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A new genus of Mesopsychidae from the late Middle Triassic Tongchuan entomofauna and its taxonomic and palaeogeographic implications

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Abstract

Mesopsychids, a long-proboscid mecopteran group, are presumably associated with the pollination of Mesozoic gymnosperms. Despite over 100 years of study on the genus *Mesopsyche*, only isolated wings have been discovered. *Mesopsyche* is now redefined as a monotypic genus with only one species, *Mesopsyche triareolata*. The other species previously classified within *Mesopsyche* have been assigned to the newly established genus *Turbidapsyche* Lian & Huang, **gen. nov.**, distinguished by its Sc with two anterior branches, in contrast to Sc with more than three anterior branches in *Mesopsyche*. Herein, we present descriptions and illustrations of new material from the middle part (late Ladinian) of the Middle–Upper Triassic Yanchang Formation. We assigned these specimens to the newly erected genus, *Turbidapsyche* Lian & Huang, **gen. nov.** *Turbidapsyche tongchuanensis* (Hong, 2007) **comb. nov.**, the first reported *Turbidapsyche* (*Mesopsyche*) from the Tongchuan entomofauna, is revised based on a new specimen. Additionally, we erect three new species of *Turbidapsyche* Lian & Huang, **gen. nov.** based on their wing size, shape, and especially the coloured patterns. *Turbidapsyche orientalis* Lian & Huang, **gen. et sp. nov.** is characterised by the distinctly shrunken wing base and dense coloured markings along anterior wing. *Turbidapsyche sparsanota* Lian & Huang, **gen. et sp. nov.** is distinguished by its relatively larger wing size and sparse coloured spots situated at the forks, crossveins, and apical longitudinal veins. *Turbidapsyche hongii* Lian & Huang, **gen. et sp. nov.** is characterised by a relatively small wing size and sparser striped coloured markings. Although hindwings of *Turbidapsyche* Lian & Huang, **gen. nov.** are described and illustrated, they are not assigned to any species. Species of both *Mesopsyche* and *Turbidapsyche* are discussed in detail. The wing coloured patterns of *Turbidapsyche* exhibit

regional differentiation, with numerous coloured spots or spots fused into striped coloured markings observed in China, transparency in Kyrgyzstan, and full pigmentation in Ukraine. Based on previous palaeomagnetic research conducted in Tongchuan area, we derive a palaeolatitude of 21° in the Middle Triassic. *Turbidapsyche* was distributed along the northern Palaeotethys, near a similar palaeolatitude, suggesting it inhabited comparable climates and perhaps had specific ecological requirements or limited dispersal capabilities.

Keywords: Mesopsychidae, Tongchuan biota, Ordos Basin, Palaeolatitude

Introduction

Mesopsychidae Tillyard, 1917, an enigmatic mecopteran family, have long intrigued researchers due to its enigmatic nature. Characterised by an elongated siphonate proboscis, Mesopsychidae are hypothesised to have played a role in the pollination of Mesozoic gymnosperms (Labandeira *et al.*, 2007; Ren *et al.*, 2009; Labandeira, 2010). This distinctive proboscis has garnered significant attention for its potential association with pollination and its close evolutionary relationship with fleas (Huang *et al.*, 2012; Tihelka *et al.*, 2020). The extinction of these peculiar mecopterans is possibly linked to the transition from gymnosperms to angiosperms, a significant event in the evolutionary history of insects and plants (Dilcher, 2000; Lloyd *et al.*, 2008; Benton *et al.*, 2022).

The genus *Mesopsyche* Tillyard, 1917 (Mesopsychidae Tillyard, 1917) was established based on an incomplete hindwing of the Upper Triassic Blackstone Formation of Australia. The original reconstruction of *Mesopsyche triareolata* Tillyard, 1917 depicted it with an anal loop and Sc with only two anterior branches (Tillyard, 1917: Text). Initially placed within the order Trichoptera, further examination revealed that *Mesopsyche* possessed separated anal veins rather than a tangling anal loop. Therefore, Tillyard (1919) established a new order, Paratrichoptera, to accommodate it. Riek (1956) suggested that Mesopsychidae should be a mecopteran family, as they share no distinction with Mecoptera, apart from the arrangement of costal veinlets. Additionally, Riek (1956) suggested that three other species previously described from the Upper Triassic Blackstone Formation of Queensland, Australia—*Triassopsyche dunstani* Tillyard, 1917 (forewing), *Aristopsyche superba* Tillyard, 1919 (forewing), and *Neuropsyche elongata* Tillyard, 1919 (hindwing)—should be considered synonymous with *M. triareolata*.

Based on Lambkin's re-examination and new illustrations of the former and his recently described material of *Mesopsyche* (Lambkin, 2014), we notice that *M. triareolata* is noteworthy in presenting a series of costal veinlets (at least three). Conversely, the species subsequently placed in the genus—from China, Korean, Kyrgyzstan, Russia, and Ukraine—typically exhibit only two costal veinlets (with rare instances of a simple veinlets observed). In light of this observed disparity, we propose the establishment of a new genus, *Turbidapsyche* Lian & Huang, **gen. nov.**, to accommodate these subsequently established species. Consequently, *Mesopsyche* would represent a monotypic genus encompassing only *M. triareolata*.

The Middle-Late Triassic Tongchuan entomofauna is regarded as a window into the evolutionary history of insects during the Triassic period. To date, numerous insect orders have been unearthed from this entomofauna, including Blattodea, Coleoptera, Diptera, Glosselytroidea, Grylloblattodea, Hemiptera, Mecoptera, Miomoptera, Odonatoptera, and Orthoptera (Li *et al.*, 2007; Hong, 2009; Zheng *et al.*, 2017, 2018; Xu *et al.*, 2020; Fu *et al.*, 2021; Lian *et al.*, 2021; Zhang *et al.*, 2022). The late Prof. Youchong Hong was a pioneering figure in the excavation and study of this entomofauna, dedicating over 30 years to its study (Hong, 1980, 2009; Hong & Li, 2012). Nevertheless, the original papers often contain outdated and low-quality photographs and drawings, which have posed challenges for subsequent researchers in comprehensively understanding the entirety of the Tongchuan entomofauna.

During the past years, we have discovered a wealth of new material from the Tongchuan entomofauna. Herein,

we leverage this new material to present descriptions and illustrations of one revised species and three new species belonging to the newly established genus *Turbidapsyche* **gen. nov.**

Material and methods

The specimens were preserved in the green-yellowish mudstone of the lower part of the Yanchang Formation, at a locality in the vicinity of Jinsuoguan Township, Tongchuan City, Ordos Basin, Shaanxi Province (for a detailed locality map, see Lian *et al.*, 2023: fig. 1). Yanchang Formation is stratified into 10 members (Ch 1–Ch 10) from top to bottom based on oil layers. The organic-rich shale Chang 7 member, from where the material are collected, comprises predominantly black shale and oil shale interbedded with fine sandstone and siltstone (He *et al.*, 2004). Precise Zircon U-Pb dating of the Chang 7 member's thin-layered tuff yielded ages of 241.06 ± 0.12 Ma at the top and 241.558 ± 0.093 Ma at the bottom (Zhu *et al.*, 2019), indicating a Ladinian age.

Photographs were captured utilising a digital camera attached to a Zeiss Discovery V20 microscope, and some specimens were moistened with 75% ethanol to enhance the contrast. The step is particularly important as many wings present colouration patterns and a coloured pterostigma. Line drawings were made using Adobe Illustrator 2019 graphic software. The specimens are housed in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China.

The terminology of the mecopteran venation is based on the nomenclature of Minet *et al.* (2010) and Bashkuev & Sukatsheva (2021).

