Palaeoentomology 002 (2): 148–170
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.2.2.6
http://zoobank.org/urn:lsid:zoobank.org:pub:C5DA379A-9C11-4669-996E-A9D7C5C92E13

First Dysmorphoptilidae from the Permian of China (Hemiptera: Cicadomorpha: Prosbolomorpha), with notes on the fossil record of the family

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Abstract

The first representative of Dysmorphoptilidae from the Middle Permian of China is described. Linglunxiellus chaohuensis **gen.** and **sp. nov.** is placed together with Permocixiella venosa Becker-Migdisova, 1961 from Kuznetsk Basin in the newly established subfamily Permocixiellinae **subfam. nov.**, Eoscarterellinae **stat. nov.** is proposed as separate subfamily within Dysmorphoptilidae. The classification and fossil record of Dysmorphoptilidae is reviewed, and an annotated catalogue of included taxa in Dysmorphotiloidea is presented.

Keywords: Permocixiellinae **subfam. nov**.; *Linglunxiellus* **gen. nov.**; *L. chaohuensis* **gen.** and **sp. nov.**; Eoscarterellinae **stat. nov**.; Permian; China; Dysmorphoptilidae; evolution; palaeobiogeography

Introduction

The family Dysmorphoptilidae Handlirsch, 1906 was established for the reception of Jurassic fossil *Dysmorphoptila liassina* (Giebel, 1856). Later, Evans (1956) included *Dysmorphoptiloides* Evans, 1956 from the Triassic of Queensland, Australia, Becker-Migdisova (1962) transferred the genus *Mesoatracis* Becker-Migdisova, 1949 from the Jurassic of Kyrgyzstan, and Riek (1976) add to the account the genus *Tennentsia* Riek, 1976 from Triassic Molteno Formation of South Africa. The generic content of the family was later reviewed by Shcherbakov (1984a, b), Hamilton (1992) and Carpenter (1992). These lists were subsequently updated with genera from Triassic of South America (Martins-Neto & Gallego, 1999, 2001, 2006; Martins-Neto *et al.*, 2003). Recently, Lambkin (2015, 2016) revised material from Triassic of Australia, and new taxa from South America were add by Lara & Wang (2016). The family was usually divided into three subfamilies: Fulgoringruinae Pinto, 1990, Dysmorphoptilinae Handlirsch, 1906 and Gallegomorphoptilinae Martins-Neto *in* Martins-Neto & Gallego, 2006 (Shcherbakov, 2000; Martins-Neto & Gallego, 2006).

Shcherbakov (1984a, b) postulated that Dysmorphoptilidae could be related to and originate from taxa similar to the Permian genera *Permobrachus* Evans, 1943 and *Orthoscytina* Tillyard, 1926 of family Prosbolidae Handlirsch, 1906 (Permian to Jurassic). Dysmorphoptilidae is known in fossil record since the Early Permian to the Late Jurassic (Szwedo, 2018). The family was the most diversified taxonomically and morphologically, and widespread during the Triassic, being one of the most typical and dominant insect groups from the Triassic sediments of both Laurasia and Gondwana (Shcherbakov, 1984a, b, 2000; Martins-Neto *et al.*, 2003; Martins-Neto & Gallego, 2006; Lambkin, 2015, 2016).

Taxonomic concept, content, and placement of Dysmorphoptilidae encountered several changes (Fig. 1). Originally the family was placed in the order Palaeohemiptera Handlirsch, 1906 (Handlirsch, 1906: 492). Later (Handlirsch, 1921: 212; 1939: 146) placed Dysmorphoptilidae as a sister group of Cicadellidae Latreille, 1802 (the latter as Jassidae Amyot & Audinet-Serville, 1843). This action was treated as synonymisation of these groups by Metcalf & Wade (1966: 215). Becker-Migdisova (1949: 40) originally placed the genus *Mesoatracis* Becker-Migdisova, 1949, described from apical fragment tegmen, in Flatidae (Fulgoromorpha Evans, 1946), but later (Becker-Migdisova, 1962) transferred it to Dysmorphoptilidae. Evans (1956: 220) placed Dysmorphoptilidae in the superfamily Cercopoidea Westwood, 1838 (Hemiptera: Cicadomorpha). Later, Becker-Migdisova (1962: 189) postulated that Dysmorphoptilidae belonged in the *incertae sedis* section of Auchenorrhycha Duméril, 1805. Metcalf

 Accepted by D. Azar: 1 Apr. 2019; published: 5 Apr. 2019

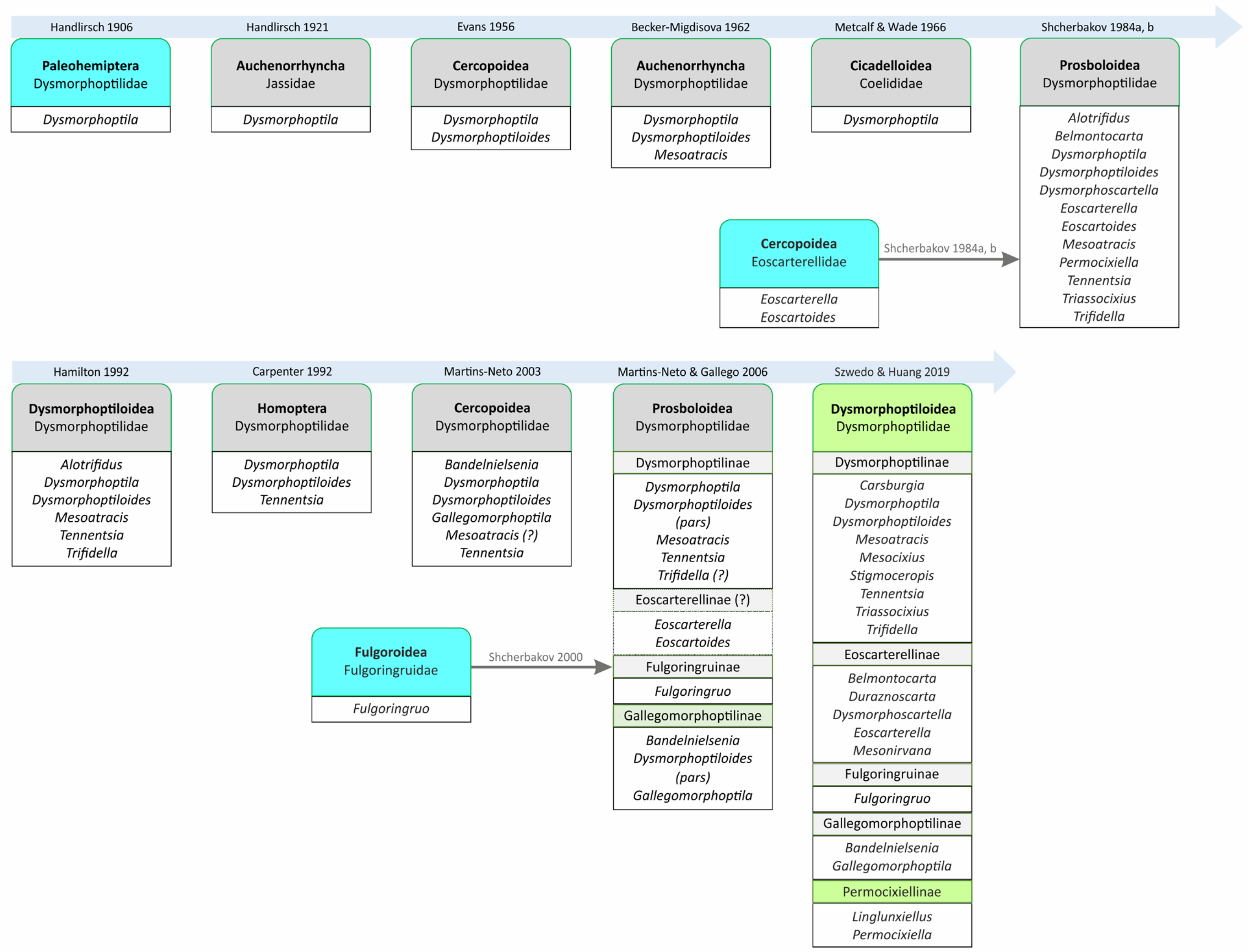

FIGURE 1. Cable car classification history of Dysmorphoptilidae.

& Wade (1966: 214) synonymized Dysmorphoptilidae under Coelidiidae Dohrn, 1859 [sic!] (recently treated as subfamily Coelidiinae in the Cicadomorpha: Cicadellidae). Carpenter (1992: 229) listed in the Dysmorphoptilidae (as family of Homoptera Leach, 1815) only the genera: *Dysmorphoptila*, *Dysmorphoptiloides*, *Mesoatracis* and *Tennentsia*. The family Eoscarterellidae Evans, 1956 was synonymized under Dysmorphoptilidae by Shcherbakov (1984a, b), followed by Nicholson *et al.* (2015), but has been treated as separated family by the other authors (Carpenter, 1992; Hamilton, 1992; Szwedo *et al.*, 2004; Jell, 2004; Szwedo, 2018). Another group with taxonomic problems is Magnacicadiidae Hong & Chen, 1981. The genus *Magnacicadia* Hong & Chen, 1981 – the sole member of the family was suggested tentatively to be included in Dysmorphoptilidae, but without formal decision (Shcherbakov, 1984a, b). Magnacicadiidae has so far been treated as a separate family (Hamilton, 1992, Carpenter, 1992; Wang *et al.*, 2006, 2010, 2012; Nicholson *et al.*, 2015; Szwedo, 2018). Shcherbakov (2000: S251) downgraded Fulgoringruidae Pinto, 1990 as a subfamily of Dysmorphoptilidae. Martins-Neto *et al.* (2003: 239) placed Dysmorphoptilidae within Cicadomorpha: Cercopoidea. Hamilton (1992: 428) proposed the superfamily Dysmorphoptiloidea for the families Eoscarterellidae, Dysmorphoptilidae and Magnacicadiidae. Contrarily, Shcherbakov (1984a, b, 2011), Shcherbakov & Popov (2002), and Szwedo (2002) placed Dysmorphoptilidae in the superfamily Prosboloidea Handlirsch, 1906, together with Prosbolidae Handlirsch, 1906, Prosbolopseidae Becker-Migdisova, 1946 and Ingruidae Becker-Migdisova, 1960. Szwedo *et al.* (2004) following Hamilton (1992), placed three families: Dysmorphoptilidae, Eoscarterellidae and Magnacicadiidae within the superfamily Dysmorphoptiloidea. Nicholson *et al.* (2015) followed the synonymisation of Eoscarterellidae and Fulgoringruidae with Dysmorphoptilidae, but treated Magnacicadiidae as a separate family. Szwedo (2018) placed the Dysmorphoptiloidea Handlirsch, 1906 (with three families Dysmorphoptilidae, Eoscarterellidae and Magnacicadiidae) in the infraorder Prosbolomorpha Popov, 1980, which was treated by Shcherbakov (1984a, b) as synonym of Cicadomorpha, but was believed to be ancestral to modern cicadomorphans by Emeljanov

(1987). Lambkin (2016) followed the synonymisation of Eoscarterellidae under Dysmorphoptilidae, but noted that the taxa comprised could be separated in two, alas weakly defined groups.

Lack of unambiguous definitions and cleraly defined characters of numerous extinct Cicadomorpha groups, present in the Palaeozoic and Mesozoic hamper the understanding of the placement, relationships and phylogeny of the Dysmorphoptilidae and whole suborder. Relationships between early representatives of the Cicadomorpha is still a melting pot.

