

Redescription of the Planthopper *Bursinia genei* (Dufour, 1849), with a New Record from Greece (Hemiptera: Fulgoromorpha: Dictyopharidae)

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Bursinia genei (Dufour, 1849) is the most widespread species of the planthopper subfamily Orgeriinae (Hemiptera: Fulgoromorpha: Dictyopharidae) in Europe, found from the Iberian Peninsula to the Western Balkans. However, its diagnostically important genitalia and biology have been insufficiently described. We employ state-of-the-art synchrotron X-ray microtomography and photomicrography to re-describe *B. genei*, and to study the morphology of both its sexes in unprecedented detail. By examining specimens from across the distribution of *B. genei*, we find that they probably belong to a single, broadly distributed morphospecies. Our morphological examination allowed us to make inferences on its jumping mechanism and capacity for vibrational communication. We also record *B. genei* for the first time from Greece, further extending the range of this elusive species. Detailed information on the habitat of *B. genei* is also provided.

Key words: Auchenorrhyncha, Orgeriinae, Snapping organ, Balkans, Taxonomy, X-ray tomographic microscopy.

BACKGROUND

The planthopper genus *Bursinia* Costa, 1862 (Hemiptera: Dictyopharidae: Orgeriinae: Almanini) comprises 18 species with a largely West Mediterranean distribution, whose centre of diversity is in the Iberian Peninsula, where 11 species are endemic (Horváth 1910 1913 1936; Emeljanov 1972 1980 2003; Emeljanov and Drosopoulos 2004; Bourgoïn 2022). *Bursinia* is split into two subgenera: *Bursinia sensu stricto*, distributed primarily in southern Europe, and *Struthionia* Emeljanov, 2009, which is found exclusively in North

Africa (Algeria, Morocco, Tunisia), Spain, Sicily and Malta (Emeljanov 2003 2009; Linnavuori 1965). However, the validity of the various *Bursinia* spp. is ambiguous, as the genus has not been revised since the work of Horváth (1910), and most species descriptions are short, with few to no illustrations of diagnostic features such as the genitalia. An updated taxonomic revision of all described taxa in this biogeographically interesting genus is urgently required.

As a first step towards the abovementioned objective, we studied the taxonomy of the most widespread species of the genus, *B. (Bursinia) genei*

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(Dufour, 1849), which was described from Sardinia and later recorded from Spain, Portugal, France (including Corsica), mainland Italy, Croatia, Bosnia and Hercegovina, and Montenegro (Horváth 1910; Melichar 1912; Metcalf 1946; Emeljanov 2003). Like most of its congeners, *B. genei* is an elusive species that has seldom been collected, and almost nothing is known regarding its biology. Furthermore, the genitalia of this species have only been illustrated partly and schematically (Emeljanov 1980), which makes it difficult to distinguish it from its congeners. It is also possible that being flightless, different subpopulations may have been isolated for millennia, leading to the evolution of multiple related cryptic species.

In the present study, we use conventional and state-of-the-art techniques to redescribe the morphology of *B. genei*, providing the first detailed description of its genitalia based on material from across the species' distribution. We used synchrotron X-ray microtomography (SR- μ -CT) to reconstruct the internal morphology of *B. genei*, which allowed us to make inferences regarding aspects of its jumping and vibrational behaviour. We also record *B. genei* from the Pindus mountain range in Epirus, Greece, for the first time, further extending its distribution to south-eastern Europe.

MATERIALS AND METHODS

Photomicrographs of the habitus of *B. genei* were taken using a Leica M165c binocular microscope equipped with a Leica DFC490 camera at the Oxford University Museum of Natural History (OUMNH), or a Keyence VHX-5000 digital microscope with VH-Z20T and VH-ZST objectives at the Department of Botany and Zoology, Masaryk University, Brno. The latter equipment was also used to image the snapping organ and genitalia of *B. genei*. All photomicrographs were stacked and combined using Helicon Focus or Keyence VHX-5000 software.

For examination of male and female genitalia, abdomina were detached from specimens and cleared in a 10% solution of warm KOH for approximately two hours. Dissections were made in distilled water. A few drops of chlorazol black (CAS No. 1937–37–7) were later added to water to dye the female ectodermic genital ducts (Carayon 1969; Bourgoin 1993).

X-ray tomographic microscopy scans of a critical-point dried male specimen of *B. genei* from Greece were obtained at the TOMCAT beamline, Swiss Light Source (SLS), Paul Scherrer Institut, Switzerland, at an X-ray beam energy of 15.99 keV with final pixel size of 1.625 μ m. Three-dimensional image processing and

segmentation was carried out using Amira 6.1 software (Mercury Systems). Image labelling and illustrations were generated in Adobe Illustrator CC/CS6 (Adobe Systems Incorporated, San Jose, California, USA).

As we did not have the opportunity to study the type material of *B. genei* or any other specimen from Sardinia, the species' type locality, we used the works of Horváth (1910), Melichar (1912), Emeljanov (1969 1972 1980 2009) and Emeljanov and Drosopoulos (2004) for the identification of the examined material. The identification of the specimens from Greece as *B. genei* was also kindly confirmed by Prof. Alexander F. Emeljanov (Zoological Institute, Russian Academy of Sciences, St. Petersburg) based on habitus photographs. The morphological terminology in the description follows Song et al. (2018) for the general morphology and male genitalia, Bourgoin (1993) for the female genitalia, and Davranoglou et al. (2019) for the vibrational (snapping) organ.

The examined specimens were deposited at the Natural History Museum in London (BMNH) and the Moravian Museum in Brno (MMBC).

RESULTS

TAXONOMY

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Duméril, 1806
Infraorder Fulgoromorpha Evans, 1946
Family Dictyopharidae Spinola, 1839
Subfamily Orgeriinae Fieber, 1872
Tribe Almanini Kusnezov, 1936
Genus *Bursinia* Costa, 1862

***Bursinia genei* (Dufour, 1849)**
 (Figs. 1–10)

Dyctiophora [sic] *senegalensis* nec Spinola, 1839 – Spinola 1839: 296 (misidentification, not conspecific with the type of *D. senegalensis*, now *Philotheria senegalensis* (Spinola, 1839), according to Melichar 1912: 93 and Metcalf 1946: 189).

Dyctiophora [sic] *genei* Dufour, 1849: 101 (original description).

Almana genei – Stål 1861: 150 (new combination, listed).

Bursinia genei – Horváth 1910: 180, 183, fig. 5 (new combination, in key, redescription); Melichar 1912: 185, 188 (in key, redescription); Metcalf 1946: 189 (catalogue); Emeljanov 1980: 27, 29, figs. 113, 126 (drawings of female gonapophysis VIII and male phallosome).

Bursinia genei var. *dispar* Horváth, 1910: 180, 184, fig. 6. Synonymy according to Nast 1972: 93.

Bursinia (*Bursinia*) *genei* – Emeljanov 2009: 48 (listed).

Material examined: Spain: Sierra de Guadarrama,

viii.1927, Uvarov leg., 1 m*, 1 f* (BMNH); Espinar, viii.1894, I. Bolivar leg., 1 f* (MMBC). France: Alpes-Maritimes, Théoule, 14.vii.1955, P. Hervé leg., 1 m*; Alpes-Maritimes, Sospel env., Albaria, Mt Razit, 700 m, 31.vii.1955, P. Hervé leg., 1 m*; Serres, 8.vii., F. Lombard leg., 2 m*m*; same data but ix., 1 m* 1 f* (all MMBC). Croatia: Murter, Slanica, 25.viii.1983, I. Vavřínová leg., 1 m*; Dalmatia, Ragusa, 2 m* m* (all MMBC). Greece: Epirus, Konitsa Municipality, outskirts of Konitsa, 40°2'56.80"N, 20°45'50.53"E,

818 m, 24.vii.2015, L.-R. Davranoglou & Z.W.W. Soh leg., 2 m*m* (BMNH).

