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The systematic position of the stonefly †*culonga* Sinitshenkova, 2011 (Plecoptera: *Leuctrida*) reassessed using Reflectance Transforming Imaging and cladistic analysis

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Abstract. The phylogenetic position of the insect species †*culonga* Sinitshenkova, 2011, recovered from the Khasurty locality (Transbaikalia, Russia; Early Cretaceous), is re-investigated. This fossil needle stonefly has been considered an *Exeuctrida* nec *Mioleuctrida* & *Eleuctrida* based on the organization of the hind wing venation opposite the arculus. We reconsidered this interpretation based on a direct observation, complemented by a Reflectance Transforming Imaging file. Our investigation indicates that the species displays the defining character state of *Eleuctrida* while it lacks the defining character state of *Mioleuctrida*. Due to inconsistencies in the character state combination displayed by the species, we carried out a cladistics analysis. The species †*culonga* is recovered as an *Eleuctrida* nec *Mioleuctrida*, and therefore represents a suitable calibration point for a node more recent than previously assumed, and incidentally demonstrates that *Mioleuctrida* belongs to *Eleuctrida*.

Key words. Leuctridae, fossil, hind wing, venation, RTI, phylogeny.

1. Introduction

The fossil record of insects is gaining an unprecedented interest in relation to attempts to time-calibrate the phylogenetic tree of the group. A side effect is that the systematic placement of putatively relevant fossils is scrutinized more carefully than it has previously been. Taxonomic assignments based on documentation perceived as insufficient are considered with caution. It is a fact that fossil insects, especially those preserved as imprints, are chronically difficult to photograph. Fortunately, computer-assisted photographic techniques which, generally speaking, are revolutionizing the field of palaeontology, offer new opportunities to ascertain the occurrence of relevant character states.

Here we revise the position of †*culonga* Sinitshenkova, 2011, an Early Cretaceous needle stonefly. The species was considered by BÉTHOUX et al. (2015) who placed it as an *Exeuctrida* nec *Mioleuctrida* & *Eleuctrida* (fig. 9 – *contra* legend to fig. 8, erroneous; i.e., a somewhat ‘remote’ crown-Leuctridae). This assignment was based on the organization of RP, M and the arculus near the hind wing base (states schematized in Fig. 1A–C), as inferred from photographs provided by colleagues. Based on direct observation of the specimen, and complemented by a Reflectance Transforming Imaging (RTI) file, a technique which delivers exhaustive and interactive photographic data (see a former application of the technique

on a fossil insect in BÉTHOUX et al. 2016), a more accurate interpretation of the hind wing base venation is provided. Because of inconsistencies in the character state combination displayed by the species, we carried out a morphology-based cladistics analysis.

2. Material and methods

2.1. Fossil material

The specimen we focus on herein was collected from Khasurty locality, Transbaikalia, Russia (Early Cretaceous; KOPYLOV 2011; SINITSHENKOVA 2011). It is kept at the Paleontological Institute (PIN; Russian Academy of Sciences, Moscow, Russia). Draft drawings were produced with the aid of a microscope equipped with a camera lucida (Zeiss SterEO Discovery V8 stereomicroscope equipped with a pair of W-PL 10×/23 eye pieces, a Plan Apo S 1.0 × FWD objective; Zeiss, Jena, Germany).

2.2. Data production

Photographs reproduced in Fig. 2B,D were taken using a Canon EOS 5D Mark III equipped with a Canon MP-E 65 macro lens (Canon, Tokyo, Japan). A set of photographs necessary to produce two RTI files (overview, and details of the left hind wing base) were obtained with the same photographic equipment driven by a hand-made Portable Light Dome, and then computed using RTIBuilder software (see BÉTHOUX et al. 2016). We provide an online Dryad dataset, cited below as “CUI et al. (2018)”, in which the RTI files (to be opened using the freely accessible software RTIViewer) are available. The photograph reproduced as Fig. 2E was extracted from the RTI file ‘PIN 5026 75 – detail LHW base’ (bookmark 2).

