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The first Sharephemeridae (Insecta: Ephemeroptera) from the Jurassic Shiti Formation of South China

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ABSTRACT

The new genus and species, *Jurassephemera zhangi* gen. et sp. nov., belonging to the extinct family Sharephemeridae (Ephemeroptera: Mesephemeroidea), is established from the late Early Jurassic interval of the Shiti Formation of Guangxi Zhuang Autonomous Region, South China. The new genus and species is characterised by its moderate size; small head with reduced compound eyes; body with ten abdominal segments; round-triangular forewing shape; vein R dividing three times, forming five veinlets and three triads; veins MA, MP, and CuA straight, all basally forking once with single triads between; crossveins well developed; and hind wing oval, much smaller than forewing, with veins generally radial and single. SEM observations also reveal that crossveins are much more developed than previously recognised under optical illumination. The forewing venation of all sharephemerid genera is compared. The first report of this family in China herein increases the diversity and palaeogeographic distribution of Sharephemeridae.

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KEYWORDS
Jurassephemera zhangi gen. et sp. nov; Sharephemeridae; Shiti Formation; Early Jurassic; Guangxi

Introduction

Sharephemeridae Sinitshenkova 2002 are a small, extinct family of Ephemeroptera (commonly known as mayflies), comprising three genera and species found in Laurasia (including Germany, Spain, Mongolia and Russia) (Sinitshenkova 2002; Bashkuev et al. 2012, 2013; Matamales-Andreu et al. 2021). This family first appeared in the Late Permian (Sinitshenkova 2013) and disappeared in the latest Jurassic (Sinitshenkova 2002). Nearly all the known genera and species were established on forewings or obscure body remains (Zhang et al. 2022). Here, we describe a new genus and species belonging to Sharephemeridae with complete and clear body and wing characters for the first time from the Early-Middle Jurassic Shiti Formation in the Guangxi Zhuang Autonomous Region, South China.

Material and methods

All specimens described in this study were collected from the Shiti Formation in the section located in the Pinggui District, Hezhou City, Guangxi Zhuang Autonomous Region in southern China (GSP: 24°26′20″ N, 111°27′85″ E, H = 132 m) (Figure 1). So far, 20 species in 18 genera representing nine insect orders have been described from the Shiti Formation (Lin 1986; Wang et al., 2011). The insect-bearing layer is dated as the late Early Jurassic, while the whole Shiti Formation ranges from the late Early to Middle Jurassic (Chen et al. 1980; Lin 1986).

The specimens studied herein are housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). The microscopes used to observe specimens include a stereomicroscope system (ZEISS Stereo Discovery V16) and Scanning Electron Microscope (SEM) with the accelerating voltage 20 kV (Tescan MAIA 3 GMU) at NIGPAS. Line drawings were made using CorelDRAW 2019 software. Mayfly body and wing venation terminology follows Tillyard (1932) and Kluge (2004). The venational abbreviations are as follows: C(+), Costa; Sc(-), subcosta; R, radius; R1(+), first branch of R; R2(-), second branch of R; iR2(+), intercalary between R2(-) and R3a(-); R3, third branch of R; R3a(-), anterior branch of R3; R3b(-), posterior branch of R3; iR3a(+), intercalary between R3a(-) and R3b(-); R4 + 5(-), last branch of R; iR3b(+), intercalary between R3b(-) and R4 + 5(-); MA, media anterior; MA1(+), anterior branch of MA; MA2(+), posterior branch of MA; iMA(-), intercalary between MA1(+) and MA2(+); MP, media posterior; MP1(-), anterior branch of MP; MP2(-), posterior branch of MP; iMP(+), intercalary between MP1(+) and MP2(+); CuA, cubital anterior; CuA1(+), anterior branch of CuA; CuA2(+), posterior branch of CuA; iCuA(-), intercalary between CuA1(+) and CuA2(+); CuP(-), cubitus posterior; AA1(+), anterior anal; AA2(+), posterior anal; iAA(-), intercalary between AA1(+) and AA2(+); (+) and (-) signify convex and concave veins respectively. The nomenclatural acts established herein are registered under Zoo-Bank LSID:http://www.zoobank.org/urn:lsid:zoobank.org:pub:FAE38691-A24F-4EE0-BAB4-8C50D45730B6.