Systematic palaeontology

Order Mecoptera Packard, 1886

Family Mesopsychidae Tillyard, 1917

Genus *Turbidapsyche* Lian & Huang, **gen. nov.**

Type species. *T. dobrokhotovae* (Novokshonov, 1997) **comb. nov.**

Included species. *T. shcherbakovi* (Novokshonov, 1997) **comb. nov.**, *T. justa* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. ordinata* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. tortiva* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. gentica* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. tongchuanensis* (Hong, 2007) **comb. nov.**, *T. incompleta* (Bashkuev, 2011) **comb. nov.**, *T. jinsuoguanensis* (Lian, Cai &

Huang, 2021) **comb. nov.**, *T. liaoi* (Lian, Cai & Huang, 2021) **comb. nov.**, *T. orientalis* Lian & Huang, **sp. nov.**, *T. sparsanota* Lian & Huang, **sp. nov.**, and *T. hongii* Lian & Huang, **sp. nov.**

Etymology. The generic name combines the Latin “*turbida*”, confused, indicating the classification of this genus is confused, and the Greek generic name “*psyche*”, soul. Gender feminine.

Diagnosis. Forewing with pterostigma distinct, generally adorned with coloured markings, costal area is broader than subcostal area, Sc with two anterior veinlets (in rare cases, one), Rs and M both have four branches, Rs_{1+2} fork and Rs_{3+4} fork nearly at same level, CuA base and crossvein cua-cup present, crossveins sparse and consistently found in specific regions. Hindwings with Sc short, terminating near wing mid-length, a crossvein connected apical Sc and R_1 ; R_1 simple or apically forked into two branches, Rs and M each with two branches.

Comparison. The new genus can be distinguished from *Mesopsyche* by having Sc with only two anterior veinlets; it differs from *Permopsyche* by the larger size of its wings, broader costal area, and CuA base inclined backward instead of being oblique to transverse.

***Turbidapsyche tongchuanensis* (Hong, 2007) comb. nov.**

(Fig. 1)

Itaphlebia tongchuanensis Hong, 2007, late Middle Triassic, Tongchuan City, China.

Mesopsyche tongchuanensis (Hong, 2007) Bashkuev, 2011

Material. NIGP204959a, b, part and counterpart, a nearly complete forewing, 12.4 mm long (preserved), 5.8 mm wide, with the lower part of the wing base not preserved.

Type Locality and horizon. Tongchuan City, Shaanxi Province; middle part of Middle–Upper Triassic Yanchang Formation (Ladinian).

Emended diagnosis. Forewing more than 10 mm long, with more than five coloured stripes, coloured markings dense at costal and subcostal areas, length of apical costal area (L1) twice as long as length of middle costal area (L2), Sc terminating at level of Rs_{1+2} fork.

Type locality and horizon. A locality near Jinsuoguan Township, Tongchuan City, Shaanxi Province, northwestern China; middle part of Middle–Upper Triassic Yanchang Formation (Ladinian).

Description (new material). Wing with five stripes of coloured markings, with an unpigmented spot located apically between longitudinal veins; first stripe along basal wing margin; second and third stripe below pterostigma, fourth stripe along apical wing margin, stripes separated by unpigmented spots or stripes; Sc long, with three branches, terminating at level of Rs_{1+2} fork; length from Sc_1 end to rise of Sc_2 (Fig. 1, L1) $2.3 \times$ longer than length

from rise of Sc_2 to rise of Sc_3 (L2); one backward-inclined crossvein connect Sc_1 middle and R_1 ; R_1 simple, relatively straight; pterostigma distinct, with deeper coloured marking, and one small unpigmented patch along upper margin; Rs_{1+2} fork and Rs_{3+4} fork nearly at same level, Rs_{1+2} stem much shorter than Rs_1 and Rs_2 branches; M_{1+2} stem more than twice as long as M_{3+4} stem, crossvein m-cua located near M_4 base and CuA; fork of Rs at same level as fork of M; CuA missing apical part, fused with M stem near wing base; crossvein cua-cup somewhat oblique; one crossvein presented between R_1 and apical part of Rs_{1+2} stem, Rs_2 and Rs_3 , Rs_4 and M_1 , Rs_{3+4} stem and M_{1+2} stem, and M_2 and M_3 , respectively.

Remarks. The assignment of specimen NIGP204959 to *T. tongchuanensis* **comb. nov.** is mainly based on the colouration pattern of the wing membrane and the size of wing. *T. tongchuanensis* **comb. nov.** can be differentiated from *T. dobrokhotovae* (Novokshonov, 1997) **comb. nov.** by several characters: wing smaller (length about 14 mm vs. 30 mm), fewer coloured markings and more hyaline areas, and Rs_{1+2} stem and Rs_{3+4} stem much shorter rather than longer than its branches Rs_1 , Rs_2 , Rs_3 , and Rs_4 ; it also differs from *T. jinsuoguanensis* **comb. nov.** and *T. liaoi* **comb. nov.** by larger wing size, coloured markings fused in stripes, more pigmentation at costal and subcostal areas, and Rs fork and M fork at same level instead of Rs fork being located distad M fork.

***Turbidapsyche orientalis* Lian & Huang, sp. nov.**

(Fig. 2)

Material. Holotype, NIGP204960, a complete forewing, 7.7 mm long, 3.5 mm wide.

Etymology. The species name is derived from the Latin word “*orientalis*”, meaning eastern. Gender feminine.

Diagnosis. Forewing with wing base notably shrunken, with dense coloured markings at anterior wing, length of apical costal area (L1) $3.6 \times$ as long as length of middle costal area (L2), space between CuP and A_1 narrow.

Type locality and horizon. A locality near Jinsuoguan Township, Tongchuan City, Shaanxi Province, northwestern China; middle part of Middle–Upper Triassic Yanchang Formation (Ladinian).

Description. Forewing with apex broad and rounded, tapering from wing mid-length to base; one elongate coloured spot present at apex of each longitudinal vein, crossveins generally accompanied with a larger rounded spot; anterior half of wing densely covered with coloured markings, with two lines of unpigmented rounded spots; costal area moderately broad, Sc with two anterior veinlets, Sc_1 long and terminating distad Rs_{1+2} fork, Sc_2 short and oblique, Sc_3 short and transverse; humeral vein present; R_1 simple, straight, one transverse crossvein connected