2.3. Systematic nomenclature

We use the cladotypic nomenclatural procedure (BÉTHOUX 2007a, 2007b, 2010; BÉTHOUX et al. 2015). Under this procedure, all the taxon names are written in italics, with a capital letter, just as names of genera under the traditional, ICZN-governed procedure.

2.4. Wings and their venation

We follow the serial insect wing venation ground plan (LAMEERE 1922, 1923). Wing venation nomenclature is repeated here for convenience: ScP, posterior Subcosta; RA, anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; Cu, Cubitus; CuA, anterior Cubitus; CuP, posterior Cubitus; AA: anterior Analis; AA1: first anterior Analis; AA2, second

Table 1. List of taxa included in the cladistic analysis (under Linnaean nomenclature).

Nemouridae	<i>Amphinemura banksi</i> Baumann & Gaufin, 1972
Capniidae	<i>Capnioneura pettipierreae</i> Aubert, 1960
Leuctridae	<i>Megaleuctra flinti</i> Baumann, 1973
Leuctridae	<i>Megaleuctra complicata</i> Claassen, 1937
Leuctridae	<i>Megaleuctra kincaidi</i> Frison, 1942
Leuctridae	<i>Megaleuctra stigmata</i> (Banks, 1900)
Leuctridae	<i>Megaleuctra williamsae</i> Hanson, 1941
Leuctridae	† <i>Rasnitsyrina culonga</i> Sinitshenkova, 2011
Leuctridae	<i>Calileuctra dobryi</i> Shepard & Baumann, 1995
Leuctridae	<i>Paraleuctra vershina</i> Gaufin & Ricker, 1974
Leuctridae	<i>Zealeuctra claasseni</i> (Frison, 1929)
Leuctridae	<i>Despaxia augusta</i> (Banks, 1907)
Leuctridae	<i>Moselia infusata</i> (Claassen, 1923)
Leuctridae	<i>Leuctra grandis</i> Banks, 1906

anterior Analis; ra-rp, rp-ma indicate the two specific cross-veins connecting RA and RP, RP and MA, respectively. The terminology for areas of the hind wing follows BRANNOCH et al. 2018); specifically, the posterior area referred to as ‘vannus’ or ‘anal area’ by some is termed ‘plicatum’. Right and left forewings are indicated as RFW and LFW respectively, and right and left hind wings as RHW and LHW, respectively.

2.5. Cladistic analysis

Taxon sample. BÉTHOUX et al. (2015) proposed a phylogenetic and nomenclatural framework including †*culonga* and other close relatives inside *Leuctrida*. Based on this framework, we selected 11 extant species (in addition to †*culonga*) as ingroup (Appendix, Table 1). One species of Nemouridae (*banksi* Baumann & Gaufin, 1972) and one species of Capniidae (*pettipierreae* Aubert, 1960) were used as outgroup representatives (the former being set as most distant one).

Character list and matrix. The only morphological matrix covering stoneflies published is from ZWICK (2000; and see ZWICK 1973, 1974). In this contribution characters derived from the wing venation are few with respect to their potential. Therefore we elaborated a new character list (see Appendix). This study used only wing venation characters because of the very limited availability of other morphological characters, such as male genitalia, in fossils. We obtained our documentation from BÉTHOUX et al. (2015) and direct observation of specimens referred to in there. The resulting matrix is provided in Table 2.

As for *kincaidi* Frison, 1942, our observations demonstrated that the drawing of the hind wing of this species in BÉTHOUX (2005: fig. 6) is inaccurate regarding **ch. 5**: the species displays the type represented in Fig. 1A (**ch.s. 5:0**; instead of that represented in Fig. 1B). As stated by BÉTHOUX et al. (2015), it is not clear whether, in hind wing, AA2α and AA2β are fused, or not, in *Mioleuctrida* (**ch. 6**). As a consequence the character was coded as