The Permian record of the Dysmorphoptilidae comprises the oldest species known − *Fulgoringruo kukalovae* Pinto, 1990 from the Artinskian (290.1 ±0.26–283.5 ±0.6 Mya; data after Cohen *et al.*, 2013: ICS 2018–8) of Brazil (Pinto, 1990; Shcherbakov, 2000), *Permocixiella venosa* Becker-Migdisova, 1961 from Wuchapingian (259.1 ±0.5–254.14 ±0.07 Mya) of Kuznetsk basin, Russia (Becker-Migdisova, 1961; Shcherbakov, 2000; Lozovsky *et al.*, 2009a, b), *Dysmorphoscarterella* Riek, 1973 from Changhsingian (254.14 ±0.07–251.902 ±0.024 Mya) of Natal, South Africa (Riek, 1973), and *Belmontocarta perfecta* Evans, 1958 from Changhsingian of Belmont, New South Wales, Australia (Evans, 1958, Shcherbakov, 2000; Beattie, 2007). Below, we are adding another taxon from the Permian period (Fig. 2C).

Material and methods

The studied specimen (impression in black shale), originates from the latest section of the Middle Permian, Capitanian (265.1 ±0.4–259.1 ±0.5 Mya) of Yinping Formation at the Paomaling Section (near the Houdong Village) at Yinping Mountain, of Chaohu City, Anhui Province. The fossil was collected by DYH in 2005, from the middle section of the black shale of Middle Permian Yinping Formation near the Houdong Village, Sanbing Township, Chaohu City, Anhui Province (Fig. 2A, B). The Yinping Formation probably represents a lagoonal palaeonenvironment where the lower section had yielded very rich marine fauna. The insects mainly found in the middle section of the Yinping Formation co-occurred with bivalves, fishes, sponges, and terraneous plants. Various insects groups are found here, primarily Hemiptera, Orthoptera and Coleoptera. There are also some Mecoptera, Odonata, and Glosselytrodea, but Blattaria have not yet been found (Huang *et al*., 2007; Lin *et al*., 2010; Ponomarenko *et al*., 2014).

The specimen was observed under light stereoscopic microscopes Nikon 1500, Olympus SZH10 and Zeiss Axio Zoom.V16, in normal reflected and polarized light, dry and under alcohol. Drawings were made using a drawing tube (camera lucida) attached to the microscope. Photographs were taken using an Olympus W5060 digital camera mounted on the microscope and an Axiocam 512

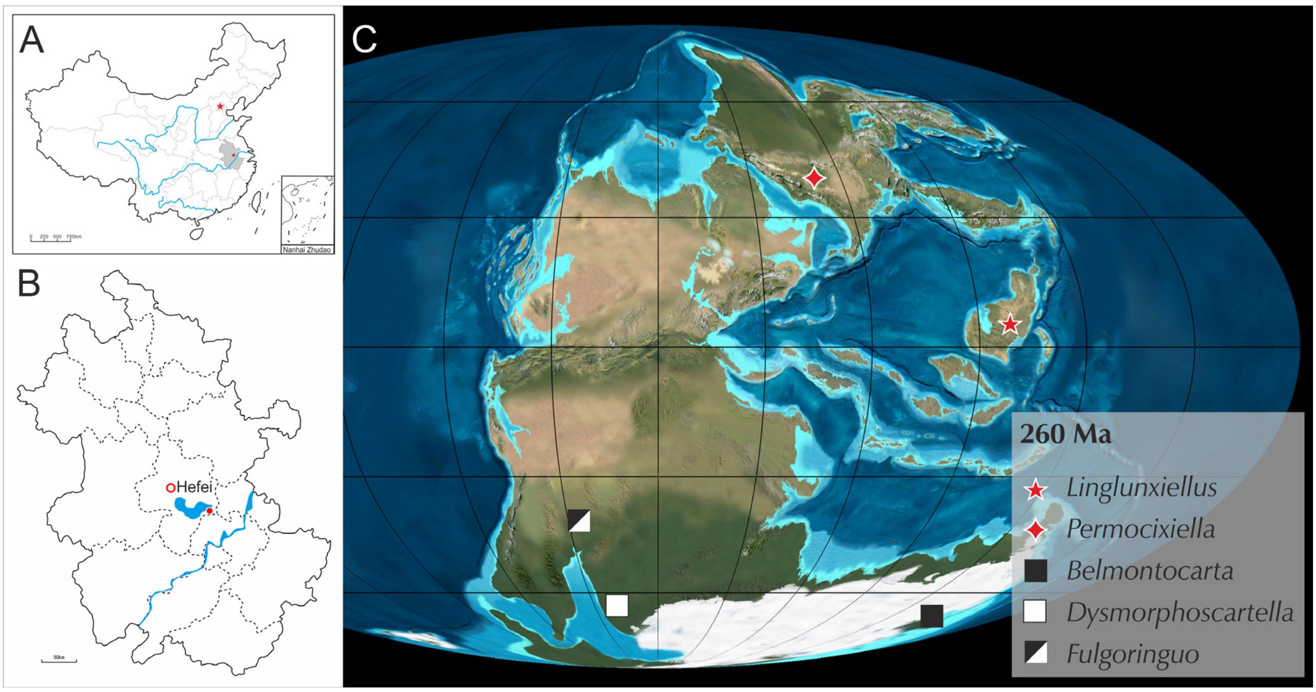

FIGURE 2. A, The location of fossil site in China. **B**, Placement of Chohu in Anhui Province, indicating the fossil locality of *Linglunxiellus chaohuensis* **gen.** and **sp. nov.** (red dot) **C**, Distribution of Permian Dysmorphoptilidae. Palaeogeographic reconstruction thanks of courtesy of Professor Ron Blakey, Colorado Plateau Geosystems.

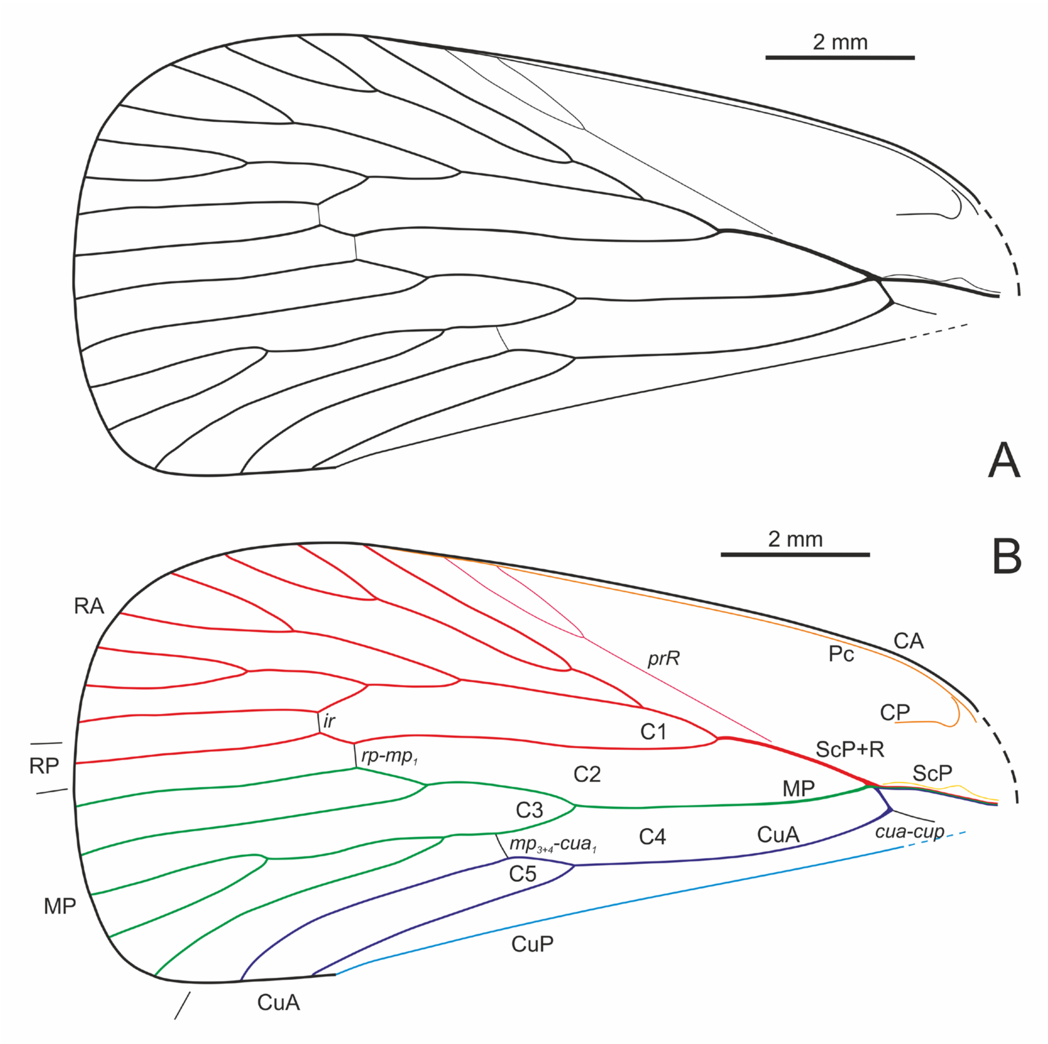

FIGURE 3. *Linglunxiellus chaohuensis* **gen.** and **sp. nov. A**, Drawing of tegmen, **B**, Scheme of tegmen venation.

color working under control of Zen 2.3 Pro software. The photographs were readjusted using Adobe Photoshop Elements 6.0 and Corel PhotoPaintX19. There is no full consensus for vein homology and nomenclature in Cicadomorpha, thus the general model proposed for Hemiptera (Nel *et al.*, 2012; Bourgoin *et al.*, 2015) and adapted to Cicadomorpha (Chen *et al.*, 2019) is followed here.

