



Two new species of *Archelcana* Sharov (Orthoptera: Elcanidae) from the Lower Jurassic of Luxembourg

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Abstract: Two new species of the genus *Archelcana* Sharov (Orthoptera: Elcanidae: Archelcaninae) are described from the Toarcian (Lower Jurassic) deposits of Uerschterhaff, near Sanem, southern Luxembourg. *Archelcana numbergerae* sp. nov. and *Archelcana tina* sp. nov. are the first fossil insects to be formally described from the Uerschterhaff locality and the first fossil orthopterans from the Lower Jurassic of Luxembourg.

Key words: Arthropoda, Insecta, Polyneoptera, Orthopterida, Elcanidea, Mesozoic, Toarcian.

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Introduction

Familiar and ubiquitous today, grasshoppers and crickets (Orthoptera) were already a diverse and important component of terrestrial ecosystems by the Early Jurassic. One of the most diverse and recognizable orthopteran clades of the Mesozoic are the Elcanidae, a group of grasshopper-like insects characterized primarily by their unique tegminal venation and the presence of prominent spurs on the metatibiae (Zessin 1987; Gorochov 1995; Heads *et al.* 2018). Despite a long and rich fossil record spanning the Triassic to the Paleocene, a precise phylogenetic placement for the elcanids has remained elusive (Heads *et al.* 2018; Fang *et al.* 2018a,b; Schubnel *et al.* 2020). Their superficial resemblance to tettigonioids, with long antennae and well-developed, sword-like ovipositors, led many authors to assign them to Ensifera (Ander 1939; Zessin 1987; Gorochov *et al.* 2006), though these characters are almost certainly plesiomorphic among orthopterans. Other work based on tegminal venation has suggested relationships with or within Caelifera (Sharov 1968; Béthoux & Nel 2001) or a position at the base of Orthoptera (Martynov 1938; Ragge 1955; Gorochov & Rasnitsyn 2002). At the time of writing, the *Orthoptera Species File Online* (Cigliano *et al.* 2022) places the family within Ensifera, though this assignment is erroneous and will certainly change following a comprehensive revision and phylogenetic analysis.

Elcanidae were divided into two subfamilies by Gorochov *et al.* (2006) based on the condition of the tegminal cubitoanal veins: the nominate subfamily, Elcaninae, comprising the genera *Cratoelcana* Martins-Neto, 1991 from the Lower Cretaceous of Brazil (Heads & Martins-Neto 2007), *Ellca* Kočárek, 2020 from mid-Cretaceous Burmese amber, *Eubaiselcana* Gorochov, 1986 from the Lower Cretaceous of Mongolia, *Minelcana* Gorochov, Jarzembowski & Coram, 2006 from the Lower Cretaceous of England, *Panorpidium* Westwood, 1845, definitively known only from the Lower Cretaceous of England, Eastern Europe, and Asia (see discussion below), and *Probaiselcana* Gorochov, 1989 from the Upper Jurassic of Kazakhstan and the Lower Cretaceous of England and China (Gorochov 1989; Tian *et al.* 2019a); and the arguably more primitive subfamily Archelcaninae, comprising the genera *Archelcana* Sharov, 1968 from the Lower Jurassic of England, Russia, and Uzbekistan (Handlirsch, 1906; Whalley 1985; Zherikhin 1985), *Cascadelcana* Fang, Muscente, Heads, Wang & Xiao, 2018 from the Triassic of North America, *Jeholelcana* Fang, Heads, Wang, Zhang & Wang, 2018 from the Lower Cretaceous of China, *Parelcana* Handlirsch, 1906 from the Lower Jurassic of England and Germany, and the Middle Jurassic of China (Tian *et al.* 2019b), *Sibelcana* Gorochov, 1990 from the Upper Jurassic of Transbaikalia, *Sinoelcana* Gu, Tian, Wang & Yue, 2020 from the Middle Jurassic of China, and *Synelcana* Zessin, 1988 from the Lower Jurassic of Germany. Several elcanid genera remain unassigned to either subfamily. *Burmelcana* Peñalver & Grimaldi, 2010 and *Elcanonympha* Heads & Thomas, 2018, both from mid-Cretaceous Burmese amber, *Hispanelcana* Peñalver & Grimaldi, 2010 from Cretaceous Spanish amber, and *Liaonemobius* Ren, 1998 from the Cretaceous of China, are all known only from nymphs, and so, the tegminal venation characters used to separate the two subfamilies are unavailable (Ren 1998; Peñalver & Grimaldi 2010; Heads *et al.* 2018). *Longioculus* Poinar, Gorochov & Buckley, 2007 from mid-Cretaceous Burmese amber is known only from a partially preserved adult in which the cubitoanal region of the tegmen is incomplete, preventing confident subfamilial assignment (Poinar *et al.* 2007). Similarly, the recently described and only Cenozoic elcanid, *Cenoelcanus* Schubnel, Desutter-Grandcolas, Garrouste, Hervey & Nel, 2020 from the Paleocene of France is known only from a single, incomplete tegmen lacking the cubitoanal region (Schubnel *et al.* 2020). The genera *Elcanopsis* Tillyard, 1918 from the Permi-Triassic of Australia, and *Macrelcana* Karny, 1932 from the Lower Miocene of Croatia are, at the time of writing, included in Elcanidae in the *Orthoptera Species File Online* (Cigliano *et al.* 2022) apparently following Jell (2004) and Cadena-Castañeda (2019) respectively. Both of these genera are of unknown affinity and require detailed redescription, though are certainly not elcanids in that neither possess the close association of RP with the stem of M+CuA that is synapomorphic of Elcanoidea *sensu* Gorochov & Rasnitsyn (2002).