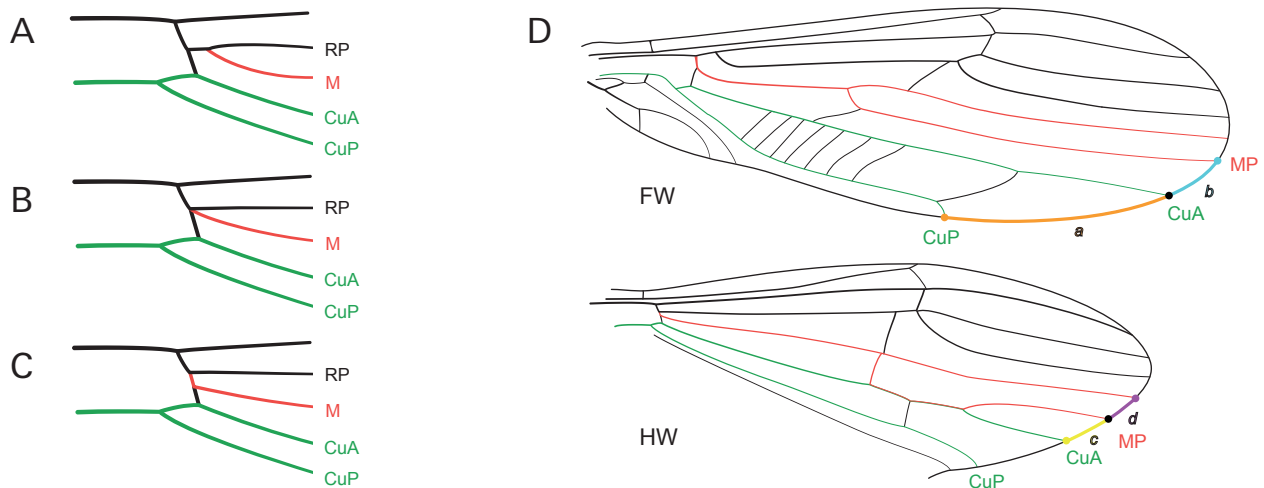


Fig. 1. A–C: Schemes representing the defining character states of various *Leuctrida* taxa (according to BÉTHOUX et al. 2015); A: *Leuctrida*; B: *Exeuctrida*; C: *Eleuctrida*. D: Schemes representing the measurement on fore- and hind wing, used as characters for cladistic analysis.

unknown in the corresponding species. Two characters, namely **ch. 7** and **ch. 8**, are based on measurements. Corresponding abbreviations are as follows (Fig. 1D): **a**, in forewing, distance between the endings of CuA and CuP; **b**, in forewing, distance between the endings of MP and CuA; **c**, in hind wing, distance between the endings of MP and CuA; **d**, in hind wing, distance between the endings of MA and MP. Note that measurements correspond to the length between two vein endings along the wing margin, i.e., length of a curve, rather than the straight distance between the two endings.

Analysis. The data matrix was subjected to a parsimony analysis in PAUP* (version 4.0a152) (Swofford 1991) using the branch-and-bound algorithm. All characters were weighted equally and were treated unordered.

3. Results

3.1. Redescription

Species †*culonga* Sinitschenkova, 2011

Fig. 2

Diagnosis. In hind wing, arculus connecting M and CuA; in hind wing, plicatum developed; in hind wing, MP fused for some distance with CuA via the m-cua cross-vein (state thereafter considered convergently acquired in *Collaleuctrida*).

Redescription. Positive and negative imprints of an almost complete individual, with abdomen poorly preserved, partly disarticulated; details of head and tarsi indistinct; thorax well visible. **Left forewing:** posterior part of the wing folded longitudinally; length about 7.2 mm, width (reconstruction) 2.3 mm; no cross-vein in the