Abbreviations used: Pc – precosta; CA – costa anterior; CP – costa posterior; ScP – subcosta posterior; ScP+R – common stem of subcosta and radius (fused); ScP+RA – common portion of subcosta posterior and radius anterior (fused); R – radius; RA – radius anterior; RP – radius posterior; in fact it is fused RP+MA (radius posterior+media anterior; see Nel *et al.*, 2012); MP – media posterior; MP_{1+2} – first branch of MP; MP_{3+4} – second branch of MP; CuA – cubitus anterior; CuP – cubitus posterior (often named claval fold; see Bourgoin *et al.*, 2015); Pcu – postcubitus; A_1 – first anal vein; A_2 – second anal vein; *prR* – prenodal branches of radius; *ra-rp (ir)* – interradial veinlet; *rp-mp* – radius posterior-media posterior veinlet; *mp-cua* – media posterior-cubitus anterior veinlet; hc – hypocostal carina; C1 – cell delimited by branches of RA and RP, after forking of stem R, closed apically by *ir* veinlet; C2 – cell delimited by stems of R and MP and closed apically by first veinlet *rp-mp*; C3 – cell delimited by branches MP_{1+2} and MP_{3+4}, after forking of stem MP; C4 – cell delimited by stems MP (MP_{3+4}) and CuA (CuA_1), closed apically by *mp-cua* veinlet; C5 – cell between the branches CuA_1 and CuA_2 after forking of CuA; anal area – commisural space, narrow field between claval vein A_1+Pcu+A_1 and posterior margin of clavus (vein A_2).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1956
Infraorder Prosbolomorpha Popov, 1980

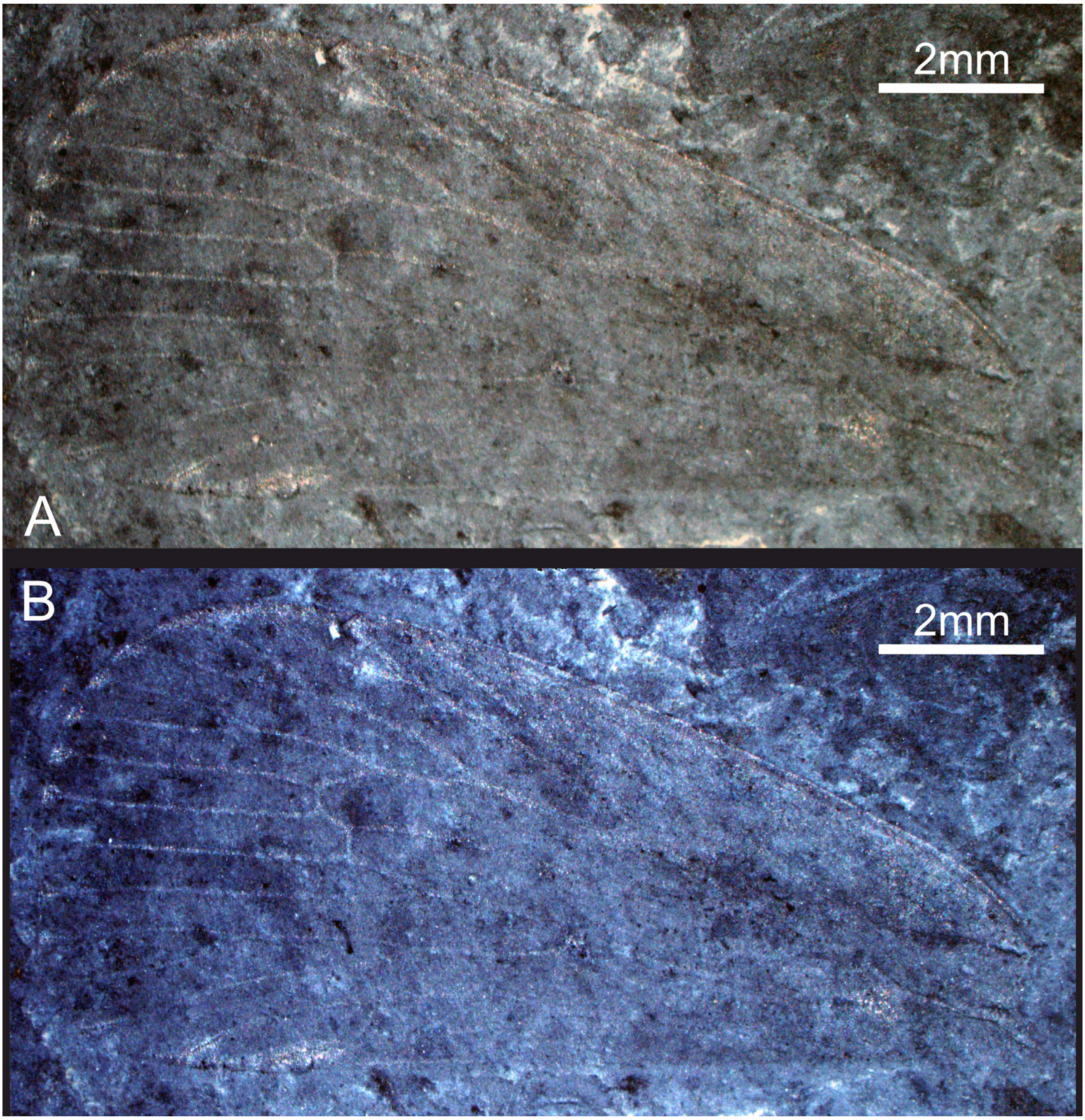

FIGURE 4. *Linglunxiellus chaohuensis* **gen.** and **sp. nov.** tegmen under various light conditions**. A**, Normal light. **B**, Utraviolet light, wavelength about 395 nm.

Superfamily Dysmorphoptiloidea Handlirsch, 1906
Family Dysmorphoptilidae Handlirsch, 1906

Type genus. *Dysmorphoptila* Handlirsch, 1906; by original designation and monotypy.

Diagnostic features. Tegmen with macrosculpture punctate, covering it uniformly; very basal portion of Pc+CA+CP thickened, then Pc very close to CA, forming narrow distinct edge along costal margin of tegmen; apical portion of CP directed to ScP; basal portion of ScP somewhat shifted from common stem R+MP+CuA, ScP concave over its whole extent; basal cell closed by 'arculus', i.e. very basal portion of CuA (or MP+CuA) separating from common basal stem ScP+R+MP+CuA or less frequently stems ScP+R, MP and CuA leaving basal cell at point with posteriad connecting point of basal *cua-cup* veinlet shifted posteriad, behind this point; branch ScP+RA longer than first segment of branch RP, more strongly inclined than postnodal branches; weak prenodal branches of ScP+R stem present; stem MP beyond basal cell usually curved towards CuA; branch MP_{3+4} forked; three transverse veinlets: *ir* (*ra-rp*), *rp-mp* and *mp-cua*, rarely more transverse veinlets on membrane; anal area (commisural space) distally shifted ventrad (Pcu+A_1 seems entering margin); stridulitrum (stridulating field) on underside, near the base of tegmen, on costal cell almost always noticeable (plectrum presumably at hind femur).

Key to subfamilies of Dysmorphoptilidae

1. Apical portion of tegmen abruptly narrowed 4
– Apical portion of tegmen not abruptly narrowed 2
2. Tegmen with postclaval margin (tornus) arcuate, convex; postnodal membrane distinctly widened; RA_1 entering anterior margin more basad, before level of claval apex.... .... Eoscarterellinae **stat. nov.**
Composition: *Eoscarterella* Evans, 1956; *Belmontocarta* Evans, 1958; *Duraznoscarta* Lara et Wang, 2016; *Mesonirvana* Evans, 1956
– Tegmen with postclaval margin (tornus) concave at base, sigmoid; RA_1 entering anterior margin more distad, beyond level of claval apex.. 3
3. Tegmen punctate only in basal portion; hypocostal carina (fused Pc+CA) short, thickened only in basal portion, then narrow; stem MP forked at level of CuA forking.......................................Permocixiellinae **subfam. nov.**
Composition: *Permocixiella* Becker-Migdisova, 1962; *Linglunxiellus* **gen. nov.**
– Tegmen punctate on costal cell and clavus; hypocostal carina (fused veins Pc+CA) thickened (more at base), reaching level of claval apex; stem MP forked apicad of stem CuA forking ....Fulgoringruinae
Composition: *Fulgoringruo* Pinto, 1990
4. Veins RA and RP distally fused; apical veinlet *ra-rp* on membrane absent; RP with secondary branching............... .... Gallegomorphoptilinae
Composition: *Gallegomorphoptila* Martins-Neto, 2003; *Bandelnielsenia* Martins-Neto & Gallego, 2003
– Veins RA and RP not fused distally, apical veinlet *ra-rp* on membrane present; RP not branched ... Dysmorphoptilinae
Composition: *Dysmorphoptila* Handlirsch, 1906; *Carsburgia* Lambkin, 2015; *Dysmorphoptiloides* Evans, 1956; *Mesoatracis* Becker-Migdisova, 1949; *Mesocixius* Tillyard, 1919; *Stigmocercopis* Lin, 1986; *Tennentsia* Riek, 1976; *Triassocixius* Tillyard, 1919; *Trifidella* Evans, 1956

Subfamily Permocixiellinae Szwedo & Huang, **subfam. nov.**

Type genus. *Permocixiella* Becker-Migdisova, 1961; by present designation.

Diagnosis. Tegmen membranous, slightly punctate at base (tegmen uniformly punctate in others); costal margin curved at base, then straight (costal margin with nodal incision in Dysmorphoptilinae and Gallegomorphoptilinae); costal cell wide, distinctly wider than cell C2, with prenodal branches of stem R; stems MP and CuA forked at same level (stem MP usually forked more apically in the others).

Remarks. The subfamily is defined based on a combination of characters, of which the puncturation being limited to the base of tegmen, the forking of stems MP and CuA at the same level, and the presence of three veinlets on the membrane could be regarded as apomorphic.

Composition. *Permocixiella* Becker-Migdisova, 1961; *Linglunxiellus* **gen. nov.**

Linglunxiellus Szwedo & Huang, **gen. nov.**

Type species. *Linglunxiellus chaohuensis* **sp. nov.**; by present designation.

Diagnosis. In general venation pattern similar to *Permocixiella* Becker-Migdisova, 1961. It differs in distinctly angulate apical angles of tegmen (apex of tegmen rounded in *Permocixiella*); strongly curved basal portion of costal margin (mildly curved in *Permocixiella*); forked prenodal branches of RA (no distinct branches in *Permocixiella*); and more numerous branches of RA and MP branch RP not forked before apex (branch RP forked apically in *Permocixiella*).

Description. Tegmen membranous, with punctuate portion only at base; apical margin with widely angulate anterior angle and distinctly angulate posterior angle, slightly widened. Costal margin distinctly curved at base, slightly thickened; costal cell with prenodal branches. Basal cell elongate, closed with arculus. Venation distinct, vein CP subparallel to lower margin of costal cell; Sc slightly shifted, adhering costal cell; stem R straight with prenodal branch basad of stem R forking, branch RA forked slightly anteriad of stems MP and CuA forkings, RA_1 forked again on membrane, RA_2 forked twice, RP distinctly curved mediad at base, not forked before apex. Stem MP curved towards stem CuA at base, branches MP_{1+2} and MP_{3+4} forked at same level, branch M_{3+4} forked on membrane. Stem CuA forked at level of stem MP forking, stem about as long as cell C5.

Etymology. The generic name is derived from Linglun The Musician – god of music in ancient Chinese mythology. Gender: masculine.

Composition. Single species *Linglunxiellus chaohuensis* Szwedo & Huang, **sp. nov.**

Linglunxiellus chaohuensis **gen.** and **sp. nov.**
(Figs. 3A, B, 4A, B)

Diagnosis. Tegmen about 2.3 times as long as wide, with apex of clavus at ⅔ of tegmen length. Prenodal branch of R strongly oblique and forked, prenodal branch of RA forked twice; five postnodal terminals of RA, RP single, MP with five terminals; CuA with branch CuA_1 reaching margin well before apical angle. Anteroapical angle widely angulate, posteroapical angle angulate, veinlet *rp-mp₁* basad of veinlet *ir*.

Description. Length of preserved part of tegmen 12.85 mm (basal portion destroyed, estimated length ca. 13.3 mm), width 5.71 mm; length/width ratio 2.33 : 1.

