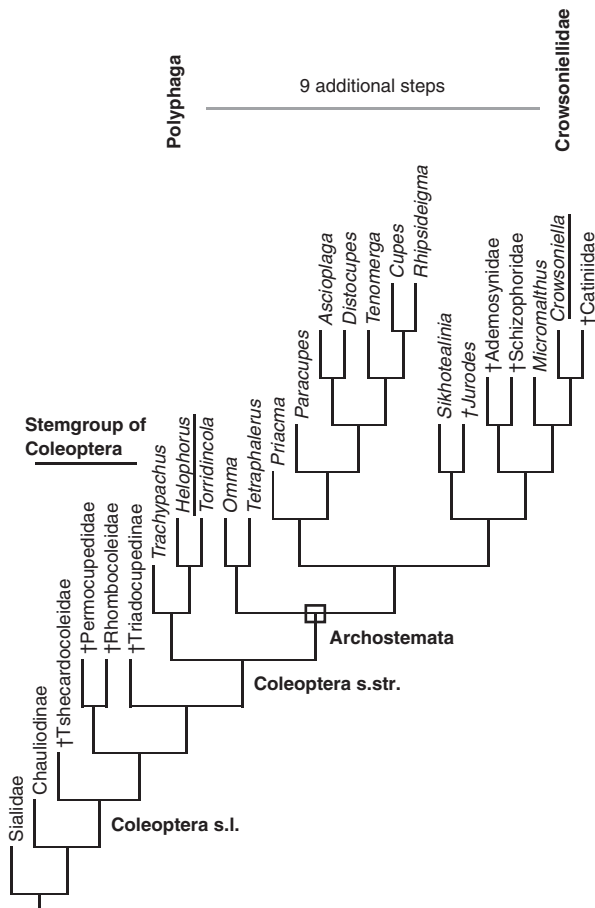
(e.g. Barlet, 1997, not cited). Partial or complete fusion of prothoracic sclerites in correlation with size reduction appears likely in the case of *Crowsoniella* and *Micromalthus*. A similar condition has evolved independently in the small males of the extant groups of Strepsiptera (H. Pohl, personal communication). The second argument is little better. The authors state that 'its metepisterna could not reach mesocoxal cavities' (Kirejtshuk *et al.*, 2010: 217). A metathoracic anepisternum reaching the mesocoxal cavity is a characteristic found in most members of Archostemata (except Micromalthidae), but also in some groups of Adephaga (e.g. Eodromeinae, Amphizoidae, Aspidytidae), Myxophaga and Polyphaga (Ponomarenko, 1977, not cited; Ge *et al.*, 2007, not cited; Beutel *et al.*, 2008; Friedrich *et al.*, 2009). Apparently this condition was acquired several times independently in the evolutionary history of Coleoptera. Mesocoxal cavities only formed by the meso- and metaventrites and the mesepimeron would by no means be an argument for removing *Crowsoniella* (or *Micromalthus*) from Archostemata. Moreover, fig. 17 in Kirejtshuk *et al.* (2010) suggests that the metanepisternum may in fact reach the coxal cavity. In any case, the presently available morphological documentation of the character is insufficient.

As additional arguments for an inclusion in Polyphaga and Cucujiformia, Kirejtshuk *et al.* (2010) point out a combination of characters of *Crowsoniella* coinciding 'with that in some [emphasis our own] Cerylonidae Billberg 1820': 'bulged preapical palpomeres, type of formation of mesocoxae, type of antennal insertions, elongate trochanters, structure of antennae, character of depressions for reception of legs on thoracic and abdominal, sclerites as well as depressions at anterior angles of pronotum as well as depressions at base of elytra congruous to posterior angles of prothorax, tendency to reduction of eyes, even some features in the structure of aedeagus' (Kirejtshuk *et al.*, 2010: 217). These features are insufficiently specified [e.g. 'type of antennal insertions', 'structure of antennae' (many varieties occur in Cerylonidae; Ślipiński & Lawrence, 2010), 'tendency to reduction of eyes', 'some features in the structure of aedeagus'], most of them are widespread in Coleoptera, and most do not belong to the ground plan of Cerylonidae (see Ślipiński & Lawrence, 2010). Kirejtshuk *et al.* (2010) only cited one study on Cerylonidae (Ślipiński, 1990), and ignored a recent treatment in the Handbook of Zoology series (Ślipiński & Lawrence, 2010).

