



<https://doi.org/10.11646/palaeoentomology.6.5.5>

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A review of the singing cicada fossils from the Pliocene Fossil-Lagerstätte Willershausen, Germany, with the description of three new species (Hemiptera: Cicadidae: Tibicinae and Cicadinae)

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Abstract

The singing cicada fossils (Cicadidae), based mainly on isolated forewings, from the Pliocene Fossil-Lagerstätte Willershausen, Germany, are reviewed, including previously published material and unpublished specimens from the collections of the Geoscience Museum of the Geoscience Centre at the Georg August University in Göttingen, the State Museum of Natural History in Stuttgart, and the Geoscience Collections of the Clausthal University of Technology, which represent the three largest collections from this outstanding locality. Three new species, *Tibicina lata* **sp. nov.**, *Tibicina bouldardi* **sp. nov.** (Tibicinae), and *Cicada tithonus* **sp. nov.** (Cicadinae) are described based on forewing characters. Other singing cicadas from Willershausen are assigned to *Tibicina* sp., *Tibicina* aff. *haematodes*, *Cicada* aff. *orni*, *Cicada* aff. *lodosi* and indeterminable species.

Keywords: fossil, Pliocene, Cicadoidea, Auchenorrhyncha, Insecta, invertebrate

Introduction

Among the true cicadas or singing cicadas, family Cicadidae, 13 fossil species have been recorded so far from Europe, six in the subfamily Cicadinae (in four genera), four in the Cicadettinae (in four genera) and three in the Tibicininae (all in the genus *Tibicina*) (Moulds, 2018; Szewo, 2019). The first fossil record of singing cicadas from the Upper Pliocene Fossil-Lagerstätte beds at Willershausen, Lower Saxony, Germany, was a brief mention by Schmidt (1949). Straus (1952) mentioned and figured a single specimen as cf. *Cicadetta montana* Scopoli

(the extant New Forest Cicada) from the Willershausen lake beds. This specimen, which was presumably lost during WWII, was later deemed by Wagner (1967) a misidentification. Wagner (1967) published on 13 Willershausen specimens from the Geoscience Museum at the Georg August University, Göttingen, which he assigned to *Tibicina haematodes* Scopoli (10 specimens), *Cicada orni* Linnaeus (2 specimens), and as “Genus? sp.?” (1 specimen). He gave brief descriptions of the preservation of the fossils but, for the most part, provided no diagnostic characters or morphological comparisons. More recently, Brauckmann & Gröning (2002) described two further specimens (isolated wings) from the Geoscience Collections of the Clausthal University of Technology from Willershausen as likely conspecific to Wagner’s “*Tibicina haematodes*”. However, due to their incomplete preservation, Brauckmann & Gröning (2002) left these two, and Wagner’s (1967) specimens, in open nomenclature as “Tibicinae?, gen. et. sp. indet.”.

Here, we review the material published by Wagner (1967) and Brauckmann & Gröning (2002) as well as 29 previously unpublished specimens, mainly isolated wings, of singing cicadas from Willershausen among which we describe three new species: *Tibicina lata* **sp. nov.**, *Tibicina bouldardi* **sp. nov.** and *Cicada tithonus* **sp. nov.**

Geological setting

The former clay pit at Willershausen has yielded one of the most diverse and important biotas of the European

Neogene, with more than 40,000 specimens collected until the 1980s when the pit was closed and protected as a geological monument (Straus, 1967). The majority of specimens (~36,000) is held in the Geoscience Centre at the University of Göttingen, including about 3,000 insects. The highly fossiliferous deposits (primarily a 30 cm thick carbonate bed in the lower part of the pit) accumulated in a pond or small lake formed in a 100–200 m wide sinkhole basin (Meischner, 2000). The deposits are regarded as Upper Pliocene, Piacenzian (3.60–2.58 Ma), based on the assemblage of palynomorphs, macroflora and vertebrates (Mohr, 1986; Mai, 1995; Knobloch, 1998).

Material and methods

The studied material comprises 44 compression fossils, mainly isolated wings, preserved as imprints or carbonaceous films (Figs 1, 2, 4, 6, 7, 9, 10); 23 specimens are preserved as part and counterpart and 21 specimens are available as part only. The singing cicadas published by Wagner (1967) plus 23 previously unpublished specimens (those found after Wagner's publication, or specimens that were not available to, or not recognised by, the latter) included here are deposited in the Geoscience Museum at the Georg August University, Göttingen (GAU) and have collection numbers prefixed by 'GZG.W.' (Geowissenschaftliches Zentrum Göttingen, Fossilagerstätte Willershausen). The specimens of Wagner (1967) bear additional original numbers 593-1 to 593-13. The two specimens in Brauckmann & Gröning (2002) are owned by the Clausthal University of Technology (TUC) under catalogue numbers In180 and In181. The six specimens housed in the Stuttgart State Museum of Natural History (SMNS) have catalogue numbers 61908, 100.206 and 100.656 to 100.659.

Specimens were photographed with a Sony Alpha 99 II camera equipped with a Tamron SP 90mm macro lens. Line drawings were prepared using CorelDraw software from the photographs and checked against the specimens. Terminology for wing morphology follows that of Moulds (2005). Higher classification of Cicadidae follows that of Marshall *et al.* (2018).

Systematic palaeontology

Subfamily Tibicininae Distant, 1905

Tribe Tibicinini Distant, 1905

Genus *Tibicina* Kolenati, 1857

Apart from fossils resembling extant *T. haematodes* recorded by Wagner (1967), Tietz *et al.* (1998) and Brauckmann & Gröning (2002), just two other fossil species of *Tibicina* have been described from Europe: *T. gigantea* Boulard & Riou, 1989 from the late Miocene (8.5–8.0 Ma) at Andance, France, and *T. sakalai* Prokop & Boulard, 2000 from the early Miocene (17.9–17.8 Ma) at Bilina, Czech Republic. We here re-examine all the *Tibicina* material from the Willershausen deposit, determining specimens either as *Tibicina* sp., *Tibicina* aff. *haematodes* (Scopoli, 1763), *T. lata* sp. nov. or *T. boulandi* sp. nov.

There is one other cicada fossil from the late Miocene of France worth noting, *Miocenoprasia grasseti* Boulard & Riou, 1999, which has similar size and form to *Tibicina*, but it clearly differs, in fact, from most Cicadidae in having vein M branching very early after leaving the basal cell and then very late branching of the anterior branch of M so that the discal cell has one exceedingly long inner mid section.

The two new species described here are assigned to *Tibicina* because the basic structure of their wing venation conforms to the majority of species in that genus, *viz.* veins M and CuA are widely separated at the basal cell, the node is at about midlength, there are 8 apical cells, the first apical cell is narrow, the eighth apical cell has its side formed by CuA₁ almost straight thus making its distal angle very sharp, and the forewing is broader than that of most Cicadidae. While these attributes together do not exclude all possible genera of Cicadidae, they do exclude all other Palaearctic genera.

Tibicina sp.

(Fig. 1)

Material. The following specimens are determined to genus *Tibicina* only (in GAU).

GZG.W.21753a+b (coll. A. Straus), part and counterpart, partial base of forewing, showing apical cell 8, medial cell (mc), cubital cell (cuc) and clavus (clv) only.

GZG.W.22815a+b (coll. A. Straus), part and counterpart, most of distal forewing, showing ulnar cells and apical cells 2–7.