Costal margin curved at base then almost straight, anteroapical angle obtuse, posteroapical angle obtuse; apical margin angulate. Costal margin slightly thickened, with indistinct uncinate thickening. Vein CP subparallel to lower margin of costal cell, reaching almost to its apex; basal portion of vein ScP adhering to lower margin of costal cell, slightly curved. Basal cell closed with short basal portion of stem CuA ('arculus'), stems R and MP leaving basal cell at same point. Stem R 2.2 mm long, with early branching of prenodal terminal, basad of forking into RA and RP, forking of stem R distinctly basad of stems MP and CuA forking, another prenodal branch apicad of stem R forking; prenodal branches with subsequent forkings; branch RA forked at nodal line, with subsequent forkings on membrane, with five postnodal terminals; nine prenodal and postnodal terminals of stem R in total. Stem MP 4 mm long, curved to stem CuA at base, forked at same level as stem CuA, basad of nodal line; branches MP_{1+2} and MP_{3+4} forked at about same level, at level of nodal line, branch MP_{3+4} with forking on membrane, stem MP with five terminals. Stem CuA 4.2 mm long, curved at base, forked at same level as stem MP forking, branch CuA_1 curved posteriad before apex, not reaching apical angle. Single row of veinlets *ir*, *rp-mp*$_1$ and *mp*$_{3+4}$*-cua* present, perpendicular to longitudinal veins; veinlet *mp*$_{3+4}$*-cua*$_1$ basad of veinlet *rp-mp*$_1$, veinlet *ir* apicad of veinlet *rp-mp*$_1$. Costal cell about as wide as combined width of cells C2 and C4. Cell C1 long, closed with oblique veinlet *ir*. Cell C3 open, reaching to apical margin; cell C5 about as long as stem CuA.

Etymology. The specific epithet is named for the locality – Chaohu.

Material examined. Holotype. Specimen No. NIGP 153693 deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Tegmen with clavus missing, the most basal portion of tegmen incomplete.

Age and occurrence. Latest section of the Middle Permian, Capitanian (265.1±0.4–259.8±0.4 Myr) of Yinping Formation of Chaohu City, Anhui Province (31.6° N, 117.8° E; palaeo-coordinates 8.4° N, 100.4° E), China.

An annotated list of taxa included in Dysmorphoptilidae Handlirsch, 1906

Family Dysmorphoptilidae Handlirsch, 1906

Type genus. *Dysmorphoptila* Handlirsch, 1906; by original designation and monotypy.

1906 Handlirsch, p. 492 [new family]
1919 Mesocixiinae Tillyard, p. 876 [new subfamily], p. 867 [key]
1921 Handlirsch, p. 212 [listed, equals Jassidae Stål emend. Oshanin; sic!]
1956 Eoscarterellidae Evans, p. 220 [new family]
1961 Eoscarterellidae Evans, p. 19 [listed]
1962 Dismorphoptilidae [sic!]: Becker-Migdisova, p. 189
1973 Eoscartarellidae [sic!]: Riek, 1973, p. 514
1974 Eoscartarellidae [sic!]: Riek, 1974, p. 21
1984a Shcherbakov, p. 94 [listed, note, placed in Prosboloidea]
1984a Eoscarterellidae Evans: Shcherbakov, p. 94 [listed, synonymy]
1984b Shcherbakov, p. 92 [listed, note, placed in Prosboloidea]
1984b Eoscarterellidae Evans: Shcherbakov, p. 92 [listed, synonymy]
1986 Dysmorphotilidae [sic!]: Lin, p. 66
1992 Dysmorphoptilidae Handlirsch, 1908 [sic!]: Hamilton, p. 428 [listed, placed in Dysmorphoptiloidea]
1992 Eoscarterellidae Evans: Carpenter, p. 228 [listed, note]
1992 Carpenter, p. 229 [listed, note]
1996 Shcherbakov, p. 37 [listed, note, synonymy]
1996 Eoscarterellidae: Shcherbakov, p. 37 [listed, note, synonymy with Dysmorphoptilidae]
2000 Shcherbakov, p. S251, S253, S255-S259, S261, S263 [listed, placed in Prosoboloidea]
2002 Shcherbakov & Popov, p. 145, 150, 152 [listed, placed in Prosoboloidea]
2002 Shcherbakov, pp. 32, 33 [listed]
2004 Szwedo *et al.*, p. 14 [listed, placed in Dysmorphoptiloidea]
2004 Eoscartellidae [sic!]: Szwedo *et al.*, p. 14 [note, listed]
2006 Dysmorphotilidae [sic!] Wang Y. *et al.*, p. 296
2006 Dysmorphoptilinae: Martins-Neto & Gallego, p. 187 [redescribed, new status]
2006 Eoscartellidae [sic!]: Martins-Neto & Gallego, p. 195
2006 Gallego & Martins-Neto, p. 1, 2, 3 [listed]
2006 Dysmorphoptilinae: Gallego & Martins-Neto, p. 3 [listed]
2010 Dysmorphotilidae [sic!]: Wang Y. *et al.*, p. 136
2011 Shcherbakov, p. 1, 5, 23, 24 [listed, note]
2012 Dysmorphotilidae [sic!]: Wang Y. *et al.*, p. 170
2013 Dismorphoptilidae [sic!]: Aristov in Aristov *et al.*, p. 672
2015 Nicholson *et al.*, p. 93
2015 Lambkin, p. 359
2016 Lambkin, p. 208
2018 Szwedo, p. 110
2018 Labandeira *et al.*, p. 679

Subfamily **Dysmorphoptilinae** Handlirsch, 1906

Type genus. *Dysmorphoptila* Handlirsch, 1906; by original designation and monotypy.

Diagnostic characters. Tegmen with apical portion abruptly narrowed; veins RA and RP not fused distally; RP not branched; apical veinlet *ra-rp* (*ir*) on membrane present; stridulitrium on ventral surface of tegmen noticeable.

Genus ***Carsburgia*** Lambkin, 2015

Type species. *Carsburgia knezouri* Lambkin 2015; by original designation and monotypy.

2015 Lambkin, p. 363

***Carsburgia knezouri* Lambkin, 2015**

2015 Lambkin, p. 365, Figs. 11–12 [new species, illustrated]
2016 Lambkin, p. 217 [listed]

Late Triassic, Norian, Blackstone Formation, Dinmore clay pit, Ipswich Queensland, Australia.

Genus ***Dysmorphoptila*** Handlirsch, 1906

Type species. *Belostomum liasinum* Giebel, 1856; by original designation by Handlirsch 1906.

1906 Handlirsch, p. 492 [new genus, described]
1918 Tillyard, p. 587 [phylogeny]
1928 Schulze *et al.*, p. 1084 [listed]
1939 Handlirsch, p. 147 [listed]
1939 Neave, p. 175 [listed]
1966 Metcalf & Wade, p. 219 [catalogued, placed in Coelidiidae (sic!)]
1992 Carpenter, p. 229 [note, listed]
2006 Martins-Neto & Gallego, p. 187, 195 [listed]
2008 Martins-Neto, p. 676 [listed]
2015 Lambkin, p. 357 [listed]
=*Belostoma* Latreille, 1807 (*partim*)

Type species. *Belostoma testaceopallidum* Latreille, 1807, p. 145; by monotypy.

= *Belostomum*: Burmeister 1835, p. 195 (*partim*)

***Dysmorphoptila liasina* (Giebel, 1856)**

1845 Hemiptera? '*Belostoma*': Westwood in Brodie, p. 127, pl. 10, fig. 13 [Notes, illustrated]
1856 *Belostomum liasinum* Giebel, p. 371 [new species]
1891 *Belostoma liasina*: Scudder, p. 168 [catalogued]
1906 Handlirsch, p. 492, pl. 43, fig. 14 [synonymy, note, illustrated, catalogued]
1939 Handlirsch, p. 147, pl. 16, fig. 302 [illustrated, catalogued]
1956 Evans, p. 218, Fig. 19C [note, illustrated]
1966 Metcalf & Wade, p. 220 [catalogued, placed in Coelidiidae (sic!)]
1992 *Belostoma liasina*: Carpenter, p. 229 [note, listed]
1999 Martins-Neto & Gallego, p. 194 [listed]
2001 Gallego *et al.*, p. 2 [listed]
2003 Martins-Neto *et al.*, p. 252 [listed]
2006 Martins-Neto & Gallego, p. 187 [listed]

Early Jurassic, (Lower Liassic), Sinemurian, Wainlode, Gloucestershire, United Kingdom.

***Dysmorphoptila notodon* Shcherbakov, 1988**

1988 Shcherbakov, p. 61, fig. 3 a, b [new species]
1999 Martins-Neto & Gallego, p. 194 [listed]
2001 Gallego *et al.*, p. 2 [listed]
2003 Martins-Neto *et al.*, p. 252 [listed]
2006 Martins-Neto & Gallego, p. 187, 194 [listed]
2015 Lambkin, p. 372 [listed]
2015 Nicholson *et al.*, p. 93 (supplementary material) [listed]

Middle Jurassic, Bajocian, Togo-Khuduk Formation (Bahar Group), Bayan-Khongor (Bakhar), 12 km north Tsetsen-Ula mountain, Bayan-Khongorskiï Aïmag, Gobiïskiï Altaï, Mongolia.

Genus ***Dysmorphoptiloides*** Evans, 1956

Type species. *Dysmorphoptiloides elongata* Evans, 1956; by original designation.

1956 Evans, p. 216 [new genus, described]
1961 Evans, p. 18 [listed]
1975 Edwards & Vevers, p. 98 [listed]
1984a Shcherbakov, p. 94 [listed]
1984b Shcherbakov, p. 92 [listed]
1992 Carpenter, 230 [note]
1999 Gallego & Martins-Neto, p. 87 [listed]
2001 Gallego *et al.*, p. 2 [listed]
2004 Jell, p. 43 [listed]
2006 Martins-Neto & Gallego, p. 195 [listed]
2008 Martins-Neto, p. 676 [listed]
2015 Lambkin, p. 365 [redesribed], p. 357, 368, 373 [note, listed]

***Dysmorphoptiloides ellisi* Lambkin, 2015**

2015 Lambkin, p. 367, Figs. 18, 19 [new species]
2016 Lambkin, p. 216 [listed]

Middle Triassic, Anisian, Gayndah Formation, road cutting 3 km ENE of Gayndah, Queensland, Australia.

***Dysmorphoptiloides elongata* Evans, 1956**

1956 Evans, p. 216, fig. 17A, B, D [new species, illustrated]
1961 Evans, p. 18 [note]
1962 Becker-Migdisova, p. 189, Fig. 540 [illustrated]
1964 Evans, p. 174 Fig. 3D [phylogeny], p. 180 [listed]
1971 Evans, p. 146, Fig. 2 [listed, illustrated, placed in Cercopoidea]
1990 Rozefelds *et al.*, p. 679 [listed]
1991 Becker-Migdisova, p. 258, Fig. 540 [illustrated]
1991 Kukalová-Peck, p. 169, Fig. 6.25G [illustrated]
1992 Carpenter, p. 230, Fig. 149–9 [listed, illustrated]
1999 Martins-Neto & Gallego, p. 194 [listed]
2003 Martins-Neto *et al.*, p. 252 [listed]
2004 Jell, p. 43, fig. [unnumbered, linedrawing of Evans 1956, and photo of the specimen]
2015 Lambkin, p. 367, Figs. 8, 13–17, 20 [redescribed, illustrated]
2016 Lambkin, p. 217 [listed]

Late Triassic, Carnian, Mount Crosby Formation, Ipswich, Queensland, Australia.

Genus ***Mesoatracis*** Becker-Migdisova, 1949
Type species. *Mesoatracis reducta* Becker-Migdisova, 1949; by original designation and monotypy.