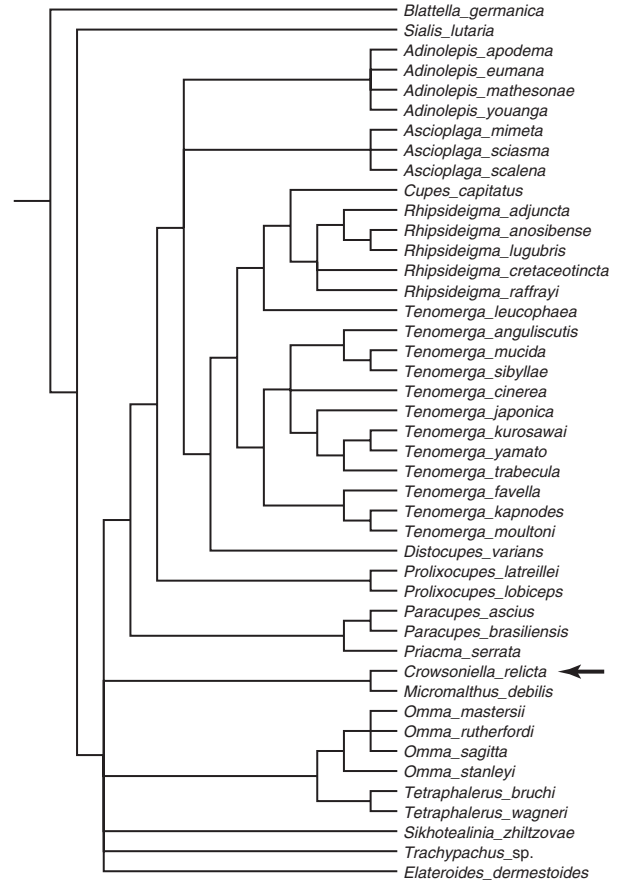
The taxonomic statement made by Kirejtshuk *et al.* (2010) would imply that the apomorphies of Coleoptera excluding Archostemata (e.g. numerous muscle losses), Myxophaga + Polyphaga (e.g. fusion of the larval tibia and tarsus, presence of prothoracic trochantinopleura of adults), Polyphaga (e.g. further muscle losses, internalization of propleura), and Cucujiformia (e.g. presence of cryptonephric Malpighian tubules; see Lawrence, 1982; Beutel & Haas, 2000, not cited) are present in Crowsoniellidae, unless secondary modification occurred. As the larvae and the internal anatomy of adults are unknown, these features do not help to resolve the relationships of *Crowsoniella* at present.

Results of the cladistic analyses

We did not reanalyse the data set presented in Friedrich *et al.* (2009), as approximately 77% of the characters could not be scored for *Crowsoniella* (internal features of adults, larval characters). *Crowsoniella* was included in the data set of Beutel *et al.* (2008) (Table S1). The analysis without enforced topologies resulted in four minimum length trees of 175 steps, and *Crowsoniella* was placed in a clade with the miniaturized and highly specialized Micromalthidae (and the extinct Catiniidae) (Fig. 2). Beutel *et al.* (2008) suggested that unambiguous apomorphies of this lineage might be the result of size reduction and possibly non-feeding in adults. In a second analysis a clade comprising *Crowsoniella* and the polyphagan terminal taxon *Helophorus* sp. (Hydrophiloidea) was enforced. This increased the length of the trees to 184 steps, i.e. nine additional evolutionary changes were required.



**Fig. 2.** Phylogenetic relationships of extinct and extant groups of Archostemata (and stem-group Coleoptera) based on 90 morphological characters. Parsimony analysis, conducted with PAUP\* 4.0b10, heuristic search, random addition and 500 replicates, yielded three equally parsimonious trees of 175 steps (one of which is presented here; for details see Beutel *et al.*, 2008). An enforced clade comprising *Crowsoniella relictata* (underlined) and the polyphagan terminal *Helophorus* sp. (Hydrophiloidea) (underlined) requires nine additional steps.



