A new specimen questions the identity of the oldest member of *Tettigonia* Linnaeus, 1758 (Orthoptera: Ensifera: Tettigoniidae) as a valid species

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Kurzfassung

Neues Fossil stellt die Gültigkeit der ältesten *Tettigonia*-Art (Orthoptera: Ensifera: Tettigoniidae) in Frage

Tettigonia bricei Greenwalt & Rust, 2014 ist die einzige bekannte fossile Art der rezenten Gattung *Tettigonia*, zu der bekannte Arten wie die Große Grüne Laubheuschrecke *T. viridissima* (Linnaeus, 1758) gehören und die in ganz Europa sowie in Teilen Asiens und Nordafrikas verbreitet ist. Der Holotyp von *T. bricei* besteht aus einem isolierten rechten Vorderflügel eines Männchens. Hier präsentieren wir ein zweites Exemplar dieser wenig erforschten Art, das sowohl beide Vorderflügel als auch Teile der Hinterbeine umfasst. Wie der Holotyp wurde auch das neue Exemplar in den miozänen Diatomitvorkommen der Montagne d'Andance in der Nähe der Gemeinde Saint-Bauzile (Ardèche) in der Region Auvergne-Rhône-Alpes in Frankreich gefunden. Das Alter dieser Ablagerung wird auf das Untere Turolium geschätzt, welches dem Oberen Miozän entspricht. Eine erneute Untersuchung der diagnostischen Merkmale von *T. bricei* legt nahe, dass einige dieser Merkmale möglicherweise nicht zuverlässig genug sind, um eine klare Unterscheidung von der heute lebenden Art *T. viridissima* zu treffen; dennoch könnte das Farbmuster der Flügel als zusätzliches Merkmal einen weiteren diagnostischen Anhaltspunkt darstellen.

Abstract

Tettigonia bricei Greenwalt & Rust, 2014 is the only known fossil species of the extant genus *Tettigonia*, which includes well-known species such as the great green bush-cricket *T. viridissima* (Linnaeus, 1758) and is distributed across Europe, as well as parts of Asia and North Africa. The holotype of *T. bricei* consists of an isolated right male forewing. Here, we present a second specimen of this poorly known species, comprising both forewings and parts of the hindlegs. As with the holotype, the new specimen was found in the Miocene diatomites of the Montagne d'Andance, near the commune of Saint-Bauzile (Ardèche) in the Auvergne-Rhône-Alpes region of France. The age of this deposit is estimated to be Lower Turolian European Land Mammal Age, corresponding to the Upper Miocene. Re-examination of the diagnostic characters of *T. bricei* suggests some of these traits may not be reliable to make a clear distinction from the extant *T. viridissima*; yet, wing color pattern as an additional trait may represent another diagnostic character.

Keywords

Evolution, bush cricket, insect, katydid, taxonomy, *Tettigonia viridissima*, *Tettigonia bricei*

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1 Introduction

The family containing the katydids or bush-crickets (Tettigoniidae Krauss, 1902) is the most species-rich in the order Orthoptera Olivier, 1789, with more than 8,500 extant species. Despite their modern diversity, only 45 species are known from the fossil record (Cigliano et al. 2026). Three occurrences from the Carboniferous (Goldenberg 1854) and Jurassic (Germar 1839, Handlirsch 1939) represent clear chronological outliers with the remaining fossil Tettigoniidae found throughout the entire Cenozoic (Cigliano et al. 2026; the Paleobiology Database, paleobiodb.org).

Among the most commonly known tettigoniids in Europe (and also Japan) are species of *Tettigonia* Linnaeus, 1758. These katydids, also known as green bush-crickets, are generally large and green, with moderately slender bodies and legs and well-developed wings. They typically inhabit vegetation at various heights, where they forage on smaller insects and plant material (Grzywacz

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et al. 2017). Despite their present-day abundance, only a single fossil specimen has so far been assigned to *Tettigonia*. *Tettigonia bricei* Greenwalt & Rust, 2014 was discovered in a Miocene deposit in France. Originally identified as *Tettigonia viridissima* (Linnaeus, 1758), it was later described as a distinct species, *T. bricei* (Brice & Laurentiaux 1963, Greenwalt & Rust 2014).
In this study, we describe a second tettigoniid specimen from the same French deposit that yielded *T. bricei*. Diagnostic characters based on the holotype of *T. bricei* are compared with those of *T. viridissima* and the new specimen. The implications of this new specimen for the taxonomy of *T. bricei* are discussed.