Tibicina aff. *haematodes* (Scopoli, 1763)

(Fig. 2)

Material. All specimens are similar in size to that of *T. haematodes* (all in GAU except In180 and In181 in TUC, and 100.659 in SMNS).

GZG.W.20912a+b (coll. A. Straus), part and counterpart, two partial forewings superimposed and partly obscured. Veins M and CuA widely separated at

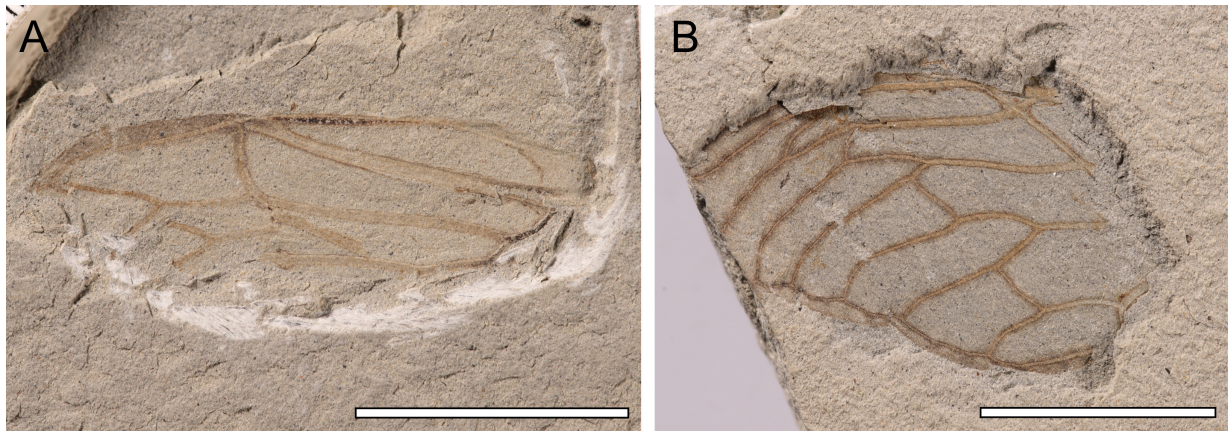


FIGURE 1. *Tibicina* sp., Pliocene of Willershausen. **A**, GZG.W.21753b. **B**, GZG.W.22518b. Scale bars = 10 mm.

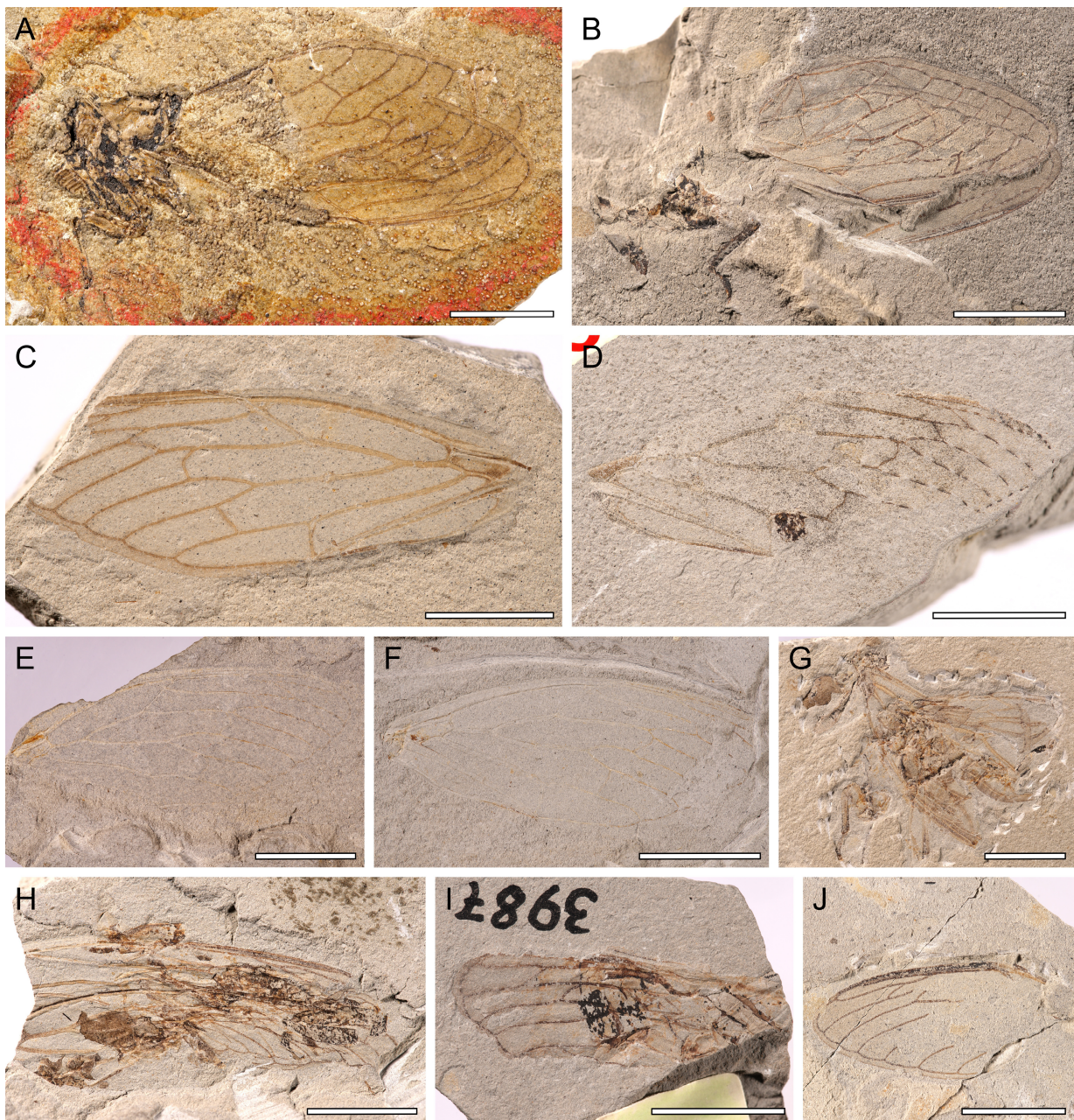


FIGURE 2. *Tibicina* aff. *haematodes*, Pliocene of Willershausen. **A**, GZG.W.11030 (593-3). **B**, GZG.W.11684b (593-1). **C**, GZG.W.12351b (593-2). **D**, GZG.W.35036 (593-11). **E**, In180, collection TUC. **F**, In181, collection TUC. **G**, GZG.W.17906. **H**, GZG.W.20912a. **I**, GZG.W.3987b (593-12). **J**, 100.659, collection SMNS. Scale bars = 10 mm.

basal cell, stem of M long, ulnar cells and apical cells slender, pigmented basal cell.

GZG.W.17906 (coll. A. Straus), part only, partial forewing base overlaying hindwings with disintegrated body. Forewing veins M and CuA widely separated at basal cell, stem of M apparently long, pigmented basal cell, visible hindwing apical cells (?2 and 3) seemingly in correct proportions.

GZG.W.35036 (593-11) (leg. H. Schmidt, 1954), part only, complete forewing. A close match in all respects to *Tibicina haematodes* or its siblings.

GZG.W.12351a+b (593-2) (coll. A. Straus), part and counterpart, complete forewing minus apex. A close match in all respects to *Tibicina haematodes* and its siblings.

GZG.W.11684a+b (593-1) (coll. A. Straus), part and counterpart, two superimposed forewings minus base. A close match to *Tibicina haematodes* and its siblings although confirmation of the basal cell is difficult but curvature of crossvein M is typical.

