The first Dysmorphoptilidae (Insecta, Hemiptera) from the Upper Triassic of South Korea

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Summary. *Tennentsia koreana* **n. sp.**, is the first representative of the family Dysmorphoptilidae described from the Upper Triassic of South Korea. This discovery extends the distribution of the genus *Tennentsia* in Asia and suggests that it was broadly distributed during the Triassic. *Tennentsia koreana* **n. sp.** differs from the other species currently included in the genus *Tennentsia*, *inter alia*, because of its tegmen not (or only slightly) emarginate at CuA, RA1 with a weak anterior branch, RA2 not strongly anteriorly curved, with two well-defined branches, strigil in basal part of costal space with coarse punctuation.

Résumé. Le premier Dysmorphoptilidae (Insecta, Hemiptera) du trias Supérieur de Corée du Sud. *Tennentsia koreana* **n. sp.**, est le premier représentant de la famille décrit du Trias supérieur de Corée du Sud. Cette découverte étend la distribution du genre *Tennentsia* en Asie et suggère qu'il était largement réparti durant le Trias. *Tennentsia koreana* **n. sp.** diffère des autres espèces actuellement incluses dans le genre *Tennentsia*, *inter alia*, car possédant un tegmen non (ou faiblement) émarginé au niveau de CuA, RA1 avec une branche antérieure faible, RA2 non fortement incurvée antérieurement, avec deux branches bien définies; et un strigile dans la partie basale de l'espace costal avec une ponctuation grossière.

Keywords. Cicadomorpha; fossil record; new species; taxonomy; *Tennentsia*

Mots clefs. Cicadomorpha; registre fossile; espèce nouvelle; taxonomie; *Tennentsia*

The extinct Dysmorphoptiloidea is an early diverged superfamily of the Cicadomorpha probably closely related to the Clypeata (Szwedo 2018). One of the families of the Dysmorphoptiloidea, the Dysmorphoptilidae spans from the Permian to the Jurassic. Recently, Fu et al. (2021) summarized the diversity within the subfamily Dysmorphoptilinae but the family Dysmorphoptilidae is much more diverse than this subfamily alone with 21 valid genera known from Eurasia, South Africa, South America, and Australia (e.g., Shcherbakov 1984; Martins-Neto et al. 2003; Lambkin 2015; Lara & Wang 2016; Szwedo 2018; Szwedo & Huang 2019; Lara et al. 2021). The Dysmorphoptilidae are morphologically diverse. Authors assumed that this reflects various ecological strategies (crypsis, camouflage, etc.). The coloration patterns along and between the veins are likely 'used' to hide from predators and mimic lichens or mosses (see Lambkin 2015: fig. 26). This mechanism is

documented across numerous lineages – even in the deep past (e.g., Fang et al. 2020). One of the most iconic examples are peppered moths hiding on trunks (e.g., Hart et al. 2010). The Dysmorphoptilidae are also known to possess structures putatively involved in acoustic communication (Shcherbakov 1988).

The family Dysmorphoptilidae is widespread but the systematics of the family remain problematical because of the lack of information on body characters and hind wing venation (Fu et al. 2021). This problem is common in insect fossils described from deposits of the Carboniferous to the Late Triassic – maybe because of fossilization process – and often results in 'taxonomic waste baskets'. Poorly defined families are a challenge for phylogenetic reconstructions and confound analyses of the fossil record at lower systematic levels (e.g., Jouault et al. 2022a).

Here we describe a new species, *Tennentsia koreana* n. sp. from the Late Triassic Amisan Formation, representing the first record of Dysmorphoptilidae from the Triassic of South Korea.