2 Materials and methods

The specimen described in this study was recovered from the Miocene diatomites of the Montagne d'Andance, near the commune of Saint-Bauzile (Ardèche), in the Auvergne-Rhône-Alpes region of France. The deposit is dated to the Lower Turolian European Land Mammal Age, corresponding to the Upper Miocene (Tortonian–Messinian, Pastre et al. 2004). The specimen is preserved as a part and counterpart, whereby the slab containing the counterpart is broken into two pieces. The larger slab, containing the part, measures ca. 25 cm × 20 cm. The specimen is disarticulated.
Photographs of the new specimen were taken by Mathias Vielsäcker at the Staatliches Museum für Naturkunde Karlsruhe (SMNK) using a Canon EOS R5 equipped with an EF100 mm f/2.8L Macro IS USM lens. Drawings were produced using GIMP v. 3.0.6-1 (www.gimp.org), and figures were assembled in Inkscape v. 1.3 (www.inkscape.org).
Two specimens of *Tettigonia viridissima* (Linnaeus, 1758) were examined in this study for comparison with the fossil specimen; both were females and are stored in the collection of the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (collection numbers ZMH71558 and ZMH71786).
The taxonomic framework follows Cigliano et al. (2026). Wing venation nomenclature follows Béthoux & Nel (2002), with the following abbreviations: ScA, ScP = anterior and posterior subcosta; RA, RP = anterior and posterior radius; M = media; CuA = anterior cubitus; CuPaα = anterior branch of the first posterior cubitus; CuPaβ = posterior branch of the first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

3 Systematic paleontology

Order Orthoptera Olivier, 1789
Suborder Ensifera Chopard, 1921
Infraorder Tettigoniidea Kevan, 1982
Superfamily Tettigonioidea Krauss, 1902
Family Tettigoniidae Krauss, 1902
Subfamily Tettigoniinae Krauss, 1902
Tribe Tettigoniini Krauss, 1902
Genus *Tettigonia* Linnaeus, 1758
Species *Tettigonia bricei* Greenwalt & Rust, 2014

Type locality and horizon (Fig. 1, 2): The male holotype, as well as the new specimen presented herein, was discovered in the Miocene diatomites of the Montagne d'Andance, near the commune of Saint-Bauzile (Ardèche), in the Auvergne-Rhône-Alpes region of France. The age of this deposit is estimated to be Lower Turolian European Land Mammal Age, corresponding to the Upper Miocene (Tortonian–Messinian).
Taxon history: The holotype was originally described by Brice & Laurentiaux (1963) as a fossil specimen of the extant *Tettigonia viridissima* (Linnaeus, 1758). In 2014, Greenwalt & Rust re-examined the specimen and described it as the new species *T. bricei*.
New material: The new material presented in this study consists of a part and counterpart (the counterpart broken into two slabs) of a disarticulated specimen that includes both forewings, parts of the hindlegs, and poorly preserved fragments of a hindwing. The specimen is housed in the paleontology collections of the State Museum of Natural History Karlsruhe (Staatliches Museum für Naturkunde Karlsruhe, SMNK), under the collection number SMNK-Pal 77018. The sex of the new specimen may be female, as no mirror in the cubital region of the forewing can be observed, in contrast to the holotype. However, due to limitations imposed by the state of preservation of the new specimen, the identification of sex should be considered tentative.
Diagnosis: See Greenwalt & Rust (2014).