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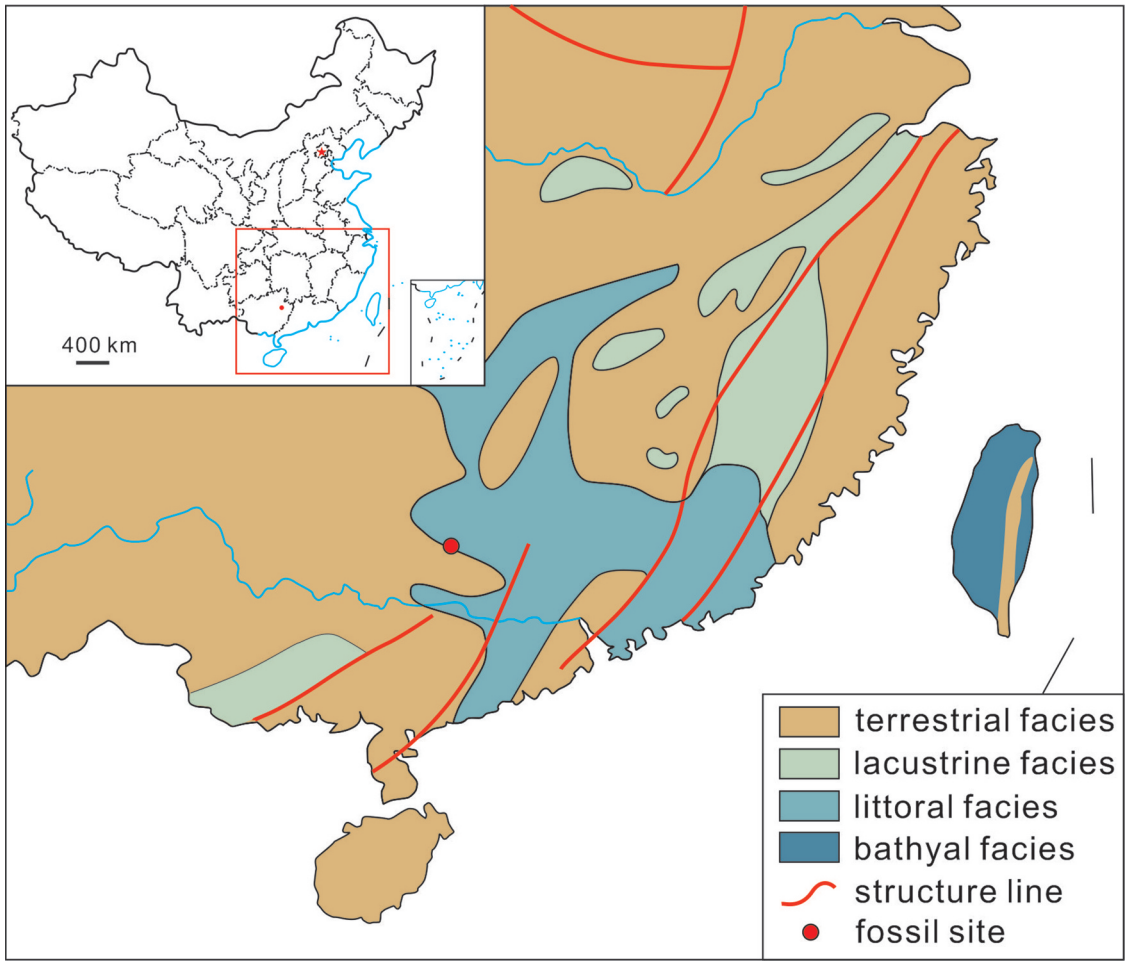

Figure 1. Geographical and geological maps of South China (modified from Wang 1985).

Systematic palaeontology

Order Ephemeroptera Hyatt et Arms, 1890

Family Sharephemeridae Sinitshenkova 2002

Type genus and species. Sharephemera cubitalis ***Sinitshenkova, 2002.***

2002 Sinitshenkova, 272, 273, 275, 276
2012 Bashkuev et al., 180, 181
2013 Sinitshenkova, 84, 85, 86

Revised diagnosis (modified from; Sinitshenkova (2002); Bashkuev et al. (2012))

Forewing twice as long as wide, with base broad, well-developed anal area, and narrow cubital area. MP divided near wing base. CuA forking, elongate, with intercalary vein. CuP long and simple. Anal veins long. Cubital and anal veins with a slight curve, otherwise straight.