Redescription: Colouration (same in both sexes). General body colour light ochreous; tegmina ochreous to dark brown, often darker than rest of body (Fig. 1A–D); cephalic process with a dark brown-greyish suffusion that runs along most of its length, becoming lighter at level of eyes (Fig. 1B–E); a dark brown band extending from paranotal lobe of pronotum to the head at the level of antennae, often reaching clypeal area

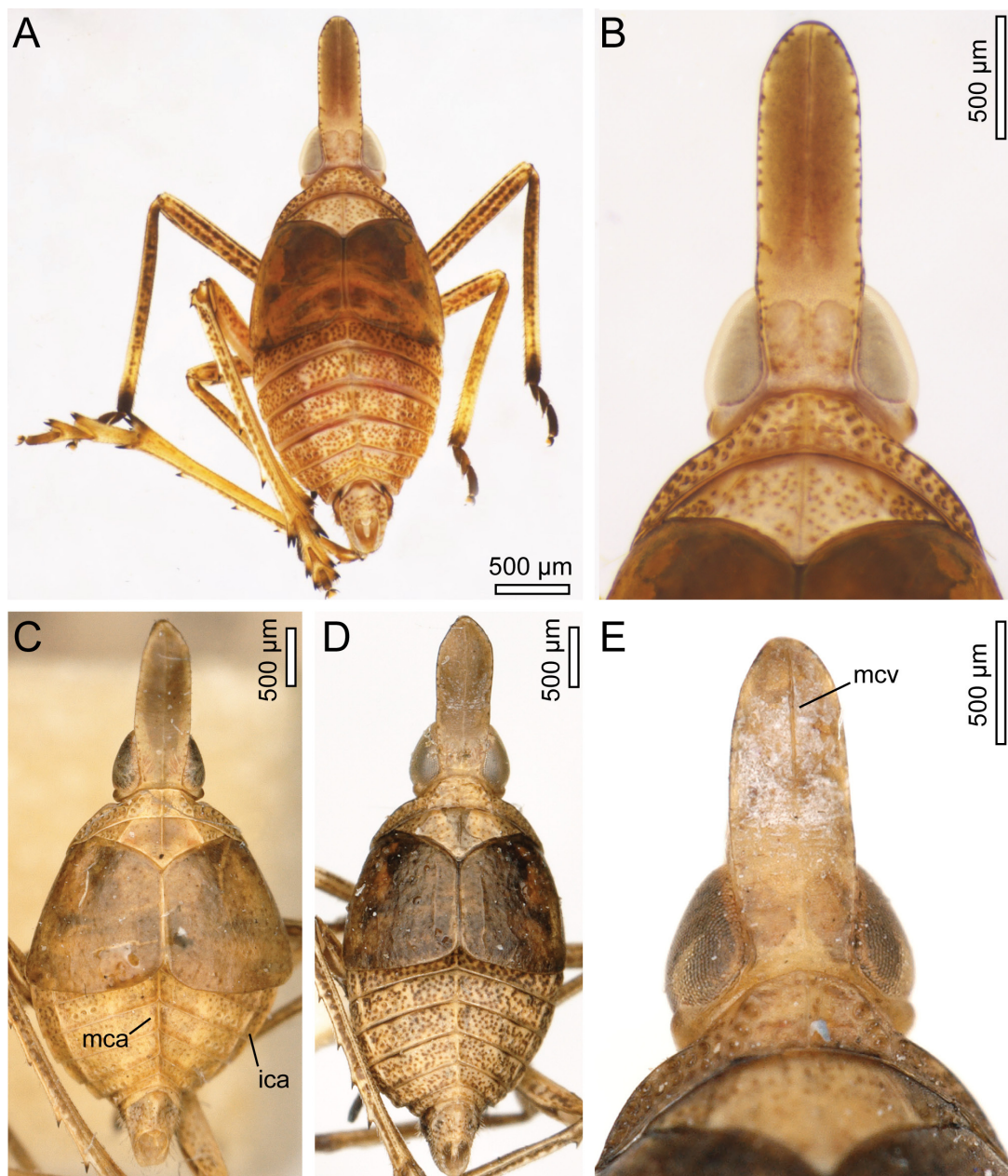


Fig. 1. Dorsal habitus of male *B. genei*. (A) Specimen from Epirus, Greece. (B) Close-up view of head. (C) Specimen from Murter, Croatia. (D) Specimen from Serres, France. (E) Close-up view of head of specimen from Serres, France. Abbreviations: ica = intermediate carina of abdomen; mca = median carina of abdomen; mcv = median carina of vertex.

(Fig. 2A–C); thorax, legs, and abdomen light ochreous, mottled with dark brown spots throughout their surface (Figs. 1, 2); fore and mid coxae and tarsi, and apices of fore and mid tibiae and metatibial spines all distinctly dark brown (Fig. 1A).

Structure: Head: vertex slightly elevated from plane of pronotum in lateral view (Figs. 2A, B; 3A, B), its base 1.65–1.85 times wider than maximum width

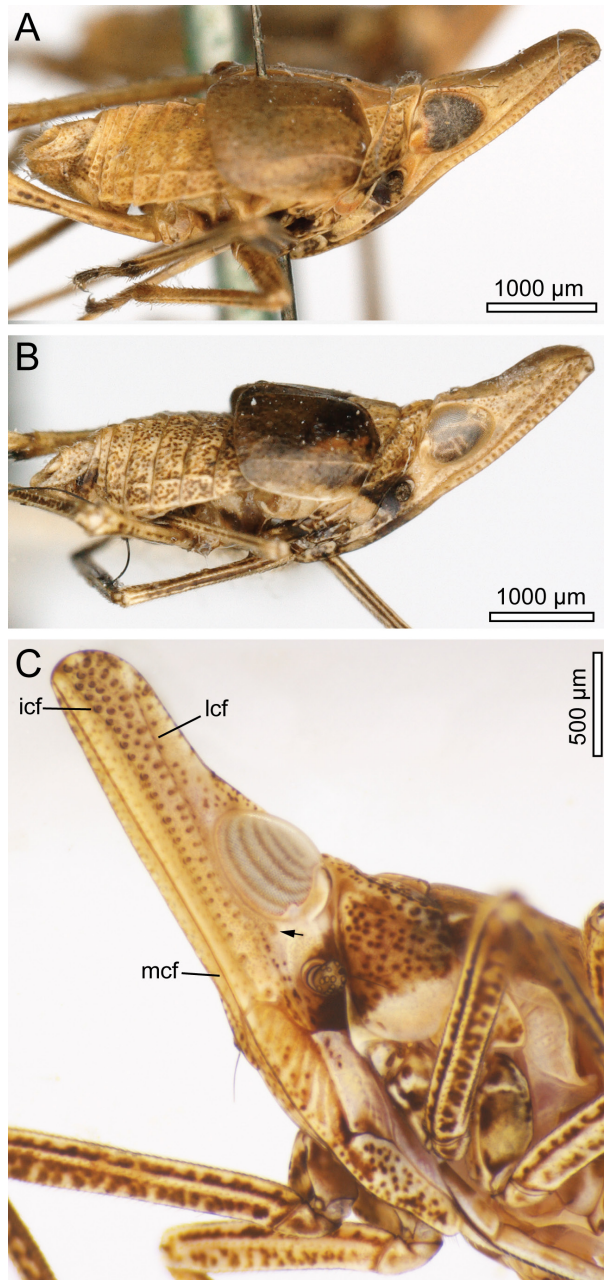


Fig. 2. Lateral habitus of male *B. genei*. (A) Specimen from Murter, Croatia. (B) Specimen from Serres, France. (C) Specimen from Epirus, Greece. Abbreviations: icf = intermediate carina of frons; lcf = lateral carina of frons; mcf = median carina of frons.

of eye in dorsal view (Fig. 1A–C); median carina of vertex distinct basally and apically, faint in the middle on cephalic process in front of eyes (Fig. 1B, E); head, in dorsal view, 2.3–3.7 times longer than vertex width at anterior eye margin; base of vertex tapered, its posterior margin straight, apex or cephalic process, in dorsal view, narrowly rounded (Fig. 1); frons with sharply delimited lateral, intermediate and median carinae (Fig. 2C); lateral carinae of frons joining lateral carinae of vertex subapically, at a clear distance from apex of cephalic process; apex of cephalic process, in lateral view, broadly, asymmetrically rounded (Fig. 2A–C), in frontal view, apical swelling (apical callus) of cephalic process longer than broad; area between intermediate and lateral carinae apically with three rows of sensory pits reaching the very apex of cephalic process, only one or two rows continue downward to level of eyes and beyond (Figs. 2C, 3B); postocular swelling (callus postocularis) well developed, distinctly concave in lateral view (Fig. 3B–D); ocelli rudimentary, only present as a small brown spot in front of eye (Fig. 2C: black arrow); antenna small: scape shortly circular; pericel bulbous, bearing ca 25 plate organs (sensilla placodea) spread over most of its surface.