Description

Measurements (mm): Forewing length (base to apex, as preserved) 42.75; maximum width (as preserved) 9.00; metafemur length at least 27.5.
Forewings: Anal and cubital area poorly preserved. Veins 1A, CuPb, CuPaβ and CuA + CuPaα apparently each with a single branch. CuPb, CuPaβ and CuA + CuPaα parallel to one another. CuA + CuPaα with secondary, nearly "horizon-

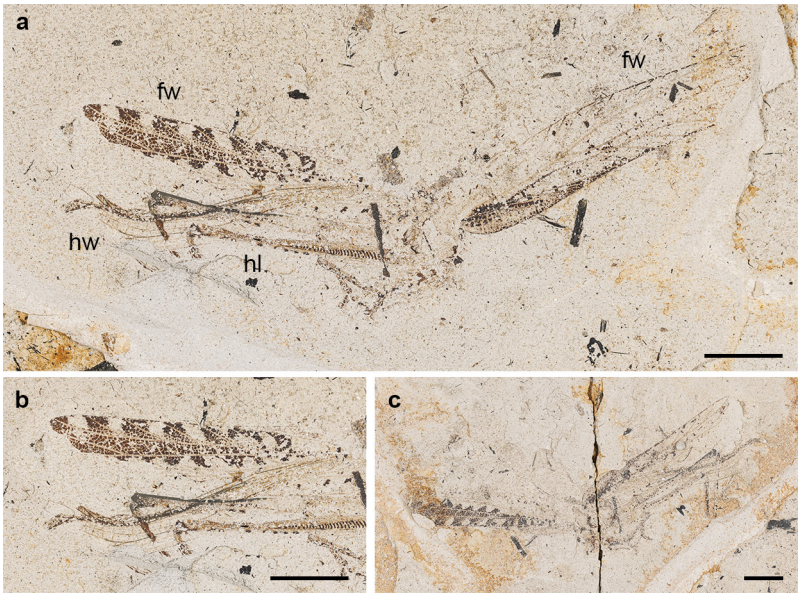
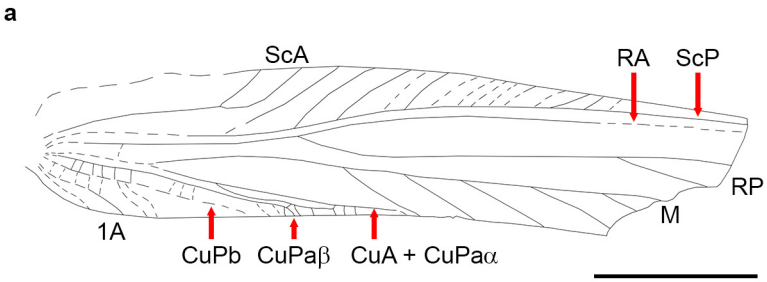


Figure 1. *Tettigonia bricei* Greenwalt & Rust, 2014, additional specimen (part and counterpart). **a.** Overview of the part. **b.** Detail of one of the forewings (part). **c.** Overview of the counterpart. Abbreviations: fw = forewing; hl = hindleg; hw = hindwing. Scale bars = 10 mm (a-c). – All photos: SMNK (Mathias Vielsäcker).