Age and occurrence

Late Permian of Russia, Middle Triassic of Germany and Spain, Early Jurassic of China, and Late Jurassic of Mongolia.

Included species

Four genera and species including *Sharephemera cubitalis* Sinitshenkova, 2002 from the Jurassic Shar-Teeg Formation of Mongolia, *Hammephemera pulchra* Sinitshenkova, 2012 from the Triassic Röt Formation of Germany (Bashkuev et al. 2012) and the Triassic Estellencs Formation of Spain (Matamales-Andreu et al. 2021), *Tunephemera tungussica* Sinitshenkova, 2013 from the Permian Pirda Formation of Russian, and *Jurassephemera zhangi* gen. et sp. nov.

Jurassephemera *gen. nov.*

Etymology

The generic name refers to the Jurassic period and the recent genus *Ephemera* L., 1758. The gender of the name is feminine.

Type species.

Jurassephemera zhangi sp. nov.

Diagnostic characters

Moderate body and forewing size. Head small and dark-coloured, with reduced compound eyes. Body with ten abdominal segments exposed. Forewing round-triangular, with comparatively straight costal margin, vein R divided three times, forming four veinlets and three triads; MA, MP, and CuA basally forking once, forming triads; CuP long and simple; vein AA divided once; crossveins well-developed. Hind wing oval, much smaller than forewing, veins commonly radial and simple.

Composition

Currently, the genus includes only the type species.