antero-apical area; RP arising obliquely from R, forked slightly basal to the point of fusion of ScP with RA; ra-rp cross-vein connected to the anterior branch of RP, very slightly oblique; M diverging from R+M slightly basal to the origin of RP; M forked slightly before the middle of the wing length, MA and MP long; rp-ma cross-vein oblique; Cu bent in the very basal part, forked into CuA and CuP slightly before the arculus; area between M/MP and CuA with four cross-veins visible in addition to the arculus; CuP curved, reaching the posterior wing margin slightly after the middle of wing length; area between CuA and CuP with 8 visible cross-veins; AA1 simple; AA2 forked. **Left hind wing:** length about 6.2 mm, width (broadest part from anterior wing margin to end of AA1) 2.2 mm; RP and MA diverge from R fused and shortly diverge; RP forked; ra-rp cross-vein connected to RP opposite the fork of this vein; point of divergence of M from RP+M located basal to the arculus (see arrows in Fig. 2C–E); course of MA indistinct for most part; MP fused with CuA via the mp-cua cross-vein, then diverging from it; Cu forked into CuA and CuP slightly basal to the arculus; AA1 simple; first anterior branch of AA2 (presumably composed of AA2α and AA2β) forked distal to the arculus (and, therefore, distal to the aa1-aa2α cross-vein); **Right forewing:** as preserved, wing venation essentially similar to that of the left forewing; area between anterior wing margin and ScP folded longitudinally; most basal and distal parts invisible/not preserved. **Right hind wing:** wing venation similar to that of the left hind wing; most basal and distal part invisible/not preserved; anal area barely visible; few veins visible, slightly distorted.

Notes. The structure formed by RP, M, and CuA at their bases, and the arculus, in the hind wing, is challenging to illustrate using traditional photographic approaches because the axis formed by RP + M, M and the arculus is perpendicular to the portions of RP and M parallel to the wing longitudinal axis. The provided RTI file allows a critical evaluation of this structure.