GZG.W.11030 (593-3) (coll. A. Straus), part only, apex and half of costal margin of one forewing partly overlying distal three-quarters of other forewing, plus lateral head, thorax and one foreleg. Wing proportions, length of rostrum to mid coxae and foreleg are all compatible with *Tibicina haematodes* and its siblings.

GZG.W.3987a+b (593-12) (coll. A. Straus), part and counterpart, distal anterior quarter of forewing, overlaid on its basal third by broken forewing cells. The size, shape and proportions of cells closely match *Tibicina haematodes* and its siblings.

In180 (coll. A. Fuhrmann), part only, forewing missing apex. The size, shape and proportions of cells closely match *Tibicina haematodes* and its siblings.

In181 (coll. A. Fuhrmann), part only, almost complete forewing missing only part of costal margin. The size, shape and proportions of cells closely match *Tibicina haematodes* and its siblings.

100.659 (ded. R. Mundlos, 1987), part only, distal two-thirds of forewing with venation on basal section ill-defined. The size, shape and proportions of cells closely match *Tibicina haematodes* and its siblings.

Remarks. Among extant cicada species in Europe, the fossils listed below closely match *Tibicina haematodes* in forewing size, shape and venation. *Tibicina haematodes* is a common species widely distributed across Europe and beyond. However, we now know there is another extant *Tibicina* species found in Europe of similar size and with similar venation, *T. steveni* (Krynicky, 1837), which provides an alternative possibility for these fossils. Further, from the wings alone we cannot be sure that these fossils represent extant species, and the possibility they represent an extinct species cannot be ignored. These fossils could, in fact, represent a mixture of all three of the above possibilities, or others not considered. Hence, we determine these fossils as being similar to *T. haematodes* but not necessarily that species.

***Tibicina lata* sp. nov.**

(Figs 3, 4)

Material. Holotype, complete forewing with counterpart, GZG.W.14592a+b (coll. A. Straus, in GAU). Paratype, complete forewing with counterpart, GZG.W.23091a+b (coll. A. Straus, in GAU).

Associated specimens (all in GAU except last in SMNS):

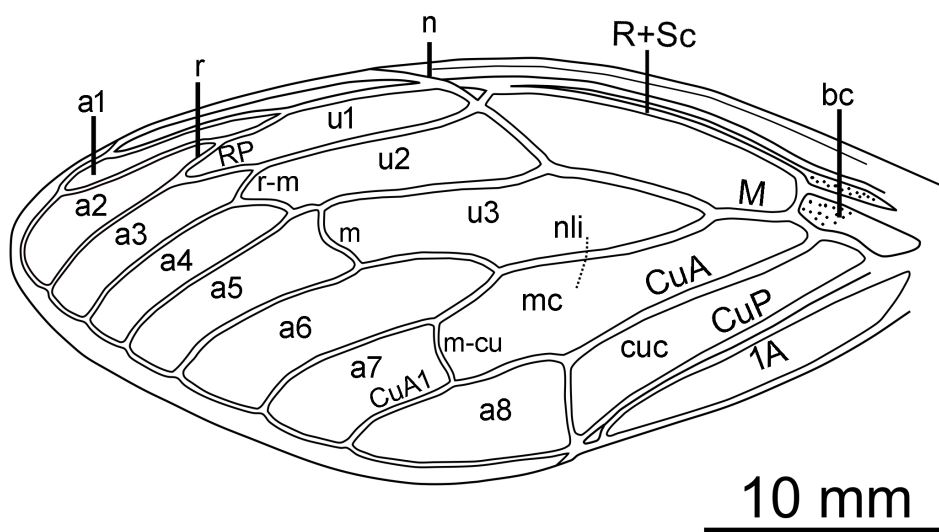


FIGURE 3. Forewing of *Tibicina lata* sp. nov., drawing based on holotype GZG.W.14592a+b and paratype GZG.W.23091a+b. a apical cell; bc basal cell; cuc cubital cell; CuA cubitus anterior vein; CuP cubitus posterior vein; M median vein; m medial crossvein; mc medial cell, (also ulnar cell 4 on forewing); m-cu mediocubital crossvein; n node; nli nodal line intersection; R radius; r radial crossvein; RA radius anterior; r-m radiomedial crossvein; RP radius posterior; Sc subcostal vein; u ulnar cell.