The genus *Archelcana* Sharov, 1968 presently comprises four species: the type species *Archelcana britannica* (Handlirsch, 1906) and *Archelcana durnovaria* Whalley, 1985, both from the Lower Jurassic of England (Handlirsch 1906; Whalley 1985), *Archelcana ornata* Zherikhin, 1985 from the Lower Jurassic of Kyrgyzstan, and *Archelcana shurabica* Sharov, 1968 from the Lower Jurassic of Uzbekistan. Here, we describe two new species of *Archelcana* from the Toarcian of Luxembourg and briefly discuss the taxonomy of the Jurassic elcanids of Europe pending their comprehensive revision.

Material and Methods

The specimens described herein were collected during fieldwork led by the National Museum of Natural History Luxembourg (MnhnL) between 2018 and 2021 at a site called Uerschterhaff near Sanem in southern Luxembourg (Figure 1). Construction works for a new prison temporarily exposed a succession

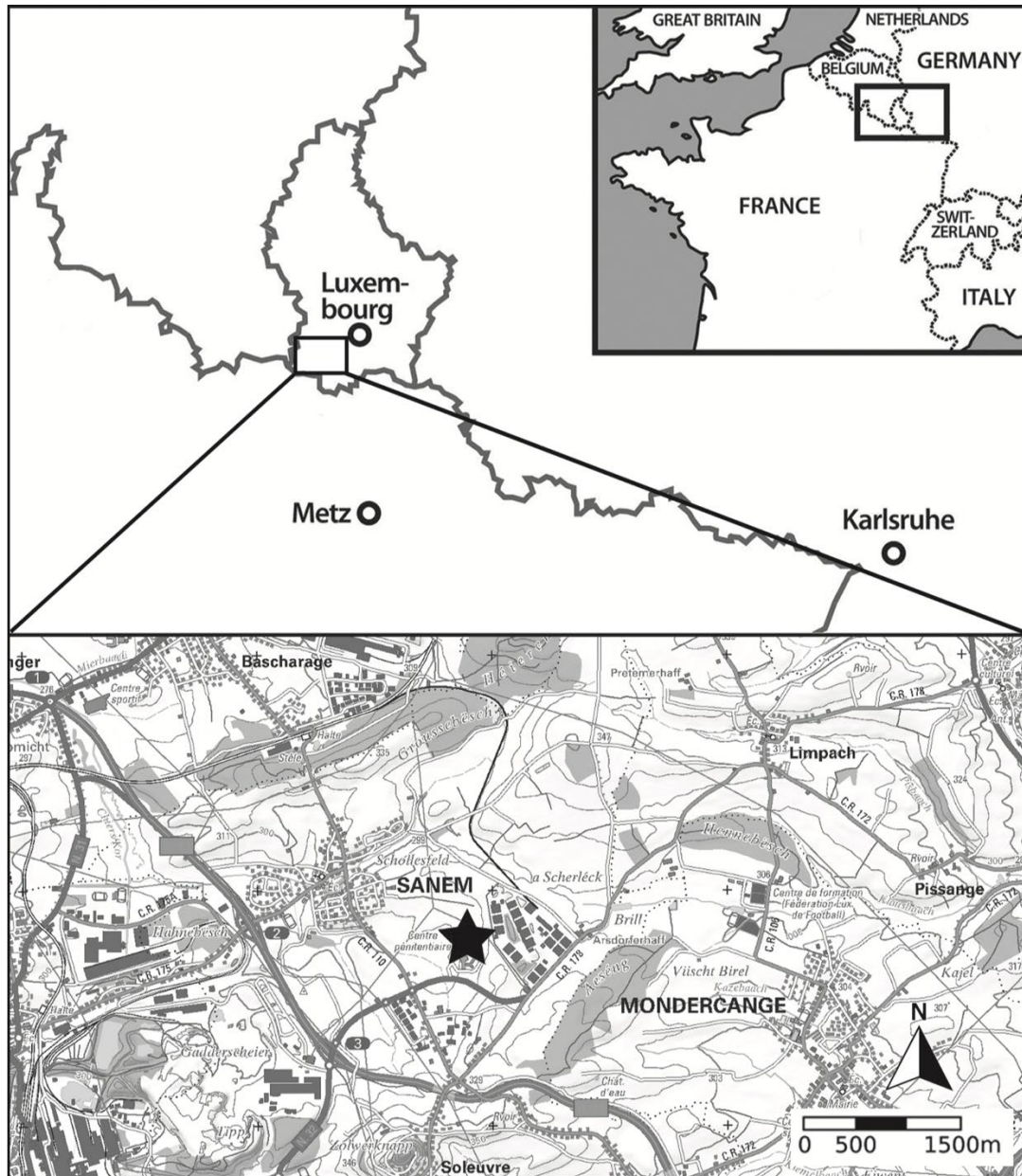


Figure 1. Map showing the location of the Urschterhaff locality near Sanem, Luxembourg.

of uppermost Pliensbachian marls and claystones, and lower Toarcian bituminous shales and limestone nodules. All the specimens were retrieved from a single layer of flat, finely laminate bituminous limestone nodules, several decimeters in diameter and approximately 10 cm thick. The nodules yield abundant shells of the small gastropod *Coelodiscus* Brösamlen, 1909. Other fossils include, in decreasing abundance, isolated bones and partly decomposed skeletons of the small teleost fish *Leptolepis* Agassiz, 1843, plant fragments, ammonites, decapod crustaceans, and coleoid cephalopods.

Ammonites found in the limestone nodules date the insect fossils to the Exaratum subchronozone, Serpentinum chronozone, lower Toarcian (*sensu* Page 2003). Similarities in stratigraphic position, lithofacies, and fossil content suggest that the insect-yielding nodule bed at Sanem is a lateral equivalent, if not direct continuation of, the nodule bed that yielded the rich insect assemblage from nearby Bascharage