1949 Becker-Migdisova, p. 40 [new genus; placed in Flatidae]
1962 Becker-Migdisova, p. 189 [listed]
1966 Metcalf & Wade, p. 133 [catalogued; placed in Flatidae]
1984a Shcherbakov, p. 94 [listed]
1984b Shcherbakov, p. 92 [listed]
1991 Becker-Migdisova, p. 259 [listed]
1992 Hamilton, p. 428 [listed]
1992 Carpenter, p. 230 [listed]
2006 Martins-Neto & Gallego, p. 187 [listed]

***Mesoatracis reducta* Becker-Migdisova, 1949**

1949 Becker-Migdisova, p. 40, Fig. 31 [new species, illustrated]
1959 Evans, p. 152 [note]
1962 Becker-Migdisova, p. 189, Fig. 541 [note, illustrated]
1991 Becker-Migdisova, p. 259, Fig. 541 [note, illustrated]
1999 Martins-Neto & Gallego, p. 194 [listed]
2004a Sukatcheva & Rasnitsyn, p. 67 [listed]
2004b Sukatcheva & Rasnitsyn, p. 185 [listed]
2006 Martins-Neto & Gallego, p. 187 [listed]

Lower Jurassic, Pliensbachian, Sagul Formation, Shurab III, ditch (excavation) No 12, layer “n”, southern Fergana Valley in the Batkenskiï District, Osh Region, Kyrgyzstan.

Genus ***Mesocixius*** Tillyard, 1919
Type species. *Mesocixius triassicus* Tillyard, 1919; by original designation and monotypy.
= *Dysmorphoptiloides* Evans, 1956 (*partim*)
Type species. *Dysmorphoptiloides elongatus* Evans, 1956; by original designation.

1919 Tillyard, p. 876 [new genus, placed in Cixiidae]
1922 Tillyard, p. 462 [comparative note]
1923 Tillyard, p. 483 [listed]
1928 Martynov, pp. 36, 37 [comparative note]
1931 Schulze *et al.*, p. 2043 [listed]
1937a Martynov, pp. 88, 161 [note]
1937b Martynov, p. 35 [note]
1939 Handlirsch, p. 17 [listed]
1940a Neave, p. 115 [listed]
1949 Jeannel, p. 83 [listed]
1956 *Dysmorphoptiloides* Evans, p. 218 [new genus] (*partim*)
1956 Evans, p. 241 [note, placed in Fulgoroidea]
1962 Becker-Migdisova, p. 186 [listed]
1966 Metcalf & Wade, p. 161 [catalogued, placed in Cixiidae]
1975 *Dysmorphoptiloides* Evans: Edwards & Vevers, p. 98 [listed]
1991 Becker-Migdisova, p. 253 [listed]
1992 Hamilton, p. 428 [listed; placed in Cercopoidea: Archijassidae]
1992 Carpenter, p. 236 [listed]
2004 Jell, p. 41 [listed]
2008 *Dysmorphoptiloides*: Martins-Neto, p. 676 [listed]
2015 Nicholson *et al.*, p. 91 (supplementary material) [note]
2015 Lambkin, p. 359 [redescribed, note], pp. 360, 364, 373 [listed, note]
2018 Labandeira *et al.*, p. 678 [listed, placed in Cixiidae]

***Mesocixius parvus* (Evans, 1956)**

1956 *Dysmorphoptiloides parva*, p. 219, Fig. 17E [new species, illustrated]
1999 *Dysmorphoptiloides parva*: Martins-Neto & Gallego, p. 194 [listed]
2003 *Dysmorphoptiloides parva* Evans 1956: Martins-Neto *et al.*, p. 253 [listed]
2004 *Dysmorphoptiloides parva* Evans: Jell, p. 43 [listed]
2006 “*Dysmorphoptiloides*” *parva*: Martins-Neto & Gallego, p. 187 [listed, note]

2015 Lambkin, p. 360, Figs. 3–6 [new combination, redescribed, illustrated]
2016 Lambkin, p. 217 [listed]

Late Triassic, Norian, Mount Crosby Formation, Ipswich Coal Measures, Mount Crosby, Queensland, Australia.

***Mesocixius triassicus* Tillyard, 1919**

1919 Tillyard, p. 877, Fig. 11 [new species, illustrated]
1923 Tillyard, p. 483 [listed]
1939 Handlirsch, p. 10 [note], p. 17 [catalogued]
1956 Evans, p. 241 [note]
1966 Metcalf & Wade, p. 162 [catalogued]
1992 Carpenter, p. 236, fig. 152–10 [listed, illustrated]
2004 Jell, p. 41, fig. [unnumbered; line drawing from Tillyard 1919 and photo of the specimen]
2015 Lambkin, p. 360, Figs. 1, 2 [redescribed, illustrated]
2016 Lambkin, p. 217 [listed]

Late Triassic, Norian, Blackstone Formation, Denmark Hill Insect Bed, Queensland, Australia.

Genus ***Stigmocercopis*** Lin, 1986
Type species. *Stigmocercopis parvis* Lin, 1986; by original designation and monotypy.

1986 Lin, p. 66 [new genus, described]
1986 *Stigmicercopis* [sic!]: Lin, p. 102
1996 Edwards *et al.*, p. 654 [listed]
2006 Wang Y. *et al.*, p. 296 [listed]

***Stigmocercopis parvis* Lin, 1986**

1986 Lin, p. 67, 102, Fig. 60, Pl. 18, Fig. 1 [new species, illustrated]
1986 *Stigmicercopis* [sic!] *parvis*: Lin, p. 102 [note]
2010 Wang Y. *et al.*, p. 136 [listed]
2012 Wang Y, *et al.*, p. 170 [listed]

Middle Jurassic, Bajocian, Shiti Formation, Shiniuwei village, Taochuan, Jiangyong County, Hunan, China.

Genus ***Tennentsia*** Riek, 1976
Type species. *Dysmorphoptiloides protuberans* Riek, 1974; by original designation and monotypy.

1976 Riek, p. 813
1984a Shcherbakov, p. 94 [listed]
1984b Shcherbakov, p. 92 [listed]
1992 Carpenter, p. 230, Fig. 149–10 [note, illustrated]
1993 Edwards & Tobias, p. 513 [listed]
2003 Martins-Neto *et al.*, p. 240, 242, 252 [listed, note]
2006 Martin-Neto & Gallego, p. 187 [listed]
2015 Lambkin, p. 368 [redescribed, note], p. 373 [listed]

***Tennentsia evansi* Lambkin, 2015**

2015 Lambkin, p. 371, Figs. 22, 26–28 [new species, illustrated]
2016 Lambkin, p. 216 [listed]

Middle Triassic, Anisian, Gayndah Formation, road cutting 3 km ENE of Gayndah, Queensland, Australia

***Tennentsia princeps* Lambkin, 2015**

2015 Lambkin, p. 368, Figs. 21, 23–25 [new species, illustrated]
2016 Lambkin, p. 2017 [listed]

Late Triassic, Norian, Mount Crosby Formation, Ipswich Coal Measures, Mount Crosby, Queensland, Australia.

***Tennentsia protuberans* (Riek, 1974)**

1974 *Dysmorphoptiloides protuberans*: p. 22, Fig. 9, Pl. 1, Fig. 5 [new species]
1976 Riek, p. 814, Fig. 15; Plate 4, fig. 4 [new status, notes, illustrated]
1984 Anderson & Anderson, p. 45, fig. 2–21 [listed, illustrated]
1988 Shcherbakov, p. 62 [listed]
1992 Carpenter, p. 230, Fig. 149–10 [note, illustrated]
1999 Martins-Neto & Gallego, p. 194 [listed]
2001 Gallego *et al.*, p. 2 [listed]
2001 Martins-Neto & Gallego, p. 108 [listed]
2003 Martins-Neto *et al.*, p. 252 [note]
2005 Labandeira, p. 16, Fig. 2f [illustrated]
2006 Martins-Neto & Gallego, p. 187 [listed]
2015 Lambkin, p. 372 [listed]
2018 Labandeira *et al.*, p. 678 [listed]

Upper Triassic, Carnian, Molteno Formation, Birds River (Bir 111), Dordrecht (C-Dt. II), Eastern Cape Province, South Africa.

Genus ***Triassocixius*** Tillyard, 1919
Type species. *Triassocixius australis* Tillyard, 1919; by original designation and monotypy.
=*Triadocixius*: Handlirsch 1939

1919 Tillyard, p. 878 [new genus], p. 865, 866 [listed],

p. 868 [key] [described in Scytinopteridae, Mesocixiinae]
1922 Tillyard, p. 462 [note]
1923 Tillyard, p. 483 [listed; placed in Cixiidae]
1928 Martynov, p. 37 [note]
1937a Martynov, pp. 88, 161 [notes]
1938 Schulze *et al.*, p. 3524 [listed]
1939 *Triadocixius* [sic!]: Handlirsch, p. 10
1939 Handlirsch, p. 17 [listed; in Homoptera *incertae sedis*]
1940b Neave, p. 533 [listed]
1949 Jeannel, p. 83 [note]
1962 Becker-Migdisova, p. 253 [listed]
1966 Metcalf & Wade, p. 125 [catalogued]
1984a Shcherbakov, p. 94 [listed, placed in Dysmorphoptilidae]
1984b Shcherbakov, p. 92 [listed; placed in Dysmorphoptilidae]
1991 Becker-Migdisova, p. 186 [listed]
1992 Hamilton, p. 428 [listed; placed in 'Cercopoidea, new family?']
1992 Carpenter, p. 237 [listed]
2004 Szwedo *et al.*, p. 129 [listed, note]
2010 Wang B. *et al.*, p. 224 [listed]
2012 Wang B. *et al.*, p. 1224 [listed]
2015 Nicholson *et al.*, p. 91 [note]
2015 Lambkin, p. 360 [redescribed], pp. 357, 358, 373 [listed]

***Triassocixius australicus* Tillyard, 1919**

1919 Tillyard, p. 878, Fig. 12 [new species, illustrated], p. 866 [listed]
1923 Tillyard, p. 483 [listed]
1939 *Triadocixius* [sic!] *australis* [sic!]: Handlirsch, p. 10
1939 *Triassocixius australis* [sic!]: Handlirsch, p. 17
1966 Metcalf & Wade, p. 125 [catalogued]
1992 Carpenter, p. 237, Fig. 152–2 [note, illustrated]
2015 Lambkin, p. 362, Figs. 9, 10 [redescribed, illustrated]
2016 Lambkin, p. 2017 [listed]
2018 Labandeira *et al.*, p. 678 [listed, placed in Cixiidae]

Late Triassic, Norian, Blackstone Formation, Denmark Hill Insect Bed, Queensland, Australia.

Genus ***Trifidella*** Evans, 1956
Type species. *Trifidella perfecta* Evans, 1956; by original designation and monotypy
= *Alotrifidus* Evans, 1956
Type species. *Alotrifidus interruptus* Evans, 1956; by original designation and monotypy.