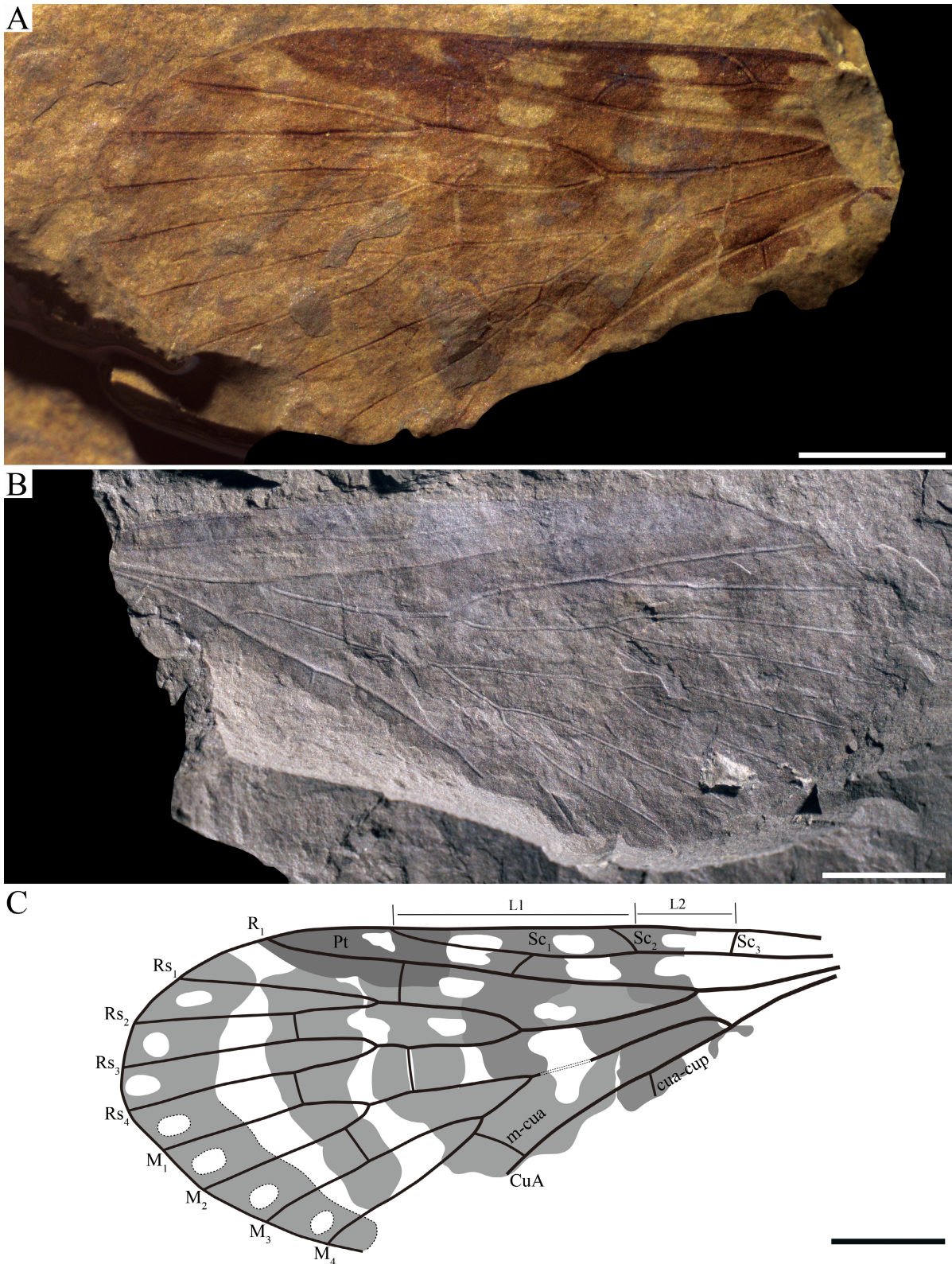


FIGURE 1. *Turbidapsyche tongchuanensis* (Hong, 2007) **comb. nov.**, paratype, NIGP204959, with part and counterpart. **A**, NIGP204959a, photograph was captured under vertical reflected light after being moistened with 75% alcohol. **B**, NIGP204959b, photograph was captured under lateral reflected light. **C**, Line drawing of wing. Scale bars = 1 mm.

Sc₁ and R₁; pterostigmal area with unregular coloured marking; Rs₁₊₂ fork slightly distad Rs₃₊₄ fork; M₁₊₂ stem more than twice as long as M₃₊₄ stem, apical part of M stem

desclerotised; crossvein m-cua located near M₃₊₄ fork; CuA sharply bent at connection of m-cua, CuP simple and apically curved, CuA base proximad M + CuA fork, CuA

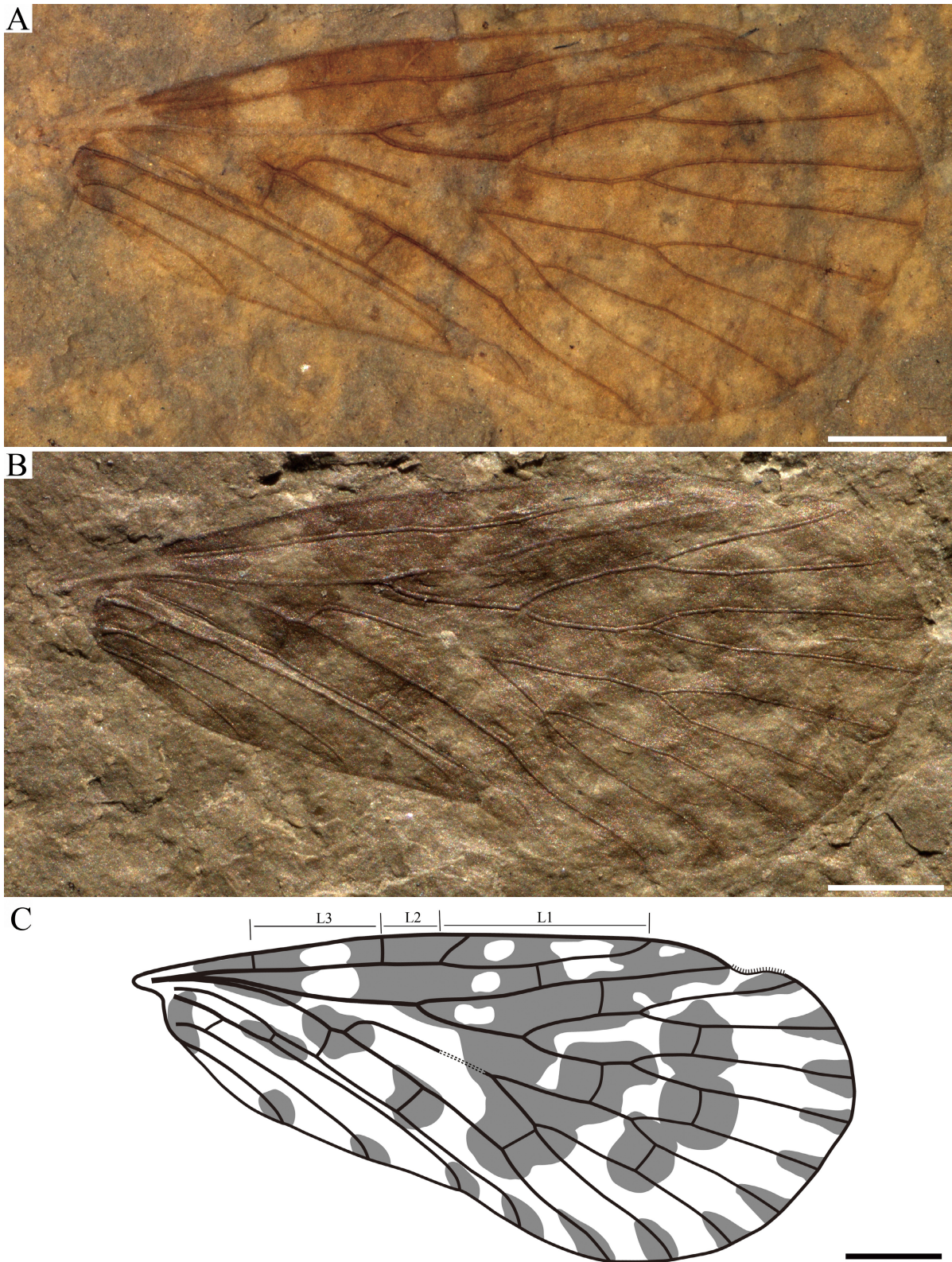


FIGURE 2. *Turbidapsyche orientalis* Lian & Huang, **sp. nov.**, holotype, NIGP204960. **A**, Photograph was captured under vertical reflected light after being moistened with 75% alcohol. **B**, Photograph was captured under lateral reflected light. **C**, Line drawing of wing. Scale bars = 1 mm.

base somewhat transverse and crossvein cua-cup inclined slightly forward; three anal veins present, space between CuP and A_1 narrow, one crossvein presented between CuP

and A_1 , A_1 and A_2 near wing base; one crossvein presented between R_1 and Rs_{1+2} stem, Rs_2 and Rs_3 , Rs_4 and M_1 , Rs_{3+4} stem and M_{1+2} stem, and M_2 and M_3 , respectively.

Remarks. The new species, *Turbidapsyche orientalis* Lian & Huang, **sp. nov.**, is characterised by its distinctly shrunken wing base, which sets it apart from most of its congeners. This character resembles that of *T. justa* from the Middle–Upper Jurassic Madygen Formation of Kyrgyzstan. However, it differs from the latter by 1) Sc with two anterior branches instead of one; 2) forks of Rs_{1+2} and Rs_{3+4} nearly at the same level instead of Rs_{1+2} fork distad Rs_{3+4} fork; 3) Rs and M each with four branches instead of more than four; and 4) the area between CuP and A_1 is very narrow. Additionally, the colouration patterns of *T. orientalis* Lian & Huang, **sp. nov.** differ from those of other *Turbidapsyche* species because of the pigmented costal and subcostal areas that are fused together, with some transparent spots lining up.