(Nel, 1989; Nel *et al.* 1993, 1994; Henrotay *et al.* 1997, 1998; Delsate *et al.* 1999) and other sites in southern Luxembourg (Nel *et al.* 2017) and adjacent parts of Belgium (Delsate *et al.* 1992).

The insect-bearing nodule bed exposed at Sanem was deposited in a quiet sublittoral setting near the southeastern shore of the emergent London-Brabant landmass (Thuy & Numberger-Thuy 2021). During the lower Toarcian, the area was part of the northeastern Paris Basin and the sediments deposited are comparable to the Posidonia Shale of southwestern Germany (Hermoso *et al.* 2014).

All specimens are deposited in the fossil collection of the Department of Palaeontology at the National Museum of Natural History Luxembourg (NMNHL) in Luxembourg City. Photographs were made using a Keyence VHX-6000 both dry and under ethanol. Drawings were made using Adobe Illustrator 2021. Vein abbreviations are as follows (from anterior to posterior): CP, posterior costa; ScA, anterior subcostal; ScP posterior subcostal; RA, anterior radius; RP, posterior radius; MA1 and MA2, first and second branches of anterior media; MP, posterior media; CuA, anterior cubitus; CuP α , anterior branch of first posterior cubitus; CuP β , second branch of posterior cubitus; AA1, first branch of first anal.

Systematic Paleontology

Order Orthoptera Olivier, 1789
 Infraorder Elcanidea Handlirsch, 1906
 Family Elcanidae Handlirsch, 1906
 Subfamily Archelcaninae Gorochov, Jarzembowski & Coram, 2006
 Genus *Archelcana* Sharov, 1968

Archelcana numbergerae sp. nov.

Figures 2, 4a

[urn:lsid:zoobank.org:act:C0E3CEF2-F430-469C-B163-45B2870D1AA7](https://zoobank.org/urn:lsid:zoobank.org:act:C0E3CEF2-F430-469C-B163-45B2870D1AA7)

Holotype. MnhnL-TV606: complete tegmen.

Type locality. Uerschterhaff, near Sanem, Luxembourg.

Type horizon. Lower Toarcian (Exaratum subchronozone, Serpentinum chronozone, Lower Jurassic) bituminous limestone nodules of Uerschterhaff.

Etymology. The species is named in honor of Dr. Lea Numberger-Thuy (MnhnL) who discovered the beautifully preserved holotype.