1956 Evans, p. 215 [new genus; illustrated, placed in Cercopidae]
1956 *Alotrifidus* Evans, p. 216 [new genus; illustrated, placed in Cercopidae]
1961 Evans, p. 18 [listed, placed in Cercopidae]
1973 Riek, p. 527 [listed]
1975 *Alotrifidus* Evans: Edwards & Vevers, p. 13 [listed]
1975 Edwards & Vevers, p. 349 [listed]
1984a Shcherbakov, p. 94 [listed; placed in Dysmorphoptilidae]
1984a *Alotrifidus* Evans: Shcherbakov, p. 94 [listed, placed in Dysmorphoptilidae]
1984b Shcherbakov, p. 92 [listed; placed in Dysmorphoptilidae]
1984b *Alotrifidus* Evans: Shcherbakov, p. 94 [listed, placed in Dysmorphoptilidae]
1992 *Alotrifidus* Evans: Hamilton, p. 428
1992 Hamilton, p. 428
1992 *Alotrifidus* Evans: Hamilton, p. 428
1992 *Alotrifidus* Evans, 1956: Carpenter, p. 231, Fig. 148–10 [listed, illustrated; placed in Cercopidae]
1992 Carpenter, p. 232 [listed, illustrated; placed in Cercopidae]
2004 *Alotrifidus* Evans, 1956: Jell, p. 36 [listed]
2004 Jell, p. 37 [listed]
2006 Martins-Neto & Gallego, p. 195 [listed]
2015 Lambkin, p. 357 [listed]
2016 Lambkin, p. 215 [redescribed, synonymy, note]

***Trifidella perfecta* Evans, 1956**
= *Alotrifidus interruptus* Evans, 1956

1956 Evans, p. 216, Fig. 16C [new species, illustrated
1956 *Alotrifidus interrutpus* Evans, p. 216, Fig. 16D [new species, illustrated]
1961 Evans, p. 18, Figs. 3A, B [described, note, illustrated]
1964 Evans, pp. 174, 175, Fig. 3C [phylogeny]
1963b Evans, p. 84 [listed]
1971 Evans, p. 146 [listed]
1990 Rozefelds *et al.*, p. 705 [listed]
2004 *Alotrifidus interruptus* Evans, 1956: Jell, p. 36, fig. [listed, unnumbered, linedrawing from Evans 1956 and photo of the specimen]
2004 Jell, p. 37, fig. [listed, unnumbered, line drawing from Evans 1956 and photo of the specimen]
2010 Wang B. *et al.*, p. 224 [listed]
2012 Wang B. *et al.*, p. 1224 [listed]
2016 Lambkin, p. 215, Figs. 13–15 [redescribed, note, illustrated], p. 217 [listed]

Late Triassic, Norian, Mount Crosby Formation, Ipswich Coal Measures, Mount Crosby, Queensland, Australia.

Subfamily **Eoscarterellinae** Evans, 1956, **stat. nov.**

Type genus. *Eoscarterella* Evans, 1956; fixed by implicit usage.

1956 Eoscarterellidae Evans, p. 220 [new family]
1958 Eoscarterellidae: Evans, p. 112
1961 Eoscarterellidae Evans, p. 19 [listed]
1962 Eoscarterellidae: Becker-Migdisova, p. 179 [listed, note]
1973 Eoscartarellidae [sic!]: Riek, 1973, pp. 514, 527
1974 Eoscartarellidae [sic!]: Riek, 1974, p. 21
1978 Eoscartarellidae: Zherikhin, pp. 28, 134 [listed]
1984a Eoscarterellidae Evans: Shcherbakov, p. 94 [listed, synonymy]
1984b Eoscarterellidae Evans: Shcherbakov, p. 92 [listed, synonymy]
1991 Eoscarterellidae: Becker-Migdisova, p. 244 [listed, note]
1992 Eoscarterellidae Evans: Carpenter, p. 228 [listed, note]
1996 Eoscarterellidae: Shcherbakov, p. 37 [listed, equals Dysmorphoptilidae]
2004 Eoscartellidae [sic!]: Szwedo *et al.*, p. 14 [note, listed]
2006 Eoscartellidae [sic!]: Martins-Neto & Gallego, p. 195

Diagnostic characters. Tegmen rugose, punctate, evenly rounded, basal portion narrowed; postclaval portion of membrane (tornus) arcuate, postnodal membrane distinctly widened; branch ScP+RA with more than two branches; RA_1 entering anterior margin before level of claval apex; RP separated from common stalk ScP+R at basal ⅓ of tegmen length; stem MP closer to stem CuA than to stem ScP+R; stems MP and CuA not forking at same level; MP with four terminals; veinlet *ir* (*ra-rp*) present, sometimes shortened; veinlets *rp-mp* and *mp-cua* present; stridulitrium noticeable.

Remarks. This subfamily and its characters are weakly known, widening of postclaval membrane, arcuate tornus and early entry of RA_1 into the costal margin could be apomorphies of this group. However, it shares with Dysmorphoptilinae number of features, e.g. weak and multiple prenodal branches of RA; not branched terminally RP and stem MP closer to stem CuA than to stem ScP+R and early entry of RA_1 into the costal margin with Prosbolidae. This taxon needs revisionary studies.

Genus ***Belmontocarta*** Evans, 1958

Type species. *Belmontocarta perfecta* Evans, 1958; by original designation and monotypy.

1958 Evans, p. 112 [new genus; placed in Eoscarterellidae]
1959 Evans, p. 152 [listed]
1975 Edwards & Vevers, p. 41 [listed]
1984a Shcherbakov, p. 94
1984b Shcherbakov, p. 92
1992 Carpenter, p. 228 Fig. 147–1 [listed, note]
2015 Lambkin, p. 357 [listed]
2016 Lambkin, p. 217 [listed]

Belmontocarta perfecta **Evans, 1958**

1958 Evans, p. 113, fig. 5 [new species, illustrated]
1959 Evans, p. 152 [note]
1963b Evans, p. 84 [listed]
1964 Evans, p. 175, Fig. 4 D [phylogeny], p. 180 [listed]
1968 Riek, p. 305 [listed]
1992 Carpenter, p. 228 [listed]
2004 Jell, p. 43 fig. [unnumbered, line drawing of Evans 1958; photo of the specimen]
2016 Lara & Wang, p. 58, 59 [listed]

Upper Permian, Changhsingian, New Castle Coal Measures, Belmont Conglomerate Member (Croudace Bay Formation), Warner's Bay, Belmont, New South Wales, Australia.

Genus ***Duraznoscarta*** Lara & Wang, 2016

Type species. *Duraznoscarta ramosa* Lara & Wang, 2016; by original designation and monotypy.

2016 Lara & Wang, p. 52 [new genus]
2017 Lara et al., p. 169 [listed]
2018 Devincenzi, p. 332 [listed]

Duraznoscarta ramosa **Lara & Wang, 2016**

2016 Lara & Wang, p. 53, Fig. 4 [new species, illustrated], p. 50, 59 [listed]
2017 Lara *et al.*, p. 169, Fig. 5G [listed, illustrated]
2018 Devincenzi, p. 332 [listed]

Late Triassic, Carnian, Potrerillos Formation, Quebrada del Durazno, Cerro Cacheuta, Cuyana Basin, Mendoza Province, Argentina.

Genus ***Dysmorphoscartella*** Riek, 1973

Type species. *Dysmorphoscartella lobata* Riek, 1973; by original designation and monotypy.

1973 Riek, p. 527 [new genus]
1992 Carpenter, p. 255 [listed; placed in family uncertain section]
1993 Edwards & Tobias, p. 152 [listed]
1997 van Dijk, p. 44 [listed]
1999 van Dijk & Gertseema, p. 140 [listed]

***Dysmorphoscartella lobata* Riek, 1973**

1973 Riek, p. 528, Fig. 13, Pl. 2, Fig. 8 [new species, illustrated], p. 514 [listed]
1992 Carpenter, p. 255 [listed]
1999 van Dijk & Gertseema, p. 140 [listed]
Late Permian, Changhsingian, Middle Beaufort Series, Estcourt Formation, Estcourt, Rondedraai Farm (Est 211), Natal, South Africa.

Genus ***Eoscarterella*** Evans, 1956
Type species. *Eoscarterella media* Evans, 1956; by original designation and monotypy.
= *Prosbolopsites Becker*-Migdisova, 1960
Type species. *Prosbolopsites tillyardi* Becker-Migdisova, 1960; by original designation and monotypy.

1956 Evans, p. 220 [new genus]
1958 Evans, p. 112 [listed]
1961 Evans, p. 19 [listed]
1960 *Prosbolopsites* Becker-Migdisova, p. 90, 96
1962 *Prosbolopsites*: Becker-Migdisova, p. 180
1973 *Eoscaratarella* [sic!]: Riek, p. 527
1975 Edwards & Vevers, p. 106 [listed]
1991 *Prosbolopsites* Bekker-Migdisova: Becker-Migdisova, p. 244 [listed]
1992 Hamilton, p. 428 [listed]
1992 *Prosbolopsites* Becker-Migdisova: Hamilton, p. 428 [listed]
1992 Carpenter, p. 228, Fig. 147–3 [listed, illustrated, note]
1992 *Prosbolites* Becker-Migdisova, 1960: Carpenter, p. 228 [listed, note]
2004 Jell, p. 43 [listed]
2016 Lambkin, p. 213 [redescribed, note]

***Eoscarterella media* Evans, 1956**

1956 Evans, p. 220, Fig. 18C [new species; illustrated]
1961 Evans, p. 19 [listed]
1961 *Prosoboloides tillyardi* Bekker-Migdisova, 1960: Evans, p. 19 [synonymy]
1962 Becker-Migdisova, p. 179, Fig. 499 [listed, illustrated]
1962 *Prosobolopsites tillyardi* Becker-Migdisova: p. 179, Fig. 500 [listed, illustrated]
1991 Becker-Migdisova, p. 244, Fig. 499 [listed, illustrated]
1991 *Prosobolopsites tillyardi* Bekker-Migdisova, Becker-Migdisova, p. 244, Fig. 500 [listed, illustrated]
1992 *Prosobolopsites tillyardi*: Carpenter, p. 228 [listed, note]
1992 Carpenter, p. 228 [listed]
2004 Jell, p. 43, fig. [unnumbered; line drawing of Evans 1956; photo of the specimen]
2016 Lambkin, p. 213, Figs. 10–12 [redescribed, illustrated, note].
2016 *Prosoboloides tillyardi* Bekker-Migdisova, 1960: Lambkin, p. 213 [listed]
2016 Lara & Wang, p. 59 [listed]
Late Triassic, Norian, Mount Crosby Formation, Ipswich Coal Measures, Mount Crosby, Queensland, Australia.

Genus ***Mesonirvana*** Evans, 1956
Type species. *Mesonirvana abrupta* Evans, 1956; by original designation and monotypy.
= *Eoscartoides* Evans, 1956 non *Eoscartoides* Matsumura, 1940
Type species. *Eoscartoides bryani* Evans, 1956; by original designation and monotypy
= *Mesocixioides* Tillyard, 1922 (*partim*)
Type species. *Mesocixiodes termioneura* Tillyard, 1922; by original designation.