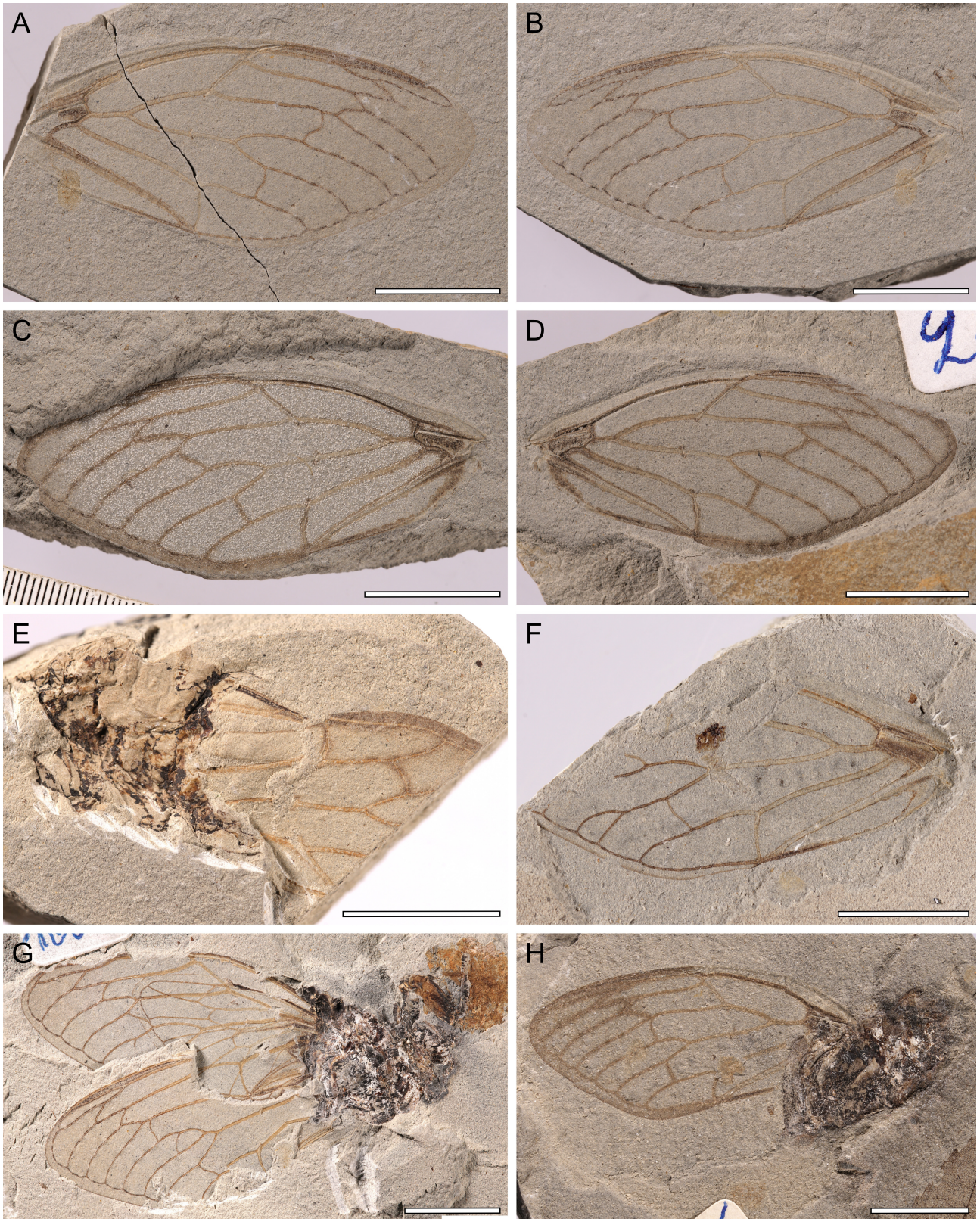


FIGURE 4. *Tibicina lata* sp. nov., Pliocene of Willershausen. **A, B**, holotype GZG.W.14592a+b. **C, D**, paratype GZG.W.23091a+b. Associated specimens: **E**, GZG.W.11666b (593-5). **F**, 100.657, collection SMNS. **G**, GZG.W.16688b. **H**, GZG.W.13308a (593-4). Scale bars = 10 mm.

GZG.W.11666a+b (593-5) (coll. A. Straus), part and counterpart, basal half of forewing but missing basal area including basal cell, together with body fragments.

GZG.W.13308a+b (593-4) (coll. A. Straus), part and counterpart, forewing with base partly covered by ventral thorax, plus head.

GZG.W.16688 (coll. A. Straus), part and counterpart, two forewings partly superimposed, distal third of hindwing beneath forewing and deformed head and thorax obscuring wing bases. Apical cells short, discal cell slender.

100.657 (ded. R. Mundlos, 1987), part only, basal two-thirds of forewing missing anterior distal quarter. Venation and pigmentation similar to *T. lata* **sp. nov.**

Etymology. From the Latin *latus* meaning broad or wide, and referring to the exceptionally broad forewing of this species.

Diagnosis. *Tibicina lata* **sp. nov.** differs from *T. haematodes* and other extant *Tibicina* species in having, in combination, a broader and more rounded forewing (holotype ratio width to length 1:2.4, paratype 1:2.3 compared to *T. haematodes* 1:2.6), veins M and CuA about as widely separated at the basal cell as the distance between M and R+Sc, the fused stem of M is usually much shorter, the nodal line intersection on vein M_{3+4} beyond midlength, and the costal margin is more ampliate so that veins C and Sc are widely separated on the basal portion of the wing.

Locality and horizon. Former clay pit at Willershäusen, Lower Saxony, Germany; Upper Pliocene, Piacenzian (3.60–2.58 Ma).

Description. Forewing (Fig. 3) unusually broad and rounded, holotype ratio width to length 1: 2.4, paratype 1: 2.3; anal angle broadly rounded; wing margin well developed; node at about mid length of costal margin; costal margin ampliate so that C is distant from Sc in basal region; perhaps with infuscation in the vicinity of crossveins r and r-m as vaguely suggested in paratype and on associated specimen GZG.W.13308 (Fig. 4H); basal cell partially pigmented; vein M with a short stem so that its length is clearly shorter than median section of discal cell; veins M and CuA clearly separated at basal cell with the distance between them similar to that between M and R+Sc; veins CuP and 1A separated or abutted for their

length; nodal line intersection beyond mid length of vein M_{3+4} ; basal cell elongate; with 8 apical cells, the first very narrow; apical cells shorter than ulnar cells; apical cells 2–7 all similar in width; apical cell 8 tending triangular; ulnar cells 1–3 all similar in width; medial cell (equals ulnar cell 4) long and narrow, its width not much more than that of apical cells; cubital cell wide, almost as wide as the medial cell; crossveins r and r-m of similar length, parallel, each only a little shorter than the distance between them along RP; crossveins m and m-cu usually bowed; vein CuA_1 divided by crossvein m-cu at about mid length.

Measurements. Holotype: forewing 37 mm long × 16.5 mm wide. Paratype: forewing 34 mm long × 15 mm wide.

Remarks. *Tibicina lata* **sp. nov.** differs from the late Miocene fossil *Tibicina gigantea* in being smaller (forewing 34–37 mm rather than 47 mm). It differs from the only other known *Tibicina* fossil from Europe, *T. sakalai* from the early Miocene, in having apical cells 2–7 all of similar width, not with apical cell 7 (not 5 as stated by Prokop & Boulard, 2000) being much wider; this is the only difference of any note but the large age difference is certainly suggestive of the two being distinct species.

***Tibicina bouldardi* sp. nov.**

(Figs 5, 6)

Material. Holotype, part and counterpart, complete forewing, GZG.W.17632a+b (coll. A. Straus, in GAU). The outer midsection of the wing has fractured and turned inward, fracturing and distorting veins M_{3+4} , distorting vein CuA_1 and crossvein m, and fracturing apical cells 5–6.

Other associated specimens (all in GAU):

GZG.W.8816 (coll. A. Straus), part only, distal third of forewing.

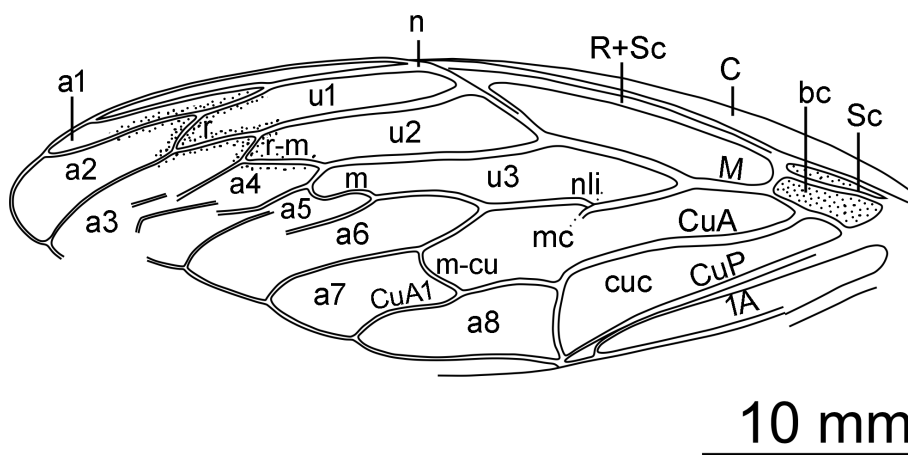


FIGURE 5. Forewing of *Tibicina bouldardi* **sp. nov.**, drawing based on holotype GZG.W.17632a+b. Abbreviations as for Fig. 4.