Diagnosis. RP1 branching into numerous diffuse veinlets at apex of tegmen; RP2 three-branched; RP-stem and RA-RP crossveins very dark with five distinct, roughly quadrangular pale spots; proximal radiomedial crossveins dark, offset from each other, creating transverse zig-zag pattern; distal region of tegmen with broad, curved band of lighter pigment following but not reaching apex.

Description. Tegmen 16.48 mm long from base to apex, 3.55 mm wide at RA-RP branch; pterostigma approximately 6.42 mm long from RA-RP branch to RA ending in costal margin. CP three-branched. ScA four-branched, linked to CP by single crossvein. ScP four-branched with branches gently curved towards tegminal apex. RA branching from ScP approximately 0.72 mm from tegmen base. RA-RP region wide, with four strong crossveins. RP branching from RA approximately 7.50 mm from tegmen base, with six main branches: RP1 branching into numerous fine diffuse veinlets apically; RP2 three-branched; RP3

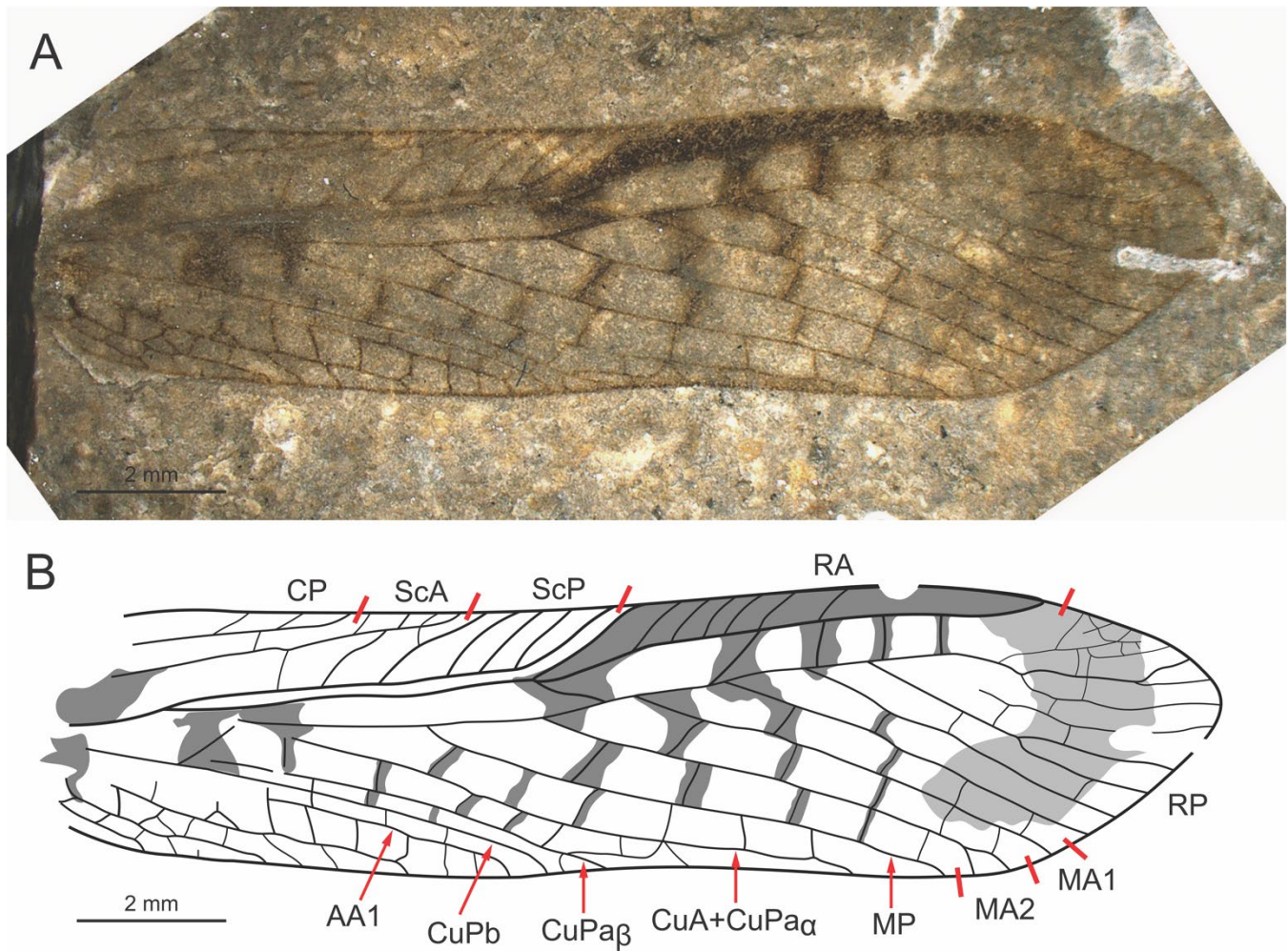


Figure 2. Holotype of *Archelcana numbergerae* sp. nov. (MnhnL-TV606). **A**, photograph under ethanol. **B**, explanatory drawing. Abbreviations are given in the text.