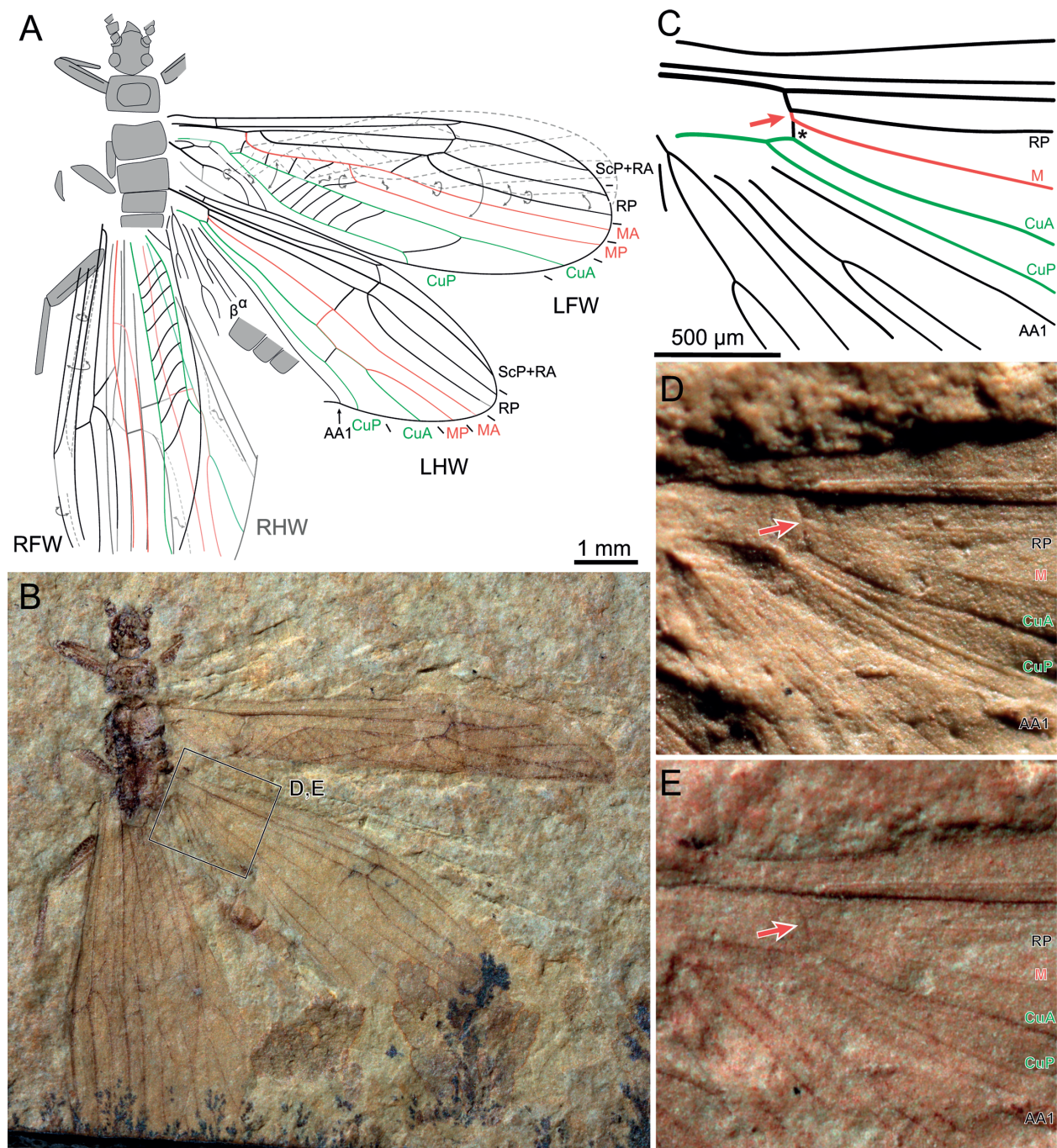


Fig. 2. *Euleuctrida* nec *Mioleuctrida* †*culonga* Sinitshenkova, 2011, specimen PIN 5026/75. **A:** Drawing of habitus (for clarity, RHW was set at 60% opacity; grey dashed lines indicate folded or creased portions of wings as preserved, while grey arrows indicate where these portions were relocated; reconstructed portions set at 60% opacity). **B:** Photograph of habitus (composite of photographs of the negative imprint under both ethanol and dry conditions, flipped, and of the positive imprint under ethanol). **C:** Drawing of LHW base (arrow indicates M diverging from RP+M, before M connects with CuA via the arcus, itself indicated by *). **D:** Photograph of LHW base (negative imprint, flipped, dry), as located on B. **E:** Photograph of LHW base (extracted from RTI data, bookmark 2 as in Cui et al. 2018), as located on B.

3.2. Cladistic analysis

The cladistic analysis delivered one most parsimonious tree (length = 13; CI = 0.769; RI = 0.900). The obtained consensus tree (Fig. 3) generally agrees with that proposed by BÉTHOUX et al. (2015). The species †*culonga* is retrieved as an *Eleuctrida* but does not belong to the *Mioleuctrida*.

4. Discussion

BÉTHOUX et al. (2015) proposed the following sequence of inclusiveness for needle stonefly taxa: *Leuctrida* > *Exeleuctrida* > *Eleuctrida* & *Mioleuctrida* > *Collaleuctrida* (the respective positions of *Eleuctrida* and *Mioleuctrida* remaining undetermined). The systematic placement of