**Fig. 3.** Phylogenetic relationships of species of Archostemata reconstructed from 84 morphological characters of adults. Parsimony analysis, conducted with PAUP\* 4.0b10, heuristic search, random addition and 500 replicates, yielded 490 equally parsimonious trees with 229 steps (for details see Hörschemeyer, 2009). Enforcing a sister-group relationship of *Crowsoniella relictata* (arrow) with the polyphagan *Elateroides dermestoides* requires three additional steps.

The reanalysis of the data set assembled for elucidating the species level phylogeny of Archostemata (Fig. 3; Hörschemeyer, 2009) was carried out without the larval character set (larvae of *Crowsoniella* unknown), leaving 84 adult characters (Table S2). Enforcing a topology with *Crowsoniella* grouping with the polyphagan terminal *Elateroides dermestoides* (Linnaeus) (Lymexyloidea) required three additional steps.

**Discussion**

The transfer of *Crowsoniella* from Archostemata to Cucujiformia is rejected here for several reasons: (i) the lack of a formal character analysis; (ii) insufficient coverage of the relevant literature; (iii) inappropriate interpretation of characters; and (iv) insufficient specification of structural affinities of *Crowsoniella* and Cerylonidae (Cucujoidea) (see above).

Even though a severe lack of data (adult anatomy, immature stages, molecular data, biology) greatly impedes a reliable

placement of *Crowsoniella*, a position within Archostemata appears very likely. This was suggested not only by two outstanding coleopterists, the late Prof. R.A. Crowson (Crowson, 1975) and Dr J.F. Lawrence (e.g. Lawrence, 1982), but is also supported in two cladistic evaluations of comprehensive morphological character state matrices (Beutel *et al.*, 2008; Hörnschemeyer, 2009). These partly overlapping data sets are not completely independent, but have a distinctly different focus of taxon and character sampling. Both studies unambiguously place *Crowsoniella* within Archostemata. Characters such as the very distinctly constricted neck region (Fig. 4C) and the median ridge of the abdominal ventrite 1 (Fig. 4C: MR) clearly are archostematan features.

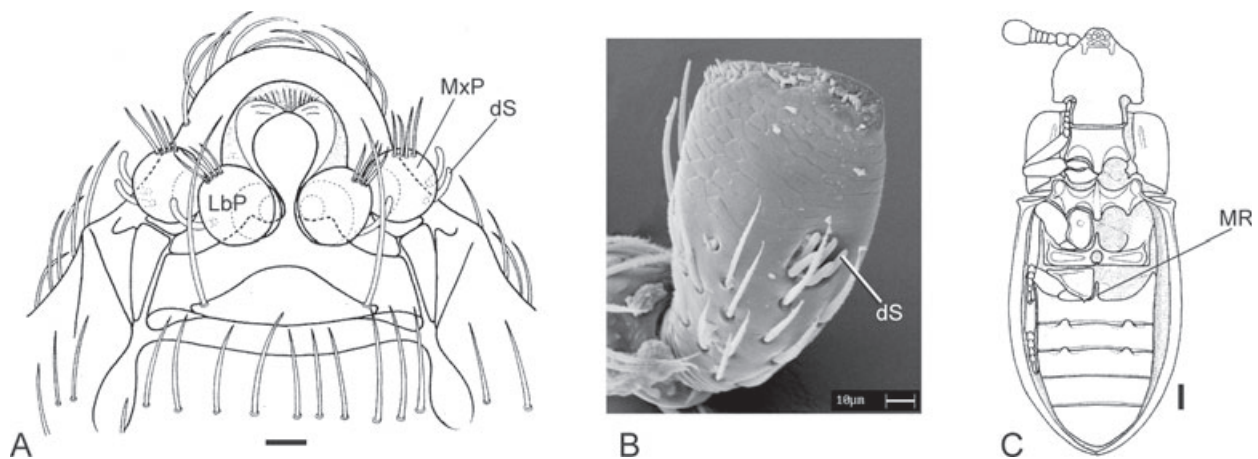
One minute but probably important character is the presence of digitiform sensilla (Fig. 4A: dS) on the palps of *Crowsoniella*. Sensilla of similar shape and size are almost generally present in the same position in Coleoptera. However, the characteristic free, nearly upright type depicted for *Crowsoniella* by Pace (1975) otherwise occurs only in Cupedidae (Fig. 4B). In other archostematan groups, the sensilla are always positioned in a more or less deep depression or pit. The presence of sensilla as such is arguably plesiomorphic for Coleoptera. Nevertheless, the specific, cupedid-like condition in *Crowsoniella* supports a phylogenetic position within Archostemata. The sensilla in Polyphaga are of a derived type, flattened and adpressed to the surface of the palpomere (S.A. Ślipiński, personal communication).