unbranched; RP4 two-branched; RP5 and RP6 unbranched. RP+MA1 fusion approximately 8.10 mm from tegmen base; fused for approximately 0.40 mm; branching approximately 8.60 mm from tegmen base. RP6-MA1 region with four crossveins. MA1 unbranched, diverging from MA2 approximately 7.40 mm from tegmen base. MA2 two-branched very close to anal margin; MA1-MA2 region with five crossveins. MA2-MP region with five crossveins. MP unbranched, diverging from M-stem approximately 5.75 mm from tegmen base. MP+ CuA+CuPa α with six crossveins. CuA+CuPa α very long, branching from M+Cu-stem approximately 2.70 mm from tegmen base, ending in anal margin well beyond midwing. CuA+CuPa α -CuPa β region with at least five crossveins. CuPa β of similar length to CuA+CuPa α and running parallel to it for almost its entire length. CuPa β -CuPb region with at least three crossveins. CuPb running parallel to CuPa β . CuPb-AA1 region with at least four crossveins. Pterostigma heavily pigmented with numerous thin crossveins. Radiomedial region crossveins and RP-stem heavily pigmented, resulting in five distinct, quadrangular pale spots in the RA-RP region. Proximal RP, MA1, MA2, and MP crossveins also heavily pigmented, offset from each other creating dark, transverse zig-zag patterns.

Distal part of tegmen with broad, curved band of lighter pigment following but not reaching apex. Tegmen apex not pigmented.

Archelcana tina sp. nov.

Figures 3, 4b

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Holotype. MnhnL-TV605: part and counterpart of partial tegmen.

Type locality. Uerschterhaff, near Sanem, Luxembourg.

Type horizon. Lower Toarcian (Exaratum subchronozone, Serpentinum chronozone, Lower Jurassic) bituminous limestone nodules of Uerschterhaff.

Etymology. The species is named in honor of Tina Heads (Center for Paleontology, wife of the senior author) in thanks for her unwavering support and help over the years.

Diagnosis. RP1 branching into four distinct veinlets apically; RP2 unbranched; RP-stem and RA-RP region crossveins very dark with four roughly quadrangular pale spots; proximal radiomedial crossveins dark, not offset from each other, creating dark, near-straight transverse bands; distal region of tegmen with broad, dark band.

Description. Tegmen 13.28 mm long from base to apex, 2.62 mm wide at RA-RP branch; pterostigma approximately 5.33 mm long from RA-RP branch to RA ending in costal margin. CP three-branched. ScA three-branched, with no crossveins between it and CP. ScP four-branched with branches strongly curved towards tegmen apex. RA-RP region wide, with five strong crossveins. RP branching from RA approximately 5.30 mm from tegmen base, with six main branches: RP1 branching into four distinct veinlets apically; RP2, RP3, RP4, RP5 and RP6 all simple and unbranched. RP+MA1 fusion approximately 6.28 mm from tegmen base and branching almost immediately. RP6-MA1 region with four crossveins. MA1 incompletely preserved, apparently unbranched, diverging from MA2 approximately 5.27 mm from tegmen base. MA2 incompletely preserved, simple, apparently unbranched. MA1-MA2 region with at least two crossveins. MA2-MP region with at least three crossveins. MP unbranched, diverging from M-stem approximately 4.20 mm from tegmen base. MP-CuA+CuP α region with four crossveins. CuA+CuP α very long, branching from M+Cu-stem approximately 2.52 mm from tegmen base, ending in anal margin well-beyond midwing. CuA+CuP α -CuP β region with at least five crossveins. CuP β incomplete, running parallel to CuA+CuP α for almost its entire length. CuP β -CuP γ region not preserved. Pterostigma heavily pigmented with numerous thin veinlets. Radiomedial region crossveins and RP-stem heavily pigmented, resulting in four distinct, quadrangular pale spots in the RA-PR region. Proximal RP, MA1, MA2, and MP crossveins not offset from each other, also heavily pigmented, creating dark, transverse nearly straight bands. Distal part of tegmen with dark, broad, curved band beginning at apex of pterostigma. Tegmen apex not pigmented.