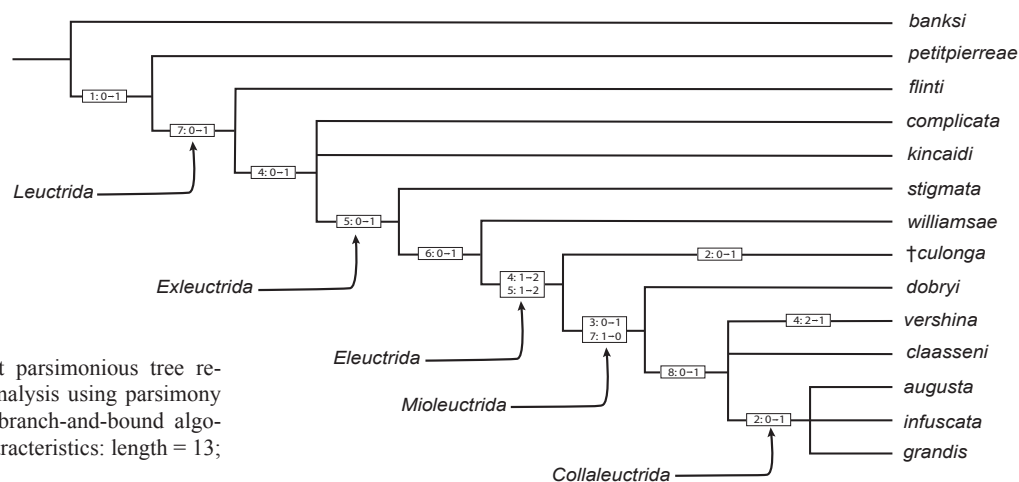


Fig. 3. The single most parsimonious tree recovered from cladistic analysis using parsimony as optimality criterion (branch-and-bound algorithm; individual tree characteristics: length = 13; CI = 0.769; RI = 0.900).

†*culonga* within this sequence was investigated, but not firmly established. According to the original description by SINITSHENKOVA (2011) the species possesses the defining character state of *Leuctrida* as defined by BÉTHOUX et al. (2015; namely, the absence of resurgence of ScP distal to its fusion with RA). This statement was confirmed by the possession of the defining character state of *Exeuctrida* ('in hind wing, arculus connecting RP+M and CuA opposite the point of the divergence of M from RP+M, or connecting M and CuA'; see Fig. 1B,C; **ch.s. 5:1, 5:2**). An assignment to *Exeuctrida* is consistent with another observed character state, viz. 'stem of AA2α and AA2β forked after the cross-vein aa1-aa2α in the hind wing' (**ch.s. 6:1**), known in *williamsae* Hanson, 1941, an *Exeuctrida* nec *Eleuctrida*, but possibly occurring as 'full fusion of AA2α and AA2β' in *Eleuctrida* and *Mioleuctrida* (BÉTHOUX et al. 2015: 324, fig. 1H). In the hind wing of †*culonga*, the presumed occurrence of **ch.s. 5:1** prompted BÉTHOUX et al. (2015) to exclude †*culonga* from *Eleuctrida*. Concurrently, the 'presence of a well-developed hind wing plicatum' (**ch.s. 3:0**), allowed †*culonga* to be excluded from *Mioleuctrida* as defined in BÉTHOUX et al. (2015). These authors then postulated that †*culonga* is an *Exeuctrida* nec *Eleuctrida* & *Mioleuctrida*. A remaining inconsistency was that the hind wing of †*culonga* exhibits the defining character state of *Collaleuctrida* (viz. 'fusion of MP with CuA'; **ch.s. 2:1**), discussed by BÉTHOUX et al. (2015).

Based on our observation of the specimen, the occurrence of **ch.s. 2:1**, **ch.s. 3:0**, **ch.s. 6:1** were confirmed. However previous accounts on **ch. 5** (SINITSHENKOVA 2011; BÉTHOUX et al. 2015) proved inaccurate: the species displays **ch.s. 5:2**. It is visible in the left hind wing of the holotype when using multiple light orientations (Fig. 2C–E; and see RTI in CUI et al. 2018). Therefore †*culonga* actually possesses the defining character state of *Eleuctrida*. Finally, the possession of a developed plicatum (**ch.s. 3:0**) indicates that the species can be excluded from the *Mioleuctrida*. However, this is inconsistent with the occurrence of **ch.s. 2:1**, suggesting an assignment to the *Collaleuctrida*, a taxon included in *Mioleuctrida* according to BÉTHOUX et al. (2015).

The formal cladistic analysis demonstrates that †*culonga* is an *Eleuctrida* nec *Mioleuctrida* (i.e. is a crown-*Eleuctrida* and a stem-*Mioleuctrida*: it can therefore be referred to as *Eleuctrida culonga*), and that the occurrence of **ch.s. 2:1** must be considered convergently acquired in †*culonga* and in *Collaleuctrida*. Owing to the unique character state combination of the species, our analysis also demonstrates that the *Mioleuctrida* belong to the *Eleuctrida*, a point that BÉTHOUX et al. (2015) could not resolve because all species known at the time displayed the definition character states of both taxa, or both antonymic character states. Finally, the species represents a calibration point for the split *williamsae*/sister-group, as opposed to the more ancient split *Exeuctrida*/sister-group, as previously assumed (BÉTHOUX et al. 2015). It will be an important asset in an ongoing project focusing on a time-calibrated phylogeny of Plecoptera (Cui et al. in prep.).