The strongest evidence for the inclusion in Archostemata comes from well-defined features of the male genital apparatus (Fig. 1), which was described in detail in Pace (1975) and analysed by Hörnschemeyer (2009). A very unusual characteristic suggesting a clade comprising *Crowsoniella* and Cupedidae is the presence of ventromarginal spines on the aedeagus (Fig. 1: Vms). Such spines occur in males of *Crowsoniella* and all species of Cupedidae, but have been reported from no other group of beetles.

Apparently many archostematan groundplan character states are lost secondarily in *Crowsoniella*. These include the absence of the transverse suture of the mesoventrite, the absence of the ventral articulations of the mesocoxa, the exposed metatrochantin and others. As pointed out in Polillov & Beutel (2010), and other studies on miniaturization, size reduction often results in the fusion or simplification of sclerites. A plesiomorphic archostematan condition that is partly preserved is the reticulate pattern of the elytra (Pace, 1975: areolae arranged in eight regular series).

The placement of *Crowsoniella* suggested by Kirejtshuk *et al.* (2010) implies this taxon re-evolved the plesiomorphic condition of the elytral pattern and the digitiform sensilla of the palps, and the convergent acquisition of several derived features such as the aedeagal spines, the median ridge of the first abdominal ventrite, and the constricted neck region. These assumptions are much less likely than the reduction or loss in *Crowsoniella* of some archostematan structures caused by miniaturization.

The precise position of *Crowsoniella* within Archostemata is somewhat ambiguous (see Beutel *et al.*, 2008; Hörnschemeyer, 2009), and will probably remain so until more evidence is available. It is uncertain whether material suitable for DNA extraction and anatomical study will become available in the near future, or whether molecular techniques will enable us to extract sufficient sequences from the type specimens. What would be possible, however, is a non-destructive investigation with micro computerised tomography ( $\mu$ -CT), a technique that was constantly improved in recent years (e.g. Friedrich *et al.*, 2008). Even though it is likely that soft tissues are not preserved (or strongly deformed), the knowledge of internal skeletal structures (e.g. tentorium, endosternites) could be obtained. As it is the case with *Crowsoniella*, it is extremely uncertain that more specimens of *Sikhotealinia* (only the holotype is known) will turn up in the foreseeable future. However, examining the holotype with  $\mu$ -CT should have high



**Fig. 4.** (A) Detail of mouthparts of *Crowsoniella relictata*, in ventral view (after Pace, 1975): note lateral digitiform sensilla on palps. Scale bar: 10  $\mu$ m. (B) Terminal segment of maxillary palp of *Cupes capitatus* (Cupedidae): note digitiform sensilla. (C) Ventral view of *C. relictata* (after Pace, 1975): note median ridge on first abdominal ventrite. Scale bar: 100  $\mu$ m. dS, digitiform sensilla; LbP, labial palp; MR, median ridge of first abdominal ventrite; MxP, maxillary palp.

priority. It is apparent that additional well-documented data on the two enigmatic and elusive taxa would greatly help to create a robust phylogeny for Archostemata – a very small key taxon within the megadiverse Coleoptera.

### Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2010.00552.x

**Table S1.** Character state matrix from Beutel *et al.* (2008).

**Table S2.** Character state matrix from Hörnschemeyer (2009).

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