***Turbidapsyche sparsanota* Lian & Huang, sp. nov.**
(Figs 3–5)

Material. Holotype, NIGP204961a, b, with part and

counterpart, a complete forewing, 10.2 mm long, 3.7 mm wide. Paratypes: NIGP204962, a complete and relatively large forewing, 12.9 mm long, 5.6 mm wide; NIGP204963a, b, with part and counterpart, a forewing missing a small part of wing base, 11.2 mm long, 4.5 mm wide; NIGP204964, a forewing missing a small part of wing base, 9.9 mm long, 4.0 mm wide; NIGP204965a, b, with part and counterpart, a forewing preserving apical part of wing.

Etymology. The specific epithet derives from the Latin “*sparsa*”, meaning sparse, “*nota*”, meaning mark, meaning that the coloured spots are distributed sparsely. Gender feminine.

Diagnosis. Forewing covered with relatively small and sparse coloured markings, Sc_2 , Sc_3 and humeral vein nearly evenly dividing costal area (L1, L2, and L3 nearly equal).

Type locality and horizon. A locality near Jinsuoguan Township, Tongchuan City, Shaanxi Province, northwestern China; middle part of Middle–Upper Triassic Yanchang Formation (Ladinian).

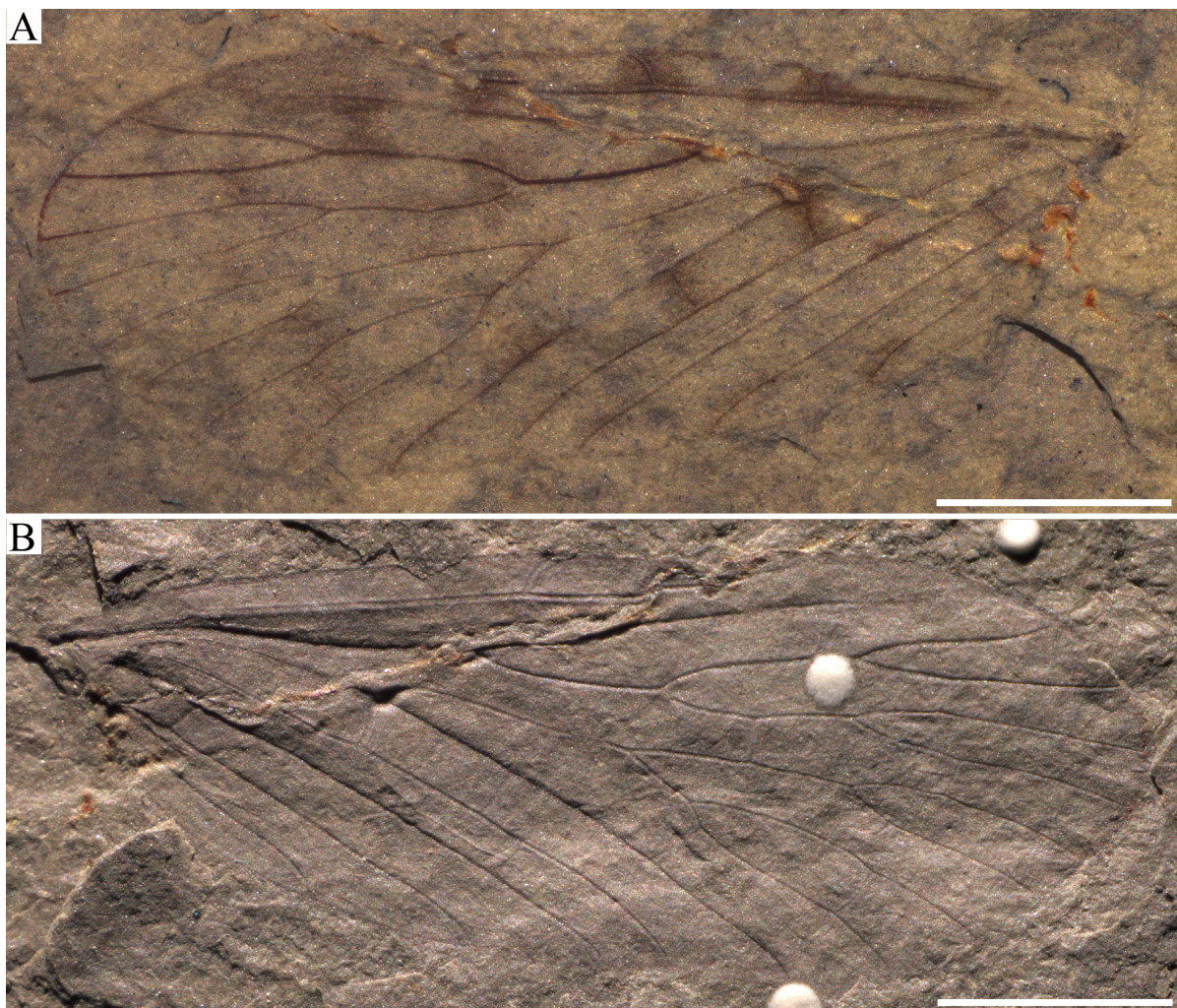


FIGURE 3. *Turbidapsyche sparsanota* Lian & Huang, **sp. nov.**, holotype, NIGP204961, part and counterpart. **A**, Photograph was captured under vertical reflected light after being moistened with 75% alcohol. **B**, Photograph was captured under lateral reflected light. Scale bars = 2 mm.