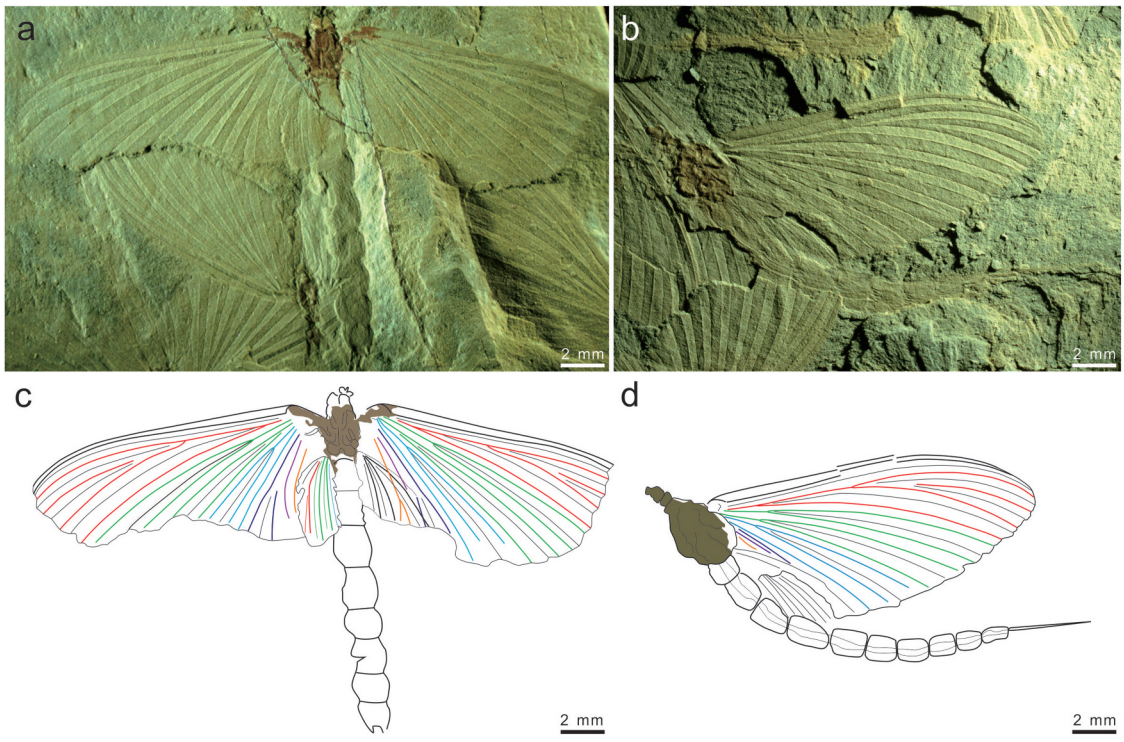

Figure 2. *Jurassephemera zhangi* gen et sp. nov. (a). Holotype photograph (NIGP180514) (in dorso-ventral aspect); (b). Paratype photograph (NIGP180515) (body lateral aspect). (c). Line drawing (crossveins not shown) of (a); (d). Line drawing of (b).

Age and distribution
Early Jurassic of Guangxi in southern China.

Remarks
Jurassephemera gen. nov. is placed in Sharephemeridae on the basis of the following characters: length: width ratio about 2:1, narrow cubital area, MP forking near base, proximal to MA branching, CuA with intercalary vein, and CuP long and simple.

Jurassephemera zhangi *gen et sp. nov.* (Figures 2, 3a, 4a–d)

Etymology
The specific epithet honours the palaeoentomologist Prof. Zhang Junfeng, and is a noun in the genitive case.

Holotype
No. NIGP180514, a nearly complete specimen.

Paratype
No. NIGP180515, a nearly complete specimen.

Locality and horizon. Xiwan outcrop in Pinggui District, Hezhou City, Guangxi Zhuang Autonomous Region, southern China; Lower Jurassic, upper interval of the Shiti Formation.

Diagnosis
As for the genus (*vide supra*).

Description
Body slender [gender uncertain], with lengths of 12.0–15.6 mm, antennae short, compound eyes small but visible, head small, thorax brown, mesothorax larger than prothorax and metathorax, forewings well-developed, hind wings reduced, and a pair of elongate cerci present at abdominal apex.

Forewings oval to round-triangular, with lengths up to 14.5 mm. Costal margin (C(+)) distinct, comparatively straight. Subcostal brace present; Sc(-) simple, approximately parallel with C(+) and R1(+). R developed, R1(+) long and simple, R2+3 divided into R2 and R3 basally at about mid-length, R2 and R3 with no branch forming a triad with intercalary iR2(+); R3 divided into R3a(-) and R3b(-) at slightly more than mid-length, and forming a triad together with intercalary iR3a(+); R4+5(-) simple and curved, diverging from stem R at basal 0.15× of wing length, forming another triad with intercalary iR3b(+) between R4+5(-) and R3b(-). MA and MP converging basally, both forking once, branching into four simple veins; MA1(+) and MA2(+) forming triad with intercalary iMA(-), similarly to two triads formed by veinlets of MP and CuA. MA forking distad MP fork. CuP simple, comparatively straight. Veinlets of AA forming triad. Pcu long, simple. Longitudinal veins generally radial and parallel with marginal intercalaries present. Crossveins developed but not distinct under optical microscopy.

Hind wing oval, much smaller than forewing, veins commonly radial and simple except stem R divided once.

Abdomen long and curved in lateral view, ten segments exposed, width narrowing gradually from abdominal segment I to X; dorsal neural tube running through middle of abdomen. Caudal filaments fragile and incompletely preserved. Legs usually incomplete, only two pairs of femora and tibiae discernable.