1922 *Mesocixiodes* Tillyard, p. 462 [new genus]
1928 *Mesocixioides* [sic!] (*partim*): Martynov, pp. 36, 37 [note]
1931 *Mesocixiodes* (*partim*): Schulze *et al.*, p. 2043 [listed]
1937a *Mesocixiodes* (*partim*): Martynov, pp. 88, 161 [note]
1937b *Mesocixiodes* (*partim*): Martynov, p. 36 [note]
1939 *Mesocixioides* (*partim*): Handlirsch, p. 10, 16 [listed]
1940a *Mesocixiodes* (*partim*): Neave, p. 115 [listed]
1949 *Mesocixiodes* (*partim*): Jeannel, p. 83 [listed]
1956 Evans p. 191 [new genus]
1956 *Eoscartoides* Evans, p. 220 [new genus]
1962 Becker-Migdisova, p. 174 [listed]
1962 *Eoscartoides* Evans, 1956: Becker-Migdisova, p. 180 [listed]
1966 *Mesocixiodes* Tillyard: Metcalf & Wade, p. 119 [catalogued]
1975 *Eoscartoides* Evans: Edwards & Vevers, p. 106 [listed]
1975 Edwards & Vevers, p. 190 [listed]
1991 Becker-Migdisova, p. 237 [listed]
1991 *Eoscartoides* Evans, 1956: Becker-Migdisova, p. 244
1992 Hamilton, p. 428 [listed]
1992 *Eoscartoides* Evans: Hamilton, p. 428
1992 Carpenter, p. 223, Fig. 144–7 [listed, illustrated, note]
1992 *Eoscartoides* Evans, 1956: Carpenter, p. 228, Fig. 147–2 [listed, illustrated, note]
1992 *Mesocixiodes* (*partim*): Carpenter, p. 257, [listed]

2004 Jell, p. 44, fig. [unnumbered, line drawing of Evans 1956; photo of the specimen]
2004 *Eoscarteroides* [sic!]: Jell, p. 44
2016 *Eoscartoides*: Lambkin, p. 208 [listed]
2016 Lambkin, p. 208 [listed, synonymy]
2016 *Mesocixiodes* (*partim*): Lambkin, p. 208 [listed]
2017 *Eoscartoides* Evans: Lambkin, 61 [synonymy]
2017 Lambkin, p. 61 [note, synonymy, new combinations]
2018 *Mesocixioides* (*partim?*): Labandeira *et al.*, p. 678 [listed, placed in Cixiidae]

***Mesonirvana abrupta* Evans, 1956**
= *Eoscartoides bryani* Evans, 1956

1956 Evans, p. 192, Fig. 5E [new species, illustrated]
1956 *Eoscartoides bryani* Evans, p. 221, Fig. 18A [new species, illustrated]
1964 *Eoscartoides bryani*: Evans, pp. 174, 175, Fig. 4C [phylogeny]
1990 Rozefelds *et al.*, p. 680 [listed]
1992 Carpenter, p. 223 [listed]
1992 *Eoscartoides bryani*: Carpenter, p. 228 [listed]
2003 Martins-Neto *et al.*, p. 253 [listed]
2004 *Eoscarteroides* [sic!] *bryani*: Jell, p. 44, fig. [unnumbered; line drawing of Evans 1956, and photo of the specimen]
2004 Jell, p. 56, fig. [unnumbered; line drawing of Evans 1956, and photo of the specimen]
2016 *Eoscartoides bryani*: Lambkin, p. 209, Fig. 1–3 [redescribed, illustrated]
2016 Lambkin, p. 209 [synonymy]
2016 *Eoscartoides bryani*: Lambkin, p. 217 [listed]
2016 *Eoscartoides bryani*: Lara & Wang, p. 59 [listed]
2017 Lambkin, p. 61 [synonymy]
2017 *Eoscartoides bryani*: Lambkin, p. 61 [synonymy]

Late Triassic, Norian, Mount Crosby Formation, Ipswich Coal Measures, Mount Crosby, Queensland, Australia.

***Mesonirvana dmitryi* (Lambkin, 2016)**
= *Eoscartoides dmitryi* Lambkin, 2016

2016 *Eoscartoides dmitryi* Lambkin, p. 211, Figs. 7–9 [new species, illustrated], p. 217 [listed]
2017 Lambkin, p. 61, Fig. 1 [synonymy, illustrated]

Late Triassic, Norian, Blackstone Formation, Dinmore clay pit, Ipswich Queensland, Australia.

***Mesonirvana orthoclada* (Tillyard, 1922)**
= *Mesocixiodes orthocladus* Tillyard, 1922
= *Eoscartoides orthocladus* (Tillyard, 1922)

1922 Tillyard, p. 463, Fig. 83 [new species, illustrated]
1923 *Mesocixiodes orthoclada*: Tillyard, p. 483 [listed]
1928 *Mesocixioides* [sic!] *orthoclada*: Martynov, p. 37 [listed]
1939 *Mesocixiodes orthoclada*: Handlirsch, p. 10 [note, listed] p. 16 [listed]
1956 *Mesocixiodes orthoclada*: Evans, p. 210 [note]
1962 *Mesocixiodes orthoclada*: Becker-Migdisova, p. 181 [listed]
1991 *Mesocixiodes orthoclada*: Becker-Migdisova, p. 246 [listed]
2004 *Mesocixiodes orthoclada*: Jell, p. 41
2016 *Eoscartoides orthocladus*: Lambkin, p. 209, Figs. 4–6 [redescribed, illustrated, synonymy], p. 217 [listed]
2017 Lambkin, p. 61 [synonymy]

Late Triassic, Norian, Blackstone Formation, Denmark Hill Insect Bed, Queensland, Australia.

Subfamily **Gallegomorphoptilinae** Martins-Neto, 2006 *in* Martins-Neto & Gallego
Type genus. *Gallegomorphoptila* Martins-Neto *in* Martins-Neto, Gallego & Melchor, 2003; fixed by implicit usage.

2005 Gallegomorphoptilinae: Gallego *et al.*, p. 294 [listed, *nomen nudum*]
2006 Gallegomorphoptilinae Martins-Neto *in* Martins-Neto & Gallego, p. 187 [new subfamily]

Diagnostic characters. Tegmen with RA and RP distally fused; veinlet *ra-rp* (*ir*) absent; RA unbranched; RP with two or three secondary branches; postclaval margin (tornus) straight, sometimes concave; apical portion of membrane narrower than basal.

Remarks. Fusion of RA and RP and secondary branching of RP could be apomorphic for this subfamily. Narrowing of apical portion of tegmen is shared feature with Dysmorphoptilinae.

Genus ***Bandelnielsenia*** Martins-Neto & Gallego *in* Martins-Neto, Gallego & Melchor, 2003
Type species. *Bandelnielsenia chilena* Martins-Neto & Gallego, 2003; by original designation and monotypy

2003 Martins-Neto *et al.*, p. 242
2005 Gallego *et al.*, p. 303
2006 Martins-Neto & Gallego, p. 187 [listed]
2011 Martins-Neto *et al.*, p. 4 [listed]
2015 Pérez & Pérez, p. 168 [listed]

***Bandelnielsenia chilena* Martins-Neto & Gallego, 2003**

2001 Gallego *et al.*, p. 2 [*nomen nudum*]
2003 Martins-Neto et Gallego in Martins-Neto *et al.*, p. 242, Fig. 6D [new species, illustrated]
2005 Gallego *et al.*, pp. 294, 296, 303, Fig. 2D; Pl. 3, Fig. 8 [listed, illustrated]
2006 Martins-Neto & Gallego, p. 186 [listed]
2011 Martins-Neto *et al.*, p. 4 [listed]

Late Triassic, Carnian, Santa Juana Formation, outcrop south of Santa Juana city, level FL2, Biobío River, Southeast Concepción, Chile.

Genus ***Gallegomorphoptila*** Martins-Neto *in* Martins-Neto, Gallego & Melchor, 2003
Type species. *Gallegomorphoptila breviptera* Martins-Neto, 2003; by original designation and monotypy.
= *Dysmorphoptiloides* Evans, 1956 (*partim*)
Type species. *Dysmorphoptiloides elongata* Evans, 1956; by original designation

2001 Gallego *et al.*, p. 2 [*nomen nudum*]
2003 Martins-Neto *in* Martins-Neto *et al.*, p. 240 [new genus, described]
2006 Martins-Neto & Gallego, p. 187 [listed]
2008 Martins-Neto, p. 674, 676 [listed]
2011 Gallego *et al.*, p. 13 [listed]
2012 Lara *et al.*, p. 6 [listed]
2015 *Gallegomorphoptila* Martens-Neto [sic!]: Lambkin, p. 367

***Gallegomorphoptila acostai* (Martins-Neto & Gallego, 1999)**
= *Dysmorphoptiloides acostai* Martins-Neto & Gallego, 1999

1999 *Dysmorphoptiloides acostai* Gallego & Martins-Neto, p. 87, Fig. 1 [*nomen nudum*, note, illustrated]
1999 Martins-Neto & Gallego, pp. 192, 194, fig. 2A [new species, illustrated]
2001 *Dysmorphoptiloides acostai*: Gallego *et al.*, p. 2 [listed]
2001 *Dysmorphoptiloides acostai*: Martins-Neto & Gallego, p. 108, Pl. 1E, Fig 1B [redescribed, illustrated], p. 109 [listed]
2003 *Dysmorphoptiloides acostai*: Martins-Neto *et al.*, pp. 239, 242 [listed]
2006 Martins-Neto & Gallego, p. 198, Figs. 1, 2 [note, illustrated, new combination]
2011 Martins-Neto *et al.*, pp. 2, 3 [listed]
2012 Lara *et al.*, p. 6 [listed]
2016 Lara & Wang, p. 50 [listed]
2017 Lara *et al.*, p. 169 [listed]
2018 Labandeira *et al.*, p. 679 [listed]

Late Triassic, Carnian, upper section of Potrerillos Formation, levels EP I and EP II of Morel (1994), 300 m west of Quebrada del Durazno, south of the Cerro Cacheuta, Mendoza, Argentina.

***Gallegomorphoptila breviptera* Martins-Neto *in* Martins-Neto, Gallego & Melchor, 2003**

2001 *Gallegomorphoptila breviptera*: Gallego *et al.*, p. 2 [*nomen nudum*]
2003 Martins-Neto *in* Martins-Neto, Gallego & Melchor, p. 240, Fig. 4H [new species, illustrated]
2006 Martins-Neto & Gallego, p. 189, 191 [listed]
2008 Martins-Neto, p. 675, Figs. 23. 32I [illustrated]
2011 Martins-Neto *et al.*, p. 3 [listed]
2016 Lara & Wang, p. 50 [listed]

Late Triassic, Carnian, Los Rastros Formation (Agua de la Peña Group), Río Gualo locality, Ischigualasto-Villa Unión Basin, La Rioja Province, Argentina.

***Gallegomorphoptila gigantea* (Martins-Neto & Gallego, 2001)**
= *Dysmorphoptila gigantea* Martins-Neto & Gallego, 2001

2001 Gallego *et al.*, p. 2 [*nomen nudum*]
2001 Martins-Neto & Gallego, p. 108, Pl. 1C, Fig. 1D. [new species, illustrated]
2003 *Dysmorphoptila gigantea* Martins-Neto & Gallego: Martins-Neto *et al.*, p. 239, Fig. 4G [listed, illustrated]
2006 Martins-Neto & Gallego, p. 189 [listed]
2011 Martins-Neto *et al.*, p. 3 [listed]
2016 Lara & Wang, p. 50 [listed]

Late Triassic, Carnian, Los Rastros Formation (Agua de la Peña Group), Río Gualo locality, Ischigualasto-Villa Unión Basin, La Rioja Province, Argentina.

***Gallegomorphoptila kotejai* Martins-Neto & Gallego, 2006**

2006 Martins-Neto & Gallego, p. 190, Figs. 4, 5 [new species, illustrated]
2016 Lara & Wang, p. 50 [listed]

Late Triassic, Carnian, Ischichuca Formation, Quebrada de Ischichuca Chica, La Rioja province, Argentina.

***Gallegomorphoptila pulcherrima* (Martins-Neto & Gallego *in* Martins-Neto, Gallego & Melchor, 2003)**
= *Dysmorphoptila pulcherrima* Martins-Neto & Gallego, 2003

2001 *Dysmorphoptila pulcherrima*: Gallego *et al*., p. 2 [*nomen nudum*]
2003 Martins-Neto et Gallego *in* Martins-Neto *et al*., p. 240, Figs. 4 E, F [new species, illustrated]
2006 Martins-Neto & Gallego, p. 194, Figs. 10, 11 [new combination, note, illustrated]
2011 Martins-Neto *et al*., p. 3 [listed]
2016 Lara & Wang, p. 50 [listed]

Late Triassic, Carnian, Los Rastros Formation (Agua de la Peña Group), Río Gualo locality, Ischigualasto-Villa Unión Basin, La Rioja Province, Argentina.