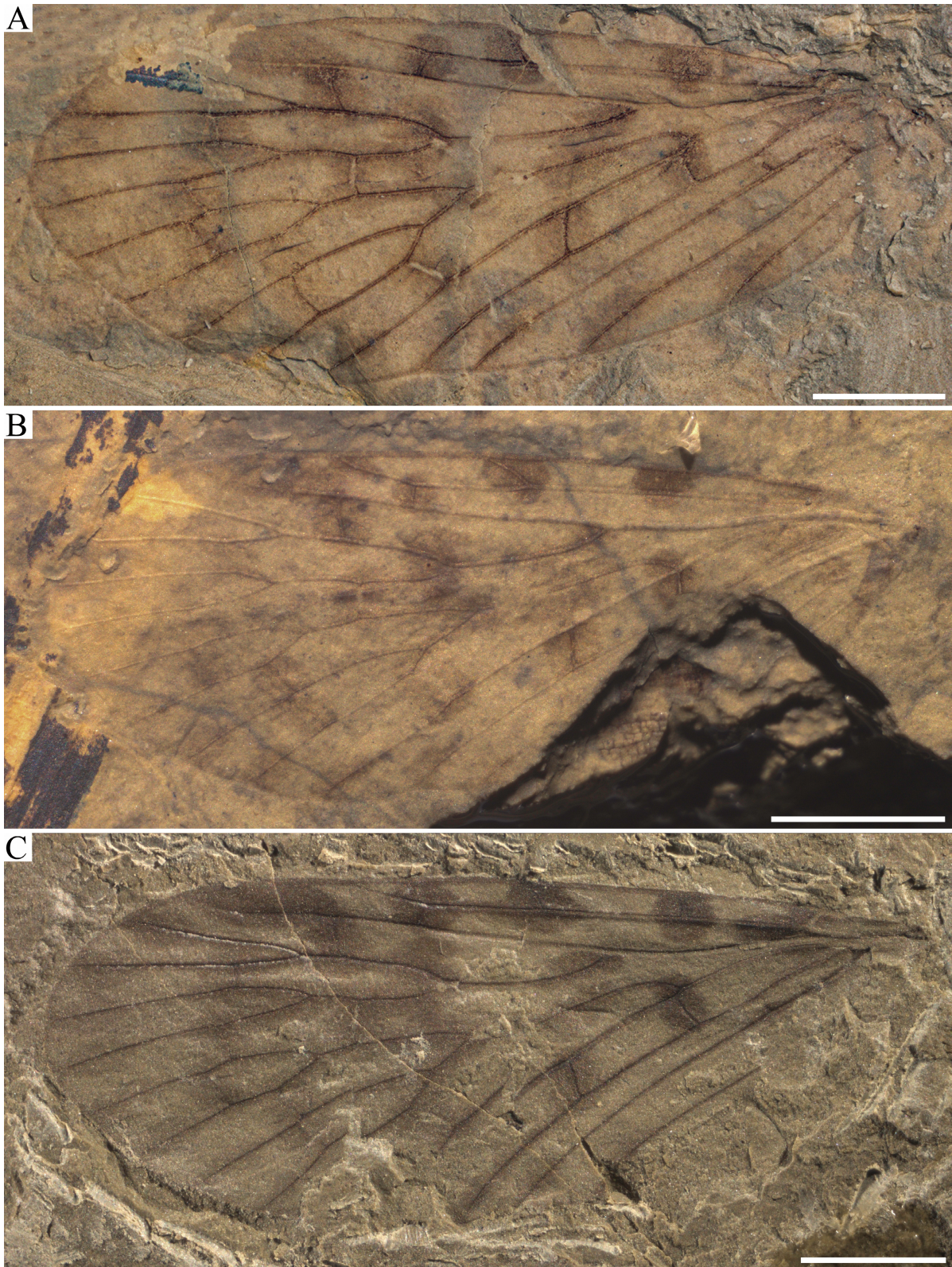


FIGURE 4. *Turbidapsyche sparsanota* Lian & Huang, **sp. nov.**, paratypes. **A**, NIGP204962. **B**, NIGP204963a. Photographs of **A** and **B** were captured when moistened with 75% alcohol under vertical reflected light. **C**, NIGP204964, photograph was captured under lateral reflected light. Scale bars = 2 mm.

Description. Holotype, NIGP204961, a forewing covered with numerous rounded and relatively small coloured spots, situated at apex of longitudinal veins, forks, and crossveins; costal space relatively broad, Sc with

two anterior veinlets, terminating proximad Rs_{1+2} fork, Sc_1 long, Sc_2 and Sc_3 short, Sc_2 oblique, Sc_3 transverse; humeral vein present; length of Sc_1 end to rise of Sc_2 (L1), length of rise of Sc_2 to rise of Sc_3 (L2), and rise of Sc_3 to

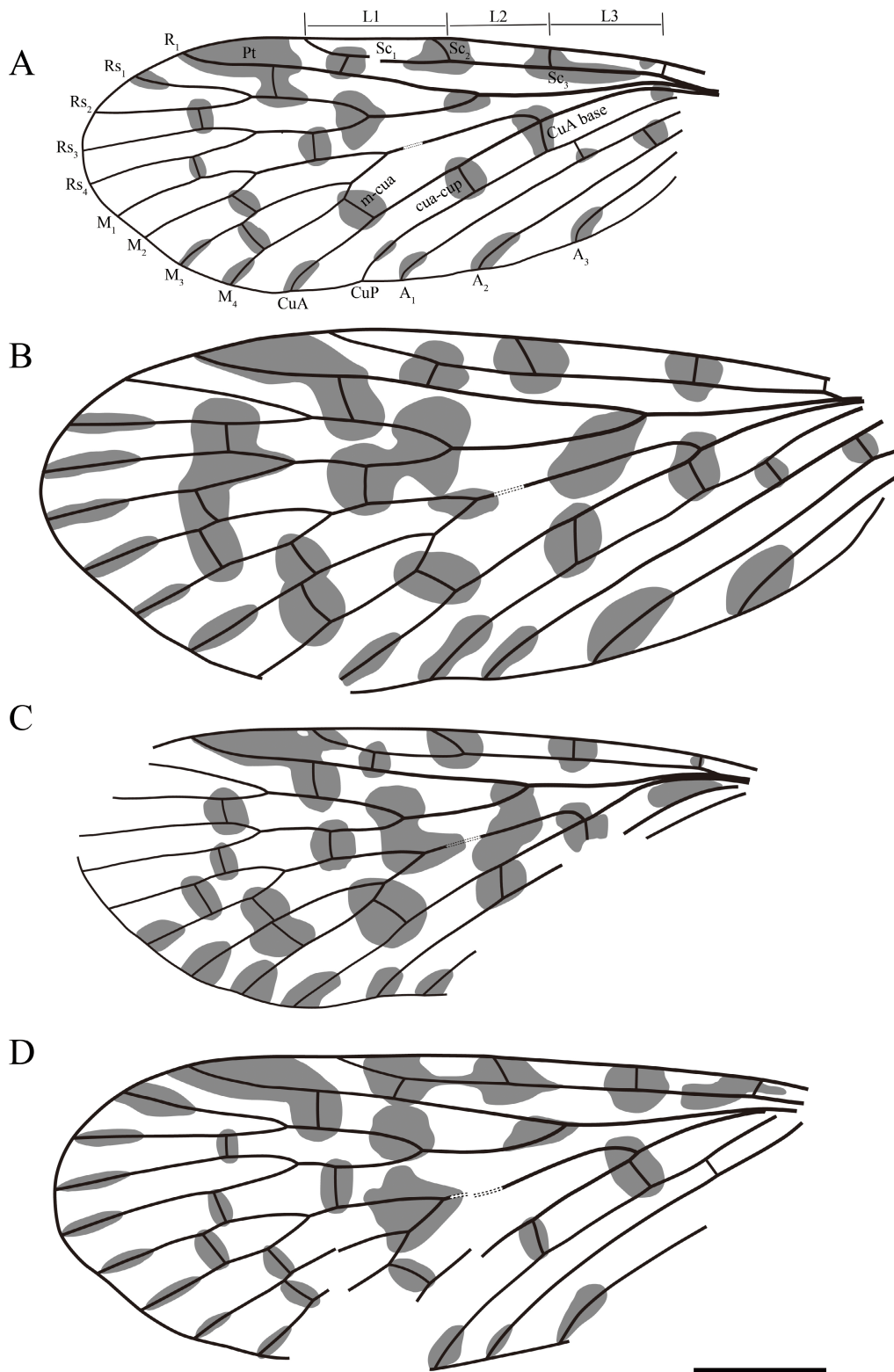


FIGURE 5. Line drawings of *Turbidapsyche sparsanota* Lian & Huang, **sp. nov.** **A**, NIGP204961 (holotype). **B**, NIGP204962. **C**, NIGP204963. **D**, NIGP204964. Scale bars = 2 mm.

humeral vein (L3) are nearly equal; R_1 curved near apex, one oblique crossvein connected R_1 and Sc_1 ; pterostigma pigmented, fused with its lower coloured spot; Rs four branched, Rs_{1+2} fork at same level as Rs_{3+4} fork, Rs_{1+2} stem

as long as Rs_1 but shorter than Rs_2 , Rs_{3+4} stem shorter than Rs_3 or Rs_4 ; M four branched, M_{1+2} stem nearly three times as long as M_{3+4} , apical part of M stem desclerotised; $m-cua$ located close to M_4 base; CuA straight, slightly curved

near apex, CuP straight, apical part curved; crossvein cua-cup transverse, CuA base inclined backward, aligned with M + CuA fork; three straight anal veins present; one crossvein presented between Rs_{1+2} and R_1 , Rs_2 and Rs_3 , Rs_{3+4} stem and M_{1+2} stem, Rs_4 and M_1 , M_2 and M_3 , M_3 and M_4 , CuP and A_1 , and A_1 and A_2 , respectively.

Paratypes. NIGP204962, wing venation overall similar to that of the holotype. One large, coloured spot at end of A_2 and A_3 ; Rs_{1+2} stem and Rs_{3+4} stem distinctly shorter than their branches, Rs_{1+2} fork slightly proximad Rs_{3+4} fork; one crossvein present between M_1 and M_2 ; crossvein cua-cup inclined backward, CuA base transverse and distad fusion of M and CuA. NIGP204963, wing venation overall similar to that of the holotype. Rs_{1+2} stem and Rs_{3+4} stem distinctly shorter than their branches, Rs_{1+2} fork distad Rs_{3+4} fork; M_3 , M_4 , and CuA broken, one crossvein connected M_1 and M_2 ; crossvein cua-cup inclined backward, CuA base transverse and distad M + CuA fork. NIGP204964, wing venation overall similar to that of the holotype. One large coloured spot presented at end of each longitudinal vein, one straight crossvein connected Sc_1 and R_1 , Rs_{1+2} fork slightly distad Rs_{3+4} fork, a crossvein connected M_1 and M_2 , crossvein cua-cup and CuA base inclined backward, CuA base slightly distad M + CuA fork.