5. Conclusion

As previously argued (BÉTHOUX et al. 2016) the RTI approach proves a suitable surrogate to the actual observation of a fossil insect specimen. This technique is particularly well-suited when critical structures (venation, or other body parts) form right angles. In such cases at least two photographs, each with a light source perpendicular to one of these structures, are needed for a proper documentation (herein, Fig. 2D,E). Indeed, in many cases of fossil insects preserved as rock imprint, the production of suitable sets of photographs can prove demanding. Moreover, the RTI data allows a critical evaluation of the favoured interpretation.

The phylogenetic position of †*culonga* suggests that *Eleuctrida* are at least Early Cretaceous. The position of the species will be essential to better appreciate the age of the *Leuctrida* and, possibly, of other major lineages of stoneflies.

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8. Appendix

List of 8 morphological characters used for the cladistic analysis. Characters 7 and 8 are based on measurements (see Fig. 1D). Where relevant the name of the taxon showing a given state is indicated.

1. In both fore- and hind wing, area delimited by the anterior wing margin and RA, and beyond the end of (the basal free part of) ScP, with a cross-vein like structure, veinlet or vein (which is the actual ending of ScP, more or less developed): **1.0** yes; **1.1** no (implying a fusion of ScP with RA without a distal free part of ScP; *Leuctrida*).
2. In hind wing, MP fused with CuA (via the m/mp-cua cross-vein): **2.0** no; **2.1** yes (*Collaleuctrida*).
3. In hind wing, plicatum, number of distinct AA2 veins reaching the posterior wing margin distal to the cup-aa1 cross-vein: **3.0** > 2; **3.1** 2 (*Mioleuctrida*).
4. In forewing, with respect to fork of M, the rp-m/ma cross-vein is located: **4.0** opposite; **4.1** proximally (it is then a ‘rp-m’ cross-vein); **4.2** distally (it is then a ‘rp-ma’ cross-vein).
5. In hind wing, arculus connecting CuA and: **5.0** RP+M basal to the split of RP and M (Fig. 1A); **5.1** RP+M at the point where RP and M split (Fig. 1B; *Exepleuctrida*); **5.2** M (therefore, distal to its split with RP; Fig. 1C; *Eleuctrida*).
6. In hind wing, stem of AA2α and AA2β forked: **6.0** before the cross-vein aa1-aa2α; **6.1** after the cross-vein aa1-aa2α.
7. In forewing, ratio *a/b*: **7.0** < 2.5; **7.1** > 2.5.
8. In hind wing, ratio *c/d*: **8.0** < 2.0; **8.1** > 2.0.

Table 2. Character matrix. “?”: character not applicable.

Taxa	Characters							
	1	2	3	4	5	6	7	8
<i>banksi</i>	0	0	0	0	0	0	0	0
<i>petitpierreae</i>	0	0	0	0	0	0	0	0
<i>flinti</i>	1	0	0	0	0	0	1	0
<i>complicata</i>	1	0	0	1	0	0	1	0
<i>kincaidi</i>	1	0	0	1	0	0	1	0
<i>stigmata</i>	1	0	0	1	1	0	1	0
<i>williamsae</i>	1	0	0	1	1	1	1	0
<i>culonga</i>	1	1	0	2	2	1	1	0
<i>dobryi</i>	1	0	1	2	2	?	0	0
<i>vershina</i>	1	0	1	1	2	?	0	1
<i>claasseni</i>	1	0	1	2	2	?	0	1
<i>augusta</i>	1	1	1	2	2	?	0	1
<i>infuscata</i>	1	1	1	2	2	?	0	1
<i>grandis</i>	1	1	1	2	2	?	0	1