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A review and phylogenetic analysis of Afrotropical Dictyopterini (Coleoptera, Lycidae)

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Abstract

The lycid tribe Dictyopterini of Africa south of Sahara is reviewed and its phylogeny is analyzed. All Afrotropical Dictyopterini are found to belong to the subtribe Flagraxina. The genera of the subtribe are redescribed. A new species, *Phaneros* (*Kleineria*) *silvicola* **sp. n.** is described from Transvaal (South Africa). *Flagrax bicoloripes* (Pic 1946), **syn. n.** is synonymized with *F. parallelus* (Pic 1922). A key to the genus-group taxa of Flagraxina is provided, accompanied by a list and a key to species of each genus.

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Introduction

The first Dictyopterini species from the Afrotropical region was described at the end of the nineteenth century from Gabon by Bourgeois (1881) who placed it in *Stadenus* Waterhouse, 1879 (Metriorrhynchini), the type species of which is an Australian insect. Shortly afterwards Bourgeois described another species from South Africa (1884) tentatively placing it in the Neotropical and Nearctic genus *Calopteron* Laporte, 1838 (Calopterini). Several more species were added by the same author later (Bourgeois 1889, 1908, 1910), also as *Stadenus.* More species of this group were introduced during the first half of the twentieth century by Pic (1915–1946) and Kleine (1933, 1942).

In 1992 types of all African "*Stadenus*" taxa, with few exceptions, were studied: they were found to belong in three different genera, *Aferos* Kazantsev, *Flagrax* Kazantsev and *Phaneros* Kazantsev, neither of them related to *Stadenus* (Kazantsev 1992). *Aferos* was separated in the subtribe Slipinskiinina (Bocák & Bocáková, 1992), which was subsequently raised to the tribal level and transferred to Calochrominae (Kazantsev 2004; 2005a; 2005b). *Phaneros*, in its turn, was divided into three subgenera, *Phaneros* s. str., *Ph.* (*Bourgeoisiella*) Kazantsev and *Ph.* (*Kleinella*) Kazantsev (Kazantsev, 1992). *Kleinella* later was substituted with *Kleineria*, and *Flagrax* and *Phaneros* together separated as Flagraxina (Kazantsev 2004). Finally, *Staepteron* Kazantsev, 1992, previously included in Erotinae *incertae sedis*, upon examination of the male of the type species, was transferred to Flagraxina as well (Kazantsev 2005a).

This paper presents a phylogenetic analysis of the Afrotropical Dictyopterini aimed at testing the monophyly of the existing supraspecific taxa and defining their possible relationships; the analysis matrix, as compared to the 2004 Erotini and Dictyopterini paper, is complemented with new data on *Kleineria* and *Staepteron*. A new species from South Africa is added to the previously monotypic *Phaneros* subgen. *Kleineria*.

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The following abbreviations are used in the paper: ICM – Insect Centre, Moscow; TMNH – Transvaal Museum of Natural History, Pretoria.

Material and methods

Specimens used as material for this study were dissected after being softened for several hours in water, with the male genitalia extracted and affixed with water-soluble glue on cardboard plates or placed in vials with glycerine. To study internal morphology some specimens were cleared with 10% KOH. All sutures, sulci, sclerites and appendages were studied on such KOH-treated specimens.

The following material was studied for the data matrix analysis:

Taphes brevicollis Waterhouse, adult male and female: Vietnam, Gialai-Contum, Buen-Loi, trop. forest, 18.–19. I. 1990 (O. Gorbunov leg.).

Dictyoptera aurora (Herbst), adult male and female: FE Russia, Kunashir Is., Mendeleevo, VI. 1985 (S. Saluk leg.).

Phaneros (*Bourgeoisiella*) *ruficeps* (Bourgeois): male, "Nguelo, D.O.Afr.".

Flagrax auberti (Bourgeois): female, Afrique occ., Guinea, Forêt Tabouna, 9. XII. 1982 (S. Murzin); male, Afrique occ., Guinea, Forêt Tabouna, 10. X. 1983 (S. Murzin).

Flagrax parallelus (Pic): male and female, Guinea Espanola, Anyundsok (Evinayong) (Dr. L. Baguena).

Flagrax atripes (Pic): male and female, S Afr., Natal, Wesa, Impetyene forest, 30°37 S – 29°42 E, beating in forest, E-Y: 2695, 19. XI. 1989 (Endrödy-Younga & Klimaszew).

Phaneros (*Kleineria*) *silvicola* sp. n.: male and female, S. Afr., E Transvaal, Marieskop, 24°35 S – 30°50 E, beaten in forest, E-Y: 1786, 6. V. 1981 (Endrödy-Younga).

Phaneros (*Phaneros*) *xanthopterus* (Bourgeois): male and female, Afrique or. anglaise, Mt. Kenya, vers^{t} ouest, zone des forêt, forêt infer^{res}, (*Podocarpus*), 2400 m (Alluaud & Jeannel).

Phaneros (*Phaneros*) *nigricollis* (Pic): male and female, Congo belge: P.N.U., Gorges de la Pelenge, 1150 m, 30. V. 1947 (Mis. G. F. de Witte).

Phaneros (*Phaneros*) *inapicalis* (Pic): male and female, Congo belge: P. N. Albert, V. Nyamuragira, Mayumbu, 2100 m, 14.–26. VI. 1945 (G. F. de Witte).

Phaneros (*Phaneros*) *costatus* (Pic): male, Guinea Espanola, Evinayong (Dr. L. Baguena); female, Gabon (OYEM) (G. le Testu).

Staepteron cyanoxanthum (Bourgeois): male and female, Jonkersberg, XI. 1944 (G. van Son).

Phylogeny

Five genus-group taxa of Dictyopterini are currently known from the Afrotropical region: *Bourgeoisiella*, *Phaneros*, *Flagrax*, *Kleineria* and *Staepteron*. The recent phylogenetic analysis of Erotini and Dictyopterini (Kazantsev 2004) did not take into consideration female characters of *Kleineria*, as no female specimens of its only species were known at that time. *Staepteron*, which was considered to belong in Erotinae *incertae sedis*, had not been included in the analysis either. With the data on *Kleineria* and *Staepteron* now available, the cladistic analysis of the Flagraxina is repeated. *Taphes brevicollis* Waterhouse (Taphini) is included as the outgroup, and *Dictyoptera aurora* Latreille, as a possible ingroup taxon (Table 1). The following set of characters was used:

1 Ultimate palpomere:
  (0) pointed distally (Figs 1–3);
  (1) flattened and widenening distally (Figs 5–7, 9).
2 Mentum:
  (0) absent or represented by paired structure (Fig. 1);
  (1) represented by free undivided sclerite (Figs 5, 9).
3 Antennomere 3:
  (0) similar in structure and vestiture to antennomere 2 (Figs 4, 12);
  (1) similar in structure and vestiture to antennomere 4 (Fig. 61).
4 Carinae making posterior sides of pronotal median cell, anteriorly:
  (0) concave (Fig. 8);
  (1) convex.
5 Elytra:
  (0) more or less parallel-sided (Fig. 61);
  (1) conspicuously widened.
6 Elytral costa 2:
  (0) fully developed;
  (1) weakened in proximal half, as compared to other primary costae.
7 Secondary elytral reticulation:
  (0) present in all interstices;
  (1) absent in last interstice.
8 Elytral cells:
  (0) elongate;
  (1) square or transverse (Fig. 61).
9 Elytral cells:
  (0) weak and uneven;
  (1) conspicuous and more or less even.
10 Last elytral interstice:
  (0) not visible from above;
  (1) visible from above, at least distally. Condition 0 was found only in Bourgeoisiella.
11 Elytral pubescence:
  (0) represented by hairs distributed along costae;
  (1) represented by hairs proximally and bristles along costae elsewhere.
12 Scuto-scutellar ridge of metascutum:
  (0) not forming loop (Figs 14, 19);
  (1) forming loop (Fig. 16).
13 Discrimen (metasternal suture):
  (0) complete (Fig. 17);
  (1) incomplete (Figs 13, 15).
14 Hind wing: wedge cell:
  (0) absent (Figs 20–21);
  (1) present (Figs 22–24).

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15 Hind wing: cu-a brace, connected to Cu_2:
(0) at Cu veins branching point or close to it (Figs 20–21, 23–24);
(1) more distally, distant from Cu branching point (Fig. 22).
16 Tarsomere 1:
(0) without plantar pad (Fig. 25);
(1) with apical plantar pad (Fig. 27);
(2) with plantar pad occupying about half of the tarsomere (Fig. 26).
17 Distal margin of male sternite 8:
(0) incised or concave (Fig. 30);
(1) straight or convex (Fig. 28).
18 Distal margin of male sternite 8:
(0) without median process (Fig. 28);
(1) with median process (Fig. 30).
19 Male sternite 9 and tergites 9 + 10:
(0) externally visible (Fig. 30);
(1) invaginated in abdomen, externally not visible (Fig. 28). Condition 1 was found only in Flagrax.
20 Spiculum ventrale:
(0) absent (Fig. 32);
(1) present (Figs 33–39).
21 Phallobase:
(0) subequal in length to median lobe (Fig. 50);
(1) considerably shorter than median lobe (Figs 51–53).
22 Phallobase: median suture:
(0) present (Figs 53, 57, 65–69);
(1) absent (Figs 50–52).
23 Parameres:
(0) free (Figs 50–53, 57–60, 62–64);
(1) fused to median lobe (Figs 65–69).
24 Coxites:
(0) not sclerotized (Fig. 44);
(1) sclerotized (Figs 40–43, 45–49).
25 Intermediate sclerite between coxites:
(0) present (Fig. 40);
(1) absent (Figs 41–49).
26 Valvifers:
(0) shorter than coxites (Fig. 40);
(1) longer than coxites, but less than twice their length (Figs 43, 45–48);
(2) more than twice as long as coxites (Figs 41–42, 44, 49)

The analysis of the data matrix by Phylip Pars, version 3.63, with unweighted characters resulted in one most parsimonious cladogram, demonstrating presence of three clades, Flagraxina, *Dictyoptera* and *Taphes*; the Flagraxina taxa are divided into two clades (Fig. 54). The monophyly of Flagraxina appeared to be confirmed. The analysis was repeated with weighted characters, weights of the 26 characters being 1, 3 or 5 (out of possible 9), i.e. 15111111111153111153115151, with highest weight (5) awarded to characters that were considered most unlikely to regain their ancestral condition: i.e. divided mentum, complete discrimen, exposed male ultimate abdominal segments, free parameres and present intermediate sclerite between coxites (2, 12, 18, 21, 23); certain conservative structures, such as wedge cell in metathoracic wing and spiculum ventrale (13, 19), were weighted as "3". The search produced the same most parsimonious cladogram and it was used for phylogenetic reconstruction.