Remarks. The new species, *Turbidapsyche sparsanota* Lian & Huang, **sp. nov.**, shares with *T. jinsuoguanensis* (Lian, Cai & Huang, 2021) **comb. nov.** and *T. liaoi* (Lian, Cai & Huang, 2021) **comb. nov.** which originate from the same layer, a similar colouration pattern. However, it differs from the latter two by having larger wings and sparser and smaller coloured spots; it differs from *T. dobrokhotovae* (Novokshonov, 1997) **comb. nov.** by its smaller wing size (length less than 13 mm vs. 30 mm), and the presence of sparse coloured spots instead of the wing being nearly fully covered with coloured markings.

Turbidapsyche hongii Lian & Huang, **sp. nov.**

(Fig. 6)

Material. Holotype, NIGP204966, a forewing missing posterior part of wing base, 7.8 mm long, 3.5 mm wide; paratype, NIGP204967, a forewing missing wing base, 6.9 mm long (as preserved), 3.7 mm wide.

Etymology. The species name, “*hongii*”, is dedicated to the late palaeontologist Prof. Youchong Hong for his contribution to the Tongchuan entomofauna.

Diagnosis. Forewing relatively small, with six or seven vertical coloured stripes, length of apical part of costal area (L1) about twice as long as length of middle part of costal area (L2).

Type locality and horizon. A locality near Jinsuoguan Township, Tongchuan City, Shaanxi Province,

northwestern China; middle part of Middle–Upper Triassic Yanchang Formation (Ladinian).

Description. Holotype, NIGP204966, a forewing covered with striped coloured markings, apical stripe along wing apex with an oval transparent spot between apex of each longitudinal vein; Sc with two anterior veinlets, terminating distad Rs_{1+2} fork, one crossvein connected Sc_1 and R_1 ; R_1 straight, somewhat curved near apex; pterostigma pigmented, fused with its under coloured markings, with one transparent spot at upper part; Rs branches much longer than its stem, Rs_{1+2} and Rs_{3+4} almost forking at the same level, one crossvein presented between Rs_2 and Rs_3 ; two crossveins presented between Rs and M ; M_{1+2} stem $2.5 \times$ as long as M_{3+4} stem, distal part of M stem desclerotised; one crossvein presented between M_2 and M_3 , M_3 and M_4 , respectively, crossvein m-cua aligned with M_{3+4} fork; Rs fork slight distad M fork; CuA straight, CuA base inclined slightly backward and aligned with M + CuA fork, CuP straight, crossvein cua-cup inclined slightly forward; only one anal vein present, the other anal veins likely missing.

Paratype, NIGP204967, length of apical part of costal area $1.7 \times$ as long as the length of middle part of costal area; M_{1+2} stem about $4 \times$ as long as M_{3+4} stem; crossvein m-cua connected M_4 base, Rs fork distinctly distad M fork; CuA base and crossvein cua-cup inclined slightly backward.

Remarks. The new species, *Turbidapsyche hongii* Lian & Huang, **sp. nov.**, shares with *T. tongchuanensis* (Hong, 2009) **comb. nov.** similar colouration patterns, but it differs from the latter by its smaller wing (length 7.8 mm vs. >12.4 mm), coloured stripes less sparse, more hyaline areas, and sparser coloured markings along the costal and subcostal area.

Turbidapsyche sp.

(Fig. 7)

Material. NIGP204968a, b, part and counterpart, a complete hindwing, 7.5 mm long, 3.3 mm wide; NIGP204969, a fragment of hindwing with base and part of apex not preserved, 6.4 mm (as preserved) long, 2.9 mm wide.

Description. Small hindwing, apical margin blunt; coloured markings presented in (roughly) second half of wing, along crossveins, and forming an intricate pattern with few hyaline spots; Sc short, terminating slightly distad Rs fork (near wing mid-length), sharply bent upward apically, one crossvein present between Sc distal-most part and R_1 ; R_1 straight, with a apical fork; pterostigma small, lentoid, located at the R_1 fork; Rs four branched, Rs_{1+2} stem $1.5 \times$ as long as Rs_{3+4} stem; M four branched, M_{1+2} stem more than twice as long as M_{3+4} stem,

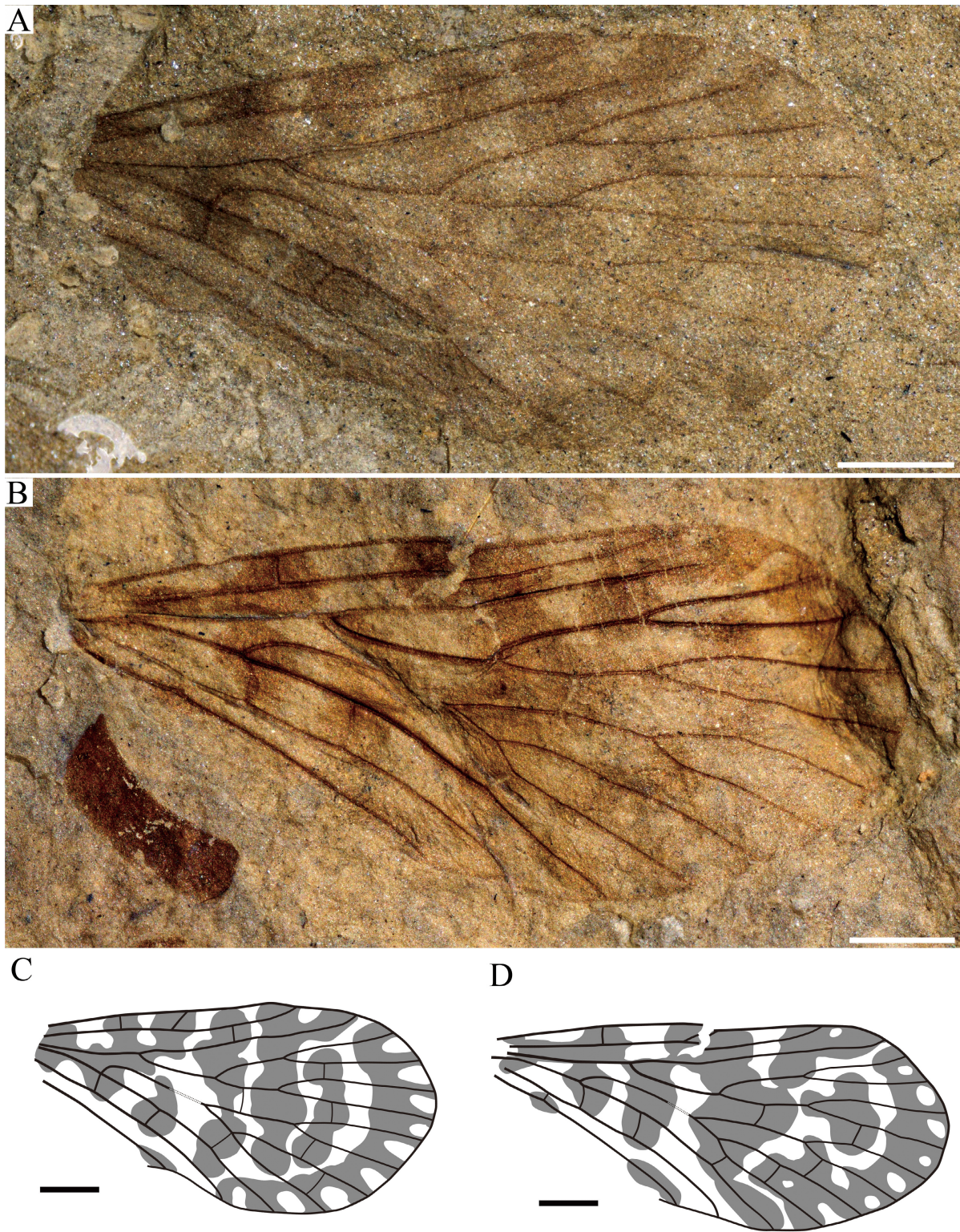


FIGURE 6. *Turbidapsyche hongii* Lian & Huang, **sp. nov.** **A**, Holotype, NIGP204966. **B**, Paratype, NIGP204967. **C**, Line drawing of NIGP204966. **D**, Line drawing of NIGP204967. Photographs of A and B were captured under vertical reflected light after being moistened with 75% alcohol. Scale bars = 1 mm.

crossvein m-cua connected M_{3+4} fork and CuA; CuA straight, fused with M near wing base; CuP simple and straight, fused with A_1 near wing base; three anal veins present; a crossvein presented between R_1 and Rs_{1+2} stem,

Rs_2 and Rs_3 , Rs_4 and M_1 , M_2 and M_3 , basal Rs and M + CuA stem, basal A_1 and A_2 , respectively.