Discussion

Elcanidae are one of the most common and diverse orthopteran families of the Lower Jurassic of western Europe, though they remain poorly studied. Handlirsch (1906, 1939) described some 67 species, all of which he placed in the waste-basket genus *Elcana*. Following the synonymization of *Elcana* with

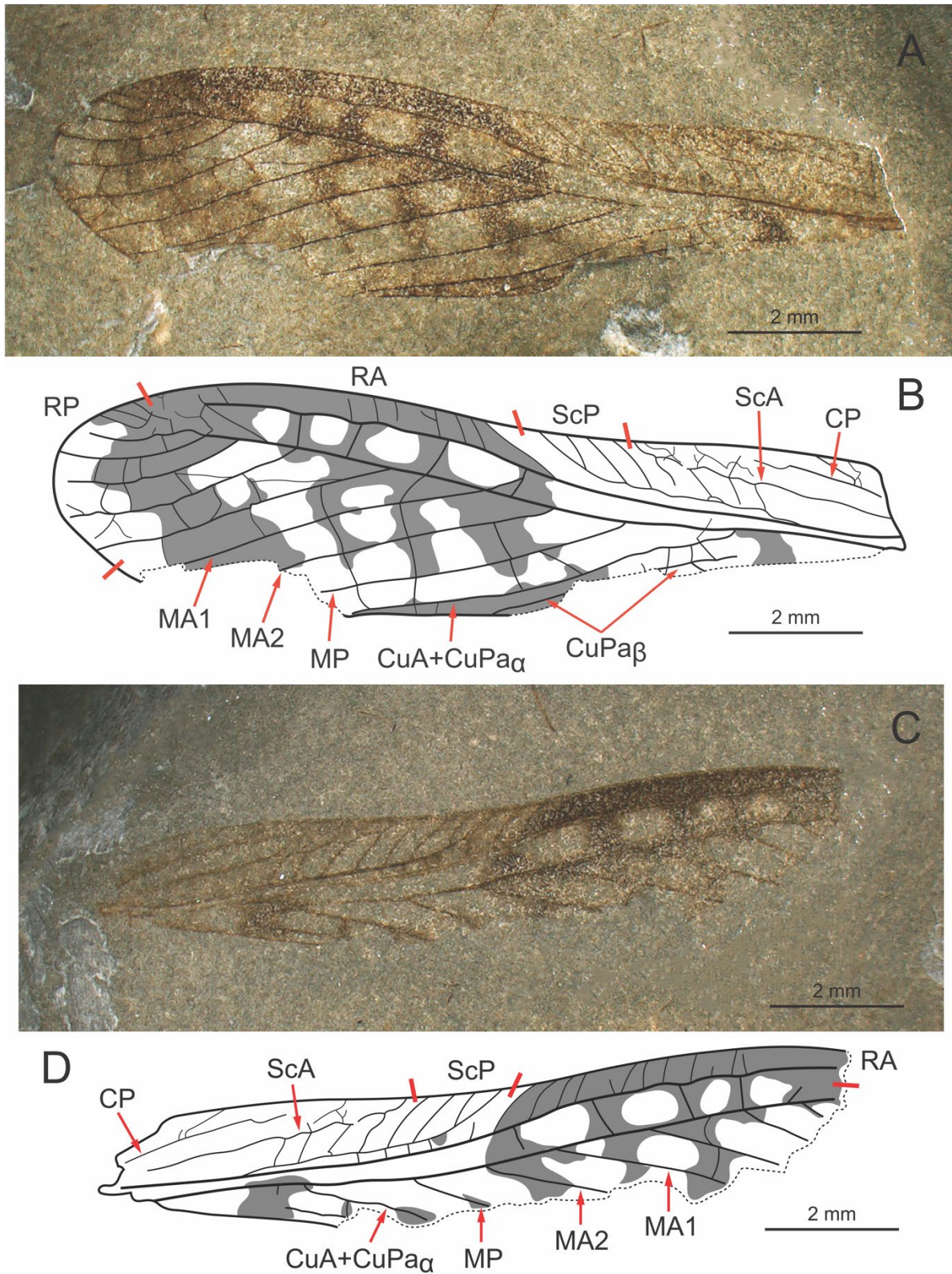


Figure 3. Holotype of *Archelcana tina* sp. nov. (MnhnL-TV605, part and counterpart). **A**, photograph of part under ethanol. **B**, explanatory drawing of part. **C**, photograph of counterpart under ethanol. **D**, explanatory drawing of counterpart. Abbreviations are given in the text.