Flagraxina is separated by such apomorphies, as the conspicuous median pronotal cell with convex posterior carinae, presence of a wedge cell in the metathoracic wing and the modified distal margin of penultimate male ventrite. On the other hand, the Flagraxina appear to have widely preserved the complete discrimen as an

Table 1
Data matrix

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Taphes brevicollis	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
Dictyoptera aurora	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	2	0	0	0	1	1	1	0	1	1	2
Bourgeoisiella ruficeps	1	1	0	1	0	1	1	1	1	0	0	0	0	1	0	1	1	0	0	?	1	0	1	?	?	?
Flagraxauberti	1	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	1	1	2
Flagrax parallelus	1	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	1	1	2
Flagrax atripes	1	1	1	1	0	0	0	0	1	1	0	0	0	1	1	2	1	0	1	1	1	0	0	1	1	1
Kleineria silvicola	1	1	0	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	1	2
Phaneros xanthopterus	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	1	1
Phaneros nigricollis	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	1	1
Phaneros inapicalis	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	1	1
Phaneros costatus	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	1	1
Staepteron cyanoxanthum	1	1	1	1	1	0	0	0	1	1	1	0	0	1	0	2	1	1	0	1	1	0	0	0	1	2

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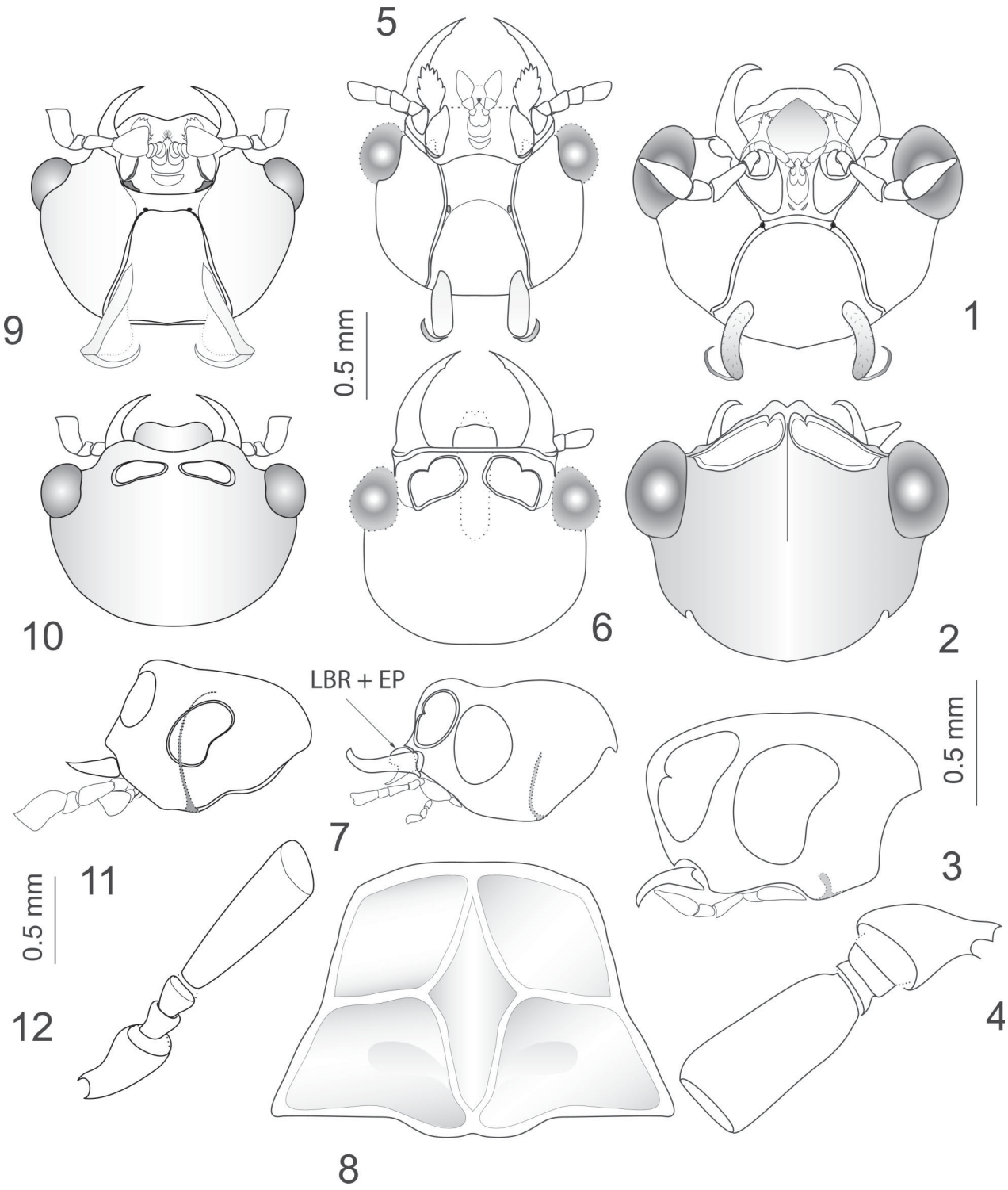

Figs 1–12. Details of Taphini and Dictyopterini. **1** – *Taphes brevicollis* Waterhouse, head, ventrally; **2** – same, dorsally; **3** – same, laterally; **4** – same, antennomeres 1–4, ventrally; **5** – *Dictyoptera aurora* (Herbst), head, ventrally; **6** – same, dorsally; **7** – same, laterally; **8** – same, pronotum; **9** – *Phaneros* (*Kleineria*) *silvicola* sp. n., head, ventrally; **10** – same, dorsally; **11** – same, laterally; **12** – same, antennomeres 1–4, ventrally. EP – epipharynx; LBR – labrum.

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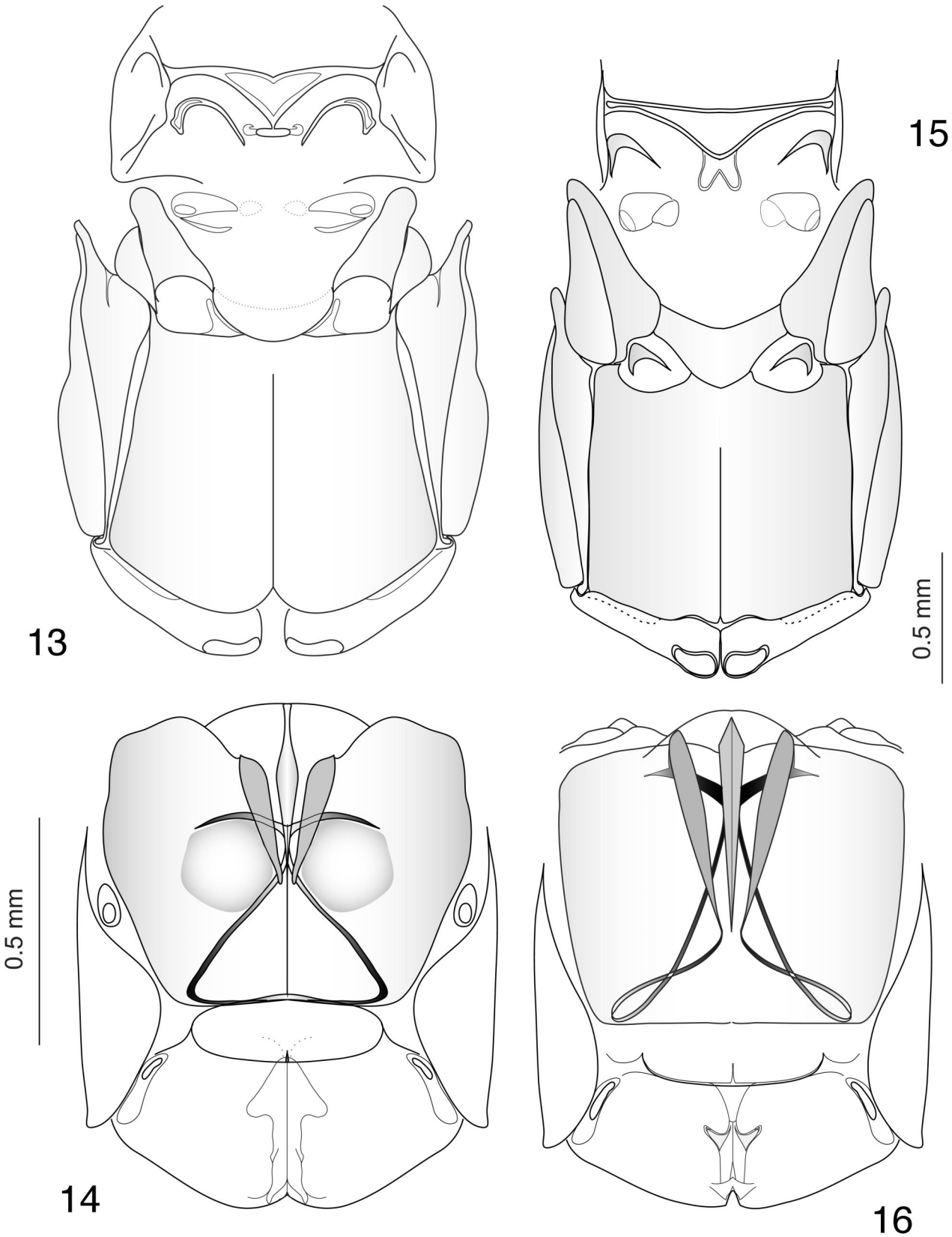

Figs 13–16. Details of Taphini and Dictyopterini. **13** – *Taphes brevicollis* Waterhouse, thorax, ventrally; **14** – same, metathorax, dorsally; **15** – *Dictyoptera aurora* (Herbst), thorax, ventrally; **16** – same, metathorax, dorsally.

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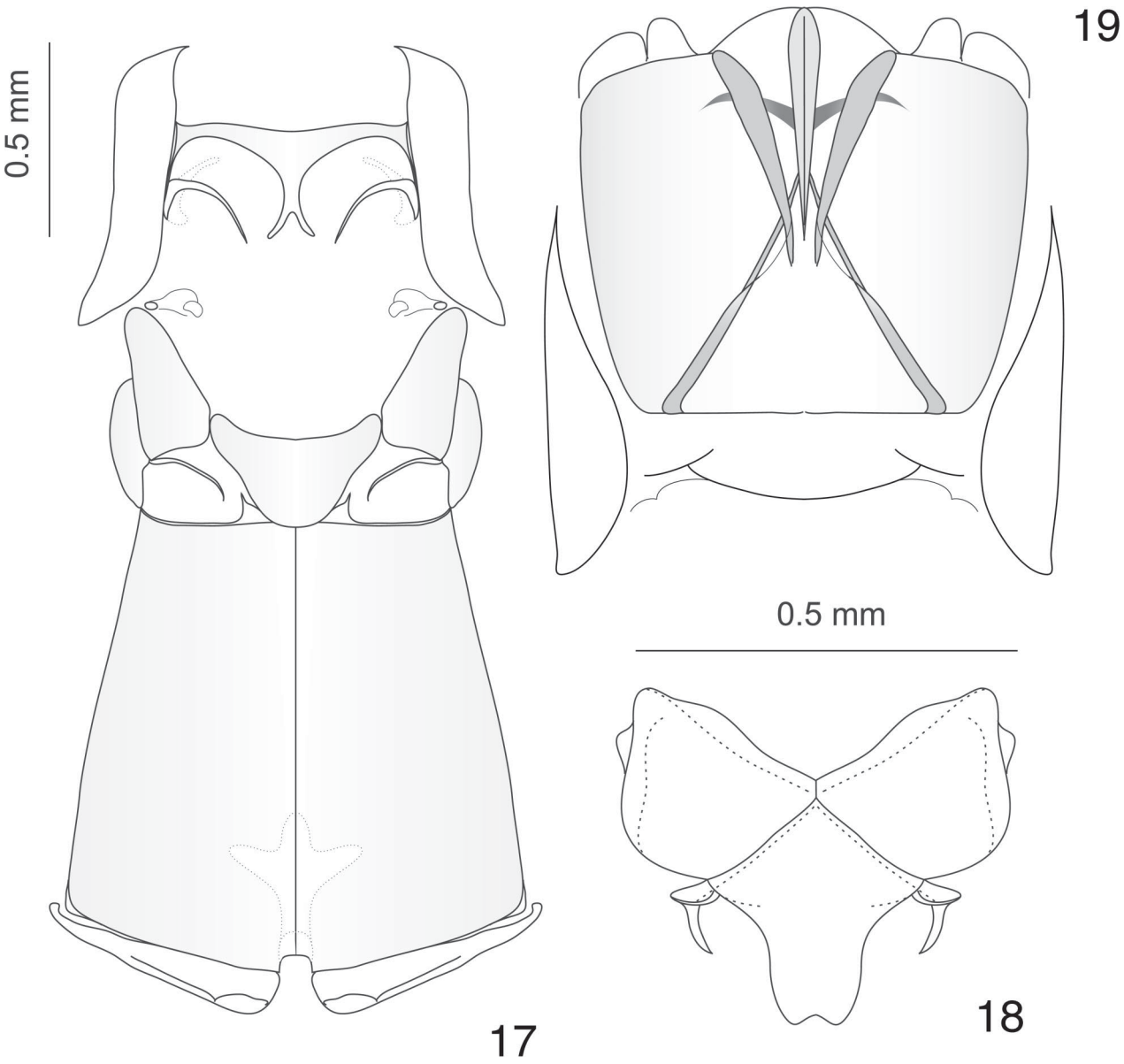

Figs 17–19. Details of *Phaneros* (*Kleineria*) *silvicola* sp. n. **17** – thorax, ventrally; **18** – mesoscutum, dorsally; **19** – metathorax, dorsally.

obvious plesiomorphy manifest in all its taxa, except several *Flagrax*, where it has acquired the apomorphic reduced condition. The latter condition is probably homoplastic with that of *Taphes* (Taphini) and *Dictyoptera* (Dictyopterina). Other symplesiomorphies of Flagraxina manifest in at least some taxa of its both branches are the simple scuto-scutellar ridge of metascutum, which does not form a loop structure, and presence of median suture of the phallobase.