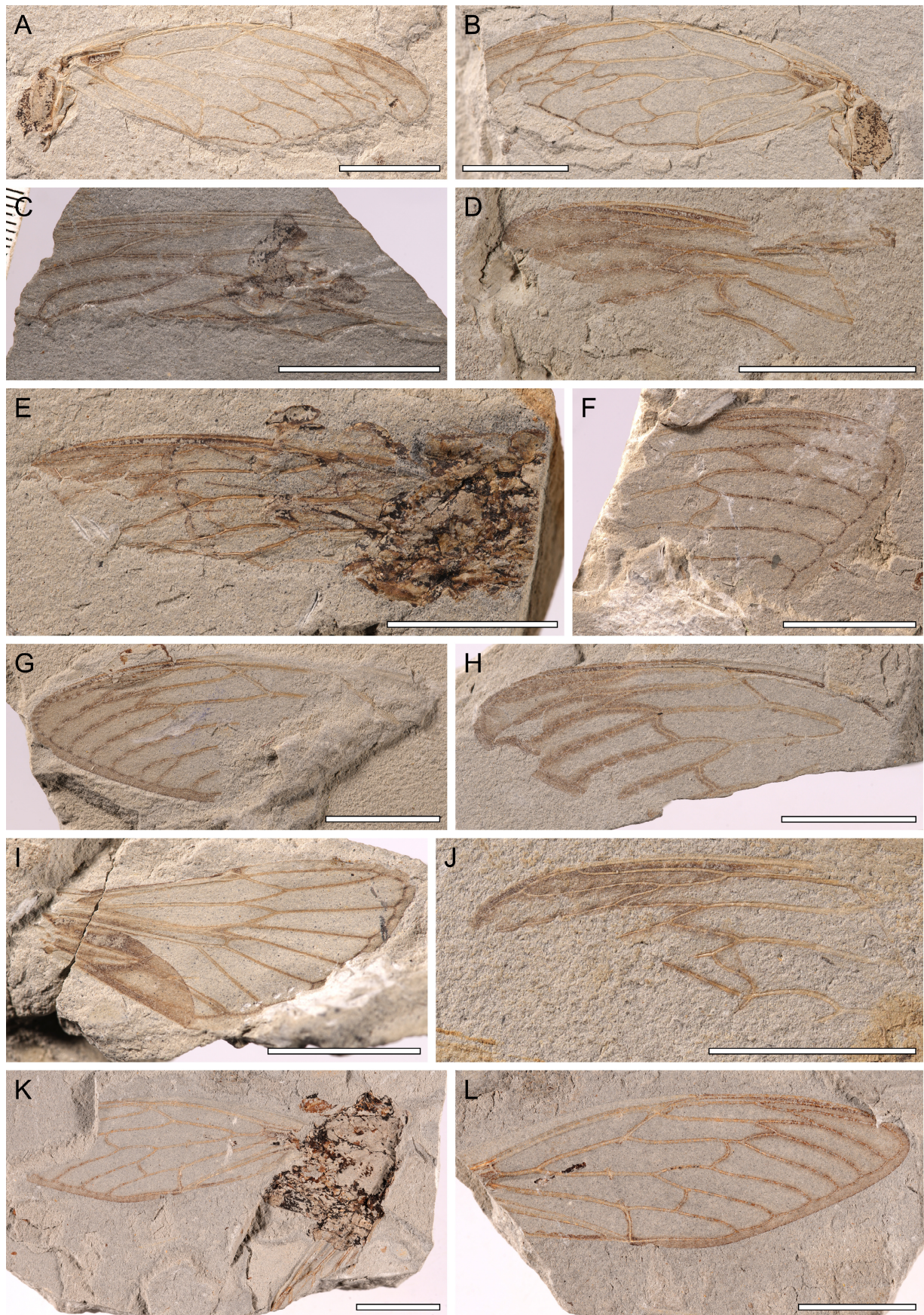


FIGURE 6. *Tibicina boulandi* sp. nov., Pliocene of Willershausen. **A, B**, holotype GZG.W.17632a+b. Associated specimens: **C**, GZG.W.9132. **D**, GZG.W.11178 (593-6). **E**, GZG.W.13689a (593-7). **F**, GZG.W.8816. **G**, GZG.W.15412b. **H**, GZG.W.16175b. **I**, GZG.W.16879a. **J**, GZG.W.17330b. **K, L**, 61908a+b, collection SMNS. Scale bars = 10 mm.

GZG.W.9132 (coll. A. Straus), part only, mid-section of forewing costal margin with some associated cells.

GZG.W.11178 (593-6) (coll. A. Straus), part only, forewing apex with partial costa and associated cells.

GZG.W.13689a+b (593-7) (coll. A. Straus), part and counterpart, forewing costal margin and associated cells minus base and apex together with head and body fragments.

GZG.W.15412a+b (coll. A. Straus), part and counterpart, distal two-thirds of forewing.

GZG.W.16175a+b (coll. A. Straus), part and counterpart, most of distal two-thirds of forewing.

GZG.W.16879a+b (coll. A. Straus), part and counterpart, hindwing. Infuscated apex*.

GZG.W.17330a+b (coll. A. Straus), part and counterpart, portion of distal forewing and basal cell.

61908a+b (ded. R. Mundlos, 1987), part and counterpart, dorsal head, thorax and first few abdominal segments (all ill-defined), with attached left forewing complete and small basal portion of right forewing.

*The single hindwing specimen, GZG.W.16879, may belong to this species with its infuscated apex and a size compatible with that of the forewings. Otherwise, it must belong to either another undescribed *Tibicina* species (as there are no other *Tibicina* with infuscated wings), or to a species in another genus. We consider it most likely to belong to *T. bouldardi* in the absence of any known alternative possibility.

Etymology. Named in honour of Michel Boulard who devoted much of his life to the study of both extant and fossil cicadas. He made enormous contributions to our understanding of their systematics and biology, especially of the European and African faunas. He is now 88.

Diagnosis. *Tibicina bouldardi* **sp. nov.** differs from all other *Tibicina* species (including those described from fossils) in having the forewings infuscated in the vicinity of crossveins r and r-m. It also differs from the similarly sized *T. haematodes* and its siblings in having a narrower forewing (holotype ratio width to length 1:2.8 compared to *T. haematodes* 1:2.6).

Locality and horizon. Former clay pit at Willershausen, Lower Saxony, Germany; Upper Pliocene, Piacenzian (3.60–2.58 Ma).

Description. Forewing (Fig. 5) of average proportions, holotype ratio width to length 1:2.8; anal angle rounded but distinct; wing margin well developed; node a little beyond mid length of costal margin; costal margin ampliate so that C is distant from Sc in basal region; infuscated in vicinity of crossveins r and r-m although not distinct in holotype and variable in extent in associated specimens; basal cell pigmented; vein M with a moderately long stem; veins M and CuA widely separated at basal cell so that the distance between them

is much more than between M and R+Sc; veins CuP and 1A not fused as one for any part of their length; nodal line intersection about mid length on M_{3+4} ; basal cell elongate; with 8 apical cells, the first very narrow; apical cells shorter than ulnar cells; apical cells 2–7 all similar in width; apical cell 8 tending triangular; ulnar cells 1–3 all similar in width; medial cell (equals ulnar cell 4) long and narrow, its width not much more than that of apical cells; cubital cell wide, almost as wide as the medial cell; crossveins r and r-m of similar length, parallel, and relatively close together so that the distance between them is no more than double their length; crossveins m and m-cu bowed (m seemingly distorted by the inward movement of the outer mid-section of the wing); vein CuA_1 divided by crossvein m-cu at about mid length.

Measurements. Holotype: forewing 36 mm long × 13.0 mm wide.

Subfamily Cicadinae Latreille, 1802

Tribe Cicadini Latreille, 1802

Genus *Cicada* Linnaeus, 1758

Cicada aff. *orni* Linnaeus, 1758

(Fig. 7A–E)

Material. All specimens are similar in size to that of *C. orni* (all in GAU).

GZG.W.21944a+b (coll. A. Straus), part and counterpart, costal part of forewing overlaid with part of hindwing. In one forewing veins M and CuA are visible close together at the basal cell and the long, fused stem of hindwing veins RP and M, are typical attributes of *Cicada orni*.