Material and methods

A single forewing with preserved venation was discovered in the middle shale unit of the Amisan Formation exposed in the Myeongcheon section (36°20'21"N, 126°37'34"E; see Park et al. 2022, figure 1). The Amisan Formation, 1,000 m thick, consists in lower sandstone unit, lower shale unit, middle sandstone unit, middle shale unit, and upper sandstone unit (Yang 1999). The Amisan Formation has been thought to be of Triassic age but the floral analyses of Kimura & Kim (1984) have to be challenged because of the life span extension (to the early Jurassic or Cretaceous) of numerous genera initially assumed to be restricted to the Late Triassic (Kim & Kimura 1988; Kim 1990, 2009, 2013; Kim et al. 2002; Lee et al. 2004; Kim

& Roh 2008). The analysis of the clam shrimp fauna supports a Triassic age (Kim & Lee 2015), but the only bivalve genus *Margaritifera* Schumacher, 1816, known from the formation is possibly indicative of a post-Triassic age (Kim et al. 2015), although a recent phylogenetic analysis of the Margaritiferidae supports a Triassic origin for this family (Araujo et al. 2017). Radiometric analyses established a Jurassic age for the Nampo Group, encompassing the Amisan Formation, questioning the Triassic age derived from the paleontological evidence (Koh 2006; Jeon et al. 2007). Finally, the composition of insect fauna, with Titanoptera and Triadophlebiomorpha, indicates a Triassic age for the formation (Park et al. 2022; Jouault et al. 2022b). Herein, we consider the age of the Amisan Formation to be Late Triassic until clear-cut analyses suggest otherwise.

The sample was photographed using a Canon EOS 6D camera with an attached Canon EF 100 mm f/2.8 USM macro lens. Images were cropped and enhanced using Adobe Illustrator and Adobe Photoshop CC2019. The specimen of *Tennentsia koreana* n. sp. is housed in the Gongju National University of Education under the collection number GNUE112006.

We follow the wing venation terminology of Nel et al. (2012) for the acercarian insects, complemented by Lambkin (2015), and modified by Schubnel et al. (2020).

Venation abbreviations are as follows: A anal vein; C costa; CuA cubitus anterior; CuP cubitus posterior; cua-cup crossvein between CuA and CuP; cv costal veinlets; hcc hypocostal carina; MA media anterior; MP media posterior; m-cua1 crossvein between M and CuA1; PCu postcubital vein; RA radius anterior; RP radius posterior; ra2-rp crossvein between RA2 and RP; rp-ma crossvein between RP and MA; str strigil.

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Systematic paleontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Dysmorphoptiloidea Handlirsch, 1906 (*sensu* Szwedo 2018)

Family Dysmorphoptilidae Handlirsch, 1906

Genus *Tennentsia* Riek, 1976

Type species. *Tennentsia protuberans* Riek, 1976 (235.0 to 221.5 Ma, Carnian–Norian, South Africa). Other species: *Tennentsia evansi* Lambkin, 2015 (247.2 to 242.0 Ma, Anisian, Australia), *Tennentsia princeps* Lambkin, 2015 (221.5 to 205.6 Ma, Norian, Australia), *Tennentsia orientalis* Fu et al., 2021 (Ladinian, Yanchang Formation, China), *Tennentsia koreana* **n. sp.** described herein.

Tennentsia koreana n. sp.

(Figures 1-2)

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Type material

Holotype. GNUE112006 (part and counterpart of a nearly complete forewing, with apical part partly missing on one side), housed in the collection of the Gongju National University of Education, Gongju, South Korea.

Locality and horizon. Amisan Formation, Upper Triassic, Myeongcheon Section, Seongju-myeon, Boryeong City, Chungcheongnam-do, Republic of Korea.

Etymology

The specific epithet refers to the originating country of the fossil South-Korea.

Diagnosis

Based on forewing characters. Tegmen not (or only slightly) emarginate at CuA; RA1 with a weak anterior branch; RA2 with two well-defined branches, not strongly curved anteriorly; strigil in basal part of costal space with coarse punctuation.