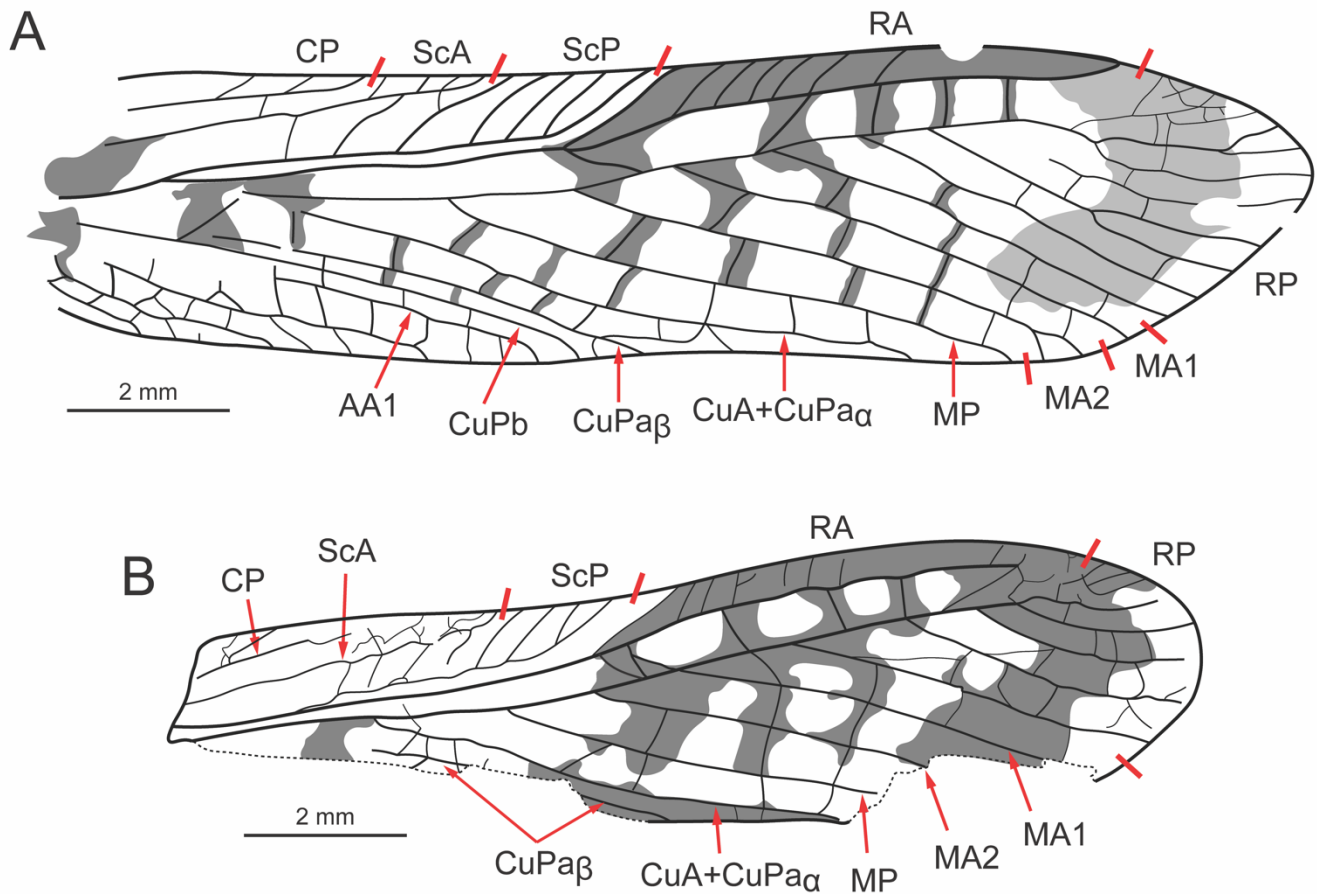


Figure 2. Comparison venation of *Archelcana numbergerae* sp. nov. and *Archelcana tina* sp. nov. showing differences in venation and marked difference in size. **A**, *A. numbergerae*. **B**, *A. tina*. Abbreviations are given in the text.

Panorpidium (see Gorochov *et al.* 2006), all of Handlirsch's species were transferred to the latter genus, where the vast majority are currently considered synonyms in *Orthoptera Species File Online* (Cigliano *et al.* 2022). However, when revising the Early Cretaceous Orthoptera of southern England, Gorochov *et al.* (2006) noted that *P. tessellatum* and other *Panorpidium* species possess a unique distal fusion of veins in the cubitoanal region of the tegmen; a diagnostic character of the Elcaninae. This distal fusion is not present in the Archelcaninae, in which $CuPa\beta$, $CuPb$, and the anal veins remain largely parallel to each other and are free distally (i.e. not fused). The former condition is typical of Early Cretaceous members of *Panorpidium* (e.g. *P. bimaculatum*, *P. minutum*, *P. parvum*, *P. proximum*, *P. tessellatum*) and other elcanine genera (*Cratoelcana*, *Eubaiselcana*, *Minelcana*, and *Probaiselcana*). In contrast, none of the species described in *Elcana* by Bode (1905) Germar (1842), Giebel (1856), Handlirsch (1906, 1939), and Heer (1865, 1880) from the Lower Jurassic of Western Europe possess this condition, indicating that they are archelcanines and thus, incorrectly placed in *Panorpidium*. Of these 79 species, only 15 are currently considered valid in the *Orthoptera Species File Online* (Cigliano *et al.* 2022): *P. angustior* (Handlirsch, 1939), *P. beyrichi* (Giebel, 1846), *P. deichmuelleri* (Handlirsch, 1906), *P. geinitzi* (Heer, 1880), *P. liasinum* (Giebel, 1846), *P. lithophilum* (Germar, 1842), *P. longicorne* (Handlirsch, 1906), *P. magnum* (Handlirsch, 1906), *P. medium* (Handlirsch, 1906), *P. mesostenum* (Handlirsch, 1939), *P. minimum* (Handlirsch, 1906), *P.*