GZG.W.15819a+b (coll. A. Straus), part and counterpart, male, lateroventral head, thorax and basal abdomen with right forewing. The large eye, leg markings, wing infuscations and wing cell proportions all closely match extant *C. orni* from France.

GZG.W.35037 (593-9) (leg. H. Schmidt, 1938), part only, female, ventral body, with wings attached but only partly visible. Forewing with typical infuscations on crossveins r and r-m; basal cell not visible but wing proportions and other cells typical of *C. orni*.

GZG.W.5144 (593-13) (coll. A. Straus), part only, portion of ventral head, thorax and base of abdomen with basal half of both forewings overlaying hindwings partly obscured. Typical infuscations on crossveins r and r-m; basal cell ill-defined but wing proportions and other cells typical of *C. orni*.

GZG.W.13310a+b (593-8) (coll. A. Straus), part and counterpart, ventro-lateral head and thorax with flat forewing basally obscured and apex of second forewing. Figured by Wagner (1967) and reproduced in Moulds (2018).

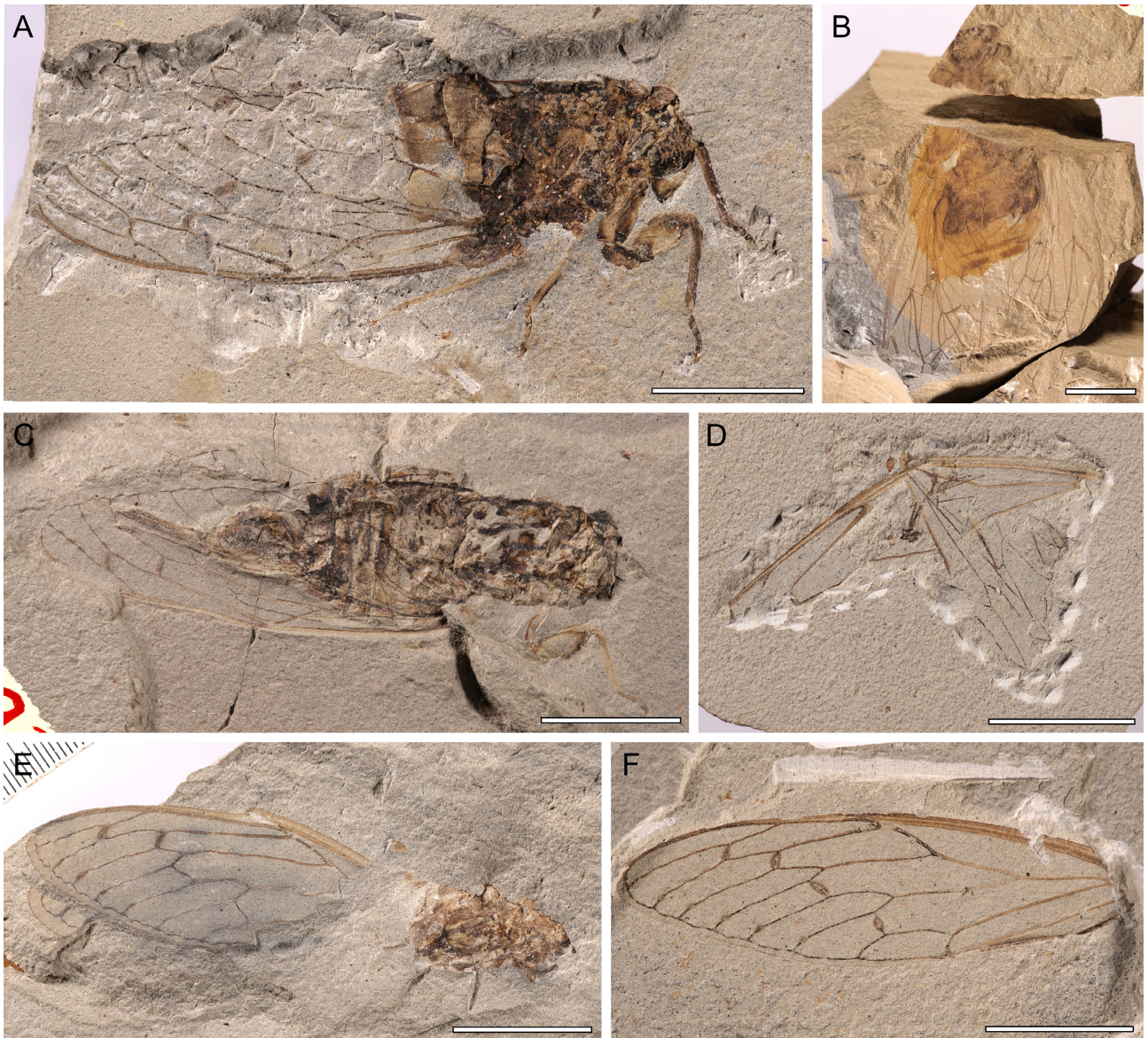


FIGURE 7. *Cicada* species, Pliocene of Willershausen. *Cicada* aff. *orni* (A–E): A, GZG.W.15819b. B, GZG.W.5144 (593-13). C, GZG.W.35037 (593-9). D, GZG.W.21944b. E, GZG.W.13310b (593-8). *Cicada* aff. *lodosi*. F, GZG.W.21609b. Scale bars = 10 mm.

Locality and horizon. Former clay pit at Willershausen, Lower Saxony, Germany; Upper Pliocene, Piacenzian (3.60–2.58 Ma).

Remarks. *Cicada orni* is a common and widespread species throughout much of Europe, North Africa, and western parts of Asia. Other species in the genus are confined to Europe and North Africa (Dlabola, 1984; Quartau & Simões, 2005). The Willershausen fossils closely match *Cicada orni* and its siblings, in the position of wing infuscations, cell proportions, position of nodal line intersection on M_{3+4} , and in wing size and shape, although apical cell 1 tends, on average, to be slightly larger. In view of the relative abundance of *C. orni*, these fossils may represent true *C. orni*. However, we cannot rule out the possibility that they do represent a sibling species

or an extinct species. Hence, we determine the fossils as being closely similar to *C. orni* but not necessarily that species.

***Cicada* aff. *lodosi* Boulard, 1979**
(Fig. 7F)

Material. GZG.W.21609a+b (coll. A. Straus, in GAU), part and counterpart, almost complete forewing.

Remarks. *Cicada lodosi* was originally described from Turkey but later recorded from Greece (Boulard, 1979; Quartau & Simões, 2005). The Willershausen fossil GZG.W.21609 shows affinities with *Cicada lodosi* in the position of wing infuscations, position of the nodal line intersection on M_{3+4} , in wing size and shape, and more

significantly, in the proportions of the apical cells to ulnar cell lengths although the apical cells are a little longer than in *C. lodosi* and the inner central section of the discal cell is a little longer. While we cannot rule out the possibility that GZG.W.21609 represents an undescribed species, we refrain from describing it as such without more convincing evidence. We therefore treat it as showing affinities with *C. lodosi*.

***Cicada tithonus* sp. nov.**
(Figs 8, 9)

Material. Holotype, part only (no counterpart), ?male. Head, thorax and sternites ?II–IV, with wings attached; the whole specimen on its back but tilted to one side; with distal two-thirds of forewings partly visible with one mostly obscured; hindwings almost entirely obscured. In SMNS, Inv. Nr. 100.206.