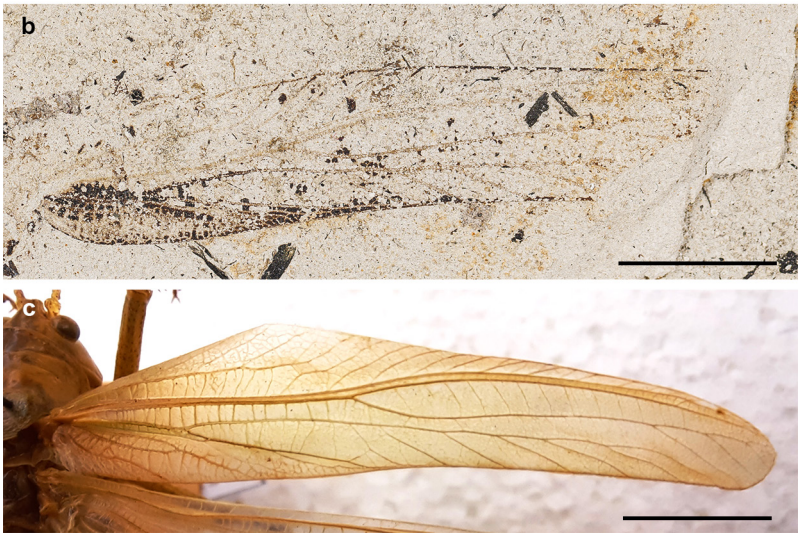


Figure 2. *Tettigonia bricei* Greenwalt & Rust, 2014, additional specimen. **a.** and **b.** Detail of one of the forewings (part), drawing (top) and photo (bottom). **c.** Forewing of *Tettigonia viridissima* (Linnaeus, 1758) for comparison (female specimen in the collection of the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg; coll. no. ZMH71558). Scale bars = 10 mm (a-c). – Drawing **a**, photo **c**: Ole-Kristian Odin Schall (LIB); photo **b**: SMNK (Mathias Vielsäcker).

tal cross-vein" in distal half (a similar structure is present in the extant *Tettigonia viridissima*, see Fig. 2a, c). Cross-veins in cubital and anal areas numerous and tightly spaced. M diverging from CuA + CuPaα at ca. one-third of its length and bearing at least five comb-like cross-veins. RP diverging from RA slightly anterior to the first cross-vein of M and with at least one distal secondary branch, diverging from main branch approximately at the level of the fifth cross-vein of M. Area between RA and RP narrow. Cross-veins of RA not visible, possibly not preserved. ScP long, reaching close to wing apex (however, apex of ScP not preserved), with numerous comb-like cross-veins. ScA reaching wing margin approximately at the level at which RP diverges from RA, with only a single comb-like cross-vein preserved. Forewing coloration forming a conspicuous melanistic pattern interspersed with lighter areas.

Hindlegs: Preservation generally poor. Only the femora and ca. proximal third of the tibiae preserved. Hind femur long and slender.

Remarks: Greenwalt & Rust (2014) proposed three characters to differentiate *Tettigonia bricei* from *T. viridissima*, the extant species with which the holotype of *T. bricei* was originally associated (Brice & Laurentiaux 1963):

1. The forewing length/width ratio of *T. bricei* was given as 6.25, whereas for *T. viridissima* it was reported as 4.52 (male) and 4.74 (female) (after Greenwalt & Rust 2014). Unfortunately, we cannot evaluate this character in the new specimen because the forewing is incomplete. However, we measured this character in two additional female specimens of *T. viridissima* from the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg, Germany). In specimen ZMH71558 the forewing length/width ratio was 4.6 for the right wing (Fig. 2c) and 4.8 for the left wing. In specimen ZMH71786 it was 5.2 for the right wing and 4.9 for the left wing. Our measurements suggest a noticeable degree of variation in regard to this character, i.e. specimen ZMH71786 had a forewing length/width ratio ca. 0.5 higher than the value reported for females of *T. viridissima* by Greenwalt & Rust (2014) (at least for the proportionally longer right wing). However, the forewing length/width ratio reported for *T. bricei* is still more than 1.0 higher than in specimen ZMH71786.
2. In *T. viridissima*, RP diverges from RA at 36.8% (male) and 37% (female) of the total wing length, compared with 32.4% in *T. bricei* (Greenwalt & Rust 2014). Again, we are unable to measure this character in our specimen of *T. bricei*, as the total wing length is not preserved. However, in the two additional specimens of *T. viridissima* mentioned above RP diverges from RA after 42.7% (right wing) and 41.9% (left wing) in specimen ZMH71558, and 39.6% (right wing) and 41.1% (left wing) in ZMH71786. These values generally confirm the tendency of RP to diverge more distally in *T. viridissima* than in *T. bricei*, but they also indicate a rather wide range for this character between individuals of the same species, i.e. 37-42.7%, which is a difference of 5.7%, based on only a few specimens, suggesting a high natural variability. This range towards the higher value would also include the value recorded for *T. bricei*, if applied towards the lower value (difference to the lowest value recorded for *T. viridissima* 4.4%).
3. The secondary branches of M in *T. viridissima* are closer together, separated by a distance approximately half the length of the individual branches. Most of the secondary branches (sb) of M in *T. bricei* are separated by a distance about equal to the lengths of these branches. In our specimen of *T. bricei*, the distance between secondary M-branches 2 and 3 (measured along the posterior wing margin; branches counted from the direction of wing base) / length of sb 2 was 0.84; the same for sb 3 was 0.72. In the two additional *T. viridissima* specimens, we obtained measurements of 0.57 (sb 2) and 0.68 (sb 3) for ZMH71786, and 0.70 (sb 2) and 0.71 (sb 3) for ZMH71558 (all values obtained from the right forewing). These measurements show that the values for sb 3 are nearly identical in all three specimens and therefore do not provide a reliable diagnostic difference. The ratio for sb 2 appears more distinct; however, as in the previous character, the range observed within *T. viridissima* (0.57-0.70; range 0.13) is not much smaller than the range between ZMH71558 and our specimen of *T. bricei* (0.14), again indicating considerable intraspecific variability.