Remarks. Hindwings of congeneric mecopterans typically exhibit very similar venation schemes, making

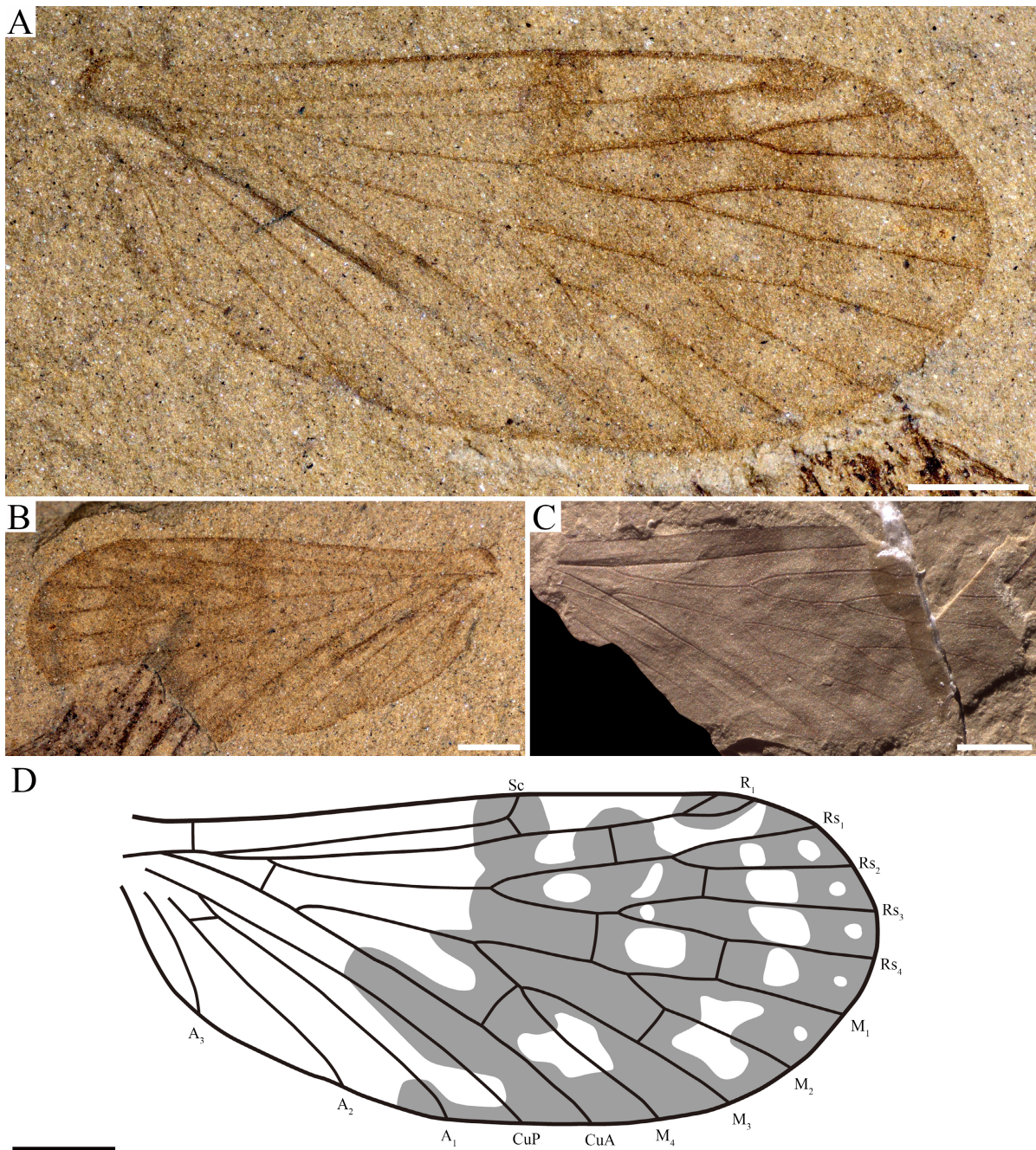


FIGURE 7. Hindwings of *Turbidapsyche* sp. **A**, NIGP204968a, part. **B**, NIGP204968b, counterpart. Photographs of **A** and **B** were captured under vertical reflected light after being moistened with 75% alcohol. **C**, NIGP204969, photograph was captured under lateral reflected light. **D**, Line drawing of NIGP204968. Scale bars = 1 mm.

them generally indistinguishable. Therefore, it is not advisable to establish a species solely based on hindwings. However, based on current evidence, the hindwings of *Permopsyche* exhibit an apical fork in R_1 , distinguishing them from the simple R_1 found in current known *Turbidapsyche*. Yet, we cannot discount the possibility that *Turbidapsyche* may also possess a forked R_1 . Since no *Permopsyche* specimens have been discovered in the Tongchuan entomofauna, we tentatively assign these hindwings to the genus *Turbidapsyche*, which is the most commonly mesopsychids in this fauna.

Discussion

Systematic placement

The revised genus, *Turbidapsyche*, displays a stable venation pattern. However, relying solely on venation for classification can be challenging, as species within this genus share subtle differences such as shifts and tilts of crossveins, making distinctions between them quite nuanced. The Tongchuan specimens are preserved with light-coloured markings, providing valuable