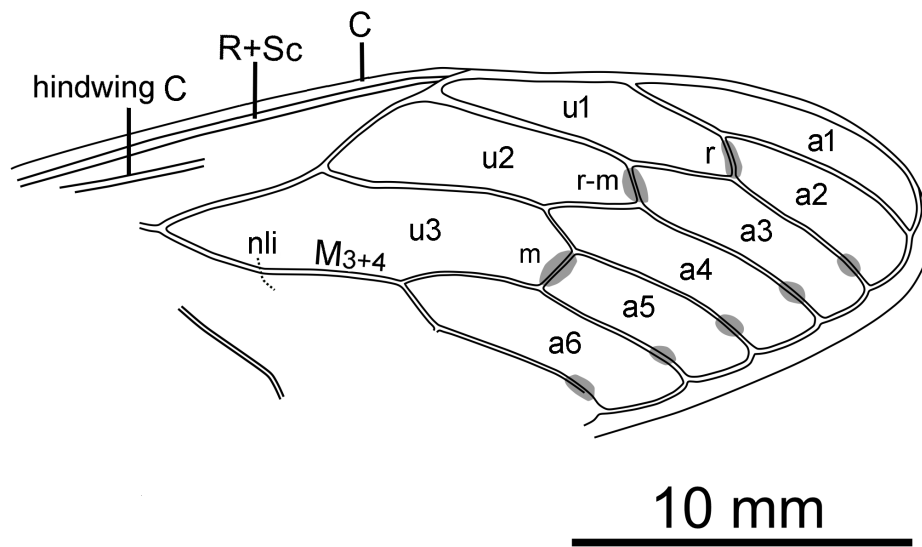


FIGURE 8. Forewing of *Cicada tithonus* sp. nov., drawing based on holotype 100.206 (collection SMNS). Abbreviations as for Fig. 4.

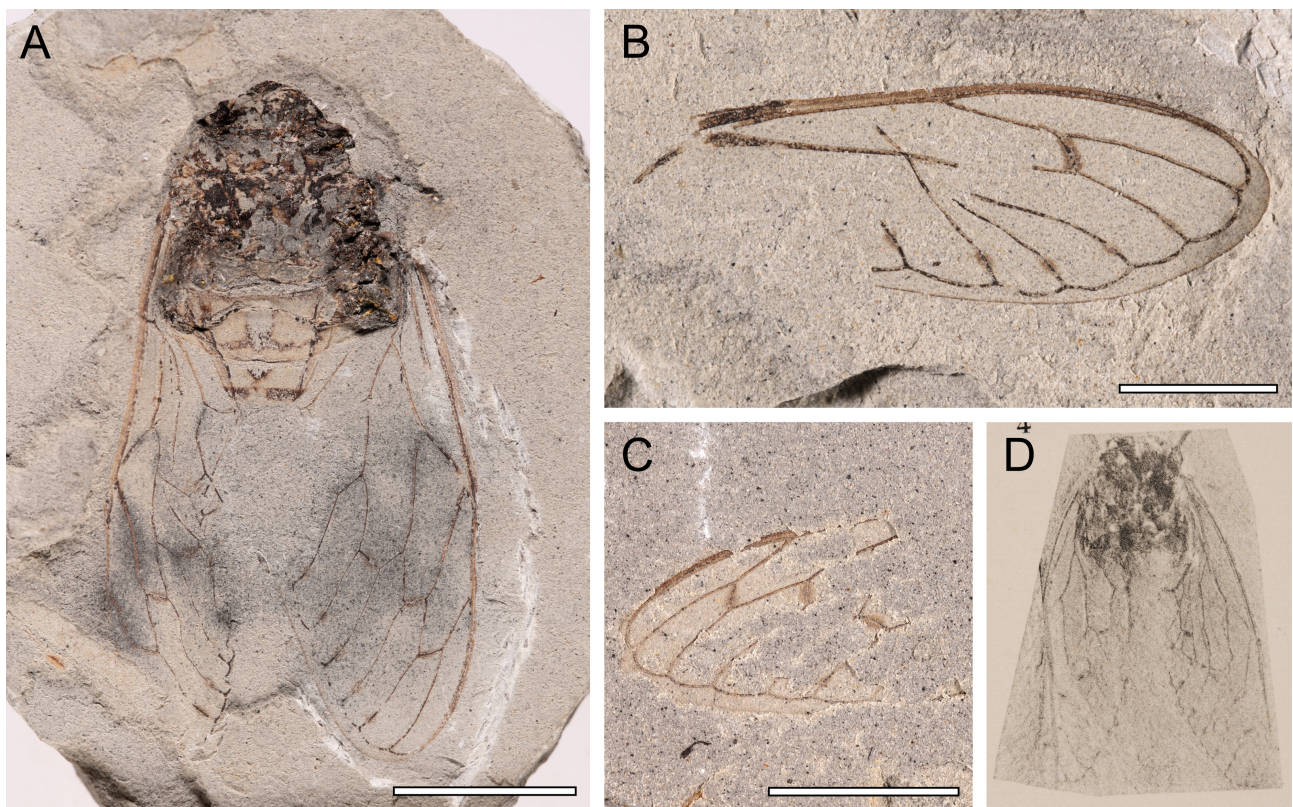


FIGURE 9. *Cicada tithonus* sp. nov., Pliocene of Willershausen. **A**, holotype 100.206. **B**, 100.656. **C**, 100.658, all collection SMNS. **D**, specimen figured in Straus (1952, pl. 4, Fig. 11). Scale bars = 10 mm.

Associated specimens (in GAU):

100.656 (ded. R. Mundlos, 1987), part only, distal half of forewing fractured longitudinally so that the posterior of the wing partly overlays the anterior as implied by the position of vein M_3 , and part of the central venation is missing; this has distorted the wing shape making it appear narrower than it should be.

100.658 (ded. R. Mundlos, 1972), part only, portion of distal forewing. The lost specimen figured by Straus (1952) also appears to belong to this species (see discussion below).

Etymology. From *Tithonus* (a Latin proper noun, in apposition), the Greek mythical lover of Aurora (or Eos), symbolic of old age, and changed into a cicada.

Diagnosis. The spot-like forewing infuscations in conjunction with the position of crossveins r, r-m and m in relation to their comparative angles and positions on veins RA, RP and M are all typical of the genus *Cicada*. Among extant species of *Cicada*, and other available fossils in the genus, *Cicada tithonus* sp. nov. is unique in having a very wide apical cell 1, as wide as apical cells 2–6, and in

having the apical cells similar in length to the ulnar cells rather than being much shorter.

Locality and horizon. Former clay pit at Willershausen, Lower Saxony, Germany; Upper Pliocene, Piacenzian (3.60–2.58 Ma).

Description. Forewing (Fig. 8) tending broad, ratio width to length approximately 1:2.5; wing margin well developed; node at about mid length of costal margin; costal margin narrow so that C is adjacent to R+Sc; with spot-like infuscations overlaying crossveins r, r-m, m and doubtfully m-cu, and also near extremities of veins forming apical cells 1–6 (other cells not visible); basal cell not visible; nodal line intersection a little proximal of mid-length of vein M_{3+4} ; apical cells about as long as ulnar cells; apical cell 1 exceptionally broad, as broad as other visible apical cells 2–6; ulnar cells 1 and 2 similar in width, ulnar cell 3 just a little wider; crossveins r and r-m of similar length, parallel, each shorter than the distance between them along RP. The specimen appears to be a male suggested by its broad sternites that would be sternites II–IV, although there is no clear indication of opercula or timbals.