oppenheumi (Handlirsch, 1906), *P. phyllophorum* (Handlirsch, 1906), *P. reticulatum* (Handlirsch, 1939), and *P. westwoodi* (Handlirsch, 1906). Given their obvious generic and subfamilial misplacements, all of the European Lower Jurassic elcanids require comprehensive revision, and while many resemble *Archelcana*, we refrain from reassigning them without having examined all available type material. It is possible, if not likely, that once such a revision is complete, *Archelcana* itself may be divided into several genera, but at present we consider it as comprising only the six species listed alongside all other archelcanine genera and species in Table 1. At present, the true scale of European Jurassic elcanid diversity remains unenumerated, but the description herein of two distinctive new species from the Toarcian of Luxembourg hints at the existence of a potentially rich assemblage across western Europe in the Early Jurassic.

Table 1. List of genera and species currently included in the subfamily Archelcaninae (Elcanidae). Asterisks indicate type species for that genus.

| Taxa | Locality and Age |
|--|--|
| Family Elcanidae Handlirsch, 1906 | |
| Subfamily Archelcaninae Gorochov, Jarzembowski & Coram, 2006 | |
| Genus <i>Archelcana</i> Sharov, 1968 | |
| <i>A. britannica</i> (Handlirsch, 1906)* ¹ | Binton, England (Lower Jurassic) |
| <i>A. durnovaria</i> Whalley, 1985 | Dorset, England (Lower Jurassic) |
| <i>A. numbergerae</i> Heads, Thuy & Tamarri, herein | Sanem, Luxembourg (Lower Jurassic) |
| <i>A. ornata</i> Zherikhin, 1985 | Ust-Baley, Russia (Lower Jurassic) |
| <i>A. shurabica</i> Sharov, 1968 | Shurab, Kyrgyzstan (Lower Jurassic) |
| <i>A. tina</i> Heads, Thuy & Tamarri, herein | Sanem, Luxembourg (Lower Jurassic) |
| Genus <i>Cascadelcana</i> Fang, Muscente, Heads, Wang & Xiao, 2018 | |
| <i>C. virginiana</i> Fang, Muscente, Heads, Wang & Xiao, 2018* | Solite, Virginia, USA (Upper Triassic) |
| Genus <i>Jeholelcana</i> Fang, Yan, Heads, Wang, Zhang & Wang, 2018 | |
| <i>J. yanensis</i> Fang, Yan, Heads, Wang, Zhang & Wang, 2018* | Liaoning, China (Lower Cretaceous) |
| Genus <i>Parelcana</i> Handlirsch, 1906 | |
| <i>P. anglica</i> Handlirsch, 1939 | Binton, England (Lower Jurassic) |
| <i>P. dubia</i> Handlirsch, 1939 | Gloucester, England (Lower Jurassic) |
| <i>P. pulchmacula</i> Tian, Gu, Yin & Ren, 2019 | Daohugou, China (Middle Jurassic) |
| <i>P. tenuis</i> Handlirsch, 1906* | Dobbertin, Germany (Lower Jurassic) |
| Genus <i>Sibelcana</i> Gorochov, 1990 | |
| <i>Sib. rossica</i> Gorochov, 1990* | Unda, Russia (Upper Jurassic) |
| <i>Sib. transbaicalica</i> Gorochov, 1990 | Shev'ya, Russia (Upper Jurassic) |
| Genus <i>Sinoelcana</i> Gu, Tian, Wang & Yue, 2020 | |
| <i>Sin. minuta</i> Gu, Tian, Wang & Yue, 2020* | Daohugou, China (Middle Jurassic) |
| Genus <i>Synelcana</i> Zessin, 1988 | |
| <i>Sy. muelleri</i> Zessin, 1988* | Dobbertin, Germany (Lower Jurassic) |
| Note: ¹ Original combination: <i>Elcana britannica</i> Handlirsch, 1906 | |

Acknowledgments

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