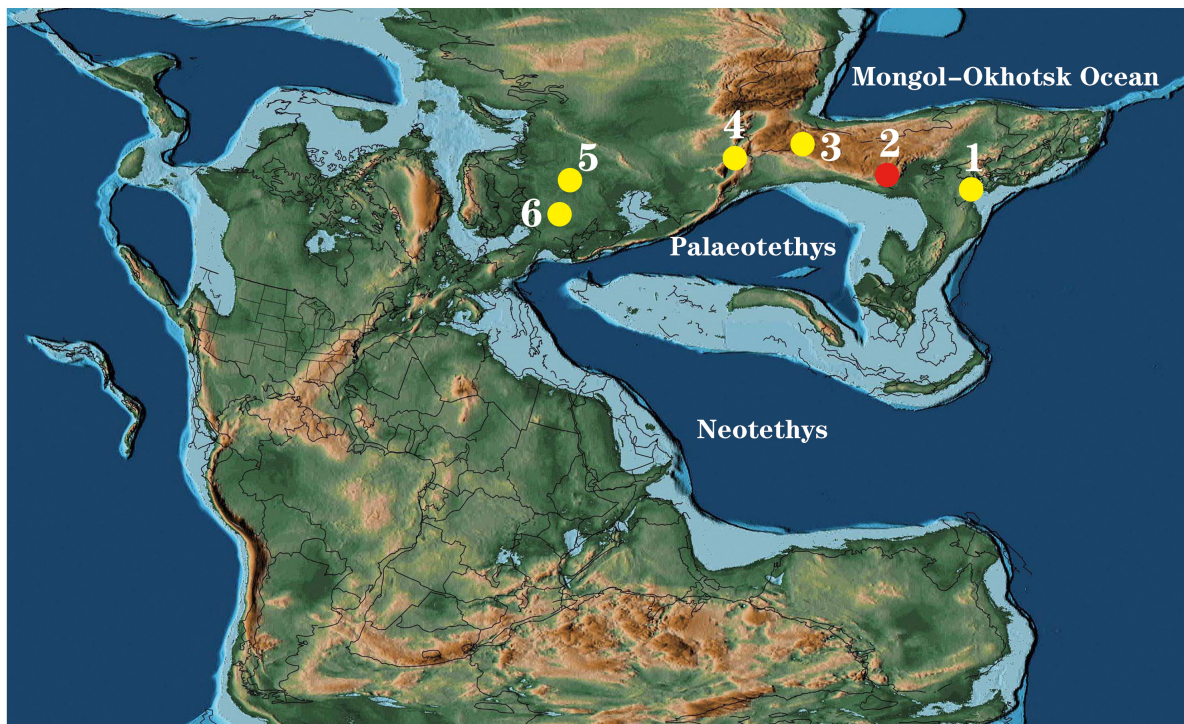


FIGURE 8. Palaeogeographical map of the Triassic (Ladinian) according to Scotese (2016) showing the distribution of *Turbidapsyche*. 1. Chungnam, Korea, Late Triassic: *T. dobrokhotovae* (Novokshonov, 1997) **comb. nov.**; 2. Shaanxi Province, China, late Middle Triassic: *T. tongchuanensis* (Hong, 2007) **comb. nov.**, *T. jinsuoguanensis* (Lian, Cai & Huang, 2021) **comb. nov.**, *T. orientalis* Lian & Huang Lian & Huang, **gen. et sp. nov.**, *T. sparsanota* Lian & Huang Lian & Huang, **gen. et sp. nov.**, and *T. hongii* Lian & Huang Lian & Huang, **gen. et sp. nov.**; 3. Xinjiang, China, Late Triassic: *T. liaoi* (Lian, Cai & Huang, 2021) **comb. nov.**; 4. Madygen, Kyrgyzstan, Middle–Late Triassic: *T. shcherbakovi* (Novokshonov, 1997) **comb. nov.**, *T. justa* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. ordinata* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, *T. tortiva* (Novokshonov & Sukatsheva, 2001) **comb. nov.**, and *T. gentica* (Novokshonov & Sukatsheva, 2001) **comb. nov.**; 5. Vladimir Province, Russia, latest Permian: *T. incompleta* (Bashkuev, 2011) **comb. nov.**; 6. Kharkiv Oblast, Ukraine, Late Triassic: *T. dobrokhotovae* (Novokshonov, 1997) **comb. nov.**

characteristics for classification and allowing us to readily categorise these specimens within a genus and family.

The first reported species of *Turbidapsyche* from the Tongchuan entomofauna is *Turbidapsyche tongchuanensis* (Hong, 1997) **comb. nov.** Initially reported by Hong (2007) as a species of *Itaphlebia* (Nannochoistidae) and was later transferred to the genus *Mesopsyche* by Bashkuev (2011). However, we did not examine the holotype specimen of this species, making it challenging to reconstruct detailed venation characters based solely on outdated drawings. The holotype specimen (82TH2-2 T144) exhibits coloured markings, that the original author overlooked. These markings provide valuable information for the diagnosis of *T. tongchuanensis* (Hong, 2007) **comb. nov.**, which was revised based on the complementary examination of the newly discovered specimen.

Nam and Kim (2014) reported a specimen (KNU-2009023) from the Upper Triassic Amisan Formation of Korea, which they assigned to *Turbidapsyche dobrokhotovae* (Novokshonov, 1997) **comb. nov.**

While the specimen undoubtedly belongs to the genus *Turbidapsyche*, not enough details were described and illustrated to confidently assign it to the aforementioned species. A re-examination and revision of this specimen is needed.

After our revision, *T. incompleta* (Bashkuev, 2011) **comb. nov.** from the Upper Permian of European Russia currently represents the oldest known *Turbidapsyche*. This species was described based on an incomplete hindwing (holotype) and four partly preserved forewings (paratypes). Firstly, establishing a new species solely based on a hindwing is not advisable, as discussed previously. Furthermore, the incomplete forewings lack the inclination of CuA base, a key character that Bashkuev (2011) proposed for separating *Turbidapsyche* (*Mesopsyche*) and *Permopsyche*, besides, their costal space is quite narrow, and the Sc has only one anterior branch, the combination of characteristics indicates that this species does not fit the typical *Turbidapsyche*. Although more complete specimens are needed to definitively

determine its taxonomical placement, we provisionally retain this species within the genus *Turbidapsyche* until further revision are conducted.

Bittacopanorpa javorskii Zalesky, 1935, from the uppermost Permian or basal Triassic of the Kuznetsk Basin in Russia, was synonymised with *Mesopsyche* (Bashkuev, 2011). However, it is important to note that the holotype of *B. javorskii* is only a small fragment of a hindwing base, rendering it insufficient for any definitive taxonomical placement.

Turbidapsyche justa (Novokshonv & Sukatsheva, 2001) **comb. nov.** has forewings displaying a Sc with one anterior branch, whereas this genus typically exhibits a Sc with two anterior branches, which is one of the key characters of *Turbidapsyche*. It is noteworthy that the holotype (PIN, no. 2240/2570(2565)) features M_1 with an additional fork (Novokshonv & Sukatsheva, 2001: Fig. 1a), and the paratype (PIN, no. 2785/4021(3971)) shows Rs_3 with an extra branch (Novokshonv & Sukatsheva, 2001: Fig. 1b). These characters are not commonly observed in *Turbidapsyche*. We interpret *T. justa* as a species exhibiting venational variation.

Biogeographic implications

Turbidapsyche exhibits a regional differentiation in coloured patterns. In China, specimens from regions such as Xinjiang and Shaanxi Province are characterised by pigmentation in the form of rounded spots, coloured stripes formed by fused coloured spots, and the spots located in stable areas such as crossveins, forked areas, and apical longitudinal veins. The forewing of the Ukrainian species (*T. dobrokhotovae*) displays nearly complete pigmentation with several rounded unpigmented patches. In contrast, *Turbidapsyche* wings from Kyrgyzstan appear to be transparent, showing no evidence of pigmentation. The specimen (*T. dobrokhotovae* ?) from Korea exhibits likely patched pigmentation. The putative *Turbidapsyche* from European Russian, *T. incompleta* **comb. nov.**, shows indistinct pigmented pterostigma and coloured spots along some crossveins.

The genus *Turbidapsyche* currently comprises 13 species (10 previous described and three newly erected). Except for the putative *Turbidapsyche* (*T. incompleta*) discovered in the latest Permian of Russia, all other species are known from the Middle and Late Triassic epochs, suggesting that *Turbidapsyche* flourished during the Triassic periods.

To further explore the palaeogeographic characters of Tongchuan City during the Middle Triassic, we examined palaeomagnetic research conducted in the area (Yang *et al.*, 1991; Ma *et al.*, 1993). In Tongchuan, grey clastics and sandstones were collected, yielding a palaeomagnetic direction with a magnetic declination of 327°, magnetic inclination of 37°, and a_{95} of 4.9. In Hancheng, mudstone

was collected, resulting in a palaeomagnetic direction with a magnetic declination of 335°, magnetic inclination of 38°, and a_{95} of 9.4. These two adjacent regions obtained nearly consistent Middle Triassic remanent magnetisation directions, both passing fold tests. We consider these results to be reliable and indicative of primary remanent magnetism from the Middle Triassic. Therefore, using the inclination of this remanent magnetisation direction as 37.5°, calculated via the formula $\tan I = 2 \tan r$, where I is the inclination, R is the palaeolatitude (Butler, 1992), the palaeolatitude of the sampling site was estimated to be 21°.

Turbidapsyche are known from South Korea, northwestern China, Kyrgyzstan, Russia, and Ukraine (Novokshonov, 1997, Nam & Kim, 2004; Hong, 2007; Lian *et al.*, 2021). All known species are confined to Eurasia, along the Northern Palaeotethys (Fig. 8). The Ordos Basin, where most Chinese species of *Turbidapsyche* have been found, experienced a temperate to subtropical climate during the Middle and Late Triassic (Ji *et al.*, 2010). All species of *Turbidapsyche* were found in deposits from similar palaeolatitudes, suggesting that they likely inhabited similar climates and may have had specific ecological requirements or limited dispersal capabilities.

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