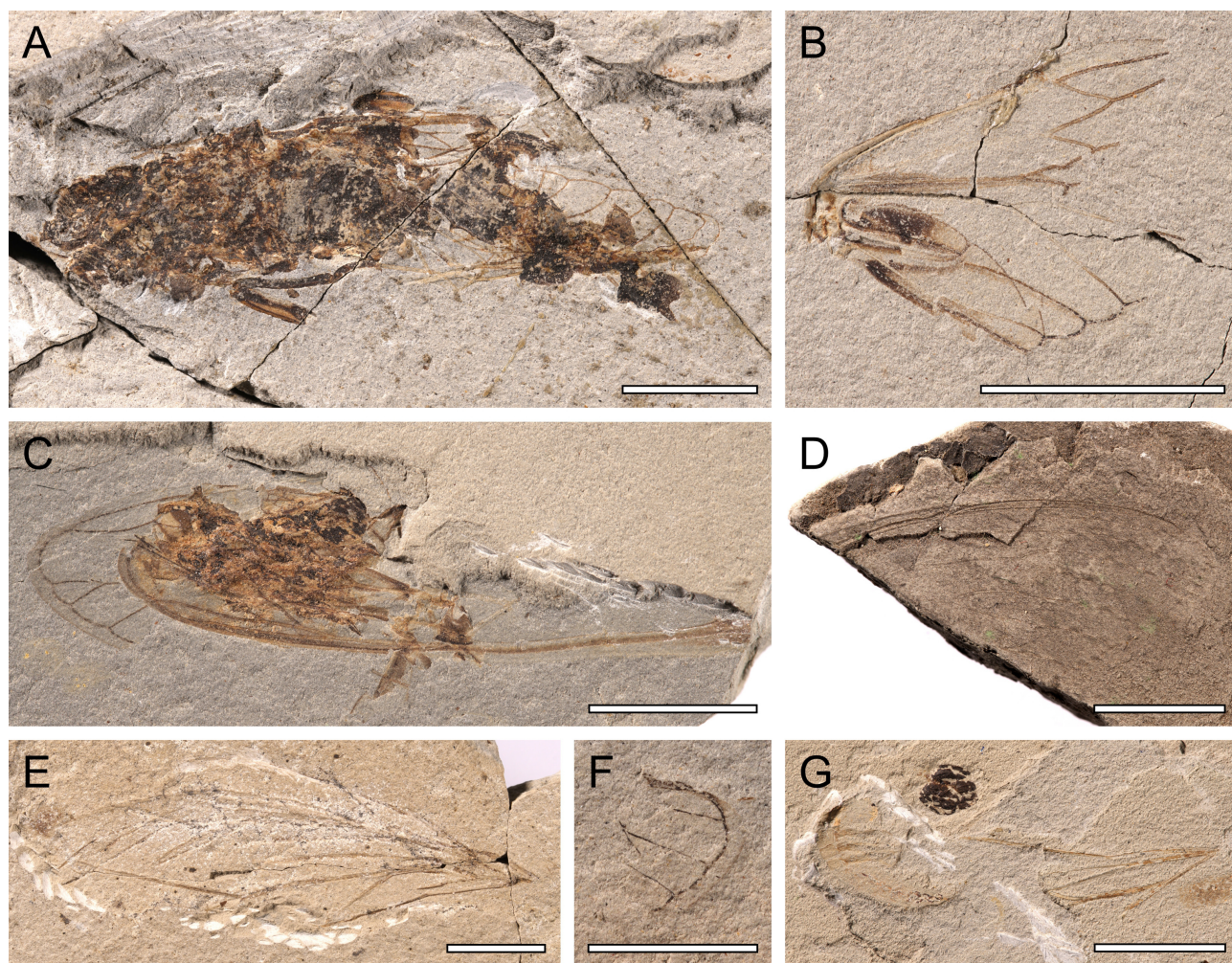


FIGURE 10. Indeterminable Cicadidae specimens, Pliocene of Willershausen. **A**, GZG.W.15826. **B**, GZG.W.40308b. **C**, GZG.W.11005a (593-10). **D**, GZG.W.15114. **E**, GZG.W.15113. **F**, GZG.W.40310. **G**, GZG.W.18044a. Scale bars: **A–E, G** = 10 mm, **F** = 5 mm.

Measurements. Holotype: total length (head, body and wings) 38 mm; forewing length approximately 30 mm; width of forewing approximately 12 mm.

Remarks. Straus's (1952) fossil image (pl. 4, fig. 11, with caption 'cf. *Cicadetta* sp. '), which we have reproduced here (Fig. 9D) shows clear affinities with *Cicada tithonus* **sp. nov.** Of note are its protruding eyes typical of the genus *Cicada*, the row of submarginal spots on the veins forming the apical cells of the forewing that are typical of the genus, the apical and ulnar cells at roughly the same length (in most *Cicada* species the ulnar cells are longer as in *C. orni*), the departure of forewing vein M_{3+4} from the discal cell more basal so that the central section of the inner margin of the discal cell is much longer than the distal section, and its similar size (forewing length estimated at 31 mm). Although the distal apical cells of Straus's specimen are only visible in the right forewing as well as being somewhat blurred, apical cell 1 does appear to be very broad, a key attribute of *Cicada tithonus* **sp. nov.**

Indeterminable specimens

(Fig. 10)

Material. The identity of the following Cicadidae specimens remains unknown (all in GAU).

GZG.W.40308a+b (leg. H. Grabenhorst, ded. H. Grabenhorst 2019), part and counterpart. basal half of hindwing, large anal lobe.

GZG.W.40310 (leg. H. Grabenhorst, ded. H. Grabenhorst 2019), apex of forewing.

GZG.W.18044a+b (coll. A. Straus), part and counterpart, remnants of basal veins and wing apex. Possible part of forewing venation overlaid by hindwing, plus apparent hindwing apex, unidentifiable but by size apparent Cicadidae.

GZG.W.15826 (coll. A. Straus), disintegrated body with partial wings, ventral view.

GZG.W.15114 (coll. A. Straus), distal two-thirds of forewing in poor definition.

GZG.W.15113 (coll. A. Straus), apparent forewing, distorted with most venation ill-defined.

GZG.W.11005a+b (593-10) (coll. A. Straus), part and counterpart, ill-defined body fragments (probably head and thorax) with forewing apex and other wing fragments.

Conclusion

Our review of singing cicadas from the Pliocene of Willershausen confirms the presence of the two subfamilies Tibicinae and Cicadinae in this lacustrine

deposit. The more common Tibicinae (28 out of 38 identifiable specimens) are all in the tribe Tibicinini and include *Tibicina* sp., *Tibicina* aff. *haematodes* and *Tibicina lata* **sp. nov.** and *Tibicina bouldardi* **sp. nov.** The less common Cicadinae (9 specimens) are represented by *Cicada* aff. *orni*, *Cicada* aff. *lodosi* and *Cicada tithonus* **sp. nov.** in the tribe Cicadini. Including these and seven Cicadidae specimens of uncertain identity, singing cicadas numerically account for less than 1% of the insect finds from the Pliocene of Willershausen.

Acknowledgements

We are grateful to Carsten Brauckmann, Brigitte Brauckmann and Elke Gröning for fruitful discussions and for making the material in TUC available to us. We are also grateful to Michael Rasser for the loan of the SMNS material. We thank Stéphane Puissant for helpful discussion regarding *Tibicina* and *Cicada*, and Albert Orr kindly helped with nomenclature matters. André Nel and an anonymous reviewer kindly gave helpful comments on a final draft of the manuscript.

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