Pronotum: Distinctly raised in lateral view (Figs. 2A, B; 3A–C); in dorsal view, anterior margin tapered, nearly straight (Figs. 1, 3A), with distinctly ridged median and intermediate carinae; discal area enclosed by inner margin of intermediate carina with three sensory pits (Fig. 3A, C), remainder of disk bare; lower lateral carina distinct, arc-shaped in dorsal view, enclosing about 14 sensory pits (Fig. 3A–C); area enclosed by lower lateral carina and paranotal lobe of pronotum with two sensory pits (Fig. 3B, D); paranotal lobe of pronotum expanding ventrally into a rounded plate, with a distinct carina and a single sensory pit (Fig. 3D); posterior margin of pronotum only slightly concave, with a nearly indistinct median notch (Fig. 3A).

Mesonotum: broad, 1.65–1.77 times longer than maximum length of pronotum; median carina distinct, almost reaching scutellar apex (Figs. 1B–D; 3A); lateral carinae of mesonotum short, straight, diverging laterally (Figs. 1C, 3A); part of mesonotum enclosed by the external margin of the lateral carina with six sensory pits (Fig. 3A–C).

Tegmina: micropterous, coriaceous, firmly interlocked, not reaching (Fig. 1A, D) or slightly surpassing (Fig. 1C) posterior margin of tergum III; apical margin truncate (Fig. 1A, C, D); wing surface glabrous, reticulation very faint (Fig. 1D) or entirely absent (Fig. 1A, C); hind wings absent.

Legs: femora on all legs unarmed; hind tibia with 3–6 lateral spines and 6–10 apical teeth; each hind

tarsomere with 12–14 platellae ventrally and a pair of apical teeth laterally.

Pregenital abdomen: short and broad (Fig. 1A, C, D), 1.15–1.3 times longer than maximum width, with a distinct median carina on each tergite, and an intermediate one, towards the junction between tergum and sternum (Fig. 1C, D); terga IV–VI with 3+3 and terga VII and VIII usually with 4+4 (sometimes 4+3 or 3+4), sensory pits laterally (mediad of intermediate carinae), arranged in transversal rows. Snapping organ of the fulgorid-dictyopharid type (Fig. 10).

Male genitalia: Dorsal margin of pygophore (segment IX), in profile, with a deep emargination (Figs. 4F, 5A, 6B); ratio of ventral to dorsal profile length 3.8; upper process of gonostyle short, rounded, hook-like process of gonostyle short, subtriangular, with a rounded apex (Figs. 4A–C, F; 5A; 6A–C); segment X (anal tube) in dorsal view short and broad, rounded (Figs.

4A, 6A), ratio of length to width about 1.5; anal style short, not reaching apex of segment X by its about half its length (Figs. 4A, 6A); base of phallosome broad and trapezoid, remaining portion very long and slender (Figs. 4B: white arrow; 6D: black arrow); distal margin of phallosome with a distinct emargination medially (Fig. 4B: black arrow); each dorsolateral lobe of phallosome split into two subconical lobes, unarmed (Fig. 4A, B, E, F); ventral lobe of phallosome strongly developed downwards, split in the middle (Fig. 4C–E), with a saw-like dorsal margin (Fig. 4F), without any sclerotised spines or denticles; endosomal processes strongly inflated, each with a single row of denticles, interrupted in the middle by unarmed surface (Figs. 4A, C, E, F; 5C, D); endosomal processes ending in an acute spine (Fig. 5D). Uninflated phallosome as in figure 6B, F.

Note: The genitalia of the male specimen from Pindos, Greece, were damaged during maceration, but

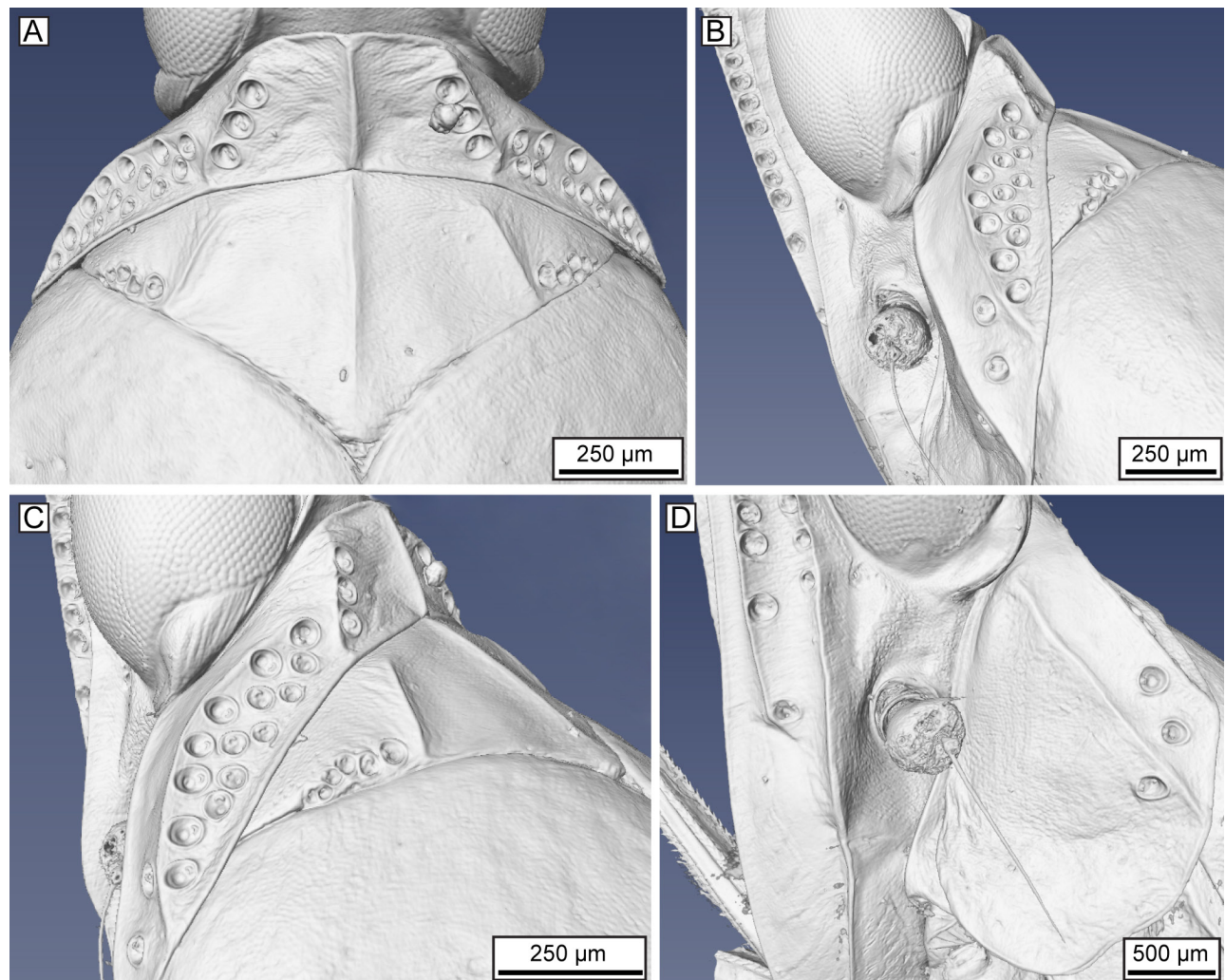


Fig. 3. Three-dimensional reconstruction of synchrotron microtomographic scans of male specimen of *B. genei* from Greece. (A) Head, pro- and mesonotum, dorsal view. (B) Same, lateral view. (C) Same, dorsolateral view. (D) Frontolateral view, with emphasis on paranotal lobe.

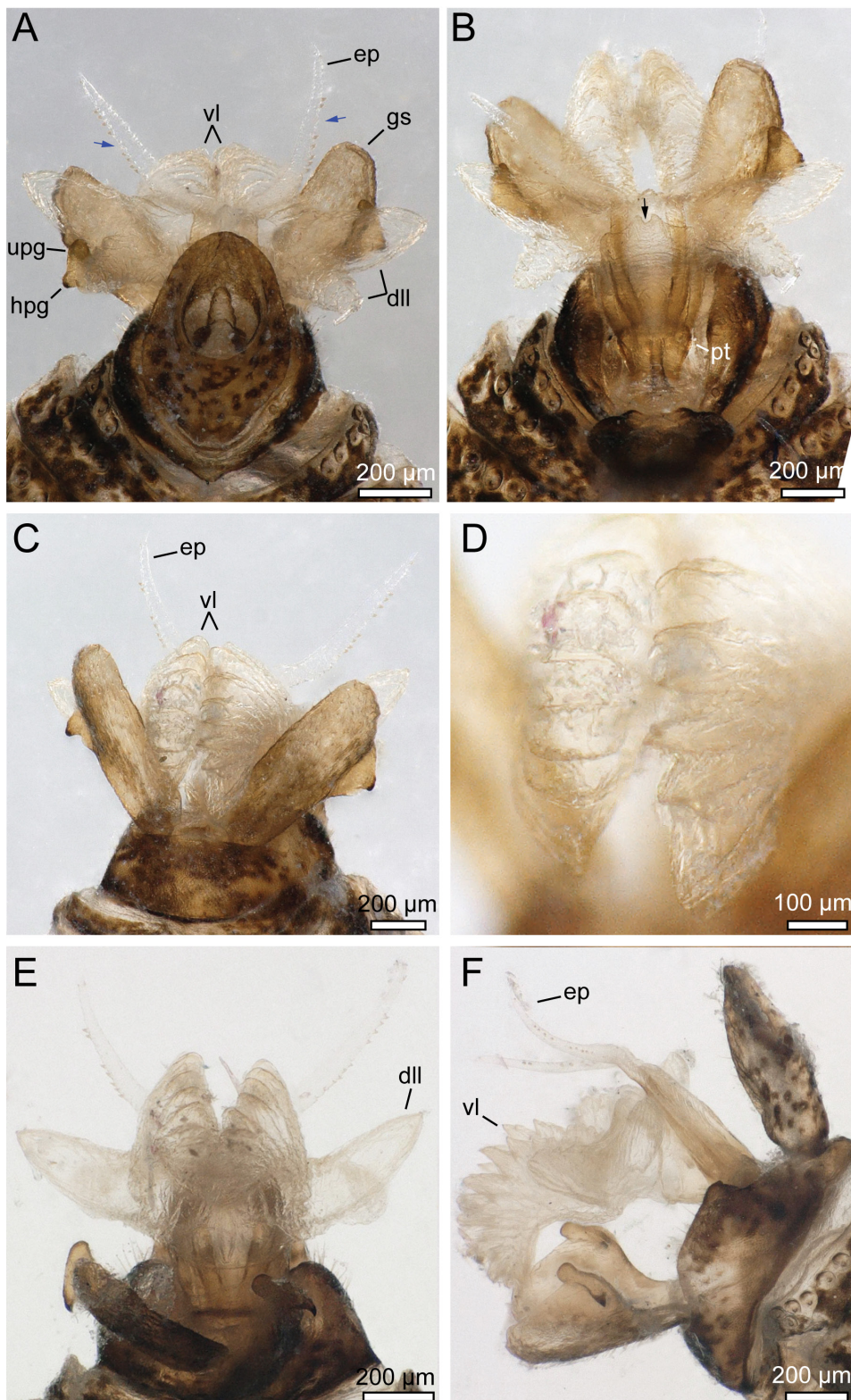


Fig. 4. Male genitalia of *B. genei* from Serres, France. (A) Dorsal view, blue arrows indicating gap between row of spines on endosomal process of phallotheca. (B) Same, with segment X raised, black arrow indicating the emargination of the phallothecal apex. (C) Ventral view. (D) Same, close-up of ventral lobe of phallotheca. (E) Ventral view, emphasising on the dorsolateral lobes of phallotheca. (F) Lateral view. Abbreviations: gs = gonostyle; ep = endosomal processes; dll = dorsolateral lobe of phallotheca; hpg = hook-like process of gonostyle; upg = upper process of gonostyle; pt = phallotheca; vl = ventral lobe of phallotheca.

they possess all the diagnostic characters found in other examined specimens of *B. genei*, namely in the overall shape and proportions of the pygophore and gonostyles (Fig. 5A), the trapezoid base of phallotheca (Fig. 5B, white arrow), and endosomal processes with a single row of denticles that are interrupted in the middle (Fig. 5D, black arrow). The morphology of the external male genitalia of the Spanish specimens is largely the same with the other populations, although the endosomal processes possess a single row of spines that are confined only towards their apex, are not interrupted, and are somewhat larger (Fig. 6A, B, E). More samples should be studied to determine whether these slight differences are fixed in most of the Spanish populations of *B. genei*. The Spanish populations, are however, likely conspecific with the remaining European ones, as

all other features are largely identical.

Female genitalia: external view of female genitalia as in figure 7A, B; segment X (anal tube) as in figure 7C, ratio of length to width about 1.2; posterior lobe Gp1 of gonoplac (valvula 3) simple, rounded, more than three times thicker than posterior lobe Gp2, without any spines, apex subtriangular (Fig. 7D); gonapophysis IX (valvula 2) with posterior connective lamina symmetrical in ventral view, completely fused at base, apex of sclerotised part harpoon-shaped (Fig. 7E); gonocoxa VIII (valvifer VIII) with anterior connective lamina consisting of six gradually enlarging, blunt teeth (Fig. 7F); endogonocoxal process largely membranous, subtriangular (Fig. 7F); bursa copulatrix with a single pouch, almost globular in dorsal (Fig. 8A) and lateral (Fig. 8B, C) views, its entire surface with distinct pit-

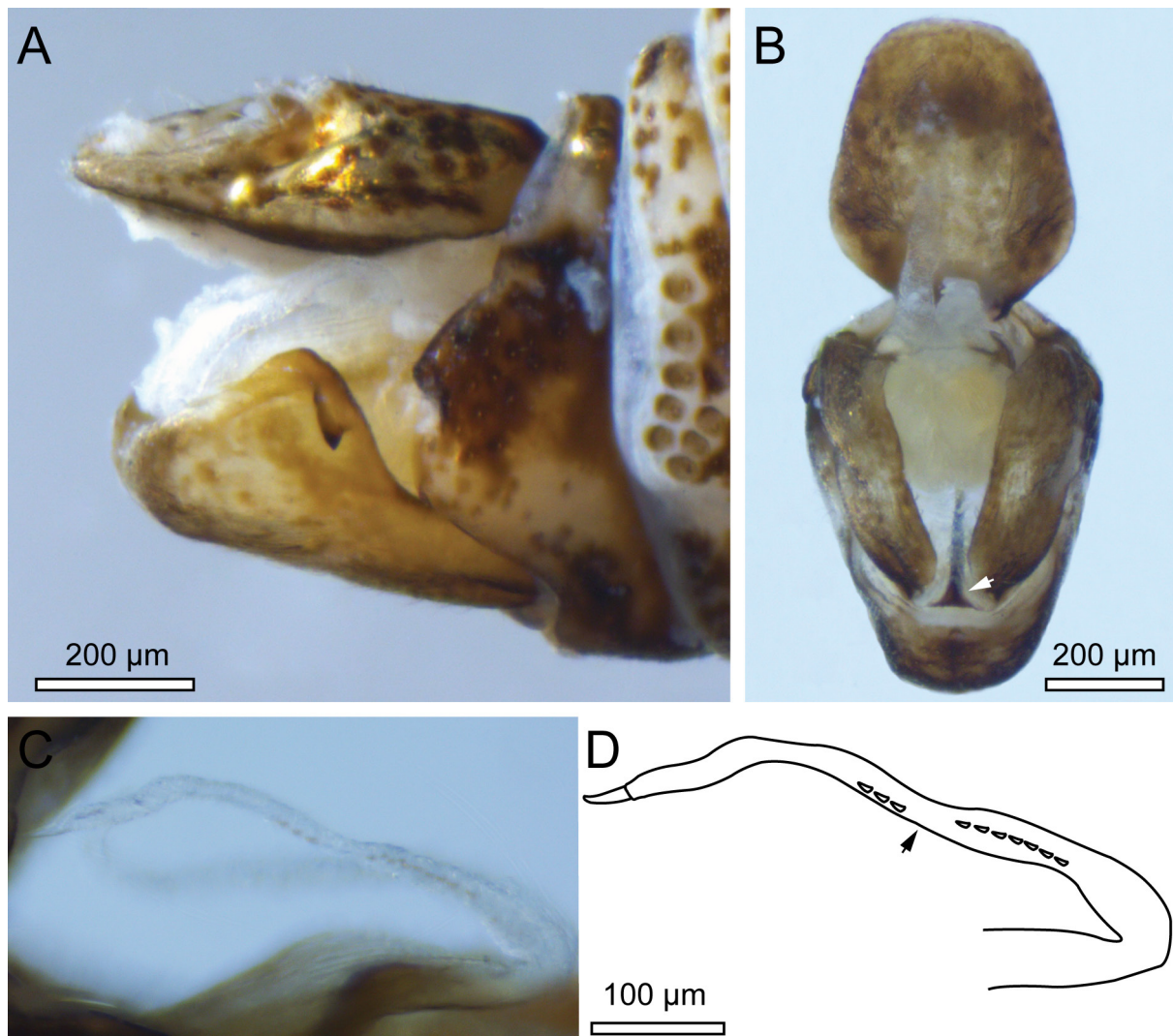


Fig. 5. Male genitalia of *B. genei* from Epirus, Greece. (A) Pygophore, lateral view. (B) Same, caudal view, white arrow indicating trapezoid base of phallotheca. (C) Low resolution image of endosomal process, lateral view. (D) Same, with outline traced, black arrow indicating unarmed area between row of spines of endosomal process.

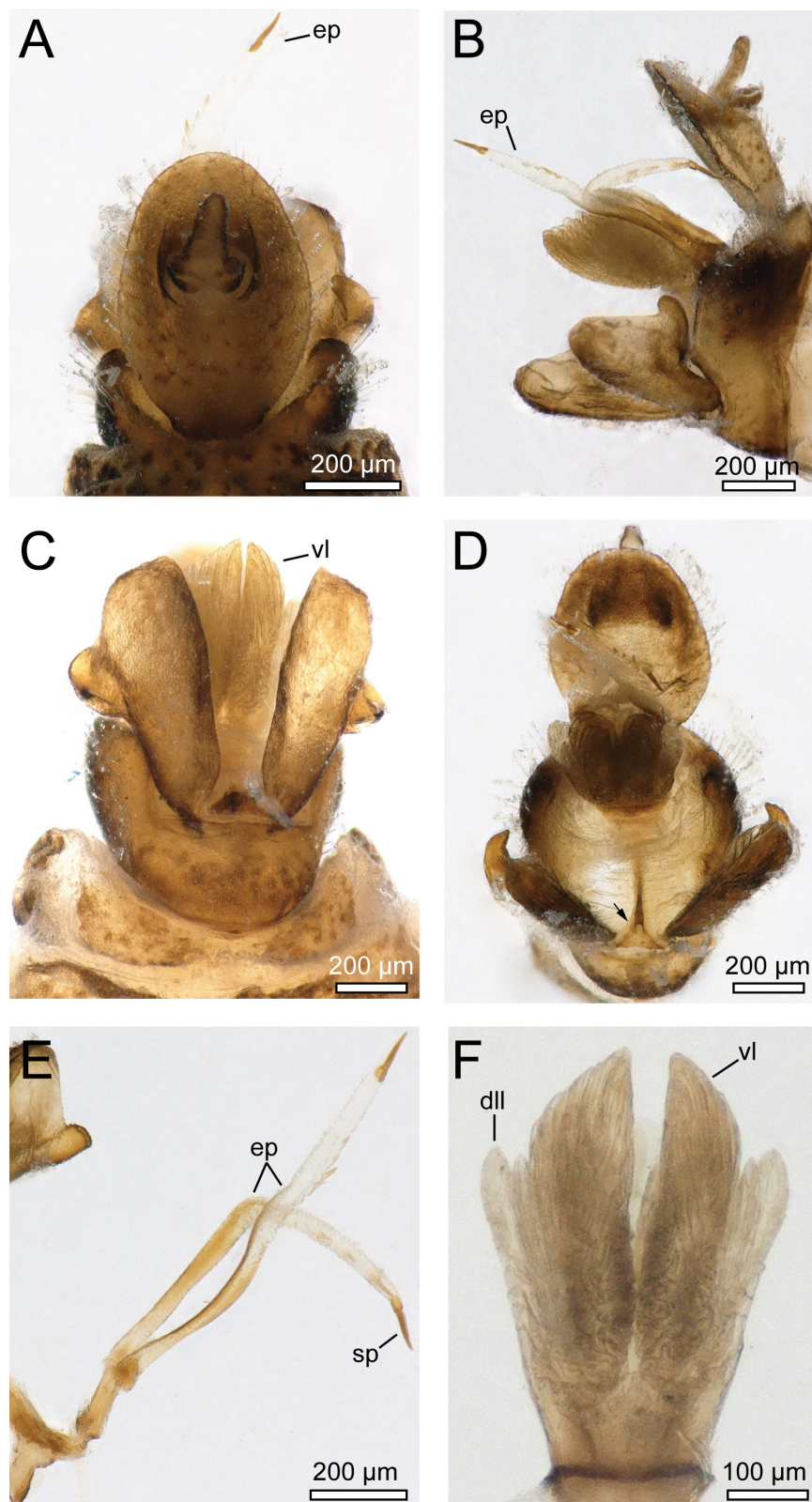


Fig. 6. Male genitalia of *B. genei* from Guadarrama, Spain. (A) Dorsal view. (B) Lateral view. (C) Ventral view. (D) Ventrocaudal view, black arrow indicating trapezoid shape of base of phallotheca. (E) Extracted endosomal process of phallotheca. (D) Phallotheca with uninflated lobes. Abbreviations: dll = dorsolateral lobe of phallotheca; ep = endosomal process of phallotheca; sp = spine at apex of endosomal process; vl = ventral lobe of phallotheca.

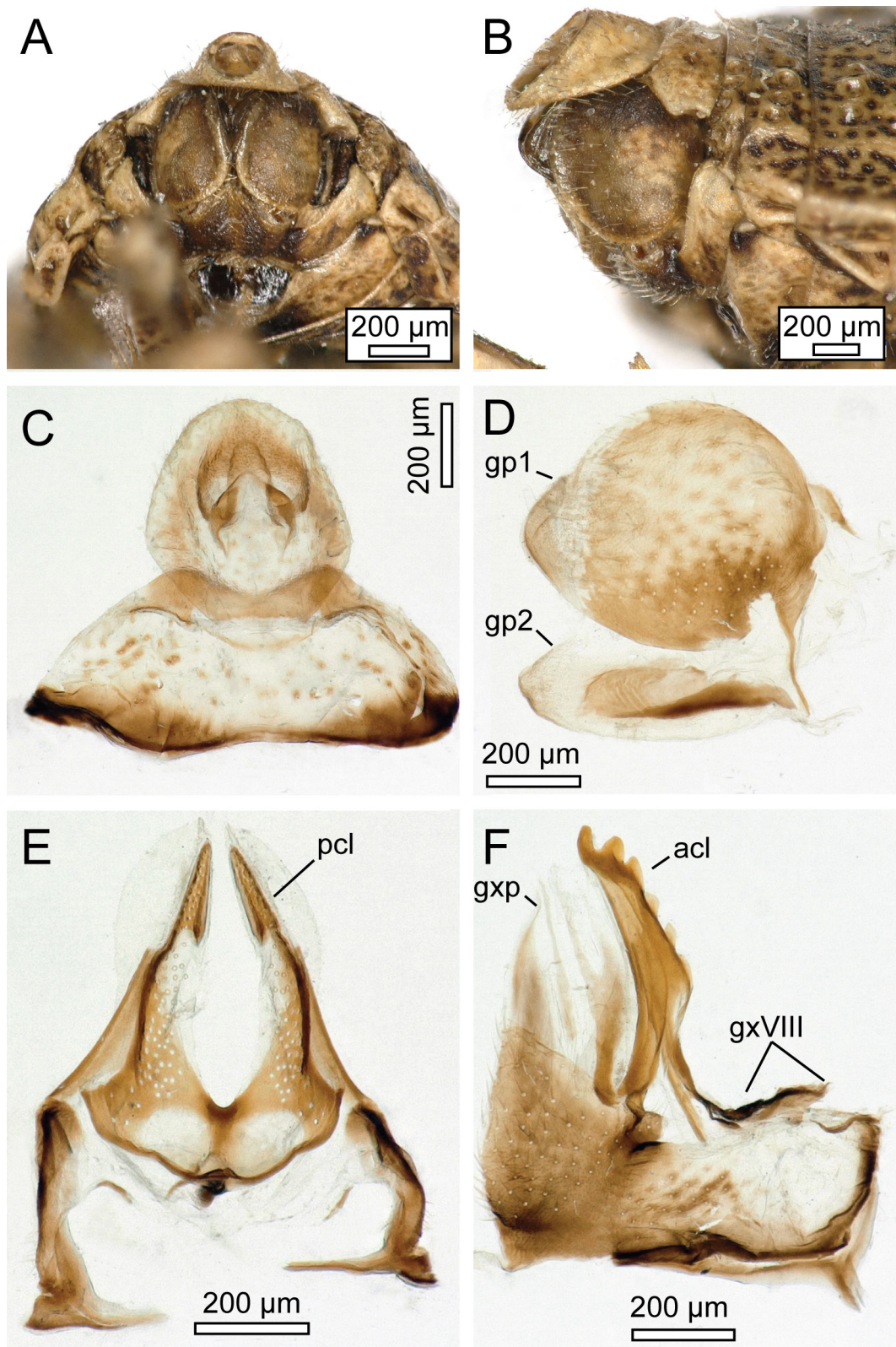


Fig. 7. Female genitalia of *B. genei* from Serres, France. (A) External genitalia, dry-mounted, ventral view. (B) Same, lateral view. (C) Segment X, macerated, dorsal view. (D) Gonoplac, outer lateral view. (E) Gonapophysis IX, ventral view. (F) Gonocoxa and gonapophysis VIII, outer lateral view. Abbreviations: acl = anterior connective lamina; gp1, gp2 = posterior lobes of gonoplac; gxVIII = gonocoxa VIII; gxp = endogonocoxal process; pcl = posterior connective lamina.

like microsculpture (Fig. 8A–C), each pit bordered by a ring of about 13 microsclerites (Fig. 8C, inset); a pair of large digitiform glands (Fig. 8B, C) branched at anterior extremity of the anterior vagina on each side of the spermatheca; spermatheca well developed (Fig. 8B–D), ductus receptaculi smooth and bulbous basally, diverticulum ductus short and distinctly swollen, pars intermedialis distinctly ribbed (Fig. 8D).

Measurements (in mm, 8 males / 2 females): total body length 4.21–6.00 / 5.15–5.78; body max. width 1.91–2.59 / 2.35–2.51; head length (in dorsal view, from base of vertex to apex of cephalic process) 1.10–1.77 / 1.16–1.74; head max. width (incl. eyes) 0.80–1.03 / 0.91–0.99; vertex width (at anterior margin of eyes) 0.42–0.57 / 0.49–0.51; pronotum max. width (at posterior angles) 1.35–1.89 / 1.63–1.72; metatibia length (incl. apical spines) 2.57–3.56. Ratios: body length / body width: 2.05–2.59; head length / head max. width: 1.27–2.21; head length / vertex width: 2.27–3.55;

metatibia length / body length: 0.52–0.61.

DISCUSSION

Diagnosis of *B. genei*

Bursinia genei shares the following combination of characters with other members of the subgenus *Bursinia s. str.* (Emeljanov 2009): apical swelling (apical callus) of cephalic process longer than broad; lateral carinae of frons complete (distinct throughout their length); area between intermediate and lateral carinae of frons with three rows of sensory pits apically (Fig. 2C). These characters should distinguish it from six species currently classified in the subgenus *Struthionia* (Emeljanov 2009).

According to Emeljanov and Drosopoulos (2004), *B. genei* is “close or identical” to *B. hemiptera* Costa,

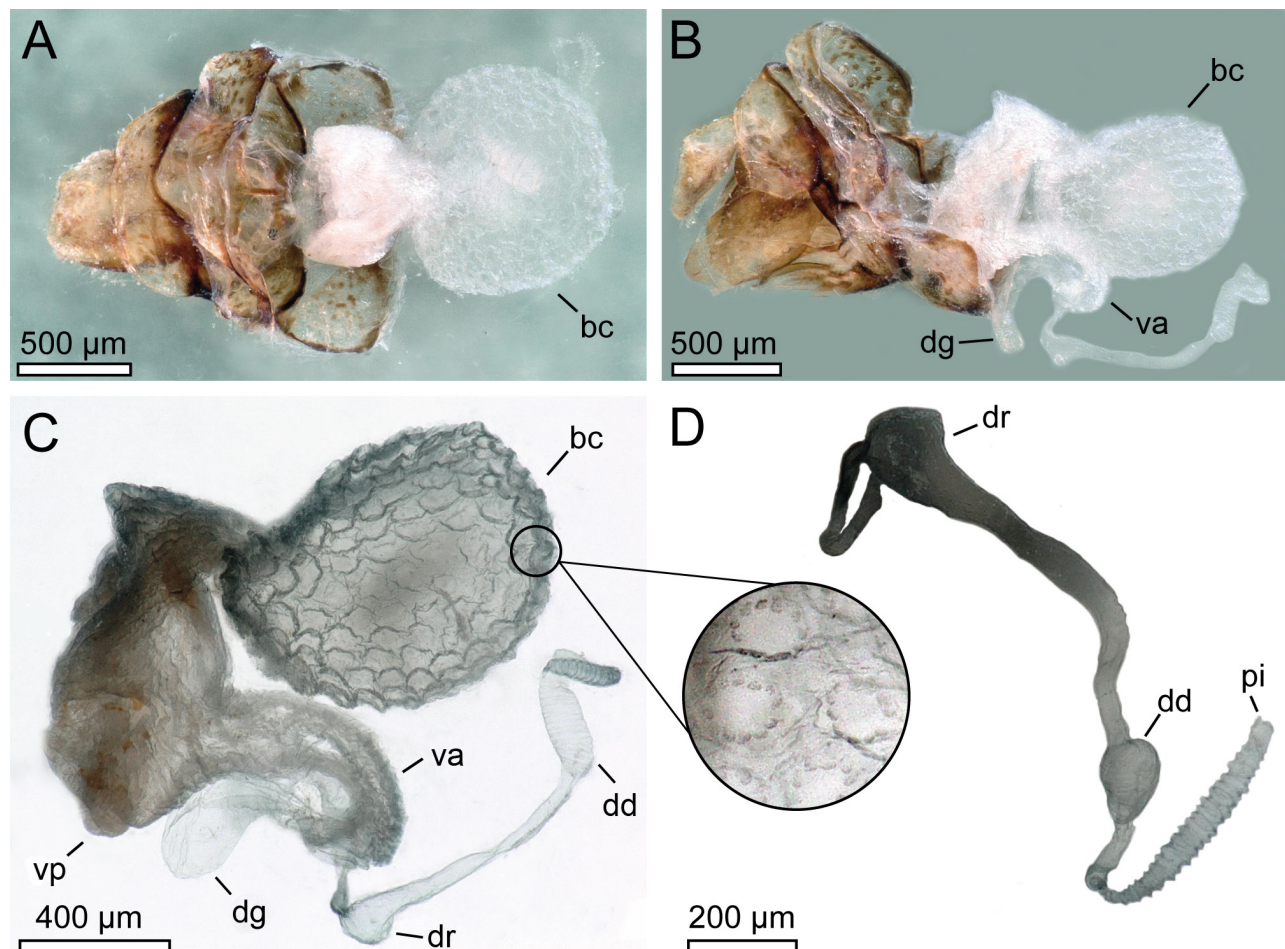


Fig. 8. Internal female genitalia of *B. genei* from Serres, France. (A) Posterior part of abdomen with ectodermal genital ducts, dorsal view. (B) Same, lateral view. (C) Extracted ectodermal genital ducts, lateral view, dyed with chlorazol black, inset showing close-up of ornamentation of bursa copulatrix. (D) Spermatheca, lateral view, dyed with chlorazol black. Abbreviations: bc = bursa copulatrix; dd = diverticulum ductus; dg = digitiform gland; dr = ductus receptaculi; pi = pars intermedialis; va = anterior vagina; vp = posterior vagina.

1840, described from southern Italy; both species should share smooth tegmina, with reticulation very faint or entirely absent. Based on Horváth (1910) and Melichar (1912), *B. genei* differs from *B. hemiptera* in lateral carinae of frons that are joining lateral carinae of vertex subapically, at a clear distance from apex of cephalic process (Fig. 2C); in *B. hemiptera*, the lateral carinae of frons are extended up to the apex of cephalic process (Costa 1840: pl. 1, fig. 4; Horváth 1910: fig. 3; Melichar 1912).

According to Horváth (1913), *B. genei* differs from *B. breviceps* Horváth, 1913, described from southern Spain, by a much longer cephalic process (which is short and broad, and parabolic in dorsal view in *B. breviceps*).

According to Horváth (1913), *B. genei* can be easily distinguished from *B. latipes* Horváth, 1913, described from eastern Spain, by its slender fore femora and tibiae (they are enlarged and lamellate in *B. latipes*) and uniformly coloured tegmina (bearing a broad, transverse, contrasting white band apically in *B. latipes*).

According to Emeljanov (1972), *B. genei* differs from *B. rugosa* Emeljanov, 1972, described from central and southern Spain, in the sensory pits between lateral and intermediate carinae of frons present up to very apex of cephalic process. Based on a comparison of our material of *B. genei* with the holotype male, a paratype female and three additional males of *B. rugosa* (labelled as from “Hispania” and “Ribas”, all specimens deposited in MMBC), we can add that those sensory pits on frons are also smaller in *B. genei* than in *B. rugosa*, and that *B. genei* also differs from *B. rugosa* in a more slender body and smooth tegmina (the body is distinctly broader and tegmina distinctly reticulate in *B. rugosa*).

Compared with *B. galaxia* Emeljanov and Drosopoulos, 2004, described from southern Portugal, the body size of *B. genei* is smaller and its cephalic process in dorsal view is slightly broader and with more or less smoothly arcuate, not angular lateral margins subapically (Emeljanov and Drosopoulos 2004).

Unfortunately, the original descriptions of *B. carinata* Horváth, 1936, *B. discolor* Horváth, 1936, *B. fallax* Horváth, 1936, *B. griseola* Horváth, 1936 (all described from Spain), and *B. pithyusa* Emeljanov, 1972 (described from Ibiza) are not accompanied by clear diagnoses from other previously described taxa or illustrations (Horváth 1936; Emeljanov 1972). These taxa need to be redescribed, illustrated and compared with other *Bursinia* spp. based on their type specimens in future studies.

Horváth (1910) also described *B. genei* var. *parvula* Horváth, 1910 from central Spain (Espinar), which he distinguished from the typical form of *B.*

genei based on a smaller body size and more elongated cephalic process (Horváth 1910: fig. 6). Horváth (1936) elevated this variety to species rank. In our opinion, the body size and the length and shape of the cephalic process in *B. genei* are quite variable (Figs. 1, 2) and *B. parvula* is likely to fall within this range, but future studies based on a more numerous material, particularly from Spain, should come to a more solid conclusion.

Besides external and morphometric characters, future revisions of *Bursinia* should take into account also male genitalia (including their inflatable elements), which are likely to provide diagnostic details for individual species as in other groups of Dictyopharidae and related Fulgoridae (Seidel and Wessel 2013; Song et al. 2017 2018). These characters, as well as the female genitalia, have been neglected in *Bursinia* so far and are described in detail for *B. genei* for the first time here.

Description of the jumping muscles

Most Auchenorrhyncha are capable of jumping, by using mechanisms that likely evolved independently in the Cicadomorpha and the Fulgoromorpha (Ogawa and Yoshizawa 2017). The mechanism of Fulgoromorpha is characterised by a greatly enlarged IIIpcm5 muscle, which inserts on a distinct funnel-shaped tendon and is the principal jumping muscle (Emeljanov 1981 1987; Ogawa and Yoshizawa 2017; Sander 1957). This mechanism is also present in *B. genei* (Fig. 9). However, the micropterous condition of this species has rendered its wings non-functional, as most of the associated dorsoventral and dorsal longitudinal muscles have disappeared (Fig. 9). As a result, most of the space in the thorax that was dedicated to flight is now occupied by a greatly enlarged jumping muscle (Fig. 9). This suggests that the jumping ability of *B. genei* might be greater than in macropterous dictyopharids. *Bursinia genei* has a similar body shape and only a slightly smaller body size compared to another micropterous dictyopharid species, *Engela minuta* Distant, 1906 (Dictyopharinae: Dictyopharini) from South Africa. The jumping capacity of *E. minuta* was studied in detail by Burrows (2014) who reported a very high take-off velocity of 5.8 m s⁻¹, which is the fastest achieved by any insect described to date, and predicted *E. minuta* to be able to jump to a distance of more than 3 m, i.e., 500 times its body length. This was longer than jumps predicted for three other, larger macropterous dictyopharid species studied in detail as well (Burrows 2014). In general, Dictyopharidae are very strong jumpers probably due to a power amplification mechanism in a catapult-like action (described in some other planthopper groups but not detailed in Dictyopharidae yet) and streamlined body including the cephalic process which further

improves jumping performance by reducing drag (Burrows 2014).

Snapping organ and capacity for vibrational communication

All planthoppers have been found to possess a snapping organ, which they use to generate substrate-borne vibrational signals (Davranoglou et al. 2019). Members of Orgeriinae have been shown to communicate with vibrational signals (Tischechkin 2003), although no recordings from *Bursinia* spp. are available. We have found that *B. genei* possesses a fully developed snapping organ (Fig. 10A, B). By virtually dissecting the specimen, we revealed hypertrophied dorsal longitudinal muscles (Fig. 10C), which are the primary operators of the snapping organ, suggesting that it is certainly functional. Unlike most other planthoppers, the apodemes for the snapping organ muscles are fused into a single central apodeme (Fig. 10B), which is visible only in microtomography scans and macerated specimens. Upcoming research (Davranoglou and Malenovský, in preparation) will show that a fused apodeme of the snapping organ is a synapomorphy of the Fulgoridae-Dictyopharidae clade.

Habitat and ecology

The two specimens of *B. genei* from Greece were collected under flat stones from a disturbed xerothermic locality in the outskirts of the town of Konitsa. The locality is at the edge of a *Pinus nigra* forest that is intersected by a rural road (Fig. 11). During the day, temperatures reached up to 36°C, and the stones that the specimens were collected from were scorching hot. These conditions are congruent with previously known collecting data in the literature (Emeljanov 2003; Mazzoni 2005) – *B. genei* is a xerothermic species that can be found at a range of altitudes (40–1300 m), primarily in open areas with sparse herbaceous vegetation and sparse trees, Mediterranean macchia, or at the edge of forests.

Adults of *B. genei* have been collected from July to September from *Acer* sp. Linnaeus, *Juniperus* sp. Linnaeus, *Ostrya* sp. Scopoli, *Quercus* sp. Linnaeus, *Thymus longicaulis* Prest and grasses, as well as in dry leaf litter and herbs at the base of trees (Horváth 1910; Emeljanov 2003; Mazzoni 2005). Although we did not collect specimens feeding on plants, we should note that the micropterism and cryptic brownish coloration of this species may indicate its preference for a way of life close to the ground rather than on larger trees or shrubs.

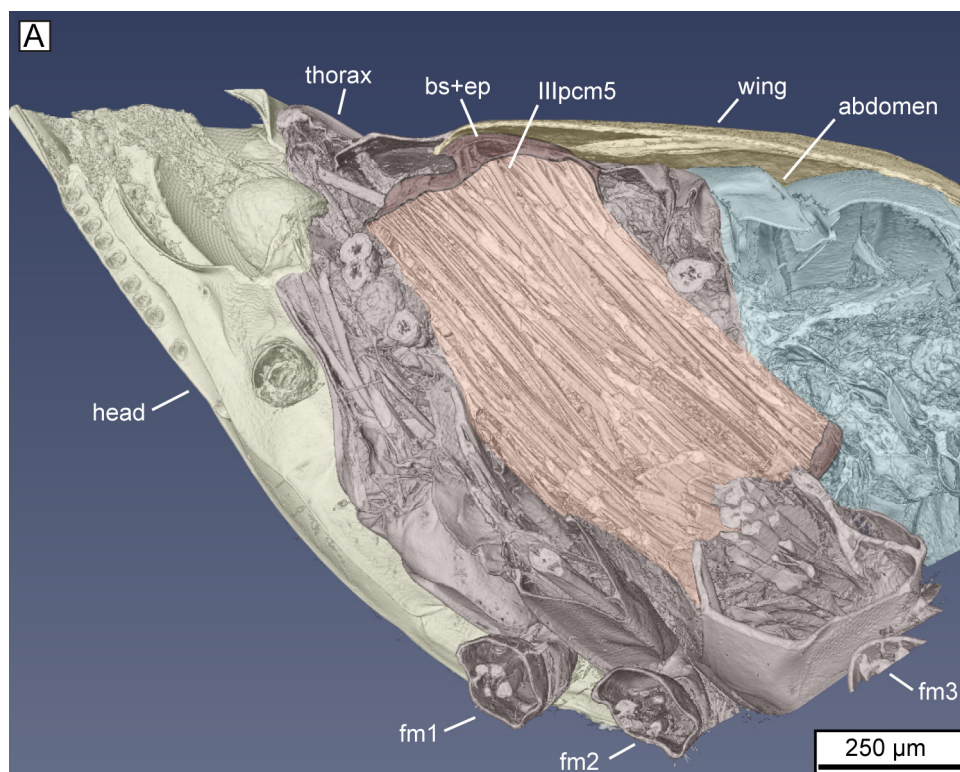


Fig. 9. False-coloured three-dimensional reconstruction of *B. genei* from Greece, longitudinal section, lateral view. Abbreviations: bs + ep = basisternum + episternum; fm = femur; IIIpcm5 = musculus episterno-trochanteralis.

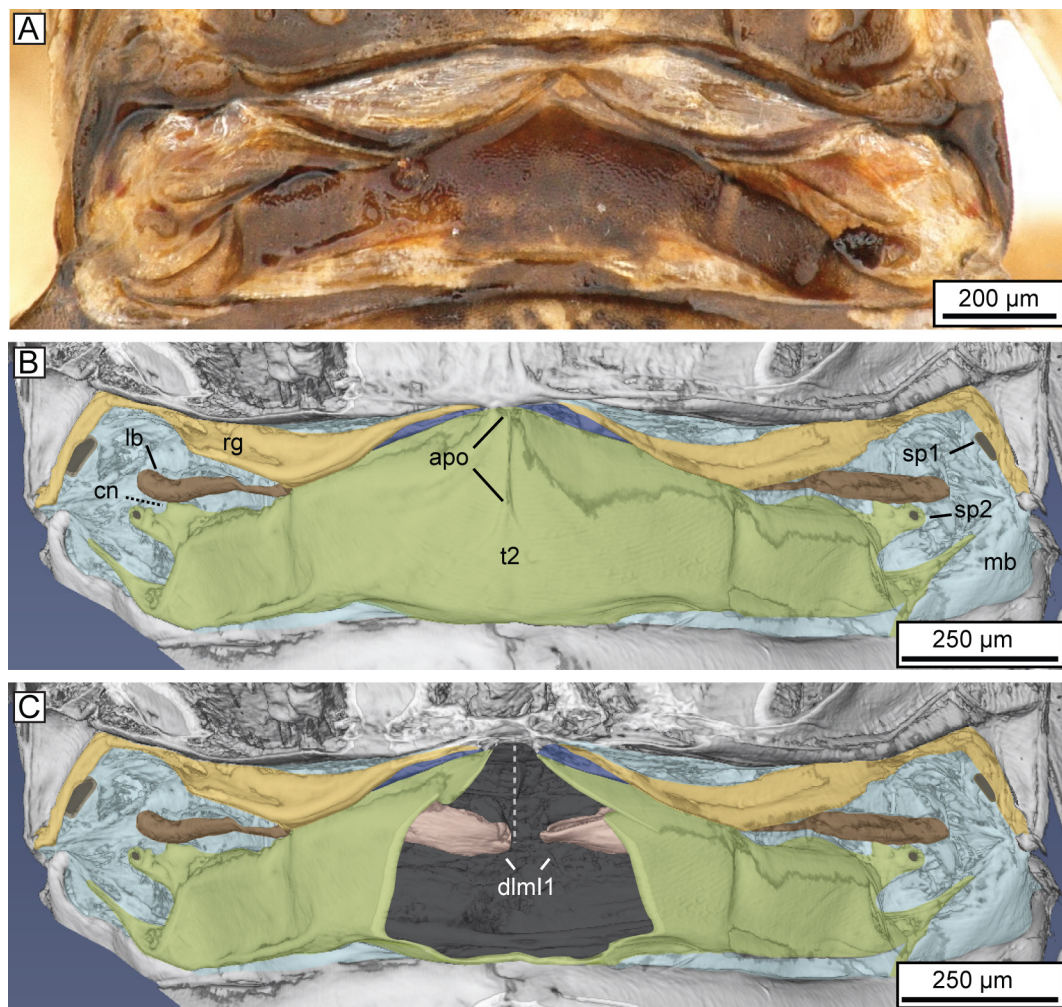


Fig. 10. Snapping organ morphology of *B. genei*. (A) dorsal view of specimen from Serres, France. (B) False-coloured three-dimensional reconstruction of snapping organ of *B. genei* from Greece. (C) Same, with top part excised to reveal the snapping organ muscles. Abbreviations: apo = apodeme for snapping organ muscles; cn = membranous connector; dlmI = dorsal longitudinal muscle of tergum one; lb = lobe of snapping organ; sp = spiracle; mb = membrane; rg = ridge of snapping organ; t2 = tergum II.



Fig. 11. Collecting locality in Konitsa, Epirus, Greece, where two specimens of *B. genei* were collected.

Distribution

In terms of biogeography, *B. genei* is a West-Mediterranean element, spread from the Iberian Peninsula (Horváth 1910 1936; Lallemand 1929; Emeljanov 2003; this paper) through southern France (Horváth 1910; Emeljanov 2003; this paper), Corsica (Emeljanov 2003), Sardinia (Spinola 1839 – misidentified as *Dyctiophora* (sic) *senegalensis* Spinola, 1839, see Metcalf 1946; Dufour 1849; Servadei 1967) and Italy (Horváth 1910; Servadei 1967; Emeljanov 2003; Mazzoni 2005), eastwards to the Adriatic coast, and the southwestern Balkans, including northwestern Greece (this paper, new record). The records from former Yugoslavia (Metcalf 1946; Nast 1972 1987) refer to what is now Croatia (Horváth 1910; Melichar 1912; Emeljanov 2003; this paper), Montenegro (locality “Sutomore” listed in Horváth 1910 and Melichar 1912), and Bosnia and Herzegovina (“Herzegowina” listed by Melichar 1912). The records from “Hungaria” and “Ungarn” listed by Horváth (1910) and Melichar (1912), respectively, both refer to the same locality “Zengg”, which is now Senj, a town on the upper Adriatic coast of Croatia. *Bursinia genei* has not been recorded from what is today Hungary (cf. Györffy et al. 2009). Its records from Hungary in the catalogues by Metcalf (1946) and Nast (1972) are thus based just on erroneous geographical interpretation of historical data. It is very likely that *B. genei* will be also found in Albania, whereas we doubt it is present in central, southern and eastern Greece where intense collecting efforts by eminent hemipterists (e.g., Sakis Drosopoulos, Pavel Lauterer) for several decades have yielded no results.

Some other hemipteran species have a similar distribution to *B. genei* and likely followed a similar West-to-East dispersal route from southwestern Europe to the Balkans, e.g., *Gardena insignis* Horváth, 1887 (Heteroptera: Reduviidae) (Putshkov and Moulet 2010).

CONCLUSIONS

Based on a thorough examination of the morphology of *B. genei*, we provide evidence that it constitutes a single morphospecies. Its ultimate biogeographic origin likely lies in the Iberian Peninsula, which contains the core diversity of *Bursinia*, alongside North Africa (Horváth 1910 1913 1936; Emeljanov 1972 1980 2003; Emeljanov and Drosopoulos 2004). We suggest that all other European populations represent a subsequent spread of *B. genei* from Iberia, and it is a clearly West Mediterranean element. It is possible that the slight morphological differences in the genitalia of Spanish specimens are the result of greater

genetic variation, whereas the extra-Iberian populations likely have reduced genetic variability due to founder effects. Future molecular studies are required to reveal the population genetics and evolutionary history of *B. genei*, and to determine whether any populations represent cryptic species that are morphologically indistinguishable.

Our study provides the first step towards a reliable identification of the most widespread species of *Bursinia*, which will hopefully trigger a more comprehensive taxonomic revision of the entire genus. It also demonstrates the utility of synchrotron microtomography in reconstructing the life history of rare species based on preserved museum specimens.

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