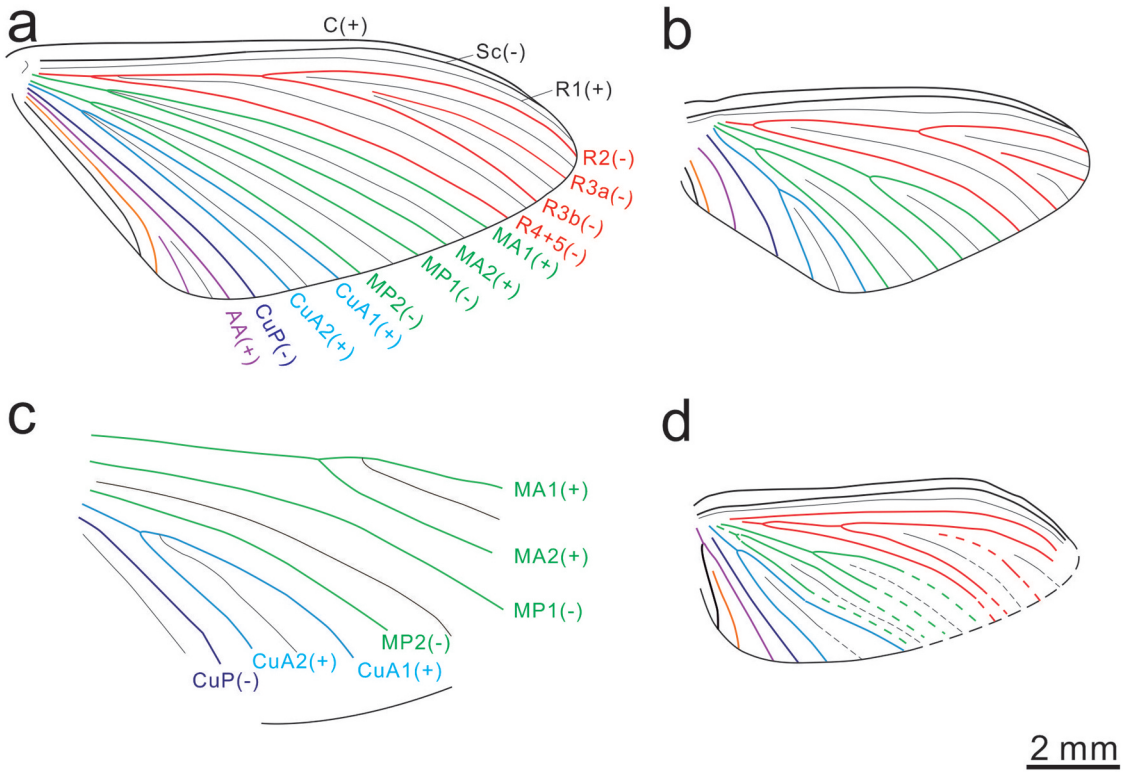

Figure 3. Forewing comparison of Sharephemeridae. (a). *Jurassephemera zhangi* gen. et sp. nov.; (b). *Hammephemera pulchra* Sinitshenkova, 2011; (c). *Tunephemera tungussica* Sinitshenkova, 2013; (d). *Sharephemera cubitalis* Sinitshenkova, 2002. Hindwings and crossveins on forewings are excluded. All to the same scale.

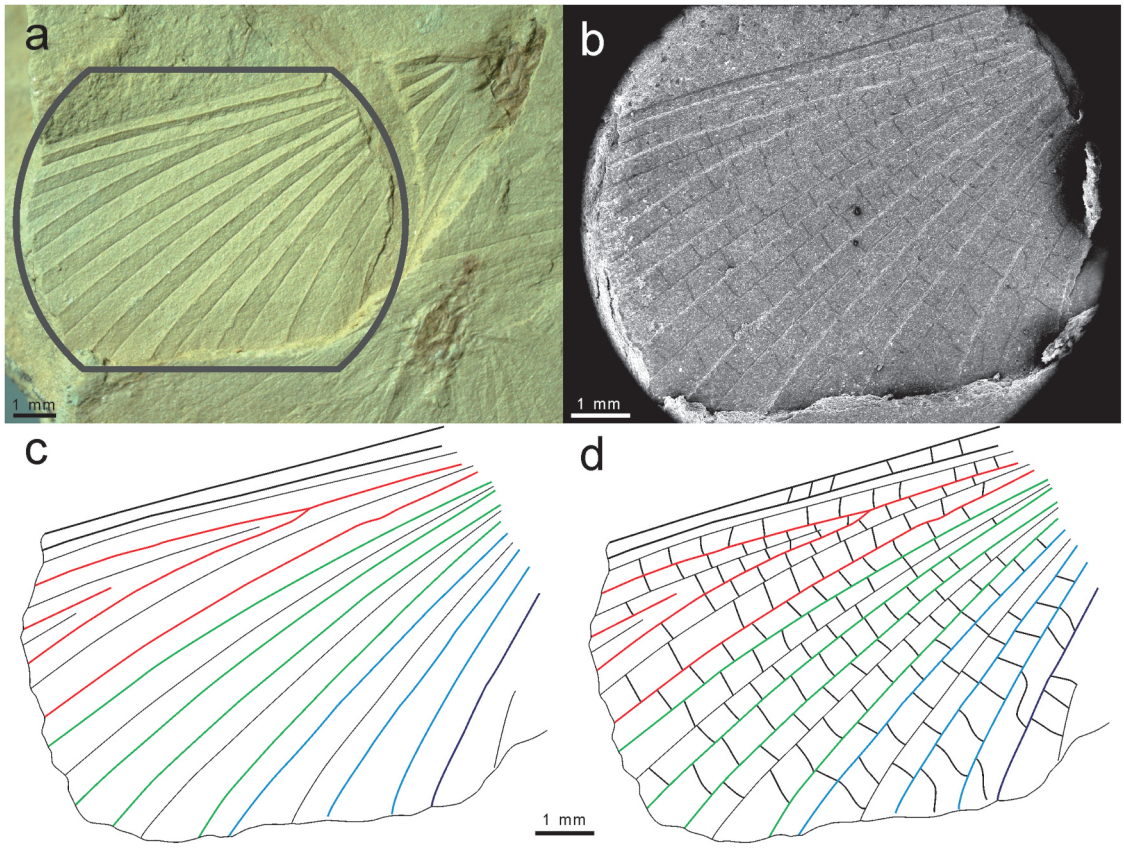

Figure 4. (a). Optical microscopy of *Jurassephemera zhangi* gen. et sp. nov.; (b). SEM image of area shown by grey border in (a); (c). forewing venation of area shown in grey border in (a); (d). forewing venation of (b).

Discussion

At least twelve out of forty fossil ephemeropteran families were recorded during the Jurassic (Huang et al. 2007a). Among Jurassic records, four families (Mesonetidae, Epeoromimidae, Ephemerellidae and Neoephemeridae) were established on the basis of nymphs and cannot be compared with the new species reported herein. Sharephemeridae including this new species differs from Mesephemeridae by possessing a straight costal margin and simpler wing venation (Lin 1986; Carpenter 1992), from Hexagenitidae by the much simpler veinlets (Carpenter 1992), from Aenigmephemeridae by its basally forked MA and simpler R (Tshernova 1968), from Siphlonuridae (adult mayfly *Olgisca schwertschlageri*) by the basally branched MA and narrower costal area (Handlirsch 1906), from Heptageniidae by the much simpler intercalated veins (Huang et al. 2007b), and from Siphluriscidae (*Stackelbergisca sibirica*) by the basally forked MA and dense crossveins in the cubital area (Tshernova 1967).

Among Sharephemeridae, *J. zhangi* differs from the other three genera and species by the proximally forked MA (Figure 3) (Sinitshenkova 2002; Bashkuev et al. 2012, 2013). The main veins are more curved apically in *Hammephemera pulchra* Sinitshenkova, 2011 than in *J. zhangi* (Figures 3a, b). *Tunephemera tungussica* Sinitshenkova, 2013 is only partly preserved, with more apical divisions to veins MA and CuA relative to that of *J. zhangi*, although the crossvein pattern is somewhat similar between the two species (Figures 3a, c) (Sinitshenkova 2013). *J. zhangi* differs from *S. cubitalis* by a less well-developed anal area, and MA and MP forking more proximally (Figures 3a, d) (Sinitshenkova 2002).

The discovery of the present fossils reveals a challenge for the study of fossil insect wings, and particularly those of Ephemeroptera. Crossveins of *J. zhangi* are not obvious under traditional optical microscopy (Figures 2a, b, 4a, 4c), but clearly visible in Scanning Electron Microscope (SEM) images (Figures 4b, 4d). This is probably associated with the carbon enrichment of the crossveins. Well-developed crossveins as a basic character in the wings of mayflies may have occurred widely and even in taxa that were previously reported to lack crossveins. Thus, the purported 'absence' of crossveins in any fossil Ephemeroptera should be considered with caution given the revelations provided by the type series of *J. zhangi*. This is particularly important where the putative absence of crossveins has been employed as a diagnostic or phylogenetically critical trait, necessitating a revision of most extinct mayfly clades.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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