Subfamily **Fulgoringruinae** Pinto, 1990
Type genus. *Fulgoringruo* Pinto, 1990; by monotypy.

1990 Fulgoringruidae Pinto, p. 4. [new family]
2000 Fulgoringruidae: Shcherbakov, p. S251 [listed]
2000 Fulgoringruinae: Shcherbakov, p. S251 [new status, note], p. S259 [listed]
2004 Fulgoringruidae: Szwedo *et al*., p. 110 [listed]
2005 Fugoringruidae [sic!]: Martins-Neto, p. 472 [listed]
2006 Fulgoringruidae: Martins-Neto & Gallego, p. 195 [listed]
2006 Fulgoringruinae: Martins-Neto & Gallego, p. 195 [listed]
2015 Nicholson *et al*., p. 93 (supplementary material) [listed]
2018 Fugoringruidae [sic!]: Moura-Júnior *et al*., p. 145 [listed]

Diagnostic characters. Tegmen punctate, not widened or narrowed at postnodal portion of membrane; costal margin arcuate, Pc shifted from CA forming distinct carination, reaching level of nodal line; RA with a few terminals; prenodal branches of RA indistinct; RP separated from common stem ScP+R apically, beyond half of tegmen length, forked apically beyond level of nodal line; stem of MP closer to stem CuA than stem ScP+R, forked distinctly caudally, beyond nodal line, apicad of ScP+R and CuA forkings; veinlet *ir* (*ra-rp*) absent, veinlets *rp-mp* and *mp-cua* present; claval veins Pcu and A_1 fused at about half of tegmen length.

Remarks. Apomorphic characters of this subfamily could be: shifting of Pc from CA at long distance; late forking of ScP+R; distal forking of RP; very late forking of MP; lack of veinlet *ir*. This taxon is very poorly known and in need of revisionary studies.

Genus ***Fulgoringruo*** Pinto, 1990
Type species. *Fulgoringruo kukalovae* Pinto, 1990; by original designation and monotypy.

1990 Pinto, p. 4 [new genus]
1995 Pinto, p. 50 [listed]
2001 *Fulguringruo* [sic!]: Adami-Rodrigues & Iannuzzi, p. 170 [listed]
2004 Szwedo *et al*., p. 110 [listed]
2005 *Fulguringruo* [sic!]: Martins-Neto, p. 472 [listed]
2006 Martins-Neto & Gallego, p. 195 [listed]
2016 Lambkin, p. 217 [listed]
2018 *Fulguringruo* [sic!]: Moura-Júnior *et al*., p. 145 [listed]

***Fulgoringruo kukalovae* Pinto, 1990**

1990 Pinto, p. 4, Figs. 4, 5 [new species, illustrated]
1995 *Fulgoringruo kukalovae* Pinto, 1987 [sic!]: Pinto, Pl. 2, Fig. 4 [illustrated]
2001 *Fulguringruo* [sic!] *kukalovae*: Adami-Rodrigues & Iannuzzi, p. 171 Fig. 3f [illustrated]
2004 Adami Rodrigues *et al*., p. 111, Fig. 3 C [listed, illustrated]
2005 *Fulguringruo* [sic!] *kukalovae*: Martins-Neto, p. 472 [listed]
2006 Martins-Neto & Gallego, p. 195 [listed]
2015 Nicholson *et al*., p. 93 (supplementary material) [listed]
2016 Ricetti *et al*., p. 185 [listed]
2018 *Fulguringruo* [sic!] *kukalovae*: Moura-Júnior *et al*., p. 145 [listed]

Lower Permian, Artinskian, Iratí Formation, a cutting at road BR-290, km 185–500 of the road Porto Allegre-Uruguaiana, near Minas do Leao, Rio Grande do Sul State, Brazil.

Subfamily **Permocixiellinae** Szwedo & Huang, **subfam. nov.**
Type genus. *Permocixiella* Becker-Migdisova, 1961.; by original designation.

Genus ***Linglunxiellus*** Szwedo et Huang **sp. nov.**
Type species. *Linglunxiellus chaohuensis* Szwedo & Huang **sp. nov.**; by original designation and monotypy.

2019 Szwedo & Huang, p. 6 [new genus]

***Linglunxiellus chaohuensis* Szwedo & Huang, sp. nov.**

2019 Szwedo & Huang, p. 6, Figs. 3A, B, 4A, B [new species, illustrated]

Upper Permian, Capitanian, Yinping Formation, Chaohu City, Anhui Province, China.

Genus ***Permocixiella*** Becker-Migdisova, 1961

Type species. *Permocixiella venosa* Becker-Migdisova, 1961; by original designation and monotypy.

1955 *Permocixiella*: Becker-Migdisova, p. 1100 [*nomen nudum*]

1956 *Permocixiella*: Miroshnikov & Pirozhnikov, p. 145 [*nomen nudum*]

1961 Becker-Migdisova, p. 361 [new genus]

1962 Becker-Migdisova, p. 185, Fig. 524 [note, illustrated]

1984a Shcherbakov, p. 94 [listed]

1984b Shcherbakov, p. 92 [listed]

1991 Becker-Migdisova, p. 252, Fig. 524 [note, illustrated]

1992 Carpenter, p. 236, Fig. 152–4 [listed, illustrated, placed in Cixiidae]

2004 Szwedo *et al.*, p. 123 [listed]

Permocixiella venosa **Becker-Migdisova, 1961**

1961 Becker-Migdisova, p. 361, Fig. 294 [new species, illustrated]

1962 Becker-Migdisova, p. 185, Fig. 524 [note, illustrated]

1991 Becker-Migdisova, p. 252, Fig. 524 [note, illustrated]

1992 Carpenter, p. 236 [listed]

Upper Permian, Wuchapingian, Gramoteinskaya Formation (Erunakovskaya Group), Sokolova II, Kemerovskiï District, Prokop'evsk Region, Kuznetsk Basin, Russia.

Discussion

The members of Dysmorphoptilidae are characterized by the convex proximally costal margin of tegmen; hypocostal expansion beyond basal bent of CA (called humeral angle), which is strongly constricted; hypocostal carina (fused Pc+CA) carinate; long C, separating from common stem Pc+CA+CP near tegmen base, with its apex directed or close to ScP, which at this point extends somewhat from stem R+MP, forming a very low-angled arc; vein ScP is concave over whole extent; basal cell elongate, weakly or not tapering caudad, closed with arculus, or rarely with anastomosis; stem ScP+RA longer than first segment of RA branch (portion between forking of ScP+RA_1 and subsequent RA terminals), more strongly inclined than postnodal (after fork of RA stem) terminals, and as a rule bearing weak prenodal (basad of RA stem forking) branches; CuA is forked before veinlet *mp-cua,* and CuA_1 is not fused with MP; veinlets *ir*, *rp-mp* and *mp-cua* present, rarely more numerous veinlets present; anal field folded back distally; macrosculpture punctate, covering uniformly the tegmen surface; almost always stridulatory field noticeable.

The characteristics given above is based mainly on the Triassic, the most diverse representatives of the family. Permocixiellinae subfam. nov. from the Permian differs by the less sclerotized tegmen, only partly punctate and details of venation, also lack of distinct stridulitrum (part of stridulatory apparatus). Tegmina shapes of the Triassic Dysmorphoptilidae are often bizarre, with enlarged costal area and disruptly narrowed membrane, sometimes with additional lobes on claval margin (see e.g. *Dysmorphoptila*, *Tennentsia*). It seems it is adaptation to crypsis among their host-plants. These Dysmorphoptilidae probably mimicked thorns or bracts of their host plants. Similar cryptic adaptations were found also in the other Cicadomorpha from the Triassic: Maguviopseidae Shcherbakov, 2011 and Saaloscytinidae Brauckmann, Martins-Neto & Gallego, 2006 (Shcherbakov, 2011). Bract, thorn, flower, or seed mimics are known among the Recent treehoppers Membracidae Rafinesque, 1815 (Cicadomorpha), and planthoppers Issidae Spinola, 1839, Flatidae Spinola, 1839, Acanaloniidae Amyot et Audinet-Serville, 1843 (Fulgoromorpha Evans, 1946). The presence of stridulatory apparatus was reported for the Triassic forms of Dysmorphoptilidae (Shcherbakov & Popov, 2002; Senter, 2008; Lambkin, 2015, 2016). It is formed by the strigil (stridulitrum) on tegmen underside (Lambkin, 2015, 2016) and scraper (plectrum) at hind knee (Evans, 1961; fig. 184). Such combination of strigil and plectrum could indicate that the knees of hind legs were concealed by tegmina and the hind legs were shortened, suggesting jumping abilities not strongly developed, as among modern Cicadomorpha. Presence of similar femoro-tegminal devices is confirmed also in some Triassic Ipsviciidae Tillyard, 1919 (Hemiptera: Scytinopteroidea Handlirsch, 1906) and various Heteroptera Latreille, 1806 (Shcherbakov & Popov, 2002; Senter, 2008). The alarm signal was possibly emitted during an escape leap in these cryptic creatures. Shcherbakov (2011) suggested that the elaborate camouflage of these extinct cicadomorphans (Dysmorphoptilidae, Maguviopseidae, Saaloscytinidae) is presumably due to increase of visual predation by small arboreal reptiles in the Triassic. Dysmorphoptilidae have not survived into the Cretaceous, presumably due to extinction of their host plants, and possible competition from the modern lineages of Cicadomorpha – the Clypeata Qadri, 1967.

The phylogenetic relationships and taxonomic content and classification of Dysmorphoptilidae is still in need of further work. Martins-Neto & Gallego (2006) suggested that that the group is monophyletic and highly flourishing in the Triassic, mainly in South America. The most ancient dysmorphoptilid came from Iratí Formation of Brazil, aged as Artinskian (Santos *et al.*, 2006), with *Fulgoringruo* (Fulgoringruinae). Martins-Neto & Gallego (2006) postulated that this area was probable cradle of the entire group. However, findings of the Permocixiellinae subfam. nov., which seems to be more basal and less specialized than Fulgoringruinae, in the Upper Permian strata of Kuznetsk Basin and China suggest a rather northern origin of this group. In the Triassic, Dysmorphoptlinae and Eoscarterellinae in South Africa and Australia, and Gallegomorphoptilinae in South America flourished. These forms exhibit more advanced characters and a higher specialization pattern, more notorious ornamentation patterns and more diversified shapes of tegmina. The poorly known Magnacicadiinae from the Triassic of China seems to have the tegmina not so bizarrely shaped, however they also present some form of crypsis. In the Jurassic, the last Dysmorphoptilinae are recorded in the deposits of Europe and Asia. This decline could be very probably related to the competition of rapidly diversifying at this time Cicadomorpha: Clypeata, global climatic and biotic changes and extinction of host-plants of Dysmorphoptilidae.

Acknowledgements

We thank Pam Wilson, Queensland Museum, for the information about the specimens. We thank Professor Ron Blakey, Colorado Plateau Geosystems Sedona, Arizona, U.S.A. for permission to use the palaeogeographic reconstructions. The paper resulted from scientific exchange projects of Chinese Academy of Sciences and Polish Academy of Sciences, and President's Fellowship Initiative grant No. 2017VBA0024 awarded to JS. Financial support was provided by Chinese Academy of Sciences (Grant No. KZCX2-YW-QN104) and the the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDB18000000), and the National Natural Science Foundation of China (41688103) to DYH.

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