Description

Tegmen without trace of coloration, ca. 19.5 mm long and ca. 6.9 mm wide, length/width ratio ca. 2.8; emargination gently obtuse; apical lobe longer than wide, occupying about 43% of total wing length; tegmen without protuberances; R with a series of ca. eight very weak and simple costal veinlets; primary fork of RA dichotomous, with RA1 nearly straight, aligned with basal part of RA, with a weak anterior branch; RA2 nearly straight, with one clear apical fork and possibly a weak more basal anterior branch; crossvein ra2-rp short and perpendicular to RA2 and RP; RP simple and nearly straight; crossvein rp-ma short and perpendicular to RP and MA; both MA and MP with a fork; crossvein m-cua1 short and perpendicular to M and CuA1; base of CuA very short; CuA1 weakly convex medially, longer than CuA2; crossvein cua-cup elongate; CuP long and straight; PCuA fading into wing membrane and sculpture; PCuP long slightly curved medially; A ‘stem’ partially fused with wing margin, then broadly curved; area of fine, dense punctation quite extensive, occupying over ½ wing length, its proximal boundary marked by a sudden change in the size of the punctuation; a rounded strigil indicated by a depression in costal area, with coarse punctuation; hind margin of clavus with six regularly spaced swellings (sensu Lambkin, 2015: fig. 8).

Discussion

The new fossil is considered to be a forewing of a cicadomorphan (Hemiptera) because of the tegminisation of the anterior part of the wing and the general pattern of venation. The wing venation and sculpture are indicative of a few Permo–Triassic families. In fact, the 'base of RP far distad the bases of MP and CuA', the 'basal to sub-basal fusion of ScP with R', and the forewing densely punctured on its all surface are characters present in taxa of few Permian and/or Triassic families, viz. Saaloscytinidae Brauckmann, Martins-Neto & Gallego, 2006, Maguviopseidae Shcherbakov, 2011, and Dysmorphoptilidae Handlirsch, 1906.

Tennentsia koreana n. sp. is included in Dysmorphoptilidae because of its proximally convex costal margin, a strigil, and a wide costal space. The new fossil differs from Manguviopseidae and Saalosctyinidae because of the size of its costal space, wider or narrow respectively (Brauckmann & Schlüter 1993; Shcherbakov 2011; Fu & Huang 2022).

Following the key to dysmorphoptilid subfamilies of Szwedo & Huang (2019), the new fossil belongs to the Dysmorphoptilinae because of the following characters: apical portion of tegmen abruptly narrowed; veins RA and RP not fused distally; apical veinlet ra-rp (ra2-rp) present; RP simple.

This subfamily currently comprises the genera *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; and *Trifidella* Evans, 1956 (Szwedo & Huang 2019).

The distal emargination of costal margin is situated at the apex of RA1 in *Mesocixius* and *Triassocixius*, vs. much more basally in *Tennentsia koreana* n. sp. (Lambkin 2015). The genus *Carsburgia* is characterized by a very weak costal emargination while the new fossil

has a strong emargination, precluding affinities with the latter genus (Lambkin 2015). The *Dysmorphoptiloides* spp. have a well-developed apical lobe with a costal emargination basad RA1 as in the new fossil but they also possess a pronounced emargination at the apex of CuA, which is absent in the new fossil (Lambkin 2015; Lara et al. 2021). They also differ from the new fossil owing to the presence of a strongly angled RA2 with a long oblique crossvein ra2-rp between RA2 and RP, vs. a straight RA2 and a short ra2-rp perpendicular to RA2 and RP (Lambkin 2015: figure 14). The *Dysmorphoptila* spp. also have a well-developed apical lobe with a costal emargination basad RA1, but RA1 is much shorter than in the new fossil (Brodie 1845, plate 10, figure 13; Giebel 1856; Handlirsch 1906–1908; Shcherbakov 1988). *Stigmocercopis* has only a weak costal emargination, RA2 simple (Lin 1986, plate 18, figure 1). *Triassocixius* strongly differs from the new fossil in the presence of a very long RA1 with a series of numerous anterior branches and an emargination much distad the base of RA1 (Tillyard 1919, text-figure 12; Lambkin 2015: figure 9). *Trifidella* has a weak costal emargination while the emargination is clearly present in *Tennentsia koreana* n. sp. (Evans 1956, figure 16C; Lambkin 2016, figure 13). *Mesoatracis* is based on the distal third of a forewing, hardly comparable with the other genera (Becker-Migdisova 1949). Note that the forewing venation as interpreted in the original description of the genus *Mesoatracis* is likely incorrect. The vein M figured in Becker-Migdisova (1949) is the RP, and the CuA a combination of MA and MP. We consider that the emargination present on the forewing of *Mesoatracis* is comparatively much more reduced than the one of *Tennentsia*. Additionally, the RP (M in Becker-Migdisova, 1949, figure 31) is distinctly bent toward anterior margin of forewing (vs. straight in the new fossil described herein), the MP (posterior branch of CuA in Becker-Migdisova, 1949, figure 31) is simple (vs. forked). Otherwise, the preserved parts of