The *Flagrax* + *Staepteron* clade is separated by the structure of the third antennomere, which is similar in shape and vestiture to fourth, and the cu-a brace of the hind wing venation that is connected to Cu_2 distant from branching point of the Cu veins. Both characters are presumed to represent apomorphies of the lineage, while their free parameres are apparently in symplesiomorphic condition with most of the Dictyopterina taxa. An evident autapomorphy of *Flagrax* is the invagination of male sternite 9 and tergites 9 + 10 in the abdomen. The apomorphies of *Staepteron* are the development of median process on distal margin of male penultimate sternite and replacement of elytral pubescence by bristles along costae beyond humeri. At the same time, its non-sclerotized coxites seem to be a unique plesiomorphy not reported elsewhere in the subfamily. In addition, *Flagrax atripes* makes quite a distinct lineage within the *Flagrax*:

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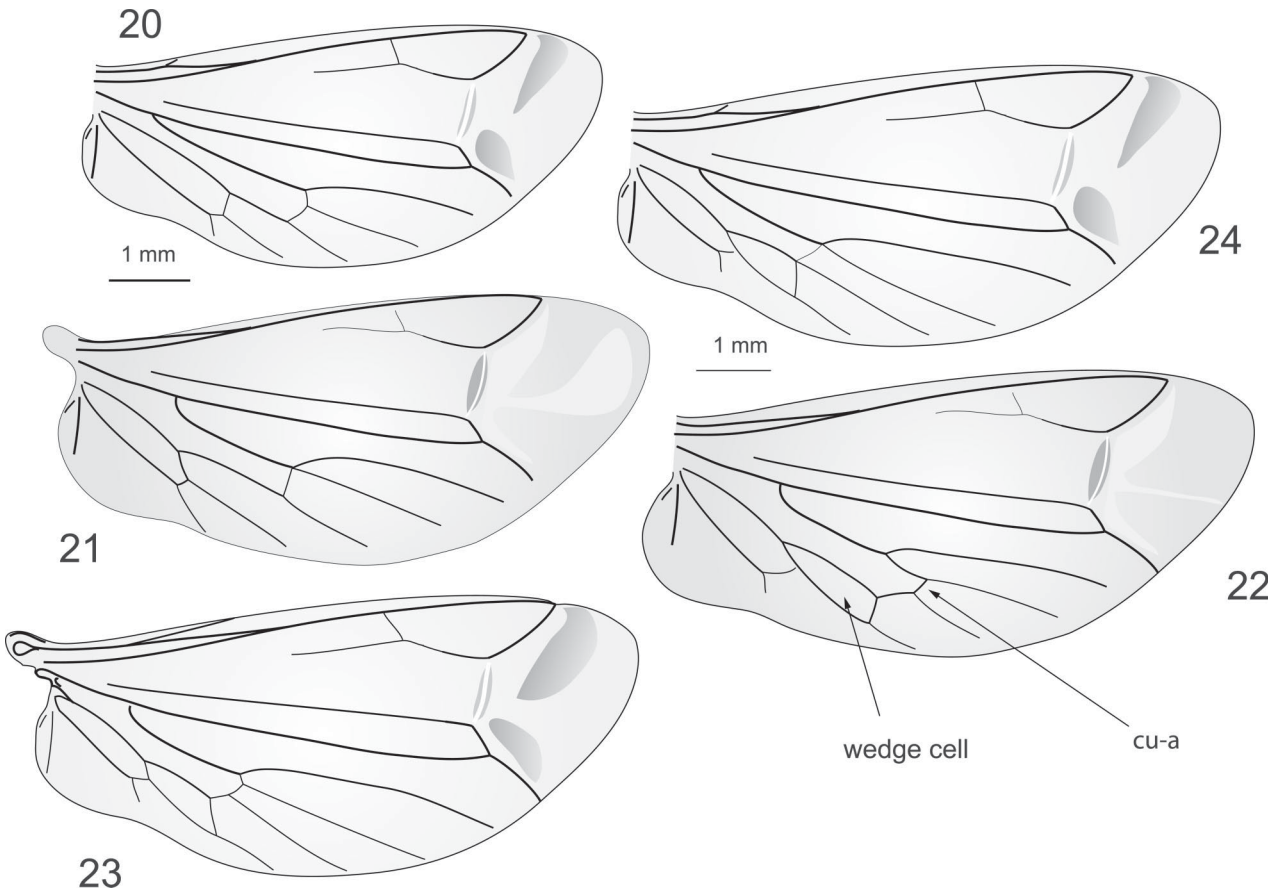

Figs 20–24. Hind wing of Taphini and Dictyopterini. **20** – *Taphes brevicollis* Waterhouse; **21** – *Dictyoptera aurora* (Herbst), thorax, ventrally; **22** – *Flagrax auberti* (Bourgeois); **23** – *Staepteron cyanoxanthum* (Bourgeois); **24** – *Phaneros* (*Kleineria*) *silvicola* sp. n.

being separated by such plesiomorphies as complete discrimen and median suture of the phallobase, which are both lost in other members of the genus, it is also distinguished by reduced parameres, which appear to be its apomorphy.

The second lineage of Flagraxina is characterized by the apparently apomorphic fused condition of parameres of aedeagus; it is subdivided into two branches, *Kleineria* and *Phaneros* + *Bourgeoisiella*. In both branches the third antennomere is similar in structure and vestiture to the second and the cu-a brace of the hind wing is connected to Cu_2 at or near the branching point of the Cu veins. The monophyly of *Kleineria* is supported by the concave distal margin of penultimate male sternite, long spiculum ventrale and valvifers that are regarded as its apomorphies, while the equally developed primary elytral costae appear to be in plesiomorphic condition. The second primary elytral costa reduced in basal half, the short spiculum ventrale and valvifers are hypothesized to be apomorphic for *Phaneros*, the latter character acquiring a homoplastic condition with *Taphes*. The *Phaneros* + *Bourgeoisiella* branch is divided into *Phaneros* and *Bourgeoisiella*, the apomorphic character of the latter taxon being one row of cells in the last interstice. However, the status of all three taxa as subgenera within *Phaneros* is preserved pending further studies: though their monophilies seem to be well supported, the hypothesized apomorphic conditions of *Kleineria* represent widespread plesiomorphies of Dictyopterini and a more representative analysis may reject some of them; besides, no females of the type species of *Kleineria* have so far been seen. Similarly, the absence of collected female specimens does not allow making a substantiated judgment on the status of *Bourgeoisiella*.

A presumed phylogenetic tree of the subtribe Flagraxina is given in Fig. 55.

The Flagraxina evidently represent a very old lineage of Dictyopterini, with a remarkably disjunct biogeographical pattern. They are characterized, for instance, by the complete discrimen (Fig. 17), which seems to be symplesiomorphic with such taxa, as *Leptolycus*, *Calopteron* and

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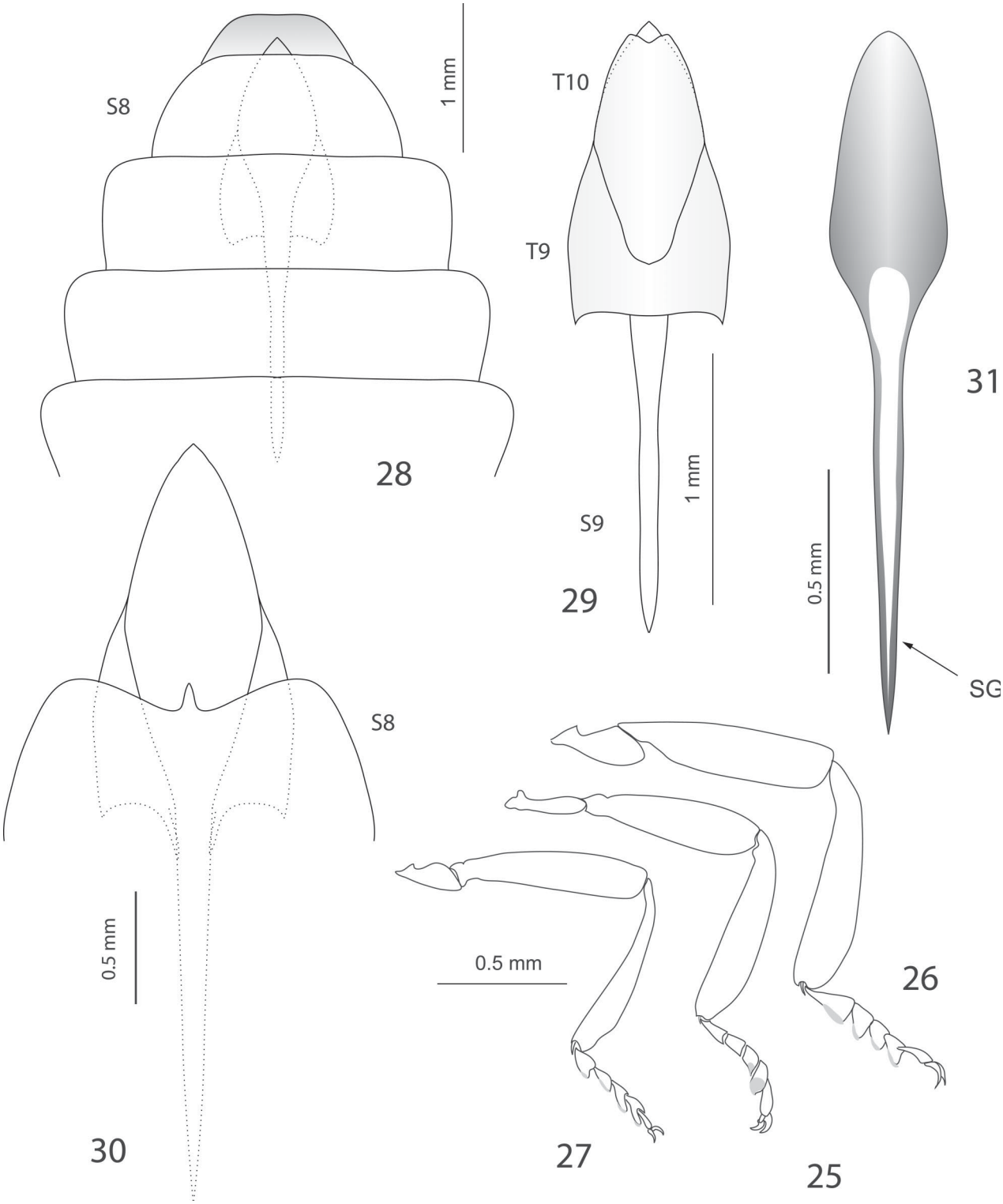

Figs 25–31. Details of Taphini and Dictyopterini. **25** – *Taphes brevicollis* Waterhouse; **26** – *Dictyoptera aurora* (Herbst); **27** – *Phaneros* (*Kleineria*) *silvicola* sp. n.; **28** – *Flagrax auberti* (Bourgeois), distal portion of abdomen, ventrally; **29** – same, sternite 9 and tergites 9 and 10, dorsally; **30** – *Staepteron cyanoxanthum* (Bourgeois), distal portion of abdomen, ventrally; **31** – *Phaneros* (*Kleineria*) *silvicola* sp. n., sternite 9, ventrally (**25**–**27**, middle leg). SG – spiculum gastrale.

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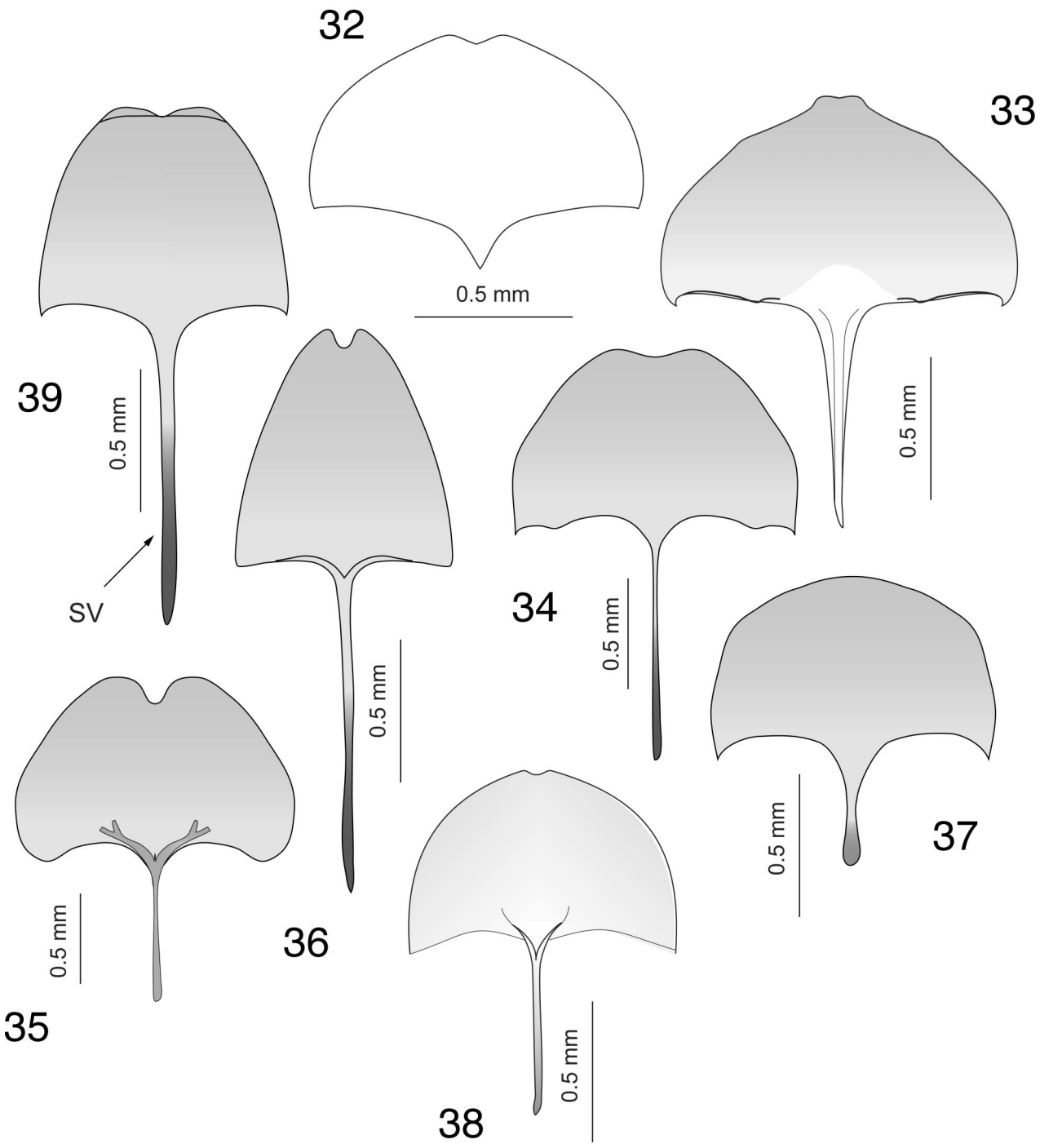

Figs 32–39. Female apical sternite of Taphini and Dictyopterini. **32** – *Taphes brevicollis* Waterhouse; **33** – *Dictyoptera aurora* (Herbst); **34** – *Flagrax auberti* (Bourgeois); **35** – *Flagrax atripes* (Pic); **36** – *Staepteron cyanoxanthum* (Bourgeois); **37** – *Phaneros* (*Phaneros*) *xanthopterus* (Bourgeois); **38** – *Phaneros* (*Phaneros*) *costatus* (Pic); **39** – *Phaneros* (*Kleineria*) *silvicola* sp. n. SV – spiculum ventrale.

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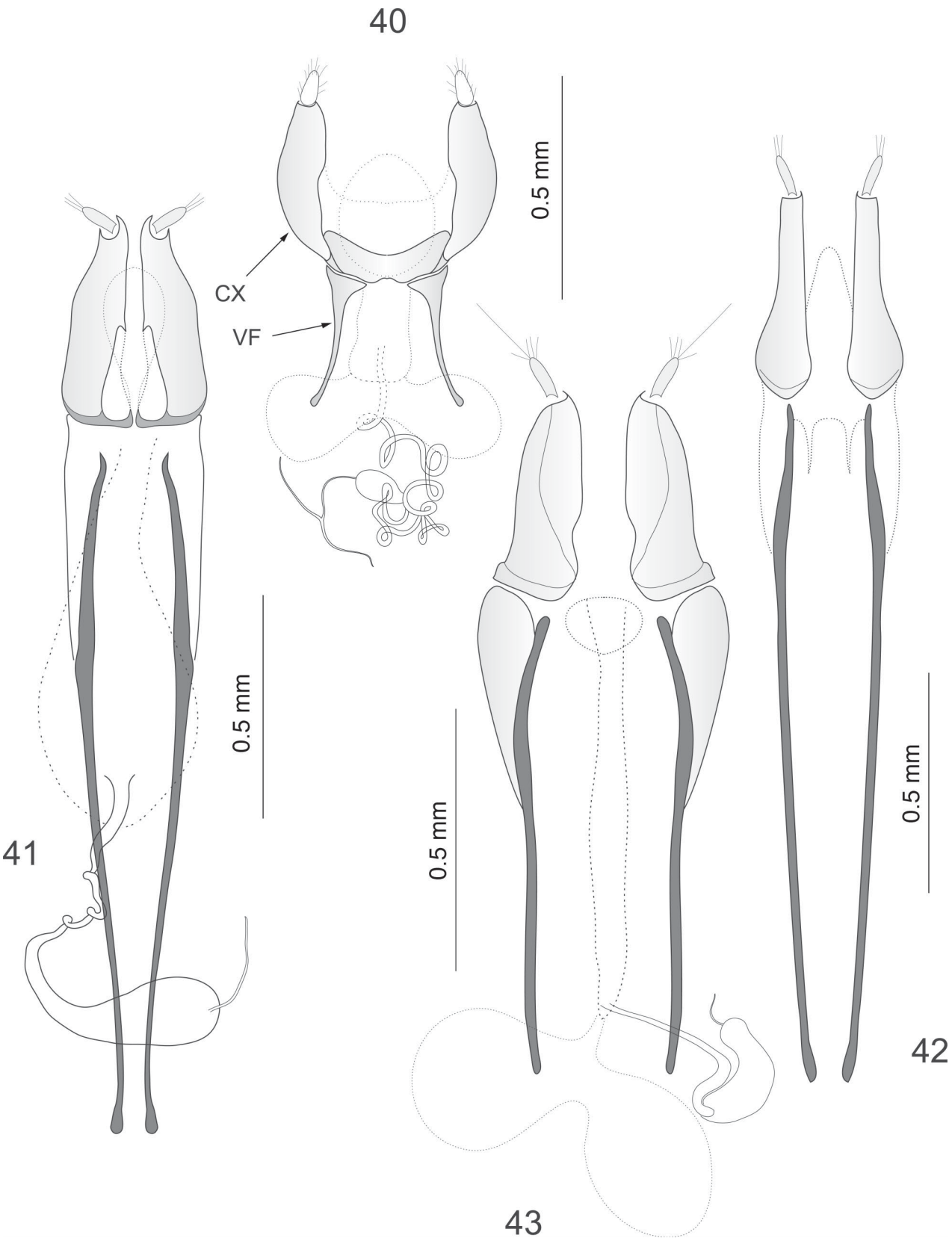

Figs 40–43. External female genitalia of Taphini and Dictyopterini. **40** – *Taphes brevicollis* Waterhouse; **41** – *Dictyoptera aurora* (Herbst); **42** – *Flagrax auberti* (Bourgeois); **43** – *Flagrax atripes* (Pic).

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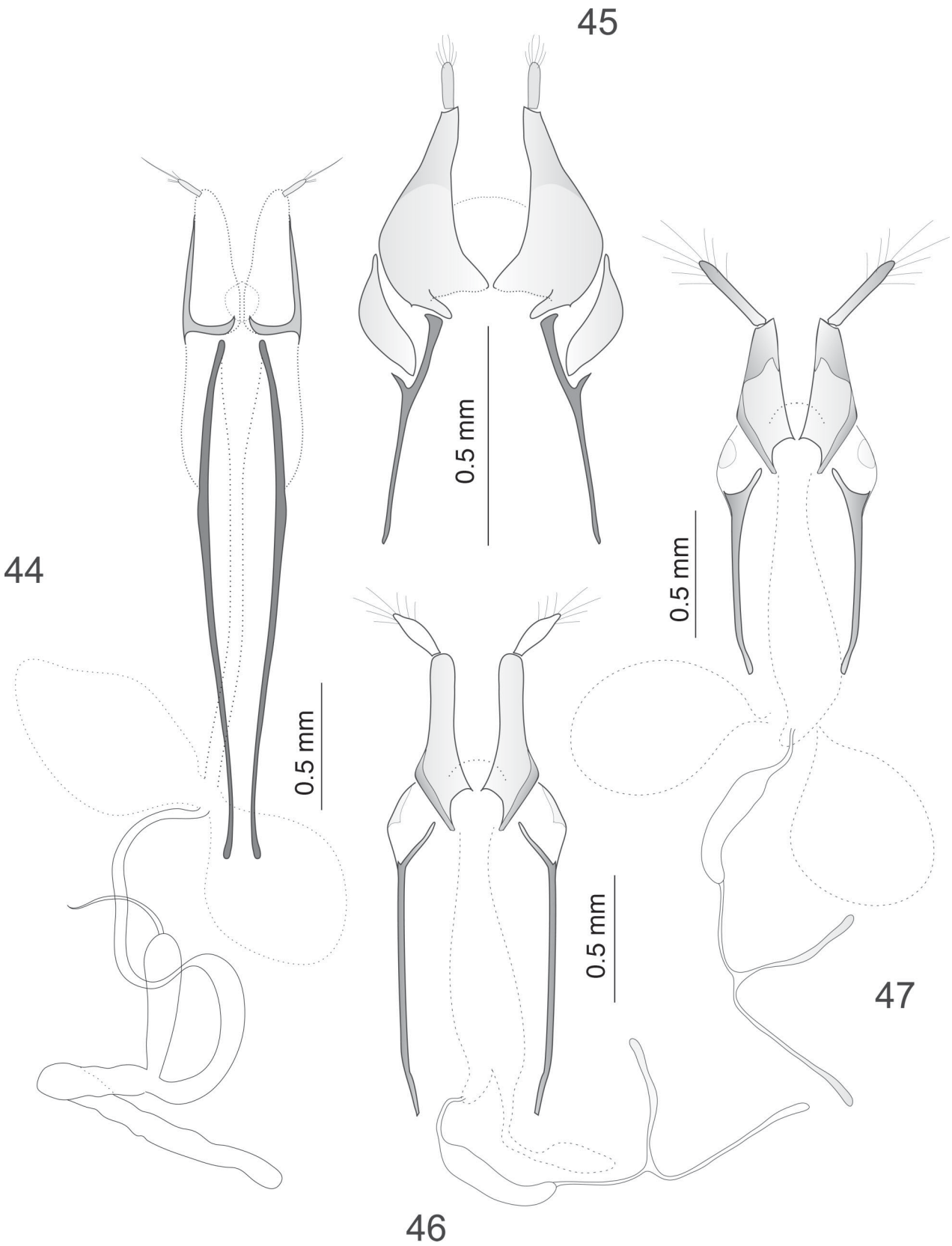

Figs 44–47. External female genitalia of Flagraxina. **44** – *Staepteron cyanoxanthum* (Bourgeois); **45** – *Phaneros* (*Phaneros*) *xanthopterus* (Bourgeois); **46** – *Phaneros* (*Phaneros*) *costatus* (Pic); **47** – *Phaneros* (*Phaneros*) *inapicalis* (Pic).

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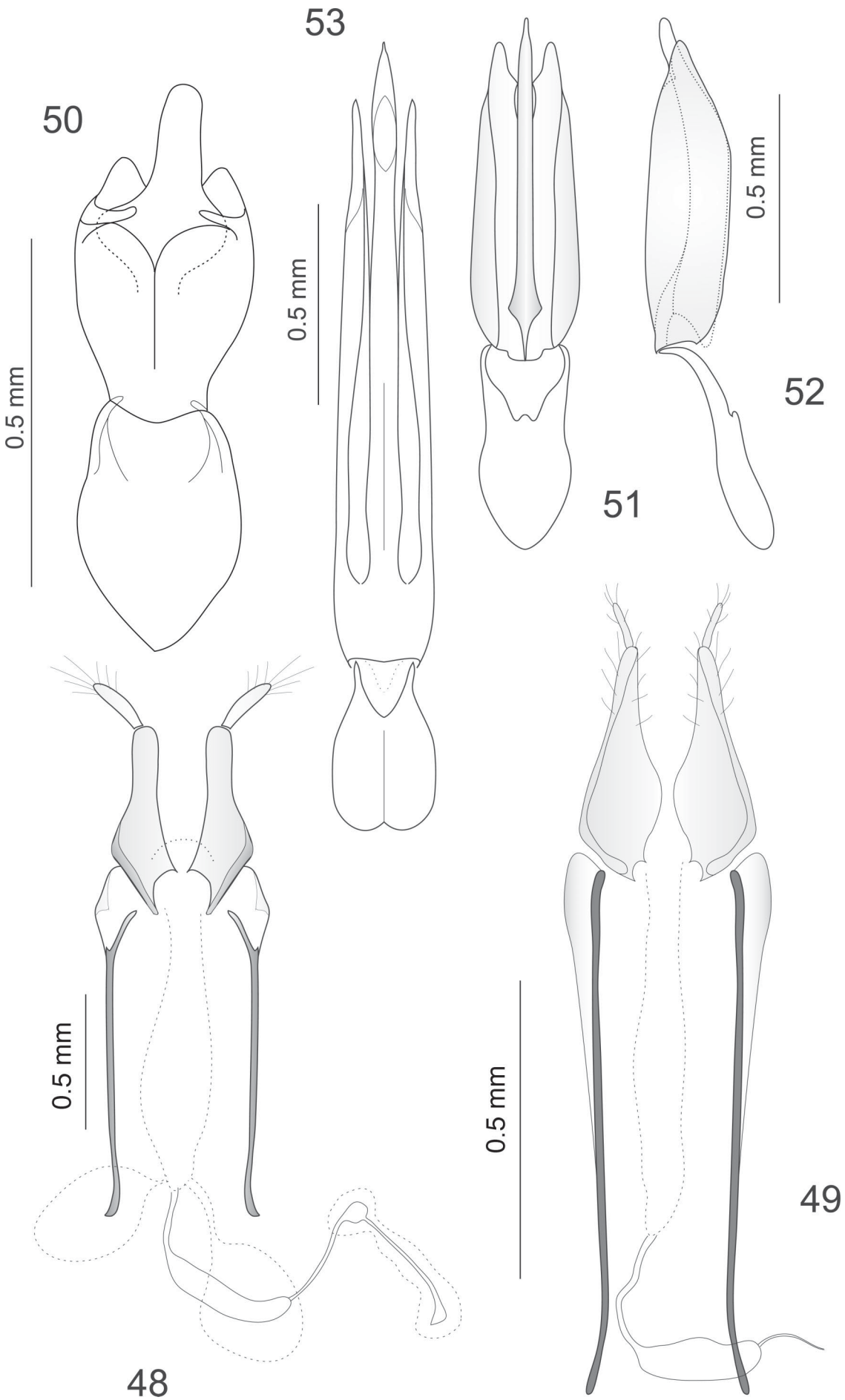

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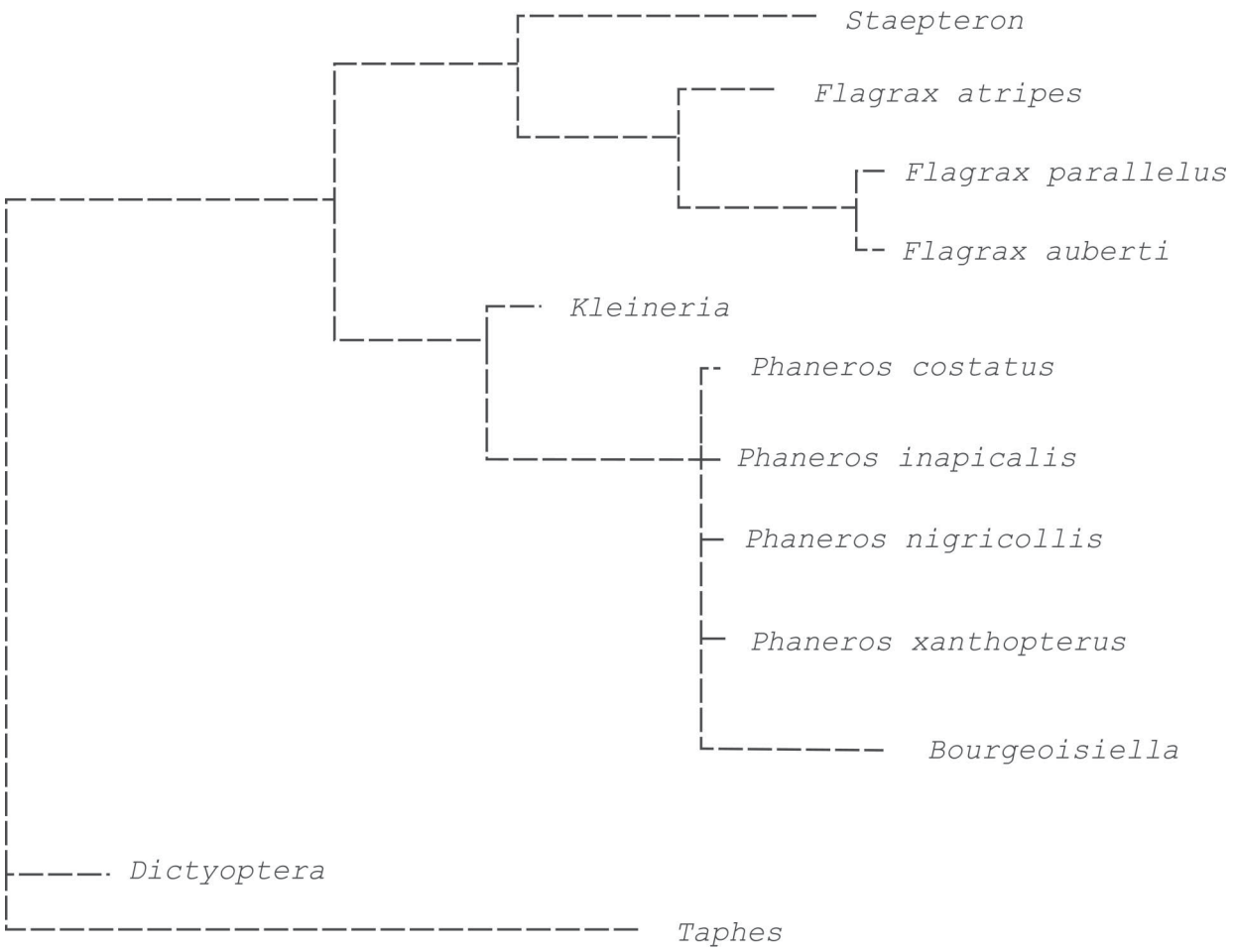

Fig. 54. Phylip Pars cladogram.

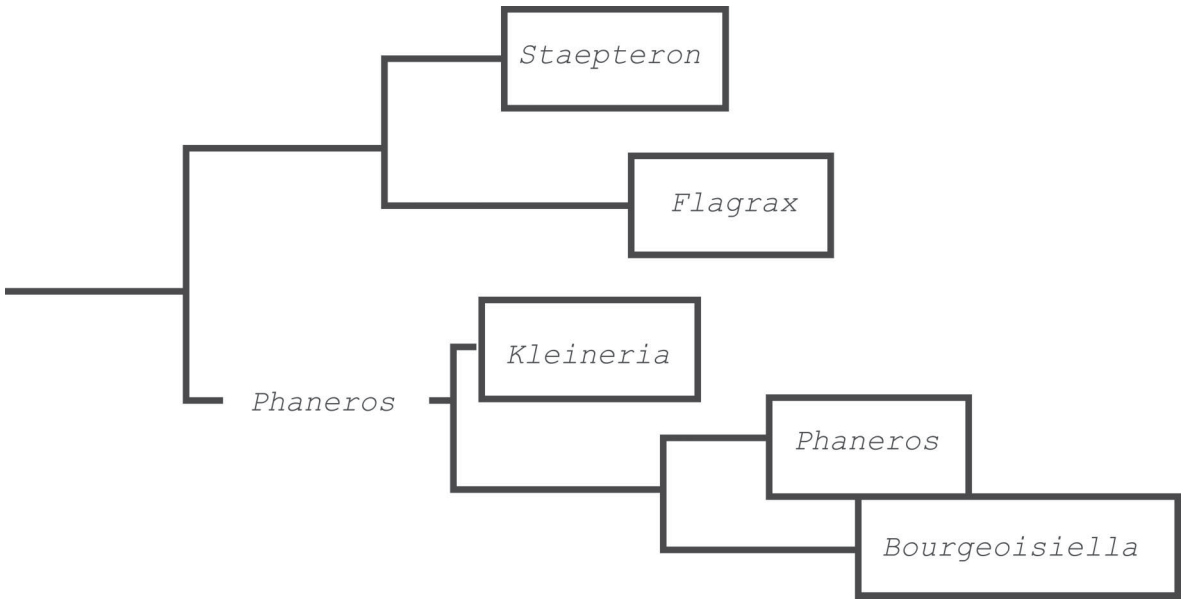

Fig. 55. Presumed phylogenetic tree of the subtribe Flagraxina.

◄

Figs 48–53. External genitalia of Flagraxina. **48** – *Phaneros* (*Phaneros*) *nigricollis* (Pic); **49** – *Phaneros* (*Kleineria*) *silvicola* sp. n.; **50** – *Taphes brevicollis* Waterhouse, aedeagus, ventrally; **51** – *Dictyoptera aurora* (Herbst), aedeagus, ventrally; **52** – same, laterally; **53** – *Staepteron cyanoxanthum* (Bourgeois), aedeagus, ventrally (48–49, female genitalia; 50–53, male genitalia).

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Lycostomus, and is absent in other studied Dictyopterini, as well as in Taphini. Another noteworthy plesiomorphy is the non-sclerotized coxites (Fig. 44), manifest in *Staepteron*. The distribution pattern of the subtribe is marked for the wide gaps between the localities where its representatives have been documented to occur. Only *Flagrax*, being somewhat better represented in collections, is known from three relatively vast areas, first in Guinea and Sierra-Leone, second in the Congo Basin and the Biafra Gulf region, including islands Bioko (Fernando Poo) and Sao Tome, and the third in Natal and Transvaal. *Phaneros* has been reported by rather few specimens from the West Coast (Gabon, Cameroon and Equatorial Guinea) and the mountains of East Africa. The distribution of *Staepteron*, the third genus of the subtribe, is limited to several slopes in the coastal ridge of Western Cape (Fig. 56).

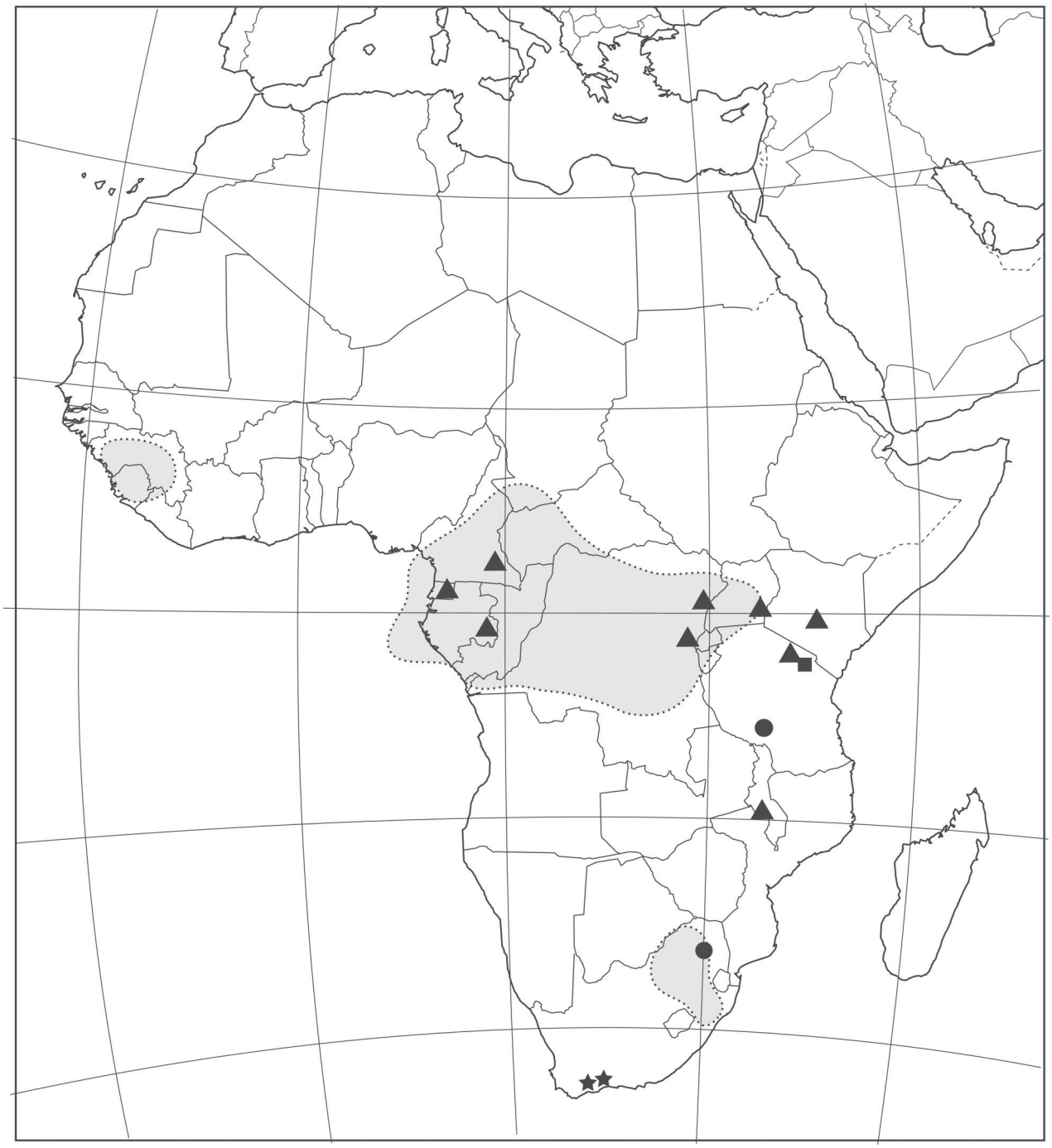

Fig. 56. Distribution of Flagraxina: *Flagrax* shown by shaded areas; *Staepteron* – by stars; *Phaneros* s. str. – by triangles; *Phaneros* (*Bourgeoisiella*) – by a square; *Phaneros* (*Kleineria*) – by circles.

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Taxonomy and descriptions

The tribe Dictyopterini is represented in the Afrotropical region by the endemic subtribe Flagraxina. The Flagraxina taxa are grouped in three genera that can be distinguished by the following characters:

Key to genera and subgenera of Dictyopterini of the Afrotropical region

1. Antennomere 3 similar in length and vestiture to antennomere 4 (Fig. 61). Elytral cells elongate. Parameres free (Figs 50–53, 57–60, 62–64) **2**
– Antennomere 3 similar in length and vestiture to antennomere 2 (Fig. 12). Elytral cells square or transverse. Parameres fused to median lobe (Figs 65–69) . . . . . [*Phaneros* Kazantsev, 1992] **3**
2. Elytra more or less parallel-sided (Fig. 61); elytral pubescence represented by hairs distributed along costae. Male ultimate abdominal segments invaginated in abdomen, distal margin of male sternite 8 without median process (Fig. 28). Coxites sclerotized (Fig. 42–43) . . . . . ***Flagrax* Kazantsev, 1992**
– Elytra conspicuously widened; elytral pubescence represented by hairs proximally and bristles along costae elsewhere. Male ultimate abdominal segments exposed, distal margin of male sternite 8 with median process (Fig. 30). Coxites not sclerotized (Fig. 44) . . . . . ***Staepteron* Kazantsev, 1992**
3. All primary elytral costae equally developed, including in proximal half. Distal margin of male sternite 8 concave. Spiculum ventrale relatively long (Fig. 39). Valvifers long (Fig. 49) . . . . . ***Phaneros* (*Kleineria*) Kazantsev, 2004**
– Elytral primary costa 2 less developed in proximal half. Distal margin of male sternite 8 straight. Spiculum ventrale relatively short (Figs 37–38). Valvifers short (Figs 45–48) **4**
4. All elytral interstices with double rows of cells. Last elytral interstice well visible from above, at least in distal half . . . . . ***Phaneros* (*Phaneros*) Kazantsev, 1992**
– Last elytral interstice with one row of cells and not visible from above, including in distal half . . . . . ***Phaneros* (*Bourgeoisiella*) Kazantsev, 1992**

FLAGRAXINA Kazantsev, 2004

FLAGRAXINA Kazantsev, 2004: 11

Type genus. *Flagrax* Kazantsev, 1992

Flagrax Kazantsev, 1992

Flagrax Kazantsev, 1992: 38

Type species. *Stadenus auberti* Bourgeois, 1881

Redescription. Head transverse. Fastigium right-angled. Labrum transverse, sclerotized, with proximal portion lying under epistoma, feebly emarginated medially. Eyes relatively small, spherical. Mandibles projected forward and strongly bent inward. Maxillary palps relatively large, 4-segmented, with ultimate palpomere more or less parallel-sided and flattened distally. Prementum undivided, labial palps 3-segmented, slender, ultimate palpomere conspicuously widened and flattened distally. Gula absent, ventral closure short. Antennal prominence relatively inconspicuous, antennal sockets separated by minute lamina. Antennae 11-segmented, long, conspicuously flattened and serrate from antennomere 3; antennomere 3 much longer and wider than antennomere 2 (Fig. 61); pubescence long and erect in male antennomeres 3–11, short and decumbent in all female antennomeres.

Pronotum transverse, with prominent median cell and weak transverse carinae; posterior angles conspicuously produced laterally. Prosternum very short, Y-shaped. Thoracic spiracles moderately sclerotized and not protruding laterally beyond coxal limits. Mesepimeron considerably smaller and shorter than mesepisternum and slightly extending beyond its base. Scutellum elongate, parallel-sided, concave at disk. Elytra almost parallel-sided, with four equally developed prominent primary costae, interstices with double rows of mostly elongate cells; pubescence distributed along costae. Metasternal suture (discrimen) incomplete, attaining to three fourths of metaventrite (complete in *Ph. atripes*). Metathoracic wing with wedge cell; cu-a brace connecting Cu_2 and A_1 distant from Cu veins branching point (Fig. 22).

Mesocoxae widely separated, metacoxae narrowly so. Protrochantins subequal in size to mesotrochantins. Trochanters elongate, noticeably widened distally, connected to femora distally; tibiae with almost straight inner margin and a pair of similar short apical spurs; tarsomeres 1–4 with plantar pads, plantar pad on tarsomere 1 occupying its apical portion; all claws simple. Abdominal spiracles located dorsally on sternite at its edge. Spiculum ventrale long (Figs 34–35); spiculum gastrale long (Figs 28–29). Valvifers long and free, styli small and elongate (Figs 42–43). Aedeagus symmetric, with elongate, free parameres; phallobase without median suture (Figs 58–60, 62–64) (shorter parameres

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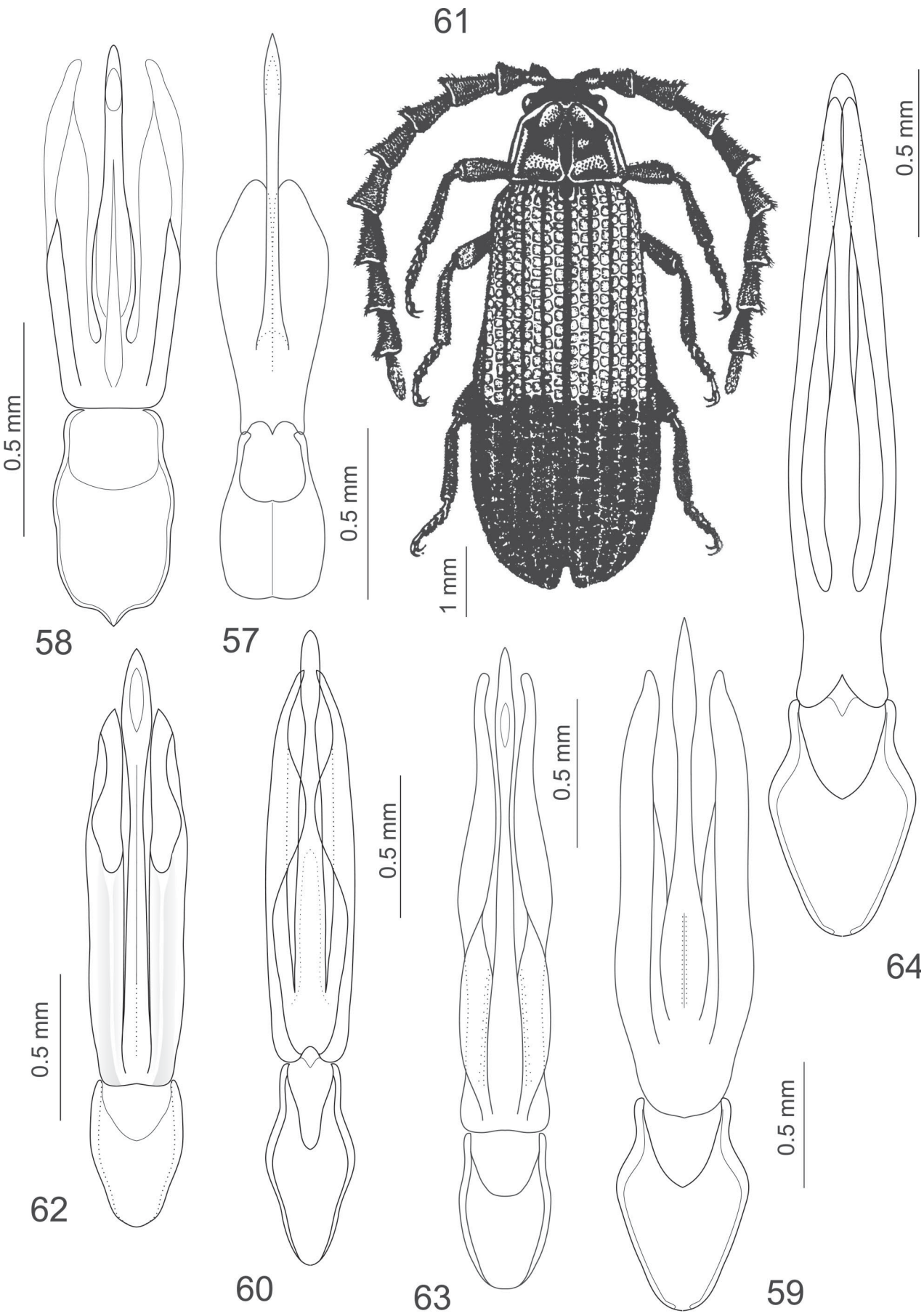

Figs 57–64. Habitus (**61**) and aedeagi (**57–60**, **62–64**) of *Flagrax* Kazantsev. **57** – *F. atripes* (Pic); **58** – *F. auberti* (Bourgeois); **59** – *F. grandis* (Kleine); **60** – *F. subelongatus* (Pic); **61**, **62** – *F. parallelus* (Pic); **63** – *F. bolivari* (Bourgeois); **64** – *F. laticornis* (Pic).

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and phallobase with complete median suture in *Ph. atripes* – Fig. 57).

Comments. Flagrax is distinguished from other Flagraxina genera by the invaginated male ultimate abdominal segments (Fig. 28). It can be easily separated from Staepteron by the parallel-sided elytra (Fig. 61), hairy elytral pubescence, absence of median process on the distal margin of male penultimate sternite (Fig. 28) and sclerotized coxites (Figs 42–43).

Distribution. The distribution area of *Flagrax* is split into three parts, first in Guinea and Sierra-Leone, second in the Biafra Gulf and the Congo Basin, it also includes Biafra Gulf islands, such as Bioko (Fernando Poo) and Sao Tome, and the third in South Africa (Natal and Transvaal) (Fig. 56).

Biology. No preimaginal forms have been observed or collected in *Flagrax*. The imagines of *F. auberti*, *F. atripes* and *F. grandis* are documented to have been taken by general collecting or beating in forest at altitudes ranging from 1410 m to 2180 m above sea level, which suggests that at least these species are restricted to mountainous forests.

Flagrax bicoloripes (Pic), the type specimen of which was illustrated in one of the previous papers (Kazantsev 1992), is assumed to represent a small specimen of *F. parallelus* (Pic), the difference from a typical *F. parallelus* being the flattened apex of the medial lobe of the aedeagus, which is believed to be a consequence of poor formation due to teratology. Therefore, *Flagrax bicoloripes* (Pic 1946) is regarded as a junior synonym of *F. parallelus* (Pic 1922).

The following species-group taxa are included in Flagrax:

***Flagrax atripes* (Pic, 1922)**. S Africa (Natal and Transvaal).

Stadenus atripes Pic, 1922: 6

***Flagrax auberti auberti* (Bourgeois, 1881)**. Gabon, Cameroon, Congo, Equatorial Guinea, Central African Republic, Fernando Poo Is., Guinea and Uganda.

Stadenus auberti Bourgeois, 1881: XXXVII
Stadenus angustatus Pic, 1946: 5
Stadenus antennalis Bourgeois, 1889: 246
Stadenus auberti var. *atricollis* Pic, 1915: 13
Stadenus breveapicalis Pic, 1946: 5
Stadenus innotatus Pic, 1928: 61
Stadenus leonensis Pic, 1946: 5
Stadenus mocquerysi Pic, 1915: 13
Stadenus mocquerysi var. *geniculatus* Pic, 1915: 14
Stadenus rufifrons Pic, 1915: 13
Stadenus subelongatus var. *notaticollis* Pic, 1946: 5

***Flagrax auberti semifulvus* (Fairmaire, 1891)**. W Africa (Sao Tome Is.).

Stadenus semifulvus Fairmaire, 1891: 116
Stadenus nodieri Pic, 1946: 6

***Flagrax bifoveolatus* (Pic, 1924)**. Ile Principe (Biafra Gulf).

Stadenus bifoveolatus Pic, 1924: 161

***Flagrax bolivari* (Bourgeois, 1905)**. W Africa (Equatorial Guinea).

Stadenus bolivari Bourgeois, 1905: 193

***Flagrax grandis* (Kleine, 1942)**. E Africa (Congo not far from Rwanda border).

Stadenus grandis Kleine, 1942: 4

***Flagrax laticornis* (Pic, 1946)**. W Africa (Gabon, Cameroon, Equatorial Guinea, Congo, Fernando Poo Is.).

Stadenus laticornis Pic, 1946: 5

***Flagrax parallelus* (Pic, 1922)**. W Africa (Gabon, Cameroon, Equatorial Guinea, Congo).

Stadenus bicoloripes Pic, 1946: 5, **syn. n.**
Stadenus parallelus Pic, 1922: 6

***Flagrax subelongatus* (Pic, 1915)**. W Africa (Gabon, Cameroon, Congo).

Stadenus lamottei Pic, 1958: 160
Stadenus subelongatus Pic, 1915: 13

Most of *Flagrax* species may be distinguished only by characters of male copulatory organs. *F. bifoveolatus* (Pic), the type of which has not been found in the Pic collection at the National Museum of Natural History in Paris, is omitted from the key.

Key to species of *Flagrax*

1. Discrimen complete. Parameres of aedeagus considerably shorter than median lobe (Fig. 57). ..... ***Flagrax atripes* (Pic)**
– Discrimen incomplete, not reaching mesoventrite. Parameres of aedeagus only slightly shorter than median lobe (Figs 58–60, 62–64). **2**
2. Aedeagus relatively short and robust, its median lobe not widened distally (Fig. 58) ..... [***Flagrax auberti* (Bourgeois)] 3**
– Aedeagus long and slender, its median lobe widened distally (Figs 59–60, 62–64) **4**
3. Elytra uniformly testaceous or with up to apical half black ..... ***Flagrax auberti auberti* (Bourgeois)**
– Apical two thirds of elytra black ..... ***Flagrax auberti semifulvus* (Fairmaire)**
4. Pronotum black. Elytra uniformly testaceous. Median lobe of aedeagus conspicuously widened and carrying median rib proximally (Fig. 59) ..... ***Flagrax grandis* (Kleine)**

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– Distal portion of elytra black **5**
5. Parameres with wide lobes in their preapical portion (Fig. 60) ..... ***Flagrax subelongatus* (Pic)**
– Parameres without conspicuous lobes in their preapical portion (Figs 62–64) **6**
6. Parameres incised distally (Fig. 62) ..... ***Flagrax parallelus* (Pic)**
– Parameres not incised distally (Figs 63–64) **7**
7. Apex of median lobe only slightly widened, its ventral surface without proximal impression (Fig. 63) ..... ***Flagrax bolivari* (Bourgeois)**
– Apex of median lobe conspicuously widened, its ventral surface with proximal impression (Fig. 64) ..... ***Flagrax laticornis* (Pic)**

Staepteron Kazantsev, 1992

Staepteron Kazantsev, 1992: 50

Type species. ***Calopteron cyanoxanthum*** Bourgeois, 1884

Redescription. Head transverse. Fastigium right-angled. Labrum transverse, almost completely lying under epistoma. Eyes small, spherical. Mandibles small, projected forward and strongly bent inward. Maxillary palps 4-segmented, with ultimate palpomere distinctly widened and flattened distally. Prementum undivided, labial palps 3-segmented, slender, ultimate palpomere large, securiform, conspicuously widened and flattened distally. Antennal prominence relatively inconspicuous, antennal sockets separated by moderately broad lamina. Antennae 11-segmented, flattened and slightly serrate from antennomere 3; antennomere 3 much longer and wider than antennomere 2; pubescence short and partly erect in all male and female antennomeres.

Pronotum transverse, with relatively narrow median cell, less conspicuous in posterior half, and almost obsolete transverse carinae; posterior angles not produced laterally. Prosternum short, T-shaped. Thoracic spiracles moderately sclerotized and not protruding laterally beyond coxal limits. Mesepimeron considerably smaller and shorter than mesepisternum, extending beyond its base. Scutellum elongate, narrow and parallel-sided, rounded distally and concave at disk. Elytra widened and inflated, with four almost equally developed prominent primary costae, interstices with double rows of conspicuous clearly elongate cells; pubescence represented by decumbent hairs proximally and erect thick bristles along costae elsewhere. Metasternal suture complete. Metathoracic wing with wedge cell; cu-a brace connecting Cu_2 and A_1 close to Cu veins branching point (Fig. 23).

Meso- and metacoxae narrowly separated. Protrochantins subequal in size to mesotrochantins. Trochanters relatively short, widened distally, connected to femora distally; tibiae with straight inner margin and a pair of similar short apical spurs; tarsomeres 1–4 with plantar pads, plantar pad on tarsomere 1 occupying its apical half; all claws simple. Male sternite 8 with median process on distal margin (Fig. 30); abdominal spiracles located dorsally on sternite at its edge; spiculum ventrale long (Fig. 36); spiculum gastrale long (Fig. 30). Valvifers long and free, coxites non-sclerotized; styli small and elongate (Fig. 44). Aedeagus symmetric, with elongate, free parameres; phallobase with median suture (Fig. 53).

Comments. *Staepteron* is readily separated from Flagrax by the widened and inflated elytra, their pubescence represented by hairs proximally and bristles along costae elsewhere, presence of a median process on the distal margin of male sternite 8 (Fig. 30) and non-sclerotized coxites (Fig. 44).

Distribution. The only known species of *Staepteron*, *S. cyanoxanthum*, is limited to a very restricted area in the coastal ridge of Western Cape (Fig. 56).

Biology. No preimaginal forms have been observed or collected in *Staepteron* and no biotope or altitude data are available for this taxon. All specimens examined were collected in November or December.

Only one species of *Staepteron* has so far been discovered.

►

Figs 65–74. Details of *Phaneros* Kazantsev. **65** – *Ph.* (*Phaneros*) *caffer* (Kleine), aedeagus, dorsally; **66** – *Ph.* (*Phaneros*) *costatus* (Pic), aedeagus, ventrally; **67** – *Ph.* (*Phaneros*) *nigricollis* (Pic), aedeagus, ventrally; **68** – *Ph.* (*Phaneros*) *xanthopterus* (Bourgeois), aedeagus, ventrally; (Pic); **69** – *Ph.* (*Bourgeoisiella*) *ruficeps* (Bourgeois), aedeagus, ventrally; **70** – *Ph.* (*Kleineria*) *pudicus* (Kazantsev), aedeagus, laterally; **71** – *Ph.* (*Kleineria*) *silvicola* sp. n., metendosternite; **72** – same, hind coxa, internally; **73** – aedeagus, ventrally; **74** – same, laterally.

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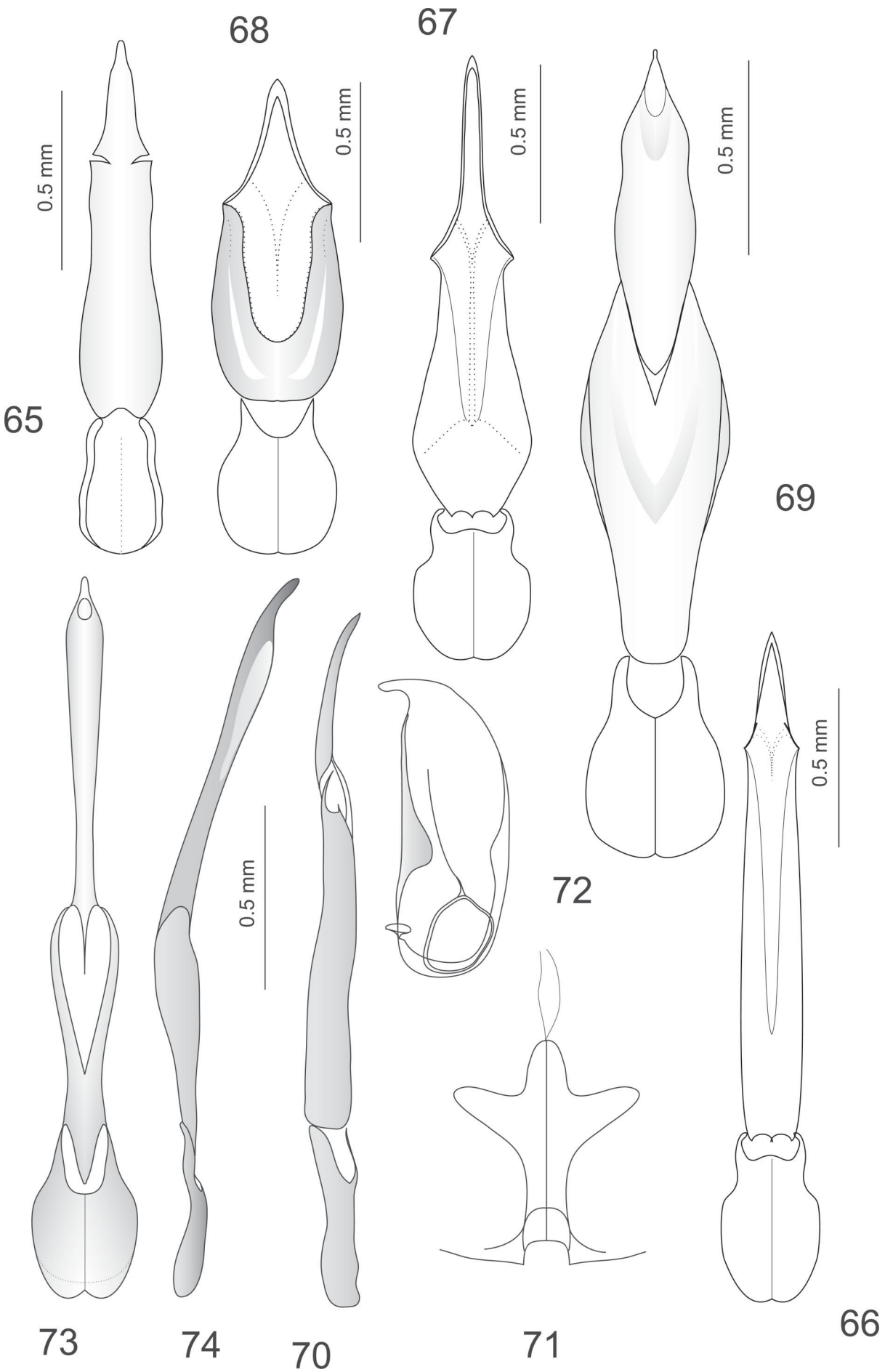

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***Staepteron cyanoxanthum* (Bourgeois, 1884).**
South Africa (W Cape).

Calopteron cyanoxanthum Bourgeois, 1908: 274

Phaneros Kazantsev, 1992

Phaneros Kazantsev, 1992: 42

Type species. *Stadenus xanthopterus* Bourgeois, 1908

Redescription. Head transverse, slightly narrowed behind eyes (Figs 9–10). Fastigium slightly blunt, almost right-angled (Fig. 11). Labrum transverse, sclerotized, with proximal portion lying inside epistoma, feebly emarginated medially (Fig. 10). Eyes relatively small, spherical. Mandibles projected forward and evenly rounded distally (Figs 9–10). Maxillary palps relatively slender, 4-segmented, with ultimate palpomere more or less parallel-sided and flattened distally (Fig. 9). Prementum undivided, labial palps 3-segmented, slender, ultimate palpomere conspicuously widened and flattened distally, ligula present (Fig. 9). Gula absent, genal sclerites connected by narrow process lying anteriad of posterior tentorial pits (Fig. 9). Ventral arms of tentorium long and narrow, almost attaining to cranial dorsal surface (Fig. 11). Antennal prominence relatively inconspicuous, antennal sockets distinctly separated (Fig. 10). Antennae 11-segmented, relatively short, slightly flattened from antennomere 4; antennomere 3 about as long and wide as antennomere 2, antennomeres 2 and 3 combined shorter than antennomere 4 (Fig. 12).

Pronotum transverse, with prominent median cell and distinct transverse carinae; posterior angles slightly produced laterally. Prosternum short, T-shaped (Fig. 17). Thoracic spiracles moderately sclerotized and not protruding laterally beyond coxal limits (Fig. 17). Mesoventrite relatively long; mesepimeron as long as mesepisternum, but conspicuously extending beyond its base (Fig. 17). Scutellum relatively small, narrowing distally (Fig. 18). Elytra slightly widening posteriorly, with four more or less equally developed primary costae (with primary costa 2 weakened proximal half in subgen. *Kleineria*), interstices with double rows of subquadrate cells (last interstice with one row of cells in subgen. *Bourgeoisiella*); sparse elytral pubescence along longitudinal costae. Metascutum with straight not loopy scuto-scutellar ridge (Fig. 19); Metasternal suture complete, attaining to mesoventrite (Fig. 17). Metendosternite with transverse suture and lateral arms (Fig. 71). Metathoracic wing with wedge cell; cu-a brace connecting Cu_2 and A_1 at Cu veins branching point (Fig. 24).

Mesocoxae widely separated (Fig. 17); metacoxae with conspicuous trochantinal and shortened meral suture (Fig. 72). Protrochantins slightly larger than mesotrochantins (Fig. 17). Trochanters elongate, slightly widened distally, connected to femora distally; tibiae curved, tibiae with pair of similar short apical spurs; tarsomeres 1–4 with plantar pads, tarsomere 1 with apical plantar pad occupying about third of its length; all claws simple (Fig. 27). Abdominal spiracles located dorsally on sternite at its edge. Spiculum ventrale short (Figs 37–38) (long in subgen. *Kleineria* – Fig. 39). Valvifers free, relatively short (Figs 45–48) (long in subgen. *Kleineria* – Fig. 49). Aedeagus symmetric, with elongate, completely fused parameres and median lobe (Figs 65–70, 73–74).

Comments. *Phaneros* is distinguished from other Flagraxina genera by the structure of antennomere 3, which is similar in length and vestiture to antennomere 2 (Fig. 12), by the square or transverse elytral cells and the structure of the aedeagus with parameres fused to median lobe (Figs 65–69). Phaneros is divided into three subgenera, *Phaneros* s. str., *Bourgeoisiella* and *Kleineria*, the difference between them shown in the key to genera and subgenera of Dictyopterini of the Afrotropical region above and their relationships discussed in the Phylogeny section.

Distribution. *Phaneros* is known from isolated locations on the West Coast and in the mountains of East Africa, from Uganda and Kenya to Transvaal (Fig. 56).

Biology. No preimaginal forms have been observed or collected in *Phaneros*. Imagines of the genus were collected in mountain forests at elevations up to 3500 m above sea level: *Ph.* (*Phaneros*) *xanthopterus* – at 2000–3500 m in the forest zone of Kilimanjaro, *Ph.* (*Phaneros*) *inapicalis* – at 1800 and 2100 m near Lake Kivu; *Ph.* (*Bourgeoisiella*) *ruficeps* – at 1800–2140 m. The lowest altitude where these beetles have been signalled from is 1150 m [*Ph.* (*Phaneros*) *nigricollis*]. The biotope data available for *Ph.* (*Kleineria*) *silvicola* sp. n. ("cloud forest") suggest this species is also restricted to mountainous areas.

Phaneros (*Phaneros*) Kazantsev, 1992: 42

Type species: *Stadenus xanthopterus* Bourgeois, 1908

1. *Phaneros* (*Phaneros*) *caffer* (Kleine, 1933).
SE Africa (L. Nyasa).

Stadenus caffer Kleine, 1933: 4

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2. *Phaneros* (*Phaneros*) *costatus* (Pic, 1915). Cameroon, Gabon, Equatorial Guinea.
Stadenus costatus Pic, 1915: 12

3. *Phaneros* (*Phaneros*) *inapicalis* (Pic, 1928). Uganda, E Congo.
Stadenus inapicalis Pic, 1928: 61
Stadenus incrassicornis Pic, 1946: 6

4. *Phaneros* (*Phaneros*) *nigricollis* (Pic, 1946). E Congo.
Stadenus nigricollis Pic, 1946: 6

5. *Phaneros* (*Phaneros*) *xanthopterus* (Bourgeois, 1908). East Africa (Kenya, Tanzania).
Stadenus xanthopterus Bourgeois, 1908: 274

Phaneros (*Bourgeoisiella*) Kazantsev, 1992: 44
Type species. *Stadenus ruficeps* Bourgeois, 1910

6. *Phaneros* (*Bourgeoisiella*) *ruficeps* (Bourgeois, 1910). Kenya, Tanzania.
Stadenus ruficeps Bourgeois, 1910: 117
Stadenus sjoestedti Bourgeois 1910: 118

Phaneros (*Kleineria*) Kazantsev, 2004: 4
Phaneros (*Kleinella*) Kazantsev, 1992: 44 HM preocc. by *Kleinella* Adams, 1860 (Mollusca)
Type species: *Kleinella pudica* Kazantsev, 1992

7. *Phaneros* (*Kleineria*) *pudica* Kazantsev, 1992. Tanzania (Tandaia).
Phaneros (*Kleinella*) *pudica* Kazantsev, 1992: 44

8. *Phaneros* (*Kleineria*) *silvicola* sp. n. (Figs 9–12, 17–19, 24, 27, 31, 39, 49, 71–74)

Description. Male. Black. Head, antennomere 1, pronotum, prosternum, elytra proximally and front legs, except tibiae and tarsi, rufous.

Head with shallow roundish impression behind antennal prominence. Eyes small (interocular distance ca. 4 times as long as the radius – Fig. 10). Labrum transverse, widely concave anteriorly (Fig. 10). Antennae attaining to elytral middle, with antennomeres 4–11 slightly flattened, but almost parallel-sided; antennomere 3 about as long as antennomere 2 and 4 times shorter than antennomere 4 (Fig. 12); antennal pubescence erect and relatively short.

Pronotum transverse (1.4 times wider than long), trapezoidal, with conspicuous median areola and less conspicuous curved transverse carinae; anterior margin slightly convex; hind angles acute. Scutellum elongate, narrowing distally and rounded at apex (Fig. 18).

Elytra long, 3.3 times longer than wide at humeri and 5.5 times longer than pronotum, slightly widenening posteriorly, with 4 equally developed primary costae; interstices with double rows of small relatively regular mostly square cells. Short pubescence distributed along longitudinal costae.

Legs slender, with conspicuously curved tibiae; tarsomeres 1–4 with plantar pads, tarsomere 1 with apical plantar pad occupying ca. one third of length of tarsomere (Fig. 27).

Spiculum ventrale long (Fig. 39). Valvifers free and long (Fig. 49). Aedeagus slender, slightly curved in lateral view, with long median lobe (Figs 3–74).

Length: 6.0–7.2 mm. Width (humerally): 1.5–1.8 mm.

Female. Similar to male, but antennae shorter and eyes smaller.

Type material. Holotype male: S. Afr., E Transvaal, Marieskop, 24°35 S – 30°50 E, beaten, cloud forest, E-Y: 1777, 5. V. 1981, Endrödy-Younga leg. (TMNH); paratypes, 2 males and 7 females, S. Afr., E Transvaal, Marieskop, 24°35 S – 30°50 E, beaten in forest, E-Y: 1786, 6. V. 1981, Endrödy-Younga leg. (TMNH and ICM).

Diagnosis. *Ph.* (*Kleineria*) *silvicola* sp. n. differs from *Ph.* (*Kleineria*) *pudica*, the only known other species of the subgenus, by the coloration and details of the aedeagus (Figs 73–74).

Etymology. The name is derived from the Latin for "inhabiting woods" alluding to the fact that all specimens of the new species were collected in a forest.

The eight *Phaneros* species grouped in three subgenera may be distinguished by the characters given in the key below.

Key to species of *Phaneros*

1. All primary elytral costae equally developed, including in proximal half. Distal margin of penultimate male sternite concave. Spiculum ventrale long (Fig. 39). Valvifers long (Fig. 49) [*Phaneros* (*Kleineria*) Kazantsev] **2**
– Elytral primary costa 2 less developed in proximal half. Distal margin of penultimate male sternite straight or convex. Spiculum ventrale short (Figs 37–38). Valvifers short (Figs 45–48) **3**
2. Only antennomere 1 rufous. Aedeagus slightly curved in lateral view, with long median lobe (Figs 73–74) . . . . . ***Phaneros* (*Kleineria*) *silvicola* sp. n.**
– Antennomeres 1–3 rufous. Aedeagus almost straight in lateral view, with short median lobe (Figs. 70) . . . . . ***Phaneros* (*Kleineria*) *pudica* Kazantsev**

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3. Last elytral interstice with one row of cells and not visible from above, including in distal half. Aedeagus with distinctly separated median lobe (Fig. 69) . . . . . ***Phaneros* (*Bourgeoisiella*) *ruficeps* (Bourgeois)**
– All elytral interstices with double rows of cells. Last elytral interstice well visible from above, at least in distal half. Aedeagus with indistinctly separated median lobe (Figs 65–68) [*Phaneros* (*Phaneros*) Kazantsev] **4**
4. Aedeagus with broad median lobe (Fig. 68) . . . . . ***Phaneros* (*Phaneros*) *xanthopterus* (Bourgeois)**
– Aedeagus with narrow median lobe (Figs 65–67) **5**
5. Parameral tube of aedeagus parallel-sided (Fig. 66) . . . . . ***Phaneros* (*Phaneros*) *costatus* (Pic)**
– Parameral tube of aedeagus widened proximally. **6**
6. Median lobe of aedeagus short (Fig. 65) . . . . . ***Phaneros* (*Phaneros*) *caffer* (Kleine)**
– Median lobe of aedeagus relatively long (Fig. 67) **7**
7. Elytra uniformly testaceous. Styli almost as long as coxites (Fig. 47) . . . . . ***Phaneros* (*Phaneros*) *inapicalis* (Pic)**
– Elytra distally black. Styli conspicuously shorter than coxites (Fig. 48) . . . . . ***Phaneros* (*Phaneros*) *nigricollis* (Pic)**

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