Altogether, the characters proposed by Greenwalt & Rust (2014) show considerable overlap and variability, when additional specimens of *T. viridissima* are examined, and do not provide strong evidence for the separation of *T. bricei* as a species distinct from *T. viridissima*.

4 Discussion

In this study, we present a new specimen of the genus *Tettigonia* Linnaeus, 1758 from the Upper Miocene of France. As the new specimen shows no characters that would justify its separation from *Tettigonia bricei* Greenwalt & Rust, 2014, which was described from the same deposit, we assign it to that species. Interestingly, measurements performed to re-evaluate the diagnostic features proposed for *T. bricei* by Greenwalt & Rust (2014) may suggest that the reported differences from *T. viridissima* fall within the range of intraspecific variation when additional specimens of the extant species are considered. However, the main diagnostic feature of *T. bricei* – the forewing length/width ratio – may be adequate to differentiate the fossil taxon from its extant congeners.

Tettigonia viridissima and *T. bricei* are separated by at least ca. 7 Ma. The longevity of individual insect species is generally estimated to be on the order of two to three (Poinar & Milki 2001) or three to ten Ma (Grimaldi & Engel 2005). However, several putative cases of much longer species durations have been reported in the fossil record, some extending up to about 45 Ma, although these records are controversial and may partly reflect coarse taxonomic concepts or insufficiently detailed comparisons. Such long survival times have been linked to persistently stable environmental conditions that may have limited opportunities for diversification (Hörnschemeyer et al. 2010). However, this scenario appears unlikely in the context of the Miocene, which was characterized by marked climatic and environmental changes (Steinthorsdottir et al. 2021).

Within this framework, the ca. 7 Ma that separate *T. viridissima* and *T. bricei* fall within the more conservative estimates of insect species durations proposed by Grimaldi & Engel (2005), suggesting that – based on age alone – one cannot rule out the possibility that both names refer to a single species. Nevertheless, the rather poor preservation precludes an assessment of the forewing length/width ratio in the new specimen. Therefore – and because our sample size of extant *Tettigonia* specimens was small – we refrain from proposing any formal taxonomic change for now. This is especially true since our new data from extant *T. viridissima* point towards the significance of the forewing length/width ratio for taxonomic purposes. In addition, the melanistic forewing pattern seen in the new specimen of *T. bricei* contrasts with the uniformly light forewing observable in *T. viridissima* (e.g. Fig. 2c), which may point to a distinct species-level identity. Although the preservation of color patterns is subject to the diagenetic history of the host sediment (McNamara 2013a), especially the temperature during burial (McNamara et al. 2013b), recent findings suggest that melanin-rich cuticle preserves well, at least in beetles (Wang et al. 2023). Thus, the color pattern of the fossil *T. bricei* may be a further indicator of a distinct species.

Altogether, our data indicate that the case of *T. bricei* versus *T. viridissima* remains unresolved, although a taxonomically distinct fossil species seems plausible. Studies on the reliability of forewing characters to inform taxonomic decision making suggest that they are stable in at least some fossil groups (e.g. the mostly Mesozoic Prophalangopsidae, another ensiferan family; Gu et al. 2021), but show considerable variation in extant species of Tettigoniidae, even between the left and right forewing of the same individual (Gu et al. 2023). In the future, additional data from well-preserved fossil specimens of *T. bricei* are necessary to confirm the stability of forewing characters in a fossil species chronologically much closer to its extant relatives than most prophalangopsids and strengthen or reject the status of the French katydid as a distinct species.

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Online Resources

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