the other veins and shape of distal part of wing resemble those of the new fossil (Becker-Migdisova, 1949, figure 31).

The new fossil has all the diagnostic characters of *Tennentsia*, viz. Tegmen over 16 mm long; emarginate at apices of RA, with a well-developed apical lobe; precostal carina and marginal membrane quite distinct; punctation quite coarse basally, much finer and much more dense apically, the size and density differential much greater than in the other genera; primary fork of R at level or about clavus mid-length; stem of RA with one or two costal veinlets which are sometimes forked; primary fork of RA proximal to apex of clavus; RA1 with two or three branches; RA2 with primary branches strongly curved anteriad; RA2 and RP joined by a crossvein; RP simple; M with four branches; basal part of CuA very short [considered as a crossvein 'a' in Lambkin (2015)].

In particular, *Tennentsia koreana* n. sp. possesses one of two putative synapomorphies of the genus as proposed by Lambkin (2015), viz. a peculiar differential punctation between basal and distal halves of the forewing. However, its RA2 has only two well-defined branches, instead of at least three in the other species. This difference alone is likely indicative of a new species or can be treated as intraspecific variability.

The other differences with the diagnosis proposed by Lambkin (2015) are as follows: tegmen not or only slightly emarginate at CuA, while it is strongly emarginate in the other species except in *Tennentsia princeps*; branches of RA2 not curved anteriorly; strigil in basal costal space with coarse punctuation, instead of very fine rugae (Riek 1976; Lambkin 2015; Fu et al. 2021).

These differences do not warrant the placement of this specimen in another genus and are rather indicative of a distinct species. Additionally, this genus is already known from

China, and not only from the Southern Gondwana land mass, suggesting a relatively broad distribution of *Tennentsia* as found in several extant or extinct genera.

Conclusion

Tennentsia koreana **n. sp.** confirms the broad distribution of the genus during the Triassic (known in South Africa, China, South Korea, and Australia). The absence of *Tennentsia* species after the Triassic is rather surprising as the family Dysmorphoptilinae survived during the Early-Middle Jurassic with *Dysmorphoptila liasina* (Giebel, 1856), *Dysmorphoptila notodon* Shcherbakov, 1988, *Mesoatracis reducta* Becker-Migdisova, 1949, and *Stigmocercopis parvis* Lin, 1986. The fossil record may indicate that the genus dies out around the Triassic-Jurassic boundary (end-Triassic extinction).

Acknowledgment

We are grateful to the editor, and the two anonymous reviewers for their valuable comments on this manuscript. This work is part of the Ph.D. project of CJ.

Disclosure statement

The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure captions

Figure 1. *Tennentsia koreana* **n. sp.**, holotype GNUE112006. Photographs of tegmen. **A**, part. **B**, counterpart. Scale bars = 2 mm.

Figure 2. *Tennentsia koreana* **n. sp.**, holotype GNUE112006. Reconstruction of tegmen. Scale